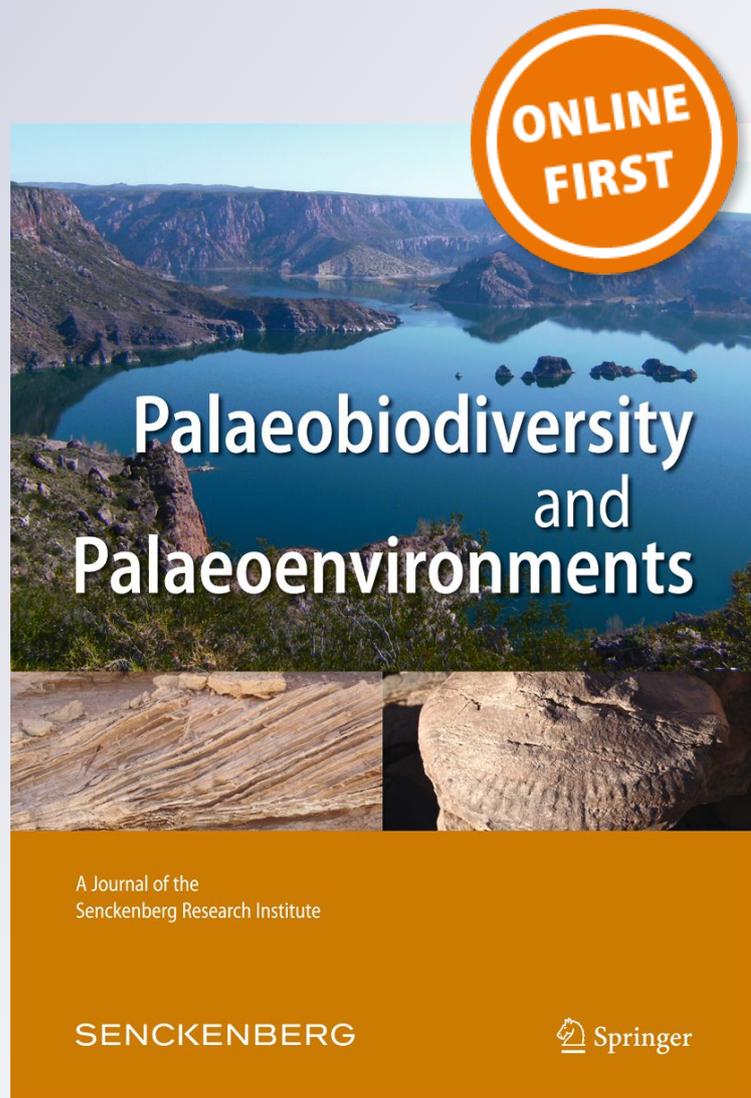*Biochronological and palaeobiogeographical significance of the earliest Miocene mammal fauna from Northern Vietnam*

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ORIGINAL PAPER

Biochronological and palaeobiogeographical significance of the earliest Miocene mammal fauna from Northern Vietnam

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Abstract Current scientific knowledge of Tertiary fossils from south of the Ailao Shan-Red River shear zone is extremely poor, in sharp contrast with the situation nowadays, as the area of Laos and Vietnam is regarded as a global hotspot of biodiversity. In this context, the few localities that yielded fossil assemblages are of first importance for the understanding of Cenozoic palaeobiogeography and the tectonic and palaeogeographical evolution of the region. Hang Mon 1 (Son La Province, Northern Vietnam) was the first site that provided evidence of Tertiary mammals, but its age remained very controversial, interpretations ranging from Oligocene to Late Miocene. Herein, we re-investigate the mammal fauna of the locality based on newly collected material and previously published fossil mammals. A new outcrop, Hang Mon 2, provides evidence of the rhinoceroses *Pleuroceros blanfordi* and *Bugtirhinus* sp. Together with the earlier finds of uncommonly small-sized *Protaceratherium*, these fossils allow a correlation to the earliest Miocene (most probably ranging from ~23 to ~21 Ma; Aquitanian) based on faunal comparison with the Sulaiman Province of Pakistan. The revision of the mammals from Hang Mon 1 is in agreement with this stratigraphic proposal. In addition, the discoveries from Vietnam (the rhinocerotid assemblage and *Hyotherium*) further support the hypothesis of strong biogeographical and environmental affinities between Europe, the Indian Subcontinent and Southeast Asia (Vietnam) during the Aquitanian.

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Introduction

While Southeast Asia is regarded nowadays as a global hotspot of biodiversity (e.g. Myers et al. 2000), current scientific knowledge of Tertiary fossils from Laos and Vietnam is paradoxically extremely poor, although the area has an excellent fossil preservation potential (e.g. Ginsburg et al. 1992; Böhme et al. 2011, 2013; Klaus et al. 2011; Neubauer et al. 2012; Schneider et al. 2013). Assessing the fossil record of Southeast Asia is of first importance for the understanding of Cenozoic palaeobiogeography, which may also constrain models of the tectonic and palaeogeographical evolution of the area. In order to fill this gap of knowledge, several field campaigns have been performed since 2008, leading to new discoveries of fossil remains (vertebrates, invertebrates, plant macro-remains, pollen and spores; e.g. Böhme et al. 2011, 2013; Neubauer et al. 2012; Schneider et al. 2013). Particular focus was on the historical locality of Hang Mon (e.g. Ginsburg et al. 1992) in order to provide confident dating of earlier mammal finds, which, in the past, led to controversial correlation of the deposits, ranging from Oligocene (Thanh and Khuc 2006) to Late Miocene (Covert et al. 2001).

The Hang Mon Basin (Fig. 1; Son La (*Son La*) Province, Yên Châu District; coordinates: N20°56.15, E104°22.22; 920 m a.s.l.) is a small pull-apart basin that is related to the Son La Fault zone, which is composed of several parallel faults and, in a wider context, associated with the Ailao Shan-Red River shear zone. Sediments of the uppermost Hang Mon formation are exposed in an abandoned coal mine near Hang Mon village (herein denoted as locality Hang Mon 1; Bao et al. 1978; see Böhme et al. (2011) for a sedimentary log). The first fossil find at Hang Mon 1, reported by Bao et al. (1978) and Dzanh and Van Hai (1995), is a mandible originally assigned to the small aceratheriine rhinocerotid *Chilotherium*, which is re-described in detail below. The scientific importance of the locality was underlined by the finds made by Ginsburg et al. (1992) who collected mammalian fossils as well as testudinoid remains. Later, Dzanh (1994) reported freshwater mussels (*Acuticosta, Cuneopsis, Oxynaia, Unio*) from Hang Mon 1, and Covert et al. (2001) collected additional mammal fossils. Furthermore, palynomorphs were described from the coal-bearing part of the mine (Thanh and Khuc 2006). Finally, Böhme et al. (2011) reported a single lower molar of a tragulid or lophiomerycid, and land snails tentatively assigned to *Lagochilus*, *Ptychopoma* and *Tortaxis*. A detailed study of the mollusc assemblage is in progress.

The age of the sediments exposed at Hang Mon 1 has been subject to debate. Based on the mammal assemblage, Ginsburg et al. (1992) inferred an Early Miocene age for the locality. In sharp contrast, Covert et al. (2001), arguing that Ginsburg et al. (1992) did not compare the concerned assemblage with Chinese

Fig. 1 The earliest Miocene localities from Hang Mon (*Son La* Province, ▶ Yên Châu District, Northern Vietnam). **a** Location of the studied area. Respectively, Hang Mon 2 (*above*) and Hang Mon 1 (*below*) in 2011. **b** Parts of an aquatic turtle (Geoemydidae/Emydidae) plastron from Hang Mon 1. **c** *Pleuroceros blanfordi* (Hang Mon 2). Left M2 with in situ breakage (*arrow*)

faunas, proposed a significantly younger, Late Miocene age for the locality, apparently consistent with the results of Dzanh (1994) based on bivalves. However, provided that the taxonomy is correct, the freshwater mussel assemblage claimed to confirm a Late Miocene age by Dzanh (1994) has no biostratigraphic significance. Two of the genera reported are part of the present day fauna of Northern Vietnam and Southern China (*Cuneopsis, Oxynaia*), while *Acuticosta* is restricted to the Yangtze Basin (China). The genus *Unio* has no living species in eastern Asia. The fossil record of *Cuneopsis* in Vietnam dates back to the Paleogene (Schneider et al. 2013). Fossil records of *Acuticosta*, *Oxynaia* and *Unio* from the area (e.g. Gou et al. 1976) are unreliable pending revision, since these genera were commonly used as waste basket taxa for poorly preserved, broadly elliptical freshwater mussels.

On the other hand, palynomorphs were thought to be indicative of an Oligocene age (Thanh and Khuc 2006). In fact, the occurrence of *Cicatricosisporites dorogensis* suggests that the sediments are not younger than 21.12 Ma, corresponding to the mid-Aquitanian stage (see details in Böhme et al. 2011).

In 2011, we re-investigated the abandoned pit at Hang Mon and also studied new exposures to the northwest of the village. The new outcrop yielded biostratigraphically useful rhinocerotid remains, which are described herein. Furthermore, we discuss the taxonomic assignment of the previously described mammal remains from Hang Mon 1, in particular with regard to systematics and biochronology.

Sample provenance

In order to settle the age dispute, a field campaign at Hang Mon 1 was launched in 2011. The groundwater-filled mine exposes the upper meters of the Hang Mon Formation. In comparison to the section described by Böhme et al. (2011), the deeper water table provided access to coaly layers that are interbedded with the lower siltstone. This siltstone contained molluscs that have been collected and are currently being studied.
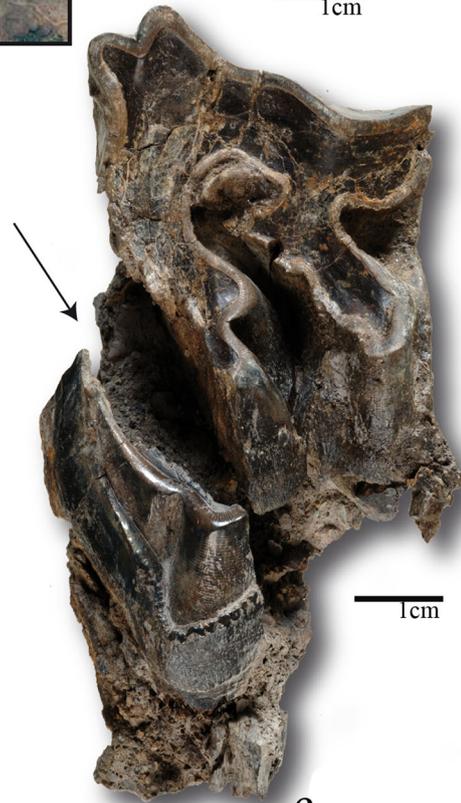
The vertebrate specimens described by Ginsburg et al. (1992) were collected by surface sampling from a 10-m-thick, partially salmon-coloured clay layer. The exact position of this layer in the outcrop could not be established during the field campaigns. Covert et al. (2001) also applied surface sampling,
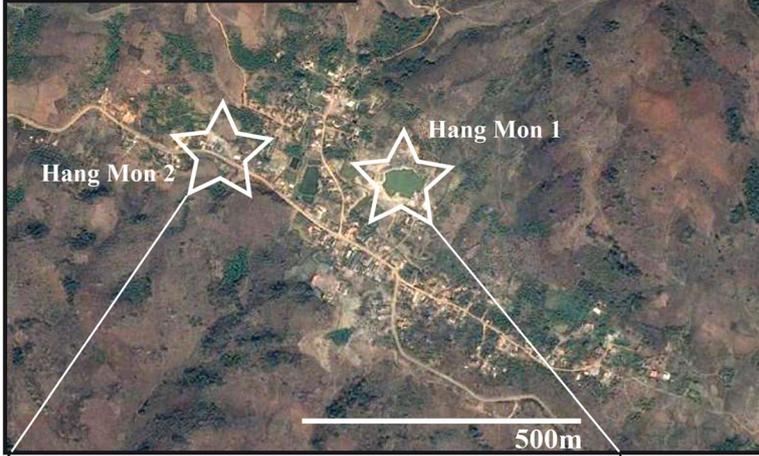
but additionally produced fossils from screen washing of sediments. Sample positions are indicated in an overview photograph of the outcrop (Covert et al. 2001: fig. 1), which, however, does not show clearly which horizons were sampled. Considering the high position of the samples relative to the water table, they might come from the same layer sampled by Ginsburg et al. (1992). The historical rhinocerotid find (Bao et al. 1978; Dzanh and Van Hai 1995), as well as the Carnivora indet. discussed below, most probably was derived from the coaly part of the section. From these sediments, aquatic turtle remains (parts of a plastron; Fig. 1b) belonging either to Geoemydidae or Emydidae families also came to light in 2011. In contrast, the purported lophiomerycid molar reported by Böhme et al. (2011) was embedded in the sandy part of the outcrop. Unfortunately, the screen washing of these sediments in 2011 did not provide any fossils. The exact origin of a single suid m1 (a cast is stored in the Museum d'Histoire Naturelle Paris under the label Hang Mon) is unclear. In conclusion, the fauna from Hang Mon 1 has to be interpreted as a composite fauna coming from at least three different sedimentary layers.

New exposures along the road TL103 to the northwest of the village (Hang Mon 2) were investigated in 2011. These exposures resulted from the road works and the creation of building sites to the north of the road. On the eastern side of the outcrop, a basal dark organic-rich layer is overlain by a 2-m-thick succession of grey clay and marl, containing reworked coal at its base. Apparently, the sediments dip at 30° towards NW. While some parts of the exposure are covered by overburden, the basal dark layer can be tracked northeastwards, where it overlays 1 m of grey marls.

The central part of the exposure consists of a ~5-m-thick fanglomerate, which terminates abruptly at the western-northwestern limit of the section. At the eastern limit of the fanglomerate, at the contact with the grey clay and marl succession, a rhinocerotid maxilla with articulated P4-M2 was excavated. While the occlusal surfaces of the maxillary teeth were embedded in the fanglomerate, the roots were stuck in the marls. Additional fragmentary tooth remains and a radius, presumably dislocated due to rainfall, were collected from the base of the exposure. Relatively large undeterminable bone fragments were also present. Because the excavated sediments were used as a basement for the road and the houses, no additional parts of the skeleton were found. Taking the position of the maxillary at the interface of the fanglomerate and the marls into account, two scenarios are possible. (1) An at least partially articulated skeleton was lying on the surface of the mud and was rapidly covered by the fanglomerate during a flooding event. The high energy of the sedimentary flow caused significant damage to the skeleton, as shown by the in situ rupture of the antero-lingual part of the M2 (Fig. 1c). (2) The rhinocerotid skeleton was transported and disarticulated in the sedimentary flow and finally dispersed over parts of the alluvial fan and into the unconsolidated mud.

Methods

The methods of study of the Suidae are conventional and need little comment. All measurements follow the protocol of Van der Made (1996a) and are given in millimetres. The tooth nomenclature is indicated in the corresponding figures.

The suprageneric systematics of the Rhinocerotidae follows the arrangement proposed by Becker et al. (2013). The dental terminology follows Heissig (1969: 11–12), Uhlig (1999: 15–16), and Antoine et al. (2010: fig. 3). The dental and osteological features described here correspond to the characters used for cladistics and listed by Antoine (2002, 2003) and Antoine et al. (2003a, 2010). Measurements of post-cranial dimensions follow the protocol defined by Guérin (1980). Dimensions are given in millimetres. Rhinocerotid stratigraphical ranges are adopted from Antoine et al. (2003b: fig. 4) and Becker et al. (2013) for the Palaeogene interval, and from Antoine et al. (2013: fig 4b) for the Neogene interval.

Abbreviations

Capital letters are used for upper teeth (P, premolar; M, molar), and lower case letters for lower teeth (d, deciduous molar; m, molar)

Anatomical orientation: ant, anterior; APD, antero-posterior diameter; H, height; l, left; L, length; lat, lateral; med, medial; post, posterior; r, right; TD, transversal diameter; W, width.

Institutions

AMNH	American Museum of Natural History, New York, USA
BNHM	Beijing Natural History Museum, Beijing, China
BSPG	Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany
CEPUNL	Centro de Estratigrafia e Paleobiologia da Universidade Nova de Lisboa, Lisbon, Portugal
GMV	Geological Museum of Vietnam, Hanoi, Vietnam
GSP	Geological Survey of Pakistan, Islamabad, Pakistan
GPIT	Paläontologische Sammlung der Universität Tübingen, Germany
HLMD	Hessisches Landesmuseum, Darmstadt, Germany
IGF	Istituto di Geologia, now Museo di Storia Naturale, Firenze, Italy
IGGML	Institut für Geowissenschaften/Geologie der Montan-Universität Leoben, Austria
IM	Indian Museum, Calcutta, India
IPS	Instituto de Paleontología, Sabadell, Spain
IPUW	Institut für Paläontologie der Universität Wien, Austria
IVAU	Instituut voor Aardwetenschappen, Utrecht, The Netherlands

IVPP	Institute for Vertebrate Palaeontology and Paleoanthropology, Academia Sinica, Beijing, China
KNM	Kenya National Museums, Nairobi, Kenya
LPUM	Laboratoire de Paléontologie, Université de Montpellier, Montpellier, France
LSPUPM	Laboratoire de Sédimentologie et Paléontologie, Université de Provence, Marseille, France
MGL	Muséum Guimet, Lyon, France
MHNT	Muséum d'Histoire Naturelle, Toulouse, France
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MSNO	Muséum des Sciences Naturelles, Orléans, France
NHM	Natural History Museum, London, UK
NMB	Naturhistorisches Museum, Basel, Switzerland
NMBe	Naturhistorisches Museum, Bern, Switzerland
NMP	National Museum, Prague, Czech Republic
NMW	Naturhistorisches Museum, Wien, Austria
PIMUZ	Paläontologisches Institut und Museum der Universität, Zürich, Switzerland
SLJG	Steiermärkisches Landesmuseum Joanneum, Graz, Austria
SMF	Forschungsinstitut Senckenberg, Frankfurt am Main, Germany
UCBL	Université Claude Bernard, Lyon, France

The fossil material from Hang Mon 1 collected by Ginsburg et al. (1992) is stored in the MNHN. The juvenile mandible of *Pleuroceros blanfordi* and the material collected by Covert et al. (2001) belong to collections of the GMV. Casts of part of the Covert collection are available at the University of Colorado at Boulder, USA. The fossils from Hang Mon 2 are also stored in the GMV or loaned for scientific studies to the GPIT. Casts of *Pleuroceros blanfordi* are also stored at GPIT.

Systematic palaeontology

Order Perissodactyla Owen, 1848
Superfamily Rhinocerotoidea Gray, 1821
Family Rhinocerotidae Gray, 1821
Subfamily Rhinocerotinae Gray, 1821
Genus *Pleuroceros* Roger, 1898

Pleuroceros blanfordi (Lydekker, 1884)
Figs. 1c and 2

2001 cf. *Chilotherium anderssoni* Covert et al.: 634–635, fig. 2

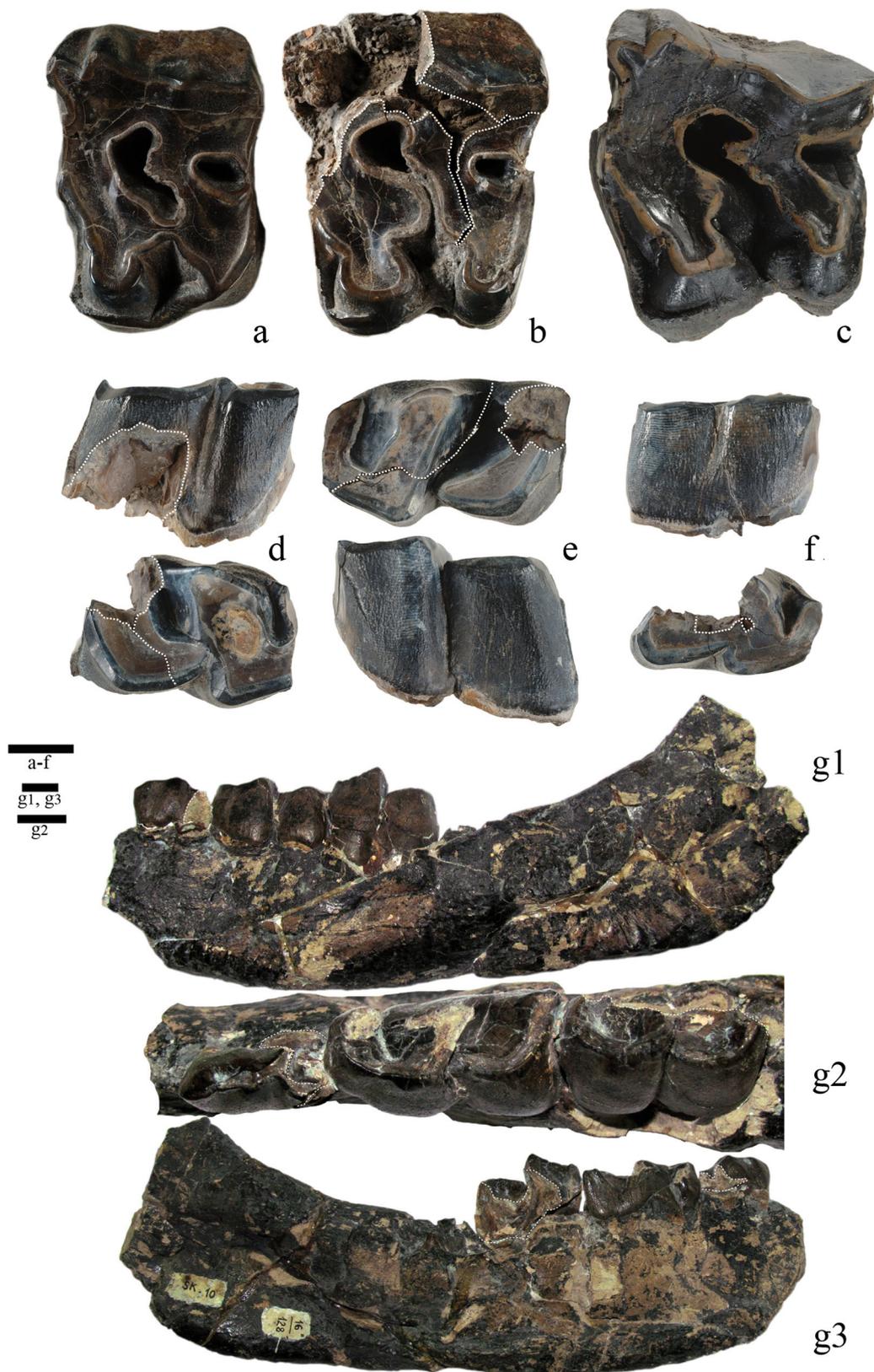2010 *Pleuroceros blanfordi* (Lydekker, 1884) comb. nov. Antoine et al.

Studied material: Left P4-M2, left broken m1, right broken m1, and right broken m3 from the same adult individual, Hang Mon 2; left P2 and left hemimandible with d2–d4, Hang Mon 1. Hang Mon Basin, Northern Vietnam.

Description

Upper teeth: Cement is only preserved in places (bottom of inner valleys and ectolophs). Enamel is thick, without folding, and thinly wrinkled both vertically and horizontally ("squared" sensu Antoine et al. 2010: 152). Teeth are rather high-crowned, but still brachydont, with ectolophs directed linguo-ventrally. The roots are not preserved or not observable.

In occlusal view, P4 is wider than long and subrectangular (metaloph shorter linguo-labially than the protoloph; Table 1). The labial cingulum is absent, while the lingual cingulum is thick and continuous, surrounding the protocone and joining the anterior cingulum (also continuous, but smoother). The protoloph is thick and continuous, with a shallow anterior constriction. The antecrochet is strongly developed. It joins the anterior side of the hypocone through a thin lingual bridge, thus closing the median valley. This valley is very deep, with a kidney-shaped outline in occlusal view. The crochet is present and multiple (pectinate), but restricted to the apical half of the crown, i.e. vanishing with wear. There is no crista. The metaloph is complete, V-shaped in occlusal view, and without a constriction. The metaloph, continuous, forms a dihedron open backwards, in which the crochet is the anterior angle; the hypocone is posterior to the metacone. The postfossette is narrow, elongate sagittally, and deep. The parastyle is sub-sagittal, slightly pointing anterolabially. The paracone groove is deep and the paracone fold thick, while the metacone fold is less developed and smoother. A deep and quadrate lingual fossa is surrounded by the protocone, the lingual bridge, the hypocone, and the lingual cingulum.

The antero-labial part of the M1 is lacking, while the protoloph of M2 is crushed and partly misaligned linguo-dorsally (Fig. 1c). The position of the protoloph has been corrected during the preparation of the fossil, as illustrated in Fig. 2c. Both M1 and M2 are lacking a labial cingulum. They have a well-developed antecrochet and a deep anterior constriction of the protocone: on both M1 and M2, the protoloph is "trefoil-shaped" (sensu Antoine 2003). The crochet is short on M1 and restricted to the apex of the metaloph, while it is spur-like, sagittally oriented, and much longer on M2. No crista, medifossette, or cristella is present on M1–2. The lingual cingulum is restricted to a thin ridge on the antero-lingual side of the protocone on M1, and to a stronger ridge surrounding the whole protocone on M2. On M2, no lingual groove

Fig. 2 *Pleuroceros blanfordi* (Lydekker, 1884) from Hang Mon 1 (**g**) and 2 (**a–f**). **a** Left P4. **b** Left M1. **c** Left M2 (cast of the reconstructed specimen Fig. 1c). **d** Right m1 (occlusal and labial views). **e** Left m1 (occlusal and labial views). **f** Right m2 (occlusal and labial views). **g** Left hemimandible with d2–d4 from labial (**g1**), occlusal (**g2**) and lingual (**g3**). *Scale bars* equal 1 cm

Table 1 *Pleuroceros blanfordi* (Lydekker, 1884). Early Miocene of Hang Mon 2, Vietnam (*left columns*) and of the Bugti Hills, Balochistan, Pakistan (*right columns*). Compared dimensions of the upper dentition (permanent cheek teeth; range, mean, number of specimens between *square brackets*), in millimetres

Tooth	L		Ant W		Post W		H	
	Hang Mon	Bugti Hills	Hang Mon	Bugti Hills	Hang Mon	Bugti Hills	Hang Mon	Bugti Hills
P4	*29*	31.5–38.5	*45*	44.5–53	*41*	44.5–54	*21*	22–33
mean	–	34.7 [6]	–	50.2 [6]	–	49.2 [5]	–	26.0 [3]
M1	–	42–56	–	53–57	*~46.5*	50–56.5	*~21.5*	34–60
mean	–	49.0 [5]	–	55.4 [5]	–	53.2 [6]	–	45.1 [4]
M2	*40*	54–56	*51.5*	58–62	*43.5*	50–53	*26.5*	38–57
mean	–	55.0 [4]	–	59.5 [4]	–	51.7 [5]	–	48.0 [3]

notches the protocone, the lingual side of which is flat and elongate antero-posteriorly. The posterior part of the ectoloph is straight on M1 (anterior half not preserved). It is more undulated on M2, with a sagittal parastyle, a strong paracone fold fading away towards the neck, a weak mesostyle, no metacone fold, and a metastyle slightly oriented postero-labially. The metaloph is long on M1 and much narrower labio-lingually on M2. A deep constriction notches the anterior side of the hypocone on both M1 and M2; this constriction is restricted to the base of the crown, deeper on M1 than that on M2. A shallow groove depresses the posterior side of the hypocone, close to the lingual tip of the posterior cingulum on M1–2. The posterior tip of the antecrochet nears the anterior side of the metaloph on M1, but there is no junction between both structures, at least at the current stage of wear. The postfossette is always present, deep and narrow, forming a closed pit on M1 due to advanced wear, and a triangle open posteriorly on M2. The wear of the upper cheek teeth is compatible with a ~10–20 years old adult individual (age classes XI–XII; Hillman-Smith et al. 1986).

Lower teeth: All three available permanent lower teeth are fragmentary. Yet, they show consistent morphological features and compatible dimensions, pointing to a single species. The molars illustrated in Fig. 2e, d are perfectly symmetrical with regard to each other, and are further identified as the left and right m1 of a single individual. Accordingly, the third molar (Fig. 2f) is referred to as a left m2 of the same individual. In all three teeth, the external groove is moderately shallow, U-shaped apically and getting shallower ventrally, and vanishing above the neck. In occlusal view, the trigonid is angular and forms a right dihedron on m1–2. The paralophid is thick and wide labio-lingually, forming a right dihedron with the protolophid. The metaconid is constricted anteriorly on m1 and m2, contrary to the entoconid (this feature can be observed on m1, but not on m2). The anterior lingual valley is a narrow strip, elongate labio-lingually. The posterior lingual valley is wider and V-shaped in lingual view. The lingual cingulid, always present, is restricted to the anterior part of the lower cheek teeth. In continuation of the anterior cingulid, it forms a thick ridge interrupted before the metaconid. A sharp ridge runs along the postero-lingual side of the metaconid on m1. The labial cingulid is reduced and forms a short ridge in the external groove. The hypolophid is more oblique on m2 than on m1, in occlusal view. There is no lingual groove on the entoconid of m1 (not observable on m2).

Juvenile mandible: The left hemimandible preserves d2–4 (Fig. 2g) and most of the *corpus mandibulae*, but lacks both the symphyseal area and the ramus. Neither *foramen mentale* nor accessory foramina are preserved. In lateral view, the *corpus mandibulae* has a constant height all along its preserved part. A very long "*spatium retromolare*" is preserved beyond d4. There is no *sulcus mylohyoideus* on the lingual side of the *corpus mandibulae*. The *ramus* is not preserved and the *angulus mandibulae* is somewhat broken. Yet, given the shape of the preserved part, the *ramus* was probably not inclined antero-dorsally, but vertical or oriented postero-dorsally instead. The specimen displays the posterior half of the alveolus of d1 (not preserved); d2–4 are functional and slightly worn; m1 is mostly included in the *pars molaris* and totally unworn. d2–3 are complete and well preserved, while the lingual side of d4 is badly broken. The whole series is lacking both labial and lingual cingulids as well as external roughness. There is no "ectolophid fold" sensu Antoine (2003), but an anterior groove is present on the ectolophid of d2–3. d2 is the smallest preserved decidual tooth, d3 being the longest one (slightly longer than d4; Table 2). The paralophid of d2 is simple, bulbous, and spur-like. The posterior valley of d2 is open postero-lingually, with a thick oblique ridge positioned postero-lingually with regard to the metaconid. The paralophid is double on d3, with a short posterior arm; the protoconid fold is hugely developed, elongate sagittally, and almost obstructing the anterior lingual valley, thus restricted to a shallow and sinuous groove in occlusal view on both d3 and d4. The posterior valley is much wider and deeper, U-shaped in lingual view on d3 (not observable on d4). The entoconid is slightly constricted on d3 in occlusal view. A shallow lingual groove notches the apical part of the entoconid on d3, as can be observed in lingual view. d4 is molariform, with a moderately deep ectolophid groove and trigonid and talonid equally developed. A thin dorso-ventral ridge runs in the middle of the

Table 2 *Pleuroceros blanfordi* (Lydekker, 1884). Early Miocene of Hang Mon 1 and Hang Mon 2, Vietnam (*left columns*) and of the Bugti Hills, Balochistan, Pakistan (*right columns*). Compared dimensions of the lower dentition (permanent and deciduous cheek teeth, range, and estimated values between *brackets*), in mm

Tooth	L		Ant W		Post W		H	
	Hang Mon	Bugti Hills	Hang Mon	Bugti Hills	Hang Mon	Bugti Hills	Hang Mon	Bugti Hills
m1	33	(37)–38	–	25–26.5	(>20.5)	27	–	24–28
m2	35–(>32)	41.5	21.5–21	28	–	25–26	16.5–	26–32
d2	22.5	26.5	9.3	9	12	12	12.5	13
d3	33.5	(39)	12.2	(15)	18	(19)	17.5	18
d4	33	38.5	–	18.5	–	22	28.5	29

anterior side of the paralophid on d4. An irregular ridge, continuous and more or less parallel to the neck, is observable on the basal third of the ectolophid of d4. We interpret it as marking a severe enamel hypoplasia, instead of being an unusually apical labial cingulid. Nothing can be said about the morphology of m1. The juvenile mandible belonged to a very young calf of an age of approximately 4–6 months (age classes II–III; Hillman-Smith et al. 1986).

Systematic discussion

All observable dental and mandibular features unambiguously recall those of the medium-sized and short-limbed stem rhinocerotine *Pleuroceros* Roger, 1898 from the Early Miocene of Eurasia, as revised by Antoine et al. (2010). The concerned morphological combination notably includes characters appearing in the generic diagnosis, such as a reduced lingual cingulum and a strong antecrochet on P4, a deeply constricted protocone and a low and reduced posterior cingulum on M1–2, and a smooth and U-shaped external groove on the lower cheek teeth (Antoine et al. 2010: 145).

Other features are consistent with those of the material referred to *Pleuroceros blanfordi* (Lydekker, 1884), be it on P4 (weak labial cingulum but continuous lingual cingulum, unconstricted metaloph, metaloph as a dihedron concave posteriorly, multiple crochet, lingual bridge originating from the strong antecrochet, and antero-lingual groove on the hypocone) or on M1–2 (squared enamel; deep anterior protocone constriction; posterior tip of the antecrochet nearing the anterior side of the metaloph without junction on M1; deep anterior groove on the hypocone of M1–2; crochet restricted to the apical half of the crown on M1–2). Although proven to be less diagnostic (e.g. Antoine 2002), the morphology of the lower permanent and deciduous molars also matches that of *P. blanfordi*: paralophid wide labio-lingually and forming a right dihedron with the protolophid, metaconid constricted anteriorly, and weak cingulids on m1–2; sharp postero-lingual ridge on the metaconid of m1; neither labial/lingual cingulid nor "ectolophid fold" on d2–3; protoconid fold hugely developed and elongate sagittally on d3. Dimensions are 10–

15% smaller than the average values of the specimens from Pakistan (*P. blanfordi*; Tables 1 and 2) and fully compatible with their Western European counterparts, referred to as *P. pleuroceros* (Duvernoy, 1853) as mentioned by Antoine et al. (2010). Yet, these dimensions are only 0–10% smaller than the smallest values measured for *P. blanfordi* (Tables 1 and 2). This disparity is far from being significant for attributing the specimens from Hang Mon to a distinct species, given that sexual size dimorphism often exceeds ~10–15% in fossil rhinocerotids (e.g. Mihlbachler 2007; Antoine et al. 2010). Moreover, body size is widely influenced by environmental parameters, such as temperature, food supply, or latitude, as exemplified in a thermal perspective by early perissodactyls (e.g. Secord et al. 2012).

The only morphological differences with the hypodigm of *P. blanfordi* are present in the lower deciduous molars, as documented by the juvenile hemimandible. The posterior valley opens postero-lingually on d2 (lingual opening in *P. blanfordi*; MHNT Pak 1784); a shallow lingual groove notches the apical part of the entoconid on d3 (absent in MHNT Pak 1784; pers. obs. POA); a thin dorso-ventral ridge is present in the centre of the anterior side of the paralophid on d4 (worn on the d4 of MHNT Pak 784; Antoine et al. 2010: 147, fig. 5F). We consider these differences to fall within the intraspecific variability of *Pleuroceros blanfordi*.

Certainly, the combination of all the features described discards assignment to any of the other Late Oligocene-Middle Miocene rhinocerotids described from Eurasia.

Interestingly, the juvenile mandible from Hang Mon 1 that is referred to *Pleuroceros blanfordi* herein, was previously described by Dzanh and Van Hai (1995), and misinterpreted as documenting an adult individual with p4–m2 (instead of having d2–d4). Based on this anatomical misidentification Covert et al. (2001: 634–635, Fig. 2) referred a "right P2" from the same locality to "cf. *Chilotherium anderssoni*". The latter specimen (GMV-214-12) rather is a left P2, the features of which somewhat recall those of Middle and Late Miocene aceratheriines such as *Acerorhinus*, *Alicornops*, *Chilotherium* and *Aceratherium*, but also and much more closely those of *Pleuroceros blanfordi* (see MHNT Pak 1031 and 751; Antoine et al. 2010: fig. 4F–G). Due to this superficial dental similarity,

P. blanfordi was long considered as an early representative of *Chilotherium* (e.g. Ringström 1924; Matthew 1929; Forster-Cooper 1934; Antoine et al. 2010). Accordingly, we consider the isolated tooth from Hang Mon 2 as belonging also to *Pleuroceros blanfordi*.

Genus *Protaceratherium* Abel, 1890
Protaceratherium sp.

1992 *Protaceratherium* cf. *minutum* Ginsburg et al.: 629, fig. 3
2010 *Protaceratherium* sp. Antoine et al.

Studied material: Right M3 and a fragmentary m3 (measurements: Ginsburg et al. 1992). Hang Mon 1. Hang Mon Basin, Northern Vietnam.

Systematic discussion

Ginsburg et al. (1992: 629) described a M3 and a fragmentary m3 from Hang Mon 1, "extraordinaires par leur petite taille", documenting an extremely small rhinocerotid, morphologically similar to *Protaceratherium minutum* but smaller than the smallest known specimens, and thus provisionally referred to *Protaceratherium* cf. *minutum*. A similar size discrepancy (~30% smaller) is observed between the M3 from Hang Mon 1 (Ginsburg et al. 1992) and that of *Protaceratherium betpakdalense* Borissiak, 1938, from the earliest Miocene of Kazakhstan (de Bonis et al. 1997).

A calcaneus (MHNT Pak 1910) and a cuboid (MHNT Pak 1876) from the earliest Miocene of Gandô 4 ("Level 4", Bugti Hills, Pakistan) closely resemble those of *Protaceratherium minutum* from Western Europe, as illustrated by Roman (1924: text-figs. 14, 17) and de Bonis (1973: 163, fig. 50), except that their size is 25–30% smaller than in the latter taxon (pers. obs. POA). They were identified as *Protaceratherium* sp. (Antoine and Welcomme 2000; Métais et al. 2009; Antoine et al. 2010, 2013), a diminutive taxon that is only known from "Assemblage A" of Antoine et al. (2013) from the Sulaiman Range (SW Pakistan).

Given their shared uncommonly small size and compatible morphological features, "*Protaceratherium* cf. *minutum*" from Hang Mon 1 (Ginsburg et al. 1992) and *Protaceratherium* sp. from SW Pakistan, as identified by Antoine et al. (2010, 2013), are here considered to belong to the same species, provisionally referred to as *Protaceratherium* sp., pending new discoveries.

Subfamily Elasmotheriinae Bonaparte, 1845
Tribe Elasmotheriini Bonaparte, 1845
Genus *Bugtirhinus* Antoine and Welcomme, 2000

Bugtirhinus sp.
Fig. 3

Studied material: proximal fragment of a left radius, Hang Mon 2. Early Miocene of Hang Mon Basin, Northern Vietnam.

Fig. 3 *Bugtirhinus* sp. from Hang Mon 2. Left radius with broken proximal extremity in anterior (**a1**) and posterior views (**a2**). *Scale bar* equals 1 cm

a1   a2

Description

The proximal articulation of the radius is in the size range of recent tapirs, i.e. very small (48-mm wide) for a rhinocerotid. The proximal-most area is fragmentary, which impedes most standard measurements. The preserved part of the shaft indicates that the bone was probably slender and that there was no proximal widening. In proximal view, the anterior border is straight and parts of the humerus facets are preserved. In anterior view, the preserved parts of the two lips of the humeral cochlea form an angle of 135° ("eggcup-shaped" humeral trochlea sensu Antoine 2002). There is no sagittal groove between the medial lip and the *capitulum humeri*. The *tuberositas radii* is not medially displaced, as it occupies the median part of the anterior side; the insertion for the *musculus biceps brachii* is wide and deeply depressed, forming a large pit in the two median quarters of the anterior side. On the medial side of the shaft, the insertion for the *musculus brachii* defines a small pinched area (10-mm high, 2-mm wide), visible in anterior view. The medial ulnar facet is broken and only part of the lateral ulnar facet is preserved; it is flat, elongated proximo-distally and concave medio-laterally. Given the poor preservation, it is impossible to tell whether both ulnar facets were fused or not. There was neither fusion nor long contact between the radius and the ulna, since the diaphysis has an oval cross section in distal view.

Systematic discussion

Although incomplete, this radius provides several morphological features (absence of a sagittal groove next to the *capitulum humeri*; "eggcup-shaped" humeral trochlea; straight anterior border; deeply depressed insertion for the *m. biceps brachii*) typical of early elasmotheriine rhinocerotids (Antoine 2002, 2003; Antoine et al. 2010). Within elasmotheriines, the morphology of the specimen matches that of the radius of *Caementodon* Heissig, 1972 from the late Early to early Late Miocene of Pakistan, although it is approximately 20% smaller than the latter (Heissig 1972a, b; Antoine 2002). No proximal radius is documented so far for the smallest and earliest elasmotheriine, *Bugtirhinus praecursor* Antoine and Welcomme 2000 from the earliest Miocene of Pakistan (Welcomme et al. 2001; Métais et al. 2009; Antoine et al. 2013). However, the size and proportions of the bone (head and diaphysis) are fully compatible with those of the distal end of specimen MHNT Pak 1702 (Antoine and Welcomme 2000: 804, Table 6). Besides, the morphology of the radius is in perfect agreement with what would be expected for the monotypic genus *Bugtirhinus*, as the corresponding traits (character states) are optimised in the phylogenetic analyses of Antoine (2002, 2003), or Antoine et al. (2010).

Although the size would be matching that of *Protaceratherium*, the radius from Hang Mon has a deep fossa for the *musculus biceps brachii* contrary to all species referred to the latter genus (Roman 1924: 27; de Bonis 1973; Antoine et al. 2011). This fossa is also absent in non-elasmotheriine genera known from the Late Oligocene–Late Miocene interval (i.e. *Pleuroceros*, *Mesaceratherium*, *Plesiaceratherium*, *Prosantorhinus*, *Brachypotherium*, *Alicornops*, or *Gaindatherium*; Heissig 1972a, 1972b; Yan and Heissig 1986; Antoine 2002; Antoine et al. 2010, 2013).

Accordingly, the radius is considered as clearly belonging to a small early elasmotheriine, closely related to *Bugtirhinus praecursor*, and thus assigned to *Bugtirhinus* and left in open nomenclature.

Order Artiodactyla Owen, 1848
Suborder Ruminantia Scopoli, 1777
Infraorder Tragulina Flower, 1883
Family Tragulidae Milne-Edwards, 1864
Genus *Dorcatherium* Kaup and Scholl, 1834

Dorcatherium sp.
Fig. 4

2001 *Dorcatherium minus* Covert et al.: 635, fig. 2a

Studied material and measurements: cast of a left maxilla preserving two molars, probably M2–3. The associated P4 was not figured by Covert et al. (2001) and cannot be studied here. Hang Mon 1. Hang Mon Basin, Northern Vietnam. Measurements are provided in Covert et al. (2001).

Description

This specimen is figured in Covert et al. (2001: fig. 2A) as "Left maxilla bearing M1–2" and ascribed, together with a left P4, to the tragulid *Dorcatherium minus*. According to this report, the fragmentary maxilla resembles those of tragulids in having:

1. Bunoselenodont teeth (Janis 1984)
2. A mesostyle that is pyramid-shaped and larger than the parastyle
3. An anterior lingual lobe (protocone) that is rounded and strongly anteriorly projecting (Gentry 1987)
4. Relatively robust paraconal labial ribs

Another distinctive and unusual trait mentioned by Covert et al. (2001) is that the first molar is larger than the second molar. The examined cast of the specimen does not show bony remains of the maxilla, and we suspect that the two molars were erroneously positioned in figure 2A of Covert et al. (2001). The more distal molar is slightly smaller, and its metaconule is reduced. Consequently, the specimen GMV 214–20 does not consist of left M1–2, but rather represents
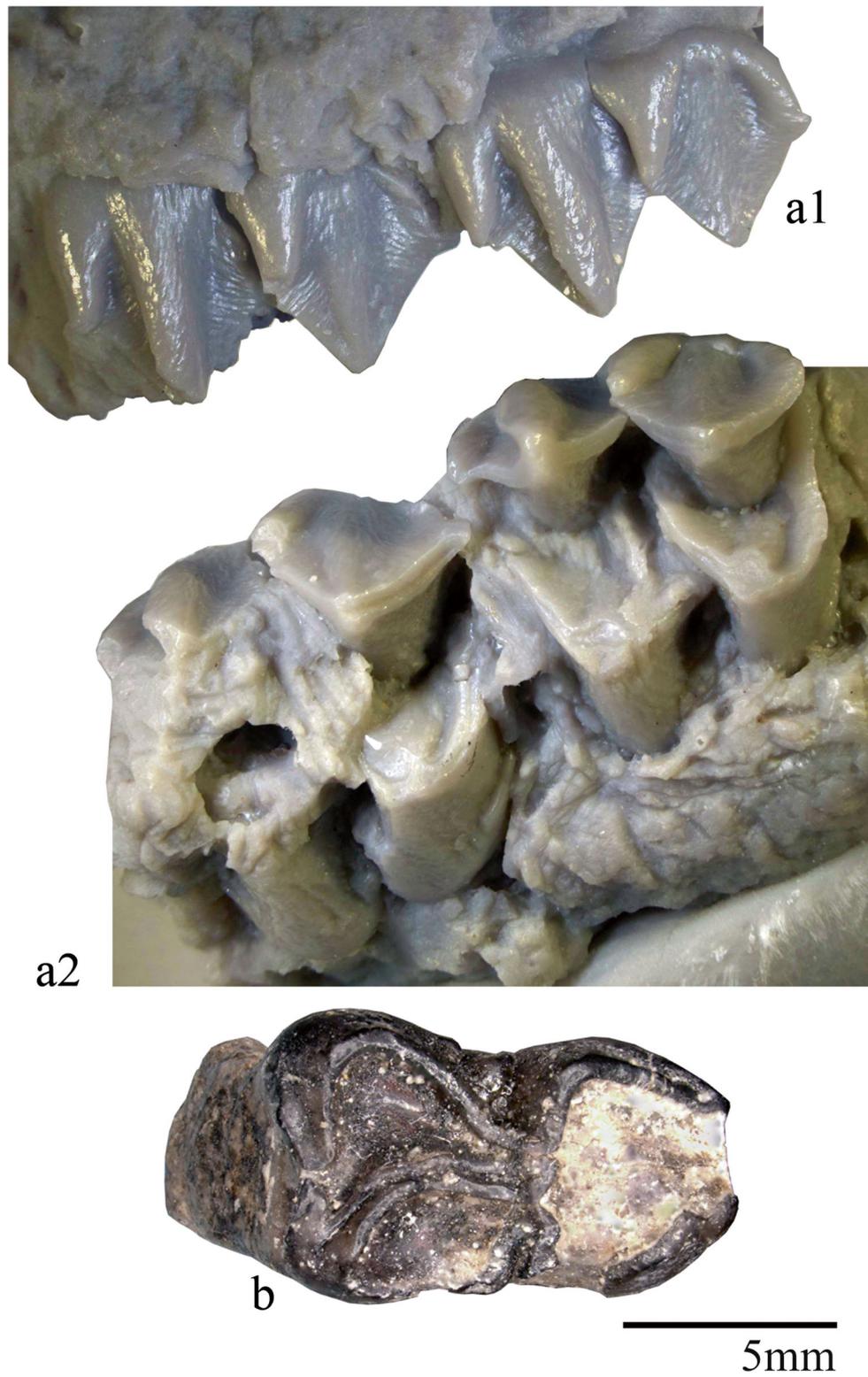
Fig. 4 Tragulids from Hang Mon 1. **a** *Dorcatherium* sp. Cast of a left maxilla preserving two molars, probably M2–3 (GMV 214–20), in labial (**a1**) and occlusal views (**a2**). **b** *Dorcabune* sp. Left lower molar (m1 or m2)

left M2–3, and the M1 is not larger than M2 as mentioned in Covert et al. (2001).

The molars are obviously not entirely prepared, thus hampering observation of several important dental features. It is difficult to assess the presence, shape and size of the lingual cingulum. There is obviously no entostyle. The mesostyle is well developed and the labial rib of the paracone is salient and prominent. On M2, the pre-protocrista is straight and reaches the base of a salient parastyle; the post-protocrista is duplicated into a transversal crest reaching the base of the paracone and a shorter disto-labial crest that joins the base of the wall formed by the higher pre-metaconule crista. The disto-labial crest is slightly arc-shaped and reaches the central valley of the tooth. The labial rib on the paracone is very strong whereas it is barely visible on the labial wall of the metacone. The enamel seems to be slightly wrinkled.

Systematic discussion

The taxonomic status of these two upper molars is difficult to establish based on such limited material. Generally, the upper molars of traguloids or basal Pecora do not show many diagnostic features for specific and even generic identification. The general tooth morphology of the specimen from Hang Mon is that of the Tragulidae. In particular the bunoselenodonty, moderate development of styles and robustness of paraconal labial ribs are characteristic for this family. However, the bifurcation of the post-protocrista is a dental feature previously unrecorded among tragulids (Gaur 1992). Beyond this specific character of the protocone, the specimen differs from *Afrotragulus* from the Early Miocene of Kenya (Sánchez et al. 2010) and *Yunnanotherium* from the Late Miocene of China (Han 1986) in having marked labial ribs on the paracone and metacone, and in its larger size. The specimen from Hang Mon is closer in morphology and size to *Siamotragulus* from the Middle Miocene of Thailand (Thomas et al. 1990), but differs from the latter in the bifurcation of the post-protocrista. Another genus very similar to the specimen from Hang Mon is *Dorcatherium*, which is fairly common in the Early to Middle Miocene of Eurasia and Africa. More than 20 nominal species of *Dorcatherium* have been described, most of them only distinguished by size differences, and the genus is clearly in need of taxonomic revision. *Dorcatherium* is based on *D. naui* Kaup 1833, and six other species are known from Europe, where the genus first appeared in the Burdigalian (MN4; ~18 Ma; Rössner 2007; Aiglstorfer et al. 2014). With regard to its selenodont morphology and size, the dental remains from Hang Mon are close to those of the smallest European species, *D. guntianum,* known from the Early and Middle Miocene (Rössner and Heissig 2013), although the latter lacks the bifurcated post-

protocrista on the molars. *Dorcatherium* is common in the Siwalik faunas of the Indian Subcontinent where it is represented by no less than nine taxa (Barry 2014). The genus is also reported from the late Early Miocene of Nepal (West et al. 1978, 1991), the Middle Miocene of Thailand (Ducrocq et al. 1994), and the Late Miocene of Myanmar (Zin Maung Maung et al. 2011). In the Early Miocene, *Dorcatherium* was already present in Africa (Pickford 2001). In Asia, tragulids are known from the Late Eocene onward (Métais et al. 2001). *Dorcatherium* sp. has its first occurrence in the earliest Miocene of the Bugti Hills, Pakistan (Aquitanian–early Burdigalian; Antoine et al. 2013). Remains from the early Burdigalian of the Bugti Hills have been determined as *Dorcatherium* cf. *parvum* (Antoine et al. 2013). Although the assignment of the specimen from Hang Mon to *Dorcatherium* is tentative, its occurrence in Vietnam would thus fit well with the confirmed palaeobiogeography of the genus in Asia.

Genus *Dorcabune* Pilgrim, 1910
Dorcabune sp.
Fig. 4b

2011 Tragulid or lophomerycid Böhme et al.: fig. 5b

Studied material and measurements: lower molar (m1 or m2) (1.05 × 0.60 cm). Hang Mon 1. Hang Mon Basin, Northern Vietnam.

Systematic discussion

Böhme et al. (2011) have reported a lower molar (m1 or m2) of a tragulid or lophiomerycid ruminant. The tooth is heavily worn. In transverse direction, the talonid is much larger than the trigonid; there is no post-entocristid, a post-hypocristid almost reaches the rear of the entoconid, where it seems to form a bulge; a distinct ectostylid is present and the enamel is wrinkled. Medially, the pre-hypocristid reaches the rear of the trigonid, where it seems to extend upwards onto the latter forming a *Tragulus* fold (Geraads et al. 1987), which is part of the "M structure", a diagnostic dental character of tragulids (e.g. Rössner 2007). Generally, a *Tragulus* fold is present in bunoselenodont tragulids, but tends to disappear in more selenodont forms (Sánchez et al. 2010). The supposed presence of a *Tragulus* fold together with the relative bunodonty suggests that the lower molar belongs to a tragulid of the genus *Dorcabune* (Pilgrim, 1910). Three species, differentiated mostly based on size have been referred to *Dorcabune*. The size of the specimen from Hang Mon 1 matches the size of *D. sindiense* from the uppermost Gaj and lower Manchar formations in Sind, Southern Pakistan (Raza et al. 1984), and *D. welcommi* from the uppermost Chitarwata Formation (level 4, earliest Miocene) of the Bugti sequence in Central Pakistan (Ginsburg et al. 2001). Due to the fragmentary nature of the material from Hang Mon,

the identification with *Dorcabune* is tentative and needs to be confirmed by additional fossil material.

Superfamily Suoidea Gray, 1821
Family Suidae Gray, 1821
Subfamily Hyotheriinae Cope, 1888
Genus *Hyotherium* von Meyer, 1834

cf. *Hyotherium youngi* (Chen, 1997)
Figs. 5, 7 and 8

1992 *Hyotherium* cf. *soemmeringi* Ginsburg et al.: 629, fig. 4
2001 *Chleuastochoerus stehlini* Covert et al.: 634–635, fig. 2b
2015 *Hyotherium* [no specific assignment] Orliac et al.: 13–14

Studied material and measurements: right M3 (MNHN no number; DAP = 16.8, DTa = 15.2, DTp = 13.3, Ta = 1.3), cast of left P4 (DAP = 10.8, DT = 11.9), cast of right M2 (DTp = 14.1), cast of right m3 (DTp = 9.6, DTpp = 7.7), cast of left m2 (DAP = 15.1, 15.1, DTa = 11.1, DTp = 10.3, Ha > 9.9). Hang Mon 1. Hang Mon Basin, Northern Vietnam.

Description

Upper molars, M3: The M3 (Fig. 5/1) has two separate lingual roots as in Suidae and unlike in Palaeochoeridae ("Old World peccaries"), where the roots are fused.

The tooth is worn, and the "protoconule" is visible as a separate dentine island, well separated from the dentine island of the protocone. A protoconule connected to the cingulum and not to the protocone is again as in most Suidae, whereas in Palaeochoeridae, Listriodontinae (Suidae) and Sanitheriinae, the protopreconule is connected to the protocone.

The tetrapreconule or "central cusp" is not recognisable as an individual cusp, but is seen as an extension of the dentine island of the tetracone. It is not a cusp blocking the transverse valley, but it remains well behind it. Within the Suidae, this is a primitive feature that is not retained in the Suinae, Babyrousinae and Tetraconodontinae. The posterior cingulum is relatively extensive, but without a well-developed cusp there (the pentacone). For the Suidae, this is again a primitive feature. The morphology in the specimen from Hang Mon 1 recalls *Hyotherium*, but differs from that of *Chleuastochoerus,* where there is a well-developed pentacone on the lingual side.

In size, the specimen from Hang Mon 1 is intermediate between the European *Hyotherium soemmeringi* and *H. meisneri* (Fig. 5), and well within the ranges of *H. major* (not shown in Fig. 5, but overlapping with the other two species). The East Asian *Hyotherium youngi* is slightly larger than the specimen from Hang Mon 1. *Chleuastochoerus* tends to have much more elongate M3.

M2: A molar fragment (Fig. 5b) is interpreted as a M2 because it is only slightly narrower than the M3, while if it were the M1, it would be much narrower. It is less worn than the M3 and it shows in a different way the morphology of the "central cusp". Because of the lesser wear, it can be seen that there is no important constriction, which separates a tetrapreconule from the tetracone. Its upper surface slopes down and ends near the middle of the transverse valley. This is a long tetraprecrista, not a separate tetrapreconule, which is a primitive feature. If seen from behind, the upper surface of the tetrapostcrista continues in the small pentacone and cingulum. In the later Suidae, the pentacone is more separate from the tetrapostcrista.

P4: The P4 (Fig. 6a) has a square outline, if seen apically. It is only slightly wider than long. This is normal but, in this respect, it differs from early Tetraconodontinae, like *Conohyus* (Fig. 6g) which have very wide and short P4.

The P4 has two buccal cusps, which are situated very close together and which have a barely visible cleft between them on the buccal side. In the later *Hyotherium* and in *Chleuastochoerus* (Figs. 6b, 6c), these cusps tend to be well separate. In early Suidae, like *Albanohyus*, *Nguruwe* (Fig. 6d) or *Bunolistriodon*, there is just one cusp or only an incipient division. In this respect, the P4 is primitive for a suid.

The lingual side of the buccal cusps is rather flat, but there is a shallow cleft, reaching about halfway down. Next to the edge of the anteriorly directed and well-marked paraectocrista, there is a shallow depression and then there is another elevation, which could be interpreted as an incipient paraprecrista. The different Suoidea have marked morphologies in the buccal cusps of their P4. In *Hyotherium soemmeringi* (Fig. 6f) and in *Chleuastochoerus* (Fig. 6c), these cusps are much more convex on the lingual side and, as a result, the cleft between them is very marked; besides, these cusps may have crests on the lingual side. In the earlier species of this genus, *H. meisneri* (Fig. 6b) and *H. youngi* (Fig. 6e), there is not yet a deep cleft, as in Hang Mon 1, and there tend to be no marked paraprecristas and metaendocristas. Also the Palaeochoeridae, Cainochoerinae, Listriodontinae and early Tetraconodontinae do not have well-separated buccal cusps, nor these lingual crests. In the later Tetraconodontinae, in *Babyrousa*, *Potamochoerus* and all Suinae, there are crests on the lingual sides of these cusps: usually a paraprecrista, that is enlarged into a parapreconule ("sagittal cusp" of Pickford 1988) and often a metaendocrista or even metaendoconule. The morphology of the lingual sides of the buccal cusps in the tooth from Hang Mon 1, are primitive for a suid.

The protocone has long pre- and postcristas and on the nearly concave buccal side, there is a low elevation, marking the endocrista. In some early suids (Fig. 6d) and in the early species of *Hyotherium*, the postcristas tend to be less long (Fig. 6b) and in the later species of that genus, they tend to be better developed (Fig. 6f) and the buccal side of the protocone is often flat and sloping. However, in *Chleuastochoerus*, the cusp is more rounded and there may be a short

and wide endocrista. In the Palaeochoeridae, the protocone tends to be rounded at the back and there is no clear protopostcrista.

The protoprecrista, is clearly visible as a narrow elongate crest that extends antero-buccally, fusing or nearly fusing to the anterior cingulum. This is also the case in *Hyotherium soemmeringi* (Fig. 6f), where it may be enlarged into a cusplet (protopreconule), but in *Chleuastochoerus* it is short and blunt and ends very clearly before reaching the cingulum, and if there is a cusplet there, it seems more related to the cingulum. Possibly the most primitive morphology in Suoidea is that of a rounded protoconid, with a short and blunt protoprecristid that is directed antero-buccally, ending before reaching the cingulum (e.g. *Eocenchoerus*, *Taucanamo*). In many Palaeochoerinae, this crest is similar to that in the specimen from Hang Mon 1. In *Nguruwe* (Fig. 6d) it is also long and in later Listriodontinae it connects to the paracone forming an anterior loph. In some early Tetraconodontinae, this crest is clearly developed and reaches the cingulum, but in the same species it may be short and blunt, as is common in the later species of this subfamily. In *Albanohyus*, the protoprecrista is short and limited in extension because of a large cusp that developed from the cingulum. In most Suidae, the protoprecrista is usually also short and blunt and does not extend much buccally because of the presence of the "sagittal cusp", which is in its way. The long and narrow protoprecristid in Hang Mon 1 recalls thus the Palaeochoerinae, but this might also be a primitive suid morphology.

In the specimen from Hang Mon 1, the postcrista is a sharp crest. In the Palaeochoerinae, the postcrista is not developed and the protocone is round here. In some early Suidae, like *Nguruwe* and *Hyotherium soemmeringi*, it is a long crest or it swelled and gave rise to a cusplet (protopostconule), as in *Albanohyus*, *Bunolistriodon* and *Chleuastochoerus*. Both morphologies may be found in the early Tetraconodontinae. In later forms, it seems that the protopostconule became more separate from the protocone and more associated to the cingulum and, as a result, the protopostcrista is rather short.

Lower molars, m2: The m2 (Fig. 7) has only little wear and only some dentine is exposed at the tip of the protoconid. The remaining crown height is clearly smaller than the width, and the unworn crown must have been low.

The "central cusp" is a small and low hypopreconulid that is separated from the hypoprecristid by a furrow on the lingual side, but not on the buccal side. If seen from the side, the upper surface of the hypoprecristid and hypopreconulid lowers gradually towards the transverse valley. In the Cainochoerinae and Listriodontinae, the central cusp is not well developed as an individual cusp. The state of this character in *Kenyasus* recalls that in the specimen from Hang Mon 1. The other Suidae, including *Hyotherium soemmeringi, H. meisneri* and *Chleuastochoerus*, tend to have hypopreconulids that are seen in side view as an elevation in the middle of the transverse

Fig. 5 cf. *Hyotherium youngi* (Chen, 1997) from Hang Mon 1: **a** MNHN no number—right M3: **a1** occlusal view—stereo photos, **a2** lingual view. **b** GMV 214-4—cast of right M1,2: **b1** occlusal view—stereo photos, **b2** posterior view. Schematic figure, on the basis of a M2 of *Sus*, showing the dental nomenclature (after Van der Made 1996a). Bivariate diagram comparing length (DAP) and width of the anterior lobe (DTa) of the M3 of: cf. *Hyotherium youngi* (Chen, 1997) from Hang Mon 1; *Hyotherium meisneri* from Cetina de Aragon (MNCN, IPS, IVAU), Laugnac (LSPUPM, NMB, UCBL), Budenheim (SMF, HLMD), Hessler (SMF); *Hyotherium soemmeringi* from Sandelzhausen (BSPG), Zangtal (SLJG), Eibiswald (IPUW), Feisternitz (SLJG), Seegraben (SLJG); *Hyotherium youngi* from Shanwang (IVPP); *Chleuastochoerus* from Baode (IVPP), Yiong Dent (BNHM), Holinger (BNHM), Yuanmou (IVPP), Hsia K'ou (AMNH)

valley. This morphology is very primitive and recalls the situation in *Palaeochoerus* and *Propalaeochoerus*. Palaeochoeridae differ from Suidae in having m1 and m2 with two roots, one below each lobe (as in ruminants), while Suidae have these molars with four roots, one below each cusp. The roots could not be studied in the cast.
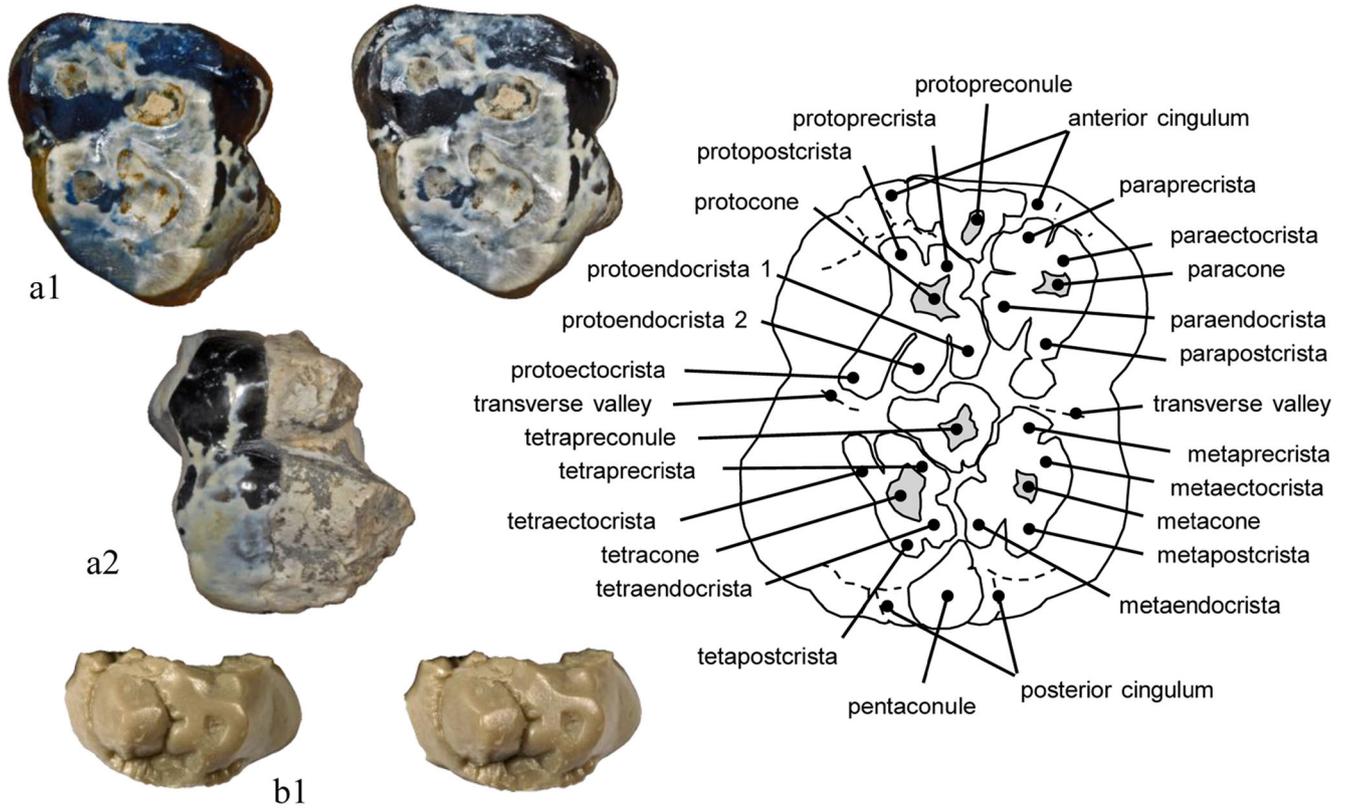
There is a well-developed round cusplet in the middle of the posterior cingulum that is not connected to the hypoconid. In *Propalaeochoerus*, this cusp is connected to the hypoconid.

The protoendocristid and metaendocristids are lobate and directed backwards and to the midline of the tooth, where they meet, but do not fuse. This is common in Suidae. In Palaeochoeridae, these structures tend to be more like slender crests that curve to each other and meet of fuse, forming a loph-like structure. This occurs also within some Cainochoerinae and the Listriodontinae, and in the latter, full lophodonty evolved.

The hypoconid and entoconid have rounded lobes that are directed to the midline of the tooth, where they meet, but do not fuse. This is like in many Suidae, while most Palaeochoeridae, some Cainochoerinae and the Listriodontinae tend to have hypoendo- and entoendocristids more slender and crest-like and oriented more transversely, in some cases suggesting and in others reaching the stage of lophodonty.

The size of the molar from Hang Mon 1 is in the upper ranges of the m2 of *Hyotherium meisneri*, is comparable to that of *H. youngi* and is clearly smaller than in *H. soemmeringi* (Fig. 7). Considering the size of the other specimens from Hang Mon 1 and comparing to *H. meisneri*, this specimen is more likely an m2 than an m1, which would be clearly smaller. The molars of *Chleuastochoerus* are on average more elongate than those of *Hyotherium*, but there is much overlap. The tooth from Hang Mon 1 is relatively elongate; it is still well in the range of *Hyotherium*, but approaches *Chleuastochoerus*.

m3: The m3 (Fig. 8) has little wear and a very low crown. Possibly it would be more low-crowned than the m2, as occurs in some brachydont suoids (e.g. *Conohyus*). The central cusp is a little more individualised than in the m2. The cusps are rounded and the lobes or crests are less defined than in the m2. There is a large pentaconid, preceded by a well-developed pentapreconulid. *Chleuastochoerus* has often, as a peculiarity, two flattened cusps in this position.
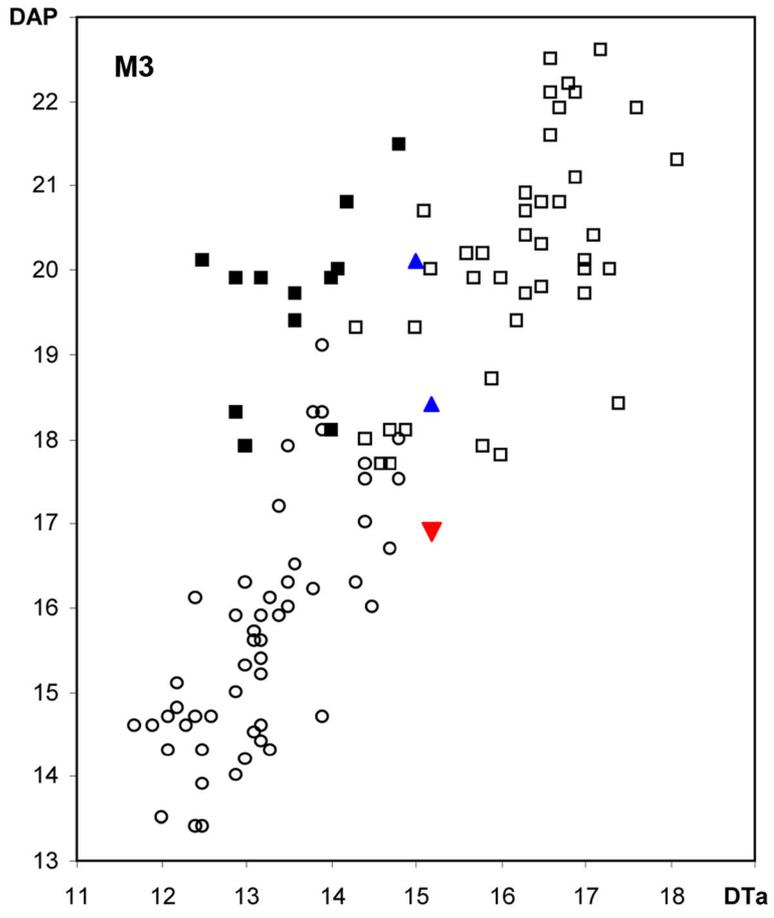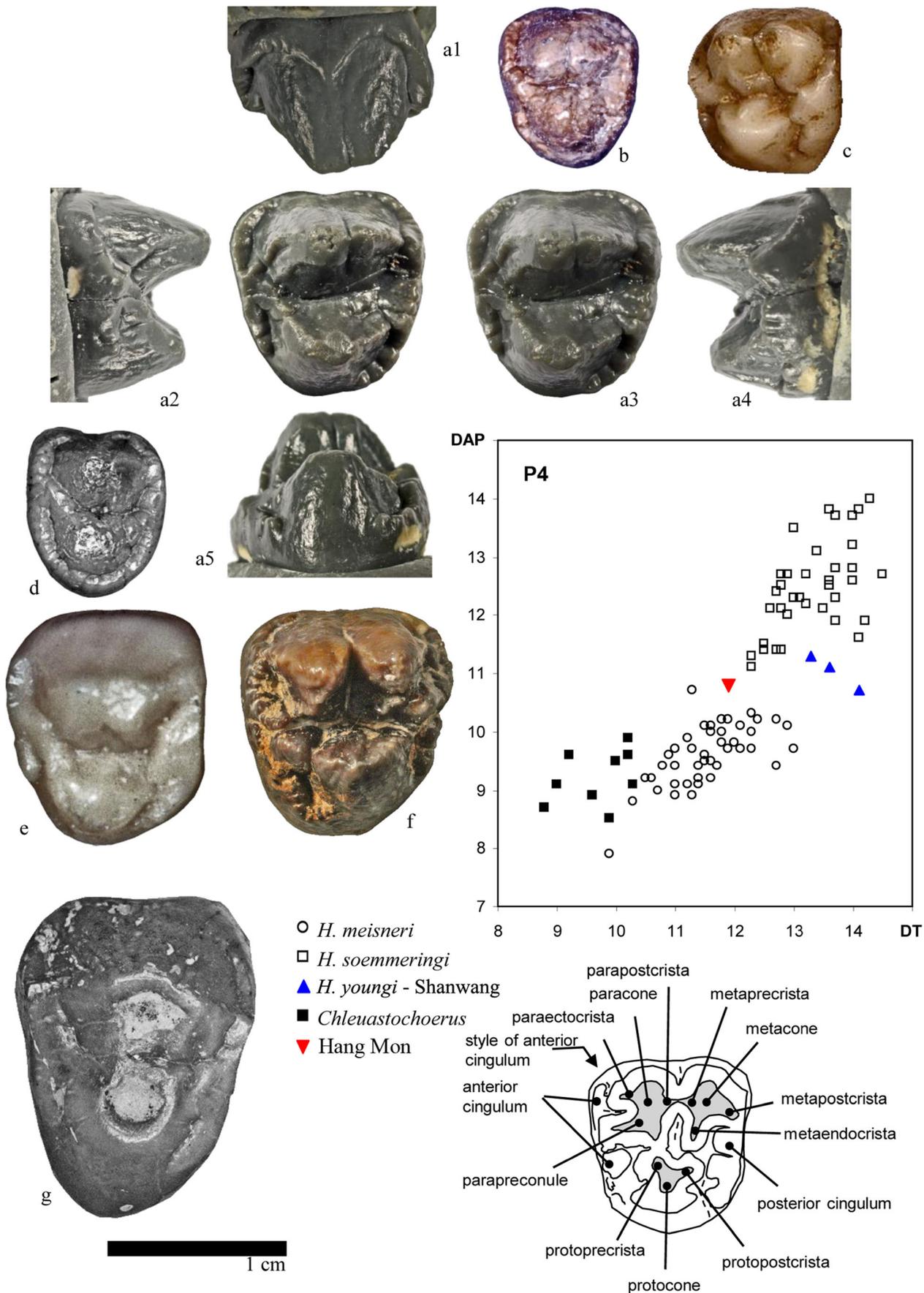
◄ **Fig. 6** The P4 of different Suidae compared: **a** 214-24—cast of left P4 of
cf. *Hyotherium youngi* (Chen, 1997) from Hang Mon 1: **a1** buccal, **a2**
anterior, **a3** occlusal (stereo), **a4** posterior, and **a5** lingual views. **b**
MNCN, no number—*Hyotherium meisneri* from Cetina de Aragon. **c**
IVPP RV2800—*Chleuastochoerus* from Baode; **d** KNM So1131—
Nguruwe kijivium from Songor. **e** *Hyotherium youngi* from Shanwang.
f IVAU Mun6 - *Hyotherium soemmeringi* from Munebrega AB. **g**
PIMUZ BP276—*Conohyus simorrensis* from Paşalar. **b**–**g** Occlusal
views. All P4 shown as if left (**c**, **d** reversed). Schematic figure, on the
basis of a P4 of *Sus scrofa*, showing the dental nomenclature (after Van
der Made 1996a). Bivariate diagram comparing the length (DAP) and
width (DT) of the P4 of: *Hyotherium?* sp. from Hang Mon; *Hyotherium
meisneri* from Cetina de Aragon (MNCN, IPS), Laugnac (LSPUPM,
NMB, UCBL), Budenheim (SMF, HLMD), Hessler (SMF); *Hyotherium
soemmeringi* from Sandelzhausen (BSPG), Schönegg (SLJG), Zangtal (SLJG), Eibiswald (IPUW), Feisternitz (NMW),
Seegraben (SLJG); *Hyotherium youngi* from Shanwang (IVPP);
Chleuastochoerus from Baode (IVPP), Yushe (IVPP), Yiong Deng
(BNHM), Yuanmou (IVPP), Hsia K'ou (AMNH)

Metrically, the m3 is smaller than in *H. youngi* (Fig. 8). It is
also smaller than in *H. soemmeringi* and in the ranges of
H. meisneri. The latter comparisons have been made, but different comparisons are shown in Fig. 8. The small and early
tetraconodonts *Tetraconodon thailandicus* and *Sivachoerus
sindiensis* (= *Conohyus sindiensis*) are small, but still clearly
larger than the suid from Hang Mon 1. Other early suids with a
primitive morphology are the African genera *Kenyasus* and
Nguruwe, the latter being of similar size.

Systematic discussion

Despite their very long history in SE Asia (Ducrocq 1994;
Ducrocq et al. 1998), all too little is known of the Suoidea
from there. Affinities with Chinese or Indian Suoidea might be
expected, but are difficult to assess, as the material is poor.
Western Eurasia and Africa have many suoid species that appeared apparently by dispersal, of which the origins are not
known.

Besides, the possibility of species endemic to SE Asia, or not
yet known from other areas, should not be overlooked. The suid
remains from Hang Mon 1 have been subject of two previous
papers. Ginsburg et al. (1992) assigned an M3 from Hang Mon 1
to *Hyotherium* cf. *soemmeringi*, did not indicate a single morphological feature to support the identification with this genus,
but used the degree of elongation of the tooth to interpret the
grade of evolution. Comparisons made here are based on observations of material in numerous collections, but descriptions of
good material of *H. meisneri* are by Van der Made (1994) and
Bouvrain and De Bonis (1999), of *H. major* by Hellmund
(1991), of *H. soemmeringi* by Van der Made (2010) and of
H. youngi by Chen (1997) and Liu et al. (2002). Most of the
features of the material studied here do not contradict the identification as *Hyotherium*, but differences from *H. soemmeringi*
include:

– The lesser separation of the paraconid and metaconid on
the P4
– The flatter lingual walls of the buccal cusps of the P4
– The lesser development of the central cusps on the molars
– Smaller size

The P4 morphology and size fit *Hyotherium youngi* much
better than *H. soemmeringi*.

Covert et al. (2001) assigned all these remains, save for the
M3, to *Chleuastochoerus stehlini* on the basis of the simple
bunodont molar pattern, lacking both "the highly variable accessory cusps and cuspules" and lophodonty. There are many
genera and species in South and East Asia, and such a general
observation on molar morphology is indeed insufficient. The
material in the metric comparisons in Figs. 5, 6, 7, 8 and 9 is
of the smaller species, while *C. tuveri* is still larger. The comparisons made here are based on observations of material in the
IVPP, BNHM, AMNH and PIN, but descriptions of good material of *Chleuastochoerus* are provided by Pearson (1928),
Vislobokova (2009) and Hou and Deng (2014). The material
from Hang Mon 1 differs from *Chleuastochoerus* in the following features:

– A lesser development of the central cusp in the upper and
lower molars
– The tetrapostcrista extends towards the posterior cingulum in the M2
– The molars are not elongated
– A lesser separation of the buccal cusps in the P4, with less
distance of the tips, and lesser developed furrows between
them on the buccal and lingual sides
– The paracone and particularly the metacone of the P4
have flatter lingual walls, that are not convex and that
have no well-developed crests there
– More marked protopre- and protopostcristas in the P4
– A flatter buccal wall of the protocone, with only an indication of the protoendocristid;
– The P4 is not elongated as in *Chleuastochoerus*;
– While in *Chleuastochoerus*, the P4 is small compared to the molars, the proportions in Hang Mon
1 resemble those in *Hyotherium*. (It should be noted
that the small P4 in *Chleuastochoerus* is probably
derived, while the relative size as in *Hyotherium* is
more widespread)

Each of the fossils from Hang Mon 1 is smaller than its
counterparts in *Hyotherium soemmeringi*, slightly or clearly
smaller than in *H. youngi*, and close to the largest specimens
of *H. meisneri*. This supports the idea that they belong to a
single species.

The features of the fossils from Hang Mon 1, which suggest that they belong to the Suidae and not to the
Palaeochoeridae, include separate lingual roots in the upper
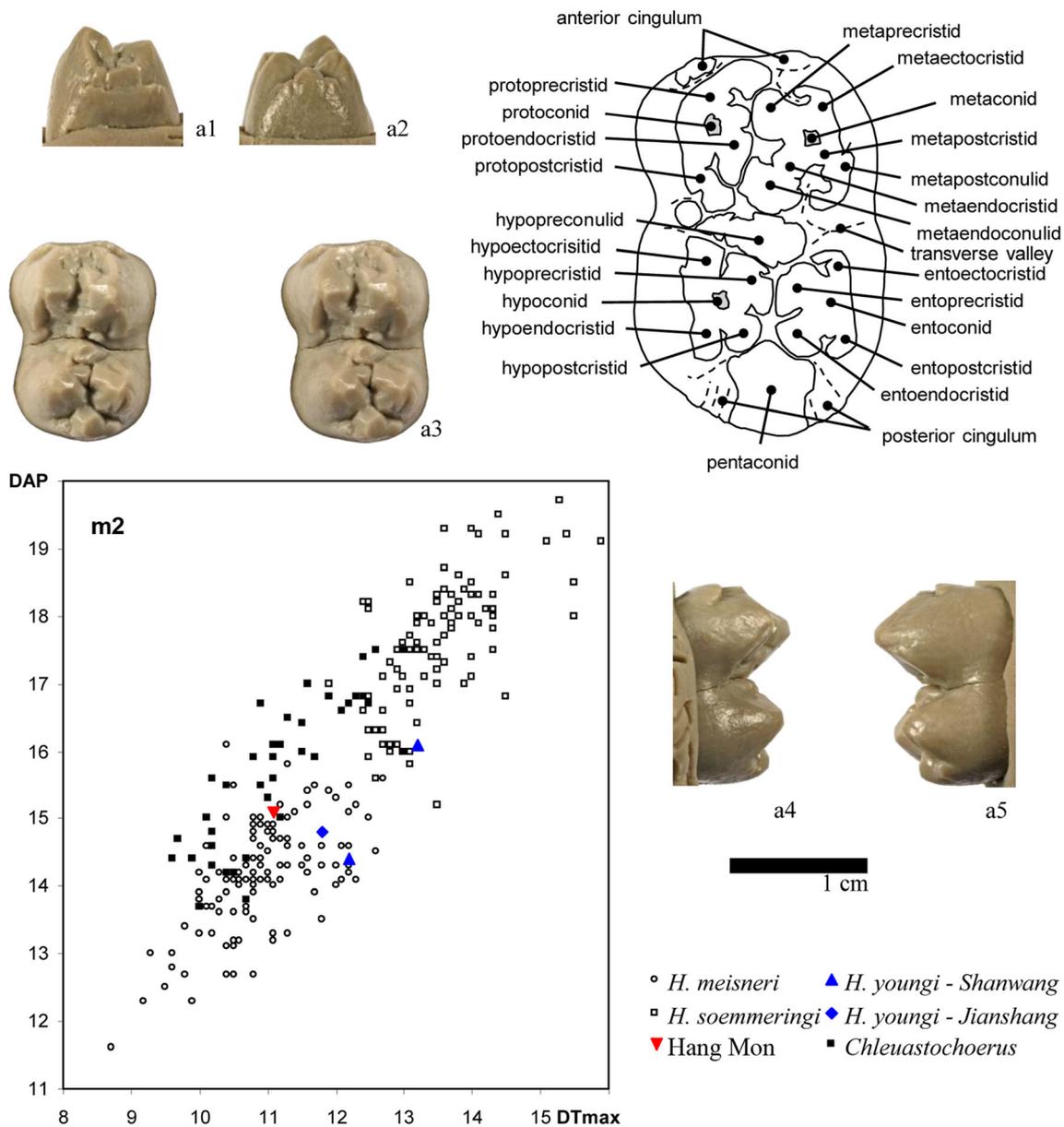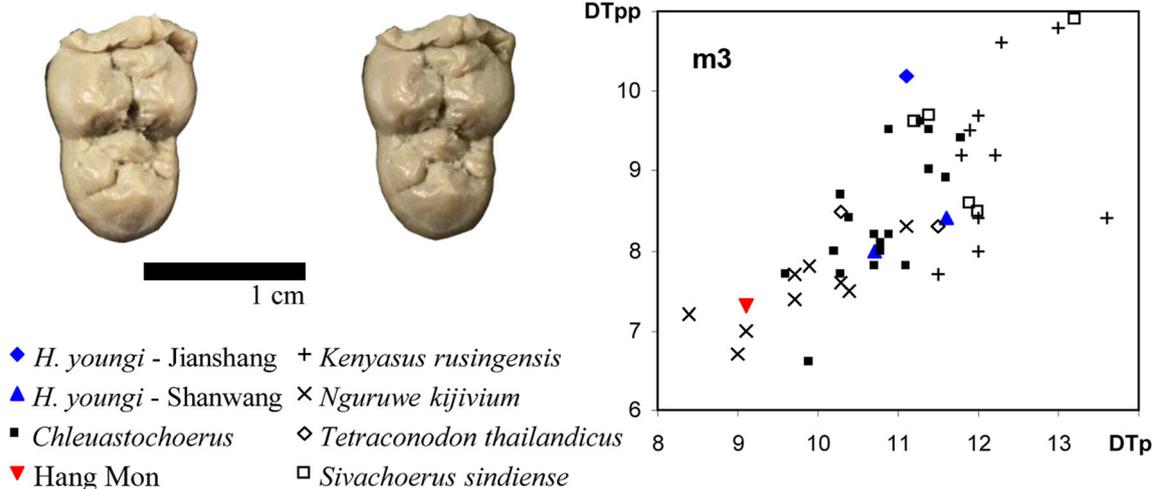
Fig. 7 cf. *Hyotherium youngi* (Chen, 1997) from Hang Mon 1, 214-03—cast of left m2: **a1** anterior, **a2** posterior, **a3** occlusal (stereo), **a4** buccal and **a5** lingual views. Schematic figure, on the basis of an m2 of *Propotamochoerus*, showing the dental nomenclature (after Van der Made 1996a). Bivariate diagram comparing the length (DAP) and width (DTmax) of the m2 of: cf. *Hyotherium youngi* (Chen, 1997) from Hang Mon 1; *Hyotherium meisneri* from Rappenfluh at Aarberg (NMBe), Hessler (SMF), Budenheim (SMF, HLMD), Cetina de Aragon (MNCN, IPS), Laugnac (LSPUPM, NMB, UCBL, MNHN), Grépiac (MHNT), Montaigu-le-Blin (NMB), Fort Ober-Eselsberg at Ulm (cast NMB), Eckingen (NMB), Tudela (IPS), Grafenmühle 2 (BSPG); *Hyotherium* *soemmeringi* from Armantes I (IVAU), Buchenthal (PIMUZ), Baigneaux-en-Beauce (NMB, MGL), Sandelzhausen (BSPG), Kalkgrube Schwanberg (SLJG), Seegraben (SLJG, IGGML), Münzenberg (SLJG), Fohnsdorf (SLJG), Vordersdorf (SLJG), Vordersdorf (NMW), Labitschberg (SLJG), Gamlitz (IPUW), Feisternitz (SLJG), Pontlevoy (MNHN), Quinta da Farinheira (CEPUNL), Georgensgmünd (SMF), Thannhausen (BSPG); *Hyotherium youngi* from Shanwang (cast and original - IVPP); *H. youngi* from Jianshang (cast IVPP); *Chleuastochoerus* from Locs. 73, 74 (IVPP), Baode (IVPP), Yuanmou (IVPP), Yiong Deng (BNHM), Locs. 12, 13, 29, 30, 49, 71, 73 (Pearson, 1928)

molars and the protoconule connected to the cingulum and not to the protocone (Van der Made 1996b), as well as a clear protopostcrista on the P4, thick lobes on the cusps of the molars, rather than thin crests that suggest a trend towards lophodonty. Early Suoidea have been described from Thailand and China (Ducrocq 1994; Ducrocq et al. 1998; Liu 2001; Orliac et al. 2011), but none of these have a "protoconule" fused with the cingulum. The tooth morphology in the suoid from Hang Mon 1 is much simpler than in the sanitheres.

Fig. 8 cf. *Hyotherium youngi* (Chen, 1997) from Hang Mon 1, 214-14—cast of right m3: occlusal view, stereo. Bivariate diagram comparing the width of the second (DTp) and third lobes (DTpp) of the m3 of: cf. *Hyotherium youngi* (Chen, 1997) from Hang Mon 1; *Hyotherium youngi* from Shanwang (cast and original—IVPP); *H. youngi* from Jianshang (cast IVPP); *Chleuastochoerus* from Locs. 73, 74 (IVPP), Baode (IVPP), Holinger (BNHM), Guanghe upper (BMNH), Yuanmou (IVPP); *Kenyasus rusingensis* from Rusinga (KNM), Baragoi (KNM); *Nguruwe kijivium* from Rusinga, Songhor, Mfwanganu (all KNM); *Tetraconodon thailandicus* from Ban San Klang (LPUM), Gyatpyegyi (cast MNCN); *Sivachoerus sindiensis* from the Chinji Fm. (IM, GSP)

Within the Suidae, the molars differ from those of the Listriodontinae in not showing any tendency towards lophodonty. The P4 has a normal width for the Suoidea, while it is widened in all early Tetraconodontinae (Van der Made and Tuna 1999). The same tooth differs from that of the later Tetraconodontinae, the Babyrousinae and the Suinae in not having a well-developed paraprecrista or parapreconule, nor a metaendocrista or metaendoconule (the sagittal cusp of Pickford (1988)). This leaves Cainochoerinae and Hyotheriinae.

The Cainochoerinae have a patchy record, suggesting that it is very incomplete. *Cainochoerus* and *Albanohyus* are much smaller, have not even the slightest hint of the development of a metacone on the P4 and have molars with a much lesser development of crests or lobes and the central cusp. *Kenyasus* does not have a well-developed metacone on the P4. The central cusps on the molars are better developed than in the other two genera, but lesser than in most Suidae, including *Hyotherium*. Their degree of development would fit that of the specimens from Hang Mon 1. In *Kenyasus*, the cristids and cristas on the molars tend to be more developed like slender crests and less than thick lobes and the endocristids and precristas tend to be more transversely directed.

The few differences with some of the Hyotheriinae have been mentioned above. Other genera of this subfamily are *Xenohyus*, which is much larger, and *Aureliachoerus*, which is much smaller than the suid from Hang Mon 1. In Europe, *Hyotherium* consists of three chronospecies that increase in size with time. The chronologically intermediate species *H. major* overlaps in size with both *H. meisneri* and *H. soemmeringi*. In size and morphology, it is most similar to the Chinese *H. youngi*, the fourth species of the genus. The main difference that could be observed with *H. youngi* is the lesser development of the central cusps in some of the specimens from Hang Mon 1, while in the m3, this cusp has a morphology that is normal for *Hyotherium*.

Even if not mentioned individually, these comparisons include virtually all known species of Suoidea from the Old World. Though there are some similarities with *Kenyasus*, most similarities are found with *H. youngi*, but many important features could not be observed because the material is limited. Though it is likely that the material represents this species, the possibility that it represents a not yet known primitive suid cannot be excluded. Therefore the material is assigned to cf. *Hyotherium youngi*.
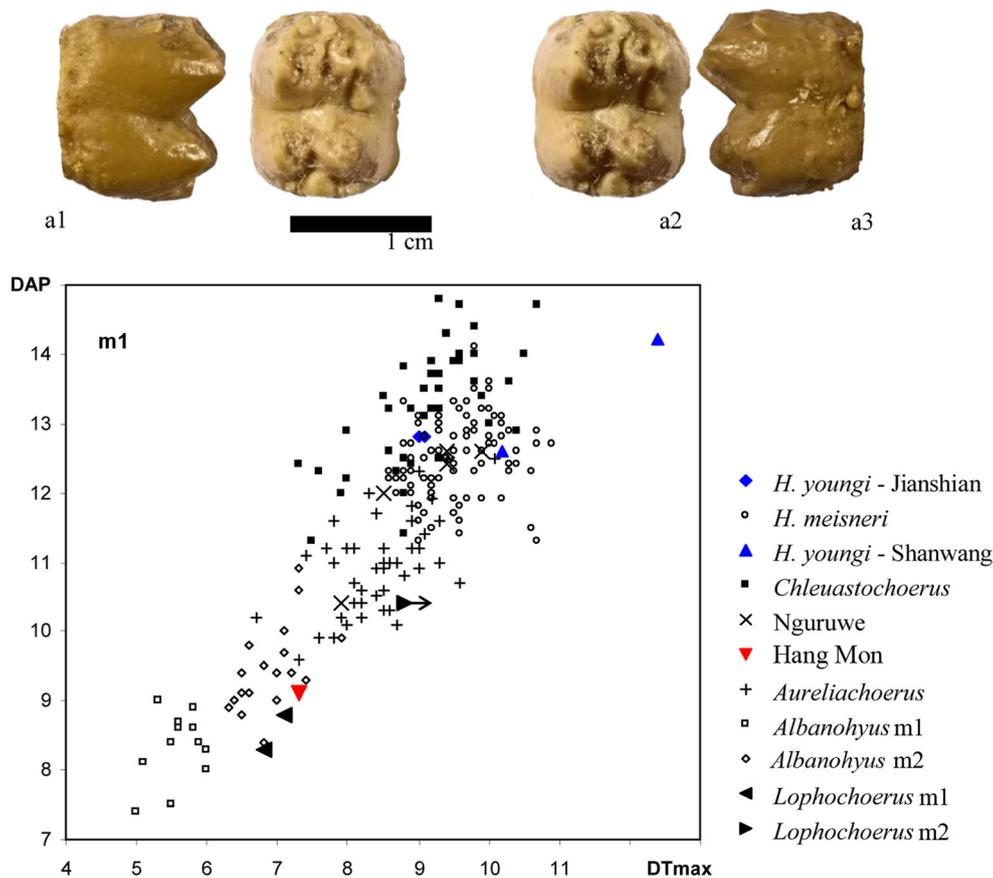
Suoidea indet.
Fig. 9

Studied material and measurements: cast of left m1/2 (DAP = 9.1, DTa = 7.3, DTp = 7.0, Ha > 7.3). Hang Mon (locality indet.), Hang Mon Basin, Northern Vietnam.

Description and systematic discussion

The m1 or m2 (Fig. 9) is a small tooth. It might be expected to be a ml of the species described above. However, those fossils tend to have sizes close to their largest homologues in *H. meisneri* (Figs. 5, 6 and 7), while this tooth is much smaller than the smallest m1 of that species. The proportions between the teeth are not constant in the Suoidea, and in the

Fig. 9 Suoidea sp. from Hang Mon (locality indet.)- MNHN no number - cast of left m1: **a1** lingual, **a2** occlusal (stereo) and **a3** buccal views. Bivariate diagram comparing the length (DAP) and width (DTmax) of the m1, 2 of Suoidea indet. from Hang Mon (locality indet.) with the m1 of *Hyotherium meisneri* from Hessler (SMF), Budenheim (SMF, HLMD), Cetina de Aragon (MNCN, IPS), Le Blanc (MHNT), Laugnac (LSPUPM, NMB, UCBL, MNHN), Grépiac (MHNT), Montaigu-le-Blin (NMB), Fort Ober-Eselsberg at Ulm (cast NMB), Tudela (IPS); *Hyotherium youngi* from Shanwang (cast IVPP); *H. youngi* from Jianshang (cast IVPP); *Chleuastochoerus* from Loc. 74 (IVPP), Baode (IVPP), Yuanmou (IVPP), Yiong Deng (BNHM), Holinger (BNHM), Locs. 12, 30, 49, 73 (Pearson, 1928); *Nguruwe kijivium* from Rusinga and Shongor (both KNM); *Aureliachoerus aurelianensis* from Fay aux Loges (MSNO), Chilleurs (MSNO, NMB), Agreda (MNCN), Tuchorice (NMW, NMP), Artenay (MSNO, NMB, MNHN), San Andreu de la Barca (IPS), Costablanca II (IPS), Chitenay (NMB), *Aureliachoerus* sp. from Moli Calopa(IPS) and *Aurliachoerus minus* from Oberdorf (SLJG), Wintershof West (BSPHG), Can Canals (IPS), La Romieu (UCBL); and the m1 and m2 of *Albanohyus pygmaeus* from La Grive (old collections; MGL, UCBL, IGF, NMB, NHM) and *Albanohyus castellensis* from Castell de Barberà (IPS); *Lophochoerus nagrii* from *Haritalyangar* (IM)

earlier species the m2 may be some 15% larger than the m1, while this may be in the order of 40% in some of the later Suidae. But the latter species tend to differ greatly in morphology from this tooth from Hang Mon 1.

The specimen studied is a cast and no observations on the roots could be made. The cristids have shapes and directions that recall Suidae, rather than Palaeochoeridae (see description above for the predominant states in these families). The central cusp is small and not well individualised. It is very similar to that described above in the m2. The cusp on the middle of the posterior cingulum is situated in the middle and not connected to the hypoconid. In general, the morphology is that of a primitive suid. The tooth is proportionally wide, as in primitive Suidae, and much wider than in *Chleuastochoerus*.

This molar is much smaller than the m1 of *Hyotherium youngi* and *H. meisneri* (Fig. 9). It is also smaller than the smallest *Aureliachoerus* molar, but it is in the ranges of the m2 of *Albanohyus*, which is the smallest suid from Europe and, together with its likely follower *Cainochoerus*, the smallest from Africa. It is close in size to the m1 of *Lophochoerus nagrii*.

Order Carnivora Bowdich, 1821
Family Amphicyonidae Haeckel, 1866
Subfamily Amphycioninae Haeckel, 1866
Genus *Amphicyon* Lartet, 1836

Amphicyon cf. *giganteus* Schinz, 1825
Fig. 10a
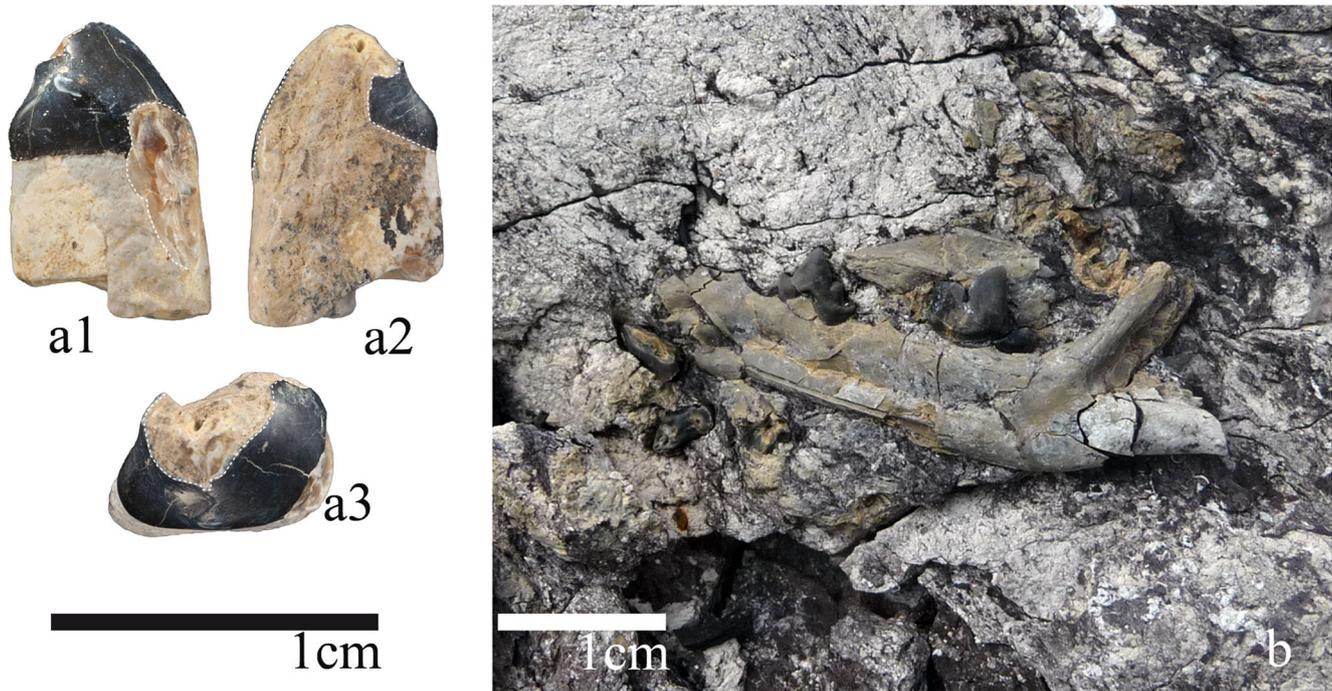
Fig. 10 Carnivores from Hang Mon 1. **a** *Amphicyon* cf. *giganteus* Schinz, 1825, right i3 (**a1**–**a3**, respectively, from labial, lingual and occlusal views). **b** Carnivora indet.: left mandible with p3 and m1 in situ and isolated fragmentary left P4 and right P3. Photography of the specimen as it has been found

1992 *Amphicyon* cf. *giganteus* Ginsburg et al.: 627, fig. 2
2006 *Amphicyon* cf. *giganteus* Peigné et al. (2006): 520, 521

Studied material and measurements: Right i3 (8.1 × 11.6 mm after Ginsburg et al. 1992). Hang Mon 1. Hang Mon Basin, Northern Vietnam.

Systematic discussion

A large lower incisor from Hang Mon 1 of a carnivore morphologically similar to *Amphicyon major* but as large as *A. giganteus* was reported by Ginsburg et al. (1992). The large size of the specimen prevents from assignment to the geographically close *Maemohcyon potisati* from the late Middle Miocene from Mae Moh (northern Thailand) (Peigné et al. 2006) or *Amphicyon tairumensis* from the late Middle Miocene Tunguur Formation (China). Affinities of the specimen from Hang Mon are thus rather with the larger species of *Amphicyon* from Asia; however their taxonomy is unsettled mostly due to the lack of appropriate material for comparison. Early Miocene records of *Amphicyon* come from the Bugti Hills, Pakistan. *Amphicyon shahbazi* occurs at the top of the Chitarwata Formation and in the lower part of the Vihowa Formation (earliest to late Early Miocene), while *A. giganteus* is found in the lower part of the Vihowa Formation (Antoine et al. 2013). The oldest record of *Amphicyon* from China comes from the late Early Miocene of Xiejiahe, and was not assigned to a species (Qiu and Qiu 2013). Similar in size is *A. ulungurensis*

from the Middle Miocene of China, which cannot be properly compared with *A. confucianus*, because the holotypes of the two species document different portions of the mandible (Peigné et al. 2006). Both do not record i3, and proper comparison with the Vietnamese material is thus impossible. Herein we follow Ginsburg et al. (1992) and tentatively assign the specimen from Hang Mon 1 to *A. giganteus*.

Remains of a second, small, primitive carnivore have recently been found at Hang Mon 1. The study of this individual, consisting of a lower mandible resting on a highly damaged skull fragment (Fig. 10b), is in progress, and the results will be published in a separate contribution.

Order Rodentia Bowdich, 1821.
Rodentia indet.
Fig. 11

1992 Hystricidae Ginsburg et al.: 627.

Studied material and measurements: upper incisor (4.7 × 7.3 mm after Ginsburg et al. 1992). Hang Mon 1. Hang Mon Basin, Northern Vietnam.

Ginsburg et al. (1992) assigned this upper incisor (actually the only find of a pre-Quaternary rodent in Vietnam) to a porcupine, based on the large size of the specimen, the shape of its cross section and the very fine elongated grooves of the enamel. However, these characteristics are not restricted to the Hystricidae. Large incisors with faint ornamentation are also

Fig. 11 Rodentia indet. from Hang Mon 1.?Left upper incisor (*from left to right*, respectively, from mesial,?labial and distal views)

reported from the Oligocene (to earliest Miocene?) *Tsaganomys altacius* from Mongolia (Matthew and Granger 1923), and this character is subject to intraspecific variability according to Bryant and McKenna (1995). Moreover, in *Hystrix* the enamel on the lateral side of the tooth extends much further than in the specimen from Hang Mon (e.g. Sulimski 1960). Other large rodents from the Late Oligocene and earliest Miocene of Asia, such as *Yindirtemys,* should thus also be taken into account for comparison. However, the taxonomic evidence from a single incisor is poor, and it is certainly more reliable to keep the assignment to the Rodentia in open nomenclature.

Mammalia indet.

2001 *Tapirus* sp. Covert et al.: 636–637, fig. 2c

Covert et al. (2001) assigned two lower molar fragments to *Tapirus*. We did not have access to the original material nor casts, and thus we can only refer to the published information. Unfortunately, the figures are too small for detailed analysis. The generic assignment was based on the presence of a "single cross loph running transversely across the posterior portion of the talonid and a very small loph-like crest on the posterior aspect of the tooth" (Covert et al. 2001: 635). This characteristic is present in tapirids (including *Tapirus*), but also in any bilophodont eutherians, such as listriodontine suids or deinothere proboscideans. As a result, a confident assignment of these specimens is presently impossible, and they are thus considered as Mammalia indet.

Biochronological significance of the assemblages

The mammalian fauna of Hang Mon comprises 11 taxa (Table 3). As outlined above, the fossiliferous layers at Hang Mon 1 and 2 cannot be directly correlated. However, the

**Table 3** The mammals from Hang Mon.

Species	Hang Mon 1	Hang Mon 2	Unknown layer
Pleuroceros blanfordi	x	x	
Protaceratherium sp.	x		
Bugtirhinus sp.		x	
Dorcatherium sp.	x		
Dorcabune sp.	x		
cf. *Hyotherium youngi*	x		
Suoidea indet.			x
Amphicyon cf. *giganteus*	x		
Carnivora indet.	x		
Rodentia indet.	x		
Mammalia indet.	x		

similarities in the sedimentary facies as well as the close vicinity of the outcrops (see Fig. 1) argue for close similarity in age, and the mammal assemblages support this hypothesis. As discussed in Antoine and Welcomme (2000) and Antoine et al. (2010, 2013), *Pleuroceros blanfordi* and *Bugtirhinus* were so far restricted to the Early Miocene of SW Pakistan (~23–18.7 Ma: Aquitanian to early Burdigalian; Bugti Hills and Zinda Pir). Based on their occurrence, a similar age can be proposed for Hang Mon 2. "Assemblage A" of Antoine et al. (2013: earliest Miocene; "Level 4"; ~23–19.3 Ma) from the Bugti Hills is notably defined by the co-occurrence of *Protaceratherium* sp., *Pleuroceros blanfordi*, and *Bugtirhinus*. The uncommonly small-sized *Protaceratherium* from Hang Mon 1 is related herein to *Protaceratherium* sp. from SW Pakistan. Tragulids are common ruminants in the Oligocene and Miocene of South and Southeast Asia (Métais et al. 2007, 2009; Thomas et al. 1990). *Dorcatherium* is reported from Aquitanian to early Burdigalian deposits of Pakistan (Antoine et al. 2013), and occurs slightly later in Northern Pakistan (lower Kamlial, ~18 Ma, Barry 2014). The other tragulid from Hang Mon is here tentatively referred to *Dorcabune* sp..While the morphological features of the tooth are hardly observable, the size best matches that of *D. sindiense* and *D. welcommi*, the smallest species of the genus. Barry (2014) noted that both species are hardly differentiable and might be synonymous. The first appearance of *D. sindiense* and *D. welcommi* is from

the uppermost Gaj (~20 Ma) of southern Pakistan (Raza et al. 1984), and the earliest Miocene (level 4 in Bugti sequence) of Bugti (Ginsburg et al. 2001) respectively. *Dorcabune* sp. is also reported from the late Early and the Middle Miocene of western Nepal (West et al. 1978, 1991).

Ginsburg et al. (1992) compared the morphology of the suid M3 from Hang Mon 1 to material from Sandelzhausen (southern Germany) and to "*Hyotherium*" *pilgrimi* from the Chinji Formation (Middle Miocene, Pakistan), concluding that Hang Mon should be older, and thus suggested an Early Miocene age. However, Sandelzhausen is now re-dated to approximately 15.2 Ma (Reichenbacher et al. 2013). The material from the Chinji Formation is now believed not to belong to *Hyotherium* (Van der Made 2010). The tentative assignment of the suid material from Hang Mon 1 to *Hyotherium youngi* suggests an age close to that of the Middle Miocene Chinese localities Shanwang and Jianshan. In addition, *H. youngi* retains primitive features that were lost in the European lineage of *Hyotherium*, suggesting that *H. youngi* has a longer, undocumented history in East Asia. The presence of large-sized *Amphicyon* in the Early Miocene of Asia, considered as likely by Ginsburg et al. (1992) has since been confirmed (e.g. Antoine et al. 2013; Qiu and Qiu 2013).

The mammal biochronology is in line with palynology, suggesting a minimum age of 21.12 Ma (Böhme et al. 2011). In conclusion, mammalian biochronology and palynostratigraphy
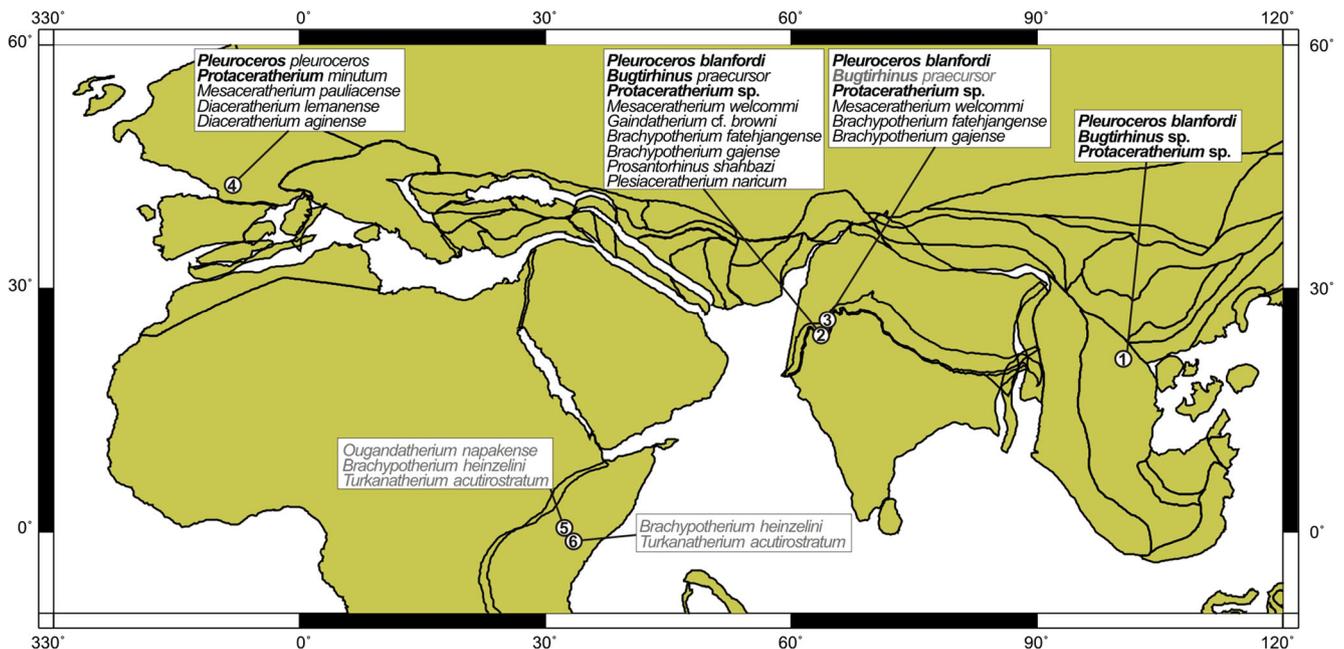
Fig. 12 Palaeogeographical map at 22 Ma BP illustrating selected Aquitanian rhinocerotid assemblages from Asia and Europe and the earliest rhinocerotid assemblages from Africa: (1) Hang Mon 1 + 2, northern Vietnam; (2) Level 4, Bugti Hills, SW Pakistan; (3) Zinda Pir, SW Pakistan; (4) Laugnac, SW France; (5) Napak I + II, Uganda; (6) Songhor, Kenya. *Bold-typed names* indicate taxa congeneric/conspecific to the Hang Mon rhinocerotid fauna. Taxa occurring in a younger interval are in grey (e.g. *Bugtirhinus praecursor*, Zinda Pir). Faunal lists revised from de Bonis (1973); Geraads (2010); Antoine et al. (2010, 2013), and the present work. Map constructed after http://www.odsn.de/cgi-bin/make_map.pl.

indicate an age of approximately 23 to 21 Ma for the composite fauna from Hang Mon, corresponding to the early Aquitanian (earliest Miocene).

Palaeobiogeographical implications

In the Early Miocene, *Pleuroceros blanfordi*, *Protaceratherium* sp., and *Bugtirhinus* were part of an exceptionally diversified rhinocerotid assemblage including up to nine associated species in SW Pakistan (e.g. Antoine and Welcomme 2000; Métais et al. 2009; Antoine et al. 2013). Together with other faunal elements and enamel isotopic values (δ^{18}O and δ^{13}C; Martin et al. 2011), this incredible specific diversity testifies to the presence of an extremely favourable, probably densely forested environment under a subtropical climate, before a global temperature decrease occurred later in the Early Miocene (Zachos et al. 2008; Martin et al. 2011).

Antoine et al. (2010) demonstrated that the earliest Miocene rhinocerotid assemblages from Pakistan, Europe, and East Africa were widely homotaxic, pointing to compatible conditions in the concerned biogeographical region. The new discoveries from Vietnam (rhinocerotid and tragulid assemblages, *Hyotherium*) may weigh in favour of this hypothesis, by documenting biogeographical affinities between the Indian Subcontinent, Southeast Asia (Vietnam) and Southwestern Europe during the corresponding interval (Fig. 12). Interestingly, zonal similarities in mammalian faunas along the northern shore of the Neotethys have been evidenced as early as the Late Eocene (Böhme et al. 2013). The distribution of the fossil-enriched Tertiary basins in SE and SW Asia is closely related to the collision of the Indian Subcontinent with the northern margin of the Neotethys. The India-Asia collision initiated the Himalayan orogeny and the eastward strike-slip extrusion of the Indochina block of the Southeast Asian continental collage along the Ailao Shan-Red River shear zone have long been recognised as the two most spectacular results of this collision (Tapponnier et al. 1986; Rangin et al. 1995). Consequently, the large strike-slip faults associated with escape tectonics are predicted to dominate the geological evolution of SE Asia. The deposits of continental clastics in small pull-apart basins, such as the Hang Mon Basin, is related to the Ailao Shan-Red River fault system that affected southern China and Vietnam from the Eocene up to now (e.g. Morley 2002). The earliest Miocene Hang Mon Formation, composed primarily of coal, coaly shales and sandstones of continental origin, was likely deposited under humid tropical climate (Dzanh 1996). The proposed age of the fauna, close to the Oligocene-Miocene transition, corresponds to a major climate change towards moister environments in SW and SE China, while inland deserts started to appear at higher latitudes as a consequence of the establishment of a monsoon-dominated system (Gao et al. 2008).

Compliance with ethical standards

Conflict of interest: The authors declare that they have no conflict of interest.

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