A NEW GENUS AND SPECIES OF HYAENODONTID CREODONT FROM THE PONDAUNG FORMATION (EOCENE, MYANMAR)

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The Pondaung Formation in central Myanmar (Fig. 1) produces one of the richest Paleogene mammalian faunas in Southeast Asia Research on the fauna, known for its diverse primates and ungulates, began in the early part of the twentieth century (e.g., Pilgrim and Cotter, 1916; Pilgrim, 1925, 1927, 1928; Colbert, 1937, 1938; Ba Maw et al., 1979; Ciochon et al., 1985; Holroyd and Ciochon, 1995, 2000; Jaeger et al., 1999; Chaimanee et al., 2000; Ducrocq et al., 2000; Tsubamoto et al., 2000, 2002a, 2003; Takai et al., 2001; Tsubamoto, 2001; Shigehara et al., 2002). However, the presence of mammalian predators was unknown in the fauna until 1997 when creodonts were discovered. Since 1997, the Pondaung mammalian fauna has been studied collaboratively by researchers from Myanmar, France, Japan, Thailand, and the United States. In subsequent field seasons, many taxa have been added to the fauna (Tsubamoto, 2001). In addition, geological study on the Pondaung Formation provided a radiometric age of 37.2 Ma at one of the fossil localities (Tsubamoto et al., 2002b), the first numerical date for the fauna

Currently, we recognize at least three types of carnivorous mammals from the Pondaung fauna. One is "*Pterodon*" *dahkoensis*, a hyaenailourine hyaenodontid creodont otherwise known from the upper Lumeiyi Formation, upper Eocene, southern China and the Rencun Member of the upper middle Eocene Heti Formation of central China (Chow, 1975; Egi and Tsubamoto, 2000). The two others are also hyaenodontids, but belong to the subfamily Proviverrinae. Proviverrine hyaenodontids are rare in the faunas near Pondaung and throughout Asia. Both of the two Pondaung proviverrine hyaenodontids are quite large among proviverrines, and belong to new taxa. In this paper, we focus on one of the new Pondaung proviverrines. Compared with the other taxon, this form is slightly smaller and differs in having less specialized and less enlarged m3.

Institutional Abbreviations—**NMM**, National Museum of Myanmar, Yangon, Myanmar; **KU**, Kyoto University, Kyoto, Japan. **NMMP-KU** denotes National Museum of Myanmar, in Paleontology, specimen numbers serially catalogued by Kyoto University.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758 Order CREODONTA Cope, 1875 Family HYAENODONTIDAE Leidy, 1869 Subfamily PROVIVERRINAE Matthew, 1909 YARSHEA CRUENTA, gen. et sp. nov.

Holotype and Only Known Specimen—NMMP-KU 0045 (field number Bhn-31), right mandibular fragment with m1; NMMP-KU 0046, right m3 trigonid; NMMP-KU 0214, right m2 and m3 talonids, metastylar blade and protocone of left M1 or M2, a tooth root fragment (Fig. 2).

Comments—The three specimens were found at the same exact location, and the right m3 trigonid of NMMP-KU 0046 and the right m3 talonid of NMMP-KU 0214 were glued together into a single tooth. Thus, NMMP-KU 0045, 0046, and 0214 belong to a single individual.

Type Locality—KU locality Bh1 (=Yarshe kyitchaung), about 4 km west to northwest of Bahin Village, Magway Division, Myanmar; 21° 44' 14.2" N, 94° 38' 14.1" E.

Distribution—"Upper Member" of the Pondaung Formation, eastern side of Pondaung Range, central Myanmar (Fig. 1).

Age-Latest middle Eocene.

Diagnosis-Yarshea cruenta is a large proviverrine hyaenodontid, but smaller than Dissopsalis and similar to Anasinopa in size. Yarshea differs from North American proviverrines (e.g., Prototomus, Sinopa, Arfia, Tritemnodon, Pyrocyon), European Proviverra-like proviverrines (e.g., Prodissopsalis, Proviverra, Allopterodon, Eurotherium, Leonhardtina), and Propterodon, in having reduction of trigonid angle from m1 to m3, reduction of metaconid from m1 to m3, reduction of talonid length from m1 to m3, and well-developed buccal cingulids on m1 and m2. Yarshea differs from some European proviverrines, such as Cynohyaenodon, Alienetherium, Paracynohyaenodon, and Asian and African advanced proviverrines (e.g., Dissopsalis, Anasinopa, Metasinopa, Masrasector, Paratritemnodon, African "Sinopa") in having in combination the following characters: m1 length greater than 90% of m3; m1 talonid as long as trigonid; m3 paraconid as tall as protoconid; m3 metaconid positioned anterolingual to protoconid; m3 talonid shorter than trigonid, but longer than half of trigonid; and presence of relatively higher preentocristid that creates a somewhat more closed talonid basin. In addition, Yarshea differs from Cynohyaenodon, Alienetherium, and Paracynohyaenodon in having smooth enamel surface, well-developed buccal cingulids on m1 and m2, m1 metaconid smaller than paraconid, and indistinct hypoconulid/entoconid separation on lower molars; from Cynohyaenodon and Alienetherium in having m3 metaconid smaller than paraconid; from African "Sinopa" and Dissopsalis in having m3 paraconid as long as protoconid and buccally positioned hypoconid on lower molars; from African "Sinopa," in having m1 metaconid positioned posterolingual to protoconid and a distinct hypoconid/hypoconulid notch; from Dissopsalis in having slender and smooth enamel, distinct metaconid and basined talonid on m3, and an indistinct hypoconulid/entoconid separation on lower molars; from Metasinopa in having smooth enamel and distinct m3 metaconid; from Anasinopa in having smooth enamel; from Paratritemnodon and Masrasector in having an indistinct hypoconulid/entoconid separation on the lower molars and in lacking buccal cingulid on m3; from Paratritemnodon in having m3 paraconid as long as protoconid.

Etymology—Yarshe, Myanmar name of the locality where the type was collected; gender of generic name is feminine. cruentus, Latin for bloody, because the specimens were collected from blood-red colored sediment.

Description—The lower dentition includes a right m1 (NMMP-KU 0045), a right m3 (NMMP-KU 0046 and 0214) and a talonid of right m2 (NMMP-KU 0214), and a right mandibular fragment was preserved (Fig. 2, Table 1). First to third lower molar length is estimated as nearly 4 cm, indicating this animal is a large hyaenodontid creodont in the size classification defined by Barry (1988). Based on natural log-transformed m1 area, the body mass of *Yarshea cruenta* is estimated to be 9.5 kg based on an equation derived from extant carnivores (Legendre and Roth, 1988) or 12.8 kg based on an all-mammal equation (Legendre, 1986).

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FIGURE 1. Map of Myanmar and the location of the Pondaung area.

From the bottom of p4 to the bottom of m2, the mandible (NMMP-KU 0045) is thick and straight. The enamel of the molars is thin, and its surface structure is smooth. The m1 is heavily worn, as usual in hyaenodontids, and the only cuspid with a preserved tip is the entoconid. The paraconid is smaller than the protoconid, and the base of metaconid is smaller than that of the paraconid. The paraconid sits anterolingual to the protoconid, and the metaconid is lingual and slightly posterior to the protoconid; thus, the trigonid angle is open. The talonid is as wide as the trigonid, but slightly shorter. It is round and well basined. On the buccal side, the cristid obliqua runs posteriorly parallel to the entocristid and connects to the hypoconid. At the posterolingual border of the talonid, there is no distinct separation between the entoconid and the hypoconulid. A distinct notch exists between the hypoconid and the hypoconulid. A cingulid begins from the precingulid at the anterior side of the paraconid, and surrounds the tooth buccally. The shape of the talonid in m2 is similar to that in m1 but slightly narrower. A small preserved portion of the trigonid base indicates that the trigonid was wider than the talonid in m2.

The anteroposterior length of m3 is about equal to that of m1, but size of the trigonid relative to the talonid greatly increases in m3. Wear due to vertical shearing is easily identifiable on the buccal surface of the carnassial blade of m3. The paraconid is as large as the protoconid at the base and slightly shorter than the protoconid in height. The paraconid position relative to the protoconid is more anterior in m3 than in m1. The m3 metaconid is greatly reduced and sits lingually and slightly anterior to the protoconid. The trigonid angle is acute in m3. The talonid of m3 is basined and two-cusped, and a clear notch separates the hypoconid and the hypoconulid-entoconid complex, similar to the talonids in m1 and m2. In contrast to the m1 talonid, the m3 talonid is narrow and about two-thirds of the trigonid in buccolingual width. A precingulid is present on the buccal side of the paraconid, but a buccal cingulid is absent on m3.

The upper dentition is represented only by two fragments, portions of the buccal and metastylar blade and the protocone of the left M2 or M1 (NMMP-KU 0214). The trigon basin is wide, and the protocone is low and buccolingually short. A weakly developed cingulum exists at the anterior side of the protocone. The metastylar blade has a strong

cingulum buccally. The metastylar blade is oriented about 25 to 30 degrees buccally relative to the buccal surface of the metastylar blade. It is discontinuous with the postmetacrista due to the presence of metastylar notch, and seems moderate in length relative to the size of upper molar as judged from the protocone size.

Discussion—The Hyaenodontidae is a highly diverse family, occurring in Paleogene through Miocene deposits in North America, Europe, Africa, Indo-Pakistan, and Central and East Asia (McKenna and Bell, 1997). Its systematic interrelationships are not well understood, although revisions to clarify the relationships among certain members of the family have been published (e.g., Lange-Badré, 1979; Barry, 1988; Gingerich and Deutsch, 1989; Ivy, 1993; Holroyd, 1994; Polly, 1996; Morlo and Habersetzer, 1999). Within the hyaenodontids, the subfamily Proviverrinae is considered a paraphyletic stem group with about 30 genera that forms half of the family. This subfamily includes many primitive hyaenodontids as well as derived later forms.

Proviverrine hyaenodontids were not very common in Asia and currently only two genera are well represented, Paratritemnodon from the early to middle Eocene of Indo-Pakistan (Kumar, 1992; Thewissen et al., 2001), and Dissopsalis from the Miocene of Indo-Pakistan (Pilgrim, 1910; Barry, 1988). More fragmentary remains have been questionably attributed to Sinopa sp. and Tritemnodon sp. from the middle Eocene of the Hetaoyuan Formation, China (Gao, 1976; Tong and Lei, 1986) and to Proviverrinae gen. et sp. indet. from the late Eocene of Mongolia (Lavrov, 1999). Both Sinopa and Tritemnodon are primarily North American taxa (Wortman, 1901; Matthew, 1909; Ivy, 1993), and these fragmental specimens probably need systematic reexamination. Indeed, the specimens of "Sinopa" reported from the late Paleocene of the Nemegt Depression, Mongolia (Dashzeveg, 1985, 1988) hav been moved from creodonts to micropternodontid lipotyphlans (Ting, 1998). Propterodon from the middle Eocene of Mongolia and Inner Mongolia of China (Li and Ting, 1983; Dashzeveg, 1985) was traditionally classified in the Proviverrinae, but we follow Polly (1996) in placing it in the subfamily Hyaenodontinae. Two other proviverrine genera, Anasinopa from the Miocene of Israel (Tchernov et al., 1987) and Masrasector from the late Eocene or early Oligocene of Oman (Crochet et al., 1990), are known from the present border of Asia and Africa, but both of the localities were on the African continent at the time (Smith et al., 1994).

Some Asian proviverrine genera are also known from Africa: Masrasector from the late Eocene to early Oligocene of Egypt (Simons and Gingerich, 1974; Holroyd, 1994), and Dissopsalis and Anasinopa from the early Miocene of Kenya (Savage, 1965; Barry, 1988). Holroyd (1994) suggested that these three Afro-Asian genera together with Paratritemnodon (Kumar, 1992; Thewissen et al., 2001) and Metasinopa and African "Sinopa," known mainly from the late Eocene to early Oligocene of Egypt (Osborn, 1909; Holroyd, 1994), form a monophyletic group relative to the other hyaenodontids. Yarshea from Myanmar has a closer relationship to this clade of Afro-Asian proviverrines than to other Asian taxa. Similarity of Yarshea to the Afro-Asian proviverrines is shown in the round and well-basined talonid and a strong buccal cingulid on m1, increase in absolute and relative trigonid size from m1 to m3, reduction of metaconid and acute trigonid angle in m3 compared with in m1, and an m3 paraconid lower than the protoconid. Currently, it is unclear which of the six Afro-Asian proviverrines Yarshea is closest to. To estimate the precise systematic position of Yarshea, we need to wait for discovery of further diagnostic materials, especially premolars and complete upper molars of Yarshea. More detailed systematic studies of other Afro-Asian proviverrines are also necessary.

Biogeographically, the discovery of a new proviverrine from the Pondaung mammalian fauna in Myanmar extends the geographic range of the Afro-Asian proviverrine group further east. It suggests that this group was widely distributed around the Tethys Sea and there was an interchange or immigration of these hyaenodontid creodonts between North Africa and Southeast Asia during the Eocene. Holroyd and Maas (1994) thought it likely that primates, rodents, and anthracotheriid artiodactyls dispersed between these two continents in the early Paleogene, and dispersal between Africa and Southeast Asia was further elaborated by Ducrocq (1994, 2001). The discovery of a proviverrine in the Pondaung fauna now clearly adds the Afro-Asian proviverrine creodonts to the list of potential immigrants and further reinforces the similarities seen among these Paleogene faunas along the borders of the Tethys.

Acknowledgments—We gratefully thank Brig.-Gen. Than Tun and Maj. Bo Bo of the International Affairs and Research Department, Min-



FIGURE 2. Yarshea cruenta, gen. et sp. nov., holotype NMMP-KU 0045, 0046 and 0214. A, right mandibular fragment with m1 in buccal view. B, buccal, and C, lingual views of right m1, m2 talonid, and right m3. Stereophotograph pairs of lower molars (D, D') and upper molar (M1 or M2) fragments (E, E') in occlusal view. Abbreviations: bc, buccal cingulum, cn, carnassial notch, mec, metacone, mecl, metaconule, mes, metastylar blade, pacl, paraconule, prc, protocone, tb, trigon basin. Scale equals 1 cm.

TABLE 1. Measurements of holotype of *Yarshea cruenta*, gen. et sp. nov. (in mm). Length and width are anteroposterior and buccolingual diameters, respectively. Mandibular depth was measured below m1.

	Total length	Trigonid length	Trigonid width	Talonid length	Talonid width	Protoconid height	Depth
m1	12.26	7.03	5.60	5.26	5.56	_	
m2				5.05	5.18		
m3	12.33	8.35	6.71	4.81	4.65	9.09	
mandible							19.40

istry of Defense of the Union of Myanmar, for their cooperation in the field research and for access to the specimens stored in the National Museum of Myanmar. Dr. H. Suzuki from Kyoto University and Dr. Maung Maung and other researchers from several Myanmar universities helped us with geological information on the Pondaung area. Drs. Dave Polly and Michael Morlo gave useful advice on classification of the material. Two anonymous reviewers provided useful comments to improve this manuscript. Financial support was provided by the MEXT Overseas Scientific Research Fund (09041161, 14405019) and the MEXT Grant-in-Aid for COE Research (10CE2005), for the 21st Century COE Program (A14 to Kyoto University), and for JSPS Fellows (15004748).

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Received 15 June 2002; accepted 7 August 2003.