

BUNOBRONTOPS SAVAGEI: A NEW GENUS AND SPECIES OF BRONTOTHERIID PERISSODACTYL FROM THE EOCENE PONDAUNG FAUNA OF MYANMAR

PATRICIA A. HOLROYD¹ and RUSSELL L. CIOCHON², ¹Museum of Paleontology, University of California, Berkeley, California 94720; ²Departments of Anthropology and Pediatric Dentistry, University of Iowa, Iowa City, Iowa 52242

The Pondaung fauna from the late middle Eocene deposits of Myanmar (Burma) continues to remain one of our few glimpses into Paleogene faunas of Southeast Asia. The fauna is best known for its abundant anthracotheriid artiodactyls (Pilgrim and Cotter, 1916; Pilgrim, 1928, 1941; Colbert, 1938) and for its enigmatic primates (e.g., Pilgrim, 1927; Colbert, 1937; Ba Maw et al., 1979; Ciochon et al., 1985; Ciochon and Holroyd, 1994; Holroyd and Ciochon, 1994). Within this fauna, the representatives of the Order Perissodactyla and especially the taxa documenting brontotheriid diversity in the area have been the least studied and most often ignored in wider systematic studies.

Pilgrim and Cotter (1916) and Colbert (1938) described a total of four brontotheriid species ultimately placed in two genera—*Metatelmatherium* and *Sivatitanops*—from the Pondaung region. No new material adequate to resolve questions regarding specific attributions within *Sivatitanops* or Burmese *Metatelmatherium* has been recovered. Instead, evidence of another new, distinct genus has been found. This taxon is sufficiently distinct on morphological grounds to differentiate it from specimens attributed to either *Sivatitanops* or *Metatelmatherium* and from other Asian as well as North American brontotheriids.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York; UCMP, University of California Museum of Paleontology, Berkeley.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order PERISSODACTYLA Owen, 1848
Family BRONTOTHERIIDAE Marsh, 1873
BUNOBRONTOPS SAVAGEI, gen. et sp. nov.
(Fig. 1A–E, G, I)

Holotype—UCMP 128416, right M2 from UCMP locality V83116 (Fig. 1B).

Hypodigm—UCMP nos. 128414, right m3 from locality V83116 (Fig. 1E); 128391, left M2 from locality V83105 (Fig. 1A); 147045, right M3 from locality V96019 (Fig. 1C); 147046, partial right upper molar from locality V96019 (Fig. 1D); 147047, left m1 or m2 talonid from locality V96019 (Fig. 1I); 147048, left m1 or m2 talonid from locality V96019 (Fig. 1G).

Type Locality—UCMP V83116, “approximately 3 mi [4.8 km] north of Bahin” village, Pale Township.

Distribution—Late middle Eocene (Sharamuruni equivalent) Pondaung sandstone as exposed at several localities within Pale Township, Sagaing Division, central Myanmar. Precise locality data on file at UCMP.

Diagnosis—Differs from all other brontotheriids in having: moderately crenulate enamel present on the lingual surfaces of the upper molars and in the basins of the lower molars; lower crowned lower molars in which the talonid is relatively longer than the trigonid, the premetacristid is absent, and the cristid obliqua meets the protolophid near the midline of the tooth rather than connecting with the metaconid and postmetacristid. Differs from more advanced brontotheriids such as *Microtitanops*, *Protitan*, *Pygmaetitan*, *Sivatitanops*, and *Metatelmatherium* in having: relatively shorter and wider upper molars with larger paraconules, more poorly developed buccal shearing crests that do not curve lingually, relatively higher lingual cusps with better developed crests, larger and more anteriorly positioned hypocone with strong prehy-

pocone crista. Differs from more primitive brontotheriids such as *Eotitanops*, *Palaeosyops*, and *Telmatherium* in having a better developed hypocone, relatively smaller and more anteriorly positioned paraconule.

Etymology—Generic name with reference to the more bunodont nature of the dentition in contrast to other Asian brontotheres. Trivial name in honor of Donald E. Savage, in recognition of his seminal role in reinitiating fieldwork in the Pondaung Hills in the latter part of the twentieth century.

Description—The upper molars are subsquare in occlusal outline, slightly wider transversely than long. Four main cusps are present and are subequal in size. A small paraconule is present. It is anteriorly positioned and confluent with a strong anterior cingulum that extends to the base of the protocone. The protocone and paracone are slightly lower than the metacone and hypocone. The paracone and metacone are joined by a W-shaped ectoloph typical of brontotheriids, on which both the para- and mesostyle are moderately developed. A much smaller metastyle is also present. External ribs are slightly developed on the buccal surfaces of both the paracone and metacone. The hypocone is well developed and surrounded by a strong distolingual cingulum. Both pre- and posthypocristae are strong, with the posthypocrista extending to the base of the metastyle. The prehypocrista takes an anteromedial course, ending just posterior of the center of the tooth. The M2 and M3 differ primarily in the relatively smaller size of the hypocone on M3 and the expansion of the lingual portion of the distolingual cingulum on M3, which occludes with the short m3 hypoconulid loop. Dimensions in mm for the three upper molars are: UCMP 128391, greatest transverse width = 43.9, length = 39.6; UCMP 128416, greatest transverse width = 43.6, length = 40.1; UCMP 147045, greatest transverse width = 46.6, length = 43.9.

Lower molar morphology is known primarily from UCMP 128414, a right m3. The tooth is low crowned and relatively wide, in contrast to other brontotheriids. The trigonid is short and slightly narrower than the talonid. The protolophid and paracristid are well developed, and no paraconid is apparent. The trigonid basin is shallow, and its enamel is deeply folded. The trigonid basin is enclosed anteriorly by a smoothly arcing paracristid that extends to the base of the metaconid. The protoconid lies only slightly anterior of the metaconid. The talonid basin is nearly twice the length of the trigonid and is also shallow and marked by deep enamel crenulations. The talonid basin is delimited lingually by a short but strong preentocristid and a longer, strong postmetacristid that is slightly expanded to form a small metaconulid. Labially, the cristid obliqua takes a mesiolingual course, meeting the protolophid near the tooth's midline. The hypolophid is low but strong. A centrally placed and well-developed hypoconulid is present, bearing strong but low crests joining it lingually to the entoconid and terminating buccally near the base of the entoconid and just below the crest of the hypolophid. A slight crenulate cingulum surrounds the base of the hypoconulid.

Two fragmentary talonids (UCMP 147047 and 147048) show evidence of strong anterior and posterior cingula that are higher medially and slope toward the base of the tooth, and these specimens are inferred to be either m1 or m2. Measurements in mm for lower molar specimens are: UCMP 128414, maximum length = 57.9, trigonid width = 28.8, talonid width = 29.0, width of hypoconulid = 19.4; UCMP 147047, talonid width = 28.9; UCMP 147048, talonid width = 25.5.

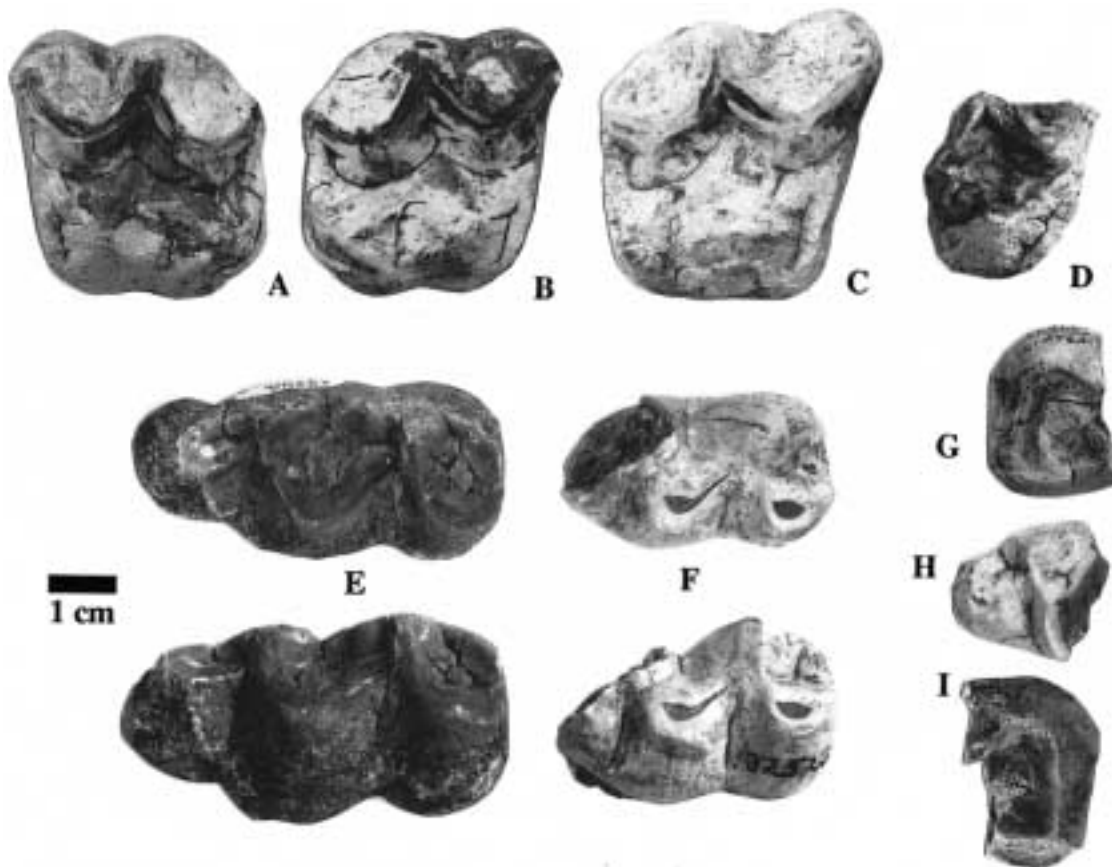


FIGURE 1. *Bunobrontops savagei*, A–E, G, I, and *Bunobrontops* sp., F, H. A, UCMP 128391, right M2; B, UCMP 128416, holotype, left M2; C, UCMP 147045, right M3; D, UCMP 147046, right M protocone; E, UCMP 128414, right m3 in both occlusal and occluso-lateral views; F, AMNH 32523b, right m3 in both occlusal and occluso-lateral views; G, UCMP 147048, left m1 or m2 talonid; H, AMNH 32523a, right m3 fragment; I, UCMP 147047, m1 or m2 talonid.

BUNOBRONTOPS sp.
(Fig. 1F, H)

Two additional fragmentary specimens, AMNH 32523a (Fig. 1H) and 32523b (Fig. 1F) collected by Barnum Brown in 1923 “1 mi [1.6 km] N. Koniwa” represent smaller individuals of this genus. AMNH 32523a is a right m3 fragment with hypoconulid and entoconulid, and AMNH 32523b is a right m3 lacking the entoconid and the lingual portion of the hypoconulid. Both are similar in morphology to UCMP 128414, but are approximately 20 percent smaller in comparable dimensions. Measurements in mm: AMNH 32523b, trigonid width = 24.5, talonid width = 24.0; AMNH 32523a, hypoconulid width = 15.1. These size differences may reflect temporal differences within a single species or specific differences. The sample is simply too small to determine which might be the case, so these specimens are referred to *Bunobrontops* without specific attribution.

Additional specimens previously described from the Pondaung may also be ultimately attributed to *Bunobrontops*. Colbert (1938) noted the presence of various postcranial elements and two incisors that belong to brontotheriids from AMNH Localities 7, A20, A21, A23, and A27. All these specimens are distinguished from amynodontids by their slightly smaller size, but whether they pertain to *Sivatitanops*, *Metatelmatherium*, or *Bunobrontops* cannot be determined with confidence.

Discussion—Although recognizing a new brontotheriid genus from molars alone is possible when the taxon is as distinc-

tive as *Bunobrontops*, providing an adequate diagnosis and assessing its phylogenetic position with respect to other brontotheriids is a difficult task. Brontotheriid genera are differentiated principally by characters of the cranium and the anterior dentition (as exemplified in Mader, 1989). Mader (1989) and Lucas and Schoch (1989) have provided revisions of the North American and European representatives of the family, respectively. However, no one has tackled the weighty problem of evaluating and synonymizing the plethora of brontotheres described from Asia (see Prothero and Schoch, 1989, for discussion of the problem).

Advanced brontotheres can be dentally typified by upper molars that are slightly longer than wide with extreme development of the buccal shearing crest and weakly developed to absent cristae on the protocone and hypocone. Most North American and Asian brontotheres (including *Sivatitanops* and *Metatelmatherium* from the Pondaung fauna) belong to this likely-monophyletic group. In lacking these derived characters, *Bunobrontops* falls outside the Brontotheriinae (sensu Mader, 1989) and would occupy a more basal position in the phylogeny of the family, along with primitive brontotheres such as *Eotitanops* and *Paleosyops*. Beard (1998) noted that the ancestry of *Paleosyops* and *Eotitanops* must be sought outside North America, although no comparably primitive brontotheriids were known in Asia or Europe. Although *Bunobrontops* is clearly autapomorphically derived with respect to either of these taxa, its retention of upper molars that are wider than long, with well

developed cristae on the lingual cusps and only moderately developed buccal shearing crests are all primitive features absent in other Asian brontotheres and elsewhere seen in *Paleosyops* and *Eotitanops*. *Bunobrontops* appears to represent a lineage near these two taxa and attests to the presence of a primitive brontothere stock that is still undetected in early middle Eocene faunas of Asia.

Acknowledgments—We are grateful to U. Ba Maw, Department of Geology, Mandalay University (retired) and D. E. Savage (deceased) for their part in recovery of these specimens. M. C. McKenna kindly provided access to the AMNH material described here, and J. Alexander provided for its curation. This work was funded in part by the Annie M. Alexander Endowment of the UCMP. This is UCMP publication no. 1693.

LITERATURE CITED

- Ba Maw, U., R. L. Ciochon, and D. E. Savage. 1979. Late Eocene of Burma yields earliest anthropoid primate, *Pondaungia cotteri*. *Nature* 282:65–67.
- Beard, K. C. 1998. East of Eden: Asia as an important center of taxonomic origination in mammalian evolution. *Bulletin of the Carnegie Museum of Natural History* 34:5–39.
- Ciochon, R. L., and P. A. Holroyd. 1994. The Asian origin of Anthropoidea revisited; pp. 143–162 in J. G. Fleagle and R. F. Kay (eds.), *Anthropoid Origins*. Plenum Press, New York.
- , D. E. Savage, Thaw Tint, and Ba Maw. 1985. Anthropoid origins in Asia? New discovery of *Amphipithecus* from the Eocene of Burma. *Science* 229:756–759.
- Colbert, E. H. 1937. A new primate from the upper Eocene Pondaung Formation of Burma. *American Museum Novitates* 951.
- 1938. Fossil Mammals from Burma in the American Museum of Natural History. *Bulletin of the American Museum of Natural History* 74:259–436.
- Holroyd, P. A., and R. L. Ciochon. 1994. The relative ages of Asian primate-bearing deposits; pp. 123–141 in J. G. Fleagle and R. F. Kay (eds.), *Anthropoid Origins*. Plenum Press, New York.
- Lucas, S. G., and R. M. Schoch. 1989. European brontotheres; pp. 485–490 in D. R. Prothero and R. M. Schoch (eds.), *The Evolution of Perissodactyls*. Oxford University Press, Oxford.
- Mader, B. J. 1989. The Brontotheriidae: a systematic revision and preliminary phylogeny of North American genera; pp. 458–484 in D. R. Prothero and R. M. Schoch (eds.), *The Evolution of Perissodactyls*. Oxford University Press, Oxford.
- Pilgrim, G. E. 1927. A *Sivapithecus* palate and other primate fossils from India. *Memoirs of the Geological Survey of India (Paleontologica Indica)*, New Series 14:1–26.
- 1928. The Artiodactyla of the Eocene of Burma. *Memoirs of the Geological Survey of India (Paleontologica Indica)*, New Series 8:1–39.
- 1941. The dispersal of the Artiodactyla. *Biological Review of the Cambridge Philosophical Society* 16:134–163.
- , and G. de P. Cotter. 1916. Some newly discovered Eocene mammals from Burma. *Records, Geological Survey of India* 48(1): 42–82.
- Prothero, D. R., and R. M. Schoch. 1989. Classification of the Perissodactyla; pp. 485–490 in D. R. Prothero and R. M. Schoch (eds.), *The Evolution of Perissodactyls*. Oxford University Press, Oxford.

Received 25 April 1999; accepted 10 November 1999.