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A new rhinoceros clade from the Pleistocene of Asia sheds light on mammal dispersals to the Philippines

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Running title A Pleistocene rhinoceros from Asia

Abstract

Rhinoceroses are among the most endangered mammalian species today. Their past diversity is well documented from the Eocene onward, although their evolutionary history is far from being fully understood. Here, we elucidate the systematic affinities of a Pleistocene rhinoceros species represented by a partial skeleton from 709±68 ka archaeological deposits in Luzon Island, Philippines. We perform a comprehensive phylogenetic analysis including all living species and a wide array of extinct rhinocerotid species. We confirm the early split between Elasmotheriinae and Rhinocerotinae at c 35.5 Ma and constrain the divergence between recent Asian and African rhinoceroses at c 24 Ma, with contrasting phenotypic evolutionary rates in Diceroti and Rhinoceroti. Dental features reveal the existence of an unsuspected Asian Pleistocene clade, referred to as *Nesorhinus* gen. nov. It includes the

rhinoceros from the Philippines and another extinct species from Taiwan, *N. hayasakai*. *Nesorhinus* is sister group to a cluster comprising *Dicerorhinus* and *Rhinoceros*. Our phylogenetic results strongly suggest an island-hopping dispersal for *Nesorhinus*, from Asian mainland towards Luzon via Taiwan by late Miocene times or later, and Pleistocene dispersals for representatives of *Rhinoceros*. *Nesorhinus philippinensis* would be the first perissodactyl species supporting the island-rule hypothesis, with decreased body weight and limb-bone robustness.

ADDITIONAL KEYWORDS: Island biogeography – island fauna – evolutionary trends – morphological phylogenetics – morphological systematics – Mammalia

INTRODUCTION

Past dispersal patterns of terrestrial vertebrates towards and within the Philippine archipelago remain a widely debated topic. As none of these islands has ever been connected to mainland Southeast Asia, even during the most severe Pleistocene sea level drops (Past Interglacials Working Group of PAGES, 2016), the question of ancient island hopping is still controversial (Braches & Shutler, 1984; Heaney, 1985; Bellwood, 2013; Morwood, 2014; Suraprasit *et al.*, 2016). Historically, three major Pleistocene dispersal routes to the islands of Southeast Asia have been considered: one along the exposed Sunda Shelf from the Siwaliks during the Early–Middle Pleistocene with extinct genera like *Stegodon* (the Siva-Malayan route), a second from China via Thailand to Indonesia with extant genera like *Pongo* in the Late Pleistocene (the Sino-Malayan route) and the third across sea barriers from Taiwan to the Philippines and elsewhere to the South and to the West. This latter hypothesis was favoured as the main route to the Wallacean islands by von Koenigswald (1956) while other scholars preferred the Sino-Malayan route with Palawan Island as the main gate to the Philippines (de Terra *et al*., 1941; Grooves, 2001). Hooijer (1951, 1958) suggested that the two routes might have acted together but not necessarily at the same time.

Recent phylogenetic studies have investigated (pre-)Pleistocene dispersals of modern land vertebrates to the pristine Philippine Islands, by a time the archipelago had not acquired its present shape and configuration yet (Brown *et al.*, 2013 and references therein). While some clades of frogs (Blackburn *et al.*, 2010) or geckos (Siler *et al.*, 2012) have benefited from the drifting of Palawan terrane from the South China's coast to its present position, other clades of amphibians (Brown & Guttman, 2002; Evans *et al.*, 2003) and birds (Jones & Kennedy, 2008) have probably migrated from the Sunda shelf fringe, either on the north from Borneo to Palawan and Mindoro or on the south via Sulu for some others (Jones & Kennedy, 2008). Among the four hypothetical gateways to the Philippines (Dickerson, 1928; Brown *et al*., 2003), the northern route from Taiwan to Luzon seems for the moment to have only been active for shrews (Esselstyn & Oliveros, 2010). Interestingly, phylogeography of termites evidences a successful West-East rafting dispersion over the South China Sea from Thailand and through Vietnam to the Philippines between 1.09 and 0.42 Ma (Singham *et al.*, 2017). These studies are generally underestimating the potential contribution of Pleistocene (and pre-Pleistocene) dispersals to the modern biodiversity of Island Southeast Asia. The scarcity of the fossil remains on those oceanic islands can be a reason for this. In the vicinity of Metro Manila, geologists from the National Institute of Geological Sciences reported, in

collaboration with German palaeontologists, on the recovery of giant land tortoise they named *Manouria sondaari* (Karl & Staesche, 2007; Rhodin *et al.*, 2015). Rhodin *et al*. (2015) nevertheless reattributed these fossils to *Megalochelys sondaari*. So far, this uncertainty regarding its systematics, which is most certainly related to its fragmentary preservation, prevents any phylogenetic interpretation. Von Koenigswald (1956) described the elephantoid *Stegodon luzonensis* based on a fragment of a mandible containing a broken last molar found within the Guadalupe tuff covering the Manila Basin area and given to him by the archaeologist H. Otley Beyer. This species is better described by additional surface-collected specimens by de Vos & Bautista (2001). The few measurable teeth at hand of this endemic taxon to the Philippines are smaller than the Javanese species *S. trigonocephalus* and the Chinese *S. orientalis* (de Vos & Bautista, 2001: 6-7). De Vos & Bautista (2001) add that the M3 of *S. luzonensis* is rather small, although it is larger than the ones of the dwarf *S. sompoensis* from Sulawesi, the small *S. sondaari* from Flores, and *S. timorensis* from East Timor. This combination of unique dimensional features and the limited number of well-preserved fossils makes difficult to link *S. luzonensis* to any other taxa at the moment. At last, Ingicco *et al.* (2017) noted the presence of the extinct suid *Celebochoerus* on Luzon Island, only known elsewhere on the southern island of Sulawesi although in a different form, suggesting a possible faunal exchange between those two islands but without being capable of knowing towards which direction.

A partial skeleton of *Rhinoceros philippinensis* von Koenigswald, 1956 (Figure S1) was recently discovered at Kalinga site in Northern Luzon from a 709±68 ka archaeological layer. Stone tools were recovered together with the skeleton and several skeletal elements exhibited evidence of butchery (Ingicco *et al.*, 2018, 2020). This early Middle Pleistocene individual considerably adds to the knowledge of Philippine rhinocerotid species, as its hypodigm was restricted to a few fossil teeth without any clear stratigraphic context, recovered from different islands in the archipelago (von Koenigswald, 1956; Bautista, 1995). The completeness of the specimen allows us to test the different phylogenetic and subsequently palaeobiogeographical scenarios at hand.

In order to constrain the taxonomical assignment and phylogenetic affinities of *R. philippinensis* and then to test potential dispersal pathways of rhinos toward the Philippine archipelago, a broad morpho-anatomical comparison was undertaken within Rhinocerotidae and a parsimony analysis was performed, allowing for discussing further the systematics and biogeographical history of rhinocerotines.

MATERIAL AND METHODS

Phylogenetic relationships were retrieved using a data matrix implemented from a proven matrix focusing on Rhinocerotidae (Antoine, 2002; Antoine *et al.*, 2010; Becker *et al.*, 2013; see Supplementary Information for details). It encompasses 278 cranio-mandibular, dental, and postcranial characters scored on 31 living and extinct perissodactyl species. Only six multistate characters were considered as non-additive (characters 66, 87, 95, 129, 177, and 263). All other multistate characters were treated as additive (see Character list in SI). Aside from outgroups (four perissodactyl species), the branching group (Antoine, 2002) consists of seven representatives of extinct rhinocerotid groups, including Teleoceratina (hippo-like rhinocerotines), Aceratheriini (hornless rhinocerotines), and an early offshoot of Elasmotheriinae (*Subhyracodon occidentalis* (Leidy, 1851)). The ingroup includes 20 terminals from the last 20 million years and consensually assigned to Rhinocerotina, i.e. the subtribe including all recent rhinoceroses and their extinct kin (see Supporting Information).

Detailed information about the morpho-anatomical characters scored and terminal taxa included in the parsimony analysis are available in Supporting Information. The program PAUP 4.0a.158 (Swofford, 2002) was used for reconstructing the most parsimonious trees. Ages for nodes in the chronologically-constrained phylogenetic tree were obtained using the approach of Brusatte *et al.* (2008), as implemented in the paleotree package (Bapst *et al.*, 2012) in R 4.0.3 (R core development team, 2020), with stratigraphical ranges as available in the NOW Database (Table S2; The NOW Community, 2020). As a prior, the first splitting event in the tree was set to 60 Ma (mean value for Perissodactyla/Ceratomorpha; Foley *et al.*, 2016) and the root of the tree was resolved using the APE package (Paradis *et al.*, 2004). Six distinct historical biogeographical models were evaluated in BioGeoBEARS package in R (Matzke, 2013; Massana *et al.*, 2015) using eight basic spatial ranges, coinciding with the geographical areas of terminal taxa included in the phylogenetic and biogeographical analyses (Americas, Afro-Arabia, Europe + Mediterranean, Central Asia, South and Southeast Asia, Indonesia, Taiwan, Philippines). Historical spatial ranges were allowed to cover from 1 to 8 areas, which in turn resulted in 163 potential ancestral states.
Body mass was estimated using regressions based either on dental (Legendre, 1989; Fortelius & Kappelman, 1993) and postcranial dimensions (Tsubamoto, 2012). Height at the shoulder was estimated by comparison with limb bones of recent rhinoceros species (Guérin, 1980) and further detailed in Supporting Information.

RESULTS

PHYLOGENETIC RELATIONSHIPS WITHIN RHINOCEROTIDAE

The first analysis, with 31 terminal taxa, recovered two equally most parsimonious trees (1321 steps each), with "*Rhinoceros*" Yanliang-Liucheng being sister taxon to either the (*R. philippinensis, R. sinensis hayasakai*) clade or to the (*Rhinoceros*, *Dicerorhinus*) clade (Fig. S2). As i) we cannot discard the possibility that "*Rhinoceros*" Yanliang-Liucheng still be a chimaera (we were not able to observe directly the referred specimens) and ii) this issue falls beyond the scope of the present work, we have chosen to remove this terminal taxon from a second analysis, hence restricted to 30 terminal taxa (see SI). In this second analysis, the heuristic search of PAUP 4.0a158 (Swofford, 2002), with ACCTRAN character-state optimization, retrieves a single most parsimonious tree (1315 steps; CI=0.2821; RI=0.4858), with exactly the same topology for all 30 taxa than in the previous analysis. We will focus on this topology detailed in the next paragraphs (Fig. 2).
Strictly speaking, monophyly of Rhinocerotidae is not retrieved, due both to the widely-undersampled Eocene–Oligocene rhinocerotid taxonomic diversity and the use of two early-diverging rhinocerotids as outgroups in the present analysis (*Trigonias osborni* Lucas, 1900 and *Ronzotherium filholi* Osborn, 1900; Figure 2). Nevertheless, suprageneric relationships among Rhinocerotidae in the chronologically-constrained tree strictly conform to those of previous comprehensive analyses (Antoine, 2003; Becker *et al.*, 2013), with a basal split between Rhinocerotinae and Elasmotheriinae (c 35.5 Mya), Aceratheriini and Rhinocerotini being sister taxa among Rhinocerotinae (both tribes split c 29.5 Mya), and Teleoceratina closely related to Rhinocerotina within Rhinocerotini and splitting c 27 Mya.
In the most parsimonious tree, two major clades diverge c 24 Mya among Rhinocerotina. The first one, strongly supported (Bremer Support [BS] > 5, 11 unambiguous synapomorphies [US]), coincides with Diceroti, an informal group of two-horned species from Eurasian and African landmasses with *Dihoplus schleiermacheri* (Kaup, 1832), "*Dihoplus*" *pikermiensis* Toula, 1906, *Stephanorhinus etruscus* (Falconer, 1868),

"*Stephanorhinus*" *megarhinus* (de Christol, 1835), *Coelodonta antiquitatis* (Blumenbach, 1799), *Ceratotherium neumayri* (Osborn, 1900), *Ceratotherium simum* (Burchell, 1817), and *Diceros bicornis* (Linnaeus, 1758) diverging successively. As revealed by the high number of derived morpho-anatomical traits at each node (between 8 and 18), Diceroti have experienced fast phenotypical evolution (Figure S3), with staggered splits ranging the middle–late Miocene time interval (c 15–8 Mya; Figure 2). The second clade only gathers Eurasian species. In terms of taxonomical composition, it fully matches the Rhinoceroti. The Miocene clade *Lartetotherium-Gaindatherium* is the first offshoot, further having close affinities with living Asian rhinoceroses (see also Antoine, 2003; Antoine *et al.*, 2010). It is sister group to a clade encompassing *Dicerorhinus* (with *Dicerorhinus sumatrensis* (Fischer, 1814) and *Dicerorhinus fusuiensis* Yan *et al.*, 2014; see Supplementary Information for further details) and all other species historically assigned to *Rhinoceros*. Rhinoceroti are supported by six US, and a BS (2) lower than in all surrounding nodes. All representatives of Rhinoceroti are much more conservative phenotypically than Diceroti, as revealed by a twice as low number of apomorphies per node (ranging from 3 to 13; Figure S3). The resulting topology for extant rhinos places the African rhinoceroses (*Diceros bicornis* and *Ceratotherium simum*) as a sister clade to Asian rhinoceroses (*Dicerorhinus sumatrensis*, plus *Rhinoceros unicornis* Linnaeus, 1758 and *Rhinoceros sondaicus* Desmarest, 1822). This topology matches that of the "geographical hypothesis", supported by most recent molecular phylogenies (Yuan *et al.*, 2014; Welker *et al.*, 2017; Kosintsev *et al.*, 2019). It differs from the "horn hypothesis" in the position of the two-horned Sumatran rhinoceros (*Dicerorhinus sumatrensis*), usually more closely related to two-horned African rhinoceroses than to the one-horned Asian *Rhinoceros*, as suggested by most morphology-based phylogenetic analyses (Antoine *et al.*, 2010; Becker *et al.*, 2013; Pandolfi *et al*., 2019), but also by a recent proteomic analysis encompassing living rhinoceroses and representatives of *Coelodonta* and *Stephanorhinus* (Cappellini *et al.*, 2019). This original result – at least on morpho-anatomical grounds – probably results from the inclusion of a more comprehensive taxonomical sample among Rhinocerotina than in any former analyses. The current sample is likely to minimise topologic biases such as long-branch attraction, due to the very low relictual diversity of rhinoceroses today.

More strikingly, a very robust clade (6 US; BS > 5) includes *Rhinoceros philippinensis* and *R. sinensis hayasakai* Otsuka & Lin, 1984 (from the Early and Middle Pleistocene of Taiwan). This bispecific clade is well distinct from its sister taxon, the *Dicerorhinus-Rhinoceros* clade (*DR*c). The *DR*c is much less supported (6 US; BS = 2), essentially on the basis of postcranial features (Table S1). All other representatives of *Rhinoceros* form a monophyletic group, with *R. sondaicus* as a first offshoot, and then *R. sinensis* Owen, 1870, *R. unicornis*, *R. kendengindicus* Dubois, 1908 and *R. platyrhinus* Falconer & Cautley, 1846-1849branching successively (Figure 2). The two first nodes are strongly supported (13, then 8 US), mostly on postcranials; BS > 5). This topology further attests to the singularity of the Javan rhinoceros, *Rhinoceros sondaicus*, as it is excluded from a compound of large-bodied extinct species either closely related to or considered as junior synonyms of the Indian rhinoceros (Antoine, 2012; Pandolfi & Maiorini, 2016), i.e., *Rhinoceros sinensis*, *R. platyrhinus*, and *R. kendengindicus*, the phylogenetic relationships of which are fully solved here (Figure 2; Supporting Information). To our knowledge, these terminals are here included for the first time into a formal phylogenetic analysis. As a result, and even if such a taxonomical revision falls beyond the scope of the current work, all of them would be valid species, mostly diagnosed by dental and, to a lesser extent, cranial features (Table S1). The chronologically-

constrained analysis suggests that intrageneric splits for *Rhinoceros* would have occurred in Pliocene times, with multiple sub-coeval speciation events until the Early Pleistocene (c 3 Mya; Figure 2). *Dicerorhinus* as a clade includes *Dicerorhinus sumatrensis* (type species) and *Dicerorhinus fusuiensis* (formerly described as *Rhinoceros fusuiensis*, from the Early Pleistocene of South China and Myanmar (Yan *et al.*, 2014; Tong & Guérin, 2009); see Supporting Information), with a strong support (8 US; BS = 4). This specific split is hypothesised to have occurred in the latest Miocene (c 6 Mya), i.e. long after the earliest unambiguous occurrence of *Dicerorhinus* in the lower Siwaliks of Pakistan (Heissig, 1972; Antoine *et al.*, 2013; Antoine, in press).

According to the topology of the most parsimonious tree and in order to maintain *Rhinoceros* as a monophyletic genus (further diagnosed by 13 cranial and postcranial features; SI), we propose to consider the clade formed by *R. philippinensis* and *R. s. hayasakai* as a distinct extinct genus among Rhinocerotina, here named *Nesorhinus* (see next section). This genus is characterised by six US (Figure 3; roots fully isolated on cheek teeth, crista absent on P3, protocone constriction always absent and posterior half of the ectoloph concave on M1-2, trigonid angular in occlusal view on lower cheek teeth, and posterior supraglenoid tubercle convex and salient on scapulae), among which four reversals (see Table S1). The type species is *Nesorhinus philippinensis* (Figure 3A–D, 3I, 3J), diagnosed by four dental autapomorphies (crochet always multiple on P2-4, metaloph transverse on P2, external groove reaching the neck on lower cheek teeth and labial cingulum usually absent on lower premolars), the latter feature being a reversal. *Nesorhinus hayasakai* (Figure 3E–H, 3K) possesses three dental autapomorphies (crochet always present on P2-4, lingual cingulum always absent on upper molars, and trigonid forming an acute dihedron in occlusal view on lower cheek teeth). The divergence between *N. philippinensis* and *N. hayasakai* is considered to have occurred by late Miocene times (c 7 Mya; Figure 2).

The taxonomic composition of *Nesorhinus* clade and the preferred timing of the corresponding intrageneric split offer a unique opportunity for discussing the biogeographical hypotheses that would explain the occurrence of rhinos in the Pleistocene deposits of the Philippine Archipelago.

SYSTEMATIC PALAEONTOLOGY

Placentalia Owen, 1837
Perissodactyla Owen 1848
Rhinocerotidae Gray, 1821
Rhinocerotina Gray, 1821
Nesorhinus gen. nov.
(Figure 3)

Etymology. From the ancient Greek *nẽsos* (*νῆσος*, island), and the suffix *-rhinus* (nose), frequently used for designating rhinocerotid genera.

Type species. *Nesorhinus philippinensis* (von Koenigswald, 1956). See SI for further details.

Referred species. *Nesorhinus hayasakai* (Otsuka & Lin, 1984).

Diagnosis. Medium-sized rhinocerotines, characterised by roots fully isolated on upper cheek teeth, a crochet usually present on P2-4, a crista absent on P3, a protocone constriction

always absent and a posterior half of the ectoloph concave on M1-2, a trigonid angular in occlusal view on lower cheek teeth, and a posterior supraglenoid tubercle convex and salient on the scapula. Differing from representatives of both *Dicerorhinus* and *Rhinoceros* in having no cement on cheek teeth, a protocone joined to the ectoloph on P2, a proximal border of the third metatarsal sigmoid in anterior view, and intermediate reliefs high and sharp on metapodials. Distinct from *Rhinoceros* in possessing a protocone and a hypocone equally developed on P2 and in having no anterior trochlear notch on the astragalus. Further differing from *Dicerorhinus* in possessing a V-shaped lingual opening of the posterior valley on lower premolars.

Geographic and stratigraphic range. Early and Middle Pleistocene of Luzon Island, Philippines, and of Taiwan Island (von Koenigswald, 1956; Ingicco *et al.*, 2018; Otsuka & Lin, 1984).

Description. See morpho-anatomical characters in Supporting Information.
Even if nasal or frontal bones are not recognised in the current hypodigm of *N. philippinensis* and *N. hayasakai*, *Nesorhinus* was most probably one-horned, i.e. with a nasal horn and no frontal horn, as inferred by the topology of the consensus tree: this is the ancestral condition in Rhinocerotina and Rhinoceroti, retained in *Rhinoceros*. According to the most parsimonious topologies, a frontal horn was acquired independently in Diceroti and *Dicerorhinus sumatrensis* (and perhaps also in *D. fusuiensis*) which is in full agreement with the most recent genomic phylogenies.
Body mass, as predicted from regressions on upper and lower teeth, but also on limb bones, with consistent results, is estimated at 998–1,670 kg for *Nesorhinus* (Table S5). *Nesorhinus philippinensis*, documented at Kalinga site by at least two individuals very similar in size, was the smallest and lightest species. Body weight ranged between 1,025–1,185 kg (mean: 1,103 kg) based on dental predictors and 998–1,140 kg (mean: 1,069 kg) based on postcranial predictors, which falls between the known ranges of the Sumatran and Javan rhinos, the smallest of the extant rhinos. *Nesorhinus hayasakai* was somewhat heavier, with more variable weight estimates based on teeth (mean: 1,263 kg; range: 1,018–1,670 kg; Table S3), and a slightly heavier estimate based on radius (1,306 kg; Table S5). A shoulder height of c 1.23-1.30 m was estimated for *N. philippinensis* through comparison of forelimb dimensions with recent rhinos (mean: 1.26 m). This estimate is similar to the smallest Javanese rhino individuals and to average Sumatran rhino individuals (Tables S6, S7). A marginally higher stature (c 1.31 m) is inferred for *N. hayasakai* (see Tables S6, S7). Nevertheless, comparison of skeletal proportions shows that *N. philippinensis* was particularly slender-limbed, with the notable exception of the scapula and the metapodials. Its gracility indices are closely similar to those of the most gracile living rhinoceros, i.e., *Dicerorhinus sumatrensis* (Table S8; Figures S5, S6). Within *Nesorhinus*, *N. philippinensis* was also much slenderer-limbed than *N. hayasakai*, which is further consistent with significantly lighter body mass estimates based on radius (998 vs 1,306 kg, respectively; Table S5). This discrepancy may be related either to inter-individual variability (e.g., sexual dimorphism – although it seems to be quite exaggerated for a rhinocerotine (Guérin, 1980)), or to a secondary adaptation to the unbalanced insular environment of the Philippines (Table S8) with respect to mainland assemblages. Strikingly, the scapula of *N. philippinensis* is neither particularly spatulate nor elongated. Its gracility equals that of *Diceros bicornis* and it is intermediate to the living

Rhinoceros species, while *Dicerorhinus sumatrensis* has by far the most robust scapula (Table S8).

DISCUSSION

BIOGEOGRAPHICAL IMPLICATIONS FOR PAST DISPERSALS OF LAND MAMMALS TO THE PHILIPPINES AND THE INFLUENCE OF INSULARITY

The current phylogenetic analysis (Figure 2) benefits from a broad taxonomic sample, particularly comprehensive for Neogene and Pleistocene-Holocene Asian rhinos with well-constrained spatiotemporal distribution. Moreover, the topology of the most parsimonious tree (Figure 2) can be interpreted in terms of historical biogeographical pattern and timing.

Parsimony, such as the least-cost pathway, in this case the shortest distance from mainland to an oceanic island, is repeatedly considered as the main argument when choosing one dispersion route over another, either passive or active (Field *et al.*, 2007; Robles, 2013), although any longer overseas travel has been proven to be statistically far to be improbable (Antoine *et al.*, 2008, 2010; Dennell *et al.*, 2014). This is why Palawan Island has been consensually viewed until recently as the most probable main gate to the Philippines during the Pleistocene (Porr *et al.*, 2012; Mijares, 2014). Some molecular phylogenies have further supported this hypothesis, although the timing of dispersal for most of them was pre-Pleistocene i.e., before the Philippines geological blocks acquired their present geographical distribution.

Per se, our results would suggest an island-hopping and/or sweepstake dispersal hypothesis for *Nesorhinus*, from the continental Indo-Malayan zoogeographic region (Figure 1) toward Luzon (*N. philippinensis*; known age: c 0.7 Myr) via Taiwan (*N. hayasakai*; considered range: 0.9–0.45 Myr). Accordingly, the current phylogenetic topology formally excludes any contribution from the well-documented Indonesian-sourced rhinos, assigned either to *Dicerorhinus* or to *Rhinoceros* from the Pleistocene of the Sundaic Region, such as *D. sumatrensis*, *R. unicornis*, *R. sondaicus*, or *R. kendengindicus*. Such a conclusion would therefore revive the north to south dispersal pattern to the Wallacean Islands as suggested by von Koenigswald (1956) and reject a dispersion from Borneo through Palawan, as one of the terminal phalanges of the Siva-Malayan and Sino-Malayan routes (Figure 1), a hypothesis favoured by all other scholars since then (Porr *et al.*, 2012; Mijares, 2014), contra Morwood, 2014). Additionally, our phylogeny may further support one other Pleistocene route between India and Java (de Vos & Long, 2001) being retrieved via the phylogenetic relationships of *R. unicornis*, *R. kendengindicus*, and *R. platyrhinus* (Figures 1, 2).

In order to evaluate objectively these hypotheses, we have undertaken historical biogeographical analyses, using BioGeoBEARS package in R (Matzke, 2013; Massana *et al.*, 2015). The model with the best Akaike Information Criterion (AIC) is BAYAREAlike + J (Table S3), in which the ancestral area of (*Nesorhinus* + (*Rhinoceros* + *Dicerorhinus*)) is mainland Asia and the geographical range of the common ancestor of *Nesorhinus philippinensis* and *Nesorhinus hayasakai* is either Taiwan or the Philippine Archipelago, with a subsequent dispersal to the Philippines or to Taiwan, respectively (Figure 4). Owing to the palaeogeographical context of the region as hypothesised for Neogene times (Hall, 2002), the first option (Taiwan toward Philippines) is much more likely to have occurred. Scenarios mostly varied whether founder speciation events were included or not, and the former option was always preferred in terms of AIC. Under that latter assumption, the geographical origin of Taiwanese and Philippine representatives of *Nesorhinus* is much more probably continental South East Asia and/or South Asia than the Sundaic Region (BAYAREAlike+J,

DIVAlike+J, DEC+J). In the absence of founder speciation events, it was found that the ancestor might have had a more widespread distribution in South East Asia before speciating in allopatry, including the Sundaic Region (BAYAREAlike) or not (DEC, DIVAlike). Under the various scenarios examined, origination for Philippine and Taiwanese *Nesorhinus* would therefore be more likely in mainland Asia rather than the Sundaic region, even if the second option is not completely ruled out for one less-supported model (DIVAlike, DIVAlike + J, DEC, or DEC +J). Indeed, wide gaps in the fossil record for these lineages impedes backtracking precisely potential shifts in their past geographical distributions.

Reaching these oceanic islands would require some rafting on floating landmasses (Houle, 1998) for the smaller terrestrial species or some excellent swimming capabilities (Johnson, 1980) for the larger ones such as the rhinos and most certainly a combination of the two for most of the species (Lomolino, 2005). With the notable exception of somewhat sagittally-flattened metapodials, the osteological differences observed on *N. philippinensis* compared to the other species of the genus should not give rise to any functional interpretation. As observed in elephants (van der Geer *et al*., 2016) and hippos (Fisher *et al.*, 2010), swimming abilities are not necessarily related to spatulate scapulae in large living ungulates, especially as the latter animals are bottom-walkers (Coughlin & Fish, 2009). Extant Asian rhinos are all excellent swimmers, capable of crossing large river streams and marine corridors (Hoogerwerf, 1970; Konwar *et al.*, 2009) and we see no reason why representatives of the new genus described here would have not acted the same. Most of Island Southeast Asia is surrounded by back-loop surface currents and the seas surrounding the Philippines are broadly flowing off the archipelago (Figure 1), a situation most likely also present during the glacial periods (Liu *et al.*, 2016). This condition is presumably unfavourable for any successful accidental dispersion. However, winds have been proven to play a main role in sea surface drift of buoys (Houle, 1998; Gästgifvars *et al.*, 2006). Prevailing Southeast Asian winds converge towards the equator and they are therefore mainly blowing to the South around and over the Philippine Islands (Liu *et al.*, 2016). This condition would obviously be helpful for any dispersal in a north-south direction. Therefore, neither the direction of wind and sea surface current nor overseas distances can be used alone to support a specific dispersion route to the Philippines. Swimming over the Luzon Strait for the rhinos does not appear to be an impossible scenario when one considers that similarly-large animals have been observed to swim over tens of kilometres (Johnson, 1980) and that the greatest distance between two of the twelve islands separating Taiwan from Luzon was no more than 57 km during the most severe glacial periods with a sea level drop of ca. 120 m – a condition met during MIS 19 (Past Interglacials Working Group of PAGES, 2016). In good agreement with early occurrences of *Gaindatherium* and *Dicerorhinus* (Antoine *et al.*, 2010; Heissig, 1972), the *Nesorhinus–DR*c split has supposedly occurred by early middle Miocene times (c 15 Mya; Figure 2; SI). *Nesorhinus hayasakai* ranges the c 0.9–0.45 Myr interval in Taiwan and *N. philippinensis* first occurs c 0.7 Mya in Luzon (see above). According to the paleotree model (Fig. 2; Brusatte *et al.*, 2008), the split between *N. hayasakai* and *N. philippinensis* has hypothetically occurred by latest Miocene times (c 7 Mya), a time interval further coinciding with a low sea level (Miller *et al.*, 2020), which may have promoted such an oversea dispersal. Nevertheless, a Pleistocene overwater sweepstake dispersal toward Luzon cannot be fully discarded either for *Nesorhinus* (Figure 1). Whether other species dispersed to the Philippines through the northern route remains to be seen. We can nevertheless note that the absence of any contribution of Sundaic rhinos to the Philippine diversity of perissodactyls recalls what is observed for artiodactyls through

the presence of the suid *Celebochoerus* in Luzon. This highly-island-endemic suid is also known from fossils from Sulawesi Island in the South but is notably absent in the well-known Javanese fossil record to the West (Ingicco *et al*., 2016). Unfortunately, the fragmentary condition of *Celebochoerus* specimens precludes any secure conclusions on the relationship between the two recognised species and the related discussion on its biogeographical implications, for instance whether this north to south dispersal can be extended further to the South from Luzon to Sulawesi. Indeed, the discovery of pre-Pleistocene large mammal fossils in the Philippine Archipelago (including Luzon), Taiwan, or in any Sundaic island would provide considerable insight into this long-lasting enigma.

BODY MASS OF *NESORHINUS* AND ISLAND RULE

The phylogenetically-constrained reconstruction of *Nesorhinus hayasakai* and *N. philippinensis* clearly points to a decreased body mass and robustness in the oceanic island species in the Philippines with respect to mainland rhinoceros' species and its continental island sister species on Taiwan (Tables S8, S9; Figures S6, S7). It appears that *N. philippinensis*, although not dwarf but only of small stoutness like the Sumatran rhino, may follow in some instances the so-called island rule (Foster, 1964) when its relative postcranial robustness, with respect to its mainland and Taiwanese relatives. Notably because perissodactyls are frequently absent from unbalanced faunal communities on oceanic islands (van der Geer *et al.*, 2010; Lomolino, 1985), it is to the best of our knowledge, the very first time that this order of mammals would be positively tested for the island rule. Following the results of our analysis, perissodactyls may add to the list of land mammals affected by this syndrome, which also includes proboscideans (van der Geer *et al.*, 2016), artiodactyls (van der Geer, 2005), rodents (McFarlane *et al.*, 1998; Marivaux *et al.*, 2020), carnivores (Lyras *et al*., 2010), and hominin primates (Bromham & Cardillo, 2007).

CONCLUSIONS

This comprehensive morpho-anatomical phylogeny of Rhinocerotina, the group encompassing all living rhinoceroses and their extinct kin, allows for providing several calibration points for molecular studies among Rhinocerotidae, with a divergence between recent Asian and African rhinoceroses at c 24 Ma, further suggesting contrasting phenotypic evolutionary rates between both lineages. On morpho-anatomical grounds, it confirms the early split between Elasmotheriinae and Rhinocerotinae (c 35.5 Mya) as recently inferred from mitogenomic data (Kosintsev *et al.*, 2019). Taxonomic affinities of a Pleistocene rhinoceros species represented by a partial skeleton found in 709±68 ka-old archaeological deposits in Luzon Island, Philippines, lead to erect a new genus, *Nesorhinus*. This genus is an unsuspected Southeast Asian Pleistocene lineage closely related to *Rhinoceros* and Sumatran rhinos. From a biogeographical perspective, the current phylogenetic results strongly suggest an island-hopping overwater dispersal for *Nesorhinus*, from Asian mainland toward Luzon via Taiwan by latest Miocene or Early Pleistocene times. Furthermore, the extinct rhinocerotine *Nesorhinus philippinensis* from Luzon Island may be the first perissodactyl species positively supporting the "island rule", with a similar height at shoulder, but significantly decreased body weight and limb bone robustness with respect to its kin.

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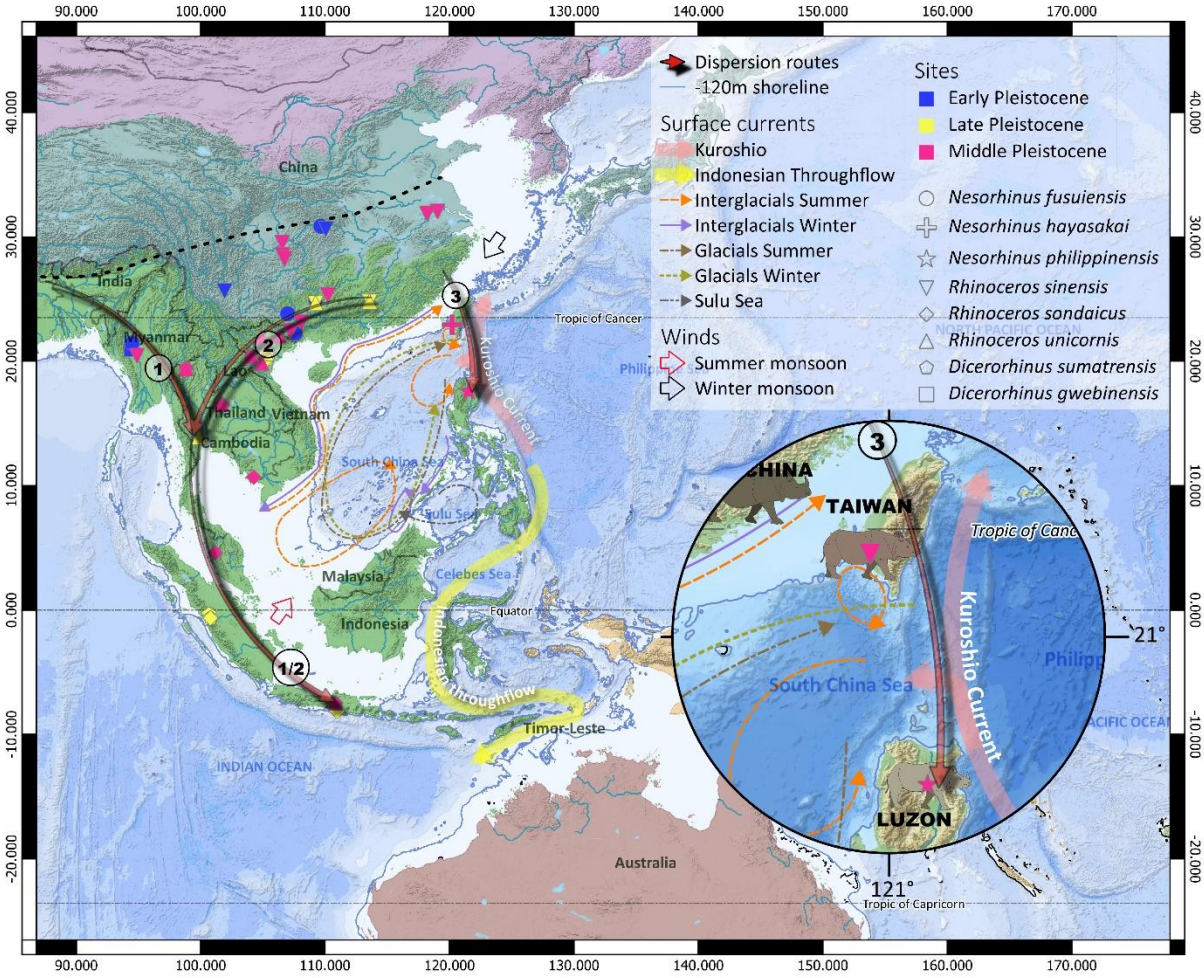


Figure 1. Physiogeographical map of Southeast Asia showing possible dispersal routes for *Nesorhinus*. Coloured lands account for the present zoogeographic regions. Palearctic in purple, Sino-Japanese in green-blue, Indo-Malayan in green, Australasian in orange and Australian in maroon (after Holt *et al*., 2013). The Palearctic-Oriental biogeographic boundary (dashed line) has been determined from several paleontological studies (see for instance Norton & Braun, 2011). The different hypothesised dispersal paths are numbered, 1) for the Indo-Malayan route (Early and Middle Pleistocene), 2) for the Sino-Malayan route (Late Pleistocene), both ending in Java Island in the south (de Vos & Long, 2001), and 3) for the Sino-Wallacean route following von Koenigswald (1956) and which we are reviving here. *[full width suggested]*

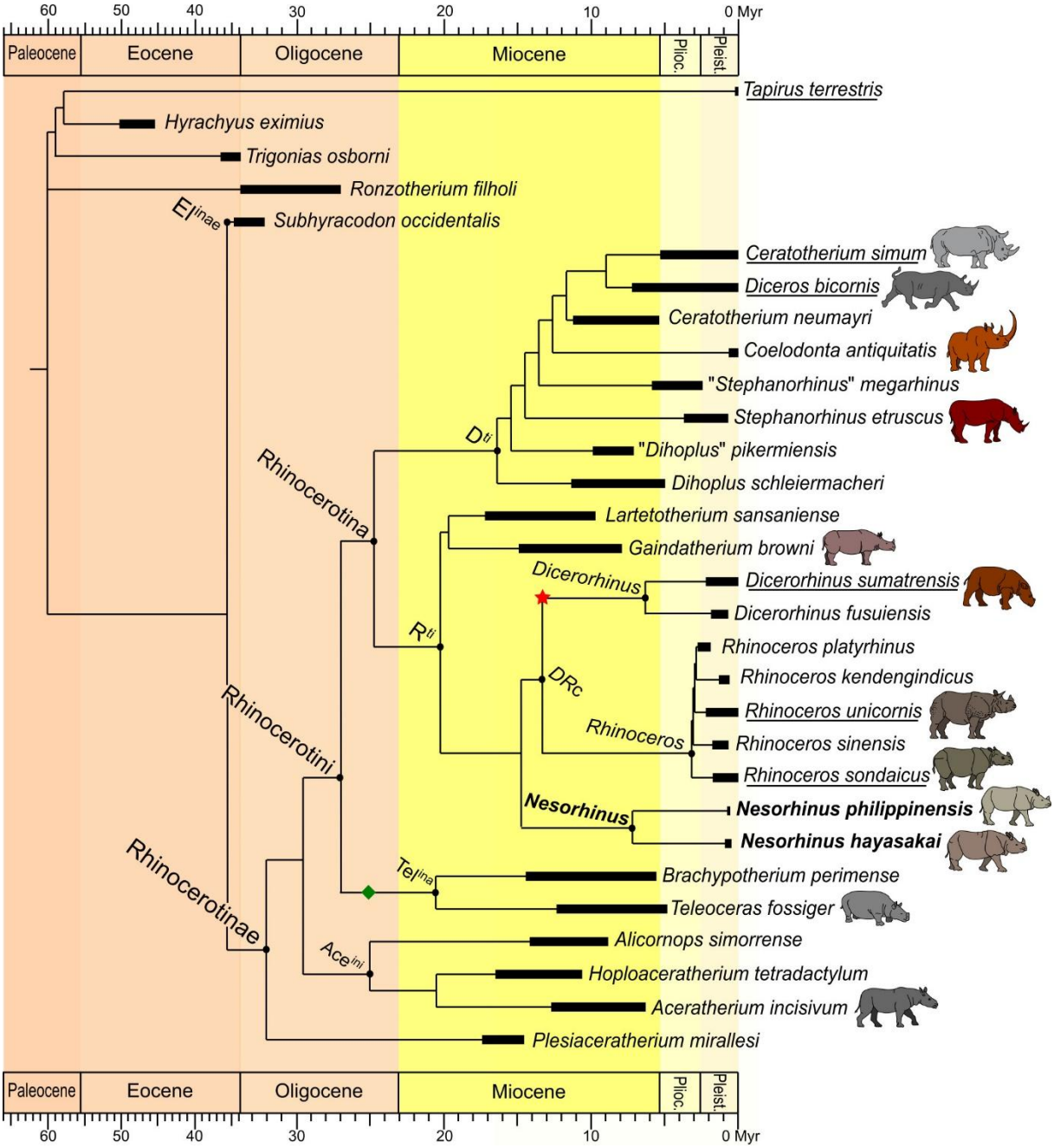


Figure 2. Phylogenetic tree of the Rhinocerotidae, built from 278 unweighted cranio-mandibular, dental, and postcranial characters scored in 30 ceratomorph species, and replaced in their stratigraphical context. *Tapirus terrestris* (Linnaeus, 1758), *Hyrachyus eximius* Leidy, 1871, *Trigonias osborni*, and *Ronzotherium filholi* were used as outgroups. Most parsimonious tree (length: 1315 steps; consistency index = 0.2821; retention index = 0.4858). Node ages were obtained using the approach of Brusatte et al. (2008), as implemented in the paleotree package (Bapst, 2012) in R 4.0.3 (R core development team, 2020), with the first splitting event set to 60 Ma. Red star and green diamond indicate the earliest occurrences of *Dicerorhinus* sensu stricto (13 Mya; Heissig, 1972; Antoine *et al.*, 2013) and Teleoceratina (25 Mya; see Supporting Information). Ace^{ini}, Aceratheriini; *DRc*, *Dicerorhinus*-*Rhinoceros* clade; D^{ti}, Diceroti; El^{inae}, Elasmotheriinae; R^{ti}, Rhinoceroti; Tel^{ina}, Teleoceratina. Recent species' names are underlined. *[Full width suggested]*

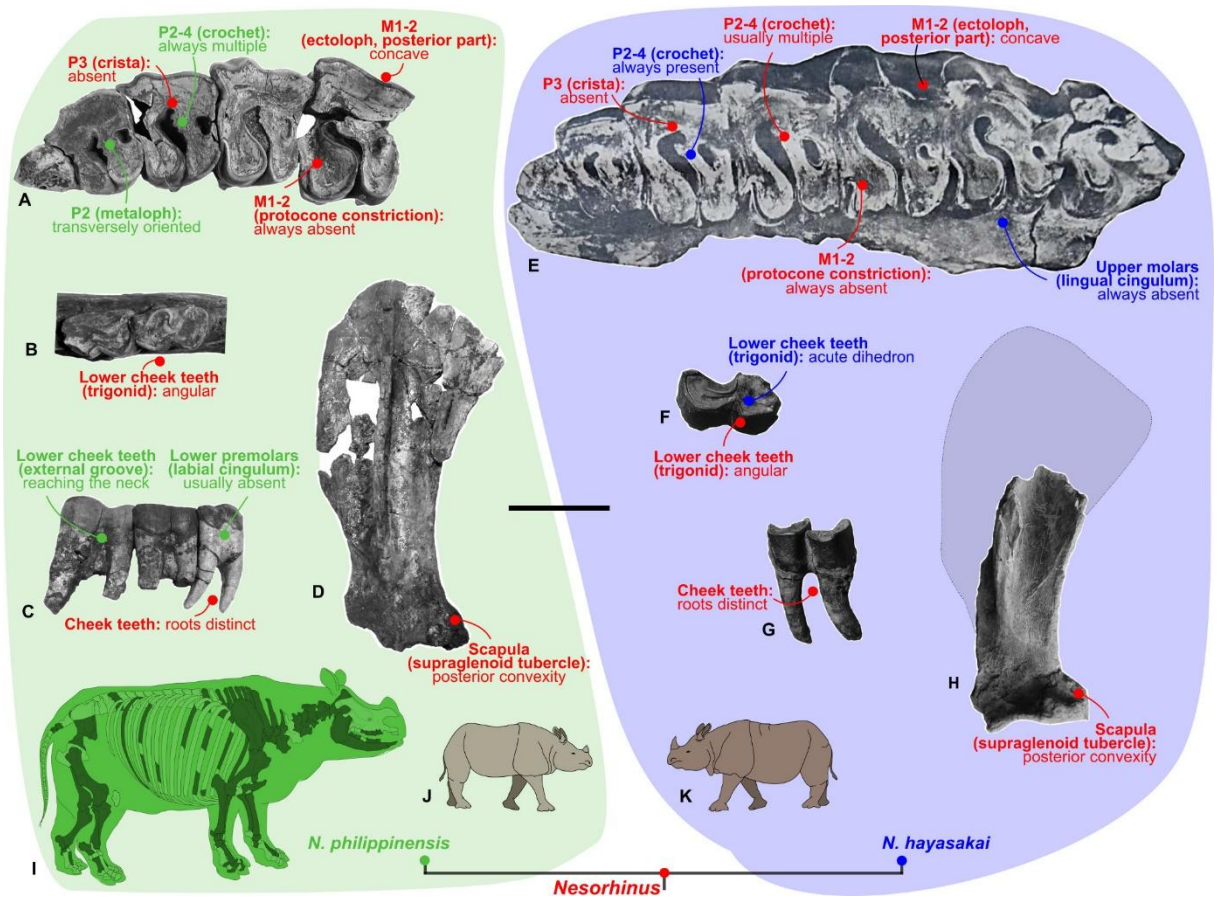


Figure 3. Dental and postcranial features characterising *Nesorhinus* n. g. in the phylogenetic framework as depicted in Figure 2. Red circles denote synapomorphies of *Nesorhinus*, whilst green and blue circles correspond to diagnostic characters (autapomorphies) of *N. philippinensis* and of *N. hayasakai*, respectively. *Nesorhinus philippinensis*: (*a*) left upper dental series (D1-M1) in occlusal view (II-2014-J1-294, 095, 409, 427); (*b*) left m2-3 in occlusal view (II-2014-J1-405); (*c*) right p3-m1 in labial view (II-2014-J1-451); (*d*) left scapula in lateral view (II-2014-J1-291). *Nesorhinus hayasakai*: (*e*) left upper dental series (D1-M3) in occlusal view (DGNTU-FV11b; modified from Hayasaka, 1942); (*f*) right m3 in occluso-labial view (HTR-55); (*g*) left m3 in labial view (HTR-91); (*h*); left fragmentary scapula (HTR-1). Completeness of the skeleton of *N. philippinensis* found at Kalinga (*i*): preserved elements appear in dark green. Tentative silhouettes of *N philippinensis* (*j*) and *N. hayasakai* (*k*) are drawn at a same scale, with a shoulder height of 1.26 m for *N. philippinensis*. See Supporting Information for further details on body size. Scale bar, 5 cm (*a*–*c*, *e*–*g*) and 10 cm (*d*, *h*). *[full width suggested]*

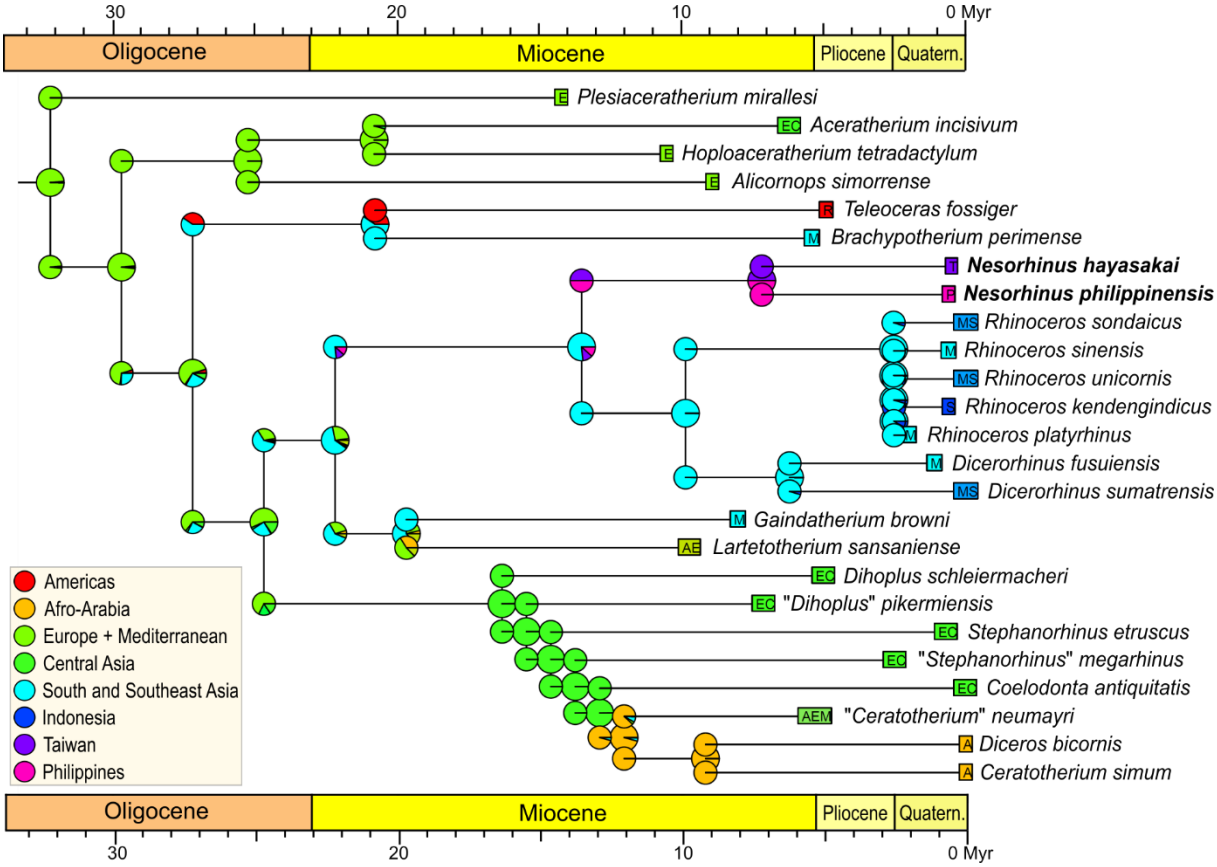


Figure 4. Ancestral biogeographical ranges of Rhinocerotinae, as calculated using BioGeoBEARS package in R (Matzke, 2013; Massana et al., 2015) and mapped on the phylogeny retrieved in Figure 3. Spatial ranges of all terminal taxa included in the phylogenetic and biogeographical analyses were split into eight domains, likely to coalesce: Americas [R], Afro-Arabia [A], Europe + Mediterranean [E], Central Asia [C], South and Southeast Asia [M], Indonesia [S], Taiwan [T], Philippines [P].