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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Submitted on 26 June 2020 | Accepted on 16 September 2020 | Published on 31 January 2022

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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 (Mammalia, Cetartiodactyla) from the middle Eocene Pondaung Formation, Myanmar. Comptes Rendus Palevol 21 (4): 115-122. https://doi.org/10.5852/cr-palevol2022v21a4

**KEY WORDS**

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

The late middle Eocene Pondaung fauna is characterized by its rich diversity of perissodactyls, anthracotherian 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; Métai 2006; Métai 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 Raaellidae, a family of Asian small Eocene artiodactyls closely related to the Cetacea. In their revision of the dental features of the family Raaellidae, 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, 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.
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 hypoconulid 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 slightly and low postmetacristid that connects with the preentocristid, and its buccal part is edged by the mesially directed cristid obliqua (prehypocrustid) 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).

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 Metais, Qi & Beard, 2005, Asiohomacodon Tsubamoto, Tun, Egi, Takai, Shigehara, Soc, Aung & Thein, 2003 and Tiganohyus Kond rashov, Lopatin & Lucas, 2004 are also more selenodont with a paraconid (Limeryx and Tiganohyus), a hypolophid and a Zha limeryx 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 Lantiania for which lower molars are known (Elaschitotherium Metais, Qi & Beard, 2004 and Eolan tianus 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). Haqueine 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 (postcristsids 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 Thewis, 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.
Neochorlakkia myaingensis n. gen., n. sp., a new Dichobunidae (Mammalia, Cetartiodactyla)

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, Limnixx chinaeaa Metais, 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 qi Metais, Guo & Beard, 2004, IVPP 12759.44, left m3 inverted (L = 3.8-4.4; W = 2.2-2.6); F, ?Elantianus 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 chorlakkiiensis 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 raellid 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 raellids. 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 raellids (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 paraconid 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 Pondaung and *C. hassani* (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. valeri) 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 linguually 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. valeri*.

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 chiiteinii* 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 linguually 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. chiiteinii* 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 distolinguinal 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 distolinguinal 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 buccolinguinal 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 paracone 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* (Tsabamoto et al. 2013) display structural differences when compared with NMMP-KU 1765, which casts doubts on their generic assignement: their paracone 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 chiiteinii* 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
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. chietseni (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 reassessment 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.

Acknowledgements

This work has been supported by the National Geographic Society Grant N° W 344-14, the Leakey Foundation, the ANR-DFG EVEPRIMASIA (ANR-18-CE92-0029 / BO 3479/7-1), the
CNRS UMR 7262, the University of Poitiers, and the Ministry of Culture of the Republic of the Union of Myanmar. We are indebted to the chairmen and villagers of Bahin and Paukkaung of Pondaung area for their help, kindness, and enthusiasm that greatly facilitated our fieldwork. We thank M. Rugbumrung for preparation and casting of the material and L. Foley-Ducrocq who corrected the English. Thanks to G. Métais, an anonymous reviewer and the editor L. Rook whose comments significantly improved the earlier version of the manuscript.

REFERENCES

AVERIANOV A. 1996. — Artiodactyla from the early Eocene of Kyrgyzstan. Palaeovertebrata 25 (2-4): 359-369. https://palaeovertebrata.com/Articles/view/212

DEHM R. & OETTINGEN-SPIELBERG T. 1958. — Paläontologische und geologische Untersuchungen im Tertiär von Pakistan. 2. Die mitteleozänen Säugerfaunen von Ganda Kas bei Basal, Nordwest-Pakistan. Abhandlungen der Bayerische Akademie der Wissenschaften 91: 1-54.

DUCROCQ S. 2019. — Pakkokhyus and Progenitohyus (Artiodactyla, Mammalia) from the Eocene of Southeast Asia are not Helohyidae: paleobiogeographical implications. Paläontologische Zeitschrift 93: 105-113. https://doi.org/10.1007/s12542-018-0425-5

DUCROCQ S., SOE A. N., BO B., BENAMM M., CHAINANE E., TUN T., THEIN T. & JAEGER J.-J. 2000. — First record of an Anthracobunidae (Mammalia, ?Ethiotheria) from the Eocene of the Pondaung Formation, Myanmar. Comptes Rendus de l’Académie des Sciences, Paris (Sciences de la Terre) 330: 725-730. https://doi.org/10.1016/S1251-8050(00)00187-7

DUCROCQ S., SOE A. N., SEIN C., LAZZARI V., CHAINANE E., VALENTIN X. & JAEGER J.-J. 2016. — First record of a diaco-dexeed artiodactyl in the middle Eocene Pondaung Formation (Myanmar). Paläontologische Zeitschrift 90: 611-618. https://doi.org/10.1007/s12542-016-0283-y

GILL T. 1872. — Arrangement of the families of mammals and synoptical tables of characters of the subdivisions of mammals. Smithsonian Miscellaneous Collections 230: 1-98. https://doi.org/10.5962/bhl.title.14607

GINGERICH P. D., RUSSELL D. E., SIGGNEAU-RUSSELL D. & HARTENBERGER J.-L. 1979. — Chorokhia hassani, a new middle Eocene dichobunid (Mammalia, Artiodactyla) from the Kuldana Formation of Kohat (Pakistan). Contributions from the Museum of Paleontology 25 (6): 117-124. http://hdl.handle.net/2027.42/48496

GUO J., DAWSON M. R. & BEARD K. C. 2000. — Zhalimeryx, a new lophiomyercyd artiodactyl (Mammalia) from the late middle Eocene of Central China and the early evolution of ruminants. Journal of Mammalian Evolution 7: 239-258. https://doi.org/10.1023/A:100943715125

MÉTAIS G. 2006. — New basal selenodont artiodactyls from the Pondaung Formation (late middle Eocene, Myanmar) and the phylogenetic relationships of early ruminants. Annals of Carnegie Museum 75: 51-67. https://doi.org/10.1007/s00114-007-0256-9

MÉTAIS G., SOE A. N., MARIVAUX L. & BEARD K. C. 2007. — Artiodactyls from the Pondaung Formation (Myanmar): new data and reevaluation of the South Asian Faunal Province during the middle Eocene. Naturwissenschaften 94: 759-768. https://doi.org/10.1007/s00114-007-0256-9

MONTEGELARD C., CATZEFLIS F. M. & DOUTZERY E. 1997. — Phylogenetic relationships of artiodactyls and cetaceans as deduced from the comparison of cytochrome b and 12S rRNA mitochondrial sequences. Molecular Biology and Evolution 14: 550-559. https://doi.org/10.1093/oxfordjournals.molbev.a025792

OHLAC M. J. & DUCROCQ S. 2012. — Eocene raoellids (Mammalia, Cetartiodactyla) outside the Indian Subcontinent: palaeogeographical implications. Geological Magazine 149: 80-92. https://doi.org/10.1017/S001675681100586

THEODOR J. M., ERFURT J. & MÉTAIS G. 2007. — The earliest artiodactyls, in PROTHERO D. R. & FOSS S. E. (eds), The Evolution of Artiodactyls. The Johns Hopkins University Press, Baltimore: 32-58.

THEWISSEN J. G. M., GINGERICH P. D. & RUSSELL D. E. 1987. — Artiodactyla and Perissodactyla (Mammalia) from the early-middle Eocene Kuldana Formation of Kohat (Pakistan). Contributions from the Museum of Paleontology 27 (10): 247-274. https://hdl.handle.net/2027.42/48532

TONG Y. & WANG J. 2006. — Fossil mammals from the early Eocene Wutu Formation of Shandong Province. Palaeontologica Sinica 192: 1-223.

TSUBAMOTO T., EGI N., TAKAI M., SEIN C. & MAUNG M. 2005. — Middle Eocene ungulate mammals from Myanmar: a review with description of new specimens. Acta Palaeontologica Polonica 50: 117-138.

TSUBAMOTO T., EGI N., TAKAI M., HITEKE T. & ZINA-MAUNG MAUNG-THIN 2012. — Dental morphology of an enigmatic artiodactyl from the Eocene Pondaung Formation, Myanmar. Journal of Fossil Research 45: 6-10.

TSUBAMOTO T., EGI N., TAKAI M., HITEKE T. & ZINA-MAUNG MAUNG-MAUNG-THIN 2013. — A new genus and species of bunodont artiodactyl from the Eocene Pondaung Formation, Myanmar. Paleontological Research 17: 297-311. https://doi.org/10.2517/1342-8144-17.4.297

TURNER H. N. 1849. — On the evidence of affinity afforded by the skull in the ungulate Mammalia. Proceedings of the Zoological Society of London 17: 147-158.

VISLOBOKOVA I. A. 2004. — Artiodactyls from the middle Eocene of Khaichin-Ula II, Mongolia. Paleontological Journal 38: 90-96.

Submitted on 26 June 2020; accepted on 16 September 2020; published on 31 January 2022.