

A RHINOCEROTID PERISSODACTYL FROM THE LATE MIDDLE EOCENE PONDAUNG FORMATION, MYANMAR

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The ungulate fauna of the upper middle Eocene Pondaung Formation in Myanmar was long thought to be composed principally of anthracotheriid artiodactyls and amynodontid perissodactyls, with rare “tapiroids” and small ruminants comprising the remainder (Pilgrim and Cotter, 1916; Pilgrim, 1925, 1928; Colbert, 1938; Métais et al., 2000; Tsubamoto et al., 2000b, 2002a). More recent work has revealed a much more diverse ungulate fauna, including helohyid and homacodontine dichobunid artiodactyls, ceratomorph and primitive brontotheriid perissodactyls, and a small and primitive indeterminate ungulate (Holroyd and Ciochon, 1995, 2000; Ducrocq et al., 2000a, b; Tsubamoto et al., 2000, 2003).

Here we add to this diversity of ungulates with the description of the first evidence for rhinocerotid perissodactyls in the Pondaung fauna and tentatively assign these fossils to *Teletaceras* (Hanson, 1989). *Teletaceras* is the oldest and most basal member of the extant family Rhinocerotidae and is previously known from the upper middle Eocene of western North America (Hancock Quarry, Oregon; Duchesnean North American Land Mammal Age) and northeastern Asia (Artyom or Artëm, Maritime Province, Russia; Sharamuruniian Asian Land Mammal Age; Hanson, 1989). Lucas et al. (2004) have offered an alternative interpretation of the age of these two records, based on the presence of some typically Uintan mammals in the Hancock Quarry fauna, and reassessment of the other perissodactyl taxa from Artyom suggesting it may be either Sharamuruniian or Ergilian in age. Interpretation of the age of these sites is problematic, as the Artyom fauna comprises only a few specimens, and as Lucas et al. (2004) noted, radiometric dates for sediments overlying the Hancock Quarry can only indicate that it is older than 30–40 Ma and that it is a mix of taxa with middle to late Eocene ranges elsewhere. Although an Asian origin has long been presumed for the family (see e.g., Beard, 1998; Prothero, 1998), the age of the oldest occurrence and area of origin of the family are not clear from these records. Recognition of the Pondaung specimens as Rhinocerotidae provides the first middle Eocene record of the family in Southeast Asia and provides one of the few Asian records that can be directly tied to radiometric dates, permitting us to more confidently establish a minimum age for the origin of Rhinocerotidae.

The specimens described here were found at localities in central Myanmar, approximately 21° 30' N to 22° N, 94° 30' to 95° E; detailed maps and locality data are provided in Tsubamoto et al. (2000a, 2003) and Gunnell et al. (2002). All these localities occur within the informally named “upper member” of the Pondaung Formation (Aye Ko Aung, 1999) and have been interpreted as floodplain deposits (Gunnell et al., 2002; Soe et al., 2002). Biostratigraphic correlations indicate the fauna is approximately coeval with the late middle Eocene Sharamuruniian Asian Land Mammal ‘Age’ and Duchesnean North American Land Mammal ‘Age’ (Holroyd and Ciochon, 1994). Recent field studies conducted by American, French, and Japanese teams working with colleagues from Myanmar have provided a more comprehensive stratigraphic framework for these sediments (e.g., Aye Ko Aung, 1999; Soe et al., 2002) and a fission-track age of 37.2 ± 1.3 Ma (Tsubamoto et al., 2002b), firmly establishing the latest middle Eocene age of the deposits.

Abbreviations—**NMMP-KU**, National Museum of Myanmar, Paleontology (Yangon, Myanmar)-Kyoto University (Japan); **UCMP**, Univer-

sity of California Museum of Paleontology, Berkeley, California. Dental nomenclature follows Antoine (2002).

SYSTEMATIC PALEONTOLOGY

Order PERISSODACTYLA Owen, 1848
Superfamily RHINOCEROTOIDEA Gray, 1825
Family RHINOCEROTIDAE Gray, 1821
Genus *Teletaceras* Hanson, 1989
cf. Teletaceras sp.
(Figs. 1, 2)

cf. Ilianodon lunanensis: Tsubamoto et al., 2000a:54–55, 88, pl. 17.

Referred material—NMMP-KU 0288, a right M3 from Mta (mesiodistal length [estimate] = 23.7 mm, buccolingual width = 27.0 mm); NMMP-KU 1060, a right M3 from Pk2 (mesiodistal length = 21.9 mm, buccolingual width = 24.5 mm); NMMP-KU 0057, a broken right M1 or M2 from Bahin area (near Paukkaung village); UCMP 128401, a right mandibular fragment with partial m1 and m2 from Mogaung area (m1 talonid width = 15.3 mm, m2 length = 24.0 mm, m2 trigonid width = 15.9 mm, m2 talonid width = 16.1 mm).

Description—The upper molars (Fig. 1) exhibit a rhinocerotid/hyracodontid dental morphology. The M3s (Fig. 1a, b) are triangular in occlusal view with very reduced metacone and metastyle and show a bilophodont structure. The parastyle is well developed. Parastyle and paracone are separated by a buccal depression. The metaloph is continuous with the ectoloph, forming a straight ecto-metaloph. The protoloph links to the parastyle. The hypocone is as large as the protocone, and its tip curves mesially in lingual view. A strong precingulum originates from the distal base of protoconid, disappearing at the mesiolingual base of the parastyle. Lingual and buccal cingula are absent. In NMMP-KU 0288, a faint postmetacrista (=metastyle) runs down distolingually from the ecto-metaloph at the point slightly closer to the hypocone rather than to the paracone. At the most distal part of the crown (below the postmetacrista), there seems to be a small distal cingulum, although this part is broken. In NMMP-KU 1060, there is a distinct but small distal cingulum. Although NMMP-KU 0057 is heavily worn and broken, its morphology indicates a rhinocerotid/hyracodontid M1 or M2 morphology. There is slight antecrochet on these three upper molars, but there is no crochet.

The lower molar dentition, UCMP 128401 (Fig. 2), has a partial and heavily worn m1 and a moderately worn m2, both of which match hyracodontid/rhinocerotid molar morphology and match the above described upper molars both in size and morphology. The lower molars have a rectangular occlusal outline and two crests (paralophid-protolophid and metalophid-hypolophid) open lingually. The talonid of m1 and the trigonid and talonid of m2 have nearly the same width, and the trigonid of m1 is slightly narrower. The mesiolingual end of the paralophid (=paracristid) is less lingually positioned than in *Teletaceras radinskyi*. Metalophid (=cristid obliqua) extends mesiodistally rather than diagonally. The talonid basin is deeper than the trigonid basin. The hypolophid is slightly oblique, but is nearly transverse in occlusal view. There are no

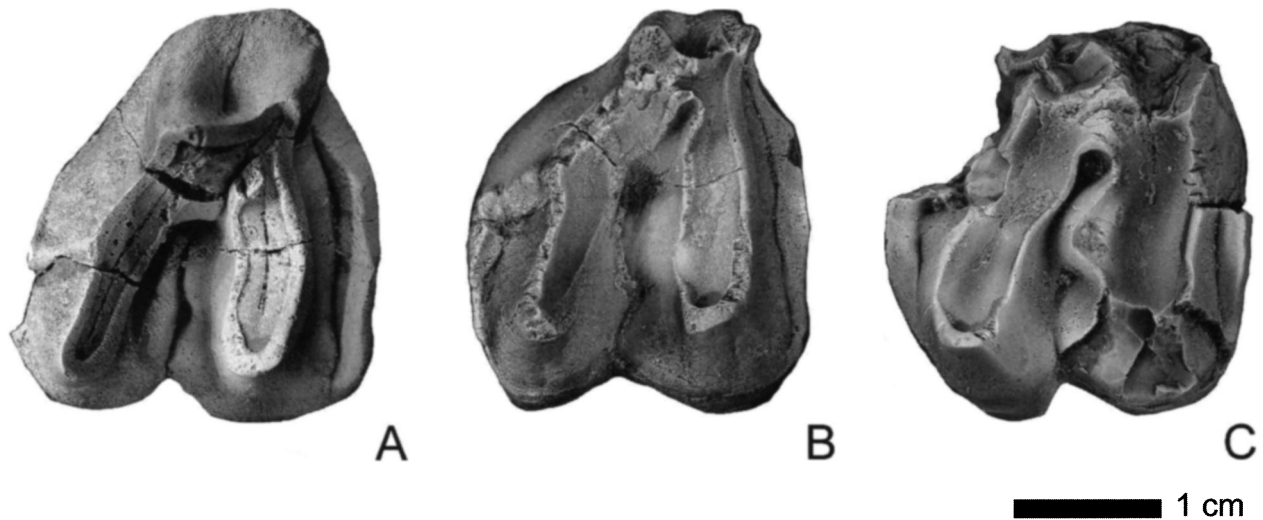


FIGURE 1. Upper molars of the Pondaung rhinocerotid. **A**, NMMP-KU-0288; **B**, NMMP-KU 1060; **C**, NMMP-KU-0057.

lingual or buccal cingulids. A weak precingulid exists on the mesiobuccal face of m2 (this part is broken on m1), and weak postcingulids traverse the distobuccal face of m1–2. There is an interstitial wear facet on the distal face of m2.

DISCUSSION

As noted by Hanson (1989) and Prothero et al. (1989), the earliest occurring hyracodontids and rhinocerotids are difficult to distinguish

dentally. Also, recognizing rhinocerotid/hyracodontid taxa based solely on molar morphology is difficult. Hanson (1989) assigned *Teletaceras* to Rhinocerotidae based largely on postcranial and incisor characters. Prothero et al. (1989) considered the incisor conformation and reduction of the M3 metacone and metastyle to be the most notable rhinocerotid features in the dentition of the Clarno rhinoceros (= *Teletaceras*). However, as illustrated by Lucas and Sobus (1989), metacone/metastyle reduction is also a feature of indricotheriine hyracodontids (or indricoth-

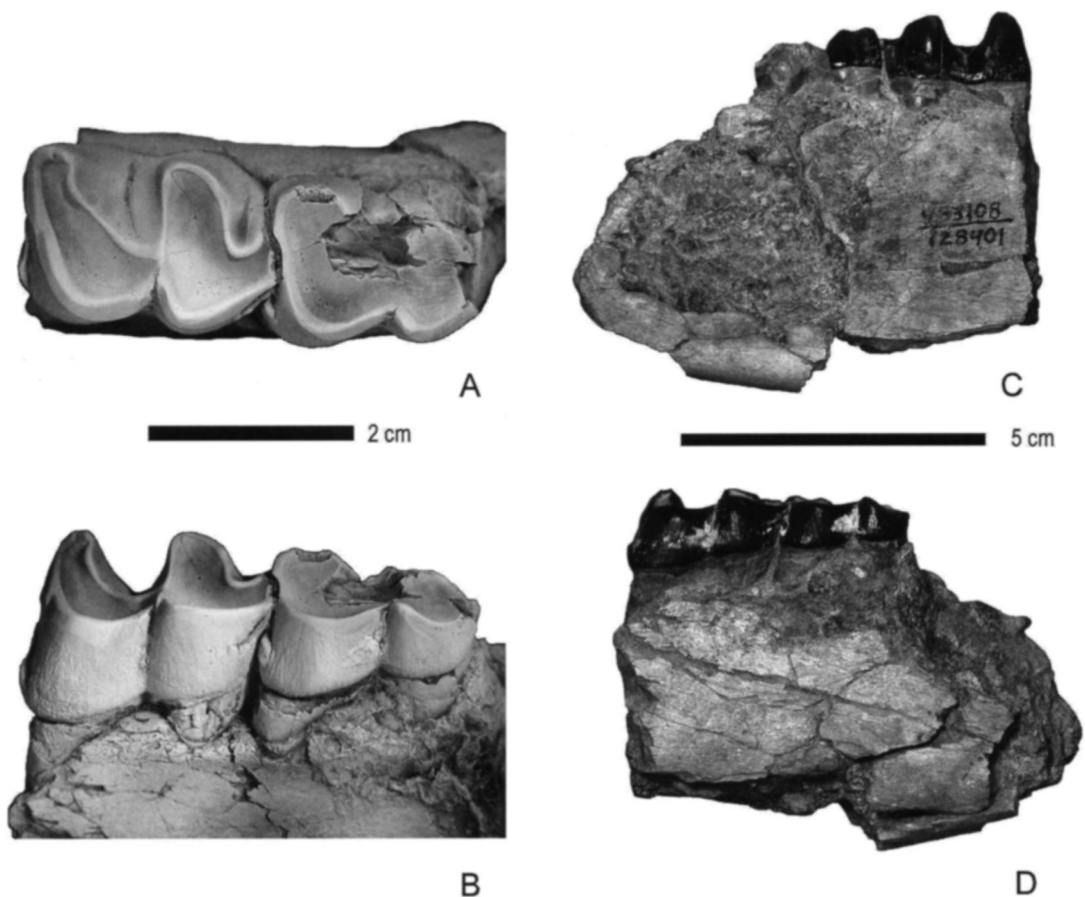


FIGURE 2. Right mandibular fragment with partial m1 and m2 of the Pondaung rhinocerotid. UCMP 128401. **A**, occlusal; **B**, occlusolateral; **C**, lingual; and **D**, lateral view.

eriids; see Heissig, 1989), a group that is widespread in the middle Eocene to Oligocene. How many times M3 metacone/metastyle reduction arose within Rhinocerotidae is open to interpretation. Heissig (1989) considered Indricotheriidae a sister taxon to Rhinocerotidae, uniting them in part based on this character. However, Radinsky (1966) contended, and Prothero et al. (1986) and Hanson (1989) further detailed, several instances of independent loss of the M3 metastyle within individual species or genera of Eocene rhinocerotids. On the other hand, Antoine (2002) and Antoine et al. (2003) mentioned that the mesiodistally oriented molar metalophid is one of the characteristics of Rhinocerotidae. The Pondaung specimens are referable not to Hyracodontidae but to Rhinocerotidae, and very closely resemble the dentition of the earliest rhinocerotid, *T. radinskyi*, both in size and dental morphology.

The M3 of the Pondaung form exhibits a complete triangular shape in occlusal view, with reduction of metacone and metastyle and a straight ecto-metaloph running from paracone to metacone. This M3 morphology is identical to that of rhinocerotids, and in contrast to that of hyracodontids in which the metacone is distinct, the metaloph curves between the hypocone and metacone, resulting in a more rectangular M3 shape (although Fig. 20.5 [Hanson, 1989] demonstrates that both morphologies are present in the population of *T. radinskyi*). The Pondaung form can be excluded from indricotheriine hyracodontids on the basis of its much smaller size and the fact that the M3 of indricotheres are longer relative to their width. In comparing the M3s of the Pondaung form with that of contemporaneous hyracodontids and rhinocerotids, we can see that the hypocone is enlarged and subequal to the protocone in size and aligned with it along the lingual border of the tooth as in rhinocerotids. This conformation is unlike the condition in hyracodontids (e.g., *Hyracodon* and *Triplopus*), in which the M3 hypocone is smaller and narrower than the protocone and is positioned more buccally. The triangular M3 morphology with reduced but distinct distal cingula and the size of the Pondaung form are almost identical to corresponding features of *T. radinskyi*. Between the two Pondaung M3 specimens, there is variation in the expression of the metastyle and posterior cingulum. In NMMP KU 1060, a small and low style is present, and there is a relatively well-developed posterior cingulum extending along the lingual half of the posterior face of the tooth. In NMMP KU 0288, there is weaker metastyle ridge, and the posterior cingulum, which seems to be smaller than that of NMMP-KU 1060, is broken. Such variability was documented by Hanson (1989:fig. 20.5) in his single-quarry study of *T. radinskyi*, and is not unexpected.

The lower dental material, UCMP 128401, most closely resembles *T. radinskyi* among described rhinocerotids and hyracodontids both in morphology and size. As noted by Hanson (1989), the lower molars of *Teletaceras* show intermediate characters between those of hyracodontids and later rhinocerotids. These intermediate characters include a paralophid that turns sharply inward at the mesiobuccal corner of the molars (vs. the more smoothly arcuate and longer paralophid of the hyracodontid *Triplopus*) and having cingula developed only along the anterior and posterior faces of the molars (vs. the presence of cingula on the labial and lingual surfaces in hyracodontids, such as *Hyracodon* and *Ardynia*). Also, the Pondaung form has a mesiodistally oriented metalophid, which is one of the characteristics of rhinocerotids (Antoine, 2002; Antoine et al., 2003). In these features, UCMP 128401 matches rhinocerotids. The lower molar dentition of the Pondaung form is almost identical to that of *T. radinskyi*, although the former differs from the latter in having a less buccally extended paralophid.

Tsubamoto et al. (2000a) tentatively referred NMMP-KU 0288 (M3 material) to *Ilianodon lunanensis* (Chow and Xu, 1961) (?Hyracodontidae) from the middle Eocene of south China. However, the only upper molar material of *I. lunanensis* is a broken M3, and it is not clear whether the Pondaung form is really related to *I. lunanensis* or not. The lower molar dentition of the Pondaung form is distinct from that of *I. lunanensis* in having much less mesiodistally elongated molar paralophid and metalophid, and so is not referable to *Ilianodon*.

Among other middle to late Eocene Asian rhinocerotids, the lower molars of the Pondaung rhinocerotid can be compared with the holotype lower dentition of *Guixia simplex* from the upper Eocene of south China (You, 1977) and an m2–m3 assigned to ?*Guixia* cf. *G. simplex* from the upper Eocene of Thailand (Antoine et al., 2003). The second molar is the only tooth that can be compared, and the m2 of the Pondaung rhinocerotid is similar in size and morphology to those of *G. simplex* and the Thai specimen. Antoine et al. (2003) distinguished their specimens from *T. radinskyi* based on the “more constricted entoconid and metaconid.” In unworn or little-worn specimens of *T. radinskyi*, the cusp tips are

markedly compressed anteroposteriorly; however, this compression disappears with wear. In comparing the range of variation in specimens of *T. radinskyi* at similar wear stages, we do not find that these cusps are noticeably more or less constricted than the Southeast Asian specimens. In fact, the morphology and size of m2 in both *Guixia* and *Teletaceras* is quite similar, and it is difficult to differentiate these taxa based solely on lower molar morphology. On the other hand, the upper molar dentition of the Pondaung rhinocerotid differs from that of *Guixia* in being smaller and in lacking a crochet, suggesting that the former is more primitive than the latter.

Comparison of the Pondaung rhinocerotid remains with other Eocene Asian and North American rhinocerotoid lineages indicates that their greatest similarity is with *Teletaceras*, the earliest rhinocerotid, and that they are referable to the Rhinocerotidae. The lower molar morphology of the Pondaung specimens is close to that of *Teletaceras* as well as to specimens assigned to *Guixia*, but the upper molars show greater similarity to those of *Teletaceras* rather than *Guixia*. Although fragmentary, the recognition of a rhinocerotid in the Pondaung fauna allows us to assign a date of approximately 37.2 Ma for the minimum age of divergence for this extant perissodactyl family and provides a tie-point that may prove useful in future attempts to correlate North American and Asian faunas.

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