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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.

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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 (Tougaard, 2001; Tougaard 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; Tougaard, 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. siva-sondaicus*; 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; Tougaard, 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-

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