

EARLY TERTIARY TAPIROIDEA  
OF ASIA

LEONARD B. RADINSKY

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# EARLY TERTIARY TAPIROIDEA OF ASIA

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## INTRODUCTION

BETWEEN THE YEARS 1922 and 1930 the Central Asiatic Expeditions of the American Museum of Natural History amassed a large collection of fossil vertebrates from several localities in Inner and Outer Mongolia. Eocene and Oligocene mammals in this collection were described in a series of papers written during the 1920's and 1930's, chiefly by Matthew, Granger, and Osborn. These were primarily short preliminary descriptions of new taxa. Despite its obvious importance as the first good record of early Tertiary life in Asia, much of the Mongolian material was never described.

Tapiroids apparently were a common element in the late Eocene faunas of central Asia, for they make up a large part of the collections of that age in the American Museum of Natural History. New taxa of tapiroids collected by the 1922 and 1923 expeditions were described in a few preliminary notices (Osborn, 1923; Matthew and Granger, 1925a, 1925b, 1925c, and 1926), but the great bulk of the tapiroid material, collected by the later expeditions and including several new genera as well as much new information on previously named forms, was never described. This wealth of undescribed material, important for the light it sheds on a hitherto poorly known Eocene tapiroid radiation, as well as for its bearing on intercontinental correlation, provided the stimulus for the present study.

As this investigation progressed it became apparent that relationships between genera of Mongolian tapiroids and those known from other parts of Asia had not been properly understood, and that many names in the literature were in reality synonyms. Therefore the scope of the present paper was expanded to include a revision of all Asiatic early Tertiary tapiroids.

Localities at which early Tertiary tapiroids have been found in Asia are shown in figure 1. The superfamily is represented in early Eocene beds by only a single specimen, from northern China, and in deposits of middle Eocene age (Ganda Kas, Pakistan, and possibly in the Zaisan basin, Kazakhstan), by one or two isolated teeth. Except for a few specimens of Oligocene age (from Ardyn

Obo, Mongolian People's Republic, and the Turgai region of Kazakhstan), virtually all our knowledge of the early Tertiary evolution of tapiroids in Asia is confined to the late Eocene. Fortunately several fairly rich late Eocene faunas from various localities in Asia, ranging in latitude from Burma to Mongolia, provide a considerable amount of information on the tapiroids of that age.

The late Eocene faunas of Mongolia serve as standards with which collections from elsewhere in Asia have been compared. Two major faunal zones are readily discernible: an earlier one, known from the Irdin Manha fauna, and a later one, represented by the Shara Murun fauna, both from Inner Mongolia. Fossils of about the same age as that of the Irdin Manha fauna are also found in the Tukhum and Ulan Shireh beds of Inner Mongolia and the Kholobolchi beds of the Mongolian People's Republic. The Arshanto beds of Inner Mongolia are slightly older than the Irdin Manha beds but may still be late Eocene in age. Faunas approximately equivalent in age to the Shara Murun fauna have been found in northern Honan and eastern Yunnan, China, and in the Pondaung Formation, Burma. A summary of the information on the Eocene and Oligocene localities in Inner Mongolia of the American Museum of Natural History expeditions has recently been published (Radinsky, 1964) and may be referred to for details of the stratigraphy in that area.

### ACKNOWLEDGMENTS

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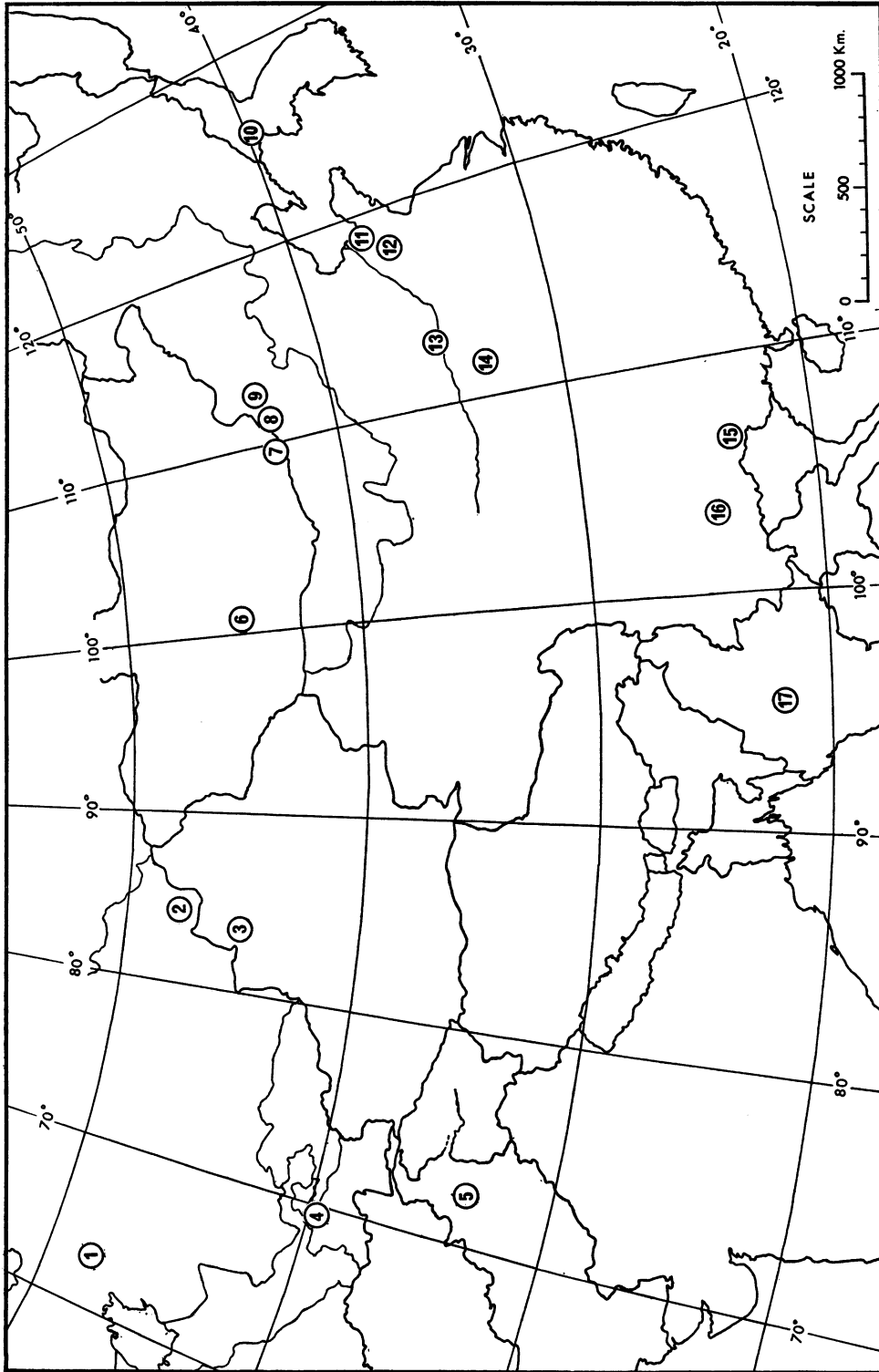


FIG. 1. Map showing localities where early Tertiary tapiroids have been found in Asia. 1. Turgai region, Kazakh S.S.R. 2. Zaisan basin, Kazakh S.S.R. 3. Luliang, northwest Dzungaria basin, Sinkiang, China. 4. Fergana basin, Kirghiz S.S.R. 5. Ganda Kas, Pakistan. 6. Kholobolchi beds, Ork Nor, Mongolian People's Republic. 7. Ardyn Obo, Mongolian People's Republic. 8. Shara Murun region, Inner Mongolia. 9. Irdin Manha, Inner Mongolia (Camp Margetts area is between 8 and 9). 10. Hosan coal field, Kokaïdo, North Korea. 11. Wutu, Changlo District, northern Shantung, China. 12. Hsintai, central Shantung, China. 13. Mienchih, northern Honan, China. 14. Sichuan, southwest Honan, China. 15. Tientong, western Kwangsi, China. 16. Lunan, eastern Yunnan, China. 17. Pondaung Formation, Burma.



ABBREVIATIONS

A.M.N.H., the American Museum of Natural History	N, number of specimens included in sample
L, anteroposterior length (maximum)	OR, observed range
W, labiolingual width (maximum)	SR, span of standard range
mm., millimeters (all measurements given in millimeters)	M, mean
	s, standard deviation
	V, coefficient of variation

## TAXONOMY

### ORDER PERISSODACTYLA

#### SUPERFAMILY TAPIROIDEA

FAMILY **LOPHIALETIDAE**, NEW RANK  
(=**LOPHIALETINAE** MATTHEW AND  
GRANGER, 1925c)

TYPE GENUS: *Lophialetes* Matthew and Granger (1925c).

INCLUDED GENERA: *Lophialetes*, *Schlosseria* Matthew and Granger (1926), and *Breviodon*, new genus.

KNOWN DISTRIBUTION: Late Eocene of Asia.

DIAGNOSIS: Small to medium-sized, lightly built tapiroids with postcanine diastemata. Premolars non-molariform. Molars of advanced forms having oblique cross crests and a rhinocerotoid-like cusp pattern, with long flat metacones and relatively high paralophids and metalophids.  $M_3$  usually with a relatively long and narrow hypoconulid. Nasal incision enlarged, and manus tridactyl in advanced forms.

DISCUSSION: Matthew and Granger (1925c, p. 7), in their original description of *Lophialetes*, erected for it a new subfamily, the Lophialetinae, which they placed in the family Lophiodontidae. The following year Matthew and Granger (1926, p. 3) described *Schlosseria*, which they placed in the Lophiodontidae without mentioning the Lophialetinae; however, from the text it is clear that they considered *Schlosseria* closely related (immediately ancestral) to *Lophialetes*. Later classifiers have not agreed on the systematic position of *Lophialetes* and *Schlosseria*. Simpson (1945, p. 140) listed them as "?Lophiodontidae or Helaletidae *incertae sedis*"; Viret (1958, p. 462), as helaletine helaletids; while Gromova (1962, pp. 313, 315) placed *Lophialetes* provisionally in the Lophiodontidae but considered *Schlosseria* of uncertain familial affinities.

*Lophialetes* and *Schlosseria* possess in common a basic dental pattern which does not conform to that of any known tapiroid or rhinocerotoid family. The upper molars of *Schlosseria* have unshortened, labially situated metacones and closely resemble those of lophiodontids and primitive helaletids (such

as *Heptodon*). This resemblance may be ascribed to a common retention, with little modification, of the basic tapiroid cusp pattern. *Lophialetes* upper molars are slightly more specialized than, but easily derivable from, those of *Schlosseria*. They approach the hyracodontid rhinocerotoid pattern in having long flat metacones, but this similarity is probably due to convergence. The lower molars of both *Schlosseria* and *Lophialetes* have relatively prominent paralophids and metalophids, crests lost in advanced tapiroids but enlarged in rhinocerotoids. The last lower molar, however, retains a long hypoconulid, a feature not seen in rhinocerotoids but characteristic of primitive tapiroids. The second to fourth upper premolars of both *Schlosseria* and *Lophialetes* have a high, continuous, protoloph-metaloph loop, a feature not seen in any tapiroid family but similar to that of the hyracodontid rhinocerotoid genus *Triplopus*.

*Schlosseria* and *Lophialetes* are classified as tapiroids rather than rhinocerotoids because the former genus, which probably gave rise to the latter, although of late Eocene age still has a typically tapiroid upper molar pattern, and the latter more specialized genus does not completely attain the rhinocerotoid molar pattern (still retaining a long  $M_3$  hypoconulid). When dentitions of the middle and early Eocene ancestors of *Schlosseria* and *Lophialetes* become known, they will probably prove to be even more tapiroid-like (with less prominent molar metalophids) than the dentition of *Schlosseria*.

Among tapiroids, the dental patterns of *Schlosseria* and *Lophialetes* appear to be equally distinct from those of the European lophiodontids and North American (and Asiatic) helaletids, and even further removed from those of North American isctolophids. Both *Schlosseria* and *Lophialetes* retain a full placental dentition, while lophiodontids and helaletids lose anterior premolars before the beginning of middle Eocene time. This fact indicates that the Mongolian forms were evolving independently from those European and North American lines before the end of the early Eocene. An additional specialization of *Schlosseria* and *Lophialetes* is a reduction of



the lateral digits. The manus of *Schlosseria* is tridactyl while that of contemporary lophiodontids and helaletids is still tetradactyl.

*Schlosseria* and *Lophialetes* appear to represent an independent line of Asiatic Eocene tapiroids which developed an increasingly rhinocerotoid-like molar pattern (with long metacones and metalophids) and acquired an unusual premolar pattern (protoloph-metaloph loop). Since they are equally distinct from lophiodontids and helaletids, and even more different from isctolophids, I propose placing *Lophialetes* and *Schlosseria* in a separate family, the Lophialetidae, new rank for Lophialetinae Matthew and Granger (1925c). *Breviodon*, a new genus described below, is included in the Lophialetidae, because its lower molars (uppers not definitely known) resemble those of *Lophialetes*. It should be noted that the diagnosis of the Lophialetidae is, of necessity, based on late Eocene members of the family only. Also, some of the new genera described in this paper are tentatively assigned to the Lophialetidae, and if these assignments prove to be correct the diagnosis of the family must be revised.

The Lophialetidae probably diverged early in Eocene time from the same basic tapiroid stock that gave rise to lophiodontids and helaletids (*Heptodon* provides an approximate morphological ancestral type). Since no lophialetid remains have yet been found in Europe or North America, it seems likely that the group was always confined to Asia.

Besides the Lophialetidae, I am proposing one other new family, the Deperetellidae, for another distinct line of Asiatic tapiroids. This makes the number of tapiroid families disproportionately high compared to that of other perissodactyl superfamilies, especially in the suborder Hippomorpha. This discrepancy may be due to the fact that, in classification, differences between groups of tapiroids have been expressed at a higher taxonomic level than those between equivalent groups in other superfamilies, or it may reflect a real greater diversity of early Tertiary tapiroids. This problem can be resolved only when one person reviews the taxonomy of the entire order and adjusts the higher-level categories so that they are at least approximately equivalent in all perissodactyl superfamilies. For the present I am arranging

the classification of the Mongolian tapiroids to be consistent within the currently accepted taxonomy of the superfamily Tapiroidea.

With new knowledge of Asiatic late Eocene ceratomorphs, it is becoming increasingly difficult to draw the line between tapiroids and rhinocerotoids. It appears that several tapiroid lines (*inter alia* Asiatic lophialetids, some North American helaletids) may have independently achieved a rhinocerotoid molar pattern. When the ancestry of the various rhinocerotoid families becomes known, the superfamily will probably turn out to be polyphyletic, including several lines that independently evolved from a primitive tapiroid level. The superfamily Tapiroidea at present encompasses the relatively unspecialized ceratomorph lines, such as isctolophids and *Lophiodon*, as well as specialized groups, such as advanced helaletids, tapirids, lophialetids, and deperetellids.

#### LOPHIALETES MATTHEW AND GRANGER, 1925c

TYPE SPECIES: *Lophialetes expeditus* Matthew and Granger (1925c, p. 5).

INCLUDED SPECIES: *Lophialetes expeditus* and closely related unnamed forms.

DISTRIBUTION: Late Eocene of Asia.

REVISED DIAGNOSIS: Medium-sized to large lophialetids with premolar series short relative to molar series. Premolar and especially molar metacones long and flat, and lophids and lophids relatively high and acute, giving molars a rhinocerotoid aspect. P<sup>1</sup> with wide posterolingual shelf. P<sup>2-4</sup> with protoloph-metaloph loop. M<sup>2-3</sup> relatively long and narrow. P<sub>1</sub> small and crowded, lacking in a few individuals. Nasal incision enlarged. Manus tridactyl.

DISCUSSION: The molars of *Lophialetes* show features that approximate the rhinocerotoid cusp pattern, including long flat metacones, prominent paralophids and metalophids, and relatively high sharp lophids and lophids. As might be expected from the cusp pattern, occlusion in *Lophialetes* also resembles that of rhinocerotoids. As Butler (1952, p. 802) pointed out, in tapiroids, at least in the early stages of wear, the upper molar cross lophids characteristically shear behind the lower cross crests and thus are worn away from in front. In *Lophialetes*, however, while the metaloph is worn away from in front, the

protoloph, even in the earliest stages of wear, is worn down from the top, with shear largely in a horizontal plane. This condition is similar to that in *Caenolophus*, *Hyracodon*, and other rhinocerotoids.

The dentition of *Lophialetes* is easily derivable from that of the slightly older lophialetid *Schlosseria* (discussed below), which exhibits a more typically tapiroid molar pattern. However, except for the long  $M_3$  hypoconulid and slightly more molariform lower premolars, the dentition of *Lophialetes* is so similar to that of a contemporary species of hyracodontid rhinocerotoid (*Caenolophus proficiens*) that a not too distant common ancestry seems quite probable, and supports the suggestion mentioned above that the Rhinoceroidea is a polyphyletic superfamily.

**DENTITION (FIGS. 2, 3):** No upper incisors or canines are known that can definitely be assigned to *Lophialetes*. Alveoli in A.M.N.H. No. 21595 indicate that  $C^1$  was separated from  $I^3$  by a short (4-mm.) gap, to accommodate  $C^1$  in occlusion.  $I_{1-2}$  (seen in A.M.N.H. Nos. 26105 and 26111) are about equal in size, almost as high as long, spatulate, with a slightly convex labial face and flat to slightly concave lingual face, and with a lingual basal cingulum.  $I_3$  is relatively much longer and lower than  $I_{1-2}$ , with the cutting edge highest in the center, descending anteriorly and posteriorly, and raised into a low posterior cusplule.

The lower canine is fairly large in A.M.N.H. Nos. 26105, 26108, and 81616, sharply pointed, circular to oval in cross section, slightly curved posteriorly, with a prominent anterior leading edge which is expanded anterolingually at its base. In A.M.N.H. No. 26111, from the same horizon and locality as the above-cited specimens,  $C^1$  is much smaller and more incisiform, with a labiolingually compressed, low, pointed crown and a faint lingual cingulum. These differences are probably indicative of sexual dimorphism. The lower canine in A.M.N.H. No. 26108 shows prominent wear facets on both anterior and posterior faces, from occlusion with  $I^3$  and  $C^1$ , respectively. The canines are separated from the cheek teeth by moderately long diastemata.

The first upper premolar ( $P^1$ ) is triangular

in outline, with short posterior and long anterolingual sides. The ectoloph consists of a sharp, undivided, central cusp and a low parastyle and metastyle. A low protoloph bounds most of the anterolingual face and merges posterolingually with the posterior basal cingulum. A low crista (incipient metaloph) is present on the lingual face of the ectoloph, posterior to the apex of the central cusp; in some individuals it extends lingually to join the protoloph. An anterolingual basal cingulum is present anterior to the protoloph only for a short distance from the parastyle.

The second upper premolar varies in outline from being approximately square to being slightly wider than long. The metacone is barely separated from the paracone. The protoloph and metaloph join lingually to form a continuous, U-shaped loop. Anterior, lingual, and especially posterior basal cingula are usually prominent; the posterior cingulum is separated from the metaloph by a narrow basin.  $P^3-4$  are progressively larger and relatively wider than  $P^2$ , with progressively more distinct metacones. Metaloph and protoloph are equally prominent and form a high, continuous, U-shaped loop. A few individuals display a slightly posteriorly extended protocone or a faint groove on the posterolingual corner of the protoloph-metaloph loop, or both, indicating incipient separation of a hypocone. A molariform extreme of this variation is seen in A.M.N.H. No. 81608, an isolated  $P^3$  or  $P^4$  of *Lophialetes expeditus* from the Irdiv Manha beds, in which the metaloph extends parallel to and is completely separated from the protoloph.

The upper molars have small to medium-sized parastyles, convex paracones, and relatively long and flat metacones (posterior ectoloph extension). The protoloph is slightly convex anteriorly, while the metaloph is straight but usually more oblique, joining the ectoloph relatively far forward, with a sharp bend (?incipient crochet). Protoloph and metaloph are high and thin, with the anterior slopes almost vertical or even overturned anteriorly. A prominent crista is situated on the lingual slope of the paracone. Basal cingula are present on anterior, posterior, and usually posterolabial sides.  $M^3$  differs from  $M^{1-2}$  in being relatively long and narrower posteriorly, with the posterior portion of the



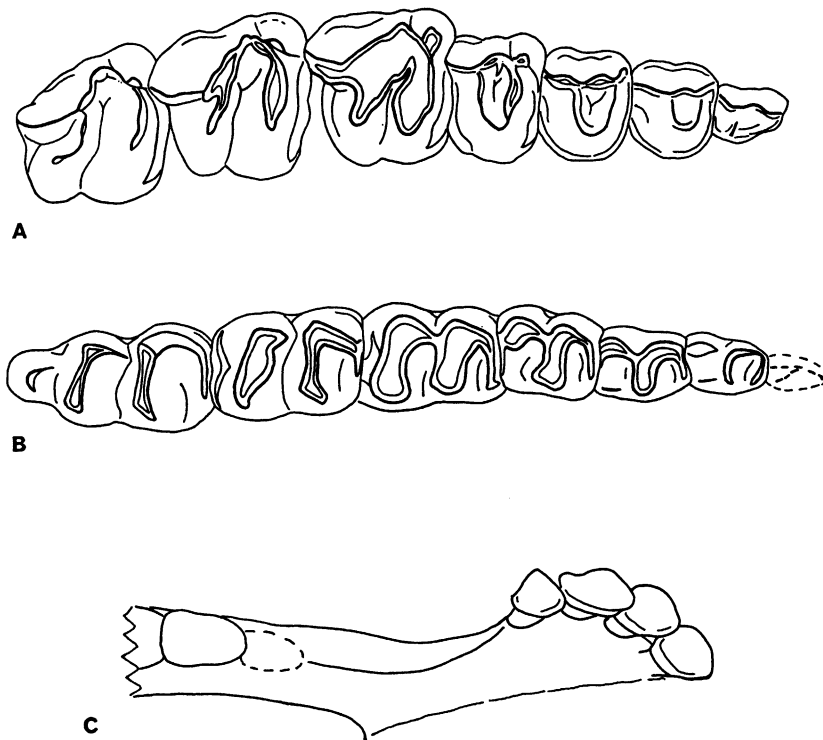


FIG. 2. *Lophialetes expeditus*. A. Type, A.M.N.H. No. 19163, with anterior premolars from A.M.N.H. No. 20160. B. A.M.N.H. No. 19162, with  $P_1$  restored from other specimens. C. Symphyseal region of A.M.N.H. No. 26111 (*L. expeditus?*), showing lower canine and incisors. A and B after Matthew and Granger (1925c, figs. 6 and 7). All  $\times 1.5$ .

ectoloph reduced and the metaloph shortened.

The first lower premolar ( $P_1$ ) is a low, single-cusped, elongate tooth, with a labial shearing surface. A low ridge descends lingually from the main cusp and merges with the lingual cingulum, separating narrow anterior and posterior lingual basins.  $P_1$  apparently was normally crowded by  $P_2$ , since in most specimens examined it was lost during life. About 5 per cent of all *Lophialetes* jaws examined had no  $P_1$  alveolus.

The second lower premolar is roughly rectangular in outline, with a high and relatively unreduced paralophid. A short, posterolingually trending protoloph connects the equal-sized protoconid and metaconid. The low talonid bears a broad hypoconid which is connected to the base of the protoconid by a short, low ridge (incipient metalophid), and a posterolingual basin bounded by a prominent posterolingual cingulum.

$P_3$ -4 are progressively larger, with relatively shorter trigonids (owing to reduction of the paralophid), longer protolophids, and wider talonids, with the posterolingual cingulum raised into a narrow entoconid.

The lower molars have relatively high, acute protolophids and hypolophids, with relatively long, unreduced paralophids and metalophids. The metalophids terminate anteriorly about one-third of the way up from the base of the protolophids; the paralophids become increasingly longer from  $M_1$  to  $M_3$ .  $M_3$  has a low, relatively long and narrow but highly variable hypoconulid, which is bounded by a low, continuous ridge.

$DP^1$  seems identical to  $P^1$  in size and cusp pattern and may be the same tooth.  $DP^1$  apparently was not replaced in *Colodon*, an advanced helaletid (Radinsky, 1963a, p. 60), and may have been retained throughout adult life in *Lophialetes* also.  $DP^2$  varies in outline from being triangular (with a long

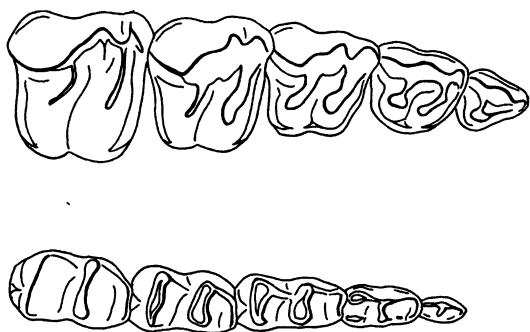


FIG. 3. Deciduous dentition of *Lophialetes expeditus*?. Above: A.M.N.H. No. 26122, DP<sup>2-4</sup> and M<sup>1</sup> (reversed from left side), with DP<sup>1</sup> from A.M.N.H. No. 26121. Below: A.M.N.H. No. 81663, DP<sub>1-4</sub> and M<sub>1</sub>. Both  $\times 1.5$ .

anterolingual side) to being roughly quadrangular, with a single sharp main ectoloph cusp and small parastyle and metastyle. The metaloph is perpendicular to the ectoloph, and the protoloph is shorter than the metaloph and more obliquely (posterolingually) oriented; these two cross lophs do not join lingually. DP<sup>3</sup> is fully molariform, but relatively longer and narrower, and has a shorter protoloph, than M<sup>1</sup>. DP<sup>4</sup> is a smaller replica of M<sup>1</sup>.

DP<sub>1</sub> is identical to P<sub>1</sub> and probably the same tooth. DP<sub>2</sub> is similar to P<sub>2</sub> but smaller and relatively longer and narrower. DP<sub>3</sub> has a molariform, but extremely long and narrow, trigonid, with the paralophid raised into a prominent anterior cingulum, almost a third cross loph, which extends parallel to the protolophid. The talonid is molariform but also relatively narrow. DP<sub>4</sub> is a smaller replica of M<sub>1</sub>.

**SPECIFIC TAXONOMY:** Specimens of *Lophialetes* are abundant at several early late Eocene localities in Mongolia and display a wide range of variation in size. The species-level taxonomy of the genus is complex and at present not well understood. For clarity of presentation, the following sections describe *Lophialetes* specimens grouped by locality. The main areas involved are at Irдин Manha, the Shara Murun valley, and around Camp Margetts.

#### IRDIN MANHA AREA

*Lophialetes expeditus* Matthew  
and Granger, 1925c

TYPE: A.M.N.H. No. 19163, maxilla with

P<sup>4</sup>-M<sup>3</sup>. Figured in Matthew and Granger (1925c, p. 6, fig. 6).

**HYPODIGM:** Type and A.M.N.H. Nos. 19162, 19164-19176, 20142-20154, 20157-20160, 20177-20229, 20231-20234, 81601, 81603-81614, 81704-81716.

**KNOWN DISTRIBUTION:** Late Eocene Irдин Manha beds, Irдин Manha escarpment, about 20 miles south-southeast of Iren Dabasu, Inner Mongolia.

**DIAGNOSIS:** Same as for genus. Mean length of M<sub>1-3</sub>, 41.08 mm. See tables 1 and 2 for complete dental measurements.

**DISCUSSION:** *Lophialetes expeditus* is represented in the American Museum collections by several fragmentary jaws and hundreds of isolated teeth, and is by far the most common species found in the Irдин Manha beds. I was not able to separate isolated M<sup>1</sup>'s from M<sup>2</sup>'s or DP<sup>4</sup>'s, P<sup>3</sup>'s from P<sup>4</sup>'s, or M<sub>1</sub>'s from M<sub>2</sub>'s and DP<sub>4</sub>'s, which accounts for the relatively small number of those teeth available for statistical calculations. Morphological variation within the sample, except for the few cases discussed below, is essentially continuous, yet the coefficients of variation for most of the dental measurements, especially on the molars, are slightly higher than would be expected for a single contemporaneous population, which suggests that the sample includes more than one population, or encompasses a long enough time span to reflect evolutionary size change.

The former hypothesis is supported by six isolated M<sub>3</sub>'s and seven isolated M<sup>3</sup>'s which fall beyond the range of continuous variation exhibited by the *Lophialetes expeditus* hypodigm. The six M<sub>3</sub>'s (A.M.N.H. No. 20230) fall in a cluster discontinuously smaller than M<sub>3</sub>'s in the main *L. expeditus* sample, averaging 13 per cent smaller than the sample mean and falling between the 95 and 99 per cent confidence limits for the hypodigm. If these teeth are included in the statistical calculations for the *L. expeditus* hypodigm, the length and width coefficients of variation of M<sub>3</sub> rise to 7.02 and 6.74 and agree more closely with those for M<sub>2</sub> and M<sub>1</sub>, and the length and width means of M<sub>3</sub> drop to 16.54 and 7.73. The seven M<sup>3</sup>'s (A.M.N.H. No. 81602) are relatively shorter and wider, have shorter and more convex metacones, and, in some cases, less oblique metalophs, than are seen in M<sup>3</sup>'s in the *L. expeditus* hypodigm.

TABLE 1

STATISTICAL DATA ON PERMANENT TEETH OF *Lophialetes expeditus* FROM THE IRDIN MANHA BEDS

	N	OR	SR	M	s	V
P <sup>1</sup>	6					
L		5.1- 6.1	—	5.43	—	—
W		4.6- 5.9	—	5.13	—	—
P <sup>2</sup>	15					
L		6.5- 8.1	3.4	7.29±0.14	0.53±0.10	7.28±1.33
W		7.2- 9.0	3.8	8.02±0.15	0.59±0.11	7.39±1.35
P <sup>3</sup>	2					
L		7.5- 7.9	—	7.70	—	—
W		9.4-10.5	—	9.95	—	—
P <sup>4</sup>	3					
L		8.1- 8.4	—	8.23	—	—
W		10.6-11.0	—	10.77	—	—
M <sup>1</sup>	4					
L		10.8-14.4	—	12.45	—	—
W		12.3-13.6	—	13.08	—	—
M <sup>2</sup>	1					
L		—	—	13.8	—	—
W		—	—	14.0	—	—
M <sup>3</sup>	39					
L		11.8-15.1	5.2	13.15±0.13	0.81±0.09	6.13±0.69
W		12.1-15.0	5.2	13.47±0.13	0.80±0.09	5.91±0.67
P <sub>1</sub>	1					
L		—	—	5.0	—	—
W		—	—	3.1	—	—
P <sub>2</sub>	12					
L		5.7- 7.1	3.0	6.50±0.14	0.47±0.10	7.28±1.48
W		3.8- 4.8	1.9	4.48±0.08	0.29±0.06	6.38±1.30
P <sub>3</sub>	22					
L		6.6- 8.4	3.1	7.38±0.10	0.48±0.07	6.56±0.99
W		5.0- 6.3	2.5	5.68±0.08	0.38±0.06	6.71±1.01
P <sub>4</sub>	29					
L		7.6- 9.6	3.8	8.59±0.11	0.59±0.08	6.89±0.90
W		5.8- 7.3	2.7	6.61±0.08	0.42±0.06	6.35±0.83
M <sub>1</sub>	26					
L		10.1-13.0	5.9	11.52±0.18	0.91±0.12	7.87±1.09
W		6.7- 8.6	3.6	7.56±0.11	0.55±0.08	7.24±1.00
M <sub>2</sub>	18					
L		11.2-14.3	6.4	12.75±0.23	0.98±0.16	7.66±1.29
W		7.1- 9.2	2.6	8.21±0.09	0.40±0.07	4.89±0.81
M <sub>3</sub>	46					
L		15.4-18.5	6.1	16.81±0.14	0.94±0.10	5.62±0.59
W		7.0- 8.8	3.0	7.84±0.07	0.46±0.05	5.81±0.61

They average about 10 per cent shorter but only 3 per cent narrower than the *L. expeditus* mean, and in both size and cusp configuration resemble M<sup>3</sup>'s of *Schlosseria magister* (see p. 200). These isolated upper and lower third molars may represent extremes of variation of *Lophialetes expeditus*, or they may represent one or possibly two distinct species in which the more anterior teeth are not so

easily separable from those of *L. expeditus*.

The hypothesis that elapsed time and evolutionary size change account for the high variability of the *Lophialetes expeditus* sample is supported by the fact that the relatively few specimens collected in 1922 fall at the large end of the observed size range, and average larger than the bulk of the sample, which was collected in 1923. According to



TABLE 2

STATISTICAL DATA ON DECIDUOUS TEETH OF *Lophialetes expeditus* FROM THE IRDIN MANHA BEDS

	N	OR	SR	M	s	V
DP <sup>1</sup>	2					
L		6.1- 6.4	—	6.25	—	—
W		5.6- 6.0	—	5.80	—	—
DP <sup>2</sup>	16					
L		7.3- 9.0	3.0	8.01±0.12	0.47±0.08	5.93±1.05
W		7.3- 8.9	2.8	8.19±0.11	0.44±0.08	5.44±0.96
DP <sup>3</sup>	21					
L		9.0-11.6	3.8	10.30±0.13	0.58±0.09	5.64±0.87
W		9.0-11.0	3.8	10.05±0.13	0.59±0.09	5.88±0.91
DP <sup>4</sup>	7					
L		11.0-12.2	2.8	11.64±0.16	0.43±0.11	3.69±0.99
W		11.3-12.5	3.4	12.03±0.20	0.52±0.14	4.32±1.15
DP <sub>1</sub>	1					
L		—	—	4.8	—	—
W		—	—	2.9	—	—
DP <sub>2</sub>	11					
L		6.1- 7.7	3.2	6.87±0.15	0.50±0.11	7.32±1.56
W		3.5- 4.7	2.5	4.09±0.12	0.39±0.08	9.50±2.02
DP <sub>3</sub>	39					
L		9.2-11.7	4.2	10.39±0.10	0.65±0.07	6.23±0.70
W		5.3- 6.9	2.8	5.97±0.07	0.43±0.05	7.15±0.80
DP <sub>4</sub>	15					
L		9.8-11.8	3.8	10.57±0.15	0.58±0.11	5.45±0.99
W		6.0- 7.6	3.2	6.62±0.13	0.49±0.09	7.44±1.35

Granger's field notes, both the 1922 and 1923 collections were made in the same general area, near where the Kalgan-Ulan Bataar road crosses the Irдин Manha escarpment, and supposedly all specimens came from the same beds. However, the difference in size between the 1922 and 1923 specimens suggests that the Irдин Manha beds include more than one horizon, or encompass enough of a time interval to show evolutionary change in *Lophialetes expeditus*.

A.M.N.H. No. 81720, a mandibular fragment with P<sub>2</sub> alveolus and worn P<sub>3-4</sub>, from the Irдин Manha beds, corresponds in cusp pattern to *Lophialetes expeditus*, but averages almost 20 per cent smaller than the *L. expeditus* mean. The P<sub>4</sub> falls outside of, and the P<sub>3</sub> just inside of, the 99 per cent confidence limits for *L. expeditus*. A.M.N.H. No. 81720 may be an extremely small variant of *Lophialetes expeditus*, or may be specifically distinct.

#### ?*Lophialetes*

A.M.N.H. No. 81719, a mandibular fragment with P<sub>1</sub> alveolus and P<sub>2-3</sub> from the Irдин

Manha beds, corresponds generally to *Lophialetes expeditus* in cusp pattern but differs in proportions. The P<sub>2-3</sub> have relatively longer trigonids and are relatively much longer and narrower, averaging 16 per cent shorter but over 30 per cent narrower than corresponding teeth of *L. expeditus*. This specimen may eventually prove to be generically distinct from *Lophialetes*.

#### SHARA MURUN REGION

Two species of *Lophialetes* are represented in the Ulan Shireh beds in the Shara Murun region of Inner Mongolia. One, a very common small form, averages about 8 per cent smaller than Irдин Manha *L. expeditus*, and the other, a rare large form, averages about 12 per cent larger than *L. expeditus*. Both forms are extremely similar in cusp pattern to *Lophialetes expeditus*, and either one could be a geographical or temporal variant of the Irдин Manha species. However, if they were sympatric, they could not both be spatial or temporal variants of the same species. *Caenolophus proficiens*, a hyracodontid rhinocero-

toid, and *Teleolophus medius*, a tapiroid (discussed below), are also represented in both the Irдин Manha and Ulan Shireh beds, and in both of these species the Ulan Shireh sample averages slightly smaller than the Irдин Manha hypodigm. Such a difference suggests (1) that the Ulan Shireh fauna is slightly older than the Irдин Manha fauna, and (2) that the smaller Ulan Shireh lophialetid is more closely related to *Lophialetes expeditus* than is the larger one. Therefore the small Ulan Shireh lophialetid is here designated *Lophialetes expeditus?*; and the larger one, *Lophialetes* sp.

#### *Lophialetes expeditus?*

REFERRED SPECIMENS: A.M.N.H. Nos. 21551, 21556, 21557, 21564-21572, 21575-21584, 21586-21595, 22096-22098, 26106-26111, 26116-26119, 26121, 26122, 81615-81680, 81682-81685, 81688, 81689, 81691-81703.

HORIZON AND LOCALITY: Late Eocene Ulan Shireh beds, 4 to 8 miles north of Tukhum in Sumu (including Buckshot Quarry at Chimney Butte), North Mesa, Shara Murun region, Inner Mongolia.

DISCUSSION: Most of the *Lophialetes* specimens collected in the Ulan Shireh beds represent a single species which is very similar to if not conspecific with *Lophialetes expeditus*. These Ulan Shireh specimens differ from Irдин Manha *L. expeditus* mainly in being of slightly smaller size; corresponding tooth measurements average 8 per cent lower, with the molars relatively smaller than the premolars (see tables 3 and 4). In addition,  $M^{1-3}$  are slightly relatively shorter and wider, and  $P^{1-4}$  and the lower cheek teeth are slightly relatively longer and narrower in the Ulan Shireh sample than in the *L. expeditus* hypodigm.

Two isolated  $M_3$ 's (A.M.N.H. Nos. 81686a, 81686b) from the Ulan Shireh beds are discontinuously smaller than the main *Lophialetes* sample, averaging 13 per cent smaller than the *L. expeditus?* mean and falling just outside the 99 per cent confidence limits for that species. These specimens may represent extreme variants of the Ulan Shireh *L. expeditus?* population or may be specifically distinct. Four lower dentitions (A.M.N.H. Nos. 21573, 21585, 21596, and 26105) are discon-

tinuously larger than the main sample in several measurements but fall within the 99 per cent confidence limits and probably are merely large variants of Ulan Shireh *Lophialetes expeditus?*

Coefficients of variation for the dental measurements of Ulan Shireh *Lophialetes expeditus?* are generally lower than those for Irдин Manha *L. expeditus*, which suggests either that the Ulan Shireh beds are temporally more restricted, or that the Ulan Shireh *Lophialetes expeditus?* sample is less likely to include more than one population. The coefficient of variation for the length of Ulan Shireh *Lophialetes*  $M_3$ 's is anomalously low, owing to omission from the statistical calculations of the discontinuously small and large specimens listed above. If all specimens are included in the calculations, the coefficient of variation for the length of  $M_3$  rises to 5.32.

The Ulan Shireh *Lophialetes expeditus?* sample is notable for the excellent preservation of most of the specimens; it includes the most complete *Lophialetes* skull (A.M.N.H. No. 21595) as well as several almost perfect lower jaws. This is in contrast to the Irдин Manha *L. expeditus* sample in which most of the specimens consist of fragmentary jaws or isolated teeth. Possibly the Ulan Shireh specimens were buried soon after death, while those from the Irдин Manha beds were exposed on the surface until they were broken up and scattered. Sedimentological studies of these strata would probably reveal paleoenvironmental differences between the two localities.

#### *Lophialetes expeditus?*, additional specimens

REFERRED SPECIMENS: A.M.N.H. Nos. 22091-22095.

HORIZON AND LOCALITY: Lower red beds of the Shara Murun Formation (?=Tukhum beds) from near the main Ula Usu pocket, Baron Sog Mesa (about 15 miles south of the Ulan Shireh locality at North Mesa), Shara Murun region, Inner Mongolia.

COMMENTS: The specimens listed above, consisting of crushed skulls, jaws, and foot bones of about five individuals, correspond in size and dentition to *Lophialetes expeditus?* from the Ulan Shireh beds and appear to represent the same species. They were col-

TABLE 3

STATISTICAL DATA ON PERMANENT TEETH OF *Lophialetes expeditus?* FROM THE ULAN SHIREH BEDS

	N	OR	SR	M	s	V
P <sup>1</sup>	2					
L		5.5-6.3	—	5.9	—	—
W		4.9-4.9	—	4.9	—	—
P <sup>2</sup>	6					
L		5.8- 7.3	—	6.48	—	—
W		6.1- 8.6	—	7.08	—	—
P <sup>3</sup>	9					
L		6.5- 8.0	3.2	7.40±0.16	0.49±0.12	6.69±1.58
W		7.7- 9.7	3.9	8.73±0.20	0.60±0.14	6.86±1.62
P <sup>4</sup>	10					
L		7.3- 8.2	1.8	7.85±0.09	0.28±0.06	3.58±0.80
W		8.9-10.7	4.0	9.85±0.20	0.62±0.14	6.27±1.40
M <sup>1</sup>	19					
L		9.6-12.5	5.2	11.20±0.19	0.81±0.13	7.22±1.17
W		11.0-13.5	5.2	11.97±0.19	0.81±0.13	6.73±1.09
M <sup>2</sup>	9					
L		10.8-12.9	4.1	12.02±0.21	0.63±0.15	5.28±1.24
W		11.4-13.7	5.2	12.61±0.27	0.81±0.19	6.41±1.51
M <sup>3</sup>	13					
L		10.9-12.9	4.0	11.75±0.17	0.62±0.12	5.27±1.03
W		11.2-13.2	4.5	12.34±0.19	0.70±0.14	5.65±1.11
P <sub>1</sub>	7					
L		3.6- 4.5	1.9	4.19±0.11	0.30±0.08	7.10±1.90
W		2.2- 2.8	1.4	2.60±0.08	0.22±0.06	8.60±2.30
P <sub>2</sub>	18					
L		5.7- 6.9	2.3	6.33±0.08	0.35±0.06	5.49±0.91
W		3.7- 5.0	2.3	4.16±0.08	0.35±0.06	8.41±1.40
P <sub>3</sub>	33					
L		6.4- 8.0	2.8	7.22±0.08	0.44±0.05	6.09±0.75
W		4.6- 6.2	2.5	5.24±0.07	0.38±0.05	7.30±0.90
P <sub>4</sub>	38					
L		7.0- 8.9	2.7	7.84±0.07	0.41±0.05	5.28±0.61
W		5.2- 6.6	2.4	5.94±0.06	0.37±0.04	6.23±0.71
M <sub>1</sub>	62					
L		8.6-11.1	3.7	10.15±0.07	0.57±0.05	5.59±0.50
W		5.9- 7.2	2.0	6.41±0.04	0.31±0.03	4.85±0.44
M <sub>2</sub>	46					
L		10.1-12.6	3.7	11.24±0.08	0.57±0.06	5.08±0.53
W		6.1- 7.8	2.7	7.01±0.06	0.42±0.04	5.97±0.62
M <sub>3</sub>	43					
L		14.3-16.5	3.9	15.53±0.09	0.60±0.06	3.88±0.42
W		6.5- 7.9	2.1	7.11±0.05	0.33±0.04	4.61±0.50

lected in 1925, apparently from the same beds that yielded the type of *Teilhardia pretiosa* in 1923.

**Lophialetes sp.**

REFERRED SPECIMENS: A.M.N.H. Nos. 81687 (P<sub>2</sub>-M<sub>3</sub>), 81690 (DP<sub>4</sub>-M<sub>1</sub>), and 81681

(DP<sub>3</sub>-<sup>4</sup>, P<sub>3</sub>-M<sub>2</sub>, isolated teeth representing at least two individuals).

HORIZON AND LOCALITY: Late Eocene Ulan Shireh beds at Chimney Butte, 8 miles north of Tukhum in Sumu, North Mesa, Shara Murun region, Inner Mongolia.

DISCUSSION: The specimens listed above

represent a species that averages between 20 to 25 per cent larger than *Lophialetes expeditus*? from the same beds and about 12 per cent larger than Irдин Manha *Lophialetes expeditus*. The upper teeth are relatively longer and the lowers, especially the premolars, relatively wider than corresponding teeth in *L. expeditus*. In the one lower jaw where it is determinable, there is no P<sub>1</sub> alveolus. *Lophialetes* sp. may represent a large geographical or temporal variant of Irдин Manha *L. expeditus* (if *L. expeditus*? does not), but more probably it is specifically distinct.

#### *Lophialetes* sp.

A.M.N.H. No. 26138, a lower jaw with P<sub>2</sub>-M<sub>2</sub> from ?"Shara Murun" beds at Urtyn Obo in the Shara Murun region about 25 miles east of the Ulan Shireh locality, corresponds in size to the large Ulan Shireh species of *Lophialetes* but has relatively narrower premolars. As in the form described immediately above, there is no P<sub>1</sub> alveolus.

A.M.N.H. No. 26138 may represent the same species as the Ulan Shireh *Lophialetes* sp., or, less likely, may represent a large geographic variant of Irдин Manha *Lophialetes expeditus*.

The only other lophialetid specimen from the same beds as A.M.N.H. No. 26138 appears more similar to *Schlosseria* than to *Lophialetes* and is tentatively assigned to the former genus (see p. 201).

#### CAMP MARGETTS AREA

At least two species of lophialetids are present at several localities in the Camp Margetts area, between 20 to 25 miles west-southwest of the type Irдин Manha beds. These include a common small form, here referred to *Schlosseria* (see p. 201), and a less common large form, which appears quite similar to *Lophialetes expeditus*. In the Irдин Manha area the beds containing *Schlosseria* underlie those with *Lophialetes*, but in the Camp Margetts area both genera are recorded as coming from the same horizon. However, the

TABLE 4

STATISTICAL DATA ON DECIDUOUS TEETH OF *Lophialetes expeditus*? FROM THE ULAN SHIREH BEDS

	N	OR	SR	M	s	V
DP <sup>1</sup>	5					
L		5.3- 6.3	—	5.78	—	—
W		4.0- 6.2	—	5.14	—	—
DP <sup>2</sup>	12					
L		7.2- 8.2	2.1	7.65±0.10	0.33±0.08	4.34±0.88
W		7.1- 8.7	3.0	7.76±0.14	0.47±0.10	6.02±1.23
DP <sup>3</sup>	13					
L		8.5-10.3	3.4	9.25±0.14	0.52±0.10	5.62±1.10
W		8.6- 9.8	2.5	9.06±0.11	0.39±0.08	4.32±0.85
DP <sup>4</sup>	10					
L		8.8-11.0	4.2	10.07±0.21	0.65±0.14	6.42-1.44
W		10.0-11.5	4.1	10.72±0.20	0.63±0.14	5.83-1.30
DP <sub>1</sub>	3					
L		4.0- 5.3	—	4.63	—	—
W		2.7- 2.8	—	2.73	—	—
DP <sub>2</sub>	22					
L		6.0- 7.5	2.7	6.66±0.09	0.42±0.06	6.32±0.95
W		3.6- 4.8	2.3	3.99±0.07	0.35±0.05	8.78±1.32
DP <sub>3</sub>	33					
L		8.9-10.8	2.8	9.86±0.08	0.44±0.05	4.42±0.54
W		4.8- 6.4	2.5	5.41±0.07	0.38±0.05	7.00±0.86
DP <sub>4</sub>	33					
L		8.4-10.7	3.0	9.53±0.08	0.47±0.06	4.90±0.60
W		5.2- 6.7	2.2	5.87±0.06	0.34±0.04	5.82±0.72

*Schlosseria* teeth from the Camp Margetts area are light brown while those of *Lophialetes* are dark blue to black, dappled with white; in addition, the bone of *Lophialetes* is usually darker than that of *Schlosseria*. These color differences suggest that the representatives of these two genera came from different horizons in this area.

Specimens of *Lophialetes* have been recorded from both the "Irdin Manha" beds and the "Houldjin gravels" in the Camp Margetts area, but those listed as from the latter, higher horizon differ in no apparent way from those from the underlying "Irdin Manha" beds. This fact suggests either that the stratigraphic data for some specimens are wrong, or that the beds called "Houldjin gravels" at some of the localities (particularly 10 miles southwest of Camp Margetts) are at least in part of the same age as the "Irdin Manha" beds, or suggests both. Stratigraphy in the Camp Margetts area is complicated and has not been satisfactorily worked out (see Radinsky, 1964, pp. 4-5); until the stratigraphy is clear, the reference of specimens from this area must be interpreted with extreme caution.

#### *Lophialetes expeditus*

MATERIAL: A.M.N.H. No. 81791 ( $M_3$ ), from "Irdin Manha" beds 5 miles east of Camp Margetts; A.M.N.H. No. 81775 ( $P_2-M_4$ ), "Houldjin gravels," at Camp Margetts; A.M.N.H. Nos. 81768 ( $M_2-M_3$ ) and 81795 ( $M^3$ ), "Irdin Manha" beds 7 miles west of Camp Margetts; A.M.N.H. Nos. 81749 ( $P_2-M_3$ ) and 81750 ( $P_4-M_2$ ), "Irdin Manha" beds 7 miles southwest of Camp Margetts; A.M.N.H. Nos. 81783 ( $P_2^2-M^3$ ), 81778 ( $P_3-M_3$ ), and 81779 ( $DP_3-M_2$ ), "Houldjin gravels," and 81780 ( $P_4-M_2$ ) and 81781 ( $P_2-M_3$ ), ?"Houldjin gravels," all from 10 miles southwest of Camp Margetts.

COMMENTS: The specimens listed above resemble *Lophialetes expeditus* from the type Irdin Manha beds in size and cusp pattern and probably represent that species. Those recorded as from the "Houldjin gravels" cannot be distinguished from those from the "Irdin Manha" beds, and all specimens probably came from the same horizon.

A.M.N.H. No. 81782 ( $P^4-M^3$ ,  $P_4-M_3$ ) from ?"Irdin Manha" beds 10 miles southwest of

Camp Margetts corresponds in size to *L. expeditus* in the lower molars but averages 20 per cent wider in the upper molars, and thus may represent another species, possibly related to *Lophialetes* sp. from the Ulan Shireh beds. Several dozen isolated carpals, tarsals, and phalanges (A.M.N.H. No. 81790), from the same horizon and locality as A.M.N.H. No. 81782, are identical to corresponding elements in the skeleton of *Lophialetes expeditus*.

A.M.N.H. Nos. 81777 ( $P_2-M_3$ ) and 81776 ( $M_3$ ), from "Irdin Manha" beds 5 miles east of Camp Margetts, are intermediate in size, proportions, degree of hypsodonty, and type of preservation between representatives of *Schlosseria* and those of *Lophialetes* from that locality and therefore cannot with certainty be assigned to one or the other genus.

#### LOPHIALETES FROM CHINA

##### *Lophialetes* sp.

Teilhard (1930, p. 331) referred an isolated  $M^3$  from the Red Sandstone Formation of Sichuan, southwest Honan, China, to *Lophialetes* sp. indet. From Teilhard's illustration (1930, fig. 1) and measurements, the specimen is inseparable from  $M^3$ 's of *Lophialetes expeditus* from the Irdin Manha beds. However, more knowledge of the dentition is necessary for specific allocation. This specimen marks the southernmost record of *Lophialetes* in Asia.

Chow (1958, p. 293) described, under the name *Lophialetes* cf. *expeditus*, an isolated  $M_3$  from Luliang, northwest Dzungaria basin, Sinkiang, China. From Chow's figure (1958, pl. 1, fig. 3) it is apparent that the tooth represents a lophialetid, but it is not possible to tell whether it is *Lophialetes* or *Schlosseria*.

#### SPECIES REMOVED FROM LOPHIALETES

Takai (1939, p. 212) proposed the species *Lophialetes tokunagai* for a mandible from the Hosan coal field, Korea, with three teeth which he designated as  $DP_3-M_1$ . From Takai's illustration (1939, pl. 4, figs. 11a-b) the anterior tooth seems to be a  $DP_2$  or  $P_2$ , and it appears that the three teeth represented are probably either all deciduous or all pre-molars. In either case they average more than twice as large and differ in proportions and cusp pattern from corresponding teeth of



*Lophialetes expeditus*. *Lophialetes tokunagai* is surely generically distinct from *Lophialetes* and appears similar to some of the undescribed rhinocerotoid genera in the late Eocene Mongolian collections at the American Museum of Natural History.

*Lophialetes minutus* Matthew and Granger, (1925c) is here transferred to a new genus, *Breviodon* (see p. 204).

# **SCHLOSSERIA MATTHEW AND GRANGER, 1926**

TYPE SPECIES: *Schlosseria magister* Matthew and Granger (1926, p. 3).

INCLUDED SPECIES: Type only.

DISTRIBUTION: Middle or late Eocene of Asia.

REVISED DIAGNOSIS: Medium-sized lophialetids with premolar series long relative to molar series. Premolar and molar metacones

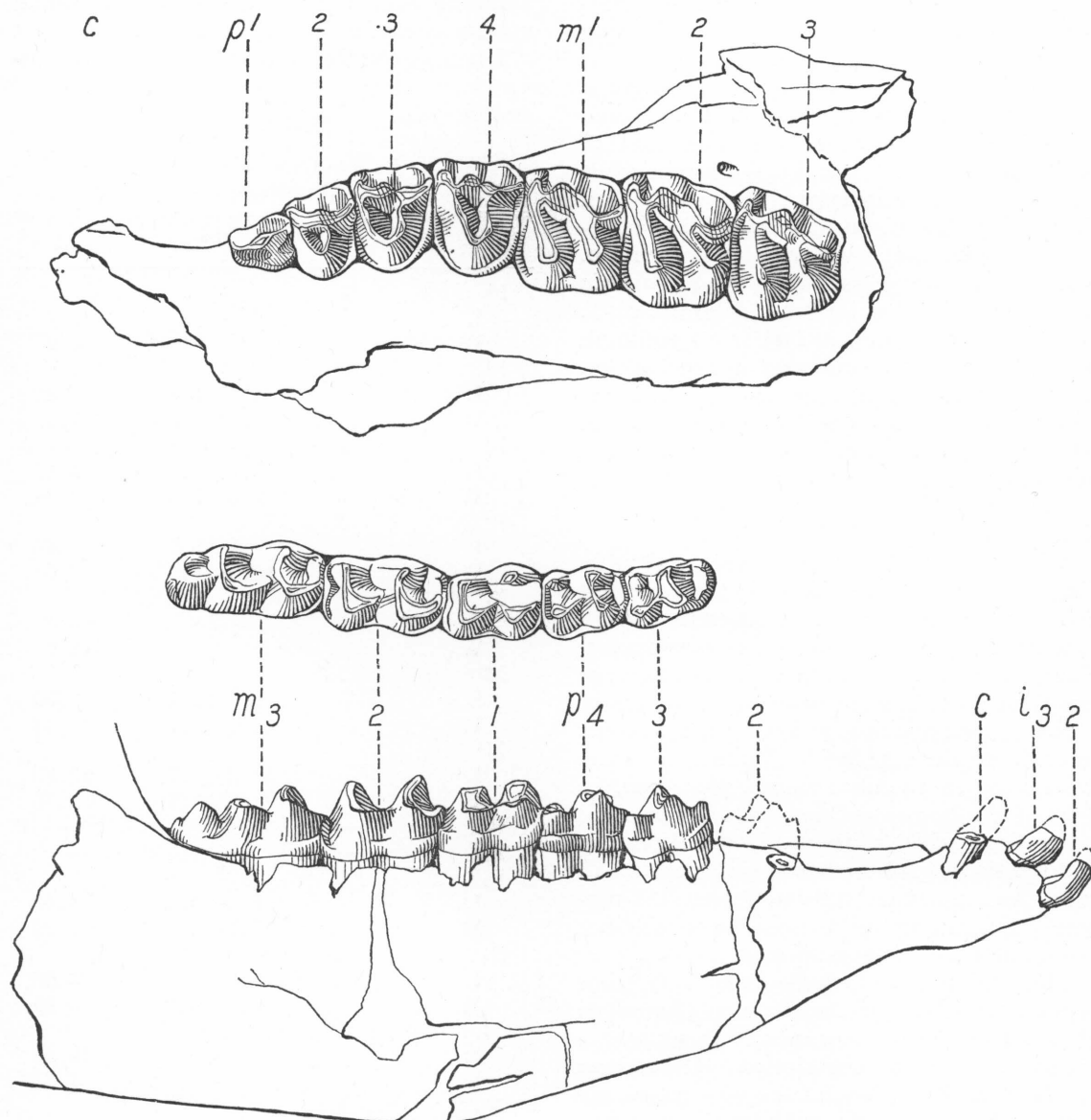


FIG. 4. *Schlosseria magister*. Above: Type, A.M.N.H. No. 20241, P<sup>1</sup>-M<sup>3</sup>. Below: Composite from A.M.N.H. Nos. 20243 and 20244, lateral and occlusal views of lower dentition. From Matthew and Granger (1926, figs. 1 and 2). Both slightly less than  $\times 1.5$ .

short and slightly convex; lophs and lophids relatively low and obtuse.  $P^1$  with narrow posterolingual shelf.  $P^{2-4}$  with protoloph-metaloph loop.  $M^{2-3}$  relatively short and wide.  $P_{2-3}$  relatively long and narrow, with long trigonids. Nasal incision not so enlarged as that in *Lophialetes*. Manus tridactyl.

DISCUSSION: The premolar and molar cusp patterns of *Schlosseria* (see fig. 4) are similar to those of *Lophialetes*, and it has been suggested by Takai (1939, p. 213) that the two genera should be synonymized. Features that distinguish *Schlosseria magister* from the type species of *Lophialetes*, *L. expeditus*, are given in the diagnosis above. The dentition of *Schlosseria magister* (see fig. 4) is somewhat more primitive (more typically tapiroid) than that of *Lophialetes expeditus*, which is specialized toward the rhinocerotoid condition. None of the lower jaws referable to *Schlosseria* show loss of  $P_1$ , and  $DP^2$  of *Schlosseria* cf. *S. magister* is slightly less molariform (protoloph smaller and more oblique) than  $DP^2$  in *Lophialetes*. Also, it appears that the nasal incision was not so deep and retracted in *Schlosseria* as in *Lophialetes*, and there are differences in the foot bones that distinguish the two (see description of skeleton in section on Osteology).

*Schlosseria magister* is definitely specifically distinct from *Lophialetes expeditus*, but whether the two species are different enough to warrant generic separation is a moot point. The differences between them in dentition are less than those that separate most genera of tapiroids, and not enough is known at present to evaluate the taxonomic significance of the differences in the foot bones. However, in light of the known differences, and since the name *Schlosseria* is already in the literature and relationships between *S. magister* and *L. expeditus* are not yet fully understood, I suggest maintaining *Schlosseria* as a distinct genus, at least for the present.

The dentition of *Schlosseria* is similar enough to that of *Lophialetes* (described above) to make it unnecessary to present a separate detailed description. Differences between the dentitions of the two genera are discussed above and need not be repeated here.

***Schlosseria magister* Matthew  
and Granger, 1926**

TYPE: A.M.N.H. No. 20241, maxilla with

$P^1$ – $M^3$ , mandible with  $P_4$ – $M_3$ , and forefeet and hind feet. Figured in Matthew and Granger (1926, p. 1, fig. 1, p. 2, figs. 3–4).

HYPODIGM: Type and A.M.N.H. Nos. 20242–20245.

KNOWN DISTRIBUTION: Late middle or early late Eocene Arshanto beds, about 1 mile east of the type Irдин Manha locality, Inner Mongolia.

DIAGNOSIS: Sole species of genus. Dental measurements are given in table 5.

DISCUSSION: The few specimens of *Schlos-*

TABLE 5  
STATISTICAL DATA ON TEETH OF *Schlosseria  
magister* FROM THE ARSHANTO BEDS

	N	OR	M
$P^1$	1		
L		—	5.8
W			4.6
$P^2$	2		
L		6.3– 6.6	6.45
W		7.8	7.8
$P^3$	3		
L		7.7– 8.6	8.17
W		9.8–10.0	9.90
$P^4$	3		
L		8.2– 8.7	8.40
W		10.5–10.8	10.63
$M^1$	1		
L		—	10.6
W			12.0
$M^2$	2		
L		11.2–12.2	11.70
W		12.8–13.5	13.15
$M^3$	3		
L		10.2–11.7	10.83
W		12.0–12.9	12.36
$P_1$	—	—	—
$P_2$	—	—	—
$P_3$	2		
L		8.2– 9.0	8.60
W		5.8– 6.5	6.15
$P_4$	2		
L		8.8– 9.0	8.90
W		6.8– 6.9	6.85
$M_1$	1		
L		—	10.6
W		—	7.6
$M_2$	2		
L		11.2–11.9	11.55
W		7.8– 8.1	7.95
$M_3$	3		
L		14.3–15.6	15.17
W		7.3– 7.9	7.50

*seria magister* listed above were, except for a tiny perissodactyl astragalus of uncertain generic affinities, the only fossils found in the Arshanto beds. Matthew and Granger (1926, pp. 3, 5) considered the dentition of *S. magister* intermediate between that of *Helalestes* and that of *Hyracotherium* and therefore regarded it as middle or possibly early Eocene in age. However, the features considered primitive by Matthew and Granger, the looped hypoconulid and prominent metalophids, are present also in the more advanced late Eocene lophialetid *Lophialetes expeditus*, the high metalophids in particular being a specialization of that line. Actually *Schlosseria magister* is more advanced than North American middle Eocene species of *Helalestes* in possessing a lingual cingulum on  $P^1$ , a high metaloph on  $P^2-4$ , and a tridactyl manus. Of course, such comparisons are not particularly pertinent for determining the age of *Schlosseria magister*, because it belongs to a different family and evolved independently and possibly at different rates than *Helalestes*. *Schlosseria magister* is quite similar to *Lophialetes expeditus* and displays all the features one would expect in the immediate ancestor of that species. *Schlosseria magister* is probably not much older than *Lophialetes expeditus* and on morphological grounds could equally well be late middle Eocene or early late Eocene in age.

#### *Schlosseria* cf. *Schlosseria magister*

REFERRED SPECIMENS: A.M.N.H. Nos. 81723–81748, 81753–81767, 81789.

HORIZON AND LOCALITY: "Irdin Manha" beds 7 miles southwest of Camp Margetts, 30 miles south-southwest of Iren Dabasu, and about 30 miles west of the type Irdin Manha locality, Inner Mongolia.

DISCUSSION: The specimens listed above represent a species that appears very similar to *Schlosseria magister* from the Arshanto beds near the type Irdin Manha locality. The specimens from the Camp Margetts area differ from *S. magister* in having more acute lophs, relatively smaller hypoconulids on  $M_3$ , slightly different tooth proportions (see table 6), and in being about 5 per cent smaller. Owing to the small size of the type *Schlosseria magister* hypodigm, the last two comparisons may not be valid. The narrower and sharper lophs of the specimens from the Camp Margetts area suggest that they may differ

specifically from *S. magister*, although more should be known about the range of variation of that species before a new one is erected. Measurements of the deciduous teeth are given in table 7.

In A.M.N.H. No. 81752 (maxilla with  $P^2-M^3$ ), the molars average 6 per cent shorter and 13 per cent narrower, and the premolars 10 per cent shorter and 23 per cent narrower, than the means for the rest of the sample (specimens listed above). A.M.N.H. No. 81752 may merely be an extreme variant of the *Schlosseria* cf. *S. magister* population with which it was found, or it may represent a new species.

#### *Schlosseria* cf. *Schlosseria magister*, additional specimens

MATERIAL: A.M.N.H. No. 81838, from "Irdin Manha" beds 5 miles east of Camp Margetts; A.M.N.H. No. 81837, from "Irdin Manha" beds at Camp Margetts; A.M.N.H. Nos. 81769–81774, 81793–81794, from "Irdin Manha" beds 7 miles west of Camp Margetts; A.M.N.H. Nos. 81787–81788, from ?"Houldjin gravels," and 81784–81786, from ?"Irdin Manha" beds, 10 miles southwest of Camp Margetts.

COMMENTS: The specimens listed above closely resemble *Schlosseria* cf. *S. magister* from 7 miles southwest of Camp Margetts and probably represent the same species. The specimens from 10 miles southwest of Camp Margetts have shorter  $M_3$  hypoconulids than those from 7 miles west and 7 miles southwest of Camp Margetts, but otherwise are indistinguishable. Two out of the six *Schlosseria* specimens from 10 miles southwest of Camp Margetts are recorded as coming from ?"Houldjin gravels," and the other four from ?"Irdin Manha" beds; all six specimens are virtually identical in size, cusp pattern, and preservation and probably came from the same horizon.

Although *Lophialetes* is recorded as coming from the same horizon as *Schlosseria* in the Camp Margetts area, the preservation is different enough between representatives of the two genera to suggest that they actually did come from different horizons (see p. 198).

#### ?*Schlosseria*

A.M.N.H. No. 26139, a lower jaw with  $P_2-M_2$  from ?"Shara Murun" beds at Urtyn Oba, Shara Murun region, corresponds in

TABLE 6

STATISTICAL DATA ON PERMANENT TEETH OF *Schlosseria* cf. *S. magister*  
FROM THE "IRDIN MANHA" BEDS IN THE CAMP MARGETTS AREA

	N	OR	SR	M	s	V
P <sup>1</sup>	3					
L		5.8- 6.5	—	6.13	—	—
W		4.4- 4.8	—	4.57	—	—
P <sup>2</sup>	4					
L		6.1- 6.8	—	6.50	—	—
W		6.5- 7.9	—	7.32	—	—
P <sup>3</sup>	5					
L		7.3- 8.0	—	7.62	—	—
W		8.5-10.6	—	9.56	—	—
P <sup>4</sup>	9					
L		7.0- 9.1	4.2	8.04±0.21	0.64±0.15	8.02±1.89
W		9.5-11.4	4.2	10.46±0.21	0.64±0.15	6.15±1.45
M <sup>1</sup>	13					
L		9.4-11.7	5.3	10.72±0.23	0.82±0.16	7.62±1.49
W		10.3-12.4	3.8	11.55±0.16	0.59±0.12	5.08±1.00
M <sup>2</sup>	9					
L		10.2-12.5	4.5	11.21±0.23	0.70±0.16	6.27±1.48
W		11.6-13.2	3.8	12.52±0.20	0.59±0.14	4.74±1.12
M <sup>3</sup>	6					
L		9.8-11.8	—	10.77	—	—
W		11.0-13.0	—	12.02	—	—
P <sub>1</sub>	1					
L		—	—	5.3	—	—
W		—	—	2.5	—	—
P <sub>2</sub>	4					
L		5.8- 7.8	—	6.48	—	—
W		3.8- 4.3	—	4.05	—	—
P <sub>3</sub>	7					
L		6.9- 8.4	3.3	7.44±0.19	0.51±0.14	6.90±1.84
W		4.4- 5.5	2.8	4.99±0.16	0.43±0.11	8.63±2.30
P <sub>4</sub>	10					
L		7.5- 8.6	2.7	7.88±0.13	0.41±0.09	5.15±1.15
W		5.2- 6.5	2.6	5.91±0.13	0.40±0.09	6.70±1.50
M <sub>1</sub>	20					
L		8.9-10.8	2.9	9.91±0.10	0.45±0.07	4.54±0.72
W		5.9- 7.0	2.1	6.44±0.07	0.32±0.05	4.94±0.78
M <sub>2</sub>	15					
L		9.9-11.5	3.5	10.87±0.14	0.54±0.10	4.94±0.90
W		6.3- 7.7	2.0	7.09±0.08	0.31±0.06	4.39±0.80
M <sub>3</sub>	12					
L		13.0-15.7	6.2	14.49±0.27	0.95±0.19	6.54±1.33
W		6.5- 7.3	1.4	6.98±0.06	0.21±0.04	3.06±0.62

size and proportions both to *Lophialetes expeditus*? from the Ulan Shireh beds 25 miles to the east, and to *Schlosseria* cf. *S. magister* from the Camp Margetts area, about 60 miles to the northeast. The P<sub>3</sub> trigonid is relatively long, as in *Schlosseria*, but this feature is not

definitely diagnostic. Three small mental foramina, under P<sub>2-3</sub>, P<sub>1-2</sub>, and the middle of the diastema, resemble more closely those in *Schlosseria* than those in *Lophialetes*, but again such a resemblance is not definitely diagnostic. The one other lophialetid speci-

TABLE 7

STATISTICAL DATA ON DECIDUOUS TEETH OF *Schlosseria* CF. *S. magister* FROM THE  
"IRDIN MANHA" BEDS IN THE CAMP MARGETTS AREA

	N	OR	SR	M	s	V
DP <sup>1</sup>	2					
L		5.3- 5.5	—	5.40	—	—
W		4.4- 4.7	—	4.55	—	—
DP <sup>2</sup>	5					
L		7.0- 7.7	—	7.26	—	—
W		7.4- 8.0	—	7.56	—	—
DP <sup>3</sup>	6					
L		8.5- 9.4	—	8.95	—	—
W		8.9- 9.7	—	9.23	—	—
DP <sup>4</sup>	6					
L		9.0-10.0	—	9.68	—	—
W		10.2-10.9	—	10.47	—	—
DP <sub>1</sub>	1					
L		—	—	4.9	—	—
W		—	—	2.4	—	—
DP <sub>2</sub>	5					
L		6.4- 7.2	—	6.72	—	—
W		3.4- 4.0	—	3.76	—	—
DP <sub>3</sub>	10					
L		8.4- 9.9	3.0	9.36±0.15	0.46±0.10	4.93±1.10
W		4.8- 6.0	2.3	5.37±0.11	0.36±0.08	6.74±1.50
DP <sub>4</sub>	11					
L		8.7- 9.6	2.1	9.21±0.10	0.32±0.07	3.48±0.74
W		5.5- 6.5	1.9	6.01±0.09	0.30±0.06	5.08±1.08

men found in the ?"Shara Murun" beds at Urtyn Obo appears to represent a species of *Lophialetes* (see p. 197).

#### BREVIODON,<sup>1</sup> NEW GENUS

TYPE SPECIES: *Breviodon acares*, new species.

INCLUDED SPECIES: *Breviodon acares*, *Breviodon? minutus*, new combination.

KNOWN DISTRIBUTION: Late Eocene of Asia.

DIAGNOSIS: Very small lophialetids, with premolar series extremely short relative to molar series; P<sub>1-2</sub> lost. Symphysis broad, postcanine diastema long. Lower molar cusp patterns like those in *Lophialetes*.

#### *Breviodon acares*,<sup>2</sup> new species

Plate 1, figure 1

TYPE: A.M.N.H. No. 26113, mandible with I<sub>3</sub>, C<sub>1</sub>, P<sub>4</sub>-M<sub>3</sub>.

<sup>1</sup> Greek *brevi*, short, plus *odon*, tooth; in reference to the shortened tooth row of this genus.

<sup>2</sup> Greek *acares*, little.

HYPODGM: Type and A.M.N.H. No. 81856 (worn P<sub>4</sub>-M<sub>3</sub>).

HORIZON AND LOCALITY: Late Eocene Ulan Shireh beds, North Mesa, Shara Murun region, Inner Mongolia.

DIAGNOSIS: Same as for genus. Length of M<sub>1-3</sub>, 24.5 mm.; of P<sub>3-4</sub>, 9.5 mm.

DESCRIPTION (FIG. 5): I<sub>3</sub> has a labiolingually compressed triangular crown with slightly convex anterior and slightly concave posterior edges, with a low posterior cuspule, as in *Lophialetes*. C<sub>1</sub> is relatively large and roughly triangular in cross section. The symphysis is relatively short and wide. There is a long postcanine diastema which terminates immediately anterior to the roots of P<sub>3</sub>, indicating that P<sub>1</sub> and P<sub>2</sub> were absent in this species. This condition can be observed in both A.M.N.H. Nos. 26113 and 81856 and is definitely not artificial. P<sub>3</sub> is not preserved, except for its two roots. P<sub>4</sub> is heavily worn in both specimens but appears to have had a pattern similar to that in *Lophialetes*. The lower molars are similar in cusp pattern to



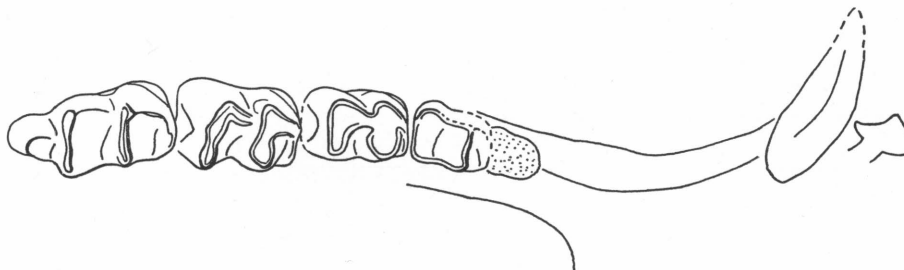


FIG. 5. *Breviodon acares*, new genus and species, type, A.M.N.H. No. 26113, left mandible with  $I_3$  (reversed),  $C_1$ ,  $P_3$  alveolus, and  $P_4$ - $M_3$ .  $\times 2$ .

those of *Lophialetes expeditus?* from the Ulan Shireh beds but are about 30 per cent smaller.

DISCUSSION: The lower molar cusp patterns of *Breviodon acares* suggest affinities to the lophialetids *Schlosseria* and *Lophialetes*, but the extreme reduction of the anterior premolars (loss of  $P_1$  and  $P_2$ ) indicates at least generic separation. The upper dentition of *Breviodon*, at present not definitely known, may reveal further significant differences from *Schlosseria* and *Lophialetes*.

*Breviodon acares* may be related to *Lophialetes minutus* (in this work transferred with query to *Breviodon*), a species known only from an isolated upper molar from the Irдин Manha beds (see below).

A few small, isolated, lophialetid teeth from the Ulan Shireh beds may also belong to *Breviodon acares*. A.M.N.H. No. 81858, an isolated  $M_3$ , is slightly larger than the two  $M_3$ 's known for *B. acares*, and has a relatively smaller hypoconulid, but may represent a large member of that species. A.M.N.H. No. 81857, an isolated  $M^3$  also from the Ulan Shireh beds, is about 20 per cent smaller than the mean of Ulan Shireh *Lophialetes expeditus?*  $M^3$ 's and therefore somewhat larger than would be expected for *Breviodon acares* (the lower teeth of which average 30% smaller than those of *L. expeditus?*). In cusp pattern A.M.N.H. No. 81857 differs from *Lophialetes expeditus?* in having a shorter, lower metacone (or posterior ectoloph extension) and a narrower, higher paracone; this latter feature is similar to that in *Rhodopagus*, a new genus described below (see p. 207). If A.M.N.H. No. 81857 does not belong to *Breviodon acares*, it represents a hitherto undescribed genus.

***Breviodon? minutus*** (Matthew and Granger, 1925c), new combination

*Lophialetes minutus* MATTHEW AND GRANGER, 1925c, p. 7.

TYPE: A.M.N.H. No. 20139, an isolated left upper molar.

HYPODIGM: Type only.

KNOWN DISTRIBUTION: Late Eocene Irдин Manha beds, Irдин Manha escarpment, about 20 miles south-southeast of Iren Dabasu, Inner Mongolia.

DIAGNOSIS: Close in size to *Breviodon acares* of the Ulan Shireh beds, and about 35 per cent smaller than Irдин Manha *Lophialetes expeditus*. The type upper molar is 7.9 mm. long and 9.0 mm. wide.

DISCUSSION: *Breviodon? minutus* is known only from an isolated upper molar (A.M.N.H. No. 20139; see fig. 6), which is intermediate in

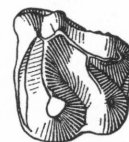


FIG. 6. *Breviodon? minutus*, new combination, type, A.M.N.H. No. 20139. From Matthew and Granger (1925c, fig. 8).  $\times 2$ .

cusp pattern between a lophialetid  $M^3$  and an  $M^2$  or  $M^1$  and thus is not assignable with certainty to a position in the tooth row. It differs from molars of *Lophialetes* in being about 35 per cent smaller, relatively shorter and wider, and in having a narrower, more pinched paracone. It cannot be compared directly with *Breviodon acares*, since no upper molars are definitely known for that species. (It differs from A.M.N.H. No. 81857, the  $M^3$

tentatively assigned to *B. acares* in having a higher, less reduced metacone, possibly because it had a different position in the tooth row, but also possibly because it comes from a different genus.) A.M.N.H. No. 20139 is here transferred to *Breviodon* because it differs from *Lophialetes* in cusp pattern, corresponds in size to *Breviodon acares*, and has a cusp pattern that could occlude with that of *B. acares*. Since most of the Ulan Shireh genera are also found in the Irдин Manha fauna, it would be no surprise to find *Breviodon* there too. Reference of *L. minutus* to *Breviodon* is queried pending knowledge of its premolars.

Of the several hundred lophialetid teeth collected in the Irдин Manha beds, only three are at all close in size to *Breviodon? minutus*. A.M.N.H. Nos. 81721A and 81721B, two isolated  $M_3$ 's, average about 25 per cent smaller than the *Lophialetes expeditus* mean. A.M.N.H. No. 81721A is probably a pathological specimen of *L. expeditus*, since it has a large protolophid but is abnormally reduced posteriorly; A.M.N.H. No. 81721B is normally proportioned and may represent *Breviodon? minutus*. A.M.N.H. No. 81722, an  $M^1$ ,  $M^2$ , or possibly a  $DP^4$ , averages between 20 to 25 per cent smaller than corresponding teeth of *Lophialetes expeditus* and also may be a large specimen of *Breviodon? minutus*. It differs from the type of *B.? minutus* in having a relatively larger parastyle and a deeper notch between paracone and metacone.

#### **?Breviodon, undescribed species**

A.M.N.H. No. 26115, a jaw with a  $DP_2$  alveolus,  $DP_{3-4}$ , and  $M_{1-2}$ , from the Ulan Shireh beds, resembles *Breviodon acares* in size and molar cusp pattern, although the  $M_1$  is slightly relatively narrower than in that species. The  $DP_4$  is smaller and relatively narrower but otherwise resembles the  $M_1$ ;  $DP_3$  has an extremely short paralophid compared to the  $DP_3$ 's of *Schlosseria* and *Lophialetes*. The  $DP_2$  alveolus indicates a double-rooted tooth which, even if it were not replaced, would have left some trace in the adult jaw. There is no evidence of a tooth anterior to  $P_3$  in the two mature jaws known for *Breviodon acares*, which suggests that A.M.N.H. No. 26115 is at least specifically

and possibly generically distinct from that species. Small size, a reduced  $DP_3$  paralophid, and short (labiolingually)  $M_1$  cross lophs separate this specimen from *Lophialetes expeditus*. A.M.N.H. No. 26115 alone is not adequate for a diagnosis of a new species; pending further information on its affinities, I leave it questionably referred to *Breviodon*.

#### **?Breviodon**

A few isolated upper and lower molars (A.M.N.H. No. 81839) from the "Irдин Manha" beds 5 miles east of Camp Margetts are smaller than *Schlosseria* cf. *S. magister* teeth from that locality and correspond most closely in size and cusp pattern to those of *Breviodon acares* and *B.? minutus*. However, the available material is inadequate for specific assignment.

#### **Cf. Breviodon acares**

##### **Plate 1, figure 2**

**MATERIAL:** A.M.N.H. No. 81751, a skull missing the snout but with all cheek teeth.

**HORIZON AND LOCALITY:** "Irдин Manha" beds, 7 miles southwest of Camp Margetts, 30 miles south-southwest of Iren Dabasu, and about 30 miles west of the type Irдин Manha locality, Inner Mongolia.

**DIAGNOSTIC CHARACTERS:** A very small tapiroid with the premolars crowded and small relative to the molars.  $P^1$  lost.  $P^2-3$  with protoloph but no metaloph;  $P^4$  with metaloph as high as protoloph and narrow protocone.  $P^3-M^3$  with strongly convex metacones. Molar metacones only slightly lingually displaced.  $M^{1-3}$  relatively short and wide. Length of  $P^2-4$ , 15.5 mm.; of  $M^{1-3}$ , 24 mm.

**DESCRIPTION:** Most of the preorbital portion of the skull, including the premaxillae, nasals, and ascending walls of maxillae, is missing, so it is not possible to determine the extent of nasal incision retraction. The infra-orbital foramen is situated above the posterior part of  $P^2$ . The posterior half of the skull appears similar to that of *Lophialetes* (described on p. 237), with a pronounced post-orbital constriction, moderately expanded braincase, and high, sharp, sagittal and lambdoidal crests. The skull differs from that of *Lophialetes* in having relatively much smaller postglenoid processes, a sharp ventral keel on

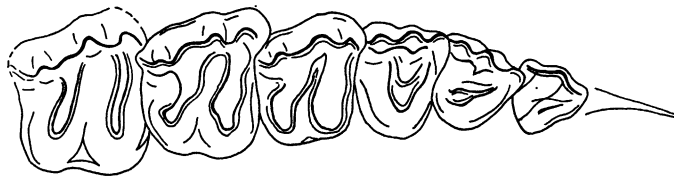


FIG. 7. Cf. *Breviodon acares*. A.M.N.H. No. 81751, P<sup>2</sup>-M<sup>3</sup> (reversed from left side).  $\times 2$ .

the basioccipital, and the foramen ovale relatively closer to (although still separated from) the foramen lacerum medius.

One side of the palate (see fig. 7) is sufficiently well preserved to show that the post-canine diastema terminated immediately anterior to P<sup>2</sup>, indicating that P<sup>1</sup> was absent. P<sup>2</sup> is triangular in outline, with a very small parastyle, prominent paracone, but no metacone differentiated from the ectoloph. A short low protoloph trends posterolingually from between the parastyle and paracone; there is no metaloph. P<sup>3</sup> is like P<sup>2</sup> but larger and wider, with a relatively larger parastyle, well-differentiated convex metacone, a relatively longer protoloph, but also without a metaloph. P<sup>4</sup> is relatively and absolutely much wider than P<sup>3</sup> and is significantly more advanced in possessing a metaloph. The P<sup>4</sup> metaloph is as high as the protoloph, as in *Lophialetes* and *Schlosseria*, but differs from that of those genera in joining the protoloph at a sharp, V-shaped angle, rather than in a broad U. The right P<sup>4</sup> has a narrow, sharply convex (lingually) protocone, while the left P<sup>4</sup> protocone shows a shallow lingual groove, apparently indicating incipient separation of a hypocone. However, the left P<sup>4</sup> is deformed, possessing a large anomalous labial cuspule between parastyle and paracone, but no metacone; the incipient hypocone separation may also be aberrant for the species. M<sup>1-3</sup> are relatively short and wide, with a moderately large parastyle, strongly convex paracone, and only slightly lingually displaced, strongly labially convex metacones. The protolophs and hypolophs are worn but seem to have been relatively low and obtuse. M<sup>3</sup> is relatively short and wide and not so different from the anterior molars as is M<sup>3</sup> in *Lophialetes* or *Schlosseria*.

The length-width measurements (in mm.) are as follows: P<sup>2</sup>, 4.9 by 4.8; P<sup>3</sup>, 5.7 by 6.3;

P<sup>4</sup>, 5.7 by 7.9; M<sup>1</sup>, 7.5 by 8.8; M<sup>2</sup>, 8.9 by 10.6; M<sup>3</sup>, 8.9 by 10.5.

DISCUSSION: The convex molar metacones of A.M.N.H. No. 81751 recall those of North American isectolophids, such as *Homogalax* and *Isectolophus*, or the Asiatic (Burmese) tapiroid of unknown affinities, *Indolophus*. However, A.M.N.H. No. 81751 differs from isectolophids in the lack of the characteristic isectolophid trapezoidal M<sup>3</sup>, loss of P<sup>1</sup>, presence of a postcanine diastema, and in having slightly less convex metacones. A.M.N.H. No. 81751 differs from *Indolophus* in the following features: molar ectolophs smaller relative to cross lophs, parastyles larger, P<sup>4</sup> with high metaloph, premolars smaller relative to molars, and teeth lower crowned. Similarities between A.M.N.H. No. 81751 and isectolophids or *Indolophus* can best be ascribed to a common retention of primitive tapiroid characters (such as convex molar metacones) and are not necessarily indicative of phylogenetic affinities below the superfamily level.

The molars of A.M.N.H. No. 81751 most closely resemble those of *Schlosseria*, but differ in being relatively shorter and wider (especially M<sup>3</sup>), and in having more convex, less lingually displaced, and apparently shorter metacones. The premolars of A.M.N.H. No. 81751 differ from those of *Schlosseria* in being relatively smaller compared to the molars, in the loss of P<sup>1</sup>, absence of P<sup>2-3</sup> metalophs, and in the acute protoloph-metaloph junction (with narrow protocone) on P<sup>4</sup>. These differences are even greater when comparisons are made with *Lophialetes*, which is more specialized than *Schlosseria* in a direction away from A.M.N.H. No. 81751.

In size and extreme reduction of the premolar series A.M.N.H. No. 81751 resembles the Ulan Shireh species *Breviodon acares*, a form known only from lower dentitions. The former is 30 per cent smaller than *Lophialetes*

*expeditus?* uppers, and the latter 30 per cent smaller than *L. expeditus?* lowers. *Breviodon acares* is unique among tapiroids in its extreme degree of premolar reduction, having lost both  $P_1$  and  $P_2$ . A.M.N.H. No. 81751 is unique among Asiatic tapiroids in having lost  $P^1$  (the European genus *Lophiodon* also lacks  $P^1$ ). Nothing in the dental pattern of the upper teeth of A.M.N.H. No. 81751 from the Camp Margetts area prevents its occlusion with the lowers of the Ulan Shireh *Breviodon acares*, and, in view of similarities in size and premolar reduction, it is possible that they represent upper and lower dentitions, respectively, of the same genus, if not the same species. This suggestion cannot be proved or disproved until the discovery of upper teeth of *Breviodon acares* in the Ulan Shireh beds or lower teeth of the species represented by A.M.N.H. No. 81751 in the Camp Margetts area. Pending such information, rather than clutter the literature with new names and possibly confuse the faunal and phylogenetic picture, I leave A.M.N.H. No. 81751 for the present unnamed, with the suggestion that it may prove to be closely related to *Breviodon*. If so, the isolated upper molars tentatively assigned to *Breviodon* (*B.?* *minutus* and others) must be assigned to a new genus, and the definition of the family Lophialetidae must be expanded to include forms with short, convex, molar metacones.

ADDITIONAL MATERIAL: A.M.N.H. No. 81836, a lower jaw fragment with  $DP_4$ ,  $M_{1-2}$ , from the same locality as the above-discussed skull, averages about 25 per cent smaller than corresponding teeth of *Schlosseria* cf. *S. magister* from that locality, and about 13 per cent larger than those of Ulan Shireh *Breviodon acares*. It is thus slightly larger than lower teeth that one would expect to go with A.M.N.H. No. 81751, but the difference is within the bounds of possible intraspecific variation. In cusp pattern the  $DP_4$ ,  $M_1$ , and  $M_2$  resemble corresponding teeth of *Schlosseria* (and *Breviodon*) but are slightly relatively wider at the base, with the cross lophs narrower on top (labial and lingual slopes less vertical). A.M.N.H. No. 81836 may be conspecific with A.M.N.H. No. 81751, but additional specimens are necessary for such allocation to be proved definitely.

A particularly puzzling specimen which

should be mentioned here is A.M.N.H. No. 81841, a lower jaw fragment with  $DP_{3-4}$  and  $M_1$  from "Irdin Manha" beds 10 miles southwest of Camp Margetts. The  $DP_{3-4}$  average 25 per cent smaller than corresponding teeth of *Schlosseria* cf. *S. magister* from the Camp Margetts area, but the  $M_1$  is disproportionately large, averaging only 10 per cent smaller than  $M_1$  in *Schlosseria* cf. *S. magister*. The  $M_1$  differs in cusp pattern from that of *Schlosseria* in having the cross lophs relatively narrower at the top. The cusp pattern is lophialetid, but the combination of large  $M_1$  and small  $DP_{3-4}$  makes it impossible to assign A.M.N.H. No. 81841 to any known genus.

#### ?FAMILY LOPHIALETIDAE

##### RHODOPAGUS,<sup>1</sup> NEW GENUS

TYPE SPECIES: *Rhodopagus pygmaeus*, new species.

INCLUDED SPECIES: Type and *R.?* *minimus*, new combination.

KNOWN DISTRIBUTION: Late Eocene of Asia.

DIAGNOSIS: Very small tapiroids with premolar series shortened relative to molars. Long postcanine diastemata.  $P^{3-4}$  relatively short and wide, with prominent protolophs and small metalophs.  $M^{1-3}$  paracones high and sharply convex, protolophs and metalophs oblique, metacones flat and increasingly posterolingually directed from  $M^1$  to  $M^3$ , so that in  $M^3$  the metacone (or posterior part of ectoloph) is confluent with metaloph. Symphysis sharply constricted.  $P_1$  lost.  $P_{2-4}$  submolariform.  $M_{1-3}$  moderately bilophodont, with oblique cross crests, and reduced metalophs and paralophs.  $M_3$  without a hypoconulid. Nasal incision not enlarged.

DISCUSSION: The peculiar upper cusp pattern of *Rhodopagus*, with its oblique, inverted U- to V-shaped shearing lophs, with the metacones parallel to or confluent with the metalophs, sets this genus apart from all other previously described tapiroids. The phylogenetic relationships of *Rhodopagus* and the reasons for the family assignment are discussed below (see p. 213) after the description of another new closely related genus.

<sup>1</sup> Greek *rhodon*, red, and *pagos*, hill, a translation of the Mongolian name (Ulan Shireh) of the type locality.

TABLE 8  
MEASUREMENTS (IN MILLIMETERS) OF UPPER  
TEETH OF *Rhodopagus pygmaeus* FROM  
THE ULAN SHIREH BEDS

	A.M.N.H. No. 21554	A.M.N.H. No. 81859	A.M.N.H. No. 81860
P <sup>1</sup>	—	—	—
P <sup>2</sup>	—	—	—
P <sup>3</sup>			
L	4.2	—	—
W	5.3	—	—
P <sup>4</sup>			
L	4.3	—	—
W	6.6	—	—
M <sup>1</sup>			
L	7.0	—	—
W	8.5	—	—
M <sup>2</sup>			
L	7.8	7.3	—
W	8.9	8.8	—
M <sup>3</sup>			
L	7.8	—	7.9
W	9.2	—	9.9

***Rhodopagus pygmaeus*,<sup>1</sup> new species**

Plate 2, figures 1-3

TYPE: A.M.N.H. No. 21554, maxillae with P<sup>1-2</sup> alveoli and P<sup>3</sup>-M<sup>3</sup>.

HYPODIGM: Type and A.M.N.H. Nos. 20330-20350, 20390-20394, 26112, 26114 (all lower dentitions), 81859 (M<sup>2</sup>), and 81860 (M<sup>3</sup>).

HORIZON AND LOCALITY: Late Eocene Ulan Shireh beds, North Mesa, Shara Murun region, Inner Mongolia.

DIAGNOSIS: Upper and lower molars with swollen, club-like, root tips. Lower jaw relatively robust. Dental measurements are given in tables 8 and 9.

DESCRIPTION (FIGS. 8-9): The type specimen (A.M.N.H. No. 21554) preserves enough of a maxilla to show that the infraorbital foramen was large and opened above P<sup>1</sup>. The relatively far forward position of this foramen suggests that the nasal incision was not enlarged.

The premolar series is short compared to the molars; the ratio of P<sup>1-4</sup> to M<sup>1-3</sup> lengths is 0.67. Only a single large alveolus is present for P<sup>1</sup>, but the maxilla is broken off immediately

anterior to it, so it is not possible to determine whether P<sup>1</sup> had one or two roots. P<sup>2</sup> is not preserved. P<sup>3</sup> is relatively short and wide and roughly rectangular in outline. The ectoloph is fairly flat, with only faint lingual indications of the parastyle and broadly convex paracone. The protoloph rises in height from the parastyle to the protocone and is the dominant lingual crest. The metaloph is a thin, low, vertical ridge on the base of the lingual face of the ectoloph and dies out before reaching the protocone; with relatively little wear the metaloph would be obliterated. Posterior to the metaloph there is a broad basined shelf bounded posteriorly by a low basal cingulum. P<sup>4</sup> is like P<sup>3</sup> but slightly larger, relatively shorter and wider, with a more prominent metaloph and a narrower posterior shelf.

The upper molars have small to medium-sized parastyles, high, sharply convex paracones, oblique protolophs and metalophs, and flat metacones which are increasingly posterolingually deflected from M<sup>1</sup> to M<sup>3</sup>. On M<sup>1</sup>, and more so on M<sup>2</sup>, the entire length of the metacone (or posterior part of the ectoloph) runs parallel and immediately adjacent to the metaloph; on M<sup>3</sup> the metacone is even more lingually deflected and is confluent with the metaloph. Even after considerable wear the paracone remains a high, narrow cusp.

The mandible is relatively deep and robust, with a convex ventral border and a prominent fossa (probably for the buccinator) behind M<sub>3</sub>. The symphysis is sharply constricted and terminates a short distance anterior to P<sub>2</sub>. A large alveolus preserved in A.M.N.H. No. 20330 indicates a relatively large canine. The postcanine diastema is relatively long. P<sub>1</sub> is absent. P<sub>2</sub>, preserved only in A.M.N.H. No. 26112, is relatively long and narrow, with a high labial ridge (paralophid) occupying most of the anterior two-thirds of the crown and a low elongate cusplule (metalophid and hypoconid) in the posterolabial corner. A low broad ridge (incipient protolophid) descends steeply linguallly from the posterior end of the paralophid, separating a shallow anterior lingual concavity from a deeper posterior one. P<sub>3</sub> has a relatively short but high paralophid which trends posterolinguallly to merge in a continuous curve with the short protolophid. The metalophid is fairly high

<sup>1</sup> Greek *pygmaios*, dwarf.



TABLE 9  
STATISTICAL DATA ON LOWER TEETH OF *Rhodopagus pygmaeus* FROM THE ULAN SHIREH BEDS

	N	OR	SR	M	s	V
P <sub>2</sub>	1					
L		—	—	4.2	—	—
W		—	—	2.2	—	—
P <sub>3</sub>	6					
L		4.3–5.3	—	4.77	—	—
W		3.1–3.8	—	3.40	—	—
P <sub>4</sub>	11					
L		5.1–6.0	2.2	5.46±0.10	0.34±0.07	6.31±1.35
W		3.8–4.6	1.4	4.25±0.06	0.21±0.04	4.87±1.04
M <sub>1</sub>	10					
L		6.3–7.3	1.6	7.00±0.08	0.25±0.06	3.56±0.80
W		4.7–5.3	1.0	4.97±0.05	0.15±0.03	3.00±0.67
M <sub>2</sub>	7					
L		7.5–8.7	3.3	8.16±0.19	0.51±0.14	6.25±1.67
W		5.1–6.0	2.0	5.50±0.12	0.31±0.08	5.65±1.51
M <sub>3</sub>	8					
L		8.0–9.0	2.7	8.46±0.14	0.41±0.10	4.85±1.21
W		5.3–6.0	1.6	5.63±0.08	0.24±0.06	4.25±1.06
DP <sub>2</sub>	5					
L		3.9–4.9	—	4.42	—	—
W		2.1–2.6	—	2.38	—	—
DP <sub>3</sub>	7					
L		5.7–6.6	2.3	6.26±0.14	0.36±0.10	5.69±1.52
W		3.2–3.8	1.3	3.61±0.08	0.20±0.05	5.42±1.45
DP <sub>4</sub>	5					
L		5.7–6.7	—	6.06		—
W		3.8–4.4	—	4.06		—

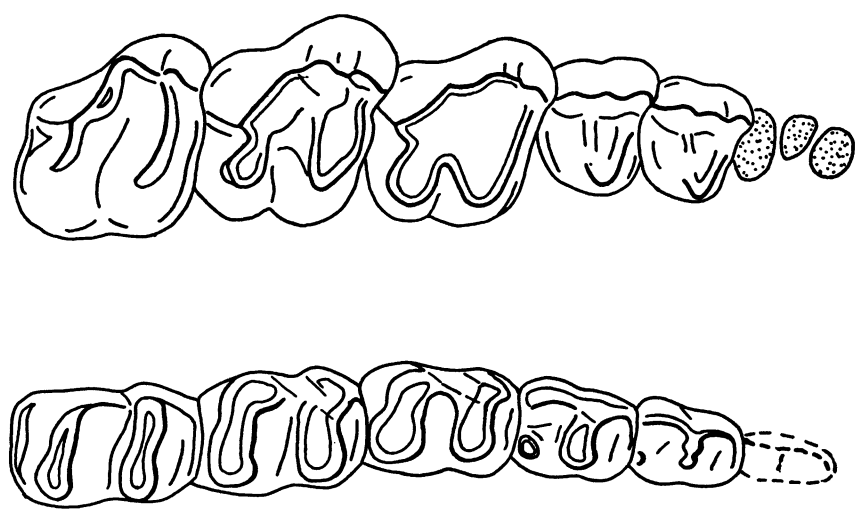


FIG. 8. *Rhodopagus pygmaeus*, new genus and species. Above: Type, A.M.N.H. No. 21554, P<sup>1-2</sup> alveoli and P<sup>3</sup>-M<sup>3</sup> (reversed from left side). Below: A.M.N.H. No. 20331, P<sub>3</sub>-M<sub>3</sub>, with P<sub>2</sub> restored from A.M.N.H. No. 26112. Both ×3.

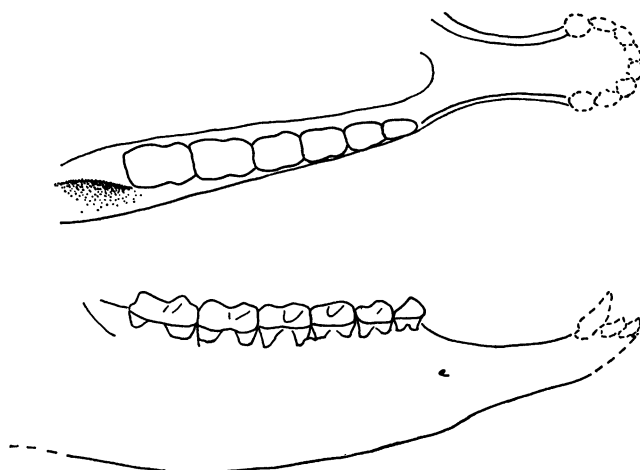


FIG. 9. *Rhodopagus pygmaeus*, new genus and species, lower jaw in occlusal (above) and lateral (below) views, composite based on A.M.N.H. Nos. 20330, 20331, and 20337.  $\times 1$ .

and continues back from the paralophid-protolophid junction along the labial margin of the tooth, rising slightly at the posterolabial corner into a broad hypoconid. The lingual slope of the hypoconid merges into a narrow posterolingual shelf with an incipient entoconid.  $P_4$  is like  $P_3$  but slightly larger, relatively shorter and wider, and has a small isolated entoconid.

The lower molars are essentially bilophodont, with oblique protolophids and hypolophids, much reduced paralophids, and somewhat less reduced metalophids. The metalophids barely reach the protolophids before dying out; in  $M_3$  the metalophid joins the hypolophid in a broad, continuous curve. There is no  $M_3$  hypoconulid.  $M_{1-3}$  are slightly wider posteriorly than anteriorly.

The upper deciduous dentition is unknown.  $DP_2$  is like  $P_2$ , except that it has a longer paralophid which terminates anteriorly in a low paraconid, and a wider talonid which bears a small entoconid.  $DP_3$  has a molariform talonid (with complete hypolophid), a wide protolophid, and a long trigonid, with the paralophid rising to a high paraconid at the anterior apex of the crown. The paraconid gives rise to a short, posterolingually trending ridge which parallels the protolophid.  $DP_4$  is like  $M_1$  except that it is smaller and slightly relatively longer and narrower.

An unusual feature of both upper and lower molars in *Rhodopagus pygmaeus* is the expansion of the root tips into bulbous, irregular, club-like processes. This apparently does not occur in the premolars or deciduous teeth.

DISCUSSION: The lower dentition of *Rhodopagus pygmaeus* resembles that of the North American helaletid *Dilophodon leotanus*, differing mainly in the relatively smaller and less molariform premolars, more oblique cross crests, and less reduced metalophids. The resemblances between the lower teeth of these two species is so great that, having only the lower teeth, one would probably assign the Mongolian form to *Dilophodon*. However, the association of the upper and lower teeth of *Rhodopagus pygmaeus* can hardly be doubted—they agree in size and degree of premolar reduction, occlude perfectly, and both have club-like molar root tips. The striking differences between the upper molars of *Rhodopagus* and those of *Dilophodon* or any other helaletid indicate that the similarities seen in the lowers must be due to convergence. Two unrelated tapiroid lines, one in Asia and one in North America, independently evolved into small forms with bilophodont lower molars, shortened the premolar series, and lost the  $M_3$  hypoconulid.

The significance of the peculiar upper

molar pattern of *Rhodopagus* in occlusion becomes obvious upon examination of the molar wear facets. The high narrow paracone and, after some wear, the parastyle shear vertically against the posterolabial side of the protoconid (or protolophid) and labial side of the metalophid. This shear is the major one between the ectoloph and the labial sides of the lower molars and accounts for the prominence of the paracone and the incomplete reduction of the metalophid. The extreme lingual displacement of the metacone precludes the possibility of vertical shear against the labial edge of the paralophid, which accordingly is greatly reduced.

The main occlusal action of *Rhodopagus* molars is transverse shear, which occurs between the anterior sides of the protolophs and metalophs above and posterior sides of the protolophids and hypolophids, respectively, below. The functional significance of the extreme lingual deflection of the metacone and its alignment along the metaloph apparently is to increase the thickness of the posterior upper cross loch edge available for shear across the back of the hypolophid. This feature is the unusual specialization of *Rhodopagus* molars, and it is carried to an even greater extreme in another new genus described below (see p. 212).

The shortening of the premolar series relative to the molars in *Rhodopagus pygmaeus* suggests decreasing importance of the anterior cheek teeth in mastication. The function of the club-like processes on the molar root tips of *R. pygmaeus* is open to conjecture. Presumably they strengthened the tooth attachments in the mandible and maxilla and, taken in conjunction with the short, robust mandible and the large buccinator fossa, suggest adaptation for chewing tough vegetation.

#### ?*Rhodopagus pygmaeus*

An isolated  $P_3$  or  $P_4$  and an unassociated lower molar (catalogued together as A.M.N.H. No. 81842) and a lower jaw fragment with  $M_{1-3}$  (A.M.N.H. No. 81843), all from the type Irдин Manha beds, are similar in cusp pattern to *Rhodopagus pygmaeus* from the Ulan Shireh beds. The lower molars average about 10 per cent longer (but no wider) than those of *R. pygmaeus* and have relatively longer trigonids.

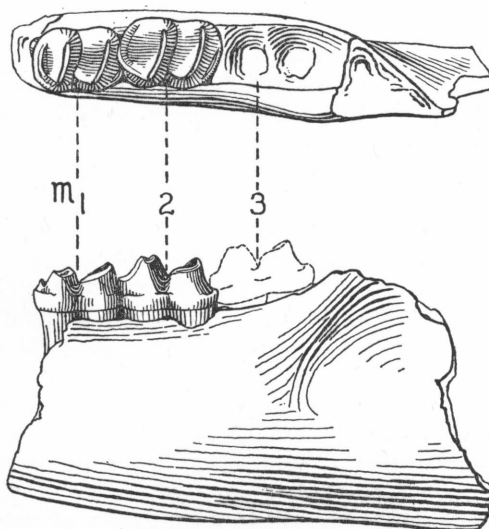


FIG. 10. *Rhodopagus? minimus*, new combination, type, A.M.N.H. No. 20310, in occlusal and lateral views. From Matthew and Granger (1925b, fig. 9).  $\times 1.5$ .

***Rhodopagus? minimus*** (Matthew and Granger, 1925b), new combination

*Caenolophus? minimus* MATTHEW AND GRANGER, 1925b, p. 7.

TYPE: A.M.N.H. No. 20310, lower jaw fragment with  $M_{1-2}$ .

HORIZON AND LOCALITY: Late Eocene Shara Murun beds, Ula Usu, Baron Sog Mesa, Shara Murun region, Inner Mongolia.

HYPODIGM: Type only.

DIAGNOSIS: About the same size as *Rhodopagus pygmaeus*, but  $M_{1-2}$  slightly wider and root tips not expanded.

DISCUSSION: Matthew and Granger (1925b, p. 7) erected the species *Caenolophus? minimus* for a lower jaw fragment (A.M.N.H. No. 20310) with  $M_{1-2}$ , from the Shara Murun beds. Assignment to *Caenolophus* was made provisional because of the specimen's small size. However, the trigonids of *C.? minimus* are shorter and the metalophids more reduced than those in other species of *Caenolophus* or any other rhinocerotoid. In fact, A.M.N.H. No. 20310 closely resembles in size and cusp pattern *Rhodopagus pygmaeus* from the underlying Ulan Shireh beds.

*Caenolophus? minimus* differs from comparable teeth ( $M_{1-2}$  only) of *Rhodopagus pygmaeus* in having relatively wider molars,

a slightly wider  $M_2$  protolophid (the protoconid is situated slightly more labially and its labial edge is somewhat steeper), and in lacking bulbous root tips. Had A.M.N.H. No. 20310 been found in the same beds with *R. pygmaeus*, it would probably have been considered an extreme morphological variant of that species. However, *C.? minimus* should be kept taxonomically separated from *Rhodopagus pygmaeus* for the following reasons: (1)  $M_{1-2}$ , the only teeth available for comparison, are among the least diagnostic teeth in the dentition and would be less likely to show generic or specific differences than, for example, the premolars or upper molars; and (2) the Shara Murun fauna is younger and quite different from that of the Ulan Shireh beds. These factors suggest that discovery of more teeth of *C.? minimus* will reveal further differences between it and *Rhodopagus pygmaeus*. However, until such information is forthcoming, the similarities in lower molar pattern between these two species are great enough to allow at least questionable assignment of *minimus* to *Rhodopagus*.

#### ?*Rhodopagus*

Zdansky (1930, pp. 40-42, pl. 3, figs. 1-2) described and figured a small ceratomorph lower jaw with  $M_{2-3}$ , from Eocene or Oligocene beds near Hsintai, central Shantung, China, which he referred to as "Hyracodontid, gen. et sp. indet." Zdansky's specimen is similar in size and cusp pattern to comparable parts of *Rhodopagus pygmaeus*, differing from the Mongolian species mainly in the apparent further reduction of the  $M_3$  metalophid. The Chinese form appears to be most closely related to species assigned to *Rhodopagus*, but more information is necessary before its affinities can be clarified.

An isolated lower molar from late Eocene beds near Mienchih, northern Honan, China, described and figured by Zdansky (1930, p. 38, pl. 1, figs. 36-37), also appears similar to lower molars of *Rhodopagus*.

#### **PATAECUS,<sup>1</sup> NEW GENUS**

TYPE SPECIES: *Pataecus parvus*, new species.

INCLUDED SPECIES: Type only.

<sup>1</sup> Greek *Pataikos*, an odd-shaped, dwarf-like, Phoenician deity.

KNOWN DISTRIBUTION: Late Eocene of Asia.

DIAGNOSIS: Diminutive tapiroids with premolar series not shortened relative to molars. Upper molars more specialized than those of *Rhodopagus*, with longer, more lingually displaced ectolophs and shorter metalophs, with the posterolingual corner of the crown truncated and rounded.

DISCUSSION: The upper molars of *Pataecus* have the same basic pattern as those of *Rhodopagus*, with oblique, inverted U- to V-shaped shearing lophs, and the posterior ends of the ectolophs parallel to or confluent with the metalophs. However, the upper molars of the former are even more specialized than those of the latter (see diagnosis above), with the degree of difference indicative of generic separation. This is supported by the lesser degree of premolar shortening and further differences noted in a partial lower dentition assigned to *Pataecus* (see description below).

#### ***Pataecus parvus*,<sup>2</sup> new species**

Plate 2, figures 4-5

TYPE: A.M.N.H. No. 21747, maxilla with  $P^1$  roots and  $P^2-M^3$ .

HYPODIGM: Type and A.M.N.H. Nos. 21746 ( $P^2-M^3$ ) and 81861 ( $DP_4-M_1$ ).

HORIZON AND LOCALITY: Late Eocene Kholobolchi Formation, about 5 miles north of Orok Nor, Mongolian People's Republic.

DIAGNOSIS: Sole known species of genus. Dental measurements are given in table 10.

DESCRIPTION (FIG. 11): The infraorbital foramen is slightly smaller than that of *Rhodopagus pygmaeus* and opens above  $P^2$ . An isolated upper canine associated with A.M.N.H. No. 21747 has a small crown, oval in cross section, and a long, swollen, labiolingually flattened root. The premolar series is not shortened relative to the molars: the ratio of  $P^{1-4}$  to  $M^{1-3}$  is 0.85.  $P^1$  has two roots and, from the fragment preserved in A.M.N.H. No. 21747, appears to have had a single, labiolingually compressed cusp, with no lingual cingulum.  $P^2$  is roughly triangular in outline, with a relatively large parastyle, indistinctly separated paracone and metacone, a short, posterolingually trending protoloph, and a crista on the middle of the

<sup>2</sup> Latin *parvus*, little.

TABLE 10  
MEASUREMENTS (IN MILLIMETERS) OF UPPER  
TEETH OF *Pataecus parvus*

	A.M.N.H. No. 21746	A.M.N.H. No. 21747
P <sup>1</sup>	—	—
P <sup>2</sup>	—	—
L	—	4.2
W	—	4.4
P <sup>3</sup>	—	—
L	5.1	5.3
W	5.9	6.5
P <sup>4</sup>	—	—
L	6.0	5.6
W	7.1	8.0
M <sup>1</sup>	—	—
L	7.3	—
W	9.0	—
M <sup>2</sup>	—	—
L	7.8	8.3
W	9.6	8.9
M <sup>3</sup>	—	—
L	7.2	7.2
W	9.0	8.6

lingual face of the ectoloph representing the metaloph. There is a wide, slightly basined, posterolingual shelf with an elongate cuspule at the posterolingual corner. This cuspule is separated from the protoloph by a notch but otherwise seems a continuation of that ridge. A basal cingulum is present only labially. P<sup>3-4</sup> are similar to those teeth in *Rhodopagus pygmaeus*, differing mainly in being of relatively larger size, the possession of a labial basal cingulum, and in the tendency for the protocones to be lengthened posteriorly for a short distance.

The upper molars of *Pataecus* differ from

those of *Rhodopagus* in having longer, more lingually displaced ectolophs, with the posterolabial root also shifted lingually, and shorter metalophs, with the whole posterolingual corner of the crown truncated in a smooth sweeping curve from the anterolingual corner to the middle of the posterior side. Also, root tips appear slightly less swollen in *Pataecus*.

A lower jaw fragment (A.M.N.H. No. 81861) with what appears to be DP<sub>4</sub> and M<sub>1</sub>, from the same locality as the *Pataecus parvus* upper dentitions, probably represents the same species. A.M.N.H. No. 81861 differs from corresponding teeth in *Rhodopagus pygmaeus* in the following features: M<sub>1</sub> absolutely and relatively narrower, with a shorter protolophid and more distinct protoconid and metaconid; DP<sub>4</sub> relatively longer and narrower, with a more prominent anterior cingulum and a short ridge running anteriorly from the entoconid (this latter feature occurs also in *Rhodopagus pygmaeus* but not so prominently).

**DISCUSSION:** The upper molars of *Pataecus* are even more specialized than those of *Rhodopagus*, with longer, more posterolingually directed ectolophs and shortened metalophs. Because of these modifications, the back of the hypolophid sheared mainly against the lingually depressed ectoloph rather than the free portion of the metaloph, which in *Pataecus* is very short.

While the upper molars of *Pataecus parvus* are more specialized than those of *Rhodopagus pygmaeus*, the premolar series of the latter is more reduced relative to the molars than that of the former species, which precludes the possibility that either species was ancestral to the other. We may thus suppose a common



FIG. 11. *Pataecus parvus*, new genus and species, type, A.M.N.H. No. 21747, P<sup>2</sup>-M<sup>3</sup>, with hypothetical restoration of P<sup>1</sup>. ×3.

ancestor for both forms which had molars similar to (or no more specialized than) those of *Rhodopagus*, and premolars unreduced relative to the molars, as in *Pataecus*.

The familial affinities of *Rhodopagus* and *Pataecus* are open to speculation. Similarities in dentition to that of the Helaletidae are probably due to convergence. In the advanced helaletid *Colodon*, while the molar metacone is lingually displaced, it is shortened, not lengthened, and the posterior end of the ectoloph is perpendicular, not parallel, to the metaloph. The metacone in *Colodon* does not appreciably thicken the metaloph for transverse shear, most of which occurs along the long free metaloph.

The dentition of *Rhodopagus* and *Pataecus* could be derived from that of a primitive lophialetid, such as the (unknown) ancestor of *Schlosseria*, but no intermediate forms are known. These may turn up in early or middle Eocene faunas when such become known for central Asia. The two new genera and the lophialetids possess in common a feature unusual in tapiroids—long ectolophs. However, *Rhodopagus* and *Pataecus* represent a stock characterized by small size and evolution toward a functionally bilophodont dentition (by lingual depression of the metacone), while the *Schlosseria-Lophialetes* group shows evolutionary size increase and development of rhinocerotoid-like molar occlusion. The size difference is not an important criterion on the family level (cf. the dwarf *Dilophodon* lineage in the Helaletidae), but the difference in molar pattern between these two groups of Asiatic tapiroids may be indicative of supra-generic separation. However, until more is known of the early evolutionary history of the genera involved, it seems best to assign *Rhodopagus* and *Pataecus* provisionally to the Lophialetidae. Should it eventually become desirable to include these genera definitely in the Lophialetidae, the definition of the family must be expanded.

#### DEPERETELLIDAE, NEW FAMILY

TYPE GENUS: *Deperetella* Matthew and Granger (1925b).

INCLUDED GENERA: *Deperetella* and *Teleolophus* Matthew and Granger (1925c).

KNOWN DISTRIBUTION: Middle to late Eocene of Asia.

DIAGNOSIS: Medium-sized to large tapiroids with full placental dentition and post-canine diastemata. Premolars submolariform to molariform. Molars high-crowned for a tapiroid and bilophodont. Upper molar protoloph, paracone, and metaloph forming a slightly oblique inverted U, with the metacone (posterior ectoloph extension) greatly reduced and lingually displaced in  $M^{1-2}$ , and lost completely in  $M^3$ ; lower molars with two parallel cross lophs, and paralophid and metalophid extremely reduced.  $M_3$  without a hypoconulid. Manus tridactyl in advanced forms.

DISCUSSION: Matthew and Granger (1925b, p. 5; 1925c, p. 5) considered *Teleolophus* and *Deperetella* clearly related to the helaletid *Colodon* and therefore assigned them to the Helaletidae. Simpson (1945, p. 140), Viret (1958, p. 463) and Gromova (1962, p. 312) followed this allocation, listing *Teleolophus* and *Deperetella* as colodontine helaletids.

The molars of *Teleolophus* and *Deperetella* resemble those of *Colodon* but are even more extremely bilophodont, with more reduced metacones and paralophids and no  $M_3$  hypoconulid. The dentition of *Teleolophus* and *Deperetella* further differs from that of contemporary helaletids in having higher and more acute cross crests, more molariform upper premolars, relatively longer and narrower lower premolars, a two-rooted  $P_1$ , large canines, and a posterior lobe on  $I_3$ . In *Teleolophus* the premolar series is shorter than the molar series, as in most tapiroids, but in the later genus *Deperetella*, the anterior part of the cheek tooth row is disproportionately lengthened and the premolar series is longer than the molars, with  $P_2$  in particular transformed into an elongate shearing blade. This development of the premolars is opposite to the trend in the Helaletidae, in which  $P_1$  is lost early and  $P_{2-4}$  become relatively short and wide.  $P_1$  was lost in helaletids before the beginning of the middle Eocene, which indicates that *Teleolophus* and *Deperetella* (like the lophialetids) must have been separate from that family before the end of the early Eocene. The differences in dentition between the *Teleolophus-Deperetella* line and the Helaletidae are basic enough to indicate that the similarities in molar pattern (approach to



a bilophodont condition) are the result of convergence rather than immediate common ancestry.

Similarities in canines, incisors, and premolars between *Teleolophus* and contemporary lophialetids suggest common ancestry, but the extremely different trends in molar evolution (bilophodont in *Teleolophus*, rhinocerotoid-like in lophialetids) indicate that the two groups were probably separate before middle Eocene time. The differences in molar pattern between the *Teleolophus-Deperetella* line and the Lophialetidae are so great that, in order to maintain a consistent higher-level taxonomy within the Tapiroidea, the two groups should be separated on the family level. *Teleolophus* and *Deperetella* are therefore here placed in a separate family, designated the Deperetellidae, after the type genus, *Deperetella*. Like the lophialetids, deperetellids seem to have been confined to Asia throughout their evolutionary history.

**TELELOPHUS** MATTHEW AND GRANGER, 1925C

TYPE SPECIES: *Teleolophus medius* Matthew and Granger (1925c, p. 3).

INCLUDED SPECIES: *Teleolophus medius*, *T. magnus*, new species, *T.? ferganicus*, new combination, and *T.? daviesi*.

DISTRIBUTION: ?Middle to late Eocene and ?early Oligocene of Asia.

REVISED DIAGNOSIS: Deperetellids with premolar series shorter than molar series and submolariform premolars.  $P^2-4$  with paracone broadly convex, metacone completely merged into ectoloph but unshortened and only slightly lingually displaced, and protoloph and metaloph equally prominent and in contact lingually.  $P_3-4$  with small, isolated entoconids. Cement present on cheek teeth.

DENTITION: (FIGS. 12, 13): Upper incisors are not known for *Teleolophus*. Lower incisors (except for  $I_1$ ) and canines are preserved in A.M.N.H. Nos. 81799 and 81854 (*T.* cf. *T. medius*).  $I_2$  is unusually short and high, with just a trace of a lingual cingulum.  $I_3$  is long and low, with a prominent posterior lobe which gives the crown a mitten-like appearance, as in *Lophialetes*. A broad, shallow pit anterolingual to the posterior lobe probably accommodated the anterior edge of  $I^3$  in occlusion.  $C_1$  is relatively small and labio-

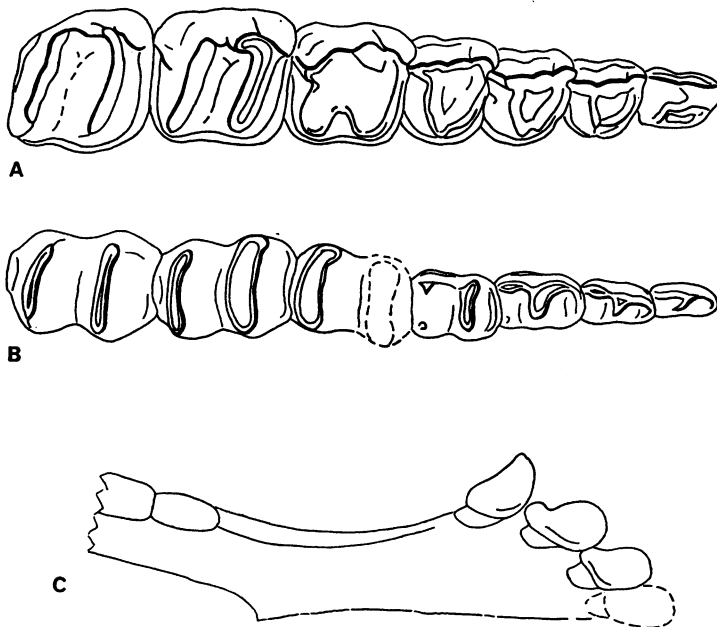


FIG. 12. *Teleolophus medius* and related forms. A. A.M.N.H. No. 26286 (*T. medius?*),  $P^1-M^3$ . B. A.M.N.H. No. 20166, type of *T. medius*,  $P_1-M_3$ . After Matthew and Granger (1925c, fig. 4). C. A.M.N.H. No. 81854 (*Teleolophus* cf. *T. medius*), symphyseal region, showing lower canine and incisors. All  $\times 1$ .

lingually compressed, with the leading (anterior) edge produced into a prominent ridge which curves anterolingually at the base (as in *Lophialetes*), and has a less prominent posterior ridge. A broad notch in the middle of the anterior edge apparently resulted from occlusion with the posterior edge of  $I^3$ . The upper and lower canines in *T. magnus* are relatively larger, less compressed, and more elongate than those in *T. cf. T. medius*, and  $C_1$  shows no notch for  $I^3$ .

The postcanine diastema is relatively longer in *T. cf. T. medius* than in *T. magnus*.

The following description of the upper premolars of *Teleolophus* is based largely on A.M.N.H. Nos. 26286 (*T. medius?*) and 26063 (*T. magnus*):  $P^1$  is relatively long and narrow, with a broad, centrally situated paracone dominating the ectoloph, a small parastyle, and a larger posterior ectoloph cusp (?metacone or metastyle). There is a broad, lingually directed, posterior, transverse crest (short metaloph or lophoid hypocone) and, in *T. medius?*, an isolated, anteroposteriorly oriented, elongate protoloph; in *T. magnus* the protoloph is connected to the ectoloph and is slightly more lingually oriented. Prominent cingula almost completely encircle  $P^1$ .  $P^2-4$  are increasingly relatively shorter and wider, but have virtually identical cusp patterns. The paracone is broadly convex, and the metacone is completely merged into the ectoloph, unshortened, and only slightly lingually displaced. The protoloph and metaloph are of equal height, the former slightly shorter and curving posterolingually to join the latter a short distance before its lingual end (hypocone). This premolar cusp pattern resembles that in *Lophialetes* and *Caenolophus proficiens*, except that the lingual ends of the crests in *Teleolophus* are separate and not joined in a continuous loop. Prominent cingula are present on all sides of  $P^2-4$ .

The upper molars are square to slightly wider than long, with a prominent parastyle and high, slightly oblique protoloph and metaloph crests which are connected by a broad paracone into an inverted, U-shaped ridge. The protoloph and metaloph are relatively very high and thin and bent anteriorly at their tops. The metaloph-paracone junction is often marked by a narrow shallow notch. The metacone, or posterior end of the

ectoloph, is extremely short and lingually displaced in  $M^{1-2}$ , and in unworn teeth is not so high as the top of the metaloph; in  $M^3$  the metacone is completely lost and the posterolabial corner of the tooth slightly truncated. There are prominent cingula on anterior, lingual, and posterior sides and, in  $M^{1-2}$ , at the posterolabial corner.

Knowledge of the lower premolars is derived largely from A.M.N.H. No. 20166 (*T. medius*) and A.M.N.H. No. 26063 (*T. magnus*).  $P_1-4$  have increasingly prominent labial cingula, apparently more prominent in the larger *T. magnus* than in *T. medius*.  $P_1$  is two-rooted, long and narrow, with a high, short, convex, anterior cutting edge (paralophid), a barely differentiated metaconid, and a low, concave, posterolabial ridge (metalophid).  $P_2$  has a prominent paralophid which leads to a small paraconid (relatively larger in *T. magnus*), a short posterolingually directed protolophid, a low metalophid which swells posteriorly into a hypoconid, and a narrow posterolingual shelf bounded by a lingual cingulum.  $P_3$  is relatively wider than  $P_2$ , with a larger paraconid, wider protolophid, and wider talonid, with the lingual cingulum raised into a low entoconid.  $P_4$  is still relatively wider, with a squared-off, shortened, virtually molariform trigonid (with the paralophid greatly reduced) and a larger entoconid. A low ridge descends from hypoconid to entoconid but dies out before connecting the two cusps.

The lower molars increase in size from front to rear and are completely bilophodont, with paralophid and metalophid almost entirely suppressed (a low ridge descending lingually across the anterior face of the protolophid is the only remnant of the paralophid). Protolophid and hypolophid are parallel, slightly oblique, and relatively high and acute, with unworn apices bent posteriorly. There are prominent anterior and posterior cingula but no hypoconulid on  $M_3$ .

Molar occlusion in *Teleolophus* (and *Deperetella*) is typically tapiroid, consisting almost entirely of shear between anterior sides of protolophids and metalophs and posterior sides of protolophids and hypolophids, respectively.

$DP^{1-4}$  are preserved in A.M.N.H. No. 21560 (*T. medius?*).  $DP^1$  is relatively long

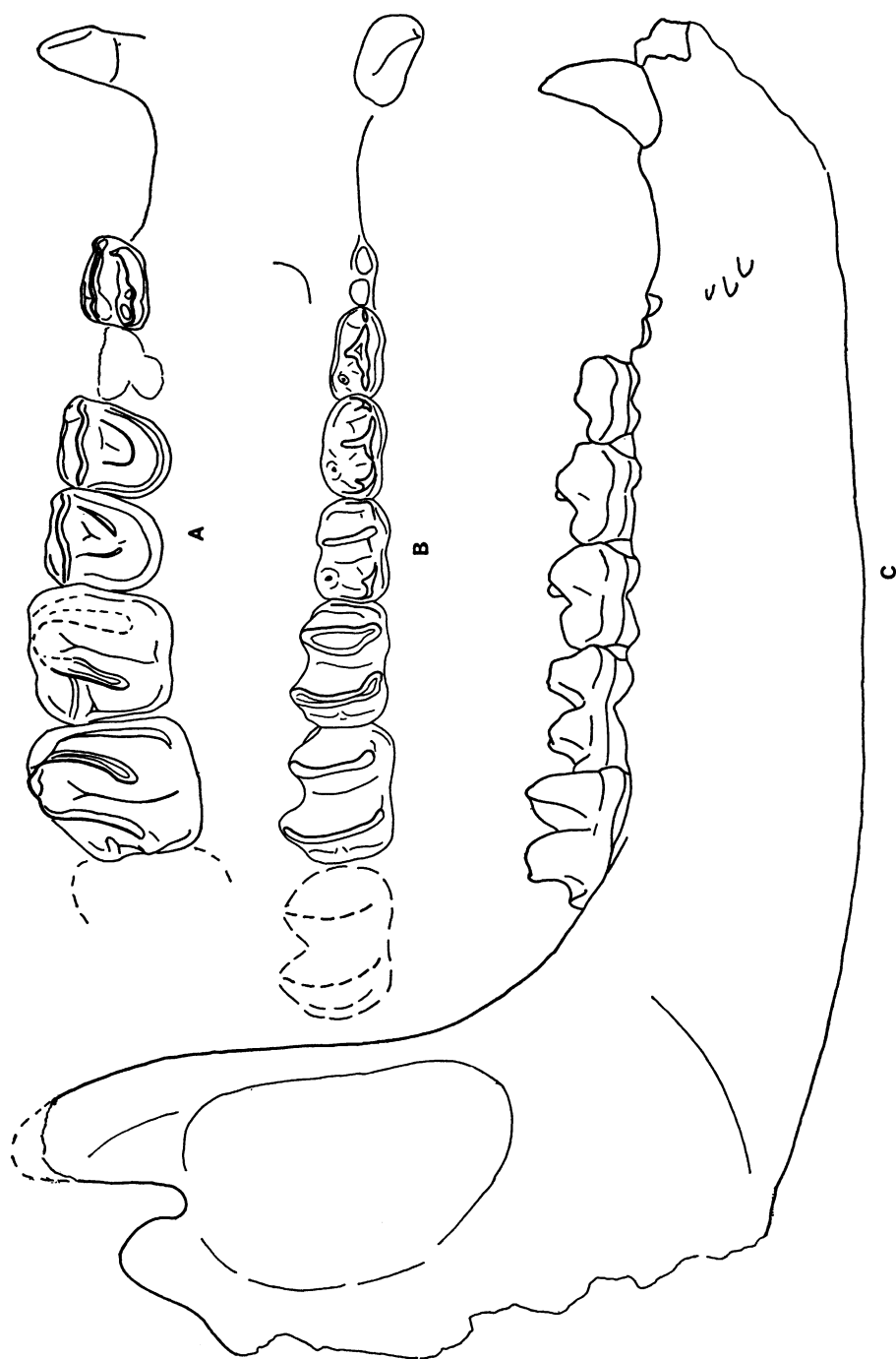


FIG. 13. *Teleolophus magnus*, new species, type, A.M.N.H. No. 26063. A. Occlusal view of  $C_1$ - $M_2$  (reversed). B. Occlusal view of  $C_1$ - $M_3$  (unrupted  $M_3$  shown in broken line). C. Lateral view of lower jaw. All  $\times 4$ .

and narrow, with the ectoloph raised into a single main central cusp and low parastyle and metastyle, as in  $P^1$ . The lingual portion of the tooth is missing, but the roots indicate that it probably was about as wide as  $P^1$ . In  $DP^2$  the ectoloph is like that in  $DP^1$ , but lingually there is a short straight metaloph and a posteriorly curving protoloph.  $DP^2$  resembles  $P^1$  except that the protoloph and metaloph are more separated lingually.  $DP^3$  is fully molariform, but differs from  $M^1$  in being relatively longer and narrower, with a shorter protoloph and less reduced and less lingually displaced metacone.  $DP^4$  is a smaller replica of  $M^1$  except that the metacone is slightly less reduced (mainly in height).

$DP^1$  and  $DP^2$  are not known.  $DP^3$  and  $DP^4$  in A.M.N.H. Nos. 81800 and 81850 (*Teleolophus* cf. *T. medius*) are extremely similar to those teeth in *Caenolophus proficiens* from the Ulan Shireh beds, differing mainly in the greater reduction of the  $DP^4$  paralophid.  $DP^3$  has an extremely elongate trigonid, with the paraconid produced into a short cross crest which parallels the protolophid and, in one of the two specimens (A.M.N.H. No. 81800), is preceded by an anterior cingulum which resembles a miniature paralophid. The hypolophid is complete and is connected to the protolophid by a low but complete metalophid.  $DP^4$  is molariform and differs from  $M^1$  only in being of slightly smaller size and in having a slightly less reduced metalophid.

**CEMENTUM:** One of the most unusual features of *Teleolophus* teeth is the presence of what appears to be cement on the molars and premolars. In many specimens it was apparently mistaken for matrix and removed in preparation, but it is preserved in A.M.N.H. No. 26063 (*T. magnus*) and most of the Ulan Shireh *T. medius*? specimens. It occurs as a yellowish white deposit usually at the base of the premolar ectolophs, in the premolar and molar valleys, and along the anterior base of the protoloph. Evidence that this coating was deposited during life and is not a product of fossilization is seen most clearly in A.M.N.H. Nos. 26063 and 26286, where it was worn down during chewing and bears an extension of the metaloph wear facet. If this yellowish white coating is cement, as it definitely appears to be, *Teleolophus* is unique among tapiroids in possessing it, although ce-

ment occurs in hypsodont equoids and rhinocerotoids (*Ceratotherium*). Since deperetellids are more hypsodont than any other tapiroid, it is perhaps not surprising to find cement developed in that family alone.

***Teleolophus medius* Matthew and Granger, 1925c**

**TYPE:** A.M.N.H. No. 20166, lower jaw with  $P_1-M_3$ . Figured in Matthew and Granger (1925c, p. 4, fig. 4).

**HYPODGM:** Type and A.M.N.H. Nos. 20163 ( $P_4-M_3$ ), 20164 ( $DP^4-M^1$ ), 20165 (mostly isolated upper and lower molars), and 20168A ( $M^2$ ).

**KNOWN DISTRIBUTION:** Late Eocene Irдин Manha beds, Irдин Manha escarpment, about 20 miles south-southeast of Iren Dabasu, Inner Mongolia.

**DIAGNOSIS:** Size relatively small: length of  $M_{1-3}$ , 54 mm. Ratio of  $P_{1-4}$  to  $M_{1-3}$ , 0.80. See table 11 for complete measurements.

**DISCUSSION:** *Teleolophus medius* molars resemble those of the contemporary helaetid *Helaletes mongoliensis*, from which they can be distinguished by their higher and sharper cross crests and more reduced metacones and paralophids. The premolars of *Teleolophus medius* are extremely similar to those of the contemporary rhinocerotoid *Caenolophus proficiens*, and isolated teeth are easily confused. The lower premolars of *T. medius* can be distinguished from those of *C. proficiens* by the following features:  $P_1$  slightly relatively longer and not crowded;  $P_2$  and  $P_3$  without lingual posterior crest;  $P_3$  protolophid slightly wider and more lingually oriented;  $P_4$  trigonid shortened (paralophid reduced), hypoconid slightly more lingually situated, hypolophid not so well developed. Except for the hypolophids, the lower premolars of *Caenolophus proficiens* are slightly less molariform than those of *Teleolophus medius*,  $P_{2-4}$  of the former resembling  $P_{1-3}$  of the latter. Upper premolars of *T. medius* and *C. proficiens* are rare at Irдин Manha, and comparisons can best be made between representatives of each genus in the Ulan Shireh beds. The upper premolars of *Teleolophus medius*? differ from those of the Ulan Shireh *Caenolophus proficiens* in the following features:  $P^1$  relatively larger and longer;  $P^{2-4}$  with protoloph in con-

TABLE 11

STATISTICAL DATA ON TEETH OF *Teleolophus medius* FROM THE IRDIN MANHA BEDS

	N	OR	M
P <sup>1</sup>	1		
L		—	10.1
W		—	7.7
P <sup>2</sup>	1		
L		—	9.9
W		—	11.0
P <sup>3</sup>	—		
P <sup>4</sup>	—		
M <sup>1</sup>	1		
L		—	17.2
W		—	17.5
M <sup>2</sup>	2		
L		19.0–21.9	20.45
W		18.1–22.2	20.15
M <sup>3</sup>	2		
L		—	21.1
W		22.6–25.8	24.20
P <sub>1</sub>	1		
L		—	9.1
W		—	4.6
P <sub>2</sub>	1		
L		—	10.7
W		—	6.0
P <sub>3</sub>	1		
L		—	12.3
W		—	7.6
P <sub>4</sub>	2		
L		12.5–12.7	12.60
W		8.9–9.9	9.40
M <sub>1</sub>	4		
L		14.7–16.4	15.65
W		11.1–12.1	11.73
M <sub>2</sub>	7		
L		17.7–19.9	18.83
W		12.4–14.2	13.31
M <sub>3</sub>	3		
L		19.5–22.7	20.87
W		14.0–16.4	15.03

tact with metaloph a short distance labial to the hypocone, not joined in a continuous loop or completely separated; P<sup>3–4</sup> metacones flat, not convex. The premolars of *Teleolophus medius* are also similar to those of *Lophialetes expeditus* in cusp pattern but are easily distinguished by their larger size as well as other differences (protoloph-metaloph loop not continuous, lower premolars relatively longer and narrower).

**Teleolophus medius?**

Plate 3, figure 1

REFERRED SPECIMENS: A.M.N.H. Nos. 21559, 21560, 26128, 26286, 26287, 81796, and 81797.

HORIZON AND LOCALITY: Late Eocene Ulan Shireh beds, 4 to 8 miles north of Tukhum in Sumu (including Chimney Butte), North Mesa, Shara Murun region, Inner Mongolia.

DISCUSSION: Several upper dentitions and one lower jaw fragment in the Ulan Shireh beds represent a form extremely similar to if not conspecific with *Teleolophus medius* from the Irдин Manha beds. Relatively few upper teeth of *T. medius* are known from the Irдин Manha beds, and few lower teeth of this form are available from the Ulan Shireh beds, so comparisons between the two samples are limited. From the available specimens, the Ulan Shireh species of *Teleolophus* appears to average slightly smaller (see table 12) than Irдин Manha *T. medius* and to have slightly squarer (relatively longer) M<sup>3</sup>'s. A slight size difference between Ulan Shireh and Irдин Manha *Teleolophus* would be consistent with

TABLE 12

STATISTICAL DATA ON TEETH OF *Teleolophus medius?* FROM THE ULAN SHIREH BEDS

	N	OR	M
P <sup>1</sup>	1		
L		—	10.5
W		—	7.9
P <sup>2</sup>	1		
L		—	10.4
W		—	11.0
P <sup>3</sup>	1		
L		—	11.1
W		—	13.5
P <sup>4</sup>	1		
L		—	11.6
W		—	15.0
M <sup>1</sup>	3		
L		15.9–17.2	16.57
W		16.9–18.2	17.50
M <sup>2</sup>	3		
L		19.6–20.0	19.83
W		18.9–20.0	19.30
M <sup>3</sup>	4		
L		19.0–21.0	20.08
W		19.5–21.2	20.28

differences observed between representatives of *Lophialetes* and *Caenolophus* from the two localities.

The Ulan Shireh *Teleolophus* sample is especially important because it includes a complete upper premolar and molar series (A.M.N.H. No. 26286) and also several dentitions with what appears to be cement still present. The Ulan Shireh *Teleolophus* sample is unusual in consisting almost entirely of upper dentitions.

#### *Teleolophus* cf. *Teleolophus medius*

REFERRED SPECIMENS: A.M.N.H. Nos. 81851 (incomplete  $P^3-M^3$ ), 81799 ( $I_3-M_3$ ), 81850 ( $DP_3-M_1$ ), and 81800 ( $DP_{3-4}$ ), from 7 miles southwest of Camp Margetts; A.M.N.H. Nos. 81853 ( $M^{2-3}$ ), 81854 ( $I_2-M_3$ ), and 81855 ( $P_3-M_2$ ), from 10 miles southwest of Camp Margetts; and A.M.N.H. No. 81798 ( $P_{2-4}$ ), from 5 miles east of Camp Margetts. Probably all from "Irdin Manha" beds.<sup>1</sup>

DISCUSSION: The specimens listed above represent a form very similar to and possibly conspecific with *Teleolophus medius*. The specimens from the Camp Margetts area differ from *T. medius* in the following features:  $P^{2-4}$  relatively shorter and wider,  $M^2$  metacone less reduced, and  $P_3-M_3$  parolophids slightly less reduced. In A.M.N.H. No. 81799 the labial slope of the  $P_4$  metalophid is unusually concave. None of the *Teleolophus* specimens from the Camp Margetts area display cement on the cheek teeth.

Xu and Chiu (1962, p. 316) referred to *Teleolophus medius* a lower jaw with  $P_4-M_3$  from the late Eocene or early Oligocene Anrencun Formation, Lunan basin, Yunnan, China. From the illustration (1962, pl. 1, fig. 7) the Anrencun specimen appears similar to *Teleolophus medius* in both size and cusp pattern. Xu and Chiu (1962, p. 332) considered the Anrencun fauna intermediate in age between the late Eocene Shara Murun and

early Oligocene Ardyn Obo faunas. This age is anomalously late for *Teleolophus*, a species of which evolved into the more advanced genus *Deperetella* by Shara Murun time, which suggests that the Anrencun fauna may be temporally mixed.

#### *Teleolophus* sp.

A.M.N.H. No. 81852, a mandible with  $P_4-M_3$ , listed as coming from ?"Houldjin gravels," 7 miles west of Camp Margetts, is similar in cusp pattern to *Teleolophus medius* but about 20 per cent larger. Since *Teleolophus* cf. *T. medius* from "Irdin Manha" beds in the same area (7 and 10 miles southwest of Camp Margetts) is about the same size as the type *T. medius* hypodigm, it seems more likely that the larger size of A.M.N.H. No. 81852 reflects evolutionary size increase (or specific differentiation) rather than geographic variation. A.M.N.H. No. 81852 may thus have actually come from a higher horizon than the "Irdin Manha" beds; it is, however, unlikely that it came from the "Houldjin gravels," because A.M.N.H. No. 81807, an undescribed species of *Deperetella* (a more advanced deperetellid than *Teleolophus*), is recorded from those beds.

#### *Teleolophus magnus*,<sup>2</sup> new species

Plate 3, figures 2-3

TYPE: A.M.N.H. No. 26063, maxilla with  $C^1-P^1$ ,  $P^3-M^2$ , and lower jaws with  $C_1-M_2$  ( $M_3$  unerupted).

HYPODIGM: Type only.

HORIZON AND LOCALITY: ?"Ulan Gochu" beds, Urtyn Obo, Shara Murun region, Inner Mongolia.

DIAGNOSIS: About 35 per cent larger than *Teleolophus medius*, with relatively more robust canines, shorter postcanine diastema, relatively longer premolar series, and slightly relatively wider upper molars. Ratio of  $P_{1-4}$  to  $M_{1-3}$ , about 0.90.

DISCUSSION: *Teleolophus magnus* is about as large as *Deperetella cristata* but is assigned to *Teleolophus* because its premolars are submolariform (protolophids not separated lingually from metalophids, and hypolophids incomplete) and essentially enlarged replicas of those of *Teleolophus medius*. In its more

<sup>1</sup> A.M.N.H. Nos. 81854 and 81855 are recorded as coming from ?"Houldjin gravels," but they are virtually identical in size and cusp pattern with A.M.N.H. No. 81799 from "Irdin Manha" beds 7 miles southwest of Camp Margetts and so similar to *T. medius* from the type Irdin Manha beds that they must almost certainly have come from the "Irdin Manha" beds rather than the "Houldjin gravels."

<sup>2</sup> Latin *magnus*, large.

robust canines, shorter postcanine diastema, relatively longer premolar series, and slightly relatively wider upper molars, *T. magnus* is intermediate between *T. medius* and *Deperetella cristata*. Like *T. medius*? from the Ulan Shireh beds, *T. magnus* has cement on the cheek teeth.

*Teleolophus magnus* is recorded as coming from the base of the "Middle Red" (considered equivalent to the Ulan Gochu beds) at Urtyn Obo, East Mesa, about 23 miles northeast of the type Ulan Gochu beds at Baron Sog Mesa. The type Ulan Gochu beds are considered early Oligocene in age and overlies the late Eocene Shara Murun beds containing *Deperetella cristata*, a more advanced deperetellid than *Teleolophus magnus*. There are three possible explanations to account for the apparent superposition of *T. magnus* over *D. cristata*: (1) the type of *T. magnus* actually was collected in so-called "Shara Murun" or older beds at Urtyn Obo and the horizon mistakenly recorded as "Ulan Gochu"; (2) at least some of the "Ulan Gochu" beds at Urtyn Obo are older than the type Ulan Gochu beds; or (3) *T. magnus* is a large but otherwise primitive late survivor of the *Teleolophus* line, persisting after the extinction (at least in that area) of *Deperetella*.

No consistent differences in preservation have been observed between specimens from "Shara Murun" and those from "Ulan Gochu" beds at Urtyn Obo, so there is no evidence either for or against the first suggestion. The second suggestion can be properly evaluated only when the entire fauna from the Urtyn Obo "Ulan Gochu" beds is compared with that from the type Ulan Gochu beds. Morphologically *Teleolophus magnus* appears intermediate between the Irdin Manha *T. medius* and Shara Murun *Deperetella cristata*. However, the third suggestion cannot be dismissed, especially since *Teleolophus* is recorded in the supposedly post-Shara Murun Anrencun fauna (see p. 220).

*Teleolophus magnus* is of about the same size as *Deperetella ferganica* Beliajeva, 1962 (here transferred to *Teleolophus*), from Kirghiz S.S.R., and possibly represents the same or a closely related species. However, *D. ferganica* is known only from an isolated P<sup>2</sup>, a tooth not known for *T. magnus*, so direct comparison is not possible.

***Teleolophus? ferganicus* (Beliajeva, 1962),  
new combination**

*Deperetella ferganica* BELIAJEVA, 1962, p. 144.

Beliajeva (1962, p. 144) proposed the species *Deperetella ferganica* for an isolated P<sup>2</sup> (Paleontological Institute, Academy of Sciences, U.S.S.R., No. 1996-1), from the Fergana basin, Kirghiz S.S.R. Beliajeva's illustration (1962, p. 143) shows that the P<sup>2</sup> protoloph of *D. ferganica* joins the metaloph lingually, a feature characteristic of *Teleolophus* (illustrated for the first time in the present paper). P<sup>2</sup> of *Deperetella* is more molariform, with the lingual end of the protoloph separated from the metaloph by a broad notch. For this reason I transfer *D. ferganica* to *Teleolophus*. The assignment is tentative pending further knowledge of the dentition of the Kirghiz species.

*Teleolophus? ferganicus* is about the same size as *Teleolophus magnus* from Inner Mongolia, and the two species may be closely related, or possibly synonymous. However, P<sup>2</sup> is unknown for *T. magnus*, and no other teeth are known for *T.? ferganicus*, so direct comparison is not yet possible.

Beliajeva (*loc. cit.*) recorded a middle Eocene age (Alai Stage) for *T.? ferganicus*, which seems too old for the degree of P<sup>2</sup> molarization in that species. Comparison with the Mongolian deperetellids suggests an early late Eocene age for *T.? ferganicus*.

***Teleolophus? daviesi* Dehm and Oettingen-Spielberg, 1958**

Dehm and Oettingen-Spielberg (1958, pp. 24-25, pl. 2, figs. 10a-c) described under the name *Teleolophus? daviesi* an isolated M<sub>3</sub> from the middle Eocene Ganda Kas fauna of northwestern Pakistan. The relatively wide cross lophs and virtually complete reduction of the paralophid and metalophid are diagnostic of the Deperetellidae. The tooth is 25 per cent smaller than M<sub>3</sub>'s of *Teleolophus medius* and further differs from the tooth in that species in having the cross crests more widely separated and apparently not curved posteriorly at the top. In view of the early (middle Eocene) age of the specimen, assignment to *Teleolophus* rather than *Deperetella* is probably more accurate. However, the lower molars are among the least diagnostic teeth in the family, and generic assignment of *T.?*



*daviesi* can only be tentative until more is known about the rest of the dentition. Since it is older than *Teleolophus medius* and does show some morphological differences (besides smaller size) in an otherwise relatively undiagnostic tooth, it is quite possible that *T.?* *daviesi* will eventually prove to be generically distinct from *Teleolophus*.

**DEPERETELLA MATTHEW AND GRANGER, 1925B**

*Cristidentinus* ZDANSKY, 1930, p. 32.

*Diplolophodon* ZDANSKY, 1930, p. 35.

TYPE SPECIES: *Deperetella cristata* Matthew and Granger (1925b, p. 6).

INCLUDED SPECIES: *Deperetella cristata*, *D. depereti*, *D. similis*, and *D. birmanicum*.

DISTRIBUTION: Late Eocene of Asia.

REVISED DIAGNOSIS: Deperetellids with premolar series longer than molars and posterior premolars molariform.  $P^{2-4}$  protoloph and metalophs slightly convergent to parallel, and separated lingually.  $P_1$  and especially  $P_2$  lengthened into shearing blades;  $P_{3-4}$  with complete hypolophids. Molars relatively shorter and wider than those of *Teleolophus*. Manus tridactyl.

DISCUSSION: The upper and lower molars of *Deperetella cristata* are similar in cusp pattern to those of *Teleolophus medius*, differing mainly in being slightly relatively shorter and wider. The posterior premolars of *D. cristata*, however, are more molariform than those of *Teleolophus*, and the anterior premolars are extremely lengthened and specialized for vertical shear. (The ratio of  $P_{1-4}$  to  $M_{1-3}$  is 1.13 in *Deperetella cristata* and 0.80 in *Teleolophus medius*.) These differences, particularly the premolar lengthening, seem basic enough to justify generic separation of *Deperetella* from *Teleolophus*.

Zdansky (1930, p. 32) proposed the genus *Cristidentinus* for a lower jaw with the  $P_3$  talonid and  $P_4$ - $M_3$ , from late Eocene beds near Mienchih, northern Honan, China. He distinguished *Cristidentinus* from *Teleolophus* and *Deperetella* by the degree of  $P_4$  molarization, which supposedly was intermediate between that of *Teleolophus* and that of *Deperetella*. However a comparison of Zdansky's excellent photographs of *Cristidentinus depereti* (*ibid.*, p. 2, figs. 1-2) with deperetellid specimens in the American Museum of Natural History collections shows that the  $P_3$

talonid and  $P_4$  in *Cristidentinus* are identical in cusp pattern with those teeth in *Deperetella*. Zdansky may have been misled by Matthew and Granger's (1925b, p. 5, fig. 5) poor illustration of the lower dentition of *Deperetella cristata*, and their statement (p. 4) that  $P_4$  in *D. cristata* was fully molariform (it differs from the molars in retaining a high metalophid). *Cristidentinus depereti* cannot be distinguished from *Deperetella cristata* on the basis of cusp pattern and should not be separated generically. *Cristidentinus* Zdansky (1930) is therefore here synonymized with *Deperetella* Matthew and Granger (1925b).

Zdansky (1930, p. 35) proposed another new genus and species, *Diplolophodon similis*, for a maxilla with worn  $P^2$ - $M^3$  from the same locality as that for *Cristidentinus*. He distinguished *Diplolophodon* from *Deperetella* by its relatively shorter teeth, less flat  $P^4$  ectoloph (the paracone is more convex), more prominent metastyle (posterolabial cingulum), relatively larger  $M^3$ , and less prominent cingula. Young (1937, pp. 419-420) described another specimen of *Diplolophodon similis* with  $P^{2-4}$ , in which  $P^4$  apparently has a flatter paracone and less prominent posterolabial cingulum than does that tooth in Zdansky's type specimen.<sup>1</sup>  $P^2$  in *D. similis* differs from that tooth in *Deperetella cristata* in being relatively shorter and wider (length-width ratio is 0.83, as opposed to 0.91 in *D. cristata*), with the protoloph more parallel to the metaloph, a fact that suggests that the anterior lower premolars in *Diplolophodon similis* may not have been so elongate as those in *Deperetella cristata*. However, the ratio of  $P^{2-4}$  to  $M^{1-3}$  in *Diplolophodon similis* (calculated from combined measurements of Zdansky's and Young's specimens, in both of which  $P^4$  is the same size) is the same as that for *Deperetella cristata* (0.77). Therefore it appears that the premolars in *Diplolophodon similis* were as long relative to the molars as those in *Deperetella cristata*.

From the illustrations given by Zdansky (1930, pl. 1, fig. 35) and Young (1937, p. 420, fig. 5), *Diplolophodon similis* appears to differ from *Deperetella cristata* in the following

<sup>1</sup> Young mistook  $P^{2-4}$  for  $P^4$ - $M^1$ . The posteriormost tooth in his specimen has a straight ectoloph, with the metacone situated labially, as in deperetellid promolars; in the molars the metacone is lingually displaced.

features: about 50 per cent smaller; cheek teeth, especially  $P^2$  relatively shorter and wider;  $P^2$  protoloph parallel to metaloph;  $P^3-4$  protolophs perhaps slightly shorter relative to metalophs;  $M^{1-3}$  posterolabial cingula more prominent and lingual cingula lacking. However, *Diplolophodon similis* has essentially the same upper premolar and molar cusp patterns as does *Deperetella cristata*, and in my opinion the similarity is basic enough to warrant placing the two species in the same genus. The size difference and relatively minor differences in proportions, premolar molarization, and prominence of molar cingula seem to me indicative of specific separation only. *Diplolophodon* Zdansky (1930) is therefore here synonymized with *Deperetella* Matthew and Granger (1925b).

**DENTITION:** (Unless otherwise noted, specimens referred to are of *Deperetella cristata*). No upper incisors or canines are known for *Deperetella*. The lower incisor alveoli in A.M.N.H. No. 20291 indicate relatively large, subequal  $I_1$  and  $I_2$ , and a smaller  $I_3$ . The roots of  $C_1$  indicate a relatively robust canine.

The dentition of *Deperetella* (see fig. 14) is advanced over that of *Teleolophus* primarily in the relative lengthening of the premolar series (with the greatest size increase in the anterior premolars), and the increased molarization of the premolars.  $P^1$  is not known for *Deperetella*.  $P^2-M^3$  are known from A.M.N.H. Nos. 20290 and 20293.  $P^2-4$  differ from those teeth in *Teleolophus* in the following features:

lophs relatively higher and sharper; paracones less convex, more merged into ectolophs; less of a posterolabial cingulum; protoloph and metaloph separate lingually, with protocone as lingually situated as hypocone. In  $P^2$  the protoloph still converges lingually toward the metaloph, and the transverse valley is partly blocked. In  $P^3-4$  the protoloph and metaloph are essentially parallel, and the valley is completely open.  $M^{1-3}$  are extremely similar to those teeth in *Teleolophus*, differing mainly in being slightly relatively shorter and wider.

The lower cheek teeth are preserved in A.M.N.H. Nos. 20291 and 20292.  $P_{1-4}$  are longer relative to the molars than are those in *Teleolophus*, with the greatest increase in length in  $P_2$  and  $P_1$ , and progressively less posteriorly, but with the effect noticeable as far back as  $M_1$  (see fig. 15).  $P_{1-4}$  cusp patterns differ from those of *Teleolophus* in the following features:  $P_1$  with larger paraconid and higher metalophid;  $P_2$  with larger paraconid, higher metalophid and a rudimentary hypolophid;  $P_3$  with a higher metalophid and complete hypolophid;  $P_4$  with a complete hypolophid.  $M_{1-3}$  differ from those teeth in *Teleolophus* mainly in being slightly relatively wider and in having a (faint) labial cingulum.

Only  $DP_{3-4}$  are known from the deciduous dentition. These teeth are preserved in A.M.N.H. No. 26027 (*Deperetella* cf. *D. cristata*).  $DP_3$  has the same cusp pattern as  $P_3$ .  $DP_4$  is fully molariform and differs from

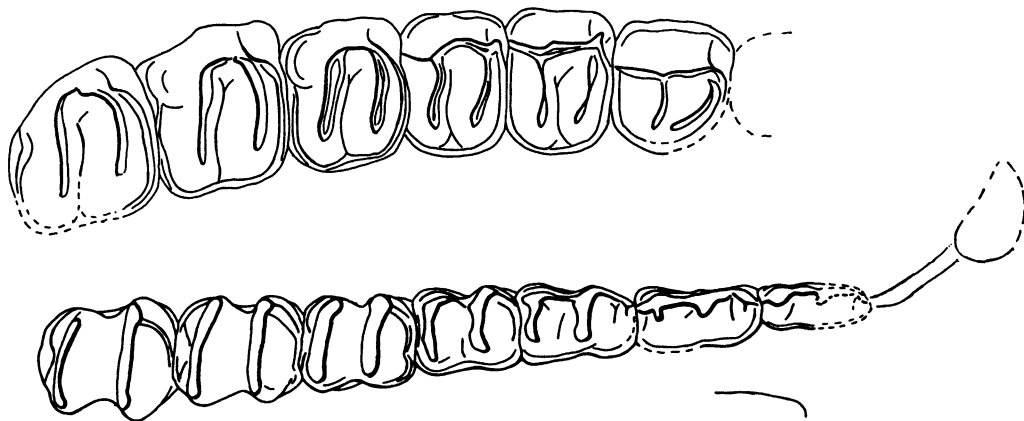


FIG. 14. *Deperetella cristata*. Above: Type, A.M.N.H. No. 20290,  $P^2-M^3$  (reversed). After Matthew and Granger (1925b, fig. 4). Below: A.M.N.H. No. 20291,  $C_1-M_3$ . Both  $\times \frac{3}{4}$ .

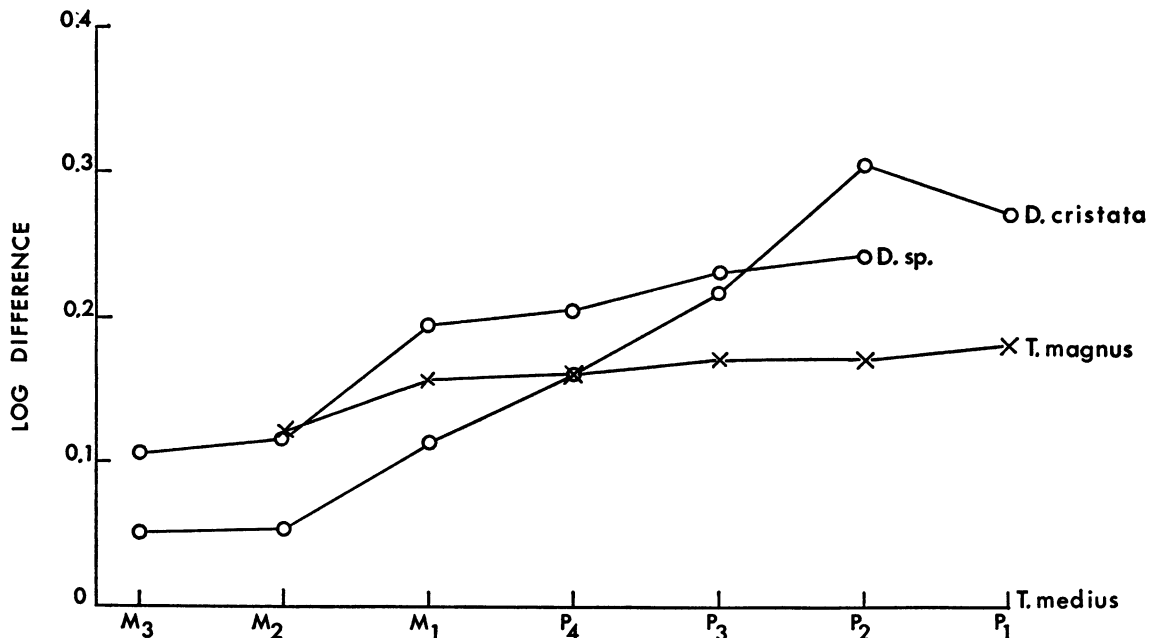


FIG. 15. Log ratio diagram of lengths of lower cheek teeth of species of *Teleolophus* and *Deperetella*. *T. medius*, A.M.N.H. No. 20166; *T. magnus*, A.M.N.H. No. 26063; *D. sp.*, A.M.N.H. No. 81807; *D. cristata*, A.M.N.H. No. 20291.

M<sub>1</sub> only in being slightly relatively longer and narrower.

***Deperetella cristata* Matthew and Granger, 1925b**

Plate 3, figure 4

TYPE: A.M.N.H. No. 20290, skull fragments with P<sup>2</sup>, P<sup>4</sup>-M<sup>3</sup>. Figured in Matthew and Granger (1925b, p. 5, fig. 4).

HYPODIGM: Type and A.M.N.H. Nos. 20291-20295, 20300-20302, 20305, 20306, 20329, 81805, 81808-81835.

KNOWN DISTRIBUTION: Late Eocene Shara Murun beds at Ula Usu, Baron Sog Mesa, Shara Murun region, Inner Mongolia.

DIAGNOSIS: Size large: length of M<sub>1-3</sub>, 67 mm. Ratio of P<sub>1-4</sub> to M<sub>1-3</sub>, 1.13. P<sup>2-4</sup> paracones and metacones merged into ectoloph, P<sup>3-4</sup> protoloph as long as metaloph. See tables 13 and 14 for complete measurements.

DISCUSSION: The size given for *Deperetella cristata* (M<sub>1-3</sub>, 67 mm.) is based on the only two specimens with all the lower molars, A.M.N.H. Nos. 20291 and 20292. Two isolated M<sub>3</sub>'s (A.M.N.H. Nos. 81805A, 81805B) average 8 per cent larger than M<sub>3</sub> in

A.M.N.H. Nos. 20291 and 20292, which suggests that the average size of the species is somewhat larger than is indicated by the measurements given in the diagnosis.

A.M.N.H. No. 81806, an isolated depere-tellid M<sup>3</sup> from the Ula Usu locality, is 19 per cent longer and 14 per cent wider than the two M<sup>3</sup>'s in the hypodigm (A.M.N.H. Nos. 20290 and 20293). It differs in cusp pattern from the other *D. cristata* M<sup>3</sup>'s in the following features: paracone narrower and metaloph converging more labially toward the protoloph; paracone confluent with parastyle along the top of the crest, bypassing the protoloph; parastyle separated from anterior cingulum by a notch, lingual to which the anterior cingulum bulges anteriorly; and no lingual cingulum. A.M.N.H. No. 81806 may be an extremely large and somewhat abnormal variant of *Deperetella cristata*, or it may represent another species (a slightly relatively larger depere-tellid occurs at Twin Oboes, East Mesa; see discussion below). The large size and the lack of a lingual cingulum suggest possible affinities to *Teleolophus magnus*.

***Deperetella* cf. *Deperetella cristata***

A.M.N.H. No. 26027, a lower jaw with  $DP_3$ - $M_1$  and unerupted (but excavated)  $P_{2-4}$  and  $M_2$ , from "Shara Murun" beds at Twin Oboes, East Mesa (about 20 miles east of the type Shara Murun at Ula Usu), resembles *Deperetella cristata* in cusp pattern but is about 25 per cent larger than the two specimens of *D. cristata* available for comparison (A.M.N.H. Nos. 20291 and 20292). The  $M_1$  paralophid appears to be slightly less reduced in A.M.N.H. No. 26027 than in *D. cristata*, possibly owing to the larger size of the former. The average size difference between the Ula Usu *D. cristata* hypodigm and the population represented by the Twin Oboes specimen is probably less than 25 per cent, because the two *D. cristata* specimens used for comparison appear to be small individuals of the species. There may be a significant size difference between deperetellids from Ula Usu and those from Twin Oboes, but its magnitude should be more reliably determined than is possible at present before a new species is based on it. The Twin Oboes specimen is closely comparable in size to

TABLE 13

MEASUREMENTS (IN MILLIMETERS) OF UPPER  
TEETH OF *Deperetella cristata* FROM  
THE SHARA MURUN BEDS

	A.M.N.H. No. 20290	A.M.N.H. No. 20293
$P^1$	—	—
$P^2$		
L	19.9	—
W	21.8	—
$P^3$		
L	—	18.7
W	—	24.4
$P^4$	—	—
$M^1$		
L	20.8	—
W	23.5	—
$M^2$		
L	24.6	24.3
W	25.7	28.7
$M^3$		
L	24.7	24.6
W	—	29.4

TABLE 14

STATISTICAL DATA ON LOWER TEETH OF  
*Deperetella cristata* FROM THE  
SHARA MURUN BEDS

	N	OR	M
$P_1$	2		
L		17.0-17.4	17.20
W		7.8- 8.1	7.95
$P_2$	2		
L		20.3-21.6	20.95
W		10.3-11.2	10.75
$P_3$	2		
L		20.3-21.7	21.00
W		13.8-14.2	14.00
$P_4$	2		
L		18.1-19.4	18.75
W		14.1-15.6	14.85
$M_1$	2		
L		20.0-20.0	20.00
W		15.7-16.7	16.20
$M_2$	3		
L		21.2-22.3	21.67
W		17.9-18.9	18.30
$M_3$	5		
L		23.0-27.0	24.56
W		19.5-21.6	20.44

A.M.N.H. No. 81806, an isolated deperetellid  $M^3$  from the Ula Usu locality.

***Deperetella* sp.**

A.M.N.H. No. 81807, a mandible with lower dentition complete except for  $P_1$ , is recorded as coming from ?"Houldjin gravels," 7 miles west of Camp Margetts. It represents a species about the size of *Deperetella cristata* but with relatively shorter anterior premolars (the ratio of  $P_{1-4}$  to  $M_{1-3}$  is about 1.00), a smaller canine, and slightly narrower  $P_{3-4}$  hypolophids. In the degree of anterior premolar lengthening, A.M.N.H. No. 81807 is intermediate between *Teleolophus magnus* and *Deperetella cristata* (see fig. 15). This specimen is assigned to *Deperetella* rather than to *Teleolophus* because its premolars have complete (although narrow) hypolophids. Formal designation of the species is postponed until we have further knowledge of the range of intraspecific variation in deperetellid premolars.

***Deperetella depereti* (Zdansky, 1930),  
new combination**

*Cristidentinus depereti* ZDANSKY, 1930, p. 32.

TYPE: Lower jaw with  $P_3$  talonid and  $P_4-M_3$ , in the collections of the Paleontological Institute of the University of Uppsala, Sweden. Figured in Zdansky (1930, pl. 2, figs. 1, 2).

HYPODIGM: Type only.

KNOWN DISTRIBUTION: Late Eocene beds in northern Honan, China.

REVISED DIAGNOSIS: Slightly smaller than *Deperetella cristata*: length of  $M_{1-3}$ , 62.5 mm. Lower dentition, as far as known, similar to that of *D. cristata*.

DISCUSSION: The type of *Deperetella depereti* is about 7 per cent smaller than the two lower dentitions of *D. cristata* which preserve the molars (A.M.N.H. Nos. 20291 and 20292). Based on so few specimens, this estimate of population size difference can hardly be considered reliable. The type of *D. depereti* may be a small member of the population it represents, in which case the species would not differ significantly in size from the Mongolian species. Conversely, the type may be a large member of the population, in which case the average size difference would be greater than is apparent at present. If I were describing this specimen for the first time, I would name it "*Deperetella* cf. *D. cristata*." However, since the species name is already in the literature, it seems best to retain it until more information is forthcoming. The unknown upper dentition or anterior lower premolars may prove to have distinctive features. Also, *Deperetella cristata* may be even larger than is indicated at present, in which case there may be significant size difference between it and *D. depereti*.

Young (1937, p. 416, fig. 2) described and figured an incomplete deperetellid lower molar, also from northern Honan, which he referred to *Cristidentinus* (= *Deperetella*) cf. *depereti*. From the illustrations, Young's specimen appears indistinguishable from *D. depereti*.

***Deperetella similis* (Zdansky, 1930),  
new combination**

*Diplophodon similis* ZDANSKY, 1930, p. 35.

*Diplophodon major* YOUNG, 1937, p. 421.

TYPE: Maxilla with the lingual half of  $P^3$

and  $P^4-M^3$ , in the collections of the Paleontological Institute of the University of Uppsala, Sweden. Figured in Zdansky (1930, pl. 1, fig. 35).

REFERRED SPECIMENS: Maxilla with  $P^{2-4}$  and an isolated  $M^1$  or  $M^2$ , figured in Young (1937, p. 420, fig. 5, p. 421, fig. 6).

KNOWN DISTRIBUTION: Late Eocene beds in northern Honan, China.

REVISED DIAGNOSIS: About one-half of the size of *Deperetella cristata*: length of  $M^{1-3}$ , 35.5 mm. Upper cheek teeth, especially  $P^2$ , relatively shorter and wider than those of *D. cristata*.  $P^2$  protoloph parallel to metaloph;  $P^{3-4}$  protoloph slightly shorter than metalophs.  $M^{1-3}$  without lingual cingula.

DISCUSSION: Young (1937, p. 421) proposed the species *Diplophodon* (= *Deperetella*) *major* for an isolated  $M^1$  or  $M^2$  from northern Honan, China. The features cited by Young as diagnostic are differences between the type upper molar and the last upper premolar in Young's specimen of *D. similis*, which he mistook for  $M^1$  (see my footnote, p. 222). *Deperetella major* differs from  $M^2$  in the type of *D. similis* only in being about 10 per cent longer and 3 per cent wider; some of the difference in length might be due to the fact that the *D. similis*  $M^2$  is heavily worn and apparently somewhat shortened by interstitial wear. In any event, the difference in size between the two specimens is not great enough to warrant specific separation, and *D. major* is therefore relegated to synonymy.

The differences between *Deperetella similis* and *D. cristata* and the reasons for placing them in the same genus are discussed above (see p. 222). *Deperetella similis* is more advanced than *D. cristata* in having the  $P^2$  protoloph parallel to the metaloph, but this fact may reflect a slightly more extreme elongation of the anterior premolars in *D. cristata* rather than a more extensive molarization field in *D. similis*. Apparently two conflicting growth fields (molarization versus elongation) overlapped in the anterior part of the premolar series in species of *Deperetella*.

*Deperetella similis* is less than two-thirds of the size of *D. depereti* from the same locality and therefore probably represents a distinct species. *Deperetella similis* is about the same size as *D. birmanicum* from Burma (see be-

low) and may be related to that species. Both forms lack molar cingula (upper lingual in *D. similis*, lower labial in *D. birmanicum*) which are present in *D. cristata*.

***Deperetella birmanicum* (Pilgrim, 1925)**

*Chasmotherium? birmanicum* PILGRIM, 1925, p. 25.

*Deperetella? birmanicum*: COLBERT, 1938, p. 348.

TYPE: Geological Survey of India No. C348, lower jaw with  $P_4$ - $M_3$ . Figured in Pilgrim (1925, pl. 2, fig. 9) and in Colbert (1938, p. 349, fig. 40).

HYPODIGM: Type only.

KNOWN DISTRIBUTION: Late Eocene Pondaung Formation, Burma.

DIAGNOSIS: About 40 per cent smaller than *Deperetella cristata*: length of  $M_{1-3}$ , 41.3 mm.

DISCUSSION: When Pilgrim (1925, pp. 25-28) described *Chasmotherium? birmanicum* he had no knowledge of the Mongolian deperetellids. Matthew (1929, p. 514) noted that *C.? birmanicum* appeared to be related to *Teleolophus* and *Deperetella*, but he did not formally change the taxonomy. Colbert (1938, pp. 348-350) made detailed comparisons between *C.? birmanicum* and the Mongolian deperetellids, and concluded that the Burmese form represented a new genus closely related to *Deperetella*. Since the available material was so scanty, Colbert refrained from naming a new genus and referred *birmanicum*, with a query, to *Deperetella*.

*Deperetella birmanicum* differs from *D. cristata* in being smaller, lacking labial cingula on  $M_{2-3}$ , and having what appears to be a short, posteriorly projecting spur on the hypoconid of  $P_4$ . In these features *D. birmanicum* is intermediate between *Teleolophus medius* and *Deperetella cristata*. The Burmese species is assigned to *Deperetella* rather than to *Teleolophus* because its  $P_4$  has a complete hypolophid. On the basis of the available evidence, I can see no reason for believing that *D. birmanicum* represents a new genus. *Deperetella birmanicum* may be related to *D. similis* from China since both species are of about the same size, and both lack molar cingula which are present in *D. cristata* and *D. depereti*.

**Deperetellid, gen. indet.**

Young and Bien (1939, p. 531) and Bien (1940, p. 185) listed *Teleolophus* sp. and *Deperetella* sp. in preliminary faunal lists of vertebrates from late Eocene beds in Lunan, Yunnan, China. Chow (1957, p. 205, pl. 1, fig. 7) described and figured the specimen which had been cited as *Deperetella* sp., a protolophid 18 mm. wide, with traces of what appears to be cement. In size, the Lunan deperetellid is comparable to *Deperetella cristata*, *D. depereti* (which may not be specifically distinct from *D. cristata*), and *Teleolophus magnus*; if the coating on the tooth is cement, *Teleolophus* is the probable genus.

The specimen cited as *Teleolophus* sp. by Young and Bien was not mentioned by Chow, who noted, however, that some of the specimens in the collection had been lost during the war.

Chow (1957, p. 205, pl. 1, fig. 6) noted and figured another deperetellid molar fragment from late Eocene beds in Tientong, Kwangsi, China, which is too incomplete for generic determination.

Takai (1944, p. 741) referred to *Cristidentinus* (= *Deperetella*) an isolated lower molar from the Hosan coal field, Korea, which he had previously (1939, p. 211) assigned to *Desmatotherium* (= *Colodon?*) *grangeri*. From the illustrations (Takai, 1939, pl. 4, fig. 7; 1944, p. 721, fig. 6) it appears to me that Takai's original assignment was correct and that the tooth does actually represent *Colodon? grangeri*. There is to my knowledge no record of a deperetellid from Korea.

**FAMILY HELALETIDAE**

**HELALETES MARSH, 1872**

***Helaletes mongoliensis* (Osborn, 1923),  
new combination**

Plate 4, figures 1-4

*Desmatotherium mongoliense* OSBORN, 1923, p. 2.

TYPE: A.M.N.H. No. 19161, right premaxilla and maxilla, with  $I^1$ - $P^1$  alveoli and  $P^2$ - $M^2$ . Figured in Matthew and Granger (1925c, p. 2, fig. 1).

HYPODIGM: Type and A.M.N.H. Nos. 20155, 20156A-20156F, 81717, 81718, and 81792.

KNOWN DISTRIBUTION: Late Eocene Irдин Manha beds, Irдин Manha escarpment, about

TABLE 15  
STATISTICAL DATA ON TEETH OF *Helalestes*  
*mongoliensis* FROM THE IRDIN MANHA BEDS

	N	OR	M
P <sup>1</sup>	—		
P <sup>2</sup>	1	—	—
L		—	9.0
W		—	9.5
P <sup>3</sup>	2		
L		9.3–9.4	9.35
W		11.3–12.0	11.65
P <sup>4</sup>	2		
L		10.2–10.4	10.30
W		12.8–13.6	13.20
M <sup>1</sup>	1		
L		—	12.1
W		—	14.0
M <sup>2</sup>	2		
L		14.3–15.2	14.75
W		16.0–16.1	16.05
M <sup>3</sup>	3		
L		14.7–16.0	15.17
W		15.8–16.9	16.47
P <sub>2</sub>	—		
P <sub>3</sub>	2		
L		9.5–9.9	9.75
W		7.2–7.4	7.30
P <sub>4</sub>	3		
L		9.9–10.1	10.00
W		8.6–8.9	8.77
M <sub>1</sub>	4		
L		12.0–12.5	12.28
W		9.0–9.1	9.05
M <sub>2</sub>	2		
L		14.1–15.0	14.55
W		10.2–10.5	10.35
M <sub>3</sub>	1		
L		—	17.5
W		—	10.3

20 miles south-southeast of Iren Dabasu, Inner Mongolia.

REVISED DIAGNOSIS: About the size of the North American *Helalestes intermedius*, but with M<sup>1–3</sup> metacones slightly shorter and more concave, and P<sub>4</sub>–M<sub>2</sub> relatively shorter and wider than in that species. Measurements are given in table 15.

DESCRIPTION (FIGS. 16, 17): From the type specimen, A.M.N.H. No. 19161, it can be seen that *Helalestes mongoliensis* possessed a greatly enlarged nasal incision, as did the North American species *H. nanus* and *H.*

*intermedius*, with the infraorbital foramen opening above the posterior end of P<sup>4</sup> and with a broad vertical groove in front of the orbit for the nasal diverticulum. The I<sup>3</sup> alveolus is slightly larger than that for I<sup>1</sup> or that for I<sup>2</sup>. The C<sup>1</sup> alveolus is considerably larger than that for I<sup>3</sup>, indicating a moderately large canine, as in *H. intermedius*. P<sup>1</sup> is missing, but the alveolus indicates that it was not vestigial, as Osborn (1923, p. 2) stated, but was perhaps even wider than P<sup>1</sup> in *H. intermedius* (known only from the roots). P<sup>2</sup> is slightly wider than long, with well-separated paracone and metacone. A prominent protoloph begins low at the ectoloph and rises to the anterolingual corner, where it curves posteriorly and extends along the broad lingual border of the tooth. A shallow vertical groove on the lingual face marks the incipient separation of the hypocone from the protocone. The metaloph is very low and thin and extends from the metacone to the hypocone. P<sup>3</sup> in A.M.N.H. No. 19161 is like P<sup>2</sup> but larger, relatively shorter and wider, and has a higher metaloph (which is still not so high as the protoloph). As in P<sup>2</sup>, the metaloph extends lingually to the posterior end of the curved protoloph. In P<sup>3</sup> of A.M.N.H. No. 20156A, the only other specimen of *H. mongoliensis* with upper premolars, the metaloph appears lower than in the type and extends slightly more anterolingually, toward the protocone. In P<sup>4</sup> of A.M.N.H. No. 19161 the posteriorly trending lingual portion of the protoloph is shorter than in P<sup>3</sup> and the metaloph, which is almost as prominent as the protoloph, converges more lingually toward the protoloph. In A.M.N.H. No. 20156A, the P<sup>4</sup> metaloph is short and extends anterolingually toward the protocone, bypassing the incipient hypocone. Among North American species of *Helalestes*, the premolar metalophs extend either anterolingually to the protocone (in *H. intermedius*) or lingually to the incipient hypocone (in *H. nanus*); apparently both kinds of premolar patterns occur in *H. mongoliensis*. The upper molars of *Helalestes mongoliensis* are similar to those of *H. intermedius*, except that the metacones in the former are slightly shorter and more concave, approaching the condition seen in the North American late Eocene species *Colodon kayi* and *C. woodi*.





FIG. 16. *Helalestes mongoliensis*, new combination, type, A.M.N.H. No. 19161,  $P^2-M^2$ , with  $M^3$  from A.M.N.H. No. 20156B. Above  $P^3-4$  of the type are  $P^3-4$  of A.M.N.H. No. 20156A (reversed).  $\times 1$ .

No  $P_2$  is preserved in the *Helalestes mongoliensis* sample.  $P_3$  resembles that tooth in the only lower dentition known for *H. intermedius*, A.M.N.H. No. 12672, except that the entoconid is slightly larger and the talonid slightly narrower in the Mongolian form. These differences may merely be due to individual variation.  $P_4$  is like  $P_3$  but has a shorter and less triangular (i.e., more molariform) trigonid and a relatively larger entoconid.  $P_4$  and  $M_{1-2}$  are relatively shorter and wider in *H. mongoliensis* than in *H. intermedius*. The posterior part of the only  $M_3$  known for *H. mongoliensis* (A.M.N.H. No. 20155) is damaged, but it appears to have

had a small hypoconulid (contra Matthew and Granger, 1925c, p. 1).

DISCUSSION: Osborn (1923, p. 2) based his original brief description of *Desmatotherium mongoliense* in part on specimens of *Lophialetes expeditus* from the same locality. Matthew and Granger (1925c, p. 1) noticed the error and published a short revised description, with illustrations, of *D. mongoliense*. Both Osborn and Matthew and Granger stressed the similarities between *Desmatotherium mongoliense* and the North American species *Desmatotherium guyotii*. In a recent revision of North American tapiroids (Radinsky, 1963a, pp. 41-42, 49-50), *Desmatotherium guyotii*, the type species of *Desmatotherium*, was synonymized with *Helalestes intermedius*, and the North American late Eocene species previously referred to *Desmatotherium* (*D. kayi* and *D. woodi*) were assigned to *Colodon*. Thus the genus *Desmatotherium* no longer exists, and *Desmatotherium mongoliense* must be assigned to either *Helalestes* or *Colodon*.

In some features, such as the relatively wide  $P_4-M_2$  and the degree of metacone reduction and depression in  $M_{1-3}$ , the Mongolian species seems closer to *Colodon* than to *Helalestes*. However, in other features, mainly the degree of premolar molarization and the proportions of  $M^1$ ,  $P^{2-4}$ , and  $P_{2-3}$  (all relatively long and narrow), it is more like *Helalestes*.

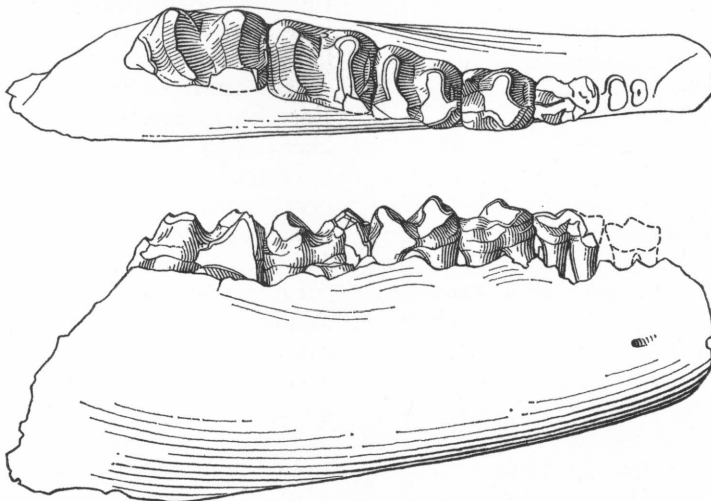


FIG. 17. *Helalestes mongoliensis*, new combination, A.M.N.H. No. 20155, in occlusal and lateral views. Teeth included are  $P_3-M_3$ . From Matthew and Granger (1925c, fig. 2).  $\times 1$ .

*letes* than *Colodon*. The generic assignment of *Helaletes mongoliensis* was an unusually subjective decision; I assigned it to *Helaletes* rather than to *Colodon* mainly because of its submolariform premolars.

*Helaletes mongoliensis* is more advanced than North American species of *Helaletes* (see diagnosis) and not far removed from primitive species of *Colodon*. Its morphology is thus in accordance with its occurrence in late Eocene beds.

***Helaletes fissus*** (Matthew and Granger, 1925c),  
new combination

*Desmatotherium fissum* MATTHEW AND GRANGER, 1925c, p. 3.

TYPE: A.M.N.H. No. 20161, maxillary fragment with P<sup>2-4</sup>.

HYPODIGM: Type only.

KNOWN DISTRIBUTION: Late Eocene "Irdin Manha" beds near Camp Margetts, 25 miles south-southwest of Iren Dabasu, Inner Mongolia.

DIAGNOSIS: Slightly smaller than *Helaletes mongoliensis*, with P<sup>2-4</sup> relatively shorter and wider, and hypocones better separated from protocones than in that species. P<sup>2-4</sup> metalophs not so prominent as protolophs, and directed toward protocones.



FIG. 18. *Helaletes fissus*, new combination, type, A.M.N.H. No. 20161, P<sup>2-4</sup>. From Matthew and Granger (1925c, fig. 3).  $\times 1$ .

DESCRIPTION (FIG. 18): Enough of the maxilla is preserved to show that the infraorbital canal opened above P<sup>4</sup>, apparently slightly anterior to its position in the type specimen of *Helaletes mongoliensis*. Immediately anterior to the infraorbital foramen the maxilla wall trends anterolaterally, abruptly terminating the broad nasal diverticulum groove which in *H. mongoliensis* continues along the maxilla as far anterior as P<sup>2</sup>. This feature is probably rather variable and not necessarily indicative of specific differentiation.

The upper premolars (P<sup>2-4</sup>) have well-separated, labially convex paracones and

metacones, moderately large parastyles, and narrow anterior and posterior basal cingula. The P<sup>2</sup> hypocone is slightly more lingually situated than the protocone and separated from it by a deep valley. No distinct metaloph is evident, and the broad labial slope of the hypocone descends unbroken toward the ectoloph. In P<sup>3</sup> the protocone and hypocone are separated by a lingual groove. Details are obscured by wear, but there appears to have been a short low metaloph extending from the anterolingual slope of the metacone toward the protocone. In P<sup>4</sup> the hypocone is not so large as in P<sup>3</sup>, although a lingual groove marks its incipient differentiation from the protocone. A metaloph which is almost as high as the protoloph extends from the metacone toward the protocone.

DISCUSSION: As is mentioned in the discussion of the preceding species, the genus *Desmatotherium* no longer exists, having been synonymized with *Helaletes*, and therefore *D. fissum* should be assigned to either *Helaletes* or *Colodon*. P<sup>2-4</sup> of the type and sole specimen of *Desmatotherium fissum* (A.M.N.H. No. 20161) are more advanced than those teeth in *Helaletes mongoliensis* in being relatively shorter and wider and in having the hypocone better separated from the protocone; in these features A.M.N.H. No. 20161 resembles species of *Colodon*. However, in *Colodon* P<sup>2-4</sup> metalophs are as prominent as the protolophs and extend to the hypocones; in A.M.N.H. No. 20161 the metalophs are less prominent than the protolophs and extend toward the protocones, as in *Helaletes*. For these reasons *Desmatotherium fissum* is here assigned to *Helaletes*.

Degree of premolar molarization varies greatly within species of helaletid tapiroids, especially *Helaletes* (see Radinsky, 1963a, p. 47, fig. 10), and it is possible that *Helaletes fissus* is more similar to *H. mongoliensis* than the few specimens now available seem to indicate. Had A.M.N.H. No. 20161 been found at the type Irdin Manha locality with the *Helaletes mongoliensis* sample, it would probably have been considered an advanced variant of that species. However, since the type of *Helaletes fissus* comes from a different locality and possibly a different horizon than does *H. mongoliensis*, and on the basis of the specimens now available is morphologically

distinct, *H. fissus* is at least for the present maintained as a separate species.

The upper premolars of *Helalestes fissus* are more advanced than those of any other species of *Helalestes* and provide an ideal morphological intermediate between the premolar pattern of that genus and that of *Colodon*.

#### *Helalestes fissus*

A.M.N.H. No. 81802, a mandible with  $C_1-M_3$ , from "Irdin Manha" beds at Camp Margetts, may belong to *Helalestes fissus*. It is slightly smaller than *Helalestes mongoliensis* and agrees in size with the type of *H. fissus*. The canine is small and the symphysis long, terminating at  $P_2$ ; in these features A.M.N.H. No. 81802 differs from *H. intermedius* (in which the canine is large and the symphysis terminates well anterior to  $P_2$ ) and resembles species of *Colodon*.  $P_2$  resembles that tooth in *H. intermedius* ( $P_2$  is not known for *H. mongoliensis*) and is less molariform than  $P_2$  in *Colodon*. The  $P_3-4$  trigonids are relatively short for *Helalestes*, but their narrow talonids and small entoconids are more like those of *Helalestes* than those of *Colodon*.  $M_3$  has a short, wide hypoconulid (or broad posterior basal cingulum). A.M.N.H. No. 81802 thus agrees with the type of *Helalestes fissus* in displaying features that are advanced for *Helalestes* and approach *Colodon*, namely, reduced canine, termination of symphysis at  $P_2$ , and shortened  $P_3-4$  trigonids.

A.M.N.H. No. 81804, a lower jaw fragment with  $P_4-M_3$ , is recorded as coming from the "Houldjin gravels" at Camp Margetts. In size and cusp pattern it is virtually identical with A.M.N.H. No. 81802, from "Irdin Manha" beds at Camp Margetts, and probably also comes from that horizon.

#### *Helalestes* sp.

A.M.N.H. No. 81803, a mandible with  $P_2-M_2$ , from 10 miles southwest of Camp Margetts is assignable to *Helalestes* rather than to *Colodon* on the basis of the relatively long and narrow  $P_2-4$ , which have relatively unreduced paralophids and small entoconids. It is close in size to *Helalestes mongoliensis* but has relatively narrower cheek teeth. It differs from *H. fissus*? (A.M.N.H. Nos. 81802 and 81804) from Camp Margetts in having the

termination of the symphysis well anterior to  $P_2$  (as in *H. intermedius*) and in having relatively long  $P_3-4$  trigonids (as in *H. intermedius* and *H. mongoliensis*).

A.M.N.H. No. 81803 is recorded as coming from the lower part of the "Houldjin gravels" (=early Oligocene), a fact that, if true, would indicate a surprisingly late survival for *Helalestes*. Two specimens of *Lophialetes* (A.M.N.H. Nos. 81780 and 81781), recorded as coming from the same horizon, closely resemble *Lophialetes expeditus* from the Irdin Manha beds (see p. 198). The stratigraphy in the Camp Margetts area is complicated, and the boundary between the so-called "Irdin Manha" beds and overlying "Houldjin gravels" at the locality 10 miles southwest of Camp Margetts has not been satisfactorily worked out. It is quite possible that A.M.N.H. No. 81803 came from the upper part of the "Irdin Manha" beds and thus is of about the same age as *H. mongoliensis*.

#### COLODON MARSH, 1890

##### *Colodon hodosisimai* Takai, 1939

*Colodon hodosisimai* is known from  $P^3-4$  and  $M^2-3$  (figured in Takai, 1939, pl. 4, figs. 2-4), from late Eocene beds of the Hosan coal field, Kokaiko, northwestern Korea. It differs from the Mongolian late Eocene species *Helalestes mongoliensis* and *H. fissus* in having the  $P^3-4$  metaloph as prominent as the proto-*loph*, a feature which, together with the molar structure, indicates assignment to *Colodon*. *Colodon hodosisimai* is of about the same size as *C. woodi* from the late Eocene of North America but differs from that species in having the  $P^3-4$  lingual cusps less well separated (not necessarily a valid specific distinction). In this feature *C. hodosisimai* resembles *Colodon inceptus* from the early Oligocene of Mongolia, from which it is distinguishable by the fact that it is about 25 per cent smaller.

##### *Colodon inceptus* Matthew and Granger, 1925a

*Paracolodon curtus* MATTHEW AND GRANGER, 1925a, p. 4.

TYPE: A.M.N.H. No. 20357, maxillary fragment with  $P^2-M^3$ .

HYPODGM: Type and A.M.N.H. No. 20355 ( $P^1-3$ ).

KNOWN DISTRIBUTION: Early Oligocene Ardyn Obo beds, Ardyn Obo,<sup>1</sup> Mongolian People's Republic.

DIAGNOSIS: About the size of the North American *Colodon occidentalis*. Small  $C^1$  present.  $P^1$  relatively long, with well-separated paracone and metacone, and large postero-lingual cusp.  $P^2-4$  with relatively convex paracone and metacone;  $P^3-4$  hypocone not well differentiated from protocone.

DISCUSSION: Matthew and Granger (1925a, p. 4) erected the genus *Paracolodon* for a maxillary fragment with three pre-molars (A.M.N.H. No. 20355) which they distinguished from species of *Colodon* by the supposed loss of  $P^1$ . What Matthew and Granger thought were  $P^2-4$  in the type are actually  $P^1-3$  (see fig. 19), and these teeth do not differ enough from  $P^1-3$  of other species of *Colodon* to justify generic separation. In fact, A.M.N.H. No. 20355 does not differ enough from the type of *Colodon inceptus* (A.M.N.H. No. 20357) from the same locality to warrant even specific separation. The only comparable tooth of the two specimens,  $P^3$ , is about 10 per cent wider in A.M.N.H. No. 20355 but is otherwise virtually identical in cusp pattern. Since the two specimens came from the same horizon and locality, and the size difference is within the bounds of possible intraspecific variation, they are here considered representatives of the same species. *Colodon inceptus* and *Paracolodon curtus* were named on the same page in the same work (Matthew and Granger, 1925a, p. 4). Since the type of *Colodon inceptus* (A.M.N.H. No. 20357) is the more complete specimen, it is here chosen as the type of the species. *Paracolodon curtus* thus becomes a synonym of *Colodon inceptus*.

*Colodon inceptus* is known from only two specimens in the Ardyn Obo collection (A.M.N.H. Nos. 20355 and 20357). They indicate an animal of about the same size as the North American species *Colodon occidentalis*, but they differ from that species in the following features: small  $C^1$  present (vestigial or absent in *C. occidentalis*);  $P^1$  relatively longer, with well-separated paracone and metacone;  $P^2-4$  paracones and metacones

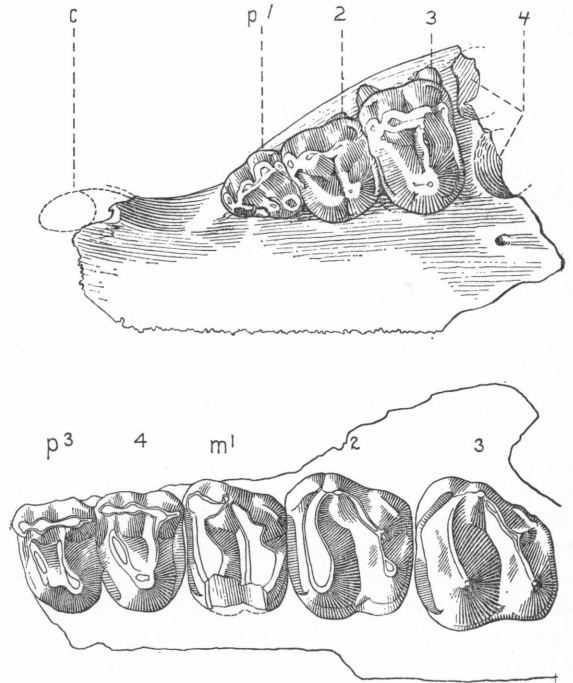


FIG. 19. *Colodon inceptus*. Above: A.M.N.H. No. 20355,  $P^1-3$ . Below: Type, A.M.N.H. No. 20357,  $P^2-M^3$ . After Matthew and Granger (1925a, figs. 4 and 5). Both  $\times 1$ .

more convex labially, not so merged into ectoloph as in most specimens of *C. occidentalis*;  $P^3-4$  hypocones not so well differentiated from protocones as in most *C. occidentalis*;  $M^2-3$  paracones narrower, less extended posteriorly. In most of these differences *Colodon inceptus* is slightly less advanced than *Colodon occidentalis*. Not enough is known of the relationships between North American species of *Colodon* to suggest to which, if any, *C. inceptus* is most closely related.

Enough of the maxilla is preserved in A.M.N.H. No. 20355 to show that *Colodon inceptus* had a greatly enlarged nasal incision, as did *Colodon occidentalis*. Matthew and Granger (1925a, p. 3, fig. 5), in their illustration of this specimen, wrongly labeled the smooth posteroventral edge of the enlarged nasal incision, behind the premaxillary-maxillary suture, as the infraorbital foramen. The infraorbital foramen is not preserved in the specimen, but it probably opened above  $P^4$ , as in *C. occidentalis*.

The occurrence of species of *Helalestes* and

<sup>1</sup> Written Ergil-Obo in Russian and Erghilyin-Dzo in Mongolian papers.

*Colodon* in temporally successive deposits in both Asia and North America raises the problem of whether *Colodon* is a monophyletic genus, with two separate migrations to account for the record, or a biphyletic genus, with parallel evolution from *Helalestes* to *Colodon* occurring independently on the two continents. As far as the available evidence shows, *Colodon hodosimai* and *C. inceptus* could have been derived from the Asiatic late Eocene *Helalestes mongoliensis* or *H. fissus*, while in North America, the middle Eocene *Helalestes nanus* or, more probably, *H. intermedius* could have given rise to the late Eocene and Oligocene North American species of *Colodon*. Or, either an Asiatic or North American species of *Helalestes* could have given rise to both Asiatic and North American species of *Colodon*. Eocene and Oligocene faunal correlations between the two continents are not yet precise enough and knowledge of the species involved is not complete enough to suggest which of the hypotheses is more probable. The problem may be more apparent than real, since the Asiatic species assigned to *Helalestes* (*H. mongoliensis* and *H. fissus*) are more advanced than the North American species of that genus and may eventually prove to be closer to *Colodon*.

***Colodon orientalis* Borissiak, 1918**

?*Colodon orientalis* BORISSIAK, 1918, p. 27.

*Colodon orientalis* is known from a maxillary fragment with  $P^4$ - $M^3$  (Paleontological Institute, Academy of Sciences, U.S.S.R., No. 1442/99), from late Oligocene beds in the Turgai region, Kazakh S.S.R. From Borissiak's illustration (1918, p. 28, fig. 1) and measurements (p. 29), the upper molars of *C. orientalis* appear identical in size and cusp pattern to those of *C. occidentalis* from the early and middle Oligocene of North America. The extraordinary feature of *C. orientalis*, one that distinguishes it from all other species of *Colodon*, is that  $P^4$  is fully molariform, with the metacone concave and lingually depressed and the protocone and hypocone as widely separated as in the molars. This degree of premolar molarization is not seen in even the most advanced variants of *Colodon occidentalis*, in which the  $P^4$  protocone and hypocone are in every case close together,

blocking the median valley, and the metacone is as labially situated as the paracone. Further evidence may show *C. orientalis* to be generically distinct from other species of *Colodon*, but for the present the difference in premolar molarization, in my opinion, warrants specific separation only.

***Colodon? grangeri* (Tokunaga, 1933),  
new combination**

*Desmatotherium grangeri* TOKUNAGA, 1933, p. 6.

Tokunaga (1933, p. 6) erected the species *Desmatotherium grangeri* for a maxillary fragment with  $P^2$ - $4$  from late Eocene beds of the Hosan coal field, Kokaido, northwestern Korea. Takai (1939, pl. 4, figs. 5, 6, 9) figured the type and a few additional specimens, including what appear to be  $M^{2-3}$  (fig. 6) and an  $M^3$  (fig. 9). Since the genus *Desmatotherium* has been synonymized with *Helalestes* (Radinsky, 1963a, p. 42), the generic assignment of *D. grangeri* must be revised.

From Takai's illustrations, *D. grangeri* appears very similar to the North American late Eocene or early Oligocene species *Colodon? hancocki* Radinsky (1963a). Both species have lingually depressed but labially convex molar metacones and relatively short and wide but otherwise non-molariform premolars. These features suggest that *D. grangeri* and *C.? hancocki* may prove to be generically distinct from *Colodon*. However, since both species are still poorly known, I think it best, for the present, to assign *D. grangeri*, with *C.? hancocki*, questionably to *Colodon*.

Takai's (1939, p. 212) measurements indicate that *C.? grangeri* is about 20 per cent smaller than *C.? hancocki*. From the illustrations cited above, the only difference apparent between the cusp patterns of the two species is that the lingual groove on  $P^2$  of *C.? grangeri* appears slightly shallower than that of *C.? hancocki*. However, the illustrations are not clear enough to confirm this suggestion definitely, and, in any event, such slight differences in degree of premolar molarization are usually not indicative of specific differentiation in early Tertiary tapiroids.

An isolated lower molar referred by Takai (1939, pl. 4, fig. 7) to *Desmatotherium grangeri* was later referred by him (1944, p. 741) to *Cristidentinus* (= *Deperetella*). From

Takai's illustrations and measurements, it appears that his original assignment was correct. An isolated  $P_4$  referred by Takai (1939, pl. 4, fig. 8) to *Desmatotherium grangeri* is too large to belong to that species, or to *Colodon hodosimai*. Three lower teeth ( $P_2$ ,  $P_4$ , and  $M_1$ ) later referred by Takai (1944, p. 738) to *Desmatotherium grangeri* are not well enough illustrated to allow comparisons with *C. ? hancocki*.

**VERAGROMOVIA** GABUNIA, 1961

***Veragromovia desmatotheroides***  
Gabunia, 1961

Gabunia (1961, p. 711) proposed a new genus and species of helaletid tapiroid, *Veragromovia desmatotheroides*, for an isolated  $M^3$  (see fig. 20) from the middle or late Eocene Obailinski beds of the Zaisan basin, Kazakh S.S.R. (A more detailed discussion of the spe-

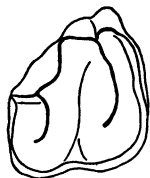


FIG. 20. *Veragromovia desmatotheroides*, type,  $M^3$ .  
After Gabunia (1961, fig. 6).  $\times 1.6$ .

cies is given in Gabunia, 1962, p. 20.) In size and cusp pattern  $M^3$  of *Veragromovia desmatotheroides* seems extremely similar to  $M^3$ 's of *Helaletes nanus* from the middle Eocene of North America. Species of *Helaletes* (*H. mongoliensis*, *H. fissus*) were present in the late Eocene in Mongolia, so it is quite possible that representatives of the genus ranged as far west as Kazakhstan. On the basis of the  $M^3$  alone, *Veragromovia* does not appear generically separable from *Helaletes*. However, further knowledge of the dentition of *Veragromovia desmatotheroides* is necessary before its relationship to other helaletid genera can be definitely established.

**Cf. *Hyrachyus*<sup>1</sup>**

**Plate 4, figure 5**

A ceratomorph upper dentition, A.M.N.H. No. 81801, consisting of left  $P^4$ - $M^3$  and right

<sup>1</sup> *Hyrachyus* is here deliberately placed in the Helaletidae. I believe that *Hyrachyus* and the other genera now included in the family Hyrachyidae are not dif-

$M^2$ - $^3$ , from "Irdin Manha" beds 7 miles southwest of Camp Margetts, cannot be assigned to any known Asiatic genus and instead shows closest resemblances to the North American genus *Hyrachyus*. The upper molars of A.M.N.H. No. 81801 (see fig. 21) differ from those of *Hyrachyus* in one feature, the lack of a metacone rib (slight labial convexity) on  $M^2$ . The  $P^4$  of A.M.N.H. No. 81801 is slightly more molariform than that of most hyrachyid species, with the hypocone



FIG. 21. Cf. *Hyrachyus*, A.M.N.H. No. 81801,  
 $P^4$ - $M^3$ .  $\times 1$ .

separated from the protocone by a shallow groove and the metaloph almost as prominent as the protoloph and extending from ectoloph to hypocone.

Among Asiatic forms, A.M.N.H. No. 81801 is most similar to species of *Helaletes* (*H. mongoliensis*, *H. fissus*), from which it differs in having slightly longer and less depressed molar metacones and in lacking a cingulum labial to the metacones on  $M^{1-2}$  (features that distinguish *Hyrachyus* from *Helaletes*).

No specimen of *Hyrachyus* has ever been found in Asia, and it is possible that, when the complete dentition of the form represented by A.M.N.H. No. 81801 becomes known, it will be unrelated to *Hyrachyus*. The molar pattern is typical of primitive ceratomorphs in general and is similar to that seen, for example, in European lophiodontid tapiroids such as *Chasmothereium* and *Lophiodon*. However, since many North American genera also occur in late Eocene faunas of Asia, it is possible that A.M.N.H. No. 81801 actually is an Asiatic representative of *Hyrachyus* or a closely related genus.

**FAMILY ISECTOLOPHIDAE**

Chow and Li (1963, pp. 1411-1412) noted the occurrence of *Homogalax*, a genus hereto-

ferent enough from the primitive helaletid *Heptodon* to warrant separation on the family level. Evidence to support this opinion will be presented in a forthcoming paper.

fore known only from the early Eocene of North America, in the Eocene marls (Kuan-chuan Series) at Wutu, Changlo District, northern Shantung, China. This record is based on a single specimen, a maxilla with  $P^2-M^1$  which greatly resemble those teeth in the North American Wasatchian species *Homogalax protapirinus*. The age of the Chinese specimen is uncertain, since it was the only fossil found in the Eocene marls at Wutu; its close resemblance to *H. protapirinus* suggests an early Eocene age.

#### ?FAMILY ISECTOLOPHIDAE

Gabunia (1962, p. 20; p. 18, fig. 5) described and figured an isolated tapiroid  $M^1$  or  $M^2$  with a convex metacone but lacking the anterolabial corner (parastyle and paracone), from the middle or late Eocene Obailinski beds of the Zaisan basin, Kazakh S.S.R. This specimen may be an isectolophid, but more material is needed before a definite familial assignment can be made.

Zdansky (1930, pp. 38-40, pl. 1, figs. 38-40) described and figured a maxillary fragment with very worn  $P^4-M^1$ , and an isolated lower molar, from late Eocene beds near Mienchih, northern Honan, China, which he questionably assigned to the Isectolophidae. The  $P^4$  and  $M^1$  metacones appear to have been convex and situated labially, but the  $P^4$  metaloph and protoloph meet lingually in a broad U, instead of a steeply conical protocone as in isectolophids. What can be seen of the cusp patterns of these teeth

suggests a rhinocerotoid rather than a tapiroid, perhaps related to a genus recently described from the late Eocene of Mongolia, *Pappaceras* Wood (1963). The isolated lower molar is relatively wider than lower molars of known isectolophids and also appears more probably to represent a rhinocerotoid than a tapiroid.

#### FAMILY INCERTAE SEDIS

#### INDOLOPHUS PILGRIM, 1925

#### *Indolophus guptai* Pilgrim, 1925

#### Plate 4, figure 6

*Indolophus guptai* was based by Pilgrim (1925, pp. 22-25) on a single specimen (Geological Survey of India No. C347) with  $P^2-M^1$  and  $DP^4$ , from the late Eocene Pondaung Formation of Burma. Because of the convex metacones of these teeth, Pilgrim and later workers (*inter alia* Colbert, 1938, p. 346) considered *Indolophus* to be most closely allied to the North American isectolophids *Homogalax* and *Isectolophus*. However, in a recent paper (Radinsky, 1963a, pp. 9-10) I pointed out that *Indolophus* (see fig. 22) differs from all known isectolophids in several important features, including:  $P^2$  more molariform;  $P^3-4$  protocones labiolingually flattened and posteriorly elongated, with incipient hypocone differentiation as in the Helatetidae and unlike that of the Isectolophidae;  $P^2-4$  lophs high and acute;  $P^2-M^1$  parastyles extremely small;  $M^1$  metaloph very low at ectoloph. Strong metacone convexity is a

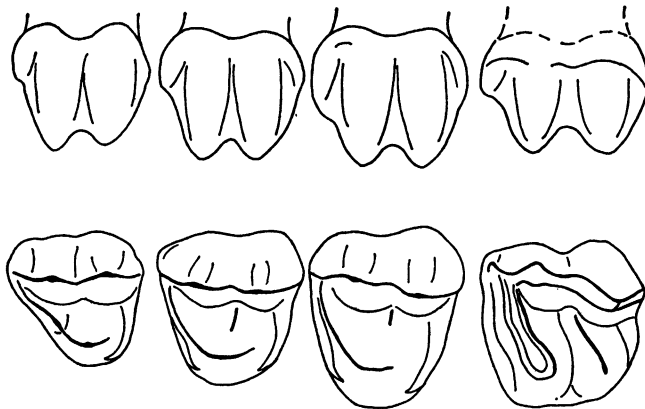


FIG. 22. *Indolophus guptai*, type,  $P^2-M^1$ , from A.M.N.H. No. 17617, a cast of the original. Above: Labial view. Below: Occlusal view.  $\times 2$ .



primitive feature in tapiroids, and it would not be very surprising to find it retained in two unrelated lineages. I consider the differences between *Indolophus* and the North American isctolophids great enough to warrant the removal of *Indolophus* from the Isectolophidae.

*Indolophus guptai* resembles A.M.N.H. No. 81751, an unnamed Mongolian tapiroid described above, in possessing convex metacones, but differs in several other features of cusp pattern (see p. 206). It differs from all other known tapiroids in having its molar metaloph almost terminate before reaching the ectoloph. The affinities of *Indolophus* are uncertain. It appears to represent a distinct, otherwise unknown line of Asiatic tapiroids.

#### GENERA REMOVED FROM THE TAPIROIDEA

##### ERGILIA GROMOVA, 1952

Gromova (1952, p. 99) proposed a new genus and species of helaletid tapiroid, *Ergilia pachypterna*, for a few foot bones and fragments of limb bones from Oligocene beds at Ardyn Obo (=Ergil Obo), Mongolian People's Republic. The most diagnostic of the skeletal elements of *Ergilia* figured in that paper are an astragalus, calcaneum, and third metatarsal. In a later paper Gromova (1960) figured a magnum of *Ergilia pachypterna* and proposed a second species, *E. kazakhstanica*,

based on a few foot bones from Oligocene beds in the Turgai region of the Kazakh S.S.R. The only tapiroid known from the Oligocene of the Ardyn Obo and Turgai areas is the helaletid genus *Colodon*, and the foot bones of *Ergilia* are distinctly different from those of *Colodon*, as Gromova pointed out. However, the foot bones on which *Ergilia* is based are identical with corresponding elements in the skeleton of *Ardynia praecox* Matthew and Granger (1923), a cursorial rhinocerotoid which occurs in the Ardyn Obo fauna, and it is evident that the two genera are synonymous. No postcranial remains are associated with dentitions of *Ardynia* at Ardyn Obo. Those that allowed a comparison with *Ergilia* are parts of front and hind feet associated with an undescribed skull and jaws of *Ardynia* (A.M.N.H. No. 26039) from the Ulan Gochu beds at Urtyn Obo, East Mesa, Shara Murun region, Inner Mongolia.

##### LUNANIA CHOW, 1957

*Lunania youngi* Chow (1957), a small perisodactyl known only from a lower jaw with  $M_{2-3}$  from the late Eocene of Lunan, Yunnan, China, was originally provisionally assigned by Chow (1957, p. 205) to the Tapiroidea. Recently Chow (1962, p. 224) transferred *Lunania* to the Chalicotherioidea. Because of the oblique molar metalophids of *Lunania*, the latter is a more satisfactory allocation.

## OSTEOLOGY

SKELETAL REMAINS are known for *Lophialetes*, *Schlosseria*, and *Deperetella*. The first two genera provide all that is known of the lophialetid skeleton; the last-named furnishes virtually all our knowledge of deperetellid osteology. A few isolated ceratomorph foot bones from the Irdin Manha beds probably belong to *Teleolophus*, *Helaletes*, or the rhinocerotoid *Caenolophus*, but cannot be assigned to a particular genus with certainty. The skeletal anatomy of the Asiatic helaletids was probably similar to that of their North American counterparts (see comments below).

Fortunately *Lophialetes* and *Deperetella* are end forms in their respective families, and each probably exhibits the most extreme specialization attained in its lineage. In the following descriptions, where possible, comparisons are made with the North American early Eocene tapiroid *Heptodon*, a genus that probably represents, at least morphologically, the ancestor of the lophialetids and deperetellids.

### FAMILY LOPHIALETIDAE

#### SKULL AND MANDIBLE

An almost complete but crushed skull of *Lophialetes* (A.M.N.H. No. 21595, Ulan Shireh *L. expeditus*?) furnished most of the information for the following remarks.

The skull of *Lophialetes* (see fig. 23) in most respects resembles that of a primitive early Eocene perissodactyl, such as *Heptodon*. It is lightly built, relatively long and low, with a pronounced postorbital constriction and moderately expanded braincase. The sagittal and lambdoidal crests are high. The anterior border of the orbit is above the anterior edge of  $M^3$ . The postglenoid process is relatively narrow but thick anteroposteriorly. The orbital foramina are obliterated by crushing in A.M.N.H. No. 21595 and are not preserved in any other specimen of *Lophialetes*. The foramen ovale is situated 8 mm. in front of the middle lacerate foramen, just anterior to the front of the postglenoid process. The postglenoid foramen appears to have been confluent with the middle lacerate foramen. As in all other known tapiroids, there is no evidence of an inflated tympanic bulla. The skull

length in A.M.N.H. No. 21595, from the anterior tip of the premaxilla to the anterior edge of the foramen magnum, is about 165 mm.; the maximum width across the zygomatic arches is about 80 mm.

The major cranial specialization apparent in the skull of *Lophialetes* is the retraction of the nasal incision. As can be seen in A.M.N.H. Nos. 19163, 20144, and 21592, the nasal incision extends posteriorly to a point above  $M^1$ , with the infraorbital canal opening above  $P^4$ . The incision is relatively narrower, with the maxilla less excavated, in *Lophialetes* than in the helaletids *Helaletes* and *Colodon*. Also, there is no evidence of a broad groove in the ascending process of the maxilla, between the orbit and the nasal incision, which in tapiroids and advanced helaletids accommodates the extended nasal diverticulum. None of the *Lophialetes* specimens includes the nasal bones, so it is not known whether they extended to the front of the premaxillae or were shortened. Without this evidence it is not possible to say whether or not *Lophialetes* had a proboscis. The relatively narrow nasal incision and lack of a groove for the nasal diverticulum suggest that it did not. If *Lophialetes* did possess a proboscis, it would have been developed independently from that of helaletids and tapiroids, since lophialetids were separated from helaletids before the appearance of that organ. Whether or not a proboscis was independently derived in both helaletids and lophialetids, the enlargement of the nasal incision is still an example of convergence between the two groups.

Evidence of nasal incision retraction in juvenile *Lophialetes* skulls is seen in A.M.N.H. Nos. 21551, 26116, and 26121 (all Ulan Shireh *Lophialetes expeditus*?), in which the notch extends back almost to a point over  $DP^4$ , with the infraorbital canal opening above  $DP^3$ .

The skull of *Schlosseria* (best preserved in several specimens from the Camp Margetts area) apparently was similar to that of *Lophialetes* except that the nasal incision does not appear to have been so extensively expanded. Matthew and Granger (1926, p. 3) stated that the nasal incision in *Schlosseria*

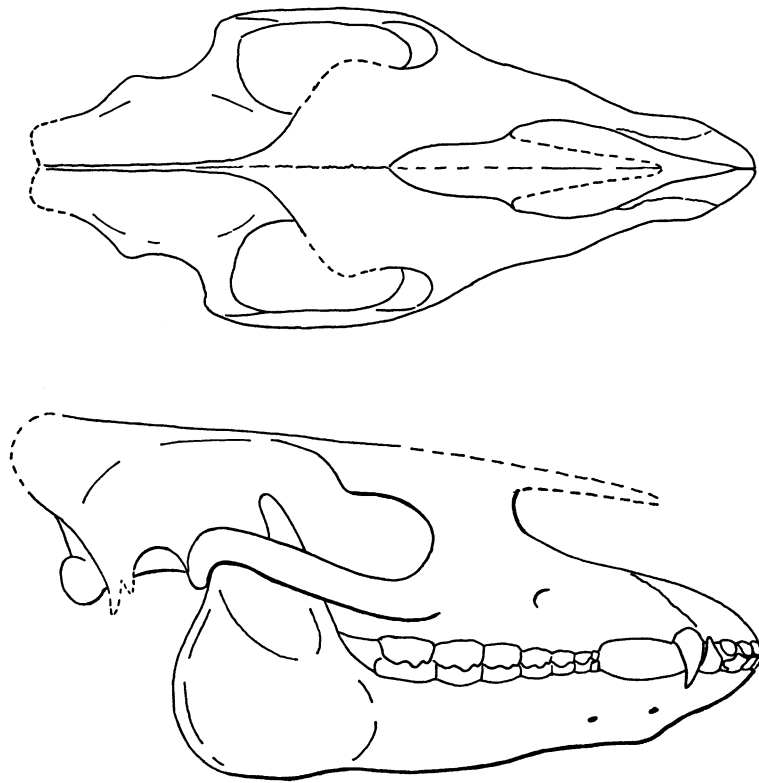


FIG. 23. *Lophialetes expeditus?*, skull and mandible, restored from A.M.N.H. No. 21595. Above: Dorsal view. Below: Lateral view  $\times \frac{1}{2}$ .

*magister* was extended far backward, as in *Heleates*. However, further preparation of the most complete cranial fragment of *S. magister* (A.M.N.H. No. 20241) showed that the preserved dorsal edge of the maxilla in that specimen is not the smooth ventral border of the nasal incision, but rather an irregular broken surface, indicating that the maxilla extended farther dorsally than is shown in Matthew and Granger's illustration (p. 1, fig. 1). The full dorsal extent of the maxilla is not known. However, the infraorbital canal in *Schlosseria* opens above  $P^{2-3}$ , which suggests a shorter nasal incision than in *Lophialetes* in which the infraorbital canal opens above  $P^4$ . One of the more advanced specimens of *Schlosseria* from the Camp Margetts area (A.M.N.H. No. 81756) preserves enough of the maxilla to show that the nasal incision extended back at least to  $P^1$ .

Several juvenile skulls of *Schlosseria* from the Camp Margetts area (A.M.N.H. Nos.

81761, 81766, 81767) preserve the facial region, but the bones are so shattered that it is not possible to determine the boundaries of the nasal incision. At first glance the nasals seem to have been in contact with the maxillae at least as far forward as  $P^1$ , but close examination suggests the possibility that in life they were separated by a narrow nasal incision which was closed during fossilization by downward crushing of the nasals. The infraorbital canal opens above  $DP^{2-3}$ , a position that is slightly more anterior than in *Lophialetes*, again suggesting that the nasal incision was not so long in *Schlosseria* as in *Lophialetes*.

The mandible of *Lophialetes* is known from several exceptionally well-preserved specimens in the Ulan Shireh *Lophialetes expeditus?* collection, the best of which are A.M.N.H. Nos. 26108 and 26111. The horizontal ramus is relatively long and slender and tapers very slightly from  $M_3$  to  $P_1$ . Its

ventral border is almost flat, with a slight convexity under the molars. The symphysis is short, terminating midway between the canine and first premolar, in contrast to the condition in most other tapiroids, in which it extends for at least the full length of the diastema. The posterior face of the symphysis is deep and vertical, meeting the dorsal surface at a right angle, and bears a relatively deep depression for the genio-hyoid muscles, with a low pointed median tubercle at the posteroventral edge. Two relatively large mental foramina are usually present on each side, one under  $P_{2-3}$ , and the other under the diastema, between  $P_1$  and  $C_1$ .

The angle is broadly convex and only slightly extended below the horizontal ramus and behind the condyle. The ascending ramus tapers sharply dorsally, with the anterior border sloping posterodorsally about 30 degrees from the vertical and the posterior border inclined anterodorsally about 20 degrees from the vertical. The coronoid process is relatively high and narrow, oriented posterodorsally in line with the anterior edge of the ascending ramus, and only very slightly curved posteriorly. The condyle is situated high above the tooth row and inclined medioventrally at about 30 degrees from the horizontal.

Juvenile mandibles of *Lophialetes*, such as A.M.N.H. No. 81663, differ in proportions from those of the adults mainly in having a relatively more slender horizontal ramus.

The mandible of *Lophialetes* differs from that of *Heptodon* in having a more broadly rounded, less posteriorly projecting angle, a narrower, posteriorly inclined (instead of vertical) coronoid process, and a shorter symphyseal region.

Mandibles of *Schlosseria* (preserved best in the Camp Margetts sample) are similar to those of *Lophialetes*, differing only in the following features: symphyseal region and diastema slightly shorter, and mental foramina usually smaller and more numerous.

#### POSTCRANIAL SKELETON

The following description of lophialetid postcranial anatomy is based almost entirely on *Lophialetes*. Except for the manus and pes, there are no postcranial remains definitely associated with dentitions of this genus, but

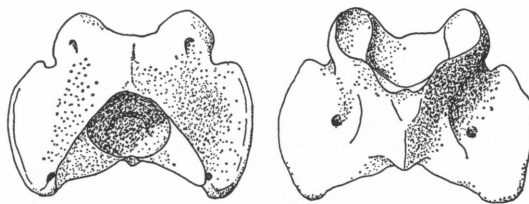


FIG. 24. Atlas, A.M.N.H. No. 19176, tentatively assigned to *Lophialetes expeditus*. Left: Dorsal view. Right: Ventral view.  $\times \frac{3}{4}$ .

several small perissodactyl skeletal elements from the Irdin Manha beds may be assigned to it on the basis of relative abundance and size. Known postcranial remains of *Schlosseria* include distal ends of radius and tibia, patella, and virtually complete manus and pes; these are so similar to corresponding bones in *Lophialetes* that additional detailed descriptions are unnecessary, and only the differences are here noted.

**VERTEBRAE:** An isolated atlas (A.M.N.H. No. 19176; see fig. 24) is of the right size to belong to *Lophialetes expeditus*. It is relatively narrower than that of *Heptodon* but resembles it in having the alar groove open; in *Tapirus* and other advanced perissodactyls that passage is bridged over by anterior growth of the transverse process. The vertebral artery entered at the dorsal edge of the posterior face of the atlas and was enclosed in a short vertebralarterial canal before passing out on the ventral side of the transverse process.

**SCAPULA:** The shoulder blade (see fig. 25) is

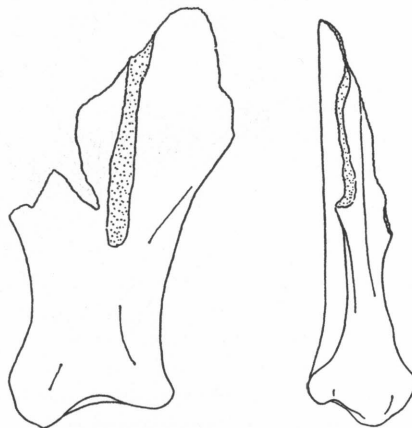


FIG. 25. Left scapula of *Lophialetes expeditus*, A.M.N.H. No. 81711b. Left: Lateral view. Right: Anterior view.  $\times \frac{3}{4}$ .

represented by three incomplete specimens (A.M.N.H. Nos. 81711a–81711c). The neck is relatively long and slender, with no coraco-scapular notch. A prominent coracoid process extends medially from the tuber scapulae. The spine does not appear to have extended quite so far ventrally down the neck as in early and middle Eocene tapiroids such as *Heptodon* and *Helalestes*.

**HUMERUS:** The humerus (see fig. 26) is known from about a dozen incomplete specimens from the Irдин Manha beds (A.M.N.H. No. 81712) and Ulan Shireh beds (A.M.N.H. Nos. 81702a, 81702b). Only one specimen (A.M.N.H. No. 81702a; *L. expeditus*?) preserves the proximal half of the humerus, but it is crushed and lacks the proximal tuberosities. It is about 125 mm. long and has a low deltoid ridge, with the deltoid tuberosity about one-quarter of the way down the shaft. The shaft is relatively long and slender, with

the nutrient foramen situated almost at the middle of the posterior side. The supinator crest is not much expanded laterally and rapidly dwindles distally. The coronoid fossa is broad and extremely shallow; the olecranon fossa is somewhat narrower but still relatively broad and low, and much deeper. A thick bony partition separates the two fossae. The trochlea has a pronounced constriction in the middle, giving it an hourglass shape. It is almost symmetrical, since the intercondylar ridge is low and broad, and there is almost no lateral condyle. Both medial and lateral epicondyles are low, but the posterior edge of the lateral epicondyle is extended unusually far distally, and forms a decidedly larger protuberance than occurs in *Heptodon* or *Tapirus*.

A lateral condyle is usually present on humeral trochlea of cursorial perissodactyls, presumably to stabilize fore-and-aft movement at the elbow joint. The absence of a lateral condyle in *Lophialetes* is somewhat surprising, for other skeletal modifications, such as the reduction of lateral digits and the elongation of metapodials, suggest a cursorial habitus. However, the deep median groove of the trochlea accommodated a ridge on the humeral facet of the radius and would have restricted lateral movement at the elbow joint, thus serving the same function.

The large posterodistal swelling on the lateral epicondyle suggests an unusually strong extensor carpi ulnaris, a muscle that in recent tapirs inserts onto the proximal end of the fifth metacarpal and acts to flex that digit. Since the fifth metacarpal was reduced to a tiny vestige in *Lophialetes*, it is somewhat surprising to find evidence for a large extensor carpi ulnaris in that genus. In recent horses, in which the fifth metacarpal has completely disappeared, the extensor carpi ulnaris has shifted insertion onto the pisiform and fourth metacarpal and acts to flex the carpal joint and extend the elbow. Presumably it served a similar function in *Lophialetes*, which has a relatively large pisiform.

**RADIUS:** No remains of this bone have been identified in the Irдин Manha collection, but A.M.N.H. No. 22091 (*Lophialetes expeditus*?) from the Ulan Shireh beds includes the distal and proximal ends of a radius which provide some knowledge of that bone. The humeral

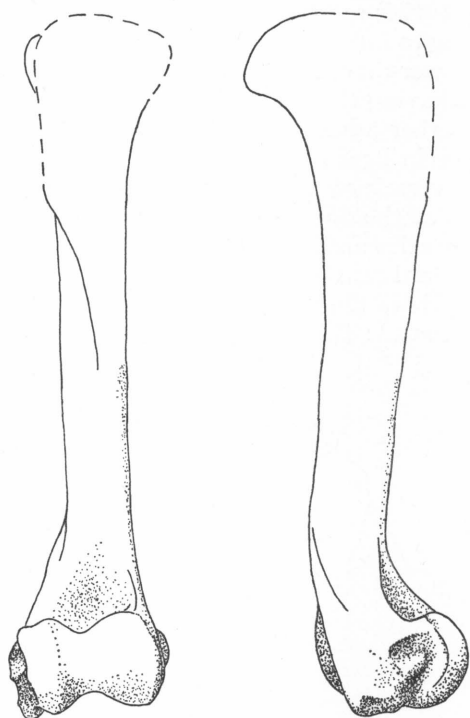


FIG. 26. Right humerus of *Lophialetes*. Distal half from A.M.N.H. No. 81712 (*L. expeditus*); proximal half from A.M.N.H. No. 81702a (*L. expeditus*?). Broken lines indicate extent of bone preserved and are not intended as a restoration. Left: Anterior view. Right: Lateral view.  $\times \frac{3}{4}$ .

facet is relatively broad lateromedially and narrow anteroposteriorly and is divided into two approximately equal, rounded concavities. At the distal end the lunar and scaphoid facets are separated by a sharp ridge; both are anteriorly concave and posteriorly convex. On the medial side the tuberosity for the attachment of the medial ligament is unusually prominent.

**ULNA:** The ulna is represented only by two proximal ends (A.M.N.H. Nos. 81716a, 81716b). The olecranon process has a vertical anterior edge and a relatively small dorsal tuberosity for insertion of the long and medial heads of the triceps.

**CARPUS:** About 20 isolated carpal bones from the Irdin Manha beds (A.M.N.H. Nos. 81704–81708) and 50 from the Ulan Shireh beds (A.M.N.H. Nos. 22091, 81697–81701) provide complete knowledge of the osteology of the carpus of *Lophialetes* (see figs. 27, 28).

The scaphoid is relatively narrow, low, and deep (anteroposteriorly), with a promi-

nent posterior process. The proximal surface is almost completely covered by a large, roughly circular facet for the radius, with the anterolateral half raised into a low convexity, and the posteromedial corner slightly concave. On the lateral side there are narrow proximal and distal facets for the lunar. The distal surface bears three long, narrow, concave facets, the central and lateral ones for the magnum and the medial one for the trapezoid. There is no evidence of a facet for the trapezium.

The lunar is relatively low and wide in anterior view and rests almost entirely on the unciform. The facet for the radius is broad and gently convex anteriorly and extends posteriorly as a narrow, slightly concave strip. On the medial side there are long proximal and small central facets for the scaphoid and a large, concave, slightly latero-distally inclined, distal facet for the high hump of the magnum. On the lateral side there are proximal and distal facets for the

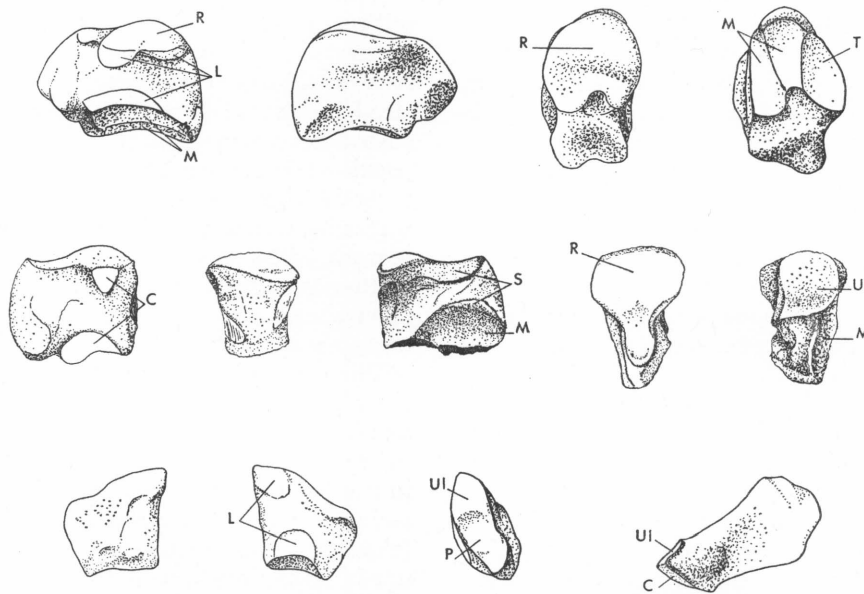


FIG. 27. Proximal carpals of *Lophialetes*. Top row: Scaphoid, A.M.N.H. No. 81704, in (from left to right) lateral, medial, proximal, and distal views. Middle row: Lunar, A.M.N.H. No. 81705, in lateral, anterior, medial, proximal, and distal views. Bottom row: Cuneiform, A.M.N.H. No. 22091, in lateral, medial, and proximal views, and pisiform, A.M.N.H. No. 22091, in medial view. Letters refer to bones with which the facets indicated articulated. All  $\times 1.25$ .

**Abbreviations:** C, cuneiform; L, lunar; M, magnum; P, pisiform; R, radius; S, scaphoid; T, trapezoid; U, unciform; UI, ulna.

cuneiform. The entire anterior half of the distal surface is taken up by an anteroposteriorly concave facet for the unciform.

The cuneiform has a relatively small, slightly convex, ulna facet and a relatively large, slightly concave, pisiform facet. Medially there is a small, flat, proximal facet and a large convex distal facet for the lunar.

The pisiform is relatively large and has a large cuneiform facet and small ulna facet which converge at an angle slightly less than 90 degrees. The neck of the pisiform is flat and thin, but distally the bone expands into a prominent club-like process.

The trapezoid and trapezium are preserved only in A.M.N.H. No. 22091. The trapezium is the most unusual bone in the carpus of *Lophialetes*. It is a long, slightly flattened, somewhat irregularly shaped rod, with a prominent facet for the trapezoid at one end and a small blunt process at the other end. When properly articulated with the trapezoid, it projects posteriorly, with the long axis approximately horizontal. In the early Eocene tapiroid *Heptodon*, and in all other tapiroids in which the carpus is known, the trapezium is a small, flat, disc-shaped bone which lies flat against the trapezoid. Evidence that the rod-shaped bone described above is the trapezium includes the perfect match of its irregularly shaped articular facet with the trapezium facet of the trapezoid, and its resemblance to the trapezium in the articulated carpus of the type of *Schlosseria magister* (A.M.N.H. No. 20241). What appears to be an elongation of the trapezium in *Lophialetes* may be the result of fusion with a vestige of the first metacarpal. An analogous situation occurs in the tarsus of rhinocerotoids in which the vestige of the first metatarsal fuses with the entocuneiform (Radinsky, 1963b). Presumably the elongate process of the trapezium served for attachment of one or more of the short digital flexors.

The trapezoid is roughly square in antero-medial view, and triangular in horizontal section, with a short base posteriorly and converging to an apex anteriorly. The proximal surface is occupied by a long, anteroposteriorly convex facet for the scaphoid; and the distal face, by a concave facet for the second metacarpal. On the medial side there is a small proximal facet and a large distal facet

for the magnum. Posteriorly there is a large slightly concave facet for the trapezium.

The magnum has a small, relatively low and wide anterior face, a high, sharp-edged, mediolaterally compressed, dorsal hump, and a very large, proximally flattened, posterior process. The facet for the scaphoid is in two parts, an anterior one which curves anteriorly onto the vertical anterior face of the magnum, and a posterior one which is mainly vertical, occupying the medial half of the thin central hump. The medial side also has small central and distal facets for the trapezoid and a thin mediolateral strip for the lateral edge of the second metacarpal. The lunar facet is latero-distally inclined and confined to the lateral side of the central hump. The unciform facet is high, covering the anterior edge of the lateral side. A concave facet below the lateral side of the posterior process articulated with the posterior process of the fourth metacarpal. On the distal surface the facet for the third metacarpal is sharply concave anteroposteriorly and slightly convex mediolaterally.

The unciform is slightly wider than high, with a relatively long, mediolaterally compressed, posterior process. The proximal surface is divided into approximately equal-sized lunar and cuneiform facets. Along the smoothly curving mediolateral edge there is a proximal facet for the magnum, a central facet for the proximolateral edge of the third metacarpal, and a distal facet for the fourth metacarpal. The same articular strip extends farther proximolaterally and posteriorly to form a concave facet for the vestigial fifth metacarpal.

The carpus of *Schlosseria*, figured by Matthew and Granger (1926, p. 2, figs. 3-4, at one-half size, not natural size as stated in the figure legend), differs from that of *Lophialetes* in the following features: scaphoid (of *Schlosseria*) with shorter anterior magnum facet (the central one of the three distal facets); ulnar facet of cuneiform smaller relative to pisiform facet; trapezoid relatively shorter and wider; proximal hump of magnum shorter (anteroposteriorly), with steeper posterior slope and shorter anterior scaphoid facet. The differences in scaphoid and magnum are the most readily recognizable ones.

The trapezium is preserved in two specimens of *Schlosseria magister* from the Ar-



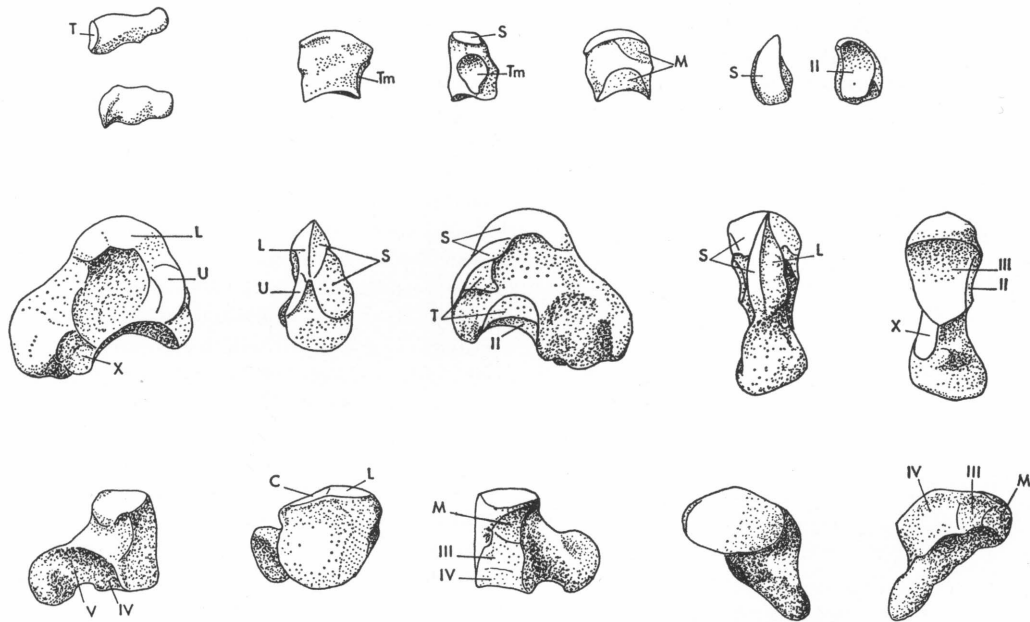


FIG. 28. Distal carpals of *Lophialetes*. Top row: From left to right: trapezium, A.M.N.H. No. 22091, in proximal (above) and medial (below) views; trapezoid, A.M.N.H. No. 22091, in medial, posterior, lateral, proximal, and distal views. Middle row: Magnum, A.M.N.H. No. 81707, in lateral, anterior, medial, proximal, and distal views. Bottom row: Unciform, A.M.N.H. No. 81708, in lateral, anterior, medial, proximal, and distal views. All  $\times 1.25$ .

Abbreviations: C, cuneiform; L, lunar; M, magnum; S, scaphoid; T, trapezoid; Tm, trapezium; U, unciform; X, facet for posterior process of fourth metacarpal; II, III, IV, and V, second, third, fourth, and fifth metacarpals.

shanto beds (A.M.N.H. Nos. 20241 and 81840). In the former (the type specimen), the trapezium is relatively long, as in *Lophialetes*, although it has a relatively smaller posterior process and may be somewhat flatter than that in the latter genus. In A.M.N.H. No. 81840, on the other hand, the trapezium is flat and disclike, as in most other tapiroids. Also, in the latter specimen the scaphoid is relatively shorter and higher than that in most other *Schlosseria* specimens. At this point not enough is known about the possible range of intraspecific variation in carpal bones of these tapiroids to indicate whether or not more than one species is represented.

**METACARPALS:** The metacarpus of *Lophialetes* (see fig. 29) is relatively extremely long and thin, with the lateral metacarpals reduced relative to the central one, and the fifth metacarpal reduced to a tiny vestige. This degree of specialization was rarely attained in other tapiroid lineages; besides

*Schlosseria*, the deperetellid *Deperetella* and possibly also the helaletid *Colodon* are the only other tapiroids known to have had a tridactyl manus. The three functional metacarpals are long and slender, with the central one slightly longer and wider than the lateral ones. Two complete third metacarpals of *Lophialetes expeditus* from the Irдин Manha beds average 92 mm. long and 10 mm. wide at the distal articulation. There are no complete lateral metacarpals of *L. expeditus*, but a second and a fourth metacarpal of the Ulan Shireh *L. expeditus*? (A.M.N.H. Nos. 81702c, 81702d), a form slightly smaller than the type of *L. expeditus*, measure 79 mm. long and 7 mm. wide across the distal end.

The first metacarpal is not present, unless as the posterior process of the trapezium. The second metacarpal has a triangular, low, proximal facet for the trapezoid and thin lateral facets for the magnum and third metacarpal. The shaft is extremely flat and thin

and bears a roughened strip along most of its length, indicating that it was bound close against the central metacarpal.

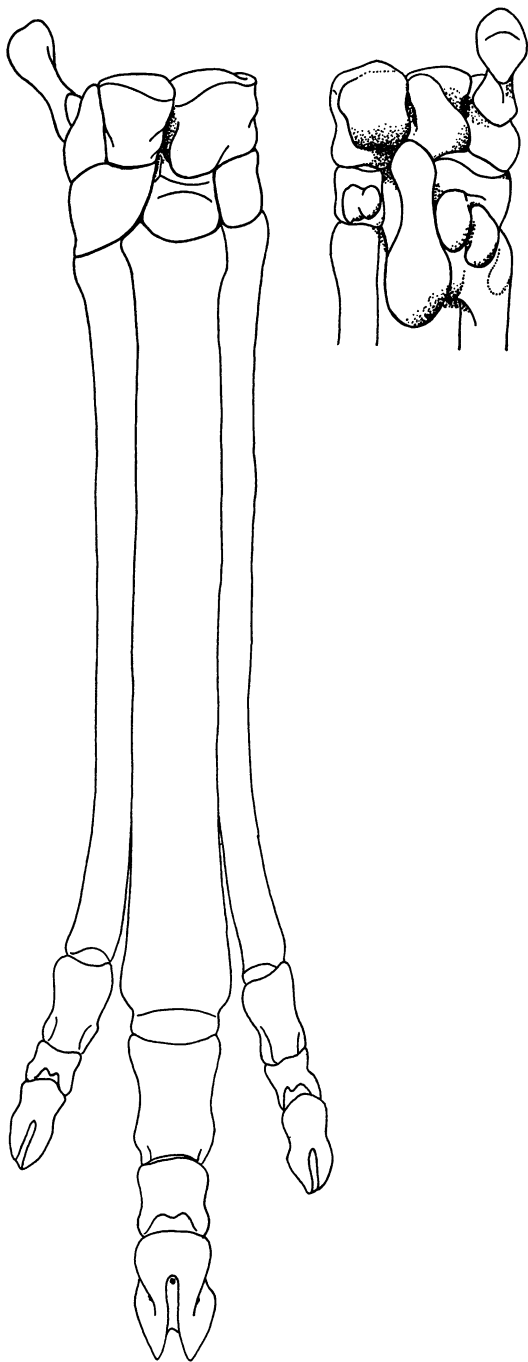


FIG. 29. Right front foot of *Lophialetes*, composite based on several specimens of *L. expeditus* and *L. expeditus*?. Right: Posterior view of carpus.  $\times 1.25$ .

The third metacarpal has a large, sharply anteroposteriorly convex, slightly medio-laterally concave, proximal facet for the magnum, and a smaller, laterodistally inclined, triangular facet for the unciform. On the medial side there is a thin facet for the second metacarpal, and on the lateral side, immediately below the unciform facet, is a large concavity with a small facet for the medial edge of the head of the fourth metacarpal. The shaft of the third metacarpal is triangular in cross section proximally (with a flat anterior face and convergent postero-medial and posterolateral sides) and flat distally. The facet for the first phalanx is evenly convex and has a sharp median keel on the posterior half. Two deep pits on the posterior face immediately above the phalangeal facet accommodated the proximal ends of the sesamoids. On each side of the distal condyle a deep pit surmounted by a prominent swelling marks the attachment of deep and superficial layers, respectively, of the collateral ligament. These features are present on the lateral metacarpals but are more transversely compressed, asymmetrical, and less pronounced.

The fourth metacarpal has narrow anterior and posterior medial facets for the third metacarpal, a large, triangular, saddle-shaped, proximal facet for the unciform, and a small, posterior, lateral facet for the vestigial fifth metacarpal. There is a prominent posterior process which in the wrist extends postero-medially under the posterior projection of the unciform and bears a large, slightly convex, posteromedially oriented facet for articulation with a concave facet on the posterior process of the magnum. The shaft of the fourth metacarpal is flat and slender, as is that of the second metacarpal.

The fifth metacarpal (preserved in A.M.N.H. No. 22091) is reduced to a short triangular nodule with a flat medial side and convex lateral (outer) surface. The unciform facet is large and shallow, and posteriorly on the medial side there is a small facet for the fourth metacarpal. The bone tapers distally and terminates in a blunt point.

The manus of *Schlosseria*, like that of *Lophialetes*, was functionally tridactyl, but the metacarpals of the former were relatively not so long and thin as those of the latter.

**PHALANGES:** The proximal phalanx of the median digit of *Lophialetes* has a shallow,

concave, metacarpal facet, with the posterior edge uplifted and cut by a median notch for the metacarpal keel. Massive prominences on each side of the median notch mark the attachment areas of collateral and possibly annular ligaments; the raised area between them served for attachment of the cruciate sesamoidean ligaments. A small tuberosity on the left and right sides of the posterior face of the shaft just above the distal articulation marks the attachment area of the tendo perforatus (superficial digital flexor tendon). The convex distal condyle faces posterodistally and is divided by a shallow median groove. At the distal end of the lateral and medial sides a shallow pit surmounted by a rough raised area indicates the attachment area of the collateral ligament and suspensory ligament of the navicular sesamoid.

The second phalanx is short, with a shallow, concave, proximal facet and a long, sharply convex, distal articular surface which extends up onto anterior and posterior sides. The distal facet is narrower anteriorly than posteriorly and is divided by a prominent median groove. A deep broad pit on each side of the distal condyle marks the attachment of strong collateral ligaments.

The ungual phalanx is relatively long, deep, and narrow, with a slight constriction below the proximal articulation and a wide, deep median fissure. On the proximal part of the posterior (volar) surface a prominent wide swelling marks the insertion of the tendo perforans (deep digital flexor tendon). On the lateral and medial sides just below the articular surface a shallow depression marks the attachment of the collateral ligament. Two large foramina on the posterior side between the tendon perforans eminence and the proximal articulation served for the entrance of the digital arteries into the ungual (into the semilunar canal); three smaller foramina on the anterior (dorsal) face, one at the proximal end of the medial fissure and one at each side, mark exits of branches of the terminal arch of the digital arteries. Phalanges of the second and fourth digits are similar to those of the median digit except that they are smaller, asymmetrical, and more mediolaterally compressed.

**DISCUSSION:** The manus of *Lophialetes* differs from that of *Heptodon* primarily in the following features: lunar, magnum, and unciform

form relatively lower and wider in anterior view; scaphoid-magnum facets narrower and longer, extending onto anterior face of magnum, allowing the scaphoid to rotate antero-distally over the magnum; anterior lunar-magnum facet lost and posterior one more vertical, so that the lunar rests less on the magnum (and more on the unciform); pisiform (and pisiform-cuneiform contact) relatively larger; magnum with narrower, more anteriorly situated, dorsal hump and more sharply concave facet for the third metacarpal; unciform-magnum facet higher and more extensive; unciform with much longer posterior process and less deep (anteroposteriorly) facet for the fourth metacarpal; trapezoid with convex instead of saddle-shaped scaphoid facet and slightly smaller posterior extension; trapezium with large, rodlike, posterior process; fourth metacarpal with posterior process which braces against the magnum; fifth metacarpal reduced to a tiny vestige and remaining metacarpals longer and narrower, with lateral metacarpals narrower relative to the central one; phalanges relatively longer and narrower; unguals deeper and with longer median fissures.

The modifications in scaphoid-trapezoid, scaphoid-magnum, and lunar-magnum articulations suggest that the carpus could have been flexed more dorsally in *Lophialetes* than in *Heptodon*, and are probably correlated with the relatively larger pisiform and more powerful extensor carpi ulnaris (a muscle that extended from humerus to pisiform and served to flex the carpal joint). The long posterior process of the unciform suggests more powerful flexors for the lateral side of the manus and is probably correlated with the development of a process to brace the fourth metacarpal against the magnum and also the larger unciform-magnum facet. On the medial side of the wrist the large posterior extension of the trapezium suggests stronger flexors for the medial side of the manus than were present in *Heptodon*, which may be correlated with the unusually prominent tuberosity for the medial ligament seen on the distal end of the radius. All these features suggest increased emphasis on flexion in the manus of *Lophialetes*. This agrees with the reduction of lateral metacarpals and the relatively great increase in length of the metacarpus, which indicate specialization for running. Addi-

tional suggestions of cursorial habitus are the reduction of the scapular spine, the relatively high position of the deltoid tuberosity on the humerus, and the relatively small size of the distal end of the ulna (indicated by the small ulnar facet on the cuneiform). The only feature in the known anatomy of the fore limb of *Lophialetes* that does not agree with the general picture of cursorial specialization is the lack of a lateral condyle on the distal end of the humerus to restrict lateral movement at the elbow joint. Presumably the same function was achieved by the deep median constriction of the humeral trochlea, which accommodated a ridge on the humeral facet of the radius. It would, of course, be extremely interesting to know the ratio of radius to humerus length in *Lophialetes*; judged from the metacarpals, it must have been relatively high.

**INNOMINATE:** The pelvic girdle is not known for *Lophialetes* or *Schlosseria*.

**FEMUR:** The femur is known only from four distal ends (A.M.N.H. Nos. 81710a–81710d), including little more than distal trochlea and condyles. The trochlea is relatively wide and asymmetrical, and the intercondyloid fossa is relatively shallow. Deep pits on the lateral and medial epicondyles mark strong ligament attachments, and an extremely deep pit on the anterodistal corner of the lateral epicondyle indicates a powerful extensor digitalis longus or peroneus tertius, or both.

**PATELLA:** The patella of *Lophialetes* is known only from the collection from the Camp Margetts area (A.M.N.H. No. 81790). It is relatively long, flat, and roughly quadrangular in outline. The anterior face is relatively smooth; the posterior face is divided by a broad low ridge into two shallow subequal grooves for the femoral trochlea.

**TIBIA:** This bone is represented by one proximal epiphysis and six distal ends (A.M.N.H. Nos. 81713a–81713g). On the proximal epiphysis the lateral tubercle of the spine is higher than the medial one. At the distal end, the articular grooves for the astragalus are relatively deep and narrow. A smooth area on the medial malleolus marks the attachment of the medial ligaments. Posterior to the medial malleolus there is the barest suggestion of a groove for the tendon of the flexor digitalis longus. On the lateral side

there is a large smooth facet for the medial side of the distal end of the fibula.

**FIBULA:** The fibula is known only from one distal fragment associated with the distal end of a tibia of *Lophialetes expeditus*? from the Shara Murun region (A.M.N.H. No. 22091A). Although the shaft of the fibula must have been extremely thin, the distal tibial articulation is a smooth facet and shows no signs of fusion. On the lateral side a swollen rough area marks the attachment of the lateral ligaments, and posterolaterally a barely distinct groove marks the path of the tendon of the peroneus brevis (lateral digital extensor). The distal end of the fibula is relatively smaller in *Lophialetes* than in *Heptodon*.

**TARSUS (FIGS. 30, 31):** About 235 isolated tarsal bones from the Irдин Manha beds may be assigned to *Lophialetes*. These include 125 astragali (A.M.N.H. No. 81715), 90 calcanea (A.M.N.H. No. 81714), and only 20 other tarsal elements (A.M.N.H. No. 81709). The great preponderance of astragali and calcanea over the other tarsals (and carpals) in the Irдин Manha collection is probably explained by collecting bias. The few tarsal elements not represented in the Irдин Manha collection are present in the *Lophialetes* sample from the Shara Murun region.

The astragalus is relatively high and narrow, averaging 23.6 mm. in proximodistal height and 13.9 mm. in distal width in *Lophialetes expeditus*. The trochlea is inclined at an angle of about 15 degrees from the neck and has a moderately deep but still broadly open median groove. The condyles are about equal in elevation; the medial one is more acute, extends distally almost to the edge of the navicular facet, and at its proximal end flares proximomedially into a backstop for the medial malleolus of the tibia. On the posterior (plantar) surface the two major planes of the proximal calcaneal facet meet at a rounded concave right angle; a short narrow strip of this facet continues distally along the lateral edge perpendicular to the adjacent face. The sustentacular facet is separated from the proximal facet by a deep narrow groove and is relatively long and narrow and very slightly convex proximodistally and concave mediolaterally. The distal calcaneal facet is a long, slightly convex, bilobed strip oriented at about 45 degrees from the plane of the sus-

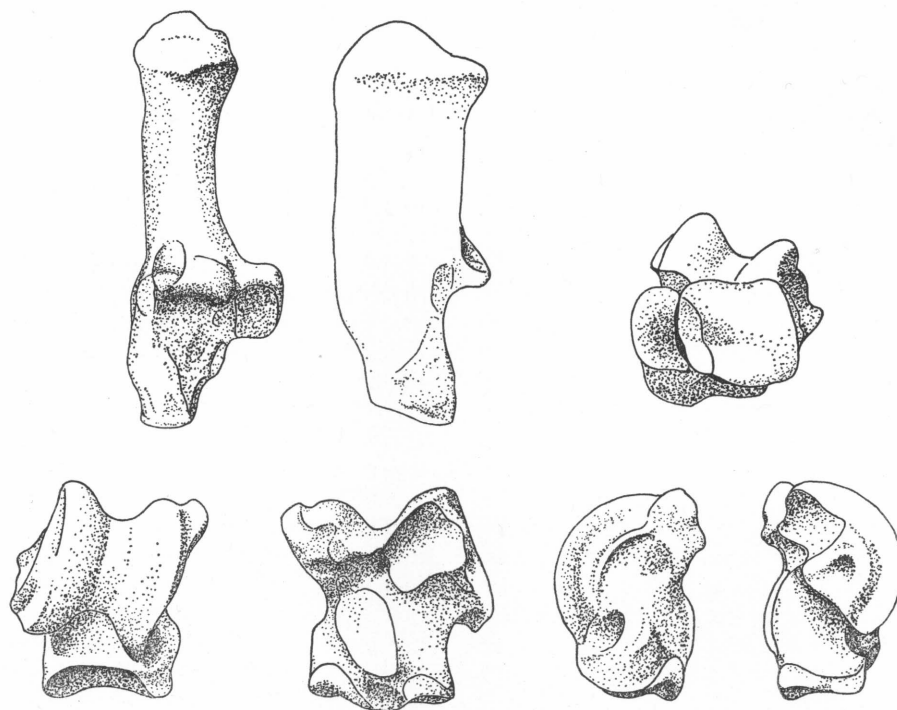


FIG. 30. Astragalus and calcaneum of *Lophialetes expeditus*. Top row: Calcaneum, A.M.N.H. No. 81714, in anterior and lateral views, and distal view of calcaneum and astragalus. Bottom row: Astragalus, A.M.N.H. No. 81715, in anterior, posterior, medial, and lateral views. All  $\times 1.25$ .

tentacular facet. On the distal end of the astragalus, the navicular facet is approximately square in outline, moderately convex anteroposteriorly and very slightly concave mediolaterally. A barely noticeable groove extends in from the lateral edge to accommodate a low ridge on the navicular which presumably served to restrict movement between the astragalus and the navicular. The cuboid facet is a laterodistally facing narrow strip which converges to a point before reaching the anterior edge; thus no astragalus-cuboid contact is visible in anterior view. A deep broad pit on the lateral side of the trochlea marks the insertion of the short lateral ligament; on the medial side a shallow proximal pit indicates the attachment area of a branch of the short medial ligament, and a distal tuberosity marks the insertion of the dorsal ligament.

The calcaneum is relatively long and thin, with the lateral astragalar facet slightly closer to the distal than to the proximal end.

The proximal half is mediolaterally compressed and terminates proximally in a moderately expanded tuber calcis (for attachment of the gastrocnemius and superficial digital flexor tendons). Immediately above the lateral astragalar facet there is a prominent pit which accommodated the posterior corner of the distal end of the fibula in extreme extension of the tarsus. The lateral astragalar facet consists of two major planes which meet at a rounded convex right angle, and a short, narrow, distal strip which extends down the lateral edge. The sustentaculum is relatively small and does not extend far medially; it bears a relatively long and narrow and very slightly concave astragalar facet on its anterior face. A broad shallow groove at the junction of the sustentaculum with the body of the calcaneum marks the passage of the deep flexor tendon. The distal astragalar facet is a long, slightly concave, bilobed strip which usually terminates before reaching the sustentaculum. The distal end of the calcaneum

is shorter anteroposteriorly than the rest of the body and bears a relatively narrow, slightly anteriorly convex and posteriorly concave, cuboid facet. On the lateral side of the calcaneum a smooth excavated area next to the lateral astragalar articulation marks the insertion of the short lateral ligament; a rough raised area on the distal end, the attachment of the long lateral ligament. The posterior (plantar) edge of the calcaneum, from tuber calcis to sustentaculum, is roughened, indicating the attachment area of the plantar ligament.

The cuboid is relatively high and narrow, with a saddle-shaped calcaneal facet and a narrow oblique astragalar facet which does not reach the anterior face. The medial surface bears proximally a thin, flat, anterior facet and a long, concave, posterior facet for the navicular. Below the latter is a short, mediodistally facing facet for the ectocuneiform. At the anterodistal corner are a small facet for the ectocuneiform and a laterodistally inclined facet for the third metatarsal. On the distal end, the facet for the fourth metatarsal is relatively long and narrow, anteriorly convex, and posteriorly concave. A shallow groove crosses the middle of the anterior face of the cuboid and descends pos-

teriorly on the lateral side, marking the passage of a blood vessel. The posterior tuberosity, or plantar hook, is quite prominent, although relatively narrow; it afforded attachment for the plantar ligament.

The navicular is moderately high, with the usual perissodactyl saddle-shaped astragalar articulation. Some specimens show a tiny oblique facet at the anterolateral corner for articulation with the calcaneum. On the lateral side there is a large, posterior, in some cases bilobed, facet for the cuboid. On the distal side the large facet for the ectocuneiform is sharply constricted posteriorly. Posteromedial to it are a small mesocuneiform facet and on the extreme posteromedial corner a small facet for the entocuneiform.

The ectocuneiform is about as high as the navicular, with a wide, rounded, anterior face and posteriorly converging, indented, medial and lateral sides. On the lateral face are a small proximal facet posteriorly and a large distal facet anteriorly for the cuboid, with the area between excavated. The medial face bears proximal and distal facets for the mesocuneiform and distal facets for the second metatarsal; these vary in number and size. Proximal and distal surfaces of the ectocuneiform are completely occupied by

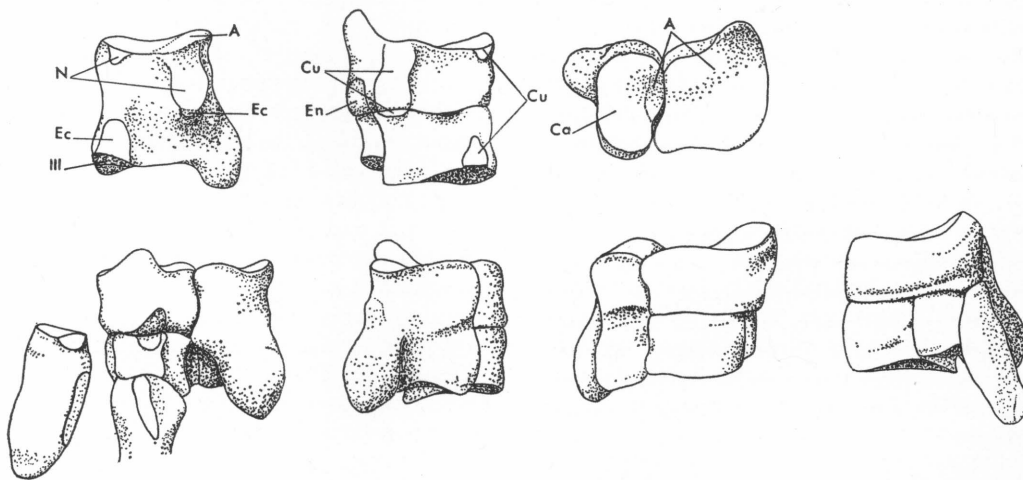


FIG. 31. Distal tarsals of *Lophialetes*, based on specimens of *L. expeditus* and *L. expeditus*?. *Top row*: Cuboid, medial view; navicular and ectocuneiform, lateral view; cuboid and navicular, proximal view. *Bottom row*: Distal tarsals in posterior, lateral, anterior, and medial views. The posterior view includes the second metatarsal and shows the entocuneiform turned over to reveal articular facets. All  $\times 1.25$ .

*Abbreviations*: A, astragalus; Ca, calcaneum; Cu, cuboid; Ec, ectocuneiform; En, entocuneiform; N, navicular; III, third metatarsal.

facets for the navicular and third metatarsal, respectively.

The mesocuneiform and entocuneiform are preserved only in the *Lophialetes* sample (A.M.N.H. No. 22091) from the Shara Murun region. The mesocuneiform is relatively high and narrow, with a rounded anteromedial face. The lateral face has four small facets, two proximal and two distal, for articulation with the ectocuneiform. Posteromedially there is a small facet for the entocuneiform.

The entocuneiform is extremely long (proximodistally), narrow, and flat. The proximal end bears a relatively large facet for the navicular and, immediately adjacent to it, on the lateral side, a small facet for the mesocuneiform. Along the anterior edge of the lateral face there is a long thin facet for the second metatarsal. Distally, the entocuneiform is slightly thickened and, although no distinct facet is evident, presumably articulated with a vestigial first metatarsal.

The only differences noted between tarsal bones of *Schlosseria* and those of *Lophialetes* are the lack of a facet for the third metacarpal on the cuboid and the slightly relatively higher navicular and ectocuneiform in *Schlosseria*. Neither of these seems particularly significant. They may be correlated with the smaller size and lighter build of *Schlosseria*.

**METATARSALS (FIG. 32):** The metatarsals, like the metacarpals, are relatively long and thin. No complete metatarsals of *Lophialetes* are preserved in the Irdin Manha collection. Two second metatarsals, apparently of *Lophialetes expeditus*?, from the Ulan Shireh beds (A.M.N.H. Nos. 81702e, 81702f), average 92 mm. long and 6 mm. wide at the distal condyle. These measurements suggest that the metatarsus was slightly longer than the metacarpus (lateral metacarpals of *Lophialetes expeditus*? average 79 mm. long). As was the case with the metacarpals, the lateral metatarsals are considerably thinner than the central one.

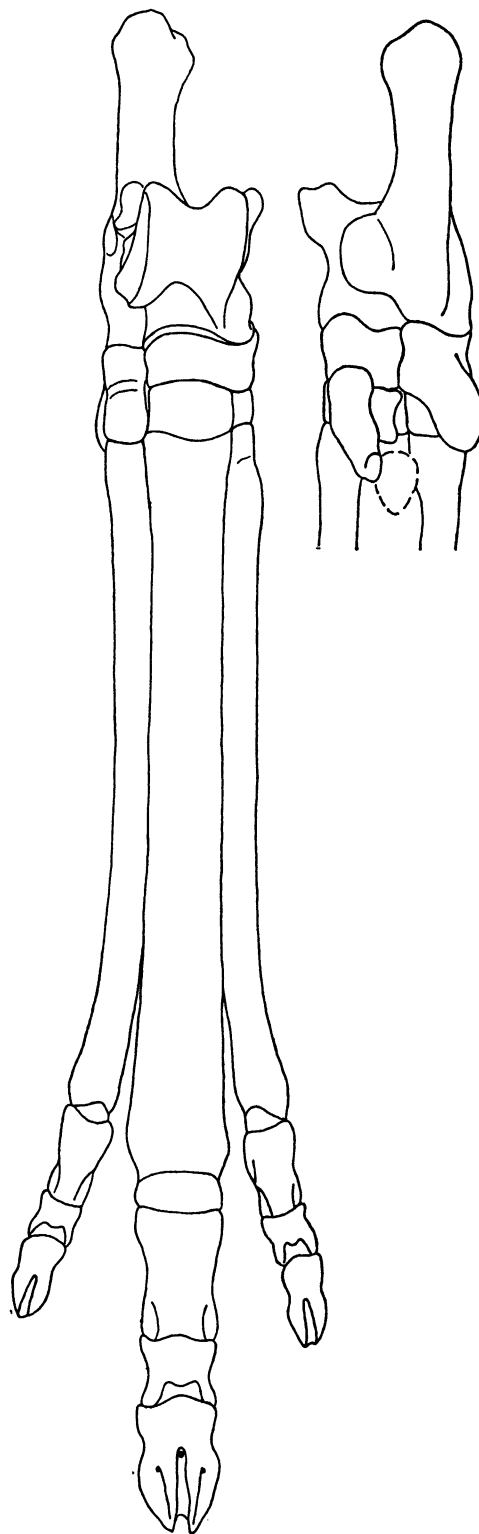


FIG. 32. Right hind foot of *Lophialetes*, composite based on several specimens of *L. expeditus* and *L. expeditus*?. Right: Posterior view of tarsus, with vestigial first metatarsal restored in broken lines.  $\times 1$ .



A vestigial first metatarsal is not preserved in the collection of *Lophialetes* foot bones, but a facet on the back of the posterior process of the third metatarsal indicates that one had been present during life. In *Schlosseria* the vestigial first metatarsal is flat and approximately triangular in posterior view, with a facet for the entocuneiform on the thin proximal edge and a facet for the third metatarsal on the thickened proximolateral corner. The vestigial first metatarsal provides attachment for the contrahentes (deep flexors of the second and fourth digits) and helps brace the tarsus (see Radinsky, 1963b).

The second metatarsal has a roughly triangular proximal facet for the mesocuneiform and an oblique, elongate, posteromedial facet for the entocuneiform. On the lateral side there are small anterior and posterior proximal facets for the ectocuneiform above and third metatarsal below. The medial side of the shaft is flat and bears a roughened area for most of its length, presumably for an interosseus ligament, which indicates that the lateral metatarsals were closely bound to the central one.

The third metatarsal has a triangular proximal facet for the ectocuneiform, with a rounded anterior edge and an indentation on the lateral side. On the medial side there are two small facets for the second metatarsal and on the lateral side a large anterior facet for the cuboid above and fourth metatarsal below, and a smaller posterior facet for the fourth metatarsal alone. The prominent posterior process of the third metatarsal bears an oblique facet for articulation with the reoriented vestige of the first metatarsal.

The fourth metatarsal has an oval, saddle-shaped, proximal facet for the cuboid and on the medial side anterior and posterior facets for the third metatarsal.

The distal ends of the metatarsals are similar to those of the metacarpals, and the phalanges of the pes are similar to those of the manus, except longer; they need no further description.

**DISCUSSION:** The pes of *Lophialetes* is similar to that of *Heptodon*, apparently differing only in the following features: astragalus (of *Lophialetes*) with slightly shorter neck and medial condyle extended proximomedially to form a stop for the medial malleolus of the

tibia; calcaneum-cuboid facet narrower; posterior process of cuboid displaced distally and slightly laterally, extending below the distal end of the cuboid; cuboid with anterior facet for third metatarsal and smaller posterior facet for ectocuneiform, so that it rests less on the ectocuneiform and more on the third metatarsal; entocuneiform much longer and the vestigial first metatarsal (known in *Schlosseria*) also lengthened distally; and lateral metatarsals thinner relative to the central one, and metatarsus relatively longer.

The entocuneiform, vestigial first metatarsal, and posterior process of the cuboid afford attachment for the digital flexors, and the distal elongation of these bones is probably correlated with the lengthening of the metatarsus. The relatively thinner lateral metatarsals, longer metatarsus, and smaller fibula indicate greater specialization for running in *Lophialetes* than in *Heptodon*.

The increase in cursorial specialization from *Heptodon* to *Lophialetes* is more evident in the manus than in the pes, possibly due to the fact that one of the basic adaptations that led to the emergence of the order Perissodactyla, specialization for running, was mainly reflected in modifications of the pes (especially the astragalus), and the biomechanical limit of specialization of the tarsus was probably attained even in the early Eocene. Thus further modifications for running (other than lengthening of the metatarsals) would be more likely to appear in the front than in the hind foot.

## FAMILY DEPERETELLIDAE

### SKULL AND MANDIBLE

The skulls of *Teleolophus* and *Deperetella* are essentially unknown. One specimen assigned to *Teleolophus medius*? (A.M.N.H. No. 26286) preserves enough of the maxilla to show that the nasal incision extended at least as far back as P<sup>2</sup> (although probably not much farther) and that the infraorbital foramen opened above P<sup>4</sup>. Several skull fragments of *Deperetella cristata* are associated with A.M.N.H. No. 20290, but most of them are too incomplete to reveal any significant details. Enough of the maxilla is preserved to show that the infraorbital canal opened above P<sup>3</sup>.

The mandible of *Teleolophus medius* is



similar in proportions to that of *Lophialetes*, with a long, slender, horizontal ramus and a relatively shallow symphysis which terminates a short distance anterior to P<sub>1</sub>. In *Teleolophus magnus* the mandible appears slightly relatively deeper than it does in *T. medius*. In both species the condyle is situated high above the tooth row and is inclined medioventrally at an angle of about 25 degrees from the horizontal. The coronoid process is small and vertical. The anterior edge of the ascending ramus is slightly less posteriorly inclined in *Teleolophus* than in *Lophialetes*.

The mandible of *Deperetella cristata* differs from that of *Teleolophus medius* in having a shorter, less procumbent symphysis and a shorter postcanine diastema.

#### POSTCRANIAL SKELETON

The following description of deperetellid postcranial anatomy is based entirely on *Deperetella cristata*, and all the specimens that are referred to belong to that species. Comparisons are made with *Lophialetes* and, where appropriate, *Tapirus*.

**VERTEBRAE:** The atlas (see fig. 33) is known from a single specimen (A.M.N.H. No. 81845) which lacks the dorsal arch and the lateral tips of the transverse processes. It is relatively longer and narrower than that of *Tapirus* and, like the atlas of *Heptodon* and *Lophialetes*, has an open alar groove. Immediately posterior to the ventral tubercle there is a large excavation which is not present in *Heptodon*, *Lophialetes*, or *Tapirus*.

The axis (see fig. 33) is represented by a single specimen (A.M.N.H. No. 81847a) which lacks the dorsal arch, transverse processes, and posterior end of the centrum. It differs from that of *Tapirus* in having a much narrower and more peglike odontoid process, more anteriorly (and less laterally) facing anterior articular facets, and a narrower and much longer body.

An incomplete cervical vertebrae (A.M.N.H. No. 81847b), probably the sixth, differs from that of *Tapirus* in being relatively longer (by at least 40%) and in having slightly convex prezygapophyseal facets. Two seventh cervical vertebrae (see fig. 34) are included in the collection of vertebrae found with limb bones and teeth of *Deperetella cristata*. One (A.M.N.H. No. 81847c) is 50

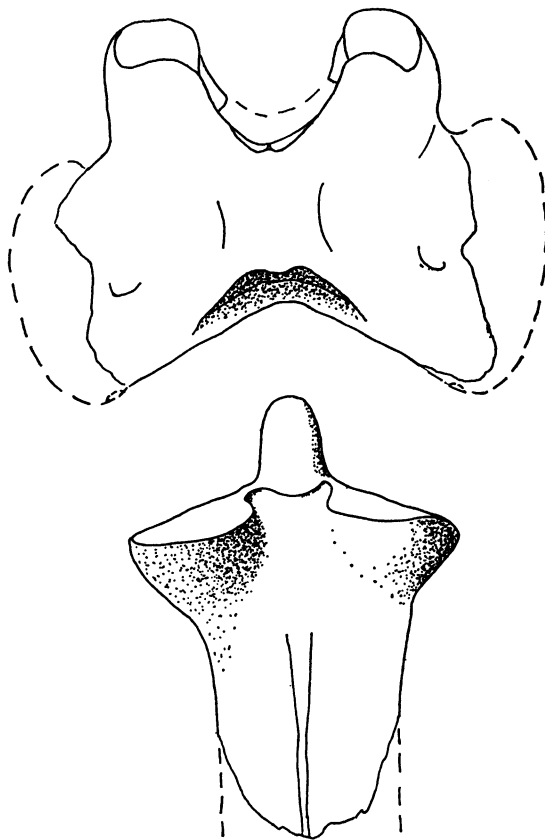


FIG. 33. Vertebrae of *Deperetella cristata*. Above: Atlas, A.M.N.H. No. 81845, in ventral view. Below: Axis, A.M.N.H. No. 81847a, in ventral view. Both  $\times \frac{1}{4}$ .

per cent longer and the other (A.M.N.H. No. 81846), 90 per cent longer, than the corresponding vertebra in *Tapirus*. The larger one is about 25 per cent longer than the smaller, and, since both are from adults, they probably represent two species, possibly from different genera. Both specimens further differ from the corresponding vertebra in *Tapirus* in having a prominent ventral keel. A.M.N.H. No. 81846 preserves the prezygapophyses and postzygapophyses. These are more elongate than those of *Tapirus*, and the pre-zygapophyseal facets are slightly convex instead of planoconcave. Finally, there is a shallow pit at the posterior side of the transverse process where it joins the body in A.M.N.H. No. 81846, but not in *Tapirus* or A.M.N.H. No. 81847c.

Five incomplete thoracic vertebrae

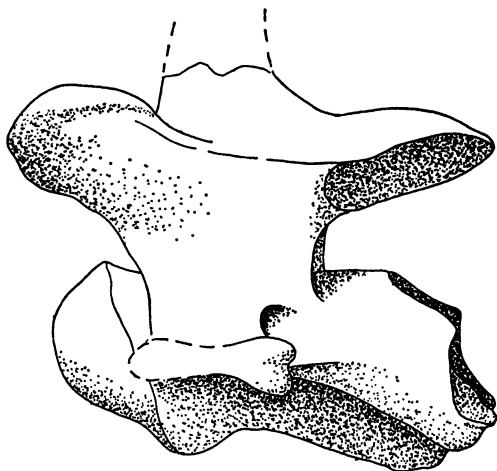


FIG. 34. Seventh cervical vertebra, A.M.N.H. No. 81846, tentatively assigned to *Deperetella cristata*, lateral view.  $\times \frac{3}{4}$ .

(A.M.N.H. No. 81848), preserving only the bodies, have slightly sharper ventral keels but otherwise resemble those of *Tapirus*.

**SCAPULA:** The scapula is not known for *Deperetella* or *Teleolophus*.

**HUMERUS:** The humerus (see fig. 35) is known from a single, slightly crushed specimen (A.M.N.H. No. 81827) which measures about 260 mm. long and 65 mm. wide across the epicondyles. It is similar to that of *Lophialetes* except that it is about twice as large, with the lateral condyle slightly more distally extended and without the posterodistal extension of the lateral epicondyle. The humerus of *Deperetella* is of about the same size and has the same proportions as that of the modern tapir *Tapirus terrestris*, but differs in the following features: deltoid tuberosity situated slightly higher on the shaft; supinator crest not so expanded laterally, and lateral epicondyle less prominent; medial wall of olecranon fossa thinner, especially distally; trochlea with deeper median constriction and much narrower lateral condyle; and lateral condyle extending farther around the trochlea. Except for the narrower lateral condyle, these differences suggest that *Deperetella* was more specialized for running than the mediportal *Tapirus*. The lack of a broad lateral condyle was compensated for by the deep median constriction of the trochlea which, as in *Lophialetes*, accommodated a ridge on the humeral facet of

the radius and restricted lateral movement at the elbow joint.

**RADIUS:** The radius (see fig. 35) is extremely long relative to the humerus. In A.M.N.H. No. 81828 (possibly, but not definitely, from the same individual as A.M.N.H. No. 81827) it measures at least 315 mm. and possibly as much as 335 mm. long, or between about 1.20 and 1.30 times as long as the humerus. In *Heptodon* and *Tapirus* the radio-humeral index is less than 1.00. The humeral articular surface of the radius is divided into two approximately equal-sized concavities, separated by a sharp median ridge. The medial tuberosity, on the medial side of the anterior face just below the humeral facet, is prominent, suggesting a strong biceps and possibly also a strong brachialis. The lateral tuberosity, for attachment of the lateral ligament and lateral digital extensor, is less prominent. On the posterior side of the shaft, just below the humeral facet, there is a roughened horizontal ridge, to which the ulna was attached. A rough-surfaced groove for the ulna can be traced about two-thirds of the way down the lateral side of the posterior face. Distally, at the posterolateral corner, a rough planoconcave area with a small articular facet marks the contact area of the distal end of the ulna. On the distal end of the anterior face a vertical, broad, deep, median groove marks the passage of the tendon of the extensor carpi radialis; lateral to it is a broad, barely discernible groove, possibly for the tendon of the common digital extensor. On the medial side the tuberosity for attachment of the medial ligaments is less prominent than in *Lophialetes*, a fact that may be correlated with the smaller posterior process on the trapezium of *Deperetella*. The anterior half of the distal articular surface is divided by a low ridge into a medial concave facet for the anterior half of the scaphoid and a lateral plano-concave facet for the anterior part of the lunar and a small part of the cuneiform. The posterior half of the carpal facet is occupied by a convex ridge, of which the medial two-thirds articulates with the posterior half of the scaphoid, and the lateral strip with the lunar.

**ULNA:** The ulna is known only from the distal end (A.M.N.H. No. 81829), which is triangular in cross section. The distal frag-



FIG. 35. Front limb bones of *Deperetella cristata*. A, B. Right humerus, A.M.N.H. No. 81827, in lateral and anterior views. C. Right radius, A.M.N.H. No. 81828, and distal end of ulna, A.M.N.H. No. 81829, in anterior view. D, E. Distal ends of radius and ulna in posterior and distal views. All  $\times \frac{1}{2}$ .

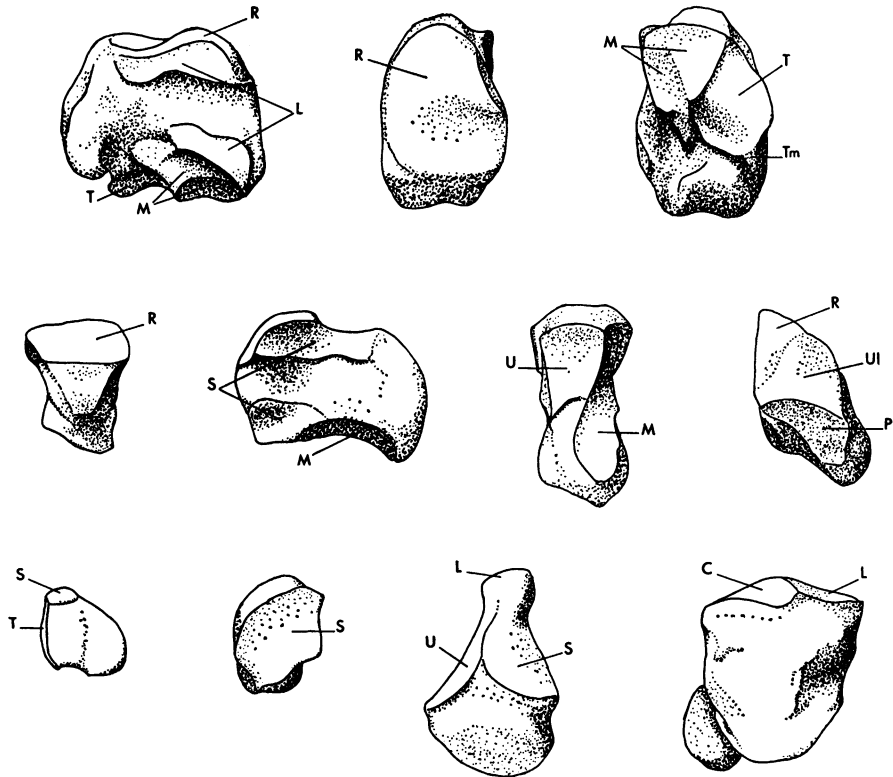


FIG. 36. Carpals of *Deperetella cristata*. Top row: Scaphoid, A.M.N.H. No. 81808, in lateral, proximal, and distal views. Middle row: Lunar, A.M.N.H. No. 81809, in anterior, medial, and distal views; cuneiform, A.M.N.H. No. 81810, in proximal view. Bottom row: From left to right: trapezium, A.M.N.H. No. 81812, medial view; trapezoid, A.M.N.H. No. 81813, proximal view; magnum, A.M.N.H. No. 81814, anterior view; unciform, A.M.N.H. No. 81815, anterior view. All  $\times \frac{3}{4}$ .

Abbreviations: C, cuneiform; L, lunar; M, magnum; P, pisiform; R, radius; S, scaphoid; T, trapezoid; Tm, trapezium; U, unciform; UI, ulna.

ment of the shaft preserved is extremely thin, indicating that the middle of the shaft was greatly reduced in width. A small facet on the medial side articulates with a corresponding strip on the radius. The distal facet is slightly wider than long and evenly convex from front to back, with no obvious division into cuneiform and pisiform portions. Apparently the anterior and central parts of the facet articulated with the cuneiform and the posterior part with the pisiform. (In ulnae of *Heptodon* and *Tapirus* the pisiform facet is lateral to the cuneiform facet.)

**CARPUS:** To facilitate description of the carpals and tarsals of *Deperetella*, they are compared with those of *Lophialetes*, which are described and figured above. Only those features in which *Deperetella* differs from

*Lophialetes* are mentioned and illustrated (see figs. 36 and 37).

The scaphoid of *Deperetella* is relatively higher and less deep anteroposteriorly than that of *Lophialetes*, and further differs in the following features: posterior process less massive; concave posterior portion of radial facet relatively larger and spread farther laterally; distal lunar facet shorter and more anteriorly situated; posterior magnum facet shorter and more vertical (the area occupied by the posterior halves of the last two facets in *Lophialetes* is deeply excavated in *Deperetella*); anterior magnum facet relatively shorter and wider; trapezoid facet saddle-shaped instead of concave; and small facet for trapezium present in some specimens.

The lunar differs from that of *Lophialetes* in

the following features: facet for radius extending farther onto the vertical anterior face; unciform facet oblique instead of horizontal, truncating the anterior half of the laterodistal edge; magnum facet more horizontally oriented, so that the lunar rests equally on magnum (posteriorly) and unciform (anteriorly); distal scaphoid facet situated anteriorly, not posteriorly; and posterior process more prominent.

The cuneiform of *Deperetella* differs from that of *Lophialetes* in having a relatively smaller pisiform facet, a large posterior tuberosity, and a small proximal facet for the lateral end of the radius. The pisiform is smaller relative to the cuneiform; the cuneiform facet of the pisiform is of about the same size as the ulnar facet (in *Lophialetes* it is larger).

The distal carpals of *Deperetella* differ from those of *Lophialetes* in the following features: trapezium with smaller posterior process and a small facet for articulation with the scaphoid; trapezoid more square in horizontal section, with saddle-shaped scaphoid and second metacarpal facets; magnum with flatter proximal hump, shorter scaphoid facets, more horizontal lunar facet, no facet on the posterior process for articulation with the fourth metacarpal; and unciform relatively higher.

The differences in articulation between the scaphoid and the trapezoid, magnum, and lunar, and between the lunar and magnum, suggest that the carpus of *Deperetella* did not have so much freedom of motion for extension and flexion between proximal and distal carpal rows as did that of *Lophialetes*. These differences agree with the relatively smaller pisiform and apparently weaker extensor carpi ulnaris (a flexor of the carpus) in *Deperetella*. The radius appears to have covered a relatively larger area of the proximal surface of the carpus in *Deperetella* than in *Lophialetes*, which may be correlated with the decrease in size of the ulna, a cursorial modification. The high radio-humeral index in *Deperetella cristata* (between 1.20 and 1.30) indicates that this species was highly specialized for running.

**METACARPALS:** The metacarpus of *Deperetella*, like that of *Lophialetes*, is tridactyl, with the fifth metacarpal reduced to a vestige. No complete metacarpals are preserved, but,

judged from the metatarsals, they were relatively long and slender, with the lateral ones thinner than the median one. Roughened areas extend down almost the entire axial sides of the lateral metacarpals, which indicates that they were bound close to the median one.

The metacarpals of *Deperetella* are basically similar to those of *Lophialetes*, differing only in the following features: second metacarpal with a more quadrangular and saddle-shaped (anteroposteriorly convex, transversely concave) trapezoid facet; third metacarpal with a small posterior projection bearing a large facet for articulation with the fourth metacarpal; posterior process of the fourth metacarpal articulating with the third metacarpal instead of the magnum; and vestigial fifth metacarpal relatively longer and thinner.

The attachment areas for muscles and ligaments are easier to see on the metapodials of *Deperetella cristata* than on those of *Lophialetes expeditus*, and those features not described before are mentioned here. The second metacarpal of *Deperetella* bears a prominent tuberosity on the posterolateral corner just below the trapezoid facet which may have served for insertion of the flexor carpi radialis or possibly a carpal ligament, and a low

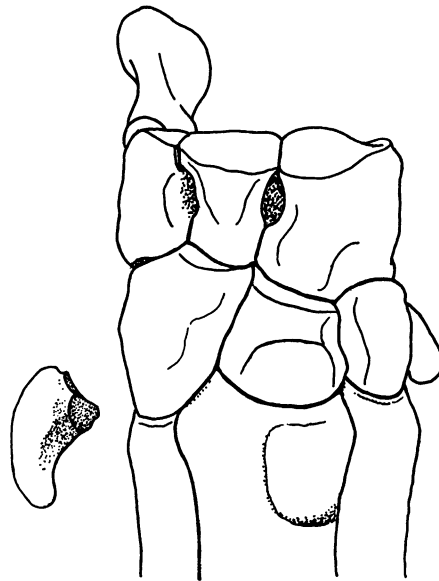


FIG. 37. Right carpus of *Deperetella cristata*, composite based on several specimens, A.M.N.H. Nos. 81808-81815. Left: Vestigial fifth metacarpal, A.M.N.H. No. 81816.  $\times \frac{3}{4}$ .

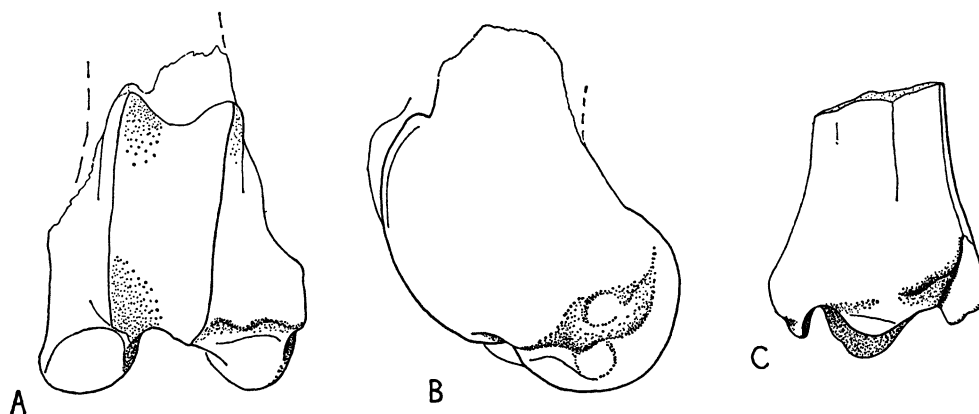


FIG. 38. Hind limb bones of *Deperetella cristata*. A, B. Distal end of left femur, A.M.N.H. No. 81830, in anterior and lateral views. C. Distal end of left tibia and fibula, A.M.N.H. No. 81844, in anterior view. All  $\times \frac{1}{2}$ .

tuberosity on the medial side which probably marks the insertion of the extensor carpi obliquus (abductor pollicis longus et extensor pollicis brevis). The third metacarpal has a low prominence on the medial side of the

anterior face, just below the magnum facet, which marks the insertion of the extensor carpi radialis. A low swelling on the lateral side of the anterior face of the fourth metacarpal, just below the unciform facet, prob-

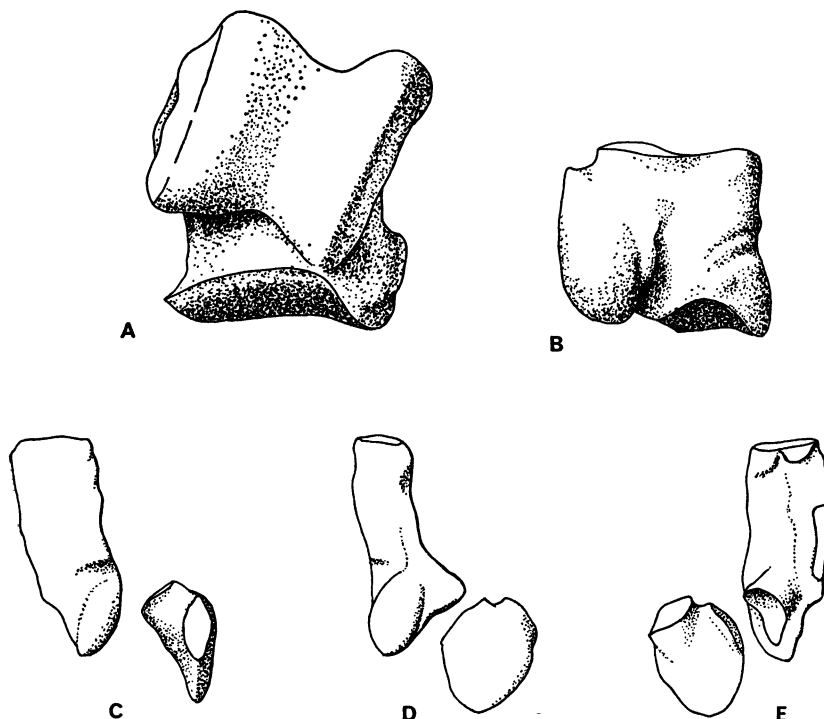
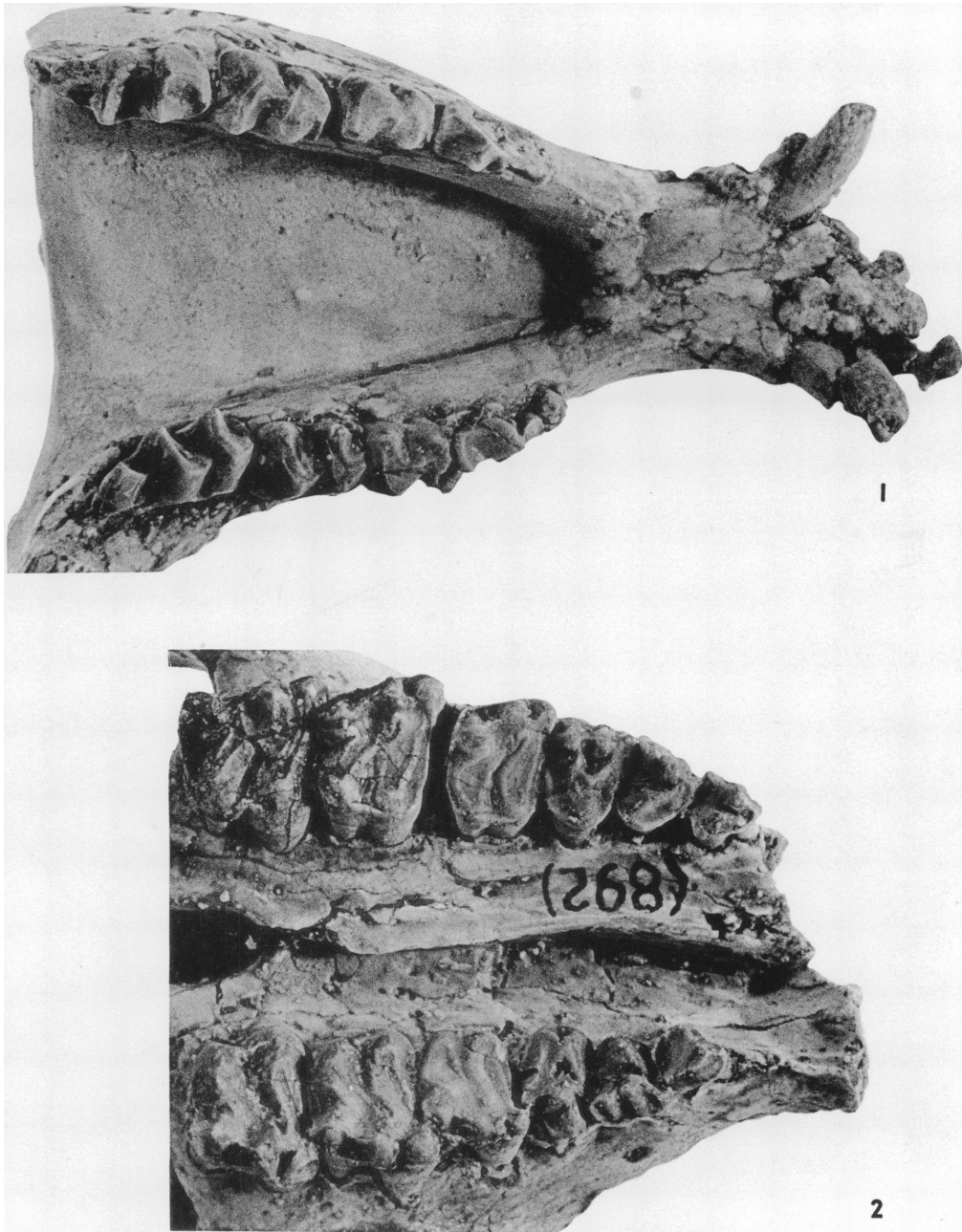
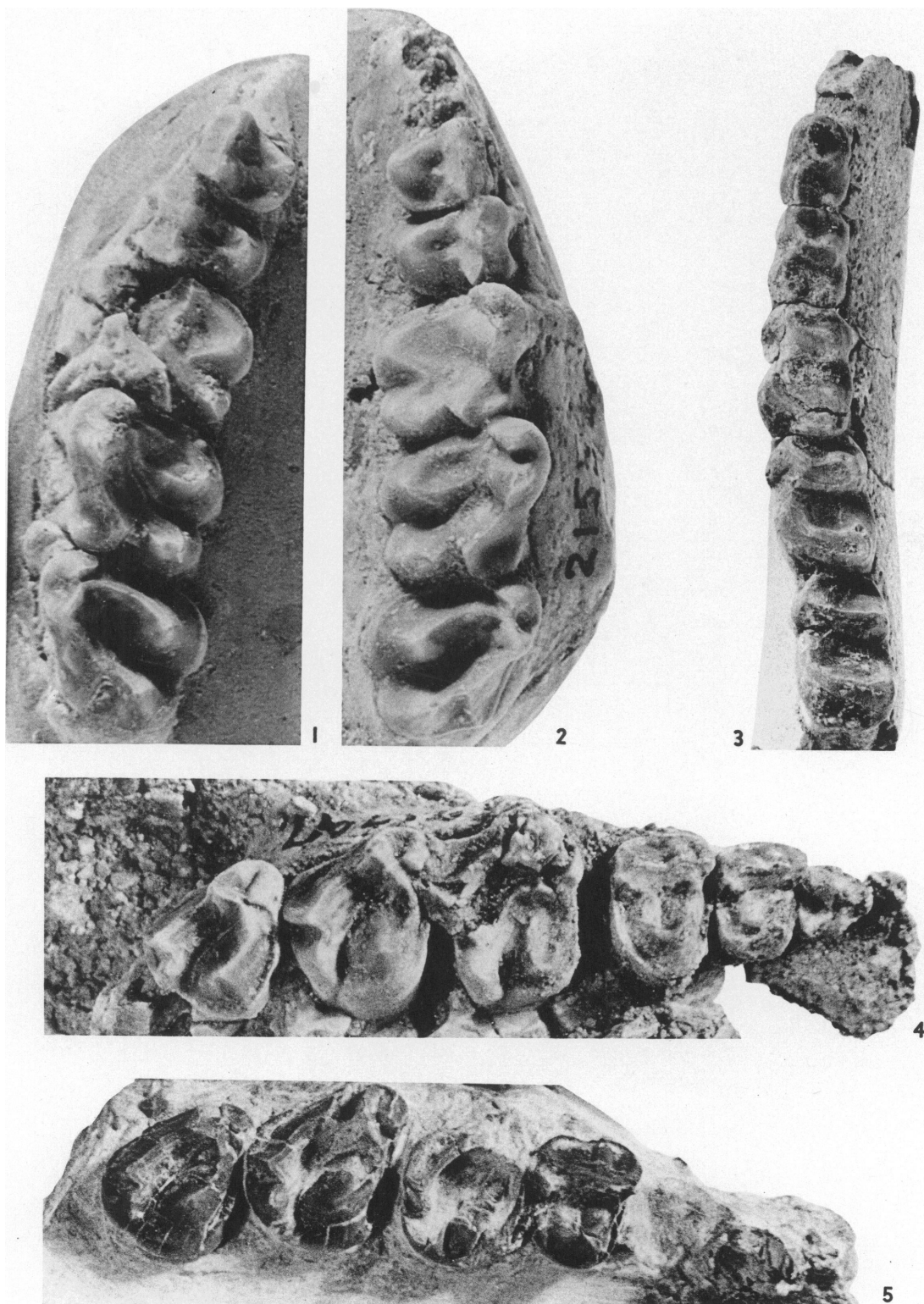


FIG. 39. Selected tarsals of *Deperetella cristata*. A. Astragalus, A.M.N.H. No. 81817, in anterior view. B. Cuboid, A.M.N.H. No. 81819, in lateral view. C, D, E. Entocuneiform, composite from A.M.N.H. Nos. 20329 and 81823, and vestigial first metatarsal, A.M.N.H. No. 81824, in medial, posterior, and lateral views. All  $\times \frac{3}{4}$ .



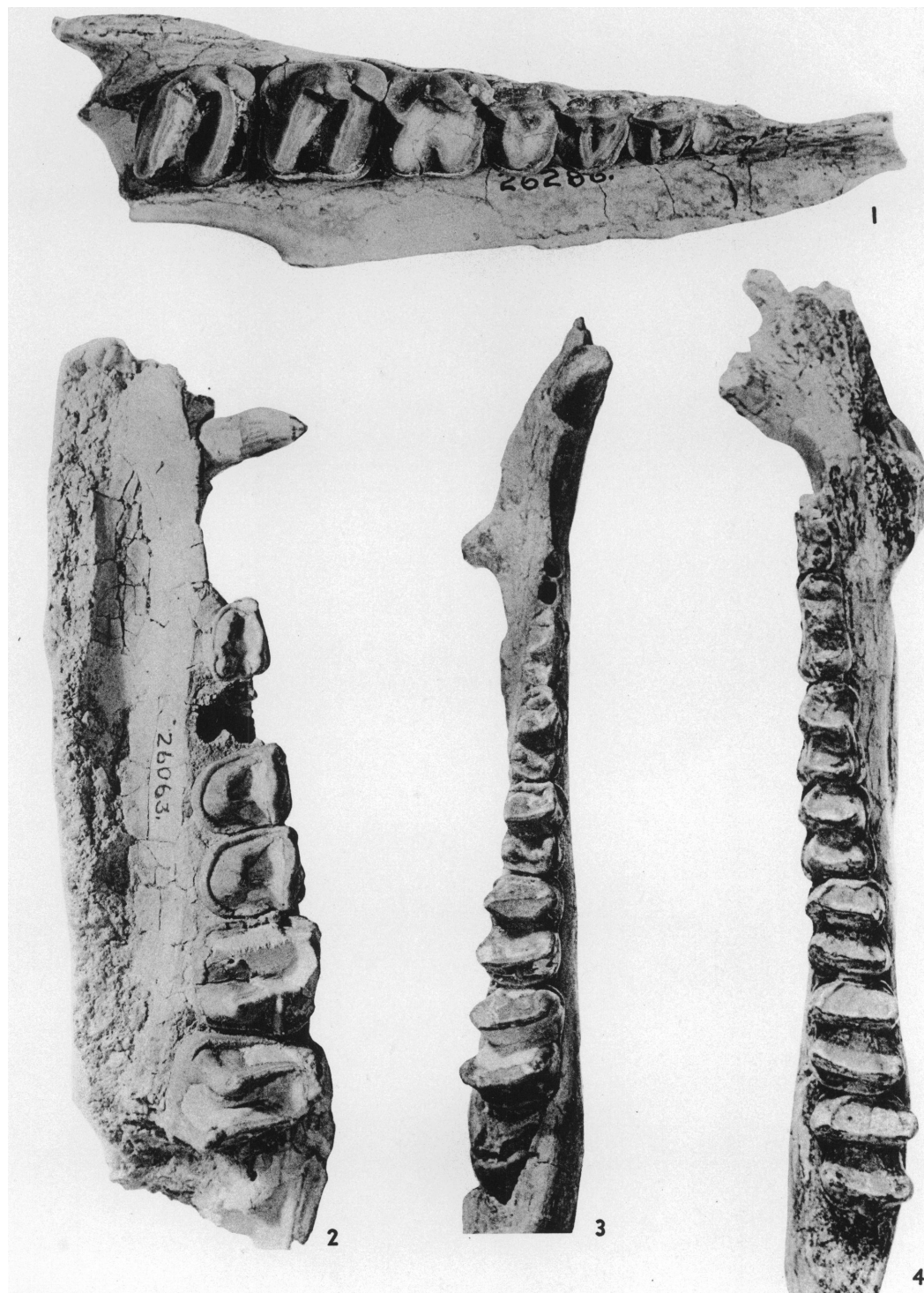
1. *Breviodon acares*, new genus and species, type, A.M.N.H. No. 26113
  2. Cf. *Breviodon acares*, A.M.N.H. No. 81751, showing palate with P<sup>2</sup>-M<sup>3</sup>
- Both  $\times 2$



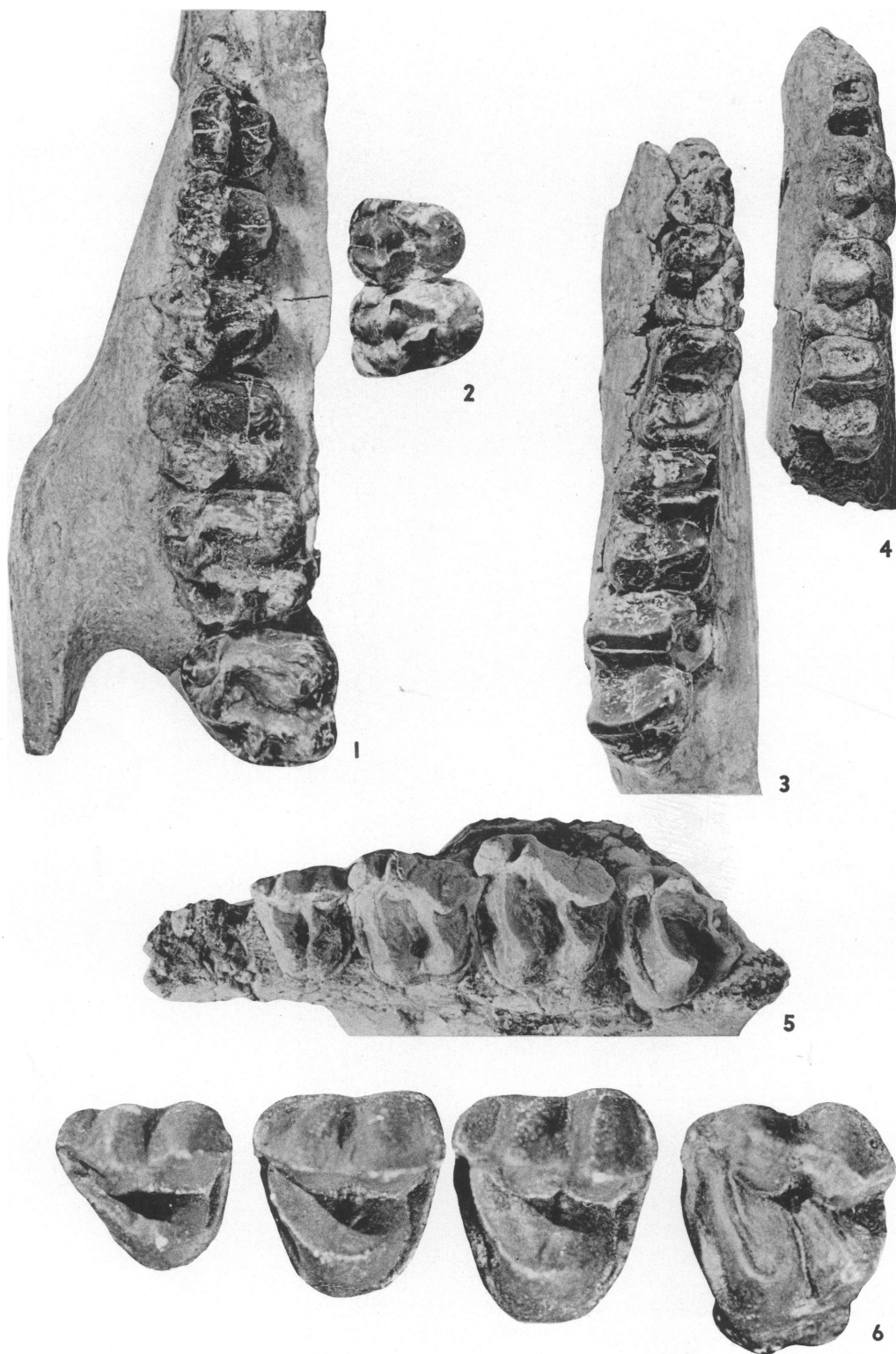
1-3. *Rhodopagus pygmaeus*, new genus and species. 1, 2. Type, A.M.N.H. No. 21554, right and left maxillae with  $P^1$ - $^2$  alveoli and  $P^3$ - $M^3$ . 3. A.M.N.H. No. 20331, left  $P^3$ - $M^3$ .  
 4, 5. *Pataecus parvus*, new genus and species. 4. Type, A.M.N.H. No. 21747, right  $P^2$ - $M^3$ . 5. A.M.N.H. No. 21746, right  $P^4$ - $M^3$

All  $\times 3$





1. *Teleolophus medius*?, A.M.N.H. No. 26286, right P<sup>1</sup>-M<sup>3</sup>.  $\times 1$
- 2, 3. *Teleolophus magnus*, new species, type, A.M.N.H. No. 26063. 2. Left C<sup>1</sup>-M<sup>2</sup>.  
3. Right C<sub>1</sub>-M<sub>2</sub>. Both  $\times \frac{3}{4}$
4. *Deperetella cristata*, A.M.N.H. No. 20291, left C<sub>1</sub>-M<sub>3</sub>.  $\times \frac{3}{4}$



1-4. *Helalestes mongoliensis*, new combination. 1. Type, A.M.N.H. No. 19161, right maxilla with P<sup>2</sup>-M<sup>2</sup>. M<sup>3</sup> added from A.M.N.H. No. 20156B. 2. A.M.N.H. No. 20156A, P<sup>3</sup>-4 (reversed). 3. A.M.N.H. No. 20155, right mandible with P<sub>3</sub> roots and P<sub>4</sub>-M<sub>3</sub>. 4. A.M.N.H. No. 81717, right P<sub>3</sub>-M<sub>1</sub>. All × 1.5

5. Cf. *Hyrachyus*, A.M.N.H. No. 81801, left P<sup>4</sup>-M<sup>3</sup>. × 1.5

6. *Indolophus guptai*, type, P<sup>2</sup>-M<sup>1</sup>, from A.M.N.H. No. 17617, a cast of the original. × 3

ably indicates the insertion of the lateral carpal ligament.

**PHALANGES:** The phalanges of *Deperetella* differ from those of *Lophialetes* in the following features: articulation between first and second medial phalanges flatter; second medial phalanx relatively shorter and wider, with the distal condyle shorter and not extending so far up the anterior face, and lacking the distal lateral pits for collateral ligaments; median ungual phalanx relatively shorter and wider; and proximal lateral phalanges with a prominent tuberosity on the axial side marking the insertion of a strong contrahens or possibly just the axial collateral ligament. The differences in the proximal and distal articular surfaces of the second phalanx suggest that there was less movement (extension and flexion) between phalanges in *Deperetella* than in *Lophialetes*.

**INNOMINATE:** No remnant of the pelvic girdle of *Deperetella* is known.

**FEMUR:** The femur (fig. 38) is known only from one distal end (A.M.N.H. No. 81830) which includes only the trochlea and condyles. The trochlea is relatively long and narrow and almost bilaterally symmetrical, with a shallow median groove. The condyles are relatively narrower, the lateral condyle more sharply convex, the pit for the extensor digitorum longus shallower, and the intercondyloid fossa deeper in *Deperetella* than in *Lophialetes* or *Tapirus*.

The patella is relatively long and narrow, and flatter than that of *Tapirus*.

**TIBIA:** The tibia is relatively long and thin. One almost complete specimen (A.M.N.H. No. 81844) has an estimated length of about 300 mm. and a proximal width of 75 mm. The proximal end of the tibia is relatively narrower and deeper (anteroposteriorly) than in *Tapirus*, with a flatter and more horizontal lateral condyle, and a steeper and much higher lateral tubercle of the spine. The lateral tubercle is higher than the median one; in modern tapirs and horses the reverse is true. On the lateral side just below the condyle there is a small shallow pit for the head of the fibula. The distal end of the tibia has moderately deep grooves for the astragalus. The medial malleolus is fairly prominent and shows a scar marking the attachment of the medial ligament. Posterior to it is a broad

groove for the tendon of the flexor digitalis longus. On the lateral side there is a roughened area, with a narrow facet for the distal end of the fibula.

**FIBULA:** The fibula is greatly reduced. Judged from the fibular fossa on the proximal end of the tibia, the head was very small. In

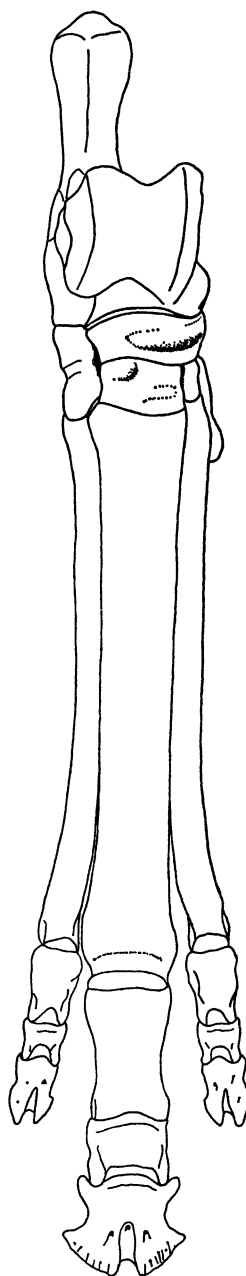


FIG. 40. Right hind foot of *Deperetella cristata*, composite based on several specimens.  $\times 2/5$ .

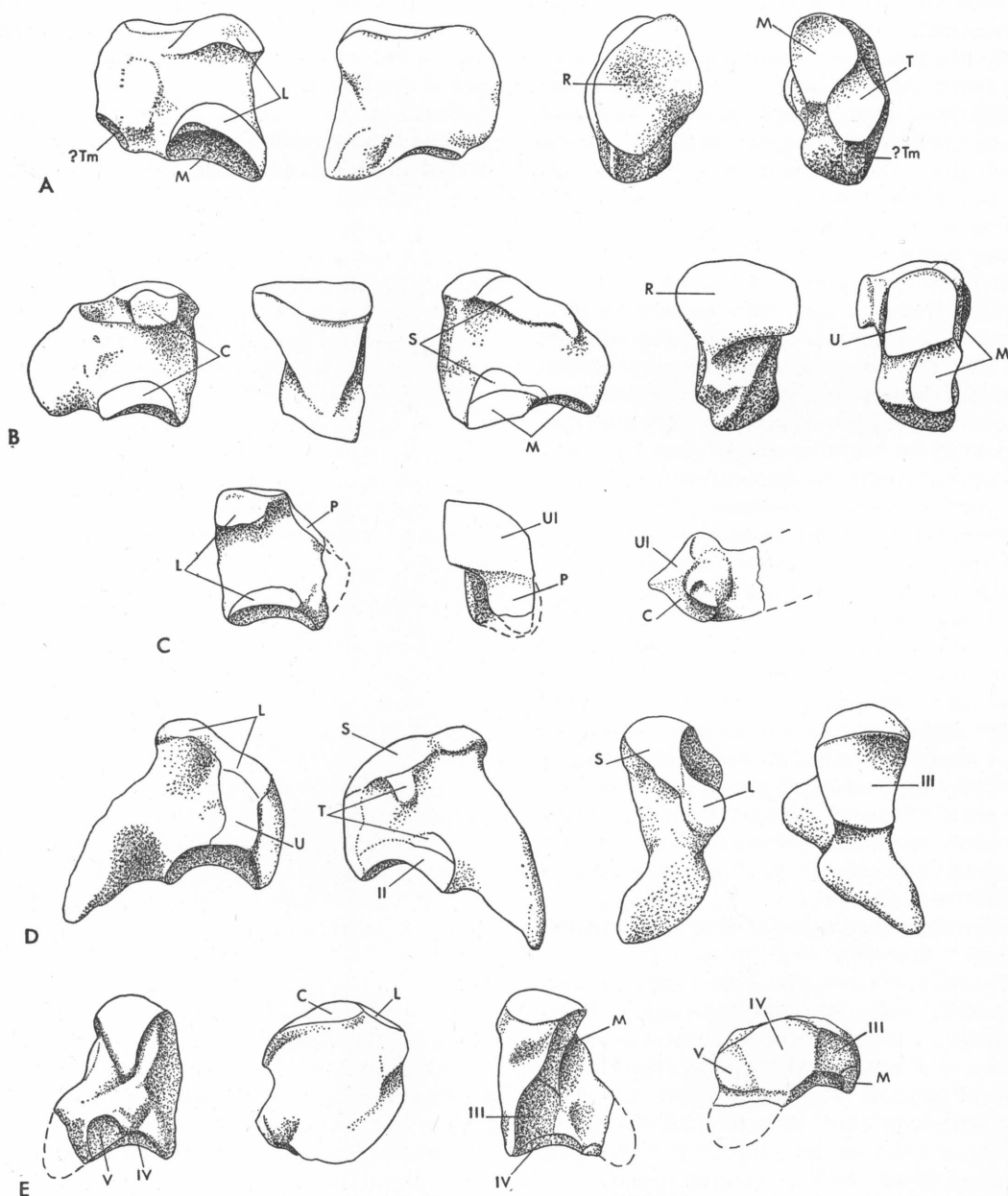


FIG. 41. Known carpals of *Colodon occidentalis*, A.M.N.H. No. 658. A. Scaphoid in (from left to right) lateral, medial, proximal, and distal views. B. Lunar in lateral, anterior, medial, proximal, and distal views. C. Cuneiform in medial and proximal views, and proximal end of pisiform in medial view. D. Magnum in lateral, medial, proximal, and distal views. E. Unciform in lateral, anterior, medial, and distal views.  $\times 1$ .

*Abbreviations:* C, cuneiform; L, lunar; M, magnum; P, pisiform; R, radius; S, scaphoid; T, trapezoid; Tm, trapezium; U, unciform; UI, ulna; II, III, IV, and V, second third, fourth, and fifth metacarpals.

A.M.N.H. No. 81844, the distal half of the fibular shaft is extremely flat and thin and is fused to the shaft of the tibia (see fig. 38). The distal end of the fibula is slightly expanded, but still flat and thin; it apparently was not fused to the tibia but articulated with it by a narrow facet. A shallow groove on the narrow posterior side accommodated the tendon of the peroneus brevis.

**TARSUS (FIGS. 39, 40):** The astragalus is similar to that of *Lophialetes* except that it is relatively lower, wider, and thicker (which would be expected in a larger, heavier animal) and lacks the proximomedial flaring of the end of the medial condyle. The facets for the calcaneum on the posterior side, the navicular and cuboid on the distal end, and ligament scars on the lateral and medial sides are essentially as described for *Lophialetes*, except that the cuboid facet extends farther anteriorly (with the cuboid, navicular, and distal calcaneal facets all converging to a point at the anterolateral corner).

The calcaneum is like that of *Lophialetes*, except that it has a smaller and shallower fibular pit above the lateral astragalar facet and a slightly more posteriorly extended cuboid facet. The cuboid differs from that of *Lophialetes* only in having a higher posterior tuberosity. The navicular, ectocuneiform, and mesocuneiform are essentially as described for *Lophialetes*. The entocuneiform is long, flat, and narrow, like that of *Lophialetes*, but more expanded distally. The distal end is enlarged anteriorly into a buttress which bears a distal facet for the vestigial first metatarsal, and posterodistally into a large tuberosity, probably for attachment of a deep flexor muscle for the second digit.

**METATARSALS:** The metatarsals are relatively long and thin. The median one averages about 185 mm. long and 27 mm. wide at the distal condyle. The lateral metatarsals are slightly shorter and considerably more slender and flatter than the central one.

The first metatarsal has been reduced to a small, flat, oval-shaped nodule, with a facet for the entocuneiform on the proximomedial corner and an anterolaterally facing facet for the back of the third metatarsal on the thickened proximolateral corner.

The proximal ends of the second, third, and fourth metatarsals are similar in shape and facet patterns to those of *Lophialetes* and need no further description here. The distal ends of the metatarsals are similar to those of the metacarpals, except that the median keel extends farther forward on the third metatarsal than on the third metacarpal.

The phalanges of the hind foot are similar to those of the front foot except that they are relatively longer and narrower. The proximal lateral phalanges of the pes do not have the prominent tuberosities that can be seen on the axial sides of those phalanges in the manus.

#### FAMILY HELALETIDAE

Skeletal elements are virtually unknown for Asiatic members of the Helaletidae. An astragalus and calcaneum, supposedly of *Colodon orientalis*, were described and figured by Gromova (1960, p. 94). These differ from the astragalus and calcaneum of the North American species *Colodon occidentalis* in lacking confluent sustentacular and inferior astragalocalcaneal facets. Knowledge of the rest of the skeleton of *Colodon* is confined to *C. occidentalis*; presumably the Asiatic species were similar to the North American one. The skull of *Colodon* is figured in a generalized drawing by Radinsky (1963a, p. 90, fig. 21). Scott (1941, pp. 766–773, pl. 81) reviewed the known postcranial elements of *Colodon occidentalis*, which include most of a forelimb and a pes. Since the carpal bones present diagnostic characters and they have never before been adequately illustrated (Scott's only figure of them is a dorsal view of the articulated carpus), they are shown here in figure 41.

## NOTES ON DISTRIBUTION

THERE WERE MORE DIFFERENT kinds of tapiroids in the early late Eocene of Asia than on any other continent or at any other time. At least eight genera are represented in faunas of Irdin Manha age in Asia, while in Europe or North America no more than three tapiroid genera existed at any one time. Hypotheses to explain this distribution should be based on thorough analyses of the entire faunas and floras involved, a project beyond the scope of the present paper. However, one factor that is immediately apparent and may be mentioned here is the scarcity of artiodactyls in the early late Eocene of Asia compared to the abundance of them in contemporaneous faunas in North America and Europe. Artiodactyls presumably were ecological competitors with tapiroids, and their scarcity in Asia may have opened environmental niches which were not available elsewhere to tapiroids.

Dehm and Oettingen-Spielberg (1958, p. 49) suggested a north-south environmental zonation of Asiatic late Eocene faunas, based on distribution of anthracothere genera. Deperetellids range from southernmost to northernmost late Eocene localities, but

lophialetids and helaletids are confined to northern faunas. In the case of the Lophialetidae, such restriction may merely reflect the fact that the southern Asiatic faunas are of latest Eocene age and thus are too late in time to contain lophialetids. Helaletids, on the other hand, are found in late late Eocene beds, but only in Korea. Their absence from more western localities in latest Eocene time may be due to environmental factors or, since they are relatively rare where they do occur, may simply reflect inadequate sampling. Thus the available data on geographic distribution of late Eocene tapiroids in Asia do not provide evidence for environmental zonation.

The occurrence of the isctolophid *Homogalax* and the helaletids *Helaletes* and *Colodon* in both Asiatic and North American faunas supports evidence from other genera that suggests that faunal exchange between the two continents, presumably by way of Alaska and Siberia, occurred during the early and late Eocene. No Eocene or Oligocene tapiroid genera have been found in both Asia and Europe.

## SUMMARY

EARLY EOCENE TAPIROIDS in Asia are known only from a single specimen, representing a form similar to the North American isctolophid *Homogalax*. The middle Eocene record is equally poor. One isolated lower molar of a form possibly ancestral to the late Eocene genus *Teleophus* is the only Asiatic tapiroid fossil of undoubted middle Eocene age. In beds that may be late middle or early late Eocene in age, *Veragromovia*, a genus based on a single upper molar, represents a form similar to the North American helaletid *Helaletes*, and *Schlosseria*, a better-known genus with a tridactyl manus, provides an approximate ancestor for the late Eocene genus *Lophialetes*.

Several relatively rich late Eocene faunas reveal a great variety of tapiroids in Asia at that time. Whether this indicates an evolutionary radiation of tapiroids in the late Eocene or merely reflects uneven knowledge of the fossil record is a moot point. Early late Eocene (Irdin Manha age) tapiroids represent at least three families, the Helaletidae, known also in North America, and two newly recognized, solely Asiatic families, the Lophialetidae and the Deperetellidae. The helaletids include advanced species of *Helaletes* (formerly assigned to *Desmatotherium*) and a form similar to the North American genus *Hyrachyus*. The lophialetids are represented by the very abundant *Lophialetes*, a genus with rhinocerotoid-like molars, and a new genus, *Breviodon*, a small tapiroid with  $P_{1-2}$  lost. A small form with  $P^1$  lost and convex molar metacones may be related to *Breviodon* or may represent a distinct new genus. Two new genera, *Rhodopagus* and *Pataecus*, both diminutive forms, appear to be divergent offshoots from the Lophialetidae, in which the long molar ectolophs were lingually dis-

placed and run parallel to or confluent with the metalophs. Early late Eocene deperetellids are represented by *Teleolophus*, a genus with bilophodont molars.

In late late Eocene (Shara Murun age) Asiatic faunas, tapiroids are less abundant in both numbers and diversity. Helaletids are represented by species of *Colodon*, a genus also known in North America. Lophialetids, the dominant elements in early late Eocene faunas, are no longer present. Deperetellids are represented by *Deperetella* (including *Cristidentinus* and *Diplolophodon*), a descendant of *Teleolophus* in which the anterior premolars are disproportionately lengthened, in specialization for vertical shear. *Indolophus*, a poorly known Burmese genus, appears to represent an otherwise unknown tapiroid lineage and cannot be assigned to any existing family.

Tapiroids are extremely rare in Oligocene deposits in Asia and are represented by only one genus, *Colodon* (including *Paracolodon*).

Postcranial remains are known for *Schlosseria*, *Lophialetes*, and *Deperetella*. In all three genera the fifth metacarpal is reduced to a tiny vestige and the remaining metacarpals are relatively long and thin, indicating specialization for running. In *Deperetella*, elongate cervical vertebrae and a high radio-humeral ratio suggest a fleet, gazelle-like animal.

It is suggested that the relatively great diversity of late Eocene tapiroids in Asia may be related to the scarcity of artiodactyls in the same faunas. The geographic distribution of late Eocene tapiroids in Asia provides no evidence for climatic zonation at that time. The occurrence of helaletid and isctolophid tapiroids in Asia supports other evidence for faunal exchange between Asia and North America during early and late Eocene time.

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