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Neochorlakkia myaingensis n. gen., n. sp., a new Dichobunidae (Mammalia, Cetartiodactyla) from the middle Eocene Pondaung Formation, Myanmar

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Occlusal view of the m3 of *Neochorlakkia myaingensis* n. gen., n. sp. (background: view of Paukkaung Kyitchaung 2 locality). Credits: Olivier Chavasseau.

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Neochorlakkia myaingensis n. gen., n. sp., a new Dichobunidae (Mammalia, Cetartiodactyla) from the middle Eocene Pondaung Formation, Myanmar

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ABSTRACT
The diversity of basal ungulates is significant in the late middle Eocene Pondaung Formation (Myanmar). However, the precise identification or attribution of some fossils is sometimes difficult because of the scarcity and poor preservation of the material. We describe here a new genus and species of a Dichobunidae from Paukkaung Kyitchaung 2 locality, that is morphologically and probably phylogenetically close to a taxon from the early-middle Eocene of Pakistan, and we discuss the attribution of dental material to *Myanmarius chitseini* Tsubamoto, Egi, Takai, Htike & Zin-Maung-Maung-Thein, 2013, an inderterminate artiodactyl from Pondaung. This study also confirms that dispersals were possible between the Indian subcontinent and Southeast Asia during the first part of the Eocene.

KEY WORDS
Myanmar,
Pondaung Formation,
late middle Eocene,
Cetartiodactyla,
Dichobunidae,
new genus,
new species.

RÉSUMÉ
Neochorlakkia myaingensis *n. gen., n. sp., un nouveau Dichobunidae (Mammalia, Cetartiodactyla) de l'Eocène moyen de la formation de Pondaung, Myanmar.*
La diversité des ongulés basaux est importante dans la formation de Pondaung (fin de l'Eocène moyen) au Myanmar. Cependant, l'identification ou même l'attribution précises de certains fossiles sont parfois difficiles du fait de la pauvreté et de la mauvaise préservation du matériel. Nous décrivons ici un nouveau genre et une nouvelle espèce de Dichobunidae de la localité de Paukkaung Kyitchaung 2, proche morphologiquement et probablement phylogénétiquement d'un taxon de l'Eocène inférieur-moyen du Pakistan, et nous proposons une discussion sur l'attribution du matériel dentaire de *Myanmarius chitseini* Tsubamoto, Egi, Takai, Htike & Zin-Maung-Maung-Thein, 2013, un artiodactyle indéterminé de Pondaung. Ce travail confirme également la possibilité d'échanges fauniques pendant la première partie de l'Eocène, entre le sous-continent Indien et l'Asie du Sud-Est.

MOTS CLÉS
Myanmar,
formation de Pondaung,
fin de l'Eocène moyen,
Cetratiodactyla,
Dichobunidae,
genre nouveau,
espèce nouvelle.

INTRODUCTION

The late middle Eocene Pondaung fauna is characterized by its rich diversity of perissodactyls, anthracothere artiodactyls, and primates. However, recent studies have revealed that a significant number of basal "ungulates" also diversified in this area and represents a large proportion of the mammalian community (Ducrocq *et al.* 2000; Métais 2006; Métais *et al.* 2007; Tsubamoto *et al.* 2012; Ducrocq *et al.* 2016; Ducrocq 2019), most of them being represented by fragmentary remains and thus of uncertain affinities. Particularly, Tsubamoto *et al.* (2005: fig. 2B, C) described two upper molars from Pondaung that they referred to an indeterminate artiodactyl. Theodor *et al.* (2007) later suggested that this material might be related to the Raoellidae, a family of Asian small Eocene artiodactyls closely related to the Cetacea. In their revision of the dental features of the family Raoellidae, Orliac & Ducrocq (2012) demonstrated that the molars described by Tsubamoto *et al.* (2005) was not part of the raoellid clade, but was probably more closely related to the Suoidea. Tsubamoto *et al.* (2013) then re-examined this material, creating the genus and species *Myanmarius chitseini* Tsubamoto, Egi, Takai, Htike & Zin-Maung-Maung-Thein, 2013, and attributed two additional upper molars and a fragmentary and worn distal part of a lower molar to this taxon. According to them, *Myanmarius* Tsubamoto, Egi, Takai, Htike & Zin-Maung-Maung-Thein, 2013 was closely related to either the raoellids or the suoids depending on the inclusion of the fragmentary lower molar or not in their phylogenetic study.

There is no strong evidence that the upper and lower molars described by Tsubamoto *et al.* (2005, 2013) belong to the same taxon because they were not found in association. Indeed, Tsubamoto *et al.* (2013) only considered matching size, bunodonty and the occurrence of a distobuccal wear facet on the worn m3 to associate this tooth with the upper molars and to attribute it to *Myanmarius*. We describe here a complete isolated m3 recently found in the locality of Paukkaung Kyitchaung 2 (Fig. 1) that is almost identical to the fragmentary m3 illustrated by Tsubamoto *et al.* (2013), and we attribute both of them to a new genus and species distinct from *Myanmarius chitseini*. This complete lower molar displays additional morphological information that will allow discussing its systematic relationships, and that also might help understanding the status of the material referred to *Myanmarius*.

Abbreviations

Site and institutional abbreviations

GSP-UM	Geological Survey of Pakistan, University of Michigan, Ann Arbor;
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing;
MFP-PK2	Myanmar French Paleontology, Paukkaung kyitchaung 2 Collections at the Myanmar Ministry of Culture, Nay Pyi Taw;
NMMP-KU	National Museum, Myanmar, Paleontology, Kyoto University, Kyoto;
ZIN	Zoological Institute, Russian Academy of Sciences, Saint Petersburg.

Other abbreviations

L	maximal length;
M/m	upper/lower molars;
W	maximal width.

All measurements are in mm.

SYSTEMATIC PALAEONTOLOGY

Superorder CETARTIODACTYLA Montgelard, Catzeflis & Douzery, 1997
Superfamily Dichobunoidea Gill, 1872
Family Dichobunidae Turner, 1849

Neochorlakkia n. gen.

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Type species. — *Neochorlakkia myaingensis* n. gen., n. sp., by monotypy.

Neochorlakkia myaingensis n. gen., n. sp.
(Fig. 2A-E)

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HOLOTYPE. — MFP-PK2-2019-003, isolated right m3, deposited in the Pondaung Collections at the Myanmar Ministry of Culture, Nay Pyi Taw, Myanmar.

ETYMOLOGY. — Genus name derives from the Greek prefix neo, meaning more recent, and *Chorlakkia* Gingerich, Russell, Sigogneau-Russell & Hartenberger 1979 in reference of the strong morphological similarity of the lower molar from Pondaung with those of *Chorlakkia hassani* Gingerich, Russell, Sigogneau-Russell & Hartenberger, 1979 from the early middle Eocene of Pakistan. Species name refers to the Myaing township where the specimens were found.

REFERRED MATERIAL. — NMMP-KU 2000 (Fig. 2D), fragmentary right m3 (Tsubamoto *et al.* 2013: figs 2C, 5A).

LOCALITY AND HORIZON. — Paukkaung Kyitchaung 2 locality, Bahin area, Pondaung Formation, Myanmar; late middle Eocene.

DIAGNOSIS. — Middle-sized ungulate characterized by its very bunodont and short m3, lacking a paraconid and most of cristids. Differs from most of the primitive artiodactyls (Diacodexeidae, Homacodontidae, European Dichobunidae, Raoellidae) by its strongly bunodont m3 with poorly expressed crests, with a short trigonid lacking a paraconid, absence of a hypolophid, with a mesiodistal cristid obliqua and a reduced hypoconulid lobe. Differs from the Asian dichobunid *Chorlakkia* by its larger size, its hypoconid taller than the entoconid and hypoconulid, its entoconid in line with the hypoconid and by its hypoconulid lobe consisting in two small cusps.

DESCRIPTION

The tooth (MFP-PK2-2019-003) is a right m3 (L = 14.8 mm; W = 9.2 mm) without any contact facet on its distal wall. The lingual and buccal roots are fused and there is a fifth tiny root under the most posterior cusp that runs along the distal roots. The molar is bunodont with four main cusps and weakly expressed crests. The trigonid is somewhat taller than the talonid. The preprotocristid and premetacristid form a low and continuous blunt crest that mesially closes the trigonid. There is no other crest in the trigonid part and only a slight furrow separates both bulbous mesial cusps. The distal wall of the trigonid is flat and mesially slanted. The lingual part of the talonid basin seems to be lined by a very slight and low postmetacristid that connects with the preentocristid, and its buccal part is edged by the mesially directed cristid obliqua (prehypocristid) that ends low on the distal wall of the protoconid. It is not possible to distinguish whether the lingual end of the transverse valley was open because this area is cracked, but the occurrence of a low postmetacristid and preentocristid suggests that they likely constitute a weak lingual edge. There is no distinct crest (hypolophid) connecting the hypoconid and the smaller and lower entoconid, but a narrow mesiodistally oriented groove separates both cusps and curves buccally between the hypoconulid and the hypoconid. The short and slightly distally protruding hypoconulid lobe is composed of two small cusps separated by a very slight furrow, and a shallow slit can be observed between the mesial hypoconulid cusp and the entoconid, suggesting that both cusps might have been twinned. The hypoconulid is not connected to the hypoconid. A narrow cingulid is present along the mesial face of the molar and a short one can be observed at the buccal end of the transverse valley between the protoconid and the hypoconid (Fig. 2A-C, E).

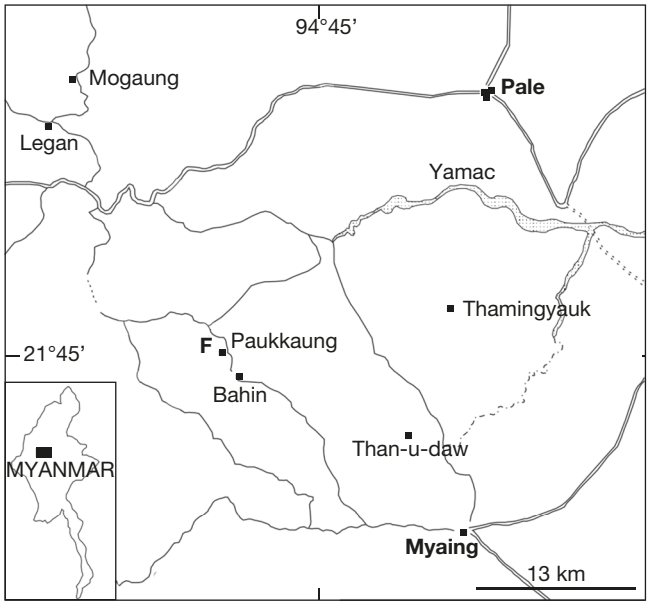

FIG. 1. — Location map of the Pondaung area. **F** indicates Paukkaung 2 locality.

COMPARISONS

Among basal cetartiodactyls, the Diacodexeidae can be distinguished from *Neochorlakkia* n. gen. by their much less bunodont lower molars with better expressed crests that often exhibit a paraconid, a talonid basin usually lingually open with a more oblique cristid obliqua, a m3 hypoconulid better developed and connected to the hypoconid and the entoconid. The Asian Homacodontidae *Limeryx* Métais, Qi, Guo & Beard, 2005, *Asiohomacodon* Tsubamoto, Tun, Egi, Takai, Shigehara, Soe, Aung & Thein, 2003 and *Tsaganohyus* Kondrashov, Lopatin & Lucas, 2004 are also more selenodont with a paraconid (*Limeryx* and *Tsaganohyus*), a hypolophid and a *Zhailimeryx* fold on the mesial face of the entoconid (*Limeryx*; see Guo *et al.* 2000), and their cristid obliqua is more obliquely oriented (Fig. 3C, D). The Asian Dichobunidae are mostly represented by fragmentary material that complicates their precise systematic affinities. For example, the Lantianiinae for which lower molars are known (*Elaschitotherium* Métais, Guo & Beard, 2004 and *Eolantianus* Averianov, 1996) display less bunodont crowns, with a more obliquely oriented cristid obliqua, a distinct paraconid (*Elaschitotherium*), a hypolophid and a stronger hypoconulid lobe (Fig. 3E, F). *Haqueina* Dehm & Oettingen-Spielberg, 1958 from the middle Eocene of Pakistan is slightly smaller than *Neochorlakkia* n. gen., but it is also less bunodont with better expressed crests (postcristids on mesial cusps), more oblique cristid obliqua, with a discrete hypolophid connecting the hypoconid and the entoconid, and a narrower and more distally protruding hypoconulid (Fig. 3G). *Pakibune* Thewissen, Gingerich & Russell, 1987 from the early-middle Eocene of Pakistan is known only from an isolated m3 that is much smaller and more elongated than the Pondaung molar, with less bunodont cusps, a paraconid, a more oblique cristid obliqua, an entoconid distinctly more distal than the hypoconid, and better developed hypoconulid and buccal cingulid (Fig. 3H).

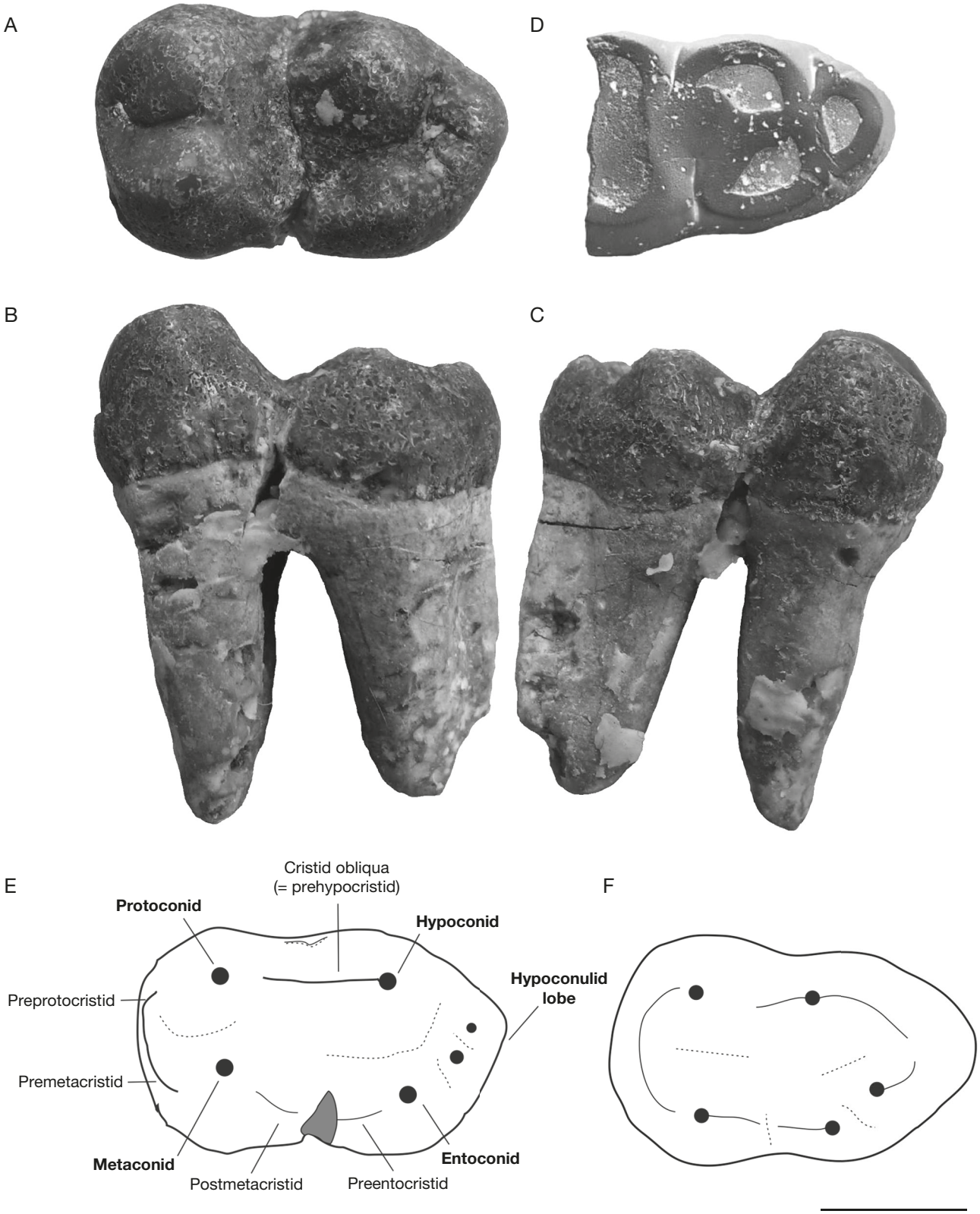

FIG. 2. — *Neochorlakkia myaingensis* n. gen., n. sp. from the late middle Eocene of Paukkaung Kyitchaung 2, Myanmar: **A**-**C**, holotype MFP-PK2-2019-003, right m3 in occlusal (**A**), lingual (**B**), and buccal (**C**) views ; **D**, NMMP-KU 2000, right m3 in occlusal view. **E**-**F**, Interpretative drawings of: **E**, *Neochorlakkia myaingensis* n. gen., n. sp. (MFP-PK2-2019-003); and **F**, *Chorlakkia hassani* Gingerich, Russell, Sigogneau-Russell & Hartenberger, 1979 (GSP-UM 77082, inverted). E and F at same scale. Scale bar: 5 mm.

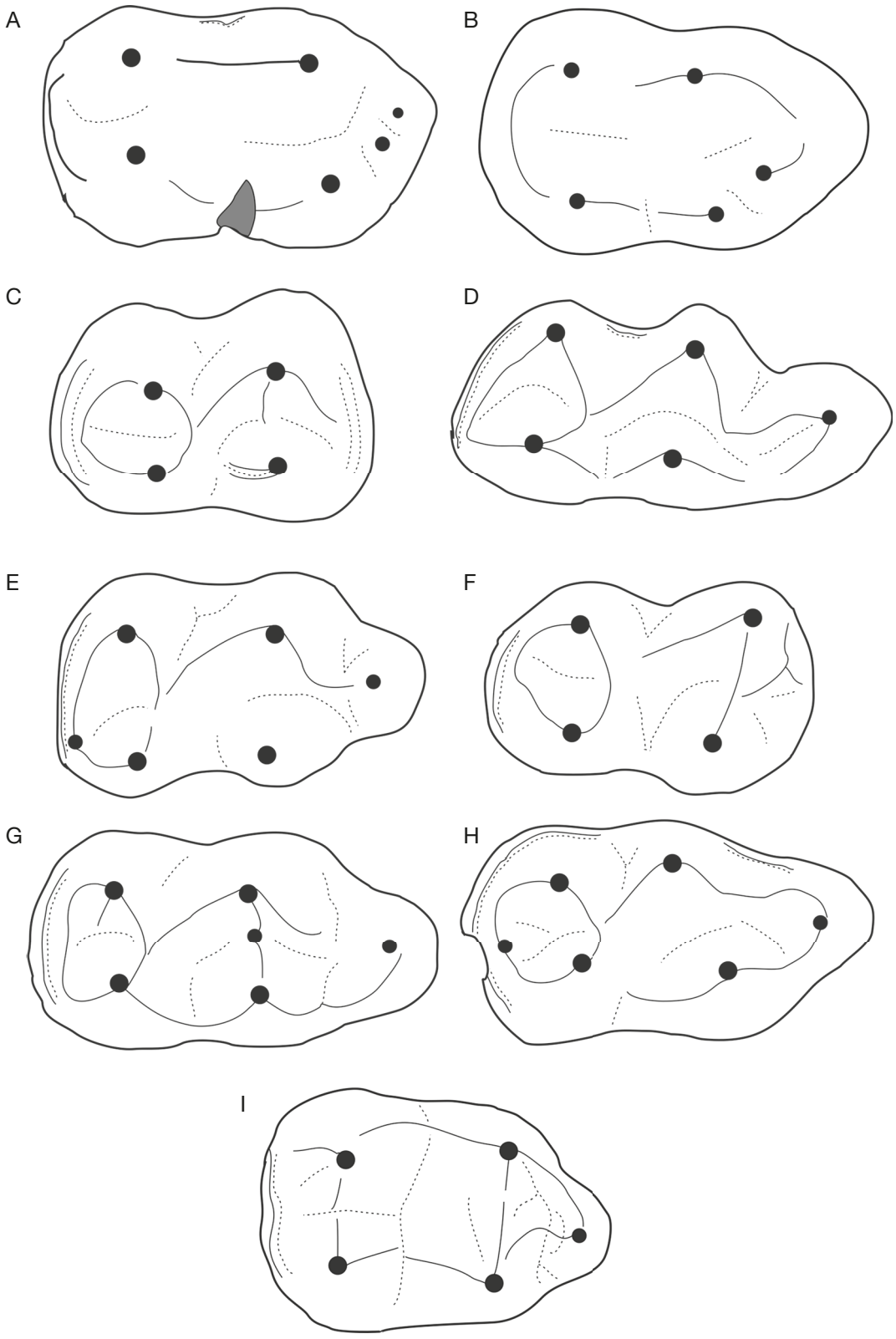

Fig. 3. — Interpretative drawings of the lower molars of the main dichobunoid taxa compared with *Neochorlakkia myaingensis* n. gen., n. sp.: **A**, *Neochorlakkia myaingensis* n. gen., n. sp., holotype MFP-PK2-2019-003, right m3 (L = 14.8 mm; W = 9.2 mm); **B**, *Chorlakkia hassani* Gingerich, Russell, Sigogneau-Russell & Hartenberger, 1979, GSP-UM 77082, left m3 inverted (L = 4.1-4.5; W = 2.8) ; **C**, *Limeryx chimaera* Métais, Qi, Guo & Beard, 2005, IVPP 34567.2, right m2 (L = 7.5; W = 5.4) ; **D**, *Asiohomacodon myanmarensis* Tsubamoto, Tun, Egi, Takai, Shigehara, Soe, Aung & Thein, 2003, NMMP-KU 0028, right m3 (L = 10.7; W = 5.6-6.0) ; **E**, *Elaschitotherium qii* Métais, Guo & Beard, 2004, IVPP 12759.44, left m3 inverted (L = 3.8-4.4; W = 2.2-2.6) ; **F**, ?*Eolantianus russelli* Averianov, 1996, ZIN 34355, right m2 (L = 4.1; W = 2.5-2.8) ; **G**, *Haqueina haquei* Dehm & Oettingen-Spielberg, 1958, holotype Sammlung München 1956 II 10, left m3 inverted (L = 10.8; W = 6.0) ; **H**, *Pakibune chorlakkiensis* Thewissen, Gingerich & Russell, 1987, holotype GSP-UM 259, right m3 (L = 5.8; W = 3.1) ; **I**, *Khirtharia dayi* Pilgrim, 1940, GSP-UM 87, right m3 (L = 9.6; W = 6.0). The molars are not at the same scale.

Although *Wutuhyus* Tong & Wang, 2006 from the early Eocene of eastern China shares bunodont cusps with the Pondaung form, it is also much smaller, with an enlarged trigonid that exhibits a prominent paraconid and a metaconid posterior to the protoconid, and an unreduced hypoconulid with two cusps. Tsubamoto *et al.* (2013) noted that the general morphology of the partial m3 NMMP-KU 2000 (Fig. 2D) somewhat reminds that of some raoellid forms: its strong bunodonty, blunt crests, absence of paraconid, reduced hypoconulid, mesially oriented cristid obliqua and well developed talonid basin ("crushing basin") are features that can also be observed in raoellids. These are features that can also be observed in *Neochorlakkia* n. gen.(Figs 2A, E; 3A). However, the lack of crests that enclose the central basin that are characteristic of raoellids (Orliac & Ducrocq 2012), especially the hypolophid that borders the basin distally and the almost absent postcristids of the mesial cusps on both m3 points to different affinities (Fig. 3I).

Interestingly enough, although the Dichobunidae *Chorlakkia hassani* from the early-middle Eocene of Pakistan is much smaller than the Pondaung specimen, the occlusal outline and morphology of the m3 of both taxa are strikingly similar. Indeed, the bunodont protoconid and metaconid not connected distally by crests, the lack of a paraconid, the deep talonid basin, the almost mesiodistally oriented cristid obliqua, the entoconid lingually protruding, and the reduced hypoconulid lobe are features shared by the Pakistani and Pondaung forms (Fig. 2E, F). However, MFP- PK2-2019-003 exhibits a hypoconid slightly taller than the entoconid-hypoconulid complex, an entoconid in line with the hypoconid, an hypoconulid consisting of two very small cusps and smaller than the entoconid (Fig. 3A, B). Vislobokova (2004) identified a new species of *Chorlakkia* (*C. valerii* Vislobokova, 2004) from the middle Eocene of Mongolia. This taxon displays several differences with *C. hassani* such as a lower molar crown more elongated, a trigonid much higher than the talonid, a hypoconulid lobe single cusped and much more developed distally, an entoconid more lingually protruding and in line with the hypoconid. It also differs from *Neochorlakkia* n. gen. by its much smaller size, more elongated crown with the trigonid much taller than the talonid, more oblique cristid obliqua, entoconid lower than hypoconid, presence of a posthypocristid, single-cusped hypoconulid separated from the entoconid by a depression, more elongated hypoconulid lobe, and weaker mesial cingulid. Nevertheless, the structural features that can be observed in the ungulate from Mongolia but not in *Chorlakkia* cast doubts on the generic attribution of *C. valerii*.

DISCUSSION

Despite its heavy wear, the general structure and size of the broken m3 (NMMP-KU 2000) described by Tsubamoto *et al.* (2013) as *Myanmarius chitseini* seem to match those of the molar described here except for its absence of a buccal cingulid between the protoconid and the hypoconid that might be caused by wear, and its slightly less lingually protruding entoconid that causes the distal part of the crown to taper (Fig. 2D). We can thus confidently refer NMMP-KU 2000 to *Neochorlakkia myaingensis* n. gen., n. sp. However, there is some doubt about the association of the upper molars attributed to *M. chitseini* with the lower ones. Indeed, most of the early and middle Eocene Asian Dichobunidae usually possess triangular and wider than long upper molars with three main cusps (paracone, metacone, protocone), distinct but small conules, sometimes a hypocone, and a protocone more lingually protruding than the distolingual cusp. The morphology of both m3 (MFP-PK2-2019-003 and NMMP-KU 2000) being similar to that of the m3 of *Chorlakkia hassani*, it is expected that the corresponding upper molars might resemble those of the Pakistani genus. The upper teeth attributed to *Chorlakkia* by Thewissen *et al.* (1987) exhibit this primitive morphology very different from that of the upper molars referred to *Myanmarius* that are more quadratic, with a well-developed distolingual metaconule and no hypocone, and that would more likely correspond to more advanced ungulates. In addition, the size and peculiar morphology of the M3 referred to *Myanmarius* (NMMP-KU 1742: position of the cusps on the buccolingual wide crown, presence of distinct crests on the paracone, metacone and protocone) do not seem to provide a proper occlusion pattern with the structure of the narrow and very bulbous m3 MFP-PK2-2019-003. Especially, Tsubamoto *et al.* (2013: 303) claimed that the distobuccal wear facet next to the hypoconulid of the m3 might correspond to the "small cusp-like structure distal to the metacone-metaconule on the corresponding M3". However, the occlusal interpretation of the upper and lower last molars provided in Figure 4 illustrates that a proper occlusion was likely not possible because of the size and position of cusps and crests on antagonist molars, and it thus strongly suggests that they do not belong to the same taxon. Indeed, although the trigonid cusps leave enough surface for the protocone and paraconule of NMMP-KU 1742, the paracone of this molar occludes against the cristid obliqua, and the accessory cusps on the distal margin of the M3 come into occlusal contact with the hypoconulid cusps of m3. Likewise, the M2 (NMMP-KU 1765) attributed to *Myanmarius* that exhibits a structure similar to that of the M3 NMMP-KU 1742 in terms of cusp and crest arrangement might also not be associated to the lower molars. Finally, the two other upper molars (NMMP-KU 2208a and NMMP-KU 2208b) tentatively attributed to *Myanmarius* (Tsubamoto *et al.* 2013) display structural differences when compared with NMMP-KU 1765, which casts doubts on their generic assignement: their paraconule is more in line with the paracone and the protocone (more mesially situated in NMMP-KU 1765), their lingual wall is inflated at the protocone level thus giving a more triangular outline to the crown (this region is more square in NMMP-KU 1765), their protocone lacks a distobuccal crest, and their mesial cingulum is somewhat weaker. As a consequence, the material included in the hypodigm of *Myanmarius chitseini* should be restricted to the holotype (right M2, NMMP-KU 1765) and possibly the right M3 (NMMP-KU 1742), whereas the two upper molars (NMMP-KU 2208a and

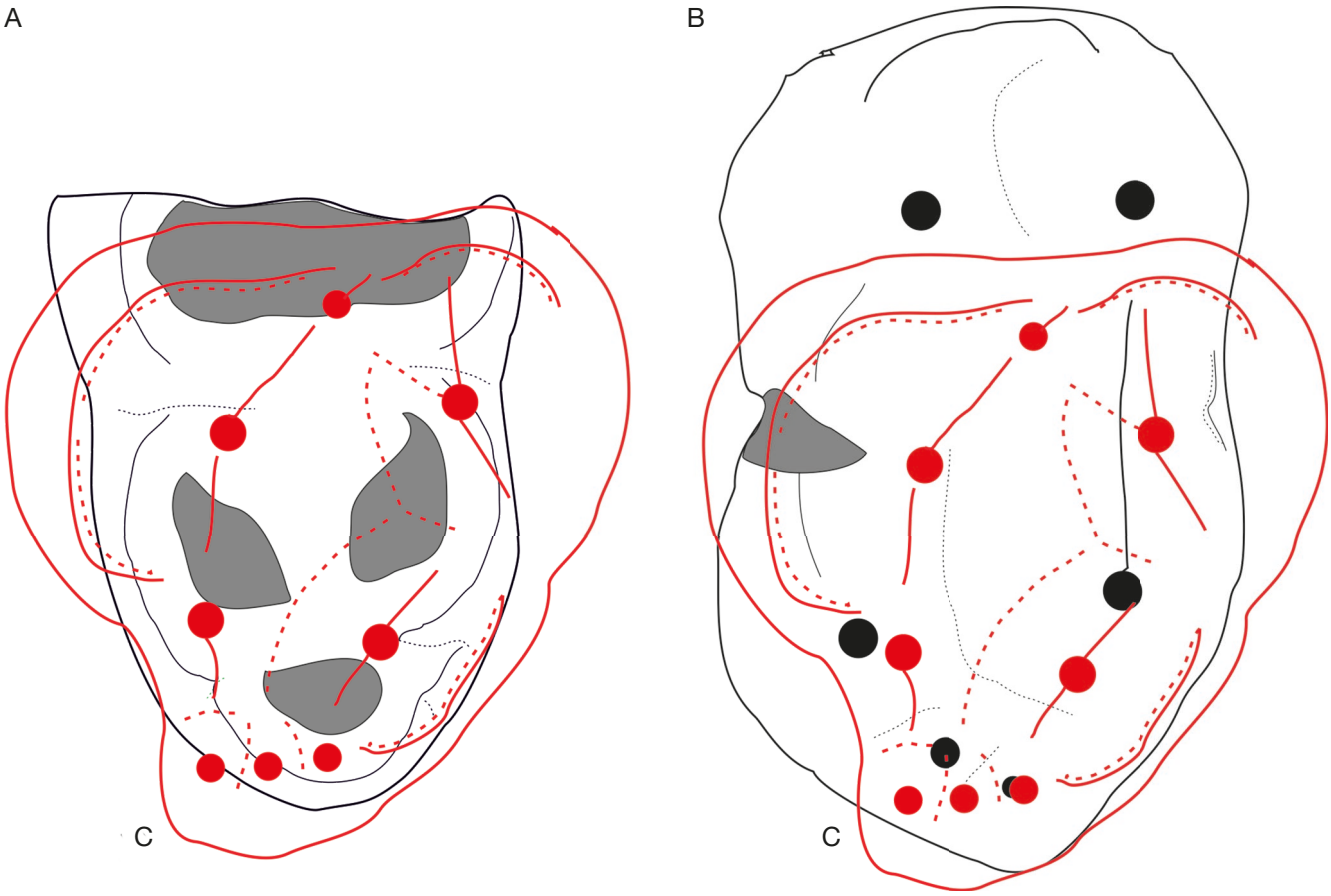

FIG. 4. — Occlusal interpretative drawings of the m3 of *Neochorlakkia myaingensis* n. gen., n. sp. (**A**, NMMP-KU 2000; and **B**, MFP-PK2-2019-003) and the M3 of *Myanmarius chitseini* Tsubamoto, Egi, Takai, Htike & Zin-Maung-Maung-Thein, 2013 (**C**, NMMP-KU 1742). **Black lines** and **circles** correspond to occlusal outline, crests, valleys and cusps of the m3 of *N. myaingensis* n. gen., n. sp. **Red lines** and **circles** correspond to occlusal outline, crests, valleys and cusps of the M3 (NMMP-KU 1742) of *M. chitseini*. Upper and lower molars are represented at the same scale.

NMMP-KU 2208b) provisionally referred to *Myanmarius* by Tsubamoto *et al.* (2013) might belong to a distinct taxon. The lower molar NMMP-KU 2000 described by Tsubamoto *et al.* (2013) can thus been removed from *M. chitseini* (the holotype of this taxon being an upper molar), and it can be transfered into *Neochorlakkia myaingensis* n. gen., n. sp. Considering the fossil material that we refer to *Myanmarius*, the raoellid or suoid affinities suggested by Tsubamoto *et al.* (2013) are very unlikely (lack of typical transverse crests that delimit the central basin, Orliac & Ducrocq 2012), and its relationships should be investigated within the dichobunids.

CONCLUSIONS

The systematic affinities of *Neochorlakkia* n. gen. can be challenging because only two lower molars are attributed to that genus so far. However, their peculiar morphology including the association of their occlusal outline, strong bunodonty, poorly expressed crests, lack of a paraconid and of a hypolophid, and mesiodistal cristid obliqua sets them apart from most of the primitive artiodactyls (Diacodexeidae, Homacodontidae, European Dichobunidae, Raoellidae). On the other hand, although they are more derived by some features (larger size, hypoconid slightly taller than the entoconid and in line with it, entoconid not twinned with the hypoconulid), the Pondaung teeth are much more similar to the m3 of the Dichobunidae *Chorlakkia*. Although morphological convergence cannot be excluded, these similarities, together with the chronological occurrence of both taxa, might reflect phylogenetic relationships between *Chorlakkia* and *Neochorlakkia* n. gen. If such relationships were proved correct, this might thus reinforce the hypothesis that dispersal events were possible between the Indian Subcontinent and southeastern Asia until the middle Eocene, as already demonstrated for the Raoellidae by Orliac & Ducrocq (2012). No additional dental material can be referred to *Neochorlakkia* n. gen. at the moment, but a detailed resassessement of the Pondaung specimens described as "indeterminate artiodactyl" as well as further discoveries from ongoing work in the Paleogene of Myanmar might lead to a better knowledge of the dental morphology of this taxon and to more precisely identify its systematic affinities.

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