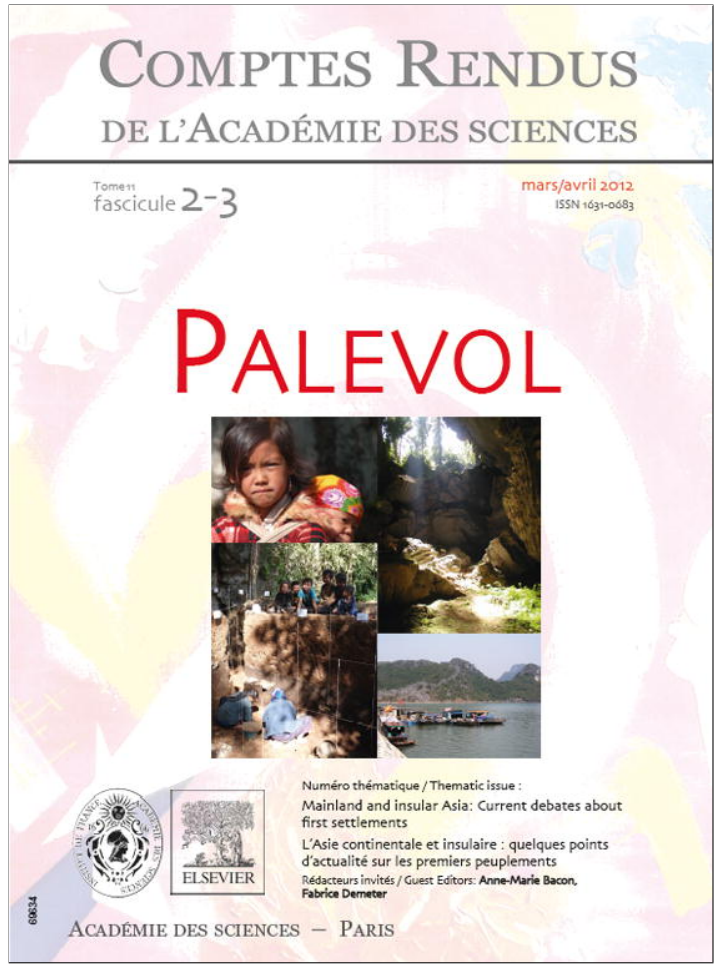

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General palaeontology, systematics and evolution (Vertebrate palaeontology)

Pleistocene and Holocene rhinocerotids (Mammalia, Perissodactyla) from the Indochinese Peninsula

Les Rhinocérotidés (Mammalia, Perissodactyla) du Pléistocène et de l'Holocène de la Péninsule indochinoise

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ABSTRACT

Rhinocerotids were abundant and diverse in southern Asia during the Pleistocene and the Holocene epochs, as shown by palaeontological and archaeological discoveries published throughout the last century, whereas the only living rhinoceros in the Indochinese Peninsula is *Rhinoceros sondaicus* (Cat Loc Reserve, Vietnam). The Pleistocene-Holocene Indochinese rhinocerotid record consists of the extinct species *Dicerorhinus gwebinensis* (Early Pleistocene, Myanmar) and representatives of the Recent Asian Species *Rhinoceros unicornis* (Middle-Late Pleistocene), *R. sondaicus* (Middle Pleistocene-Recent), and *Dicerorhinus sumatrensis* (Middle Pleistocene-Holocene). This fossil record is synthesized, mapped for Early/Middle/Late Pleistocene and Holocene/Recent times, and then compared with coeval rhinocerotid assemblages from the adjacent areas (South China), subregions (Indian, Sundaic, Philippine, and Wallacean), and region (Palearctic), from a biochronological and biogeographical perspective.

Mots clés :
Rhinocerotidae
Rhinocerotina
Systématique
Biochronologie
Biogéographie
Région indo-malaise
Sous-région sondaïque

RÉSUMÉ

Les rhinocérotidés étaient abondants et diversifiés en Asie du Sud pendant le Pléistocène et l'Holocène, comme l'ont démontré les découvertes paléontologiques et archéologiques publiées tout au long du dernier siècle. Par contraste, le seul rhinocéros vivant aujourd'hui dans la Péninsule indochinoise est *Rhinoceros sondaicus* (Réserve de Cat Loc, Vietnam). Le registre fossile pléistocène-holocène des rhinocérotidés d'Indochine inclut à la fois l'espèce éteinte *Dicerorhinus gwebinensis* (Pléistocène inférieur, Myanmar) et des représentants des espèces asiatiques actuelles *Rhinoceros unicornis* (Pléistocène moyen à supérieur), *R. sondaicus* (Pléistocène moyen à Actuel) et *Dicerorhinus sumatrensis* (Pléistocène moyen-Holocène). Ce registre est synthétisé, puis cartographié pour le Pléistocène inférieur/moyen/supérieur, l'Holocène et l'Actuel, et enfin comparé aux assemblages contemporains de Chine du Sud (sous-région indochinoise), des sous-régions adjacentes (indienne, sondaïque, philippine et wallacéenne) et de la région paléarctique, à la fois des points de vue biochronologique et biogéographique.

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1. Introduction and historical background

Asian rhinoceroses are among the most endangered mammalian species today, with populations ranging from 50 (*Rhinoceros sondaicus*) up to ca. 2850 individuals (*Rhinoceros unicornis*; source: International Rhino Foundation, http://www.rhinos-irf.org). Before hunting and poaching nearly led to their eradication in the 20th century, they used to be conspicuous elements of Cenozoic terrestrial ecosystems in southern Asia. This is particularly true for Palaeogene and Miocene vertebrate assemblages, with a remarkable rhinocerotid specific diversity (Antoine et al., 2003, 2010; Antoine et al., in press; Heissig, 1972), but also for Pleistocene and Holocene faunas (Bacon et al., 2004, 2006, 2008a, 2008b; Beden et al., 1972; Colbert and Hooijer, 1953; Hooijer, 1946; Tong, 2000, 2001; Tong and Guérin, 2009; Tougard, 2001; Zeitoun et al., 2005).

In biogeographical terms, southern Asia coincides with the Indo-Malayan region (Fig. 1; Udvardy, 1975), which is split into the Indian, Indochinese, Sundaic, Philippine, and Wallacean subregions (Corbet and Hill, 1992; Lekagul and McNeely, 1988); the Indochinese subregion includes the Indochinese Peninsula (Fig. 1; Myanmar, Thailand, Laos, Vietnam, and Cambodia) and South China (Lekagul and McNeely, 1988; Tougard, 2001).

Pleistocene and Holocene rhinocerotids were mentioned in Indochinese localities throughout the 20th century, first in Burma/Myanmar (Colbert, 1938; Pilgrim, 1913), then in northern Vietnam (Bacon et al., 2004, 2006, 2008b; Patte, 1928), in Laos (Arambourg and Fromaget, 1938; Bacon et al., 2008a; Fromaget, 1936), in Cambodia (Beden and Guérin, 1973; Beden et al., 1972; Carbonnel and Guth, 1968; Guérin and Mourer, 1969), and in Thailand (Tougard, 2001; Tougard and Montuire, 2006; Zeitoun et al., 2005). These findings were primarily compared with the Chinese, Indonesian, and Indo-Pakistani upper Siwalik records (Colbert, 1938; Colbert and Hooijer, 1953; Hooijer, 1946; Matthew and Granger, 1923; Pilgrim, 1913) and with the Quaternary record of Europe (Kahlke, 1986).

This article aims to review the Pleistocene and Holocene rhinocerotid record of the Indochinese Peninsula, and to compare it in a biochronological and biogeographical perspective with coeval rhinocerotid assemblages from the adjacent areas (South China), subregions (Indian, Sundaic, Philippine, and Wallacean), and region (Palearctic).

2. Systematic overview

Three rhinocerotid species occur in Asia today, all of them referred to the Rhinocerotina subtribe (Antoine, 2002). Their recent distribution in the Indochinese Peninsula is restricted to a single micropopulation in Vietnam (Fig. 2), whereas they were widespread and quite abundant in that region during the Pleistocene and Holocene epochs (Figs. 2 and 3; e.g., Bacon et al., 2008b; Louys et al., 2007; Tougard, 2001). Aside from the extant ones, several fossil species and/or genera were also recognized in the Pleistocene of southern Asia, notably in China (e.g., Tong, 2001) and in the Indochinese Peninsula (e.g., Zin-Maung-Maung-Thein et al., 2008; Fig. 3). All the concerned species are listed and their status is discussed hereunder.

2.1. Recent species

The greater one-horned rhino, *R. unicornis*, is the least endangered of the Asian species nowadays, with ca. 2850 individuals scattered in several reserves from the Himalayan foothills, in northern India, southern Nepal, and Bhutan (Fig. 2). Its Holocene distribution was much wider and encompassed the entire Himalayan foothills, from Pakistan to easternmost India (Indian subregion). No Holocene occurrence is reported in Indochina, whereas *R. unicornis* is recorded in Pleistocene deposits throughout southern Asia, including the Indochinese Province and South China (Fig. 3). The greater one-horned rhino occurred in the Early Pleistocene of Java (Joordens et al., 2009), South China, and Indo-Pakistan, in the Middle Pleistocene of Java and the Indochinese subregion (Thailand, Laos, Vietnam, and South China), and in the Late Pleistocene of Vietnam, South China (Fig. 3), South India, and Sri Lanka (Chauhan, 2008; Nanda, 2002).

Its sister taxon, the Javan rhino *Rhinoceros sondaicus*–or "lesser one-horned rhino"–, is critically endangered today (van Strien et al., 2008a). No more than 50 individuals survive, with a main population located in Java, Indonesia (Ujung Kulon Reserve; Fig. 2) and perhaps a small group of three or four individuals in southern Vietnam (Cat Loc, Cat Tien National Park; Fig. 2). By contrast, during the Holocene, the Javan rhino was common from east to west and from north to south of the Indochinese Peninsula (e.g., Long Spean locality, southern Cambodia; Guérin and Mourer, 1969), as well as in eastern China (Fig. 2; Rookmaaker, 2006; Tong, 2000, 2001) and in the Sundaic subregion (Fig. 2; peninsular Malaysia, Sumatra, Borneo, and Java; Cranbrook and Piper, 2007). *R. sondaicus* is well represented in the Early Pleistocene of Java (Djetis, Sangiran, and Trinil localities; Joordens et al., 2009; van den Bergh et al., 2001), in the Middle Pleistocene of Indochina (Cambodia, Thailand, and Laos) and Peninsular Malaysia (Tambun; Fig. 3), and in the Late Pleistocene of the Sundaic subregion (Sumatra, Java, and Malaysia) and northern Vietnam (Ma U'Oi, Duoi U'Oi, and Lang Trang; Fig. 3; Bacon et al., 2004, 2008a). Two fossil subspecies were named for late Middle Pleistocene remains from Phnom Loang, Cambodia (*R. s. guthi;* Beden et al., 1972) and Kedung Brubus, Java (*R. s. sivasondaicus;* Guérin and Faure, 2002).

The Sumatran rhino, *Dicerorhinus sumatrensis*, is two-horned and smaller than the representatives of *Rhinoceros* (i.e., body mass is less than 1000 kg; Groves and Kurt, 1972; Guérin, 1980). Its phylogenetic affinities are controversial on both morphological and molecular grounds (Antoine, 2002, 2005; Cerdeño, 1995; Orlando et al., 2003; Tougard, 2001). Its population, estimated at ca. 200 individuals, is highly fragmented in several small groups from Sumatra and Malaysia (Fig. 2). It is therefore considered as critically endangered, due to the drastic demographic decline suffered in the last decades (van Strien et al., 2008b). *D. sumatrensis* had a much wider Holocene range than now, covering most of the Indo-Malayan region (Fig. 2; eastern India [Indian subregion]; northern Laos [Holocene alluvium at Tam Hang]; Arambourg and Fromaget, 1938), Myanmar, Thailand, and eastern China (Indochinese subregion and Palearctic region; Fig. 2); Malaysia, Sumatra, and Bor-

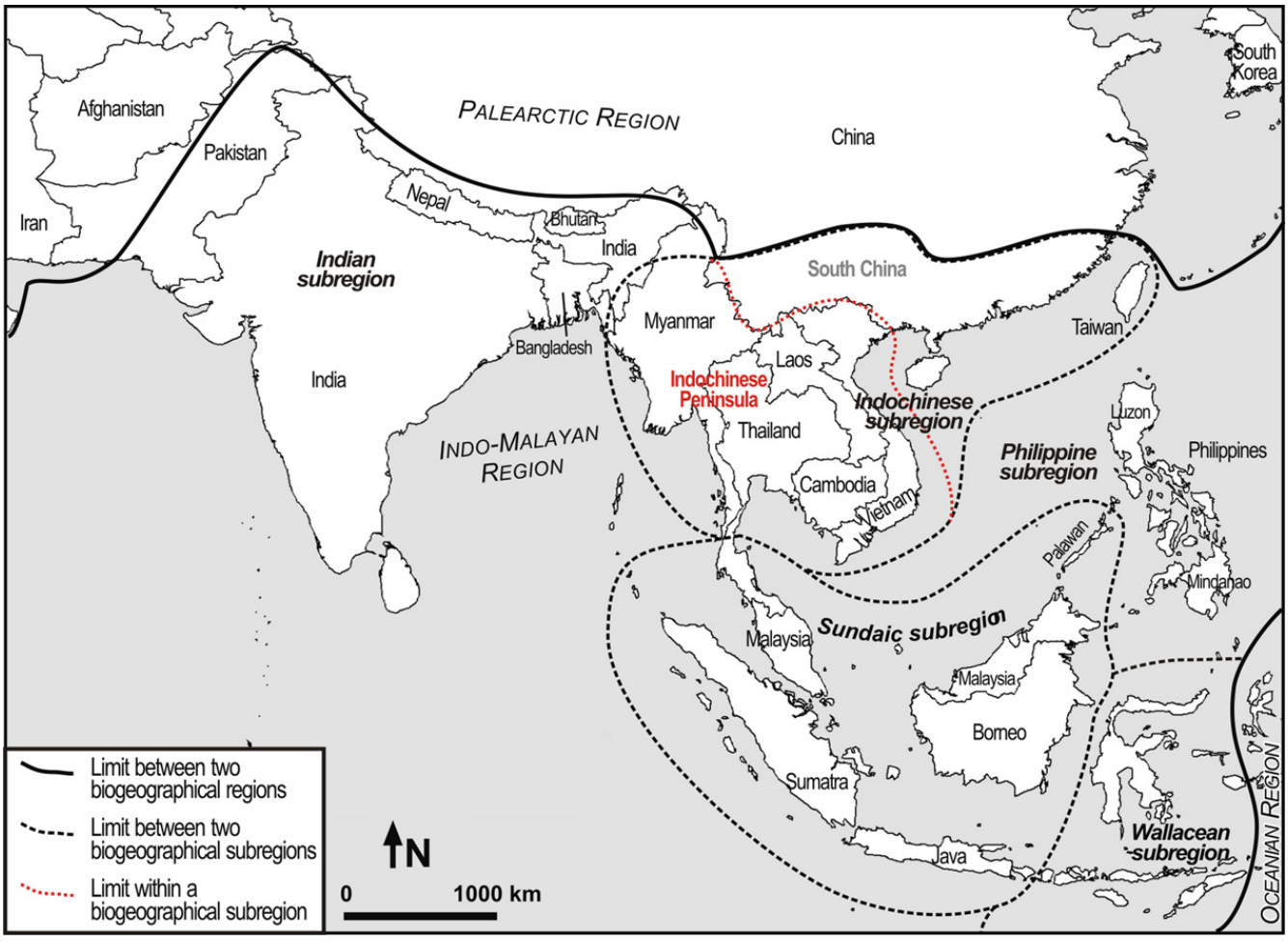

Fig. 1. Map of southern Asia showing the corresponding biogeographical regions and subregions, with a focus on the Indochinese Peninsula. Modified after Corbet and Hill (1992), Lekagul and McNeely (1988), Tougard (2001) and Udvardy (1975).
Fig. 1. Carte de l'Asie du Sud montrant les régions et « sous-régions » biogéographiques correspondantes et, en particulier, la Péninsule indochinoise. Modifié d'après Corbet et Hill (1992), Lekagul et McNeely (1988), Tougard (2001) et Udvardy (1975).

neo (Sundaic subregion). Until Recent times, the "hairy rhino" was co-occurring with *R. sondaicus* in most of its geographical range (Fig. 2). The Sumatran rhino has a scarce Pleistocene record, with a single attested occurrence for the Early Pleistocene (Liucheng or "*Gigantopithecus* cave", South China; Fig. 3; Tong and Guérin, 2009) and the late Middle Pleistocene (Ban Fa Suai, Thailand; Fig. 3; pers. obs.), but a wider Late Pleistocene range (Laos, northern Vietnam, and Sumatra; Fig. 3).

2.2. Extinct species

More than a dozen fossil species of *Rhinoceros* were named in southern Asia, the validity of which is more or less questionable (e.g., Bacon et al., 2008b; Laurie et al., 1983; Tong, 2001) (Fig. 3).

In our opinion, *R. unicornis* encompasses all large *Rhinoceros* remains from South Asia that were formerly included within the wastebasket species *R. sinensis* (and its junior synonyms *R. oweni*, *R. plicidens*, *R. simplicidens*, or *R. chiai;* Tong, 2001), the Javan *R. kendengindicus* (Bacon et al., 2008b; Hooijer, 1949), as well as the Indo-Pakistani *R. sivalensis*, *R. palaeindicus*, *R. deccanensis*, *R. sinhaleyus*, or *R. kagavena* (Tong, 2001). *Rhinoceros sinensis* was primarily described in Yengshingkuo, China and recognized in most Middle Pleistocene localities of South China (Colbert, 1938; Tong, 2001) and northern Vietnam (Fig. 3; Patte, 1928; Tougard, 2001); only a thorough revision of the hypodigm of *R. sinensis* would allow assessing the eventual availability of this species and its affinities within *Rhinoceros* and with other rhinocerotines (Tong and Wu, 2010).

The endemic ? Pleistocene species *Rhinoceros philippinensis* is based on a jaw extracted from a fossil bed of unknown location and age in Luzon, Philippines (Fig. 1; von Koenigswald, 1956; Reis and Garong, 2001; Tougard, 2001). Reis and Garong (2001: 411) consider that the "occurrence of this species may not be natural". Its specific status is therefore highly dubious.

Dicerorhinus gwebinensis is a small two-horned rhino from the Upper Irrawaddy deposits of western Myanmar (Gwebin locality, Fig. 3; Zin-Maung-Maung-Thein et al., 2008) the hypodigm of which is restricted to a skull and the associated mandible, much similar to *D. sumatrensis*, but with shorter and thicker nasals. The Upper Irrawaddy beds yielding *D. gwebinensis* are most probably of Early Pleistocene age (Louys et al., 2007).

The gigantic two-horned *Stephanorhinus kirchbergensis* is also known as the "forest rhino", with junior synonyms as widely used as *Dicerorhinus mercki* (Middle Pleistocene of the Palearctic region; van der Made, 2010), or more local names such as *D. choukoutienensis*, *D. lantianensis*, and *D. yunchuchenensis* (Early to Late Pleistocene of eastern central China; Tong, 2000, 2001). As far as South Asia is concerned, *S. kirchbergensis* occurred throughout the Pleistocene epoch in eastern central China, but only within the Beijing-Xian-Shanghai triangle, i.e. between 30° and 40°N (Tong, 2000). It is quite rare in South Chinese faunal assemblages (Tong and Wu, 2010). The presence of "*R. mercki*" (= *S. kirchbergensis*) in "Préah Vihear", Cambodia (= Phnom Loang; Fig. 3), as mentioned by Carbonnel and Guth (1968) and Louys et al. (2007), is highly dubious: other revisions of the rhinocerotine material from the same locality do not mention this taxon (e.g., Beden et al., 1972).

The fossil genus *Coelodonta* encompasses large two-horned rhinos with an ossified nasal septum. The earliest representatives of *Coelodonta* are known in the Early Pleistocene of northeastern China (Nihowan area) and referred to as *C. nihowanensis* (Tong, 2001). Later representatives document the much more widespread *C. antiquitatis*, also known as "woolly rhino" (Middle and Late Pleistocene of the Palearctic region; Guérin, 1980; Tong, 2001, 2004). No representative of *Coelodonta* is recorded in southern Asia (Tong, 2000).

Punjabitherium platyrhinus is another large two-horned rhino, ranging from the latest Pliocene to the early Middle Pleistocene in North India and Pakistan (Upper Siwaliks;

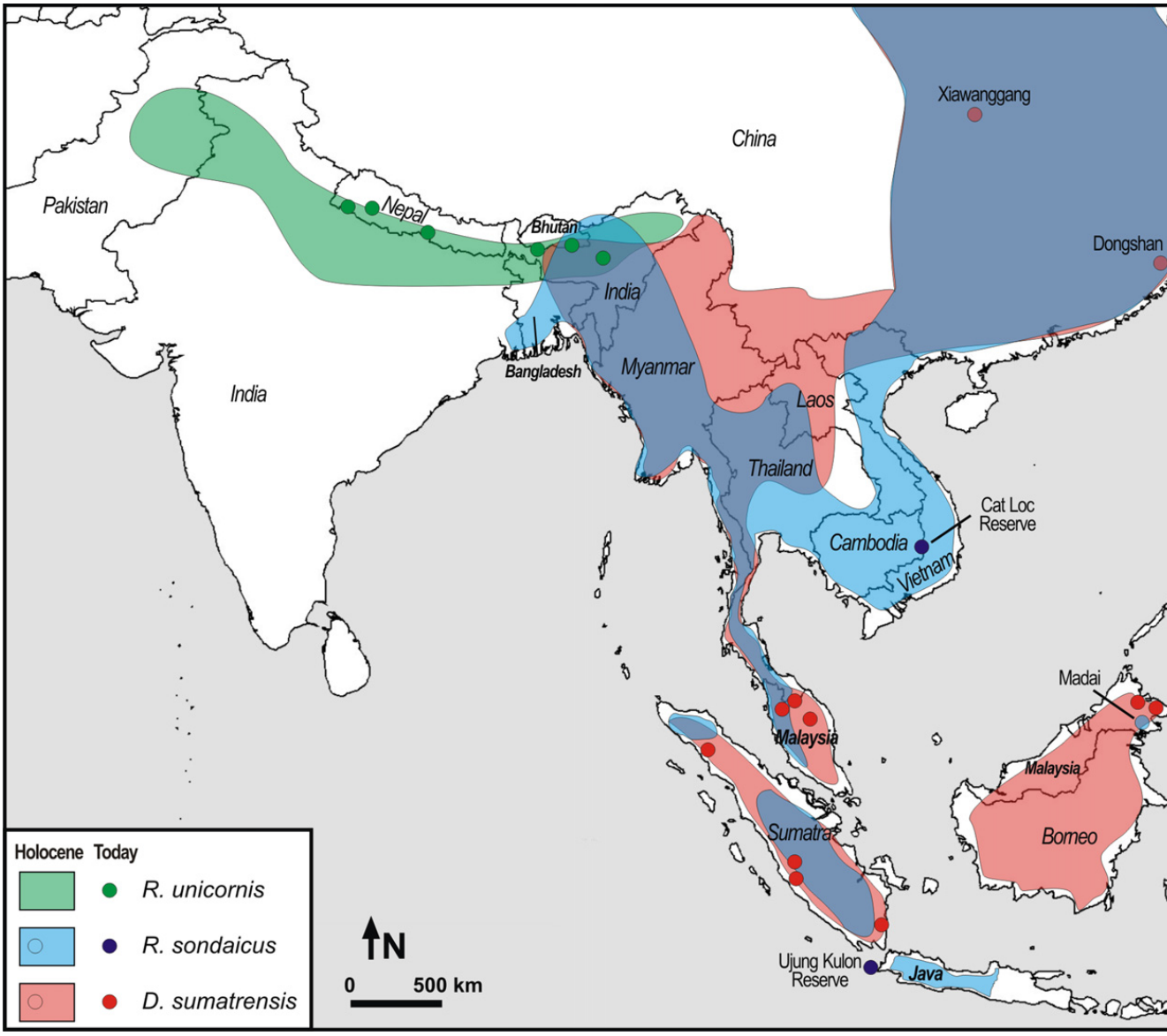

Fig. 2. Distribution map of Holocene and Recent rhinocerotids of southern Asia. Based on Arambourg and Fromaget (1938), Guérin and Mourer (1969), Tong (2000, 2001), Tong and Moigne (2000), Cranbrook and Piper (2007) for prehistorical times, and on Rookmaaker (2006), Tong and Wu (2010), Wang et al. (1993), and online data from the International Rhino Foundation for historical times and living rhinos (http://www.rhinos-irf.org).

Fig. 2. Carte de répartition des rhinocérotidés holocènes et actuels d'Asie du Sud. Fondé sur Arambourg et Fromaget (1938), Guérin et Mourer (1969), Tong (2000, 2001), Tong et Moigne (2000), Cranbrook et Piper (2007) pour les rhinocéros fossiles, sur Rookmaaker (2006), Tong et Wu (2010) et Wang et al. (1993), et sur des données disponibles sur le site de l'*International Rhino Foundation* pour les temps historiques et les rhinocéros actuels (http://www.rhinos-irf.org).

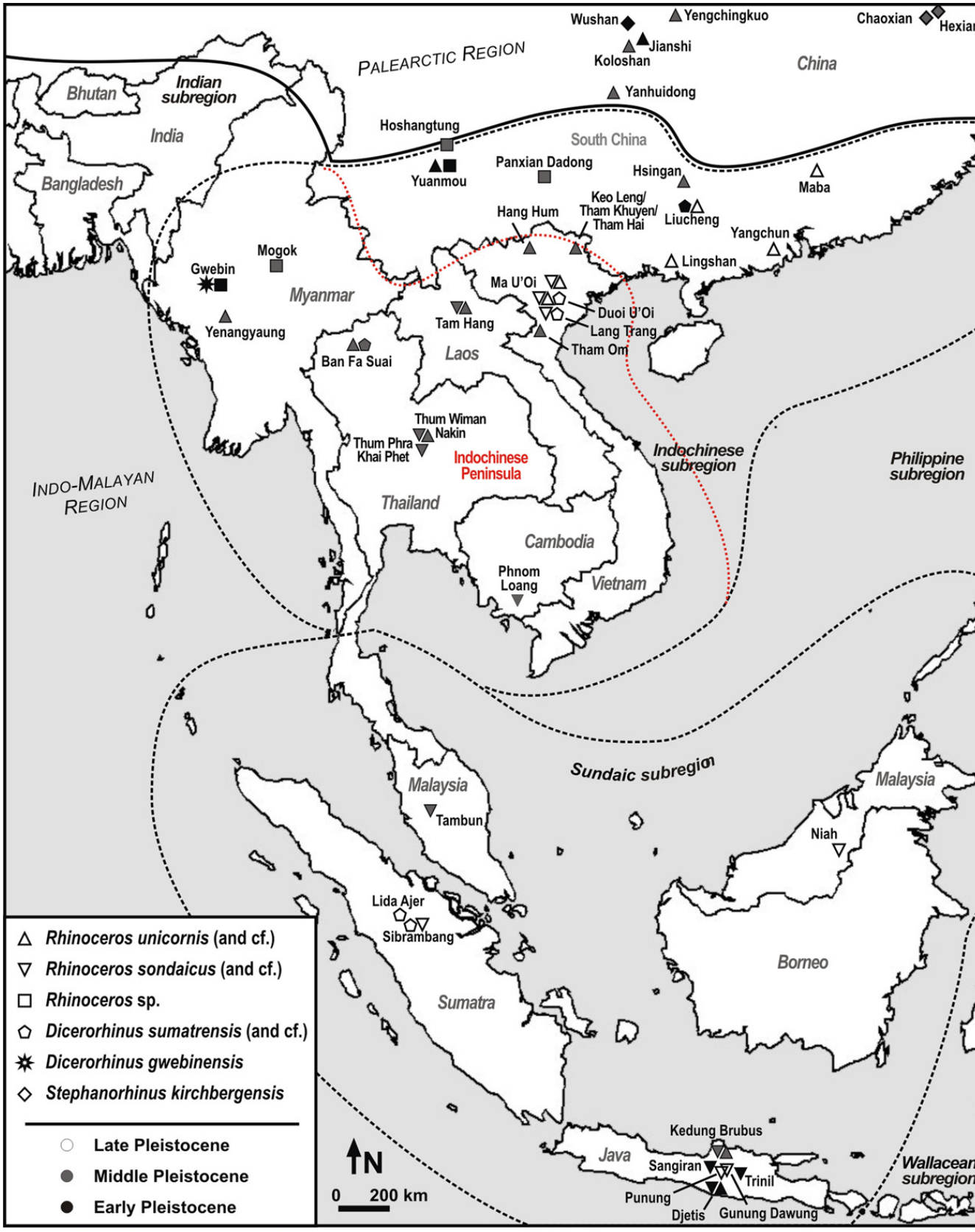
Wushan
Yengchingkuo
Chaoxian
Hexian
Jianshi
Koloshan
PALEARCTIC REGION
China
Bhutan
Indian subregion
India
Yanhuidong
Hoshangtung
South China
Bangladesh
Yuanmou
Panxian Dadong
Hsingan
Maba
Keo Leng/
Tham Khuyen/
Tham Hai
Liucheng
Hang Hum
Yangchun
Mogok
Gwebin
Lingshan
Ma U'Oi
Myanmar
Duoi U'Oi
Lang Trang
Tham Om
Tam Hang
Yenangyaung
Ban Fa Suai
Laos
Thum Wiman
Nakin
Thum Phra
Khai Phet
Indochinese Peninsula
Indochinese subregion
Philippine subregion
INDO-MALAYAN REGION
Thailand
Cambodia
Phnom Loang
Vietnam
Sundaic subregion
Malaysia
Tambun
Malaysia
Niah
Lida Ajer
Sibrambang
Borneo
Sumatra
Rhinoceros unicornis (and cf.)
Rhinoceros sondaicus (and cf.)
Rhinoceros sp.
Dicerorhinus sumatrensis (and cf.)
Dicerorhinus gwebinensis
Stephanorhinus kirchbergensis
Late Pleistocene
Middle Pleistocene
Early Pleistocene
N
0 200 km
Kedung Brubus
Java
Sangiran
Trinil
Wallacean subregion
Punung
Djetis
Gunung Dawung

Fig. 3.

Colbert, 1935; Khan, 1971; Matthew, 1929; Nanda, 2002). *P. platyrhinus* is endemic to the Indian subregion; there is no record of it in other Indo-Malayan subregions or in the Palearctic region.

3. Indochinese rhinocerotid assemblages through time in relation to neighbouring faunas

3.1. Early Pleistocene [2.588–0.781 Ma]

The Early Pleistocene period in the Indochinese subregion is poorly documented (Fig. 3); the only recognized rhinocerotids are *Dicerorhinus gwebinensis* and *Rhinoceros* sp. from Gwebin, Myanmar (Upper Irrawaddy beds; Zin-Maung-Maung-Thein et al., 2008), *D. sumatrensis* from the Liucheng *Gigantopithecus* Cave in South China (Tong and Guérin, 2009), and the bispecific assemblage [*Rhinoceros unicornis* ("*R. sinensis*") + *R.* sp.] from Yuanmou, South China (Tong, 2000). The assemblages [*Punjabitherium platyrhinus* + *R. unicornis*] and [*R. unicornis* + *R. sondaicus*] characterize the Indian subregion (Himalayan foothills; Nanda, 2002) and the Sundaic subregion (Djetis, Java; van den Bergh et al., 2001), respectively. *R. sondaicus* occurs also in Sangiran and Trinil, Java (Fig. 3; van den Bergh et al., 2001).

Central and northern China (Palearctic region) show a distinct rhinocerotine fauna, with *R. unicornis* ("*R. sinensis*"; < 30°N), *Stephanorhinus kirchbergensis* (between 30° and 40°N), and *Coelodonta nihewanensis* (> 30°N; Tong, 2000, 2001; Tong and Moigne, 2000). The assemblage [*C. nihewanensis* + *D. kirchbergensis*] is restricted to the Early Pleistocene of central eastern China (Tong, 2000).

3.2. Middle Pleistocene [0.781–0.126 Ma]

Compared to the Early Pleistocene, the middle Pleistocene period – especially the late middle Pleistocene – provides a much better fossil rhinocerotid record in Indochina (Fig. 3). All three recent rhino species occur in the Indochinese Peninsula, with *R. unicornis* (Yenangyaung, Myanmar; Hang Hum, Tham Om, Keo Leng, Tham Khuyen, and Tham Hai, Vietnam), *R. sondaicus* (Thum Phra Khai Phet, Thailand; Phnom Loang, Cambodia), both of them (Thum Wiman Nakin, Thailand; Tam Hang, Laos), or the assemblage [*R. unicornis* + *D. sumatrensis*] as in Ban Fa Suai, Thailand (Bacon et al., 2004, 2006, 2008a, 2008b; Tougard, 2001; Zeitoun et al., 2005). *R.* sp. is mentioned in Mogok Cave, Myanmar (Fig. 3).

In adjacent areas, *R. unicornis* occurs in South China (Hsingan) and central eastern China (Yanhuidong, Koloshan, Yengshingkuo), while *S. kirchbergensis* is restricted to central eastern China (e.g., Chiaoxian and Hexian; Fig. 3), and *C. antiquitatis* to northeastern China (Bacon et al., 2008b; Tong, 2000). Accordingly, the only Middle Pleistocene bispecific rhinocerotid assemblage in China consists of [*S. kirchbergensis* + *C. antiquitatis*], between 30°N and 40°N (Tong, 2000; Table 1, Fig. 1). The early Middle Pleistocene period coincides with the last occurrence of *P. platyrhinus* in the Indian subregion while *R. unicornis* is common throughout the Middle Pleistocene in the same area (Nanda, 2002). The Middle Pleistocene of the Sundaic subregion only yields *R. sondaicus* (Tambun, Peninsular Malaysia; Fig. 3) and the assemblage [*R. unicornis* + *R. sondaicus*] in Kedung Brubus, Java (Fig. 3; Bacon et al., 2008b; Hooijer, 1946, 1949).

3.3. Late Pleistocene [0.126–0.010 Ma]

Only three Vietnamese localities with rhinocerotids document the Late Pleistocene interval (Fig. 3). All of them yield distinct rhinocerotid assemblages involving recent species: [*R. sondaicus* + *D. sumatrensis*] in Lang Trang, [*R. unicornis* + *R. sondaicus*] in Ma U'Oi, and [*R. unicornis* + *R. sondaicus* + *D. sumatrensis*] in Duoi U'Oi (Bacon et al., 2006, 2008b). Aside from the Indochinese Peninsula, *R. unicornis* occurs in South China (Fig. 3), as well as in the Indian subregion (India, Sri Lanka, and Pakistan; Chauhan, 2008; Nanda, 2002). The assemblage [*S. kirchbergensis* + *C. antiquitatis*], first appearing in the early Middle Pleistocene of central eastern China, persists during the Early and Middle-Late Pleistocene in the same area (Tong, 2000). *C. antiquitatis* gets more and more documented in the Latest Pleistocene of northeastern China (Tong, 2000, 2004; Tong and Moigne, 2000). *R. sondaicus* is the only rhinocerotid species reported in the Late Pleistocene of Java (Punung and Gunung Dawung; Fig. 3) and Malaysian Borneo (Niah cave; Bacon et al., 2008b). *D. sumatrensis* occurs in Sumatra at Lida Ajer and Sibrambang (Fig. 3); it co-occurs with *R. sondaicus* in Sibrambang (Bacon et al., 2008b).

3.4. Holocene and recent times [0.010 Ma–Present]

The Holocene rhinocerotid record consists only of recent species in the Indo-Malayan region (Corbet and Hill, 1992; Nowak, 1999) and eastern China (e.g., Dongshan and Xiawanggang localities; Fig. 2; Rookmaaker, 2006; Tong, 2000; Wang et al., 1993). *R. unicornis* is the northernmost and westernmost species, with a range encompassing the Himalayan Foothills (Indian subregion) but excluding the Indochinese subregion (Fig. 2). *R. sondaicus* occurs throughout the Indochinese Peninsula and the Sundaic subregion, including the Loang Spean Neolithic site, in western Cambodia (Guérin and Mourer, 1969); the Javan rhino

Fig. 3. Distribution map of rhinocerotids in the Pleistocene of southern Asia. Based on data from Bacon et al. (2004, 2006, 2008a, 2008b), Beden et al. (1972), Bouteaux et al. (2007), Hooijer (1946, 1949), Joordens et al. (2009), Louys and Meijaard (2010), Louys et al. (2007), Patte (1928), Zin-Maung-Maung-Thein et al. (2008), Tong (2000, 2001), Tong and Moigne (2000), Tong and Guérin (2009), Tougard (2001), van den Bergh et al. (2001), Zeitoun et al. (2005) and Zhu et al. (2003).

Fig. 3. Carte de répartition des rhinocérotidés dans le Pléistocène d'Asie du Sud. Fondé sur des données de Bacon et al. (2004, 2006, 2008a, 2008b), Beden et al. (1972), Bouteaux et al. (2007), Hooijer (1946, 1949), Joordens et al. (2009), Louys et Meijaard (2010), Louys et al. (2007), Patte (1928), Zin-Maung-Maung-Thein et al. (2008), Tong (2000, 2001), Tong et Moigne (2000), Tong et Guérin (2009), Tougard (2001), van den Bergh et al. (2001), Zeitoun et al. (2005) and Zhu et al. (2003).

Table 1
Biogeographical and biochronological distribution of Pleistocene and Holocene rhinocerotids in the Indochinese Peninsula ("Indochina") and adjacent areas. Fossil taxa are indicated by (†). E, early; L, late; M, middle; Pleist., Pleistocene; Plioc., Pliocene. Based on data from Bacon et al. (2004, 2006, 2008a, 2008b), Beden et al. (1972), Bouteaux et al. (2007), Hooijer (1946, 1949), Joordens et al. (2009), Louys et al. (2007), Louys and Meijaard (2010), Rookmaaker (2006), Zin-Maung-Maung-Thein et al. (2008), Tong (2000, 2001, 2004), Tong and Guérin (2009), Tong and Wu (2010), Tougard (2001), van den Bergh et al. (2001), Wang et al. (1993), Zeitoun et al. (2005) and Zhu et al. (2003).

Tableau 1
Répartition biogéographique et biochronologique des rhinocérotidés du Pléistocène et de l'Holocène de la Péninsule indochinoise ("*Indochina*") et des régions adjacentes. Les taxons fossiles sont indiqués par (†). E, inférieur; L, supérieur; M, moyen; Pleist., Pléistocène; Plioc., Pliocène. Fondé sur des données de Bacon et al. (2004, 2006, 2008a, 2008b), Beden et al. (1972), Bouteaux et al. (2007), Hooijer (1946, 1949), Joordens et al. (2009), Louys et al. (2007), Louys et Meijaard (2010), Rookmaaker (2006), Zin-Maung-Maung-Thein et al. (2008), Tong (2000, 2001, 2004), Tong et Guérin (2009), Tong and Wu (2010), Tougard (2001), van den Bergh et al. (2001), Wang et al. (1993), Zeitoun et al. (2005) et Zhu et al. (2003).

Taxon	Region	Subregion	Area	Age/Interval
Rhinoceros unicornis	Indo-Malayan	Indochinese	Indochina	M-L Pleist.
			South China	E-L Pleist.
		Sundaic	Java	E-M Pleist.
		Indian	Himalayan foothills	E Pleist.-Recent
			Sri Lanka	L Pleist.
		Philippine	Luzon	?Pleist. ("*R. philippinensis*")
	Palearctic	Eastern	eastern China (<30°N)	E-L Pleist. ("*R. sinensis*")
Rhinoceros sondaicus	Indo-Malayan	Indochinese	Indochina South China	M Pleist.-Recent (Vietnam) Holocene
		Sundaic	Java	E Pleist.-Recent
			Peninsular Malaysia	M Pleist.-Holocene
			Malaysia, Sumatra	L Pleist.-Holocene
	Palearctic	Eastern	China	Holocene
Dicerorhinus sumatrensis	Indo-Malayan	Indochinese	Indochina	M Pleist.-Holocene
			South China	E Pleist. + Holocene
		Sundaic	Peninsular Malaysia	Holocene-Recent
			Malaysia + Borneo	Holocene-Recent
			Sumatra	L Pleist.-Recent
	Palearctic	Eastern	eastern China	Holocene
Dicerorhinus gwebinensis (†)	Indo-Malayan	Indochinese	Myanmar	E Pleist.
Stephanorhinus kirchbergensis (†)	Indo-Malayan	Indochinese	South China	E-M Pleist.
	Palearctic	Eastern	eastern central China	E-L Pleist.
		Western	northern Eurasia	M-L Pleist.
Coelodonta nihewanensis (†)	Palearctic	Eastern	northeastern China	E Pleist.
Coelodonta antiquitatis (†)	Palearctic	Eastern	China (>30°N)	M-L Pleist.
		Western	northern Eurasia	(M)-L Pleist.
Punjabitherium platyrhinus (†)	Indo-Malayan	Indian	Himalayan Foothills	L Plioc.-EM Pleist.

(*R. sondaicus*) is the only Holocene rhinocerotid species recorded in Java (Fig. 2). *D. sumatrensis* co-occurs with *R. sondaicus* in the Indian subregion (eastern India), in the western and northern parts of the Indochinese Peninsula (Myanmar, Thailand, and Laos; South China), and in the Sundaic subregion (Peninsular Malaysia and Sumatra; Fig. 2). The Holocene of Borneo yields mostly remains of *D. sumatrensis* (Fig. 2). *D. sumatrensis* is mentioned in the superficial alluvium of Tam Hang, northern Laos (Holocene; Arambourg and Fromaget, 1938).

Assam and Nagaland, in northeastern India, are the only regions which hosted the plurispecific assemblage [*R. unicornis* + *R. sondaicus* + *D. sumatrensis*] during the Holocene period (Fig. 2). The same rhinocerotid assemblage is recorded in Duoi U'Oi (Late Pleistocene, Vietnam; Bacon et al., 2008b), which would point to similar environmental conditions for both areas (subtropical moist forest under a monsoonal climate).

4. Palaeogeography

4.1. Comparison with adjacent areas

South China (Indochinese subregion) – South China's Pleistocene rhinocerotid record is highly similar to the Indochinese record, at least at genus level, with the co-occurrence of the assemblage [small-sized *Dicerorhinus* + *Rhinoceros unicornis*] in the Early Pleistocene, the prominence of *Rhinoceros* in the Middle Pleistocene of both areas, and the absence of large two-horned rhinos such as *Stephanorhinus* and *Coelodonta*, which occurred in central and northern China (Fig. 3; Tong, 2000, 2004; Tong and Moigne, 2000). On the other hand, *R. sondaicus* is common in Middle and Late Pleistocene Indochinese localities whereas it is not attested in South China before the Holocene (Figs. 2 and 3): following Wang et al. (1993) and Rookmaaker (2006), it was widespread and sometimes associated with *D. sumatrensis* south of the Yellow River from Shang up to Qing dynasties (2000 BC–200 AC). The southward retreat and final extinction of *R. sondaicus* and *D. sumatrensis* in China ca. 200 years ago was due to hunting and "the human destruction of their environment" (Rookmaaker, 2006: 104). Only a thorough revision of the wastebasket taxon "*Rhinoceros sinensis*" would allow to state about eventual Pleistocene occurrences of the Javan rhino in South China.

4.2. Comparison with adjacent subregions

Sundaic subregion–The only rhinocerotid recorded in Peninsular Malaysia is *R. sondaicus*, from the late Middle Pleistocene of Tambun (Fig. 3; Tougard, 2001). *R. sondaicus* and *D. sumatrensis* co-occurred in the Late Pleistocene of Sumatra, at Sibrambang (ca. 80–60 ka; Bacon et al., 2008b; Hooijer, 1946; Tougard, 2001). Java yields a much more documented rhinocerotid fossil record, with *Rhinoceros kendengindicus* and *R. sivasondaicus*, from the Pleistocene of Java, being considered junior synonyms of *R. unicornis* and *R. sondaicus*, respectively (Hooijer, 1949; Laurie et al., 1983). In Java, *R. sondaicus* has a continuous range from the Early Pleistocene (Fig. 3; Sangiran, Djetis, and Trinil localities) up to Recent times, whereas *R. unicornis* is restricted to Early and Middle Pleistocene deposits (Fig. 3; Djetis, Kedung Brubus; Hooijer, 1946, 1949; van den Bergh et al., 2001). There is no attested occurrence of *D. sumatrensis* or any other rhinocerotid species but *R. sondaicus* in the Late Pleistocene and the Holocene of Java (Bouteaux et al., 2007; van den Bergh et al., 2001). After Cranbrook and Piper (2007), two postcranial bones found in cave deposits attest to the presence of *R. sondaicus* in the Latest Pleistocene (Niah, ca. 14 ka; Fig. 3) and the Holocene (Madai, ca. 4 ka; Fig. 2) of Borneo. Reis and Garong (2001) do not mention any rhinocerotid in the Late Pleistocene-Early Holocene of the Palawan Island (Philippines, Sundaic subregion; Fig. 1).

Philippine subregion – Aside from the jaw of *Rhinoceros philippinensis* (unknown age, Luzon; Reis and Garong, 2001; Tougard, 2001; von Koenigswald, 1956), other unidentified rhino specimens from the Philippines Archipelago were found in Mindanao (Fig. 1); all of them are human-related or they were found without any stratigraphical control (Bautista, 1995; Reis and Garong, 2001).

Wallacean subregion – To our knowledge, there is no rhinocerotid record (fossil/recent) in the Wallacean subregion.

Indian subregion–By contrast, the Pleistocene and Holocene deposits of the Indian subregion yield many rhinocerotine rhinocerotid remains, sometimes through bispecific assemblages. The upper Siwaliks of India and Pakistan mostly yield *R. unicornis*, under the names *Rhinoceros sivalensis* and *R. palaeindicus*, with a virtually continuous fossil record from the Late Pliocene (ca. 3.3 Ma) up to recent times in northern Pakistan and northern India (Dennell et al., 2006; Nanda, 2002). In the Latest Pliocene-early Middle Pleistocene interval (2.6-0.6 Ma) of the same area, *R. unicornis* co-occurs with *Punjabitherium platyrhinus* (Colbert, 1935; Khan, 1971; Matthew, 1929; Nanda, 2002). *Rhinoceros* was also common throughout the Pleistocene of peninsular India and in the Late Pleistocene of Sri Lanka, under diverse specific names (Chauhan, 2008; Deraniyagala, 1992; Hooijer, 1946).

4.3. Comparison with adjacent regions

Oceanic region – Neither fossil nor recent rhinocerotid is recorded in the Oceanian region, with the notable exception of a P1 unambiguously referable to the western Eurasian Miocene hornless teleoceratine *Brachypotherium brachypus*, found by gold diggers in New Caledonia in the 19th century. This tooth, probably used as a jewel by a French deported convict and subsequently lost by the Diahot River, was (mis)identified as documenting an in situ diprodontid marsupial of Australian affinities (*Zygomaturus diahotensis*; Guérin et al., 1981).

Palearctic region (northern China-Mongolia) – *Rhinoceros sinensis* (= *R. unicornis*) was recognized in dozens of southern Chinese localities, as well as in the late Early to early Middle Pleistocene faunas of Taiwan (Otsuka, 1984) and Japan (Kamei, 1981; van den Bergh et al., 2001). *Coelodonta* was abundant throughout the Pleistocene epoch in most areas of the Palearctic region, including North and central China (north of 30°N; Tong, 2000, 2001). The Middle Pleistocene of

the Palearctic region also hosted the gigantic two-horned *Stephanorhinus kirchbergensis* (van der Made, 2010). The forest rhino (*S. kirchbergensis*) and the woolly rhino (*C. antiquitatis*) co-occurred in mid-latitudes of eastern China (between 30° and 40°N; Tong, 2000) but they are not recorded south of 30°N, most probably for climatic and environmental reasons (Tong, 2004).

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