

New material of *Paukkaungmeryx minutus* (Cetartiodactyla, Archaeomerycidae) from the late Middle Eocene Pondaung Formation, Myanmar Postprint

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Date: 2023-05-25T00:00:00+00:00

Abstract

This paper describes new dental material of the primitive ruminant archaeomerycid *Paukkaungmeryx minutus* Ducrocq et al., 2020 from the Myaukse Kyitchaung locality in the Pondaung Formation of central Myanmar. The upper molars of the new material exhibit only minor morphological variations compared to the holotype, such as better-developed buccal and lingual cingula. The lower cheek teeth possess primitive features, including: a simple p4, bunoselenodont lower molars, and the absence of a “fold” -like structure on the posterior wall of the trigonid. The discovery of this new material makes *Paukkaungmeryx* the second archaeomerycid member from the Pondaung Formation to preserve both upper and lower dentition, and also reveals the complex early evolutionary history of the Archaeomerycidae.

Full Text

Preamble

New material of *Paukkaungmeryx minutus* (Cetartiodactyla, Archaeomerycidae) from the late Middle Eocene Pondaung Formation, Myanmar

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Abstract

We describe here new dental material from the locality of Myaukse Kyitchaung (Pondaung Formation, central Myanmar) that we refer to the primitive Archaeomerycidae ruminant *Paukkaungmeryx minutus* Ducrocq et al. (2020). The upper molars are morphologically very similar to those of the holotype and exhibit only slight variations on features like the better development of buccal and lingual cingula. The lower teeth display primitive characters including a simple p4 and bunoselenodont lower molars that lack folds on the back of the trigonid wall.

This additional material makes *Paukkaungmeryx* the second archaeomerycid in Pondaung known by upper and lower teeth material, and documents the apparently complex early evolution of the family.

Key words

Pondaung Formation; Myanmar; middle Eocene; Cetartiodactyla; Archaeomerycidae; *Paukkaungmeryx*

Citation

Ducrocq S, Chaimanee Y, Chavasseau O et al., in press. New material of *Paukkaungmeryx minutus* (Cetartiodactyla, Archaeomerycidae) from the late Middle Eocene Pondaung Formation, Myanmar. *Vertebrata Palasiatica*.

1 Introduction

The late Middle Eocene Pondaung fauna is known for its diversified primate and ungulate communities (for example, Colbert, 1938; Jaeger et al., 1999, 2019; Chaimanee et al., 2000, 2012; Ducrocq et al., 2000a, 2021; Takai et al., 2001, 2005; Beard et al., 2007, 2009; Soe, 2008; Tsubamoto et al., 2011; Soe et al., 2017). In addition, a significant number of basal cetartiodactyls has been described during the last two decades from the Pondaung Formation including early ruminants (Métais et al., 2000, 2007a; Métais, 2006; Ducrocq et al., 2020), suggesting that southeast Asia played a significant role in the early evolution of ungulates during the Paleogene. Yet, most of these basal cetartiodactyls are documented only by fragmentary material and their precise relationships are often questionable. We report here a fragmentary maxilla preserving M1-3 associated with a partial lower jaw preserving p4-m3 collected from the locality of Myaukse Kyitchaung (about 5 km north of Pangan, Fig. 1 [Figure 1: see original paper]) that can be attributed to the archaeomerycid ruminant *Paukkaungmeryx minutus* Ducrocq et al., 2020.

Fig. 1 Location map of Kyauk Magyi Kyitchaung and Myaukse Kyitchaung

Institutional abbreviations

AMNH, Collections at the American Museum of Natural History; BM, Bang Mark Collections at the Department of Mineral Resources; BSPG, Bavarian

State Collection for Palaeontology and Geology, Palaeontological Museum Munich; GSI-B, Geological Survey of India at the Natural History Museum; GSP-UM, Geological Survey of Pakistan, University of Michigan; HGSP, Howard University/Geological Survey of Pakistan; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; KM, Kyauk Magyi Collections at the Myanmar Ministry of Culture; Li, Lissieu fossils at the Collections du Laboratoire de Géologie de la Faculté des Sciences de Lyon; MFP-PK2, Myanmar French Paleontology, Paukkaung Kyitchaung 2 Collections at the Myanmar Ministry of Culture; MYS, Myaukse Kyitchaung Collections at the Myanmar Ministry of Culture; NMMP-KU, National Museum Myanmar Paleontology, Kyoto University; PIN, Paleontological Institute, Russian Academy of Sciences; SLP, Société Laonnoise de Paléontologie, Collections de l' Université Montpellier II; TF, Thai Fossil at the Department of Mineral Resources; TUDW, Than-U-Daw Collections at the Myanmar Ministry of Culture; V, prefix to the fossil vertebrate collections stored in the IVPP; Vil, Villebramar fossils at PALEVOPRIM (Coll. M. Brunet), Université de Poitiers.

Dental terminology

The dental terminology used here follows Boisserie et al. (2010).

2 Systematic paleontology

Superorder Cetartiodactyla Montgelard et al., 1997

Suborder Ruminantia Scopoli, 1777

Superfamily Traguloidea Gill, 1872

Family Archaeomerycidae Simpson, 1945

Paukkaungmeryx Ducrocq et al., 2020

Paukkaungmeryx minutus Ducrocq et al., 2020 (Fig. 2 [Figure 2: see original paper])

Holotype

Fragmentary maxilla with left M1-3 (MFP-PK2-2010-1); Paukkaung Kyitchaung 2 locality, Bahin area, Myanmar; Pondaung Formation, late Middle Eocene.

Referred material

Fragmentary maxilla with right M1-3 (MYS-2013-2, Fig. 2A, B) associated with fragmentary lower jaw with right p4-m3 (MYS-2013-1, Fig. 2C-F).

Locality and horizon

Myaukse Kyitchaung locality (north of Pangan), Myanmar; Pondaung Formation, late Middle Eocene.

Emended diagnosis

Small size and bunoselenodont artiodactyl about the size of Xinjiangmeryx Zheng, 1978. Differs from all Archaeomerycidae in being less selenodont, in lacking a mesostyle, in having a more distally oriented postprotocrista, a distinct buccal postprotocrista and a better developed lingual cingulum, and in

lacking a paraconid and a metaconid on its p4. Differs from all other basal ruminants (Tragulidae, Lophiomerycidae, Leptomerycidae, Hypertraguloidea, Gecocidae, Bachitheriidae) in being smaller, less selenodont, in lacking a mesostyle, in having a weaker parastyle, a distally oriented postprotocrista and a well-developed lingual cingulum on upper molars, in having a more simple p4 that lacks a paraconid, and lower molars that have less developed cingulids and that lack an ectostylid.

Description

The fragmentary maxilla and lower jaw were extracted and collected from the same spot in Myaukse Kyitchaung and they exhibit the same surface wear, thus indicating that they very probably belong to the same individual.

The fragmentary maxilla preserves M1-3 (MYS-2013-2). The small size of the first upper molar might suggest that it corresponds to a D4. However, its buccal and lingual roots are not divergent and its enamel thickness is similar to that of the following teeth, which suggests that this tooth is much more likely a M1. In addition, the worn third molar does not display any contact facet on its distal wall, which indicates that it is a M3 rather than a M2. The small size of the M1 compared to that of the M2 is also reflected in the lower tooth row where the m1 is markedly smaller than the m2. The upper molars are quadrangular and bunodont with the metaconule slightly smaller than the other cusps but as lingually protruding as the protocone. The paracone and the metacone are connected by the mesiodistal postparacrista and premetacrista, and there is no mesostyle. The preparacrista joins a small mesial non-protruding parastyle and the postmetacrista extends to a minute distal metastyle. The protocone is the largest cusp and it displays three crests: the preprotocrista extends mesiobuccally along the mesiolingual face of the paracone to the parastyle. The postprotocrista is distally oriented and connects with the mesial face of the metaconule, and the buccal postprotocrista joins the lingual face of the paracone. This crest seems to be unknown in ruminants, but it is sometimes exhibited in some anthracotheres (for example, *Anthracokeryx*, *Anthracotherium*) and some suids (for example, *Conohyus*, *Hyootherium*). The M1 is too worn to observe whether a paraconule was present, but on the following teeth that are better preserved there is no trace of such a conule between the protocone and the paracone. In addition, the mesial wall of the protocone and preprotocrista is flat and there is no evidence of a groove that might have separated the protocone from a hypothetical paraconule. The postmetacristule projects along the distolingual face of the metacone and connects to the metastyle. A short cingulum is present mesially, distally, buccally except under the paracone, and lingually at the opening of the transverse valley (Fig. 2A, B).

The preserved molars on the associated lower jaw (MYS-2013-1) are worn and they thus do not exhibit much detail of structure. However, the general tooth morphology can be observed: the molars are elongated and rather narrow with the trigonid only slightly higher than the talonid. They display incipient crescentic buccal cusps and bunodont lingual cusps. The hypoconid is more distally

situated than the entoconid, and from the wear surfaces the protoconid might also be slightly more distal than the metaconid. The cristid obliqua is low and short and extends to the center of the trigonid wall. The transverse valley between the trigonid and the talonid is wide and deep. A cingulid is present mesiobuccally and buccally between the trigonid and the talonid and between the hypoconid and the hypoconulid of m3. It is not possible to observe whether a paraconid was present on the teeth, but the preserved mesial part of the trigonid on m2 and m3 does not show evidence of the presence of such a cusp. On the m3 which is the better preserved molar, the entoconid displays a very slight mesiolingual cristid (ectoentocristid), but there is no groove on the mesial face of the cusps and no postentocristid. The metaconid of the m3 also shows a faint lingual postmetacristid lined buccally with a very shallow groove. A short endohypocristid connects the hypoconid and the entoconid. A small mesiodistal posthypocristid links the hypoconid and the large hypoconulid (Fig. 2C-F).

The most significant tooth on the lower jaw is the p4. It is two-rooted, narrow and almost as long as the m2. Two cristids extend from the protoconid: the preprotocristid reaches a tiny mesial cingulid spur and the postprotocristid joins a small distostylid. There is no trace of a metaconid. A very short and shallow talonid basin is present distolingually, and only a faint cingulid occurs mesiobuccally. The p3 is missing but two sockets are visible for this tooth that suggest that it might have been at least as long as the p4 (Fig. 2C-F).

Ducrocq et al. (2020) have proposed an estimated body mass of around 1.5 kg for *Paukkaungmeryx* based on regression with M2 area (Janis, 1990). The new material allowed to confirm the body mass estimate based on regression of body mass on m1 area (Legendre, 1989).

Fig. 2 *Paukkaungmeryx minutus* from Myaukse Kyitchaung. A, B. MYS-2013-2, right M1-3, in occlusal view; C-F. MYS-2013-1, right p4-m3, in occlusal (C, D), lingual (E) and buccal (F) views. Scale bar equals 5 mm.

Measurements (length \times width in mm, * indicates minimum estimation): p4: 5.0 \times 2.5; m1: 4.5 \times 2.6; m2: 5.9 \times 3.6; m3: 8.7 \times 3.7*; M1: 4.4 \times 4.7; M2: 5.4 \times 6.5; M3: 5.8 \times 7.1.

Comparisons

Although the upper molars described here are slightly larger than those of the holotype and mainly display a slightly stronger buccal cingulum and a less developed lingual cingulum, the teeth of both maxilla exhibit the same structure and are very similar to each other. We can consider that these minor differences in morphology might correspond to intraspecific variation. In this section the upper molars attributed here to *Paukkaungmeryx* will not be compared with those of other basal ungulates because they are less well preserved than the teeth of the holotype and Ducrocq et al. (2020) made extensive comparisons.

Concerning the lower teeth, their primitive morphology reminds that of the dichobunoids, a paraphyletic superfamily that includes the Diacodexidae, Dichobunidae, Homacodontidae, Leptochoeridae, Helohyidae, Cebochoeridae and

Raoellidae according to Theodor et al. (2007). However, there are several structural differences that distinguish representatives of the dichobunoids and the Pondaung lower jaw. Even if some dichobunids have bunodont teeth (Dichobuninae, Hyperdichobuninae, some Eurodexeinae), most members of this family often display lower molars with a paraconid and a p4 with a metaconid, an association of features that is not observed on the lower jaw attributed to *P. minutus* (Fig. 3A [Figure 3: see original paper]-D). Six distinct taxa from Pondaung have been attributed to the Dichobunoidea so far, but all of them are markedly distinct from *Paukkaungmeryx*. The Pondaung dichobunoids *Myanmarius* Tsubamoto et al., 2013a and *Pakkokuhyus* Holroyd and Ciochon, 1995 (Ducrocq, 2019) are larger and more bunodont, the lower molars of *Pakkokuhyus* have the buccal and lingual cusps closer to each other and its m3 has a reduced hypoconulid lobe (Fig. 3E), and the lower molar referred by Tsubamoto et al. (2013a) to *Myanmarius* and recently attributed to the new dichobunid genus *Neochorlakkia* (Ducrocq et al., 2022) is also significantly larger than that of *Paukkaungmeryx*, it has much less developed cristids, a smaller hypoconulid and a trigonid markedly higher than the talonid (Fig. 3F). The lower molars of *Cadutherium* Métais et al. (2007a) are similar in size to those of MYS-2013-1 but they are more bunodont and also have less transversely compressed crowns with a notch on the mesial face of the entoconid, a stronger buccal cingulid and no endohypocristid connecting the entoconid and the hypoconid (Fig. 3G). The lower molars attributed to *Hsanotherium* Ducrocq et al. (2000b) by Tsubamoto et al. (2000, 2003) can easily be distinguished from those of *Paukkaungmeryx* by their larger size and more developed selenodonty, their buccal cusps mesial to the lingual ones, their mesial cingulid better developed and their trigonid basin wider and open lingually (Fig. 3H). The isolated upper molars described from Pondaung by Métais (2006) and Tsubamoto et al. (2013b) and attributed to indeterminate dichobunoids are clearly more selenodont, and the upper molar attributed to an indeterminate artiodactyl (most probably a dichobunid) by Tsubamoto et al. (2012) is significantly larger, which very likely suggests that these three isolated teeth do not belong to *Paukkaungmeryx*.

Other fragmentary known Asian dichobunids for which lower molars are known include *Haqueina* Dehm and Oettingen-Spielberg, 1958 (Middle Eocene of Pakistan and Mongolia, Vislobolova, 2004), *Chorlakkia* Gingerich et al., 1979 and *Pakibune* Thewissen et al., 1987 (both early Middle Eocene of Pakistan) that all markedly differ from *Paukkaungmeryx*. *Haqueina* is larger, and its lower molars are less elongated and retain a paraconid (Fig. 3I). *Chorlakkia* and *Pakibune* are smaller, with a buccal cingulid better developed and a shorter hypoconulid on m3, *Chorlakkia* has more bunodont lower molars (Fig. 3J, K), and *Pakibune* has lower molars that retain a paraconid and an entoconid distal to the hypoconid (Fig. 3K).

Similarly, the exclusively Asian Lantianiinae *Elaschitherium* Métais et al., 2004 from the Middle Eocene of China (the only lantianiine for which lower teeth are known) also differs from MYS-2013-1 by its p4 that retains a metaconid and by its shorter and more crescentic lower molars with a shorter hypoconulid lobe

on m3 (Fig. 3L).

The diacodexoids generally have lower molars with elevated and more lingually open trigonids, a hypoconulid that connects with the posthypocristid and the postentocristid, and a p4 that usually exhibits a metaconid, an association of features that is absent on the lower teeth of MYS-2013-1. *Diacodexis pakistanensis* Thewissen et al., 1983, an Asian diacodexoid from the early Middle Eocene of the Indian subcontinent, markedly differs from the Pondaung lower jaw mainly by its smaller size, its p4 with a strong buccal cingulid and a developed mesial cuspid, and by its lower molars that retain a paraconid, a wide talonid basin, an entoconid distal to the hypoconid and a shorter and narrower hypoconulid lobe (Fig. 3M).

The general bunodont morphology of the lower teeth of MYS-2013-1 distinguishes it from more selenodont taxa known in the Paleogene of Asia like the Homacodontidae *Asiohomacodon* Tsubamoto et al., 2003, *Limeryx Métais* et al., 2005 and *Tsaganohyus* Kondrashov et al., 2004. Indeed, these taxa markedly differ in having lower molars that retain a paraconid (*Limeryx*, *Tsaganohyus*), a marked Zhailimeryx-fold (*Limeryx*) and lacking a hypoconulid on m1-2 (*Limeryx*, *Asiohomacodon*).

Bai et al. (2023) recently described two new basal ungulates (*Obotharium* and *Tapiruloides*) from the Middle Eocene of the Erlian Basin in Nei Mongol, China that they referred to the family Tapirulidae because they exhibit a trend toward bilophodonty on lower molars. However, both of these genera markedly differ from the material described here by several aspects. The lower molars of *Obotharium* display a talonid longer and wider than the trigonid, a marked hypolophid, a hypoconulid, a variable paraconid and a postentocristid (*Obotharium parvum*), a more bulbous m3 hypoconulid, and the p4 of *O. tongi* has a well-developed paraconid and a metaconid (Fig. 3N). In addition, the isolated M1/2 attributed to ?*Obotharium parvum* is more square and slightly larger than the corresponding tooth of *Paukkaungmeryx*, it exhibits a smaller metaconule, a hypocone, a stronger parastyle, no postprotocrista, a continuous lingual cingulum and a stronger mesial cingulum.

Among the Ruminantia, the Tragulidae are poorly documented in the Middle and Late Eocene of Asia with only three basal genera that have been recognized: *Stenomeryx* Ducrocq et al., 2020 from the late Middle Eocene of Pondaung (although Menecart et al., 2021 rejected the inclusion of this genus into the ruminants), and *Archaeotragulus Métais* et al., 2001 and *Krabitherium Métais* et al., 2007b both from the Late Eocene of Krabi (Thailand). In contrast to the Archaeomerycidae, these taxa share simple and narrow lower premolars that do not exhibit a metaconid on their lingual face, as observed in the new material referred to *Paukkaungmeryx* (Fig. 4A [Figure 4: see original paper]). The three Eocene taxa probably represent two distinct radiations, with *Archaeotragulus* (and maybe *Stenomeryx*) that has narrow and elongated lower premolars and molars and selenodont upper molars, whereas *Krabitherium* is more bunodont with wider lower molars and more rounded cusps on the upper molars. The Late

Eocene taxa from Krabi are much larger than *Paukkaungmeryx*, *Archaeotragus* has a broader and more elongated p4 with a preprotocristid that curves mesiolingually and a strong paraconid, its lower molars are more selenodont and more elongated and have a much more developed mesial cingulid and a variably present ectostylid (Fig. 4B). *Krabitherium* resembles *Paukkaungmeryx* in its more rounded cusps but it has a somewhat longer p4 with two posterior cristids that originate from the apex of the protoconid, the buccal cusps of its lower molars are more selenodont with an ectostylid in the buccal end of the valley (Fig. 4C). On the other hand, *Stenomeryx* and *Paukkaungmeryx* share a similar size, elongated and narrow lower molars and a p4 that lacks a lingual metaconid. However, the p4 of *Stenomeryx* is more laterally compressed and its distal half is less steep with a shallower distolingual basin of the talonid, its lower molars are narrower, they have a weaker buccal cingulid and the entoconid is more mesially situated than the hypoconid, especially on the m3 (Fig. 4D). In addition, the horizontal ramus of *Stenomeryx* is shallower and narrower than that of *Paukkaungmeryx*. Despite the few characters shared by both genera, it is therefore very unlikely that *Stenomeryx* might be a junior synonym of *Paukkaungmeryx* based on the differences that distinguish them.

The lower teeth attributed to *Paukkaungmeryx* do not have a selenodont pattern, a paraconid or a *Dorcatherium*- and a *Zhailimeryx*-fold which are features that are usually observed in most of archaeomerycid taxa. The Archaeomerycidae for which lower teeth are known (*Indomeryx* Pilgrim, 1928, *Irrawadymeryx* Métais et al., 2007a, *Archaeomeryx* Matthew and Granger, 1925a, *Notomeryx* Qiu, 1978, *Xinjiangmeryx* Zheng, 1978 and *Miomeryx* Matthew and Granger, 1925b) have more selenodont lower molars that retain a paraconid (*Notomeryx*, *Irrawadymeryx*) and a well-marked *Zhailimeryx*-fold on the mesial wall of the entoconid (*Indomeryx*, *Irrawadymeryx*), an ectostylid (*Archaeomeryx*), a metastylid (*Notomeryx*), a continuous buccal cingulid (*Irrawadymeryx*), or no buccal cingulid (*Xinjiangmeryx*), a lingually open trigonid (*Miomeryx*), and with the exception of *Irrawadymeryx* they do not exhibit an endohypocristid (*Indomeryx*, *Archaeomeryx*, *Notomeryx*, *Miomeryx*). In addition, they all display a metaconid and a paraconid on their p4 (the p4 is unknown in *Irrawadymeryx*) (Fig. 4E-I; Fig. 5 [Figure 5: see original paper]).

3 Discussion and conclusions

Ducrocq et al. (2020) suggested that the upper molars of *Paukkaungmeryx* were morphologically closer to those of *Xinjiangmeryx* and the structure of the fragmentary lower jaw that we attribute to *Paukkaungmeryx* seems to confirm this statement, because both genera share a rather similar and simple lower molar morphology. The lower molars attributed to *Paukkaungmeryx* display features that illustrate a primitive pattern (bunoselenodonta, absence of folds on the cusps, small endohypocristid) within Ruminantia. However, some of these characters can also be observed in *Irrawadymeryx* (endohypocristid, bunoselenodonta), *Indomeryx* (buccal cuspids more distally situated than the lingual ones;

see Métais et al., 2007b) and Xinjiangmeryx (bunoselenodonty, absence of folds, buccal cingulid very weakly developed). If we further consider the morphology of its p4 (absence of a metaconid and of a paraconid, very reduced distal basin) and of its upper molars (mesiodistal postprotocrista, metaconule lingually protruding, weakly developed styles and buccal ribs (Ducrocq et al., 2020)), this supports the hypothesis that Paukkaungmeryx very likely represents a primitive archaeomerycid. However, the preservation of the material attributed to Xinjiangmeryx and Irrawadymeryx prevents more precise comparisons.

Among the Pondaung ruminants, only Indomeryx was known by its upper and lower cheek teeth so far, and the material that we describe here makes Paukkaungmeryx the second best documented basal ruminant in the Pondaung fauna. However, both of these taxa exhibit two distinct p4 morphologies. In Indomeryx this tooth has a more elongated crown with the mesial and distal halves that display a gentle slope, a mesiolingual paraconid, a metaconid twinned with the protoconid, two postprotocristids, and a small talonid basin. On the other hand, the p4 of Paukkaungmeryx has steeper mesial and distal slopes, it lacks a paraconid and a metaconid, and only one postprotocristid extends from the tip of the crown to the tiny spur on the distal end of the tooth. This latter p4 morphology is unique within the archaeomerycids (although the morphology of the p4 is still unknown for Irrawadymeryx) and was not recorded yet in the family. This suggests that two radiations might have occurred during the late Middle Eocene in Pondaung: one is illustrated by primitive premolars and molars as observed at least in Paukkaungmeryx, and the second one is documented by more selenodont and complex teeth exhibited by the other Pondaung genera (Indomeryx, Irrawadymeryx and Thandaungia). The other archaeomerycids known outside of Pondaung (except Xinjiangmeryx) also display that more derived morphology. The lower teeth morphology of Paukkaungmeryx confirms its more generalist diet that was assumed from its upper molars and very small size (Ducrocq et al., 2020). It was clearly less herbivorous than the contemporaneous Indomeryx in Pondaung and probably closer to the ancestry of basal ruminants. As stressed by Ducrocq et al. (2020), the Archaeomerycidae are diagnosed mostly on postcranial and cranial material of Archaeomeryx (Vislobokova and Trofimov, 2002), and the taxa that have been included into the family tend to exhibit a primitive dental morphology compared to that of other Asian families. However, if Paukkaungmeryx is correctly assigned to the Archaeomerycidae, the likelihood that this family might represent a paraphyletic assemblage should be considered as suggested by Métais et al. (2007b). Only the recovery of additional and more complete remains (dental and cranial) that can be attributed to Paukkaungmeryx might help to further investigate its more precise affinities.

Acknowledgements

We thank the villagers and chairmen of Pagan in the Pondaung area and their authorities for their help and kindness that greatly facilitated our field work. This study has been supported by the National Geographic Society Grant No W 344-14, the Leakey Foundation, the ANR-DFG EVEPRIMASIA (ANR-18-

CE92-0029 / BO 3479/7-1), the CNRS UMR 7262 (PALEVOPRIM), the University of Poitiers, and the Ministry of Culture of the Republic of the Union of Myanmar. This work has benefited from helpful comments by anonymous reviewers.

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