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New hyaenodonta (Mammalia) from the middle Eocene of Myanmar

Nouveaux hyaenodontes (Mammalia) de l'Éocène moyen de Birmanie

Louis de Bonis[a,*], Floreal Solé[b], Yaowalak Chaimanee[a], Aung Naing Soe[c], Chit Sein[d], Vincent Lazzari[a], Olivier Chavasseau[a], Jean-Jacques Jaeger[a]

[a] *IPHEP: Institut de paléoprimatologie et de paléontologie humaine, évolution et paléoenvironnements, UMR CNRS 7262, Université de Poitiers, 6, rue Michel-Brunet, 86073 Poitiers cedex 9, France*
[b] *Royal Belgian Institute of Natural Sciences (RBINS), Operational Directorate Earth and History of Life, 29, rue Vautier, 1000 Bruxelles, Belgium*
[c] *Department of Higher Education Ministry of Education, Naypyitaw, Myanmar*
[d] *Department of Geology, West Yangon University, 11393 Yangon, Myanmar*

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ABSTRACT

The middle Eocene Pondaung Formation in Myanmar has yielded a rich mammalian fauna including several Primate taxa. Hyaenodonta are known by the genera *Kyawdawia*, *Yarshea*, *Oriensptерodon*, and two other indeterminate taxa. We describe here new material of *Kyawdawia*, including some morphological details, a new species of the hypercarnivorous genus *Propterodon* and an indeterminate species, different from those described earlier in Myanmar, and characterized by a reduction of m3 and would belong to a third lineage with the same evolutionary trend as *Galecyon* and the Limnocyoninae. The hyainailourines (*Oriensptерodon*) and hyaenodontines (*Propterodon*) are recorded for the first time in Southeast Asia and these subfamilies appeared in quasi the same time in Europe illustrating probably a profound change in the carnivorous fauna among Laurasia.

RÉSUMÉ

La formation de l'Éocène moyen de Pondaung, en Myanmar, a livré une riche faune mammalienne, dans laquelle on a signalé plusieurs taxons de Primates. Parmi les autres ordres de mammifères, celui des Hyaenodonta était connu jusqu'à présent par les genres *Kyawdawia*, *Yarshea*, *Oriensptерodon* et deux autres taxons indéterminés. Nous décrivons dans cet article du nouveau matériel de *Kyawdawia*, qui apporte des précisions sur certains détails morphologiques, une nouvelle espèce du genre hypercarnivore *Propterodon* ainsi qu'une forme indéterminée, qui diffère de toutes les espèces décrites à ce jour en Birmanie. Elle se

* Corresponding author.
E-mail address: louis.debonis@univ-poitiers.fr (L. de Bonis).

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caractérise, en particulier, par la réduction de m3, et peut représenter une troisième lignée montrant la même tendance évolutive que les Limnocyoninae et *Galecyon*. Les hyainailourinés (*Orienspterodon*) et les hyaenodontinés (*Propterodon*) sont les plus anciens connus dans le Sud-Est asiatique. Ces sous-familles apparaissent quasiment à la même époque en Europe, et la fin de l'Éocène moyen pourrait correspondre à un changement majeur de la faune de carnassiers en Eurasie.

1. Introduction

The middle Eocene Pondaung Formation, exposed in the northwestern part of Central Myanmar, is mainly composed of fluviatile sediments, and has produced a rich vertebrate fauna. Since the first fossils reported by Pilgrim and Cotter (1916), about 50 mammalian species have been discovered such as artiodactyls (Ducrocq et al., 2000; Holroyd and Ciochon, 1995; Métais, 2006; Métais et al., 2000; Pilgrim, 1928; Tsubamoto et al., 2003, 2011, 2012, 2013), perissodactyls (Colbert, 1938; Holroyd et al., 2006; Métais et al., 2006; Rémy et al., 2005; Tsubamoto et al., 2003, 2005), rodents (Dawson et al., 2003; Marivaux et al., 2005), and primates (Ba Maw et al., 1979; Beard et al., 2005, 2007, 2009; Chaimanee et al., 2000, 2012; Ciochon, 1985; Colbert, 1938; Gebo et al., 2002; Gunnel et al., 2002; Jaeger et al., 1998, 1999; Marivaux et al., 2008a, 2008b; Shigehara et al., 2002; Takai et al., 2001). The age of the Pondaung Formation has been estimated to be late middle Eocene (ca. *37 Ma) by magnetostratigraphy (Benammi et al., 2002) and fission track dating (Tsubamoto et al., 2002). However, recent radiometric analyses (U–Pb age) on zircons obtained from a tuffacaceous bed in Pondaung Formation indicate an age range between 40.22–40.31 Ma (Khin Zaw et al., 2014), which is slightly older than that obtained from the other methods. Almost 30 fossiliferous localities have been recognized in the Pondaung Formation and its stratigraphic study, conducted by Aung Naing Soe et al. (2002), has demonstrated that sediments that yielded fossil mammal remains were deposited in the same short time interval and are issued from the upper part of the Pondaung Formation. Geochemical, sedimentological and paleoenvironmental data indicate a tropical, humid environment under strong monsoon influences (Licht et al., 2013a, 2013b, 2014). Most studies on the Pondaung fossil mammals have focused on anthracotheriid artiodactyls and primates because they are the most abundant taxa that have been collected since the beginning of the twentieth century. Here we report new discoveries that increase our understanding of the Hyaenodonta of that formation.

The first hyaenodonts recovered in Myanmar were briefly described (Egi and Tsubamoto, 2000) from specimens coming from the Pondaung area as two indeterminate species in an overall review of the fossil mammalian fauna of Myanmar. Few years later (Egi et al., 2004), one of these species was published as *Yarshea cruenta* on fragments of the same individual (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). The material was coming from the "Upper Member" of the Pondaung Formation, eastern side of Pondaung Range, central Myanmar in the Bahin basin (Egi et al., 2004). Later the other species was also described (Egi et al., 2005) as *Kyawdawia lupina*, with cranial and post-cranial elements associated with the holotype. The dentition was quite complete but, belonging to an old individual, the teeth are worn. In the same article, a fragment of mandible bearing p4 talonid and m1 coming from the same area and level is figured as Proviverrinae indet. Smaller than *Yarshea* and *Kyawdawia*, this mandible differs also by characters which seem to be more African proviverrine-like. Other remains were recorded from the same Pondaung Formation (Peigné et al., 2007). Some of them were reported as *Kyawdawia lupina* but a M3 figured as Hyaenodontidae sp. indet. is too large to belong to the other known Pondaung species at that time. The same year another genus, *Oriens pterodon* Egi et al., 2007, was created for very large specimens from Pondaung and the Chinese species *Pterodon dahkoensis* Chow Minchen, 1975 was assigned to this genus.

The new material which is described in the present article consists in mandibular fragments and isolated teeth. These new finds both increase the known diversity of the hyaenodont fauna in Pondaung and provide new morphological details for previously described taxa.

2. Systematics

Hyaenodonta Van Valen, 1967
Hyainailouroidea Pilgrim, 1932
Hyainailouridae Pilgrim, 1932
Indohyaenodontinae Solé et al., 2013
Kyawdawia Egi et al., 2005
Kyawdawia lupina Egi et al., 2005

This species is represented in the new material by an isolated p3, a fragment of mandible with p4–m2, a P4, 2 upper molars and some fragments of teeth.

2.1. Description of the lower teeth

The isolated **p3** (NMMP-PK4-5-12-10a) is identified as a lower one, but an upper one cannot be excluded; it is little worn, smaller than p4 (Table 1), with a triangular almost symmetrical lateral shape. There is a thin paracristid descending from the apex of the protoconid to meet a small paraconid and, distally, a better developed talonid.

The **dentary** (NMMP-PK2-2-11-13) is broken off at mid-height and we cannot estimate the depth (Fig. 1). The mandible would have been quite robust being 10.6 mm breadth at the level of m1–m2 (Fig. 1A–C). The **p4** is higher than m1 (Table 1), robust and without any trace of wear. The surface of enamel is slightly granular. The crown is

Table 1
Measurements (mm) of the lower teeth of *Kyawdakia lupina*.
Tableau 1
Mesures (mm) des dents inférieures de *Kyawdakia lupina*.

	p3			p4			m1					m2					m3					References
	L	w	h	L	w	h	L	TrL	trh	trw	talw	L	trL	trh	trw	talw	L	trL	trh	trw	tlw	
NMMP-PK2-11-2-2017	9.2	5.8	8.8																			
NMMP-PK2-02-11-2013				13.3	6.2	10.8	11.9	6.5	7.7	6	5.9	15.9	9.9	11.5	9.5	7.5						
NM11 Bhn 2000																	13.6	8.2		7.4	6	Peigné et al., 2007
NPL-12-2010																7.5	15	8.4		8.9		Peigné et al., 2007
PKg 1051												14.2	8		7.7	7.7						Peigné et al., 2007
NMMP-TMC-2016							12.1	6.3	9.9	5.3	4.1											
NMMP-KU 42		5.2		14.2	6.3	12.3						17.6	9.6		8.6	7.5	18.4	10.3		9.1	7.2	Egi et al., 2005
NMMP-KU1288	9.4	6.4	9.3	15.2	7	13.6	13.4	6.9	8.5	6.4	6.2						20.3	12.5	16.1	11	8.3	Egi et al., 2005
NMMP-MGW 0022				11			9.7	5.6		4.7	5											Egi et al., 2005

L: length; w: width; h: height; TrL: trigonid length; trh: trigonid height; trw: trigonid width; talw: talonid width.

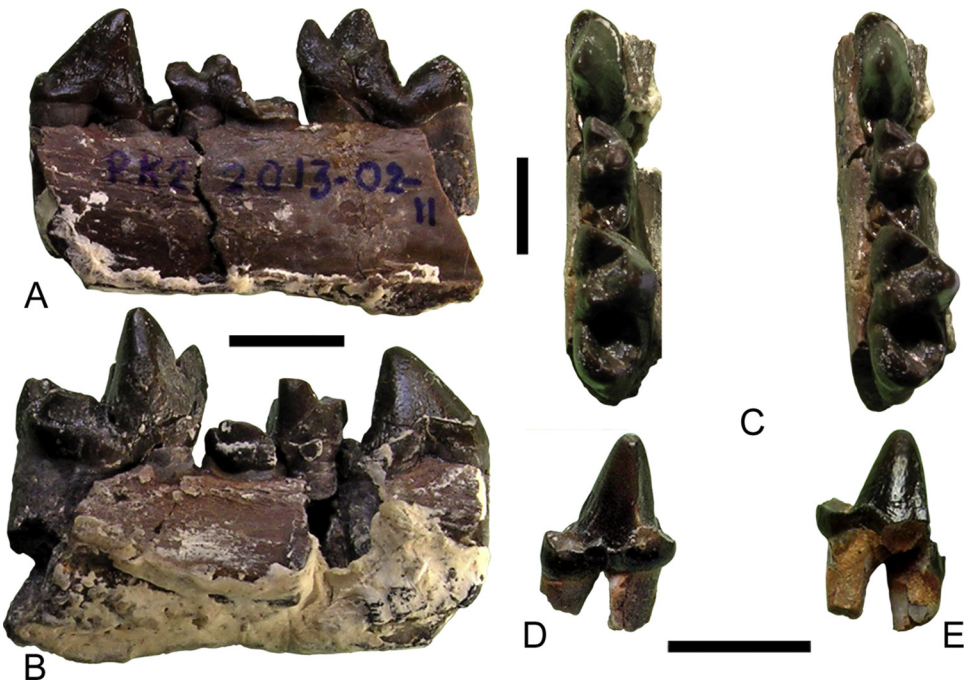

Fig. 1. *Kyawdawia lupina* (PK2-2-11-13). Fragment of dentary with p4–m2. A. Lingual view. B. Buccal view. C. Occlusal view (stereo). Isolated P4. D. Lingual view. E. Buccal view. Scale bar = 10 mm.
Fig. 1. *Kyawdawia lupina* (PK2-2-11-13). Fragment de mandibule avec p4–m2. A. Vue linguale. B. Vue buccale. C. Vue occlusale (stéréo). P4 isolée. D. Vue linguale. E. Vue buccale. Échelle = 10 mm.

bucco-lingually flattened, the mesial half being narrower than the distal one with a sharp paralophid running from the top to the base of the crown. There is another smaller crest distally from mid-height to the base. There is a well-developed talonid (3.3 mm length) without a clear cristid obliqua but with a high and powerful hypoconid and a narrow elongated lingual flat surface replacing the weak cingulid surrounding the tooth. The **m1**, slightly shorter than p4 and far smaller than m2 (Table 1), is almost complete except the disto-lingual corner of the talonid. The trigonid is complete with a swollen metaconid smaller than the paraconid but nevertheless well developed and bearing a small vertical mesio-lingual ridge. There are wear facets on the top of the three cuspids of the trigonid and we cannot know the original height of the cuspids. The wear facet is rounded and horizontal in the protoconid with appearance of the dentine in the middle, elongated and slightly buccally inclined with traces of dentine in the paraconid and it is oval and horizontal in the metaconid with also a pit of dentine. Another wear facet extends in the distal surface of the protoconid and metaconid. The talonid is slightly narrower than the trigonid (talw/trw = 98). The lingual half of the talonid is broken off. The cristid obliqua, whose a mesial part is missing, is perpendicular to the protoconid and joins the conical hypoconid, a wear facet running along the crest and the top of the hypoconid. The ratio width of trigonid/width of talonid (98.3) is slightly higher than those (77.3 to 96.8) of published m1 of *K. lupina* (Egi et al., 2005; Peigné et al., 2007). The **m2** is very well preserved. The trigonid, overlooked by the protoconid, is high without significant traces of wear in the top of the cuspids except a very tiny one, concerning only the enamel, in the apex of the protoconid. Like in specimen NMMP-Pkg-1051, the protoconid height surpasses the trigonid length.

The paraconid is very oblique, nearly perpendicular to the axis of the tooth raw and slightly separated from the metaconid. The latter is well developed but smaller and slightly lower than the former. A large vertical shearing wear facet with vertical striations extends on the buccal surface of the protoconid and partly the paraconid. There is not a clear cristid obliqua in the talonid but a large hypoconid elongated with a slightly convex buccal face and a lingual one gently sloping to the deep and wide talonid basin. The entoconid, separated from the metaconid by a deep notch, is as high as the hypoconid but thinner; it constitutes a crest separated from the hypoconulid by a small notch, the latter being separated from the hypoconid by a larger one. A moderate cingulid runs along the buccal base of the tooth except at the level of the disto-buccal part of the protoconid. The talonid breadth is smaller than the trigonid one and the ratio (79) is slightly smaller than those (87.2–100) previously published (Egi et al., 2005; Peigné et al., 2007).

2.2. Upper teeth

P4 (Fig. 1C, D) is three rooted but a root is broken off. It is fresh except a small pit of wear in the top of the main cusp and a small part of the mesio-buccal corner broken off. Its measurements are: width = 8.4 mm, height = 9.7 mm. We cannot take the length. The main cusp is triangular in lateral view; distally a thin vertical crest runs down to an elongated and trenchant talon. In the distal wall, there is a small horse-shoe shaped contact facet for M1. Another smaller mesial accessory cusp is present. Lingually a true protocone does exist as a basin limited by the cingulum in which a small transverse crest extends from the main cusp to a sharp small cusp, dividing the basin in two parts. The height of the crown is similar to the length of the teeth but the latter is may be underestimating because a missing fragment of enamel. The newly found upper molars do not differ from those described in previous publications.

3. Discussion

This is the third publication in which *Kyawdawia lupina* is reported, the first being Egi et al. (2005) and the second Peigné et al. (2007). Because of its relative abundance, this species was probably the most common carnivorous mammal in the Pondaung area during the end of the middle Eocene. It was probably an opportunistic feeder like are some of the extent canids. The morphology of the lower molars displays some cutting areas along the buccal face of the trigonid as well as large talonids dedicated to a crushing function. The new material provides new details of characters of the lower molars and principally those of the upper P4 which was quite unknown until now.

Hyaenodonta Van Valen, 1967
Hyaenodontoidea Leidy, 1869
Hyaenodontidae Leidy, 1869
Hyaenodontinae Leidy, 1869
Propterodon Martin, 1906
Propterodon panganensis nov. sp.

Holotype: dentary with p4–m1, alveoli of m2 and m3 (NMMP-Pg1-2011-29).

Etymology: from the name of the locality where the specimen was recorded. Diagnosis: small sized *Propterodon* with a low and trenchant p4 having a trenchant small talonid. Mesiodistally flattened trigonid of m1 without metaconid and short trenchant talonid with a small narrow postfossid. Presence of individualized hypoconid in m1. Complete absence of cingulid.

Differential diagnosis: differs from *Hyaenodon* and other hyaenodontids by the shape of p4, and the relative large size of m1. *Propterodon morrisi* (= *P. irdinensis*) differs by its larger size, the larger talonid of m1 and the presence of a minute metaconid in molars. *P. pishigouensis* differs by its larger size, with a relatively larger and powerful p4 of which the main cusp is distally tilted with very developed accessory mesial and distal cuspids. *P. tongi* differs by its larger size, more robust dentary, and, following Tong and Lei, 1986, a m1 similar to that of *P. irdinensis* (with a minute metaconid?).

Type locality: Pangan 1, Myanmar.

Geological age: upper part of the Pondaung Formation, 40–37 Ma, almost equivalent to the European Bartonian or MP 15–MP 16 (European Land Mammal Age).

Distribution: Pondaung formation (Myanmar) only.

Measurements in mm: p4 length 5.5, width 2.15, height 5.06. m1L 5.1, trigL 4.16, trigw 2.73, trigh 4.2, talw 1.6. m2L (6.5), m3L (7.5) Height and width of the dentary: level p3–p4 10.3×5.3; level p4–m1 10.6×4.9; level m1–m2 11×4.6; level m2–m3 11.5×7.7. Height of the coronoid process: 21.7 mm. ( ) = measured from alveoli.

4. Description

This taxon is represented by an incomplete dentary bearing p4–m1 (Fig. 2A–C) and part of the mesial alveolus and the distal alveolus of p3, alveoli of m2 and m3 with pieces of the tooth roots and the coronoid process (NMMP-Pg1-2011-29). Beyond its far smaller size, it differs dramatically from *Kyadawia lupina* by its morphology and probably by its ecology and diet. It belongs clearly to a different genus undescribed in Myanmar until now. The dentary is slender, shallow with the lower border slightly concave and slightly tapering forward. The mesial border of the coronoid process is very oblique with an angle of 134° relatively to the horizontal line of the tooth row. Part of the distal surface and the angular area are missing off, but it seems that it was ventrally pointed. The masseteric fossa is wide but not especially deep. It extends beneath m3 and is dorsally limited by a robust ridge along the mesial border of the coronoid process. Lingually, a shallow depression mesially limited by a moderate ridge corresponds to the temporal muscle. The position of the mandibular condyle is visible: it is located below the tooth row. The p4 is complete except a fragment of enamel missing from the bucco-distal corner. It is almost as high as m1 with a triangular lateral outline. A weak paralophid ends at the base of a small mesio-lingual paraconid. Distally there is a small but clear talonid with a hypoconid of which the top is obliterated by a small wear facet and, lingually a narrow and shallow basin limited by a low entocristid. There is no trace of a

Fig. 2. *Propterodon paganensis* nov. sp. (Pg1-2011-29). Fragment of dentary with p4–m1. A. Lingual view. B. Buccal view. C. Occlusal view (stereo). Scale bar = 10 mm.
Fig. 2. *Propterodon paganensis* nov. sp. (Pg1-2011-29). Fragment de mandibule avec p4–m1. A. Vue linguale. B. Vue buccale. C. Vue occlusale (stéréo). Échelle = 10 mm.

cingulid. The paraconid of m1 is lower than the protoconid and it is elongate mesially and slightly lingually directed. The protoconid is transversally flattened. The protoconid is shifted distally. A wide quasi vertical wear facet with vertical striations extends in the buccal surface of the paraconid and large part of the protoconid. The metaconid is absent. A short talonid composed by a conical hypoconid is aligned on the protoconid and separated from it by a buccal depression. A very short entocristid is present but does not reach the metaconid, leaving the small talonid basin lingually open. Like in p4, there is no cingulid.

5. Comparisons and discussion

The fossil from Pondaung fauna shares with the *Hyaenodon* species the distally shifting of the protoconid on m1, the absence of metaconid, the very oblique coronoid process, the coronoid process longer than high, the ventrally curved angular process, and the wide masseteric fossa. These features distinguish the Pondaung taxon from hyainailourines (e.g., *Pterodon*) and teratodontines (e.g., *Dissopsalis*), two hyaenodont subfamilies that convergently acquired hypercarnivorous dentition (Borths et al., 2016). The morphology of the m1 (long and distally shifting of the protoconid) distinguishes the Pondaung taxon from hypercarnivorous proviverrines such as *Oxyaenoides* – the latter genus actually shares mandibular features with *Hyaenodon* (Solé et al., 2015).

We estimated the index (Lm1/Lp4) × 100 for some of the oldest *Hyaenodon* species. It equals 74 in the North American *H. venturae* (this species possesses the relatively longest m1 among *Hyaenodon* (Lavrov and Emry, 1998)), 69 in *H. minor*, 68 in *H. brachyrhynchus*, *H. requieni*, and *H. eminus*. This index actually equals 93 in NMMP-Pg1-2011-29. Therefore, the Pondaung fossil differs from the *Hyaenodon* species by the relative size of the m1: the latter is indeed longer than in *Hyaenodon*. This feature is primitive among hyaenodontids. Moreover, the species of *Hyaenodon* have flattened and shearing lower molars without metaconid but p4 is normally more robust relative to NMMP-Pg1-2011-29, far higher than m1 and more conical. Consequently, NMMP-Pg1-2011-29 does not represent a *Hyaenodon* species despite the presence of similar dental and mandibular features.

Propterodon is the closest relative to *Hyaenodon* (Borths et al., 2016). *Propterodon morrisi*, Matthew and Granger, 1924 (= *P. irdinensis* Matthew and Granger, 1925) from the Eocene of Mongolia is founded on a dentary with p3, m1, m3 and the alveoli of p1, p2, p4 and m2. It is close by the size to NMMP-Pg1 2011-29 (Matthew and Granger, 1925, Fig. 3). Unfortunately, the absence of p4 does not allow any comparison of that tooth but m1 is different "with rather large, high-crested heel nearly as broad as the body of the tooth, a minute metaconid, paraconid considerably smaller and lower than metaconid" (Matthew and Granger, 1925, p. 4). In NMMP-Pg1-2011-29, the paraconid cannot be lower than the metaconid which is absent, the protoconid

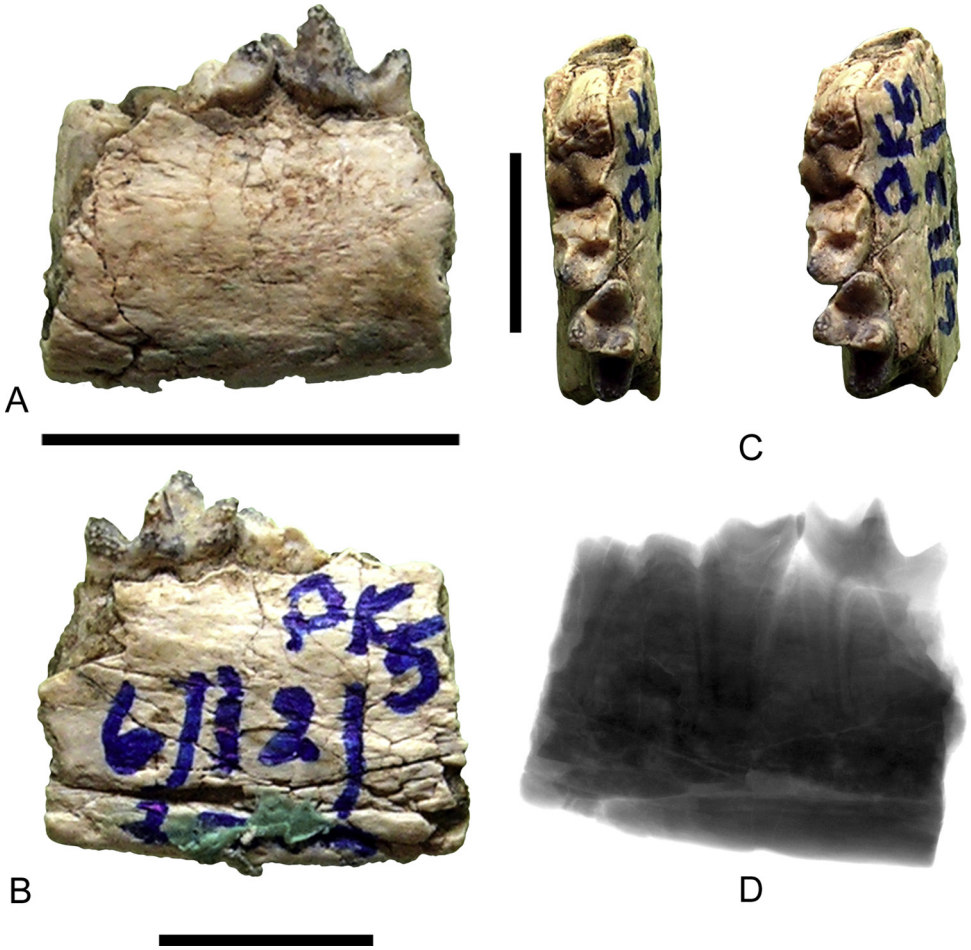

Fig. 3. Hyaenodonta indet. sp. (PK5 6-12-10). Fragment of dentary with talonid of m2 and the complete m3. A. Lingual view. B. Buccal view. C. Occlusal view (stereo). D. Radiography showing the roots of m2 and m3. Scale bar = 10 mm.
Fig. 3. Hyaenodonta indet. sp. (PK5 6-12-10). Fragment de mandibule avec le talonide de m2 et m3 complète. A. Vue linguale. B. Vue buccale. C. Vue occlusale (stéreo). D. Radiographie montrant les racines de la m2 et la m3. Échelle = 10 mm.

is less high relative to the paraconid and the talonid is relatively smaller than that of *P. irdinensis* and it is narrower than the trigonid. Another species, from the Eocene of China, is attributed to the genus with a question mark? *Propterodon pishigouensis* Tong and Lei, 1986. This taxon is known from a piece of dentary with p4–m1. It differs by the large size of p4, the protoconid of which being very high and distally tilted, with relatively larger mesial and distal accessory cuspids, the m1 with a large and high talonid (Tong and Lei, 1986, Fig. 2). Another dentary bearing p1–m3 is the type specimen of *Propterodon tongi* Liu and Huang, 2002. That mandible differs from that of Pondaung by its larger size (height of the dentary at p4–m1 14.5 against 10.6, at m1–m3 15.4 against 11.5: and length of p4 5.5 against 8, Lm1 6.5 for 5.1). The ventral border of the dentary is going up rapidly and is staying in a horizontal line in NMMP-Pg1-2011-29 (Liu and Huang, 2002, Fig. 1). The teeth are also different, p4 of *P. tongi* bears a clear paraconid and a larger talonid, while m1 of *P. tongi* is worn out and we just can see that it is smaller relatively to p4. Regarding the relative sizes of the p4 and m1, the index (Lm1/Lp4) × 100 equals 81 in *P. tongi* and 80 in *P. iridensis* (unpublished specimen). The species? *P. pishigouensis* has an index close to that of the Pondaung taxa: 95 vs 93.

To conclude, we consider that Pg1-2011-29 represents a new species of *Propterodon*.

Hyaenodonta Van Valen, 1967
Family indet.
Hyaenodonta indet. sp.

NMMP-PK5 6-12-10 is a fragment of dentary (Fig. 3A–D) with the mesial root and the talonid of m2 and the complete m3. Its tooth measurements (mm) are: L m2 = (5.43); talw m2 = 1.71; Lm3 = 3.76; Ltrg m3 = 2.12: trh m3 = 2.22; trw m3 = 2; tlw m3 = 1.2.

The dentary is deep relatively to its width [index $(w/h)100 = 45.5$]. The distal root of m1 is robust. The mesial root of m2 is large, in the talonid, a high and relatively trenchant hypoconid has a convex buccal surface and a slightly convex, almost flat, vertical lingual surface while the thin very low entocristid limits lingually an almost flat talonid basin. The talonid is slightly tapering distally. There is no

hypoconulid but a small notch separates hypoconid and entocristid. In m3, the enamel is slightly weathered. The protoconid overlooks the high trigonid with a lingual face only slightly convex. The postparacristid is very oblique, almost perpendicular, relatively to the tooth row axis. The base of the paraconid contacts that of the metaconid. The latter is less voluminous but as high as the paraconid and, in occlusal view, the trigonid is V shaped in isosceles triangle. The metaconid is slightly more distal than the protoconid. The talonid is narrow and high because the size and shape of the hypoconid. There is no talonid basin but a surface sloping gently toward the lingual border without clear entocristid nor entoconid. It is difficult to distinguish the wear facets but it seems that there is one shearing in front of the protoconid and, partly, the paraconid and another one on the wall constituted by the distal surface of the protoconid and metaconid which are both in a same plane. Like around the talonid of m2, there is no trace of any cingulid around the tooth.

6. Comparisons

The comparisons will deal with the hyaenodonts of which m3 is reduced relative to m2: our comparison thus will focus on *Galecyon* and on Limnocyoninae.

The genus *Galecyon* has been described in North America (Gingerich and Deutsch, 1989; Zack, 2011) and Europe (Smith and Smith, 2001). The relative reduction of m3 is mentioned in the original diagnosis as one of the major features of this hyaenodont genus (Zack, 2011).

We can measure the reduction of the last molar relatively to m2 (index (Lm3/Lm2) × 100). This index is 69 in the Pondaung fossil, 97 in *Galecyon morloi*, 77 in *Galecyon peregrinus*, 68 in *G. mordax* and 64 in *G. chronius* (means of several specimens for the latter), higher for the two former species but close to that of Pondaung in the latter one.

In NMMP-PK5 6-12-10, the dentary is relatively deep like in *Galecyon* but the trigonid of the m3 is more open and the lingual cuspids clearly separated, the protoconid is lower relative to the paraconid, the metaconid is slightly more distal, and the paraconid is lower with a postparacristid more elongate and directed more distomesially and not more conical as in *Galecyon*. The talonid of *Galecyon* has a robust hypoconid and a crista oblica directed toward the protoconid like in NMMP-PK5 6-12-10 but the basin is deeper with an entocristid slightly higher. Despite the common presence of a reduced m3, the differences between the m3 of the Asian fossil and the *Galecyon* species – especially the opening of the trigonid and length of the paracristid – imply that it is hard to refer the Pondaung taxon to *Galecyon*.

The Limnocyoninae are first recorded in the late Palaeocene of Asia (Meng et al., 1998), but they mainly radiated in the early and middle Eocene of North America (Gunnel, 1998). The whole subfamily Limnocyoninae is characterized by m3 reduced or absent (Morlo and Gunnell, 2003, 2005; Polly, 1996). The m3 is absent in *Limnocyon* Marsh, 1872a, *Thinocyon* Marsh, 1872b, *Oxyaenodon* Wortman, 1899, and *Iridodon* Morlo and Gunnell, 2003. In *Prolimnocyon* Matthew and Granger, 1915, m3 is dramatically reduced. The index m3/m2 is very low (63) in *P. chowi* Meng et al., 1998 – the oldest limnocyonine – and in *P. haematus* Gingerich and Deutsch, 1989 (means of several specimens for the latter), (43) in *P. atavus* Matthew and Granger, 1915, and the m3 is knob-like in *P. antiquus* (Morlo and Gunnell, 2003, fig. 18) so far more reduced than that of NMMP-PK5 6-12-10. The m3 of *P. chowi* recalls that of the Pondaung taxon in having a V shaped trigonid (in occlusal view) and a metaconid slightly more distal than the protoconid. However, the m3 of *P. chowi* differs from that of the Pondaung taxon in having a postparacristid clearly shorter and more transversally aligned and large hypoconulid and hypoconid. The m3 of *P. atavus* is more similar in having a longer and more oblique postparacristid, but, as mentioned above, the m3 is much more reduced compared to the m2 – the elongation and modification of the position of the postparacristid could correspond to a convergence towards more secant teeth. Therefore, based on these comparisons, the fossil from Pondaung could represent a taxon different from the Limnocyoninae.

Following the observations of Smith and Smith (2001) based on the hyaenodonts from Dormaal, it has been proposed that m3 was slightly smaller than m2 in the earliest hyaenodonts (Solé, 2013; Solé et al., 2013). Based on this postulate, one hypothesized that (1) the relative size of m3 increased in several groups of Hyaenodonta (e.g., Proviverrinae, Hyaenodontinae), whereas (2) the relative size of m3 decreased in the Limnocyoninae and *Galecyon*. Regarding this hypothesis, the Pondaung taxon could represent a third lineage that experienced such reduction.

7. Overall conclusion

The Pondaung Formation had produced at least three different taxa of Hyaenodonta, *Kyawdawia lupina*, *Yarshea cruenta* and *Orienspterodon dahkoensis*. Two indeterminate species, were also described, Proviverrinae indet. for a fragment of mandible in Egi et al. (2005) and Hyaenodontidae sp. indet. in Peigné et al. (2007) for a large M3, none of them matching the new material. Thus, the two new carnivorous significantly augment the list of the Pondaung predators. The larger species, *O. dahkoensis*, would occupy the place of a large hypercarnivore, the two medium-sized *Yarshea* and *Kyawdawia* acted like canids, the former being probably more carnivorous than the latter, *Propterodon* was a small hypercarnivore similar to the extant *Martes* and the smaller species was preying upon small vertebrates or invertebrates. These five species, together with the other indeterminate species, constituted a quite complete guild of predators.

Concerning the paleo-biogeography, we note that all the genera are recorded only in Myanmar (*Yarshea* and *Kyawdawia*) or in Myanmar, Mongolia or China (*Propterodon* and *Orienspterodon*). The relationships of these carnivorous with those of other continents are thus actually unknown. However, one can note that the hyainailourines (*Orienspterodon*) and hyaenodontines (*Propterodon*) recorded in the Pondaung Formation, are the first ones recorded in the Southeast Asia. It is interesting to note that these subfamilies appeared almost contemporaneously in Europe: hyaenailourines appeared around MP16 reference level (ca. 39 Ma) (Solé et al., 2013) and the hyaenodontines around

MP17a (ca. 38 Ma) (Lange-Badré, 1979). The hyaenodonts of the Pondaung Formation thus might illustrate a profound modification of the carnivorous fauna among Laurasia.

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