The systematics of *Rhodopagus,* a late Eocene hyracodontid (Perissodactyla: Rhinocerotoidea) from China

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Rhodopagus Radinsky 1965 is a diminutive genus of perissodactyls known from the late Eocene of China. Two species, *R. minimus* (Matthew & Granger 1925) (= *R. pygmaeus* Radinsky 1965) and *R. zdanskyi*, new species, here are considered valid. Formerly *Rhodopagus* and the somewhat similar genus *Pataecops* Radinsky 1966 were assigned to the Lophialetidae (Tapiroidea). However, both genera possess derived characters (e.g., relatively high-crowned teeth, lingually deflected M^3 metacone, M_3 hypoconulid absent) that justify their reassignment to the Hyracodontidae (Rhinocerotoidea).

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Introduction

Rhodopagus Radinsky 1965 is a diminutive perissodactyl genus known from the Late Eocene of China. In his original description of the genus, Radinsky (1965) recognized two species: *Rhodopagus? minimus*, known only from the type specimen of *Caenolophus? minimus* Matthew & Granger 1925, and *R. pygmaeus*, known from numerous upper and lower jaw fragments and isolated teeth. Two lower jaw fragments described by Zdansky (1930, p. 40) as "Hyracodontidae gen. et sp. indet." were reassigned by Radinsky (1965, p. 212) to "?*Rhodopagus*". Radinsky (1965, p. 207) assigned *R.* with a query to the lophialetid tapiroids but noted that "the peculiar upper cusp pattern of *Rhodopagus* ... sets this genus apart from all other previously described tapiroids". Indeed we here argue that *R.* is not a tapiroid and is best assigned to the Hyracodontidae. In addition, we revise the species-level taxonomy of *R.*, designating the specimen described by Zdansky (1930) the type of a new species. The following abbreviations are used: AMNH-Department of Vertebrate Paleontology, American Museum of Natural History, New York; PMU-Paleontological Museum, Paleontologiska Institutionen, Uppsala Universitet, Uppsala. All Chinese place names follow the Pinyin romanization, except the often used locality names in Inner Mongolia.

Systematics

Class MAMMALIA Linnaeus 1758
Order PERISSODACTYLA Owen 1848
Family HYRACODONTIDAE Cope 1879
Genus RHODOPAGUS Radinsky 1965

TYPE SPECIES: *Rhodopagus minimus* (Matthew & Granger 1925) (= *Rhodopagus pygmaeus* Radinsky 1965).

INCLUDED SPECIES: The type species and *Rhodopagus zdanskyi* Lucas & Schoch, new species.

DISTRIBUTION: Late Eocene of China (Fig. 1).

REVISED DIAGNOSIS: Very small hyracodontids: M^{1-3}_{1-3} length approximately 23,0 mm; P_1 lost; lower premolars sub-molariform; upper premolars non-molariform; crown height index (unworn M^3 paracone height measured from the base of the enamel divided by M^3 width) averages 0,6; M^3 with small metacone.

DISCUSSION: *Rhodopagus* here is diagnosed as a hyracodontid rhinocerotoid (see later discussion). Among the Hyracodontidae (*sensu* Radinsky 1967) it most closely resembles *Triplopus* (cf. Radinsky 1967, p. 7—8) but differs in its diminutive size and loss of P_1. Because only the upper molars of three specimens previously referred to *R. pygmaeus* are known (Radinsky 1965), the species-

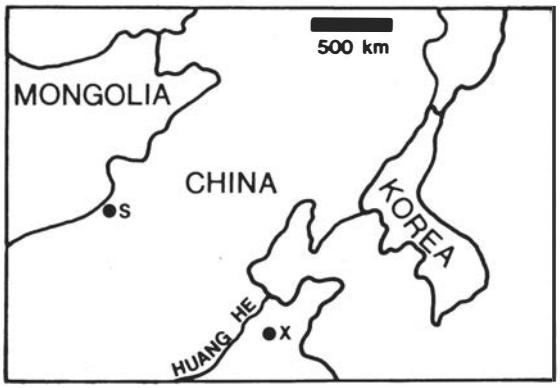

Fig. 1. The distribution of *Rhodopagus* in China. Localities are: S = Shara Murun Region, Inner Mongolia (see Radinsky 1964 for further locality information), X = Xintai County, Shandong Province (see Tan 1923 for further locality information). Less well documented occurrences of *Rhodopagus* in Inner Mongolia, Henan Province and Yunnan Province are discussed in the text.

level taxonomy of *R.* that follows necessarily relies on characters of the lower dentition.

Rhodopagus minimus (Matthew & Granger 1925)
Figs. 2, a—f; 5, a.

1925 *Caenolophus? minimus* Matthew & Granger, p. 7, Fig. 9.
1965 *Rhodopagus pygmaeus* Radinsky, p. 208—211, Figs. 8—9; Pl. 2, Figs. 1—3.
1965 *Rhodopagus? minimus*: Radinsky, p. 211—212, Fig. 10.

HOLOTYPE: AMNH 20310, left dentary fragment with M_{1-2} and M_3 alveolus.

HORIZON AND LOCALITY OF THE TYPE: Late Eocene Shara Murun beds, Ula Usu, Baron Sog Mesa, Shara Murun Region, Inner Mongolia, China (Fig. 1; see Radinsky 1964, for further locality information).

REFERRED SPECIMENS: AMNH 21554, palate with left P^{1-2} alveoli, right and left P^3—M^3 (Fig. 5, a, type specimen of *Rhodopagus pygmaeus*); AMNH 81859, isolated M^2; AMNH 81860, isolated M^3; AMNH 20330—20350, 20390—20394, 26112, 26114 (lower dentitions): all from late Eocene Ulan Shireh beds, North Mesa, Shara Murun Region, Inner Mongolia, China (Fig. 1).

REVISED DIAGNOSIS: Largest species of *Rhodopagus*: M_2 longer and M_{2-3} wider than in *R. zdanskyi*; M_2 metalophid low, meeting the protolophid just lingual of the protoconid; M_{2-3} paralophids low and straight; M_{2-3} protolophids and hypolophids subequal in height; M_3 trigonid short and rectangular in cross-section; M_3 posterior cingulid small.

DISCUSSION: Radinsky (1965 p. 211) separated AMNH 20310, the type of *Caenolophus? minimus* Matthew & Granger 1925 from specimens he referred to *R. pygmaeus* because AMNH 20310 has a "slightly wider M_{1-2}" and lacks expanded root tips. However, bivariate plots of M_1 and M_2 lengths versus widths (Fig. 3) show that AMNH 20310 falls within the cluster formed by the specimens Radinsky referred to *R. pygmaeus*, although admittedly it is near the large end of the cluster. Moreover, coefficients of variation of the plotted measurements are no higher than seven (Table 1), well within the range of values expected in a population consisting of one species (Simpson et al. 1960). We therefore see no quantitative basis for taxonomically separating AMNH 20310 from other specimens of *R.* from Inner Mongolia.

We also place little taxonomic value on the lack of bulbous root tips in AMNH 20310 because the root tips of the specimens Radinsky (1965) referred to *R. pygmaeus* are not all observable. This renders impossible an assessment of the variability of this character and thus diminishes our faith in its utility as a character of taxonomic significance.

In its crown morphology, AMNH 20310 closely resembles other specimens of *R.* from Mongolia (Fig. 2; Radinsky 1965). Therefore we see no reliable quantitative or qualitative evidence to justify assigning two trivial names to specimens of *R.* from Inner Mongolia and consider *R. pygmaeus* Radinsky 1965 to be a junior subjective synonym of *R. minimus* (Matthew & Granger 1925).

Rhodopagus zdanskyi, Lucas & Schoch, new species
Fig. 4, a—f.

1930 Hyracodontidae gen. et sp. indet.: Zdansky, p. 40—42; Pl. 3, Figs. 1—2.
1930 *Hyracotheriine*, gen. et sp. indet.: Zdansky, p. 83 (*lapsus calami*).
1965 ?*Rhodopagus*: Radinsky, p. 212.

HOLOTYPE: PMU. M. 3004, left dentary fragment with M_1 roots and complete M_{2-3} and PMU. M. 3006, left dentary fragment with C root, partial P_{2-3} and P_4 alveolus. Both dentary fragments were collected together and presumably belong to one individual (Zdansky 1930). However, if they are later shown not to pertain to a single individual, the type should be restricted to PMU. M. 3004.

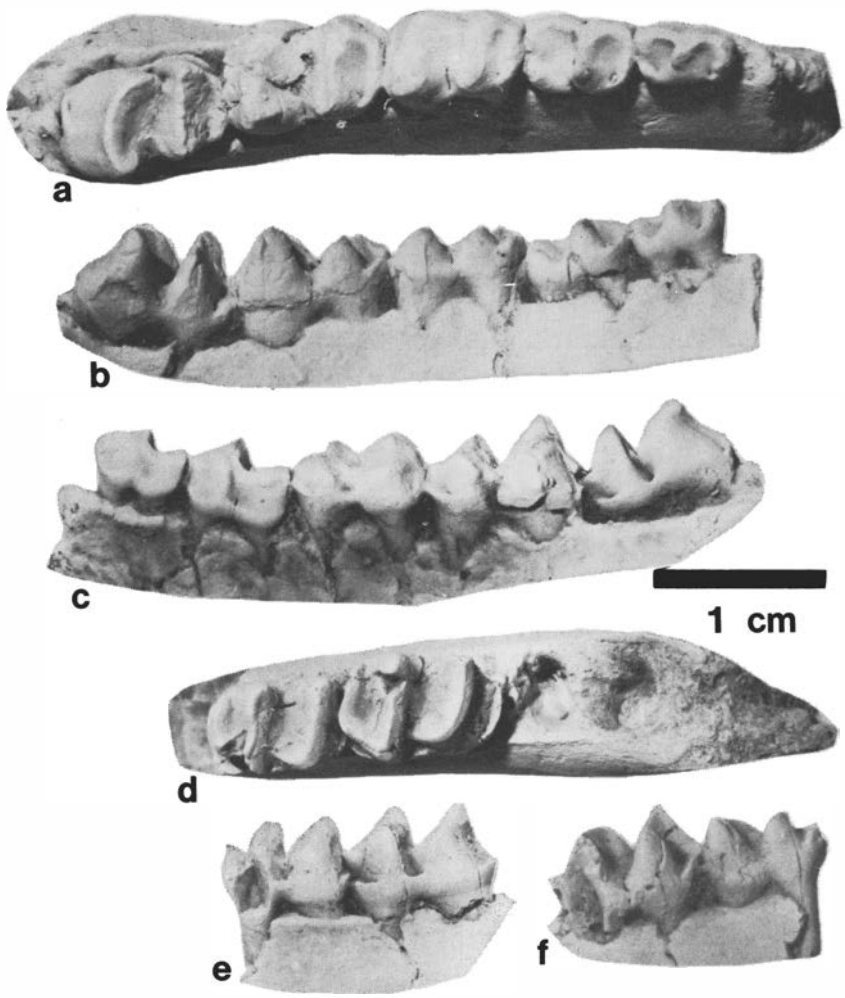

Fig. 2. Lower cheek teeth of *Rhodopagus minimus*. a—c, AMNH 26114, left dentary fragment with P_3—M_3 referred by Radinsky (1965) to *R. pygmaeus*, occlusal (a), lingual (b) and labial (c) views. d—f, AMNH 20310, left dentary fragment with M_{1-2} and M_3 alveolus, the holotype of *R. minimus*, occlusal (d), labial (e) and lingual (f) views.

HORIZON AND LOCALITY OF THE TYPE: A presumably late Eocene age horizon of the Guanzhang Series at Xi Gou, Xintai County, Shandong Province, eastern China (Fig. 1; Tan 1923; Zdansky 1930).

REFERRED SPECIMENS: Known only from the type specimen.

ETYMOLOGY: Named after Dr. Otto Zdansky who first described the type specimen and made a significant contribution to our understanding of the Chinese early Tertiary in his classic monograph (1930).

DIAGNOSIS: Smallest species of *Rhodopagus*: M_2 shorter and M_3 narrower than in *R. minimus*; M_2 metalophid high, meeting the protolophid well lingual of the protoconid; M_{2-3} paralophids high and arcuate; M_{2-3} protolophids distinctly taller than hypolophids; M_3 trigonid long and triangular in cross-section; M_3 posterior cingulid large.

DISCUSSION: Zdansky (1930, p. 40—42) described the holotype of *R. zdanskyi* (Fig. 4) in detail. It resembles Mongolian specimens of *R.* in its small size, constricted symphysis, long post-

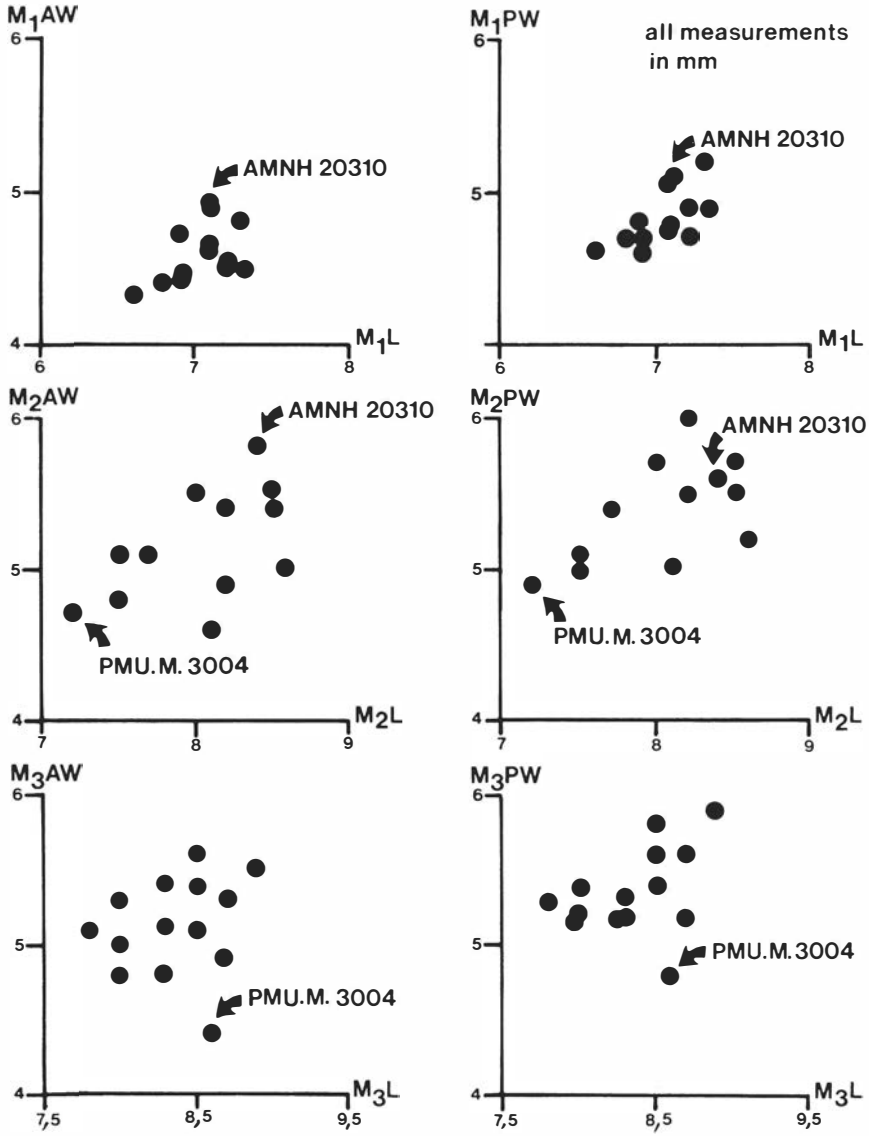

Fig. 3. Bivariate plots of measurements (Table 1) of the lower molars of *Rhodopagus*. AMNH 20310 is the holotype of *R. minimus*; PMU. M. 3004 is the holotype of *R. zdanskyi*, new species.

canine diastema, loss of P_1, relatively high protolophids and hypolophids and reduced paralophids on M_{2-3}, distinct metalophids and small posterior cingulids on M_{2-3} and lack of a M_3 hypoconulid. Assignment of the specimen to *R.* thus is certain. However, PMU. M. 3004, 3006 differs from the Mongolian specimens in the following detailed features: M_3 significantly narrower and M_2 relatively narrow as well; M_2 significantly shorter (the M_3 of PMU. M. 3004 might also be relatively short but the tooth is broken and damaged making it impossible to obtain an accurate measurement); metalophid on M_3 relatively high, joining the protolophid at a point relatively lingual of the protoconid; M_{2-3} paralophids higher and convex forward (arcuate) instead of transversely straight; M_{2-3} protolophids distinctly taller than hypolophids instead of both lophids subequal in height; M_3 trigonid open and long so that it has a nearly triangular cross-section instead of a rectangular

Table 1. Dental measurements of *Rhodopagus* (in mm. L = length, W = width, A = anterior, P = posterior; asterisks (*) indicate approximate measurements of damaged teeth).

	M_1L	M_1AW	M_1PW	M_2L	M_2AW	M_2PW	M_3L	M_3AW	M_3PW
R. minimus:									
AMNH 20310[a]	7,1	4,9	5,1	8,4	5,8	5,6*			
AMNH 20330	6,9	4,4	4,6	7,7	5,1	5,4	8.9	5,5	5,9
AMNH 20331	6.9	4,7	4,8	7,5	5,1	5,1	8,0	5,0	5,2
AMNH 20332	7,2	4,5	4,7	8,6	5,0	5,2			
AMNH 20333	6,6	4,3	4,6	7,5	4,8	5,0			
AMNH 20334	7,1	4,9	5,1						
AMNH 20335	6,9	4,4	4,7						
AMNH 20336	7,1	4,6	4,8						
AMNH 20339							8.0	5,3	5,4
AMNH 20340							8,7	5,3	5,6
AMNH 20341							7,8	5,1	5,3
AMNH 20390				8,5	5,4	5,5	8,5	5,6	5,8
AMNH 20391a				8,5	5,5	5,7			
AMNH 20391b				8,2	4,9	5,5			
AMNH 20392a							8,7	4,9	5,2
AMNH 20392b							8,3	5,4	5,2
AMNH 20392c							8,3	5,1	5,3
AMNH 20392d							8,3	4,8	5,2
AMNH 20392e							8,0	4,8	5,2
AMNH 20393a				8,1	4,6	5,0			
AMNH 20393b	7,3	4,5	4,9						
AMNH 20393c	6.8	4,4	4,7						
AMNH 20393d	7,1	4,6	4,8						
AMNH 20394							8,5	5,1	5,4
AMNH 26112	7,3	4,8	5.2	8,0	5,5	5,7*			
AMNH 26114	7,2	4,5	4,9	8,2	5,4	6,0	8,5	5,4	5,6
Mean	7,04	4,58	4,84	8,11	5,19	5,43	8,35	5,18	5,41
Standard Deviation	0,21	0,20	0,19	0,40	0,36	0,32	0,33	0,26	0,24
Coefficient of Variation	2,98	4,36	3,92	4,93	6,94	5,89	3,95	5,02	4,44
R. zdanskyi:									
PMU. M. 3004[b]				7,2	4,7	4,9	8,6*	4,4	4,8

[a] Type specimen of *R. minimus* (Matthew & Granger 1925).
[b] Type specimen of *R. zdanskyi*, new species.

one; and M_3 posterior cingulid more distinct and longer. Based on these differences we recognize it as the type of a distinct species. Comparison with *Triplopus* suggests that *R. zdanskyi* is more primitive than *R. minimus* (note, for example, the narrower molars, larger M_3 posterior cingulid, tall protolophid, etc.) and it thus may be from beds of slightly older age than the Ulan Shireh and Shara Murun.

Other occurrences of *Rhodopagus*

Three other possible occurrences of *R.* in China are known to us: 1. Zdansky (1930, p. 38, Pl. 1, Figs. 36—37) described and illustrated an isolated lower molar he referred to "Lophiodontide, gen. et sp. indet." from Mianchi County, Henan Province, eastern China. Radinsky (1965, p. 212) noted the similarity of this tooth to *R.*, and its size (length = 7,9 mm, width = 4,7 mm: Zdansky 1930, p. 38) suggests it could be a M_2 or M_3 of *R. minimus* (cf. Fig. 3, Table 1). More complete material, however, is needed to justify a definite identification. 2. Radinsky (1965, p. 211) referred AMNH 81842, an isolated P_3 or P_4 plus an unassociated lower molar, and AMNH 81843, a dentary fragment with M_{1-3} to "*?Rhodopagus pygmaeus*". Both specimens are from the type Irdin Manha beds at the Irdin Manha Escarpment, Inner Mongolia, China. Radinsky (1965 p. 211) stated that "the lower molars average about ten percent longer (but no wider) than those of *R. pygmaeus* and have relatively longer trigonids"

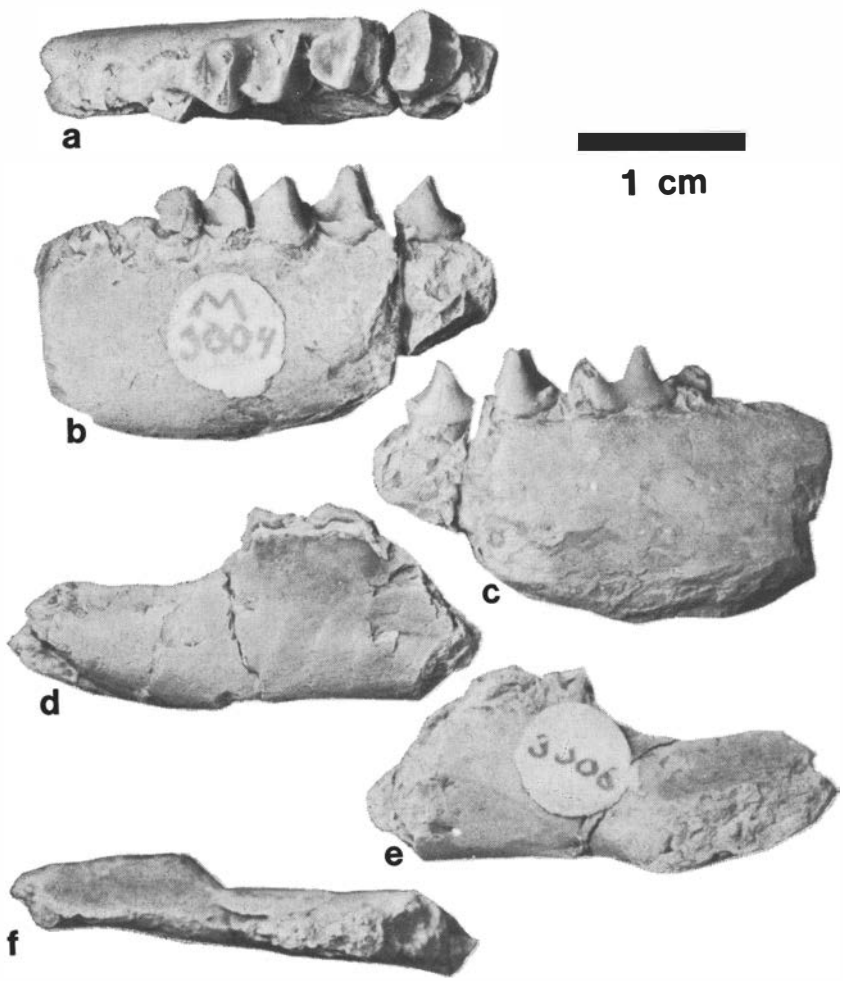

Fig. 4. The holotype of *Rhodopagus zdanskyi*, new species, PMU. M. 3004 and 3006. a—c, PMU. M. 3004, left dentary fragment with M_1 roots and M_{2-3}, occlusal (a), labial (b) and lingual (c) views. d—f, PMU. M. 3006, left dentary fragment with C root, partial P_{2-3} and P_4 alveolus, labial (d), lingual (e) and occlusal (f) views.

to justify his unwillingness to definitely assign these specimens to *R. pygmaeus*. Our measurements of the M_1 of AMNH 81843 (length = 7,5 mm, anterior width = 4,4 mm, posterior width = 4,7 mm; note that M_2 is damaged and M_3 not fully erupted) place it just at the large end of the cluster for *R. minimus* (Fig. 3). Measurements of the isolated molar that is part of AMNH 81842 (length = 8.2 mm, anterior width = 4,6 mm, posterior width = 4,7 mm) fall within the cluster of M_2 measurements of *R. minimus* (Fig. 3). It seems likely, therefore, that both specimens pertain to *R. minimus*. However, the trigonids of these specimens are relatively longer, as pointed out by Radinsky (1965), and we only refer them tentatively to *R. minimus* as *R.* cf. *R. minimus*. 3. Zheng et al. (1978) have reported *R.* from the Lunan Basin in Yunnan Province, southern China, but no specimens have been described or illustrated to substantiate this report.

Systematic position of *Rhodopagus*

Radinsky (1965, p. 207) noted that 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 meta-

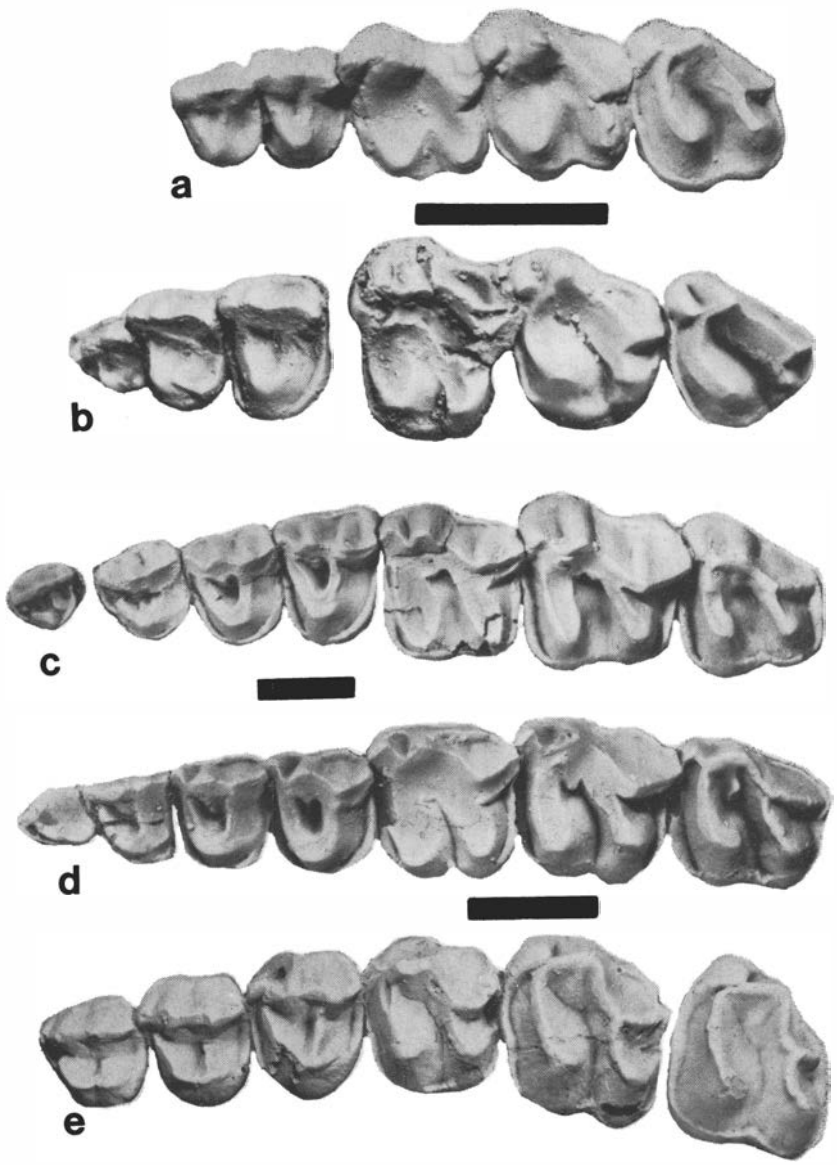

Fig. 5. The upper cheek teeth of *Rhodopagus* compared with selected tapiroids and hyracodontids. a, AMNH 21554, left P^3—M^3, type of *Rhodopagus pygmaeus*. b, AMNH 21747, right P^2—M^3 (photograph reversed), type of *Pataecops parvus*. c, AMNH 21552, left P^1—M^3 referred to *Triplopus? proficiens* by Radinsky (1967). d, AMNH 26118, left P^1—M^3 referred to *Lophialetes expeditus?* by Radinsky (1965). e, AMNH 19161, right P^2—M^3 (photograph reversed), type of *Helaletes mongoliensis*. The black bars are one cm long (one scale for a and b, one scale for c, one scale for d and e).

lophs, sets this genus apart from all other previously described tapiroids". He then tentatively assigned *R.* to the Lophialetidae, a family of tapiroids. Radinsky (1965, p. 214) further argued that similarities between the dentitions of *R.* and helaletid tapiroids were "probably due to convergence". He contended that the dentition of *R.* "could be derived from that of a primitive lophialetid, such as the (unknown) ancestor of *Schlosseria*, but no intermediate forms are known" (Radinsky 1965, p. 214). The long ectoloph of *R.* and *Lophialetes* (Fig. 5, a, d) was also cited by Ra-

dinsky to support his assignment of *R.* to the Lophialetidae.

We here approach the problem of the systematic position of *R.* by cladistic analysis aimed at discerning derived characters *R.* shares with other perissodactyls. Based on such an analysis, we consider *R.* to be a hyracodontid because it shares the following derived characters with members of the Hyracodontidae (*sensu* Radinsky 1966, 1967, 1969): 1. Relatively high-crowned teeth. The crown height index of specimens of *R.* averages 0,6, nearly the same as that of *Triplopus*, *Forstercooperia* and other hyracodontids (Radinsky 1967). 2. Long and flat M^{1-2} ectolophs resulting from the lengthening of the metacone. 3. Protoloph longer than metaloph, both lophs oblique to the transverse axis of the tooth. In *R.* this is the "peculiar upper cusp pattern ... with its oblique inverted U- to V-shaped shearing lophs" mentioned by Radinsky (1965, p. 207). 4. Reduced parastyles on the upper molars. 5. M^3 triangular (or nearly so) due to the lingually depressed and reduced metacone. 6. Metaloph confluent with the ectoloph in the upper molars. 7. Relatively high paralophids and metalophids on the lower molars. 8. No hypoconulid on M_3.

In assigning *R.* to the Hyracodontidae we point out the strong similarity of its dentition to that of *Triplopus* (cf. Fig. 5, a, c). Superficially, the upper dentition of *Lophialetes* (Fig. 5, d) resembles that of *Triplopus* and *R.* But, on closer examination, the molar metalophs are not confluent with the ectolophs and the large M^3 metacone results in a square M^3 outline in *Lophialetes*. Note also that the lower dentition of *Lophialetes* differs from that of hyracodontids in the retention of a M_3 hypoconulid, among other features (Radinsky 1965).

As noted above, Radinsky (1965) alluded to convergent similarities between *R.* and helaletid tapiroids. These similarities are largely in the lower dentition: helaletids lack an M_3 hypoconulid and have a bilophodont lower dentition similar to that of *R.* However, the upper dentition of helaletids, such as *Helaletes* (Fig. 5, e), differs greatly from that of *R.* Among other features, *Helaletes* lacks a long flat ectoloph, has large parastyles and has metalophs longer than protolophs, all characters that preclude a close relationship to *R.* and other hyracodontids.

As a final note, if *R.* is assigned to the Hyracodontidae then *Pataecops* Radinsky 1966 must also be assigned to the hyracodontids. The upper dentition of *Pataecops* (Fig. 5, b) displays all the derived hyracodontid features cited above. Indeed, *Pataecops* appears to be an even more derived hyracodontid than *R.* because its M^3 metacone is virtually absent, M^3 is more triaugular in outline and the molar metalophs are much shorter than the protolophs.

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