RESEARCH

The "Diahot Tooth" is a Miocene rhinocerotid fossil brought by humans to New Caledonia

Oscar Affholder[1] · Pierre-Olivier Antoine[1] · Robin M.D. Beck[2]

Abstract

The "Diahot Tooth" is an isolated postcanine tooth of a large herbivorous mammal, discovered in the Diahot region of northern New Caledonia in 1875. Most authors have identified it as an upper premolar of a rhinocerotid, but an alternative proposal is that it belongs to a diprotodontoid marsupial that has been named *Zygomaturus diahotensis*. Either possibility raises biogeographical difficulties, because New Caledonia has been isolated from other major landmasses for 80 million years, and neither rhinocerotids nor diprodotontoids appear to be good candidates for such a long-distance overwater dispersal event. Here, we present a novel interpretation of the affinities and origin of the Diahot Tooth, based on qualitative study of its preserved morphology and quantitative phylogenetic analyses that include both rhinocerotids and diprotodontoids. We show that the Diahot Tooth most closely resembles the first deciduous premolar of Western Eurasian Miocene teleoceratine rhinocerotid *Brachypotherium brachypus*, with the few discrepancies relating to traits that are known to be variable in *B. brachypus*. Our phylogenetic analyses also support this relationship. The preservation of the Diahot Tooth closely resembles that of *B. brachypus* teeth from the "Faluns Sea" of the Loire basin, and we propose that the New Caledonian specimen originated there and was taken to New Caledonia by a European colonist during the mid-19th century, where it was lost, rediscovered, and incorrectly assumed to be autochthonous.

Keywords Biogeography · *Brachypotherium brachypus* · France – Oceania · Phylogenetic analyses · *Zygomaturus diahotensis*

Introduction

As a remote archipelago, New Caledonia holds a special place in the current global biodiversity landscape. It is situated in the southern Pacific Ocean, around 1500 km away from the Australian coast, and is widely recognised as a terrestrial biodiversity hotspot (Pillon et al. 2017). Out of 3200 extant plant species described from New Caledonia to date, 75–80% are endemic to the archipelago (Morat 1993; Pillon

et al. 2017). The degree of endemism is even higher regarding living animal species, with 86% found only in the region (Caesar et al. 2017). Extant vertebrates are mostly represented by birds and squamates (geckos, skinks, and snakes), the only mammals naturally present being bats (Chazeau 1993); besides introduced species, non-volant mammals are absent. This endemism has long fascinated biologists and biogeographers, and led them to identify New Caledonia as an "Old Darwinian Island" (Grandcolas et al. 2008) and/or a Gondwanan refuge (Morat 1993).

Recent geological studies tend, however, to support a different scenario: it is now well established that the landmass that would become the modern archipelago of New Caledonia separated from the Australian part of Gondwana around 80 Ma, that it did not experience connections with any other major landmass subsequently, and that it was entirely submerged by the ocean at least once between 75 and 60 Ma, and then periodically between around 50 and 34 Ma (Maurizot and Campbell 2020). These submersion events would have impeded the survival of any Gondwanan continental

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ecosystems, biomes, or lineages that may have predated the Oligocene epoch on the island (Ladiges and Cantrill 2007; Espeland and Murienne 2011; Nattier et al. 2017). Genetic studies also show that most endemic New Caledonian clades are no older than 37 ± 3 Ma, i.e., late Eocene in age (Skipwith et al. 2016; Nattier et al. 2017; but see also Heads 2023), congruent with overwater colonization after the most recent emergence of the island.

Given the very limited terrestrial fossil record currently known from New Caledonia, evolutionary hypotheses regarding its insular fauna and flora have long been based on Recent species and tectonic evidence (Garrouste et al. 2021). For a long time, the only known pre-Holocene New Caledonian fossils were Permian–Jurassic mollusks and bryozoans, as well as Triassic ammonites and fragmentary marine sauropsids (Maurizot and Campbell 2020). Neogene–Pleistocene fossils are now known, however, and consist of marine and terrestrial plant macroremains (Genise et al. 2012). Recent fieldwork has also uncovered numerous and well-preserved plant fossil specimens from Mesozoic and Cenozoic times (Garrouste et al. 2021). The only terrestrial vertebrate elements unambiguously found in situ are Holocene in age: they mostly come from caves, and include the horned turtle *Meiolania mackayi*, the terrestrial crocodile *Mekosuchus inexpectatus*, the giant flightless bird *Sylviornis neocaledoniae* (Anderson et al. 2010; Maurizot and Campbell 2020), and nine bats (Hand and Grant-Mackie 2012).

Among these discoveries, a large (anteroposterior length: 26.2 mm), lophodont mammalian postcanine tooth, found by gold miners in 1875 in the Diahot region of northern New Caledonia (Grande-Terre Island; Fig. 1), is of particular interest (Filhol 1876). If autochthonous, this tooth would attest to the presence of a large extinct herbivorous mammal on the island, challenging current scenarios about its past diversity. However, the exact circumstances of this
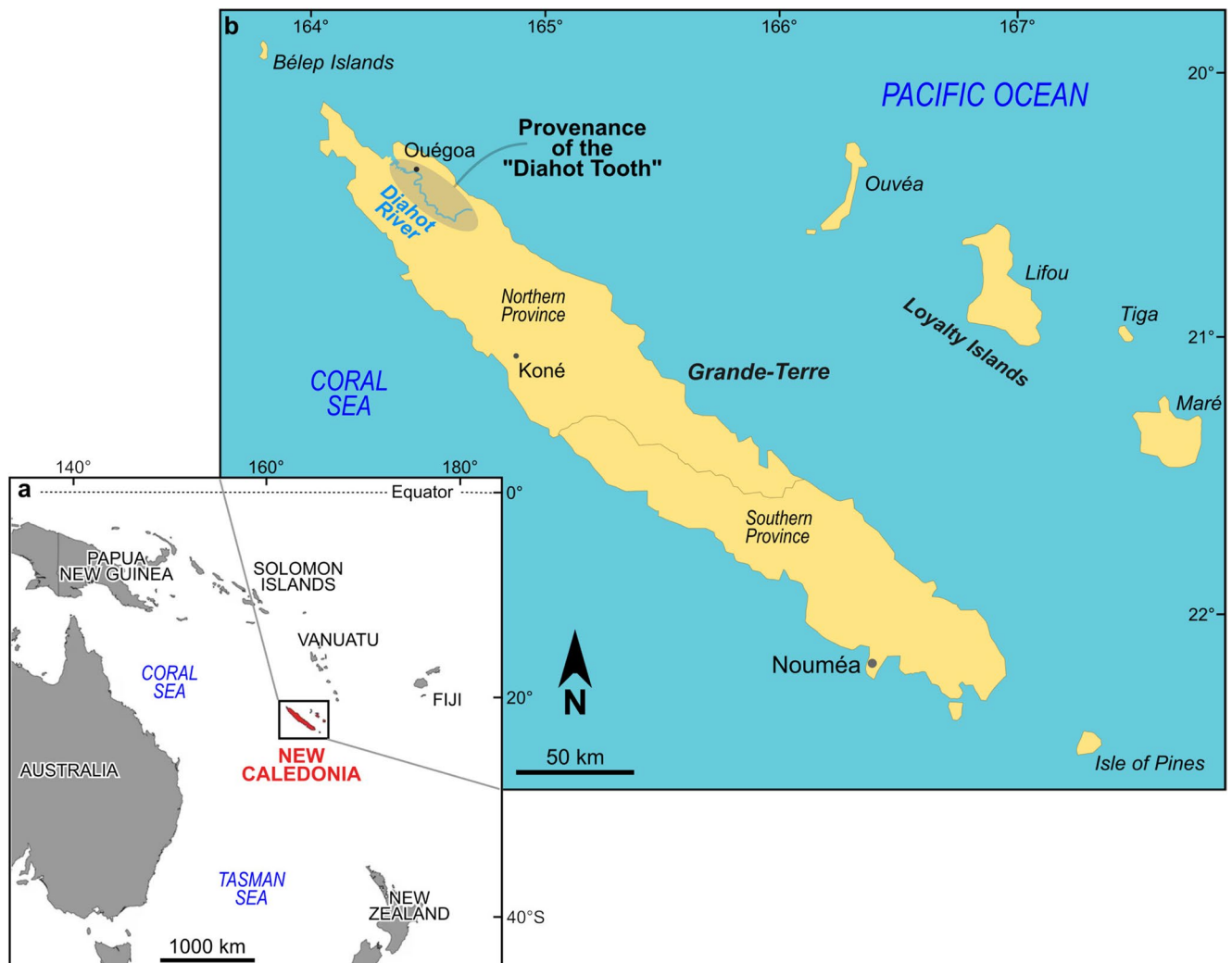

Fig. 1 Location map of Oceania and Southeast Asia (**a**), with a focus on New Caledonia (**b**) and the Ouégoa area, on the Diahot River, where the Diahot Tooth was found in the mid-1870s

find are not fully known, which may explain why the specimen has fallen into relative scientific obscurity since its discovery. Very few paleontologists have considered the implications of this specimen, but two distinctive interpretations have been proposed since its original description. The specimen, originating from the "E. Bonsignorio collection", was first mentioned by Filhol (1876) as a fully mineralized (and therefore fossil) tooth of rhinocerotid affinities. Filhol (1876) identified it as a first upper premolar, very similar to that of the living Sumatran rhinoceros *Dicerorhinus sumatrensis*. He further considered it unlikely that it could have been brought to New Caledonia by sailors or explorers. Nevertheless, he deliberately avoided drawing paleobiogeographical conclusions "based on this sole specimen found in unknown circumstances".

More than a century later, a radically different hypothesis was proposed for its taxonomic assignment, when Guérin et al. (1981) identified the Diahot Tooth as a third upper premolar of a giant extinct diprotodontid marsupial of Australian affinities, further considering it as documenting a new species, *Zygomaturus diahotensis* Guérin, Winslow, Piboule & Faure, 1981. The authors proposed the existence of a now-submerged Pliocene–Pleistocene archipelago between Australia and New Caledonia that could have facilitated sweepstake dispersal, thus explaining the presence of such a fossil Australian megaherbivore in New Caledonia (Guérin et al. 1981).

The proposal of diprotodontid affinities for the Diahot Tooth was later strongly challenged by non-invasive observations on its enamel microstructure, specifically the presence of vertical decussation as in rhinocerotids (Bertrand 1986; Rich et al. 1987). The referral of the Diahot Tooth to Rhinocerotidae was further supported on morphological grounds by Rich et al. (1987), who reasserted that it is rhinocerotid (specifically, an upper first deciduous premolar), and Guérin et al.'s (1981) biogeographical scenario has not been supported by recent geological or molecular biogeography-based data (Skipwith et al. 2016; Nattier et al. 2017 and references therein). In any event, regardless of whether the Diahot Tooth pertains to a rhinocerotid or diprotodontid, given the distances considered, only a non-testable dispersal scenario can be considered, such as by long-range swimming or passive "rafting" on a floating island (Azzaroli 1996; Antoine et al. 2022). In general, however, large herbivorous mammals appear poorly suited for long-range overwater dispersal (van der Geer et al. 2010), except for the semi-aquatic hippopotamids (van der Geer et al. 2010, 2015; but see Mazza 2014, 2015 and Mazza et al. 2019 for an opposing view), and deer and elephants, both of which are known to be excellent swimmers (Johnson 1980; van der Geer et al. 2010; Beck 2017: p. 351). A single case of overwater dispersal is reported for rhinocerotids,

with an estimated 60-km distance from mainland Asia to the Philippines during the Late Neogene or the Early Pleistocene (Antoine et al. 2022), in no way comparable to the ~1300 km separating Australia from New Caledonia during sea-level lowstands.

A third hypothesis has been suggested, one that involves direct human intervention (Rich et al. 1987: p. 777; Antoine 2012). Rich et al. (1987: p. 777) stated that "the hypothesis that the Diahot tooth had been carried to New Caledonia… by a human agency…should be seriously considered", but did not discuss this possibility further. By contrast, Antoine (2012: p. 166) specifically identified the Diahot Tooth as representing "the western Eurasian Miocene hornless teleoceratine *Brachypotherium brachypus*", and its presence in New Caledonia explained as the result of "probably [having been] used as a jewel by a French deported convict and subsequently lost by the Diahot River". Unfortunately, this hypothesis was not accompanied by supporting morphological evidence, nor can it be supported by convincing historical clues.

The present study aims at providing a quantitative, anatomy-based test of the taxonomic assignment of the Diahot Tooth to either Rhinocerotidae or to the marsupial Diprotodontoidea, and, based on the results of this test, at proposing potential scenarios for explaining its presence and recovery in New Caledonia.

Materials and methods

Material

The Diahot Tooth (Fig. 2a-f) is permanently stored in the paleontological collections of the Muséum National d'Histoire Naturelle, in Paris. To our knowledge, it lacks a specimen number. The tooth is mounted on a wood-and-brass pedestal, typical of late 19th century museum material intended to be on exhibition (Fig. 2f). It is accompanied by three hand-written labels, two of them likely being almost coeval with the discovery of the specimen (Fig. 2g). The most informative is the first label, which reads "*Rhinocéros, dent fossile trouvée au Diaho*[t] *(Nouvelle Calédonie) par M. E. Bonsignorio. Voir H. Filhol, Ann. Sc. Nat. 6me série, T.III, Catal. 1876.*" [Rhinoceros, fossil tooth found at the Diaho[t] (New Caledonia) by Mr. E. Bonsignorio. See H. Filhol, Ann. Sc. Nat., 6th series, T. III. Catalogue 1876; our translation]. This label has two holes in its lower part, coinciding with the spikes left in the pedestal of the specimen (Fig. 2f-g). The second label (Fig. 2g) reads "*Dent de Rhinocéros. Trouvée au Diahot. (N^{elle}Calédonie) Cat 7- 1879*" [Rhinoceros tooth. Found at the Diahot. (New Caledonia) Catalogue 7- 1879; our translation]. The last one (Fig. 2g)

Fig. 2 The Diahot Tooth, from the Diahot region in northern New Caledonia, in occlusal (**a**), labial (**b**), lingual (**c**), distal (**d**), and mesial (**e**) views; arrows indicate the hole crossing the roots that was used for the brooch. **f**. The same specimen mounted on its 19th-century pedestal. **g**. Labels accompanying the specimen in the paleontological collection of the Muséum national d'Histoire naturelle, in Paris; the bottom left label was originally nailed to the pedestal (the holes are evident in **f**). Scale bars equal 20 mm

postdates Guérin et al.'s (1981) publication, and reads "*Zygomaturus diahotensis nov. sp. Nouvelle Calédonie C. Guérin et alii, 1981*".

Comparison

Direct observation and measurements were first performed on the Diahot Tooth, with most descriptive features observed on this specimen included as character states in a phylogenetic character matrix (see below). The concerned character states are detailed in the anatomical description subsection, between square brackets. Following the primary homology hypotheses of the relevant authors, we compared the Diahot Tooth to first upper deciduous premolars (DP1) of rhinocerotids, and to third upper premolars (P3) of diprotodontoids (Fig. 3; Table 1). Dental nomenclature for rhinocerotids follows Heissig (1969), Uhlig (1999), and Antoine (2002), whereas that for diprotodontoids follows Stirton et al. (1967) and Murray et al. (2000).

A two-step character analysis was then undertaken, with the first step intended to test the rhinocerotid vs. diprotodontoid status of the Diahot Tooth, and the second step intended to refine its potential taxonomic assignment within the clade supported by the first step. The first-step
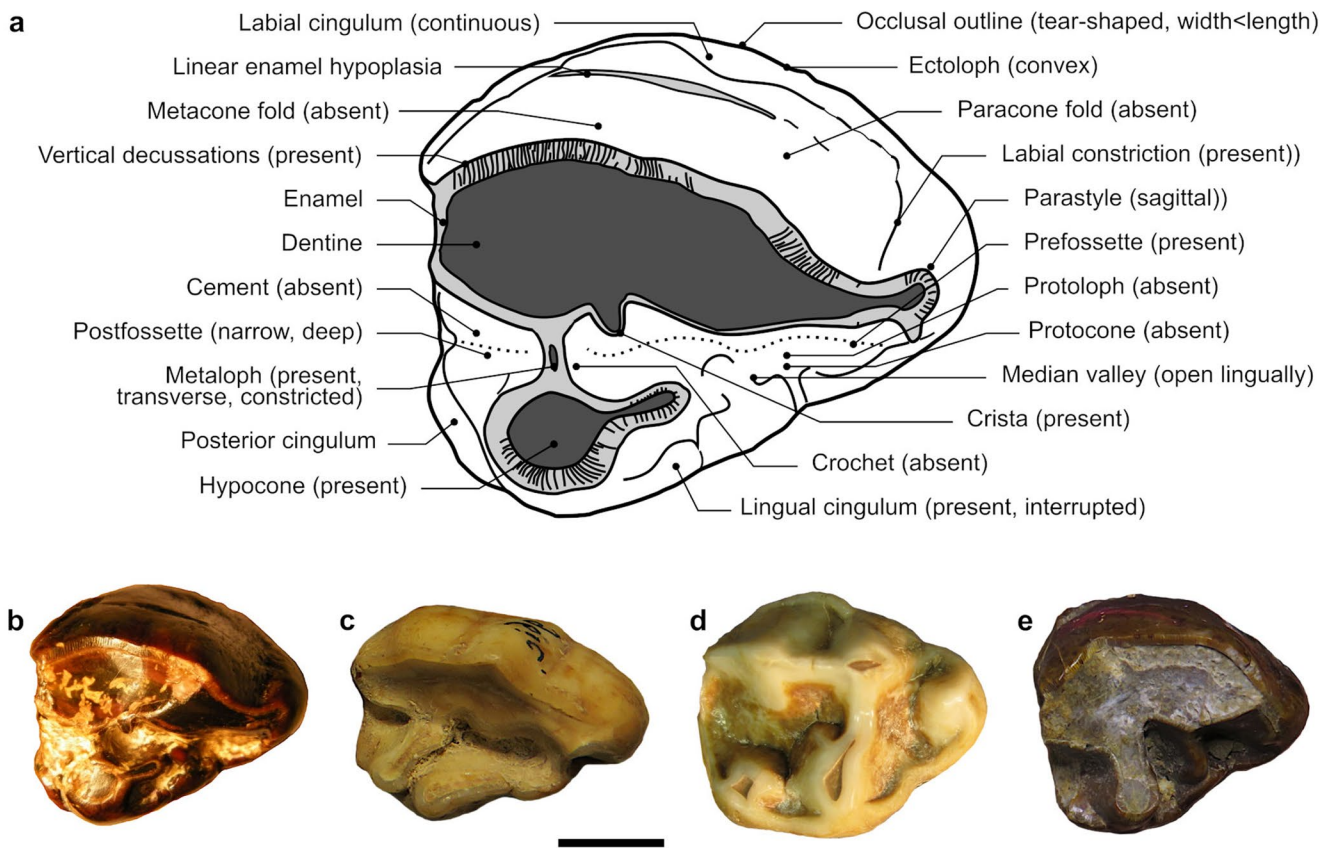
Fig. 3 a. Dental terminology used in the present work and main features of interest observed on the Diahot Tooth, in occlusal view. Comparison of the Diahot Tooth (**b**) with three candidates for taxonomic assignment (**c-e**). **c**. Left DP1 (mirrored) of a Sumatran rhinoceros, *Dicerorhinus sumatrensis* (NML, Dubois Collection, n°961c; Lida Ajer, Sumatra). **d**. Left P3 (mirrored) of *Zygomaturus trilobus*, a giant diprotodontoid marsupial from Australia, following Guérin et al.'s (1981) hypothesis (AM F49675). **e**. Right first upper deciduous premolar of *Brachypotherium brachypus*, a Miocene Western Eurasian hippo-like rhinocerotid, following Antoine's (2012) variant of Filhol's (1876) hypothesis (MHNT SIM-1995-71; Simorre, SW France). Scale bar equals 10 mm

comparison sample includes five rhinocerotid species (for testing Filhol's [1876] and Antoine's [2012] hypotheses), and three extinct diprotodontoid marsupial species (for testing Guérin et al.'s [1981] hypothesis). Four of the rhinocerotid terminals are living Asian species, which also have a Pleistocene fossil record in Asia (Antoine 2012), for addressing Filhol's (1876) hypothesis. The concerned taxa are *Dicerorhinus sumatrensis* (Sumatran rhinoceros, broad sample of fossil specimens from Sumatra), *Rhinoceros unicornis* (Indian rhinoceros; Recent specimens), *Rhinoceros sondaicus* (Javan rhinoceros, Recent specimens), and *R. sondaicus* (broad sample of fossil specimens from Java and Southeast Asian Pleistocene localities). This sample also includes the hippo-like Miocene teleoceratine *Brachypotherium brachypus*, to test Antoine's (2012) hypothesis. The diprotodontoids are all Pleistocene taxa: the diprotodontids *Zygomaturus trilobus* and *Diprotodon optatum*, and the palorchestid *Palorchestes azael*, each of which achieved adult body masses > 1000 kg (Richards et al. 2019; Beck et al. 2020). Following this, and given the results of the first step

(see Results), based on direct observation and/or available literature, we compare the Diahot Tooth to first upper deciduous premolars of 33 rhinocerotid species, spanning all Old World suprageneric taxa and the Oligocene–Holocene time interval, with sample sizes ranging from a single tooth to dozens of them within a given species (Table 1).

Institutional abbreviations; **AMF**, Australian Museum fossil collection, Sydney; **MHNT**, Muséum d'Histoire Naturelle de Toulouse; **MNHN**, Muséum National d'Histoire Naturelle, Paris; **NML**, Naturalis Museum, Leiden.

Character matrix and subsequent analyses

Observation of the Diahot Tooth, based on the restricted comparison sample (step 1, see above), and on the broader rhinocerotid sample (step 2, see above) allowed for the creation of a matrix of 36 taxa and 29 anatomical characters (Appendix 1; Online Resource 1); some of these taxa and characters are derived from Antoine (2002, 2003), Antoine et al. (2003, 2022), and Pandolfi et al. (2021), which in turn

Table 1 Diprotodontoid marsupial and rhinocerotid species included in the comparison sample for testing the taxonomic affinities of the Diahot Tooth (via morphology, distance, and parsimony analyses). Abbreviation: *N*, number of specimens observed

Taxon	*N*	Geographic range; age	Source
Diahot Tooth	1	Diahot, New Caledonia; unknown	Direct observation; this work
Diprotodon optatum	2	Australia; Pleistocene	Price and Sobbe (2011)
Palorchestes azael	2	Australia; Pleistocene	Price and Sobbe (2011)
Zygomaturus trilobus	2	Australia; Pleistocene	Direct observation
Alicornops simorrense	13	Western Europe; Miocene	Direct observation; Cerdeño and Sánchez (2000)
Brachydiceratherium aginense	6	Western Europe; Early Miocene	Direct observation; Répelin (1917)
Brachydiceratherium lemanense	>10	Western Europe; Early Miocene	Direct observation
Brachypotherium brachypus	9	Western Eurasia; Early to Late Miocene	Direct observation; Cerdeño (1993); Becker and Tissier (2020)
Brachypotherium perimense	2	South and Southeast Asia; Early to Late Miocene	Direct observation; Heissig (1972)
Ceratotherium neumayri	4	Eastern Mediterranean; Late Miocene	Direct observation; Giaourtsakis (2009)
Ceratotherium simum	4	Africa; Pleistocene-Holocene	Direct observation; Guérin (1980)
Coelodonta antiquitatis	1	Northern Eurasia; Pleistocene	Garutt (1994)
Coelodonta nihowanensis	6	China; Early Pleistocene	Tong and Wang (2014)
Diaceratherium tomerdingense	1	Germany; Early Miocene	Dietrich (1931)
Diceratherium armatum	3	North America; Late Oligocene-E Miocene	Direct observation; Wood (1933)
Dicerorhinus sumatrensis (fossil)	>30	Southeast Asia; Pleistocene-Holocene	Direct observation
Diceros bicornis (Recent)	34	Africa; Holocene	Direct observation; Guérin (1980)
Epiaceratherium cf. *magnum*	1	Pakistan; Early Oligocene	Direct observation; Antoine et al. (2003)
Epiaceratherium magnum	2	Western Europe; Oligocene	Uhlig (1999)
Gaindatherium vidali	3	South Asia; Miocene	Direct observation; Heissig (1972)
Hispanotherium matritense	4	Western Europe; Miocene	Direct observation; Antunes and Ginsburg (1983)
Hoploaceratherium tetradactylum	15	Western Eurasia; Middle to Late Miocene	Direct observation; Heissig (2012)
Lartetotherium sansaniense	5	Western Eurasia; Middle to Late Miocene	Direct observation; Heissig (2012)
Menoceras arikarense	7	North America; Early Miocene	Direct observation
Pliorhinus crusafonti	1	Western Eurasia; Pliocene	Guérin and Santafé-Llopis (1978)
Prosantorhinus germanicus	8	Western Europe; Early to Middle Miocene	Peter (2002)
Protaceratherium minutum	3	Western Europe; Early Miocene	Direct observation
Rhinoceros aff. *sondaicus*	1	Pakistan; Miocene	Heissig (1972)
Rhinoceros ?*sivalensis*	1	India; Pliocene	Matthew (1929)
Rhinoceros sinensis	2	China; Pleistocene	Colbert et al. (1953)
Rhinoceros sondaicus (fossil)	8	Southeast Asia; Pleistocene	Direct observation; Hooijer (1946)
Rhinoceros sondaicus (Recent)	>30	Southeast Asia; Holocene	Direct observation; Guérin (1980)
Rhinoceros unicornis (Recent)	8	Southeast Asia; Pleistocene	Direct observation; Guérin (1980)
Ronzotherium filholi	7	Western Europe; Oligocene	Direct observation; Brunet (1979)
Ronzotherium romani	1	Western Europe; Oligocene	Direct observation; Tissier et al. (2021)
Stephanorhinus hemitoechus	1	Eurasia; Pleistocene	Pandolfi et al. (2017)

allowed us to tentatively polarize them according to their likely plesiomorphic and apomorphic states. The matrix was edited using the Nexus Data Editor (NDE) software package, version 0.5.0 (Page 2001). The Diahot Tooth was included as a terminal taxon under its own name.

Binary and unordered multistate characters were assigned a weight of 1, whereas multistate ordered characters were scaled according to the number of character states, so that they were assigned either a weight of 0.5 (character 9, which has three states) or 0.333 (characters 6, 10, 14, 15, 17, 20, 22, 24, 25, and 26, all of which have four states).

All analyses were performed with the PAUP* software package, version 4.0a (build 169) (Swofford 2002). For the

first step, we used distance analyses (UPGMA, restricted sample) to test the general resemblance of the Diahot Tooth to our comparative sample. For the second step, maximum parsimony analyses were run on a broad rhinocerotid sample, with no topological constraints, using the Oligocene rhinocerotids *Ronzotherium filholi* and *R. romani* as outgroups, and specifying 1000 replicates of a stepwise random addition sequence, with 10 trees held at each step, and a tree-bisection-reconnection branch-swapping algorithm (reconnection limit set at 8). Reversals are denoted by dashes ("-21^0").

Results

Anatomical description

Total height of the crown plus roots of the Diahot Tooth is 49 mm, length (L) is 26.2 mm, width (W) is 23.0 mm, and crown height (H) is 23.0 mm. The tooth has a dark brown crown and lighter brown roots, while the cementum layer covering parts of the two long and straight roots is almost black. The crown is complete, except for several small (~1 mm by 1 mm) pits in the enamel, whilst the roots are straight and have broken tips. The tooth has a smooth and polished aspect, suggesting significant surface erosion (see also comments by Rich et al. 1987: p. 775). A few splinters (~1 mm by 1 mm) were lost from the labial side of the posterior root after exhumation of the tooth (Fig. 2b). A man-made round hole, used to attach the tooth to the pedestal, further crosses the apical part of the roots.

The tooth has a teardrop occlusal outline [1¹], being longer than wide (L > W [2⁰]). The enamel is thick (reaching a maximum of 1.4 mm), and is much thicker in the labial region than in the lingual region (0.2 mm). It has a smoothly corrugated surface, with vertical raised striations (< 1 mm in width) running all over the labial surface of the tooth [3²]. These striations (vertical decussations; see Bertrand 1986; Rich et al. 1987: p. 776–777) run transversely throughout the occlusal section of the enamel. There is a horizontal pit (5 mm horizontally by 1 mm vertically) hollowing out the median part of the outer wall, on its apical third. This enamel defect progressively vanishes both anteriorly and posteriorly, and appears to be an example of linear enamel hypoplasia (Hullot et al. 2021). The tooth is brachydont (H < L [4⁰]). There is no cementum, either covering the outer walls or filling the valleys [5⁰]. There is no anterior loph ("protoloph" [6⁰] if belonging to a rhinocerotid, hence the quotation marks here and for other anatomical features in this paragraph), which prevents comparison of its height to that of the posterior loph or cusp [7⁻], or scoring of its shape [8⁻]. However, a posterior loph ("metaloph"), strongly constricted in its median part, extends transversely [9¹]. The outer wall ("ectoloph") is thick and continuous, with a convex outline in occlusal view [10³]. There is a short anterior spur ("parastyle" [11⁰]), which is sagittally oriented [12⁰] and labially constricted on most of the crown height [13⁰]. The ectoloph is regularly convex, with no anterior or posterior vertical swellings (the "paracone fold" [14⁰] and "metacone fold" [15⁰], respectively). A deep sagittal pit hollows out the lingual side of the tooth ("prefossette" [16⁰]), and is bordered lingually by a strong cingulum [17⁰] with irregular enamel knobs. This lingual cingulum in interrupted [18¹] around the postero-lingual circle-shaped cusp ("hypocone" [19⁰]). On the labial side, a thick and continuous cingulum

is present [20⁰] [21⁰], with a M-shape in labial view (and anatomical position). There is no antero-lingual cusp ("protocone" [22³]), and hence no protocone-hypocone connection [23⁻], but a short and narrow crest runs anteriorly from the hypocone leaving the deep median valley open lingually [24⁰]. There is no spur running anteriorly from the median part of the metaloph ("crochet" [25⁰]), but a small and sharp transverse spur ("crista") arises from the lingual side of the ectoloph [26³]. This crista is developed only at mid-height of the median valley. There are no secondary enamel folds [27⁰]. The posterior valley ("postfossette") is narrow transversely [28⁰] and as deep as the median valley [29⁰].

### Distance and parsimony analyses

Restricted sample, UPGMA analysis (Online Resources 2, 3)

The tree, rooted using midpoint method, includes two main clusters. The first one includes the Diahot Tooth and all rhinocerotids (Fig. 4a). The Diahot Tooth and *Brachypotherium brachypus* are connected by the longest internal branch of the tree, and this cluster is sister to all living Asian rhinocerotid species, with *Dicerorhinus sumatrensis* being the sister taxon to all three *Rhinoceros* terminals (Fig. 4a). The second cluster includes the diprotodontoids *Diprotodon optatum*, *Zygomaturus trilobus*, and *Palorchestes azael*. The high level of similarity between the Diahot Tooth and *Brachypotherium brachypus* within rhinocerotids allows for narrowing the taxonomic scope of the second step (see below), with a broader sample of living and extinct rhinocerotids (Table 1).

Broad rhinocerotid sample, maximum parsimony analysis (Online Resources 2, 3)

The maximum parsimony analysis recovers four most parsimonious trees of 111.958 steps (consistency index = 0.2679; retention index = 0.5363). In all these trees, and in the strict consensus (Fig. 4b), the Diahot Tooth is closely related to *B. brachypus*, with the small and hornless aceratheriine *(A) simorrense* (Middle–Late Miocene, Western Eurasia) as a sister taxon to that clade. This three-taxon clade has the huge teleoceratine *Brachypotherium perimense* (Middl to Late Miocene, South and Southeast Asia) as a sister taxon. All Pleistocene–Recent South Asian representatives of *Dicerorhinus* and *Rhinoceros* are distantly related to the Diahot Tooth (Fig. 4b). This analysis further allows the identification of features that are unambiguously shared by the Diahot Tooth and *Brachypotherium brachypus* (Online Resource 5): a continuous labial cingulum [-21⁰], and a postfossette as deep as the median valley [-29⁰]. Both taxa further share a tear-shaped occlusal outline [1¹] and a labial

Fig. 4 Morpho-anatomical affinities of the Diahot Tooth, as retrieved through a 29-character analysis. **a**. "First-step analysis": distance tree retrieved via a UPGMA analysis with selected rhinocerotid species (living Asian rhinoceroses, following the hypothesis of Filhol 1876; Miocene hippo-like *Brachypotherium brachypus*, following the hypothesis of Antoine 2012) and three diprotodontoid marsupial species (*Diprotodon optatum*, *Zygomaturus trilobus*, and *Palorchestes azael*); **b**. "Second-step analysis", with a comparison to 33 rhinocerotid species (Recent and extinct); strict consensus tree of four most parsimonious trees obtained through a parsimony analysis, with the Oligocene rhinocerotids *Ronzotherium romani* and *R. filholi* as outgroups
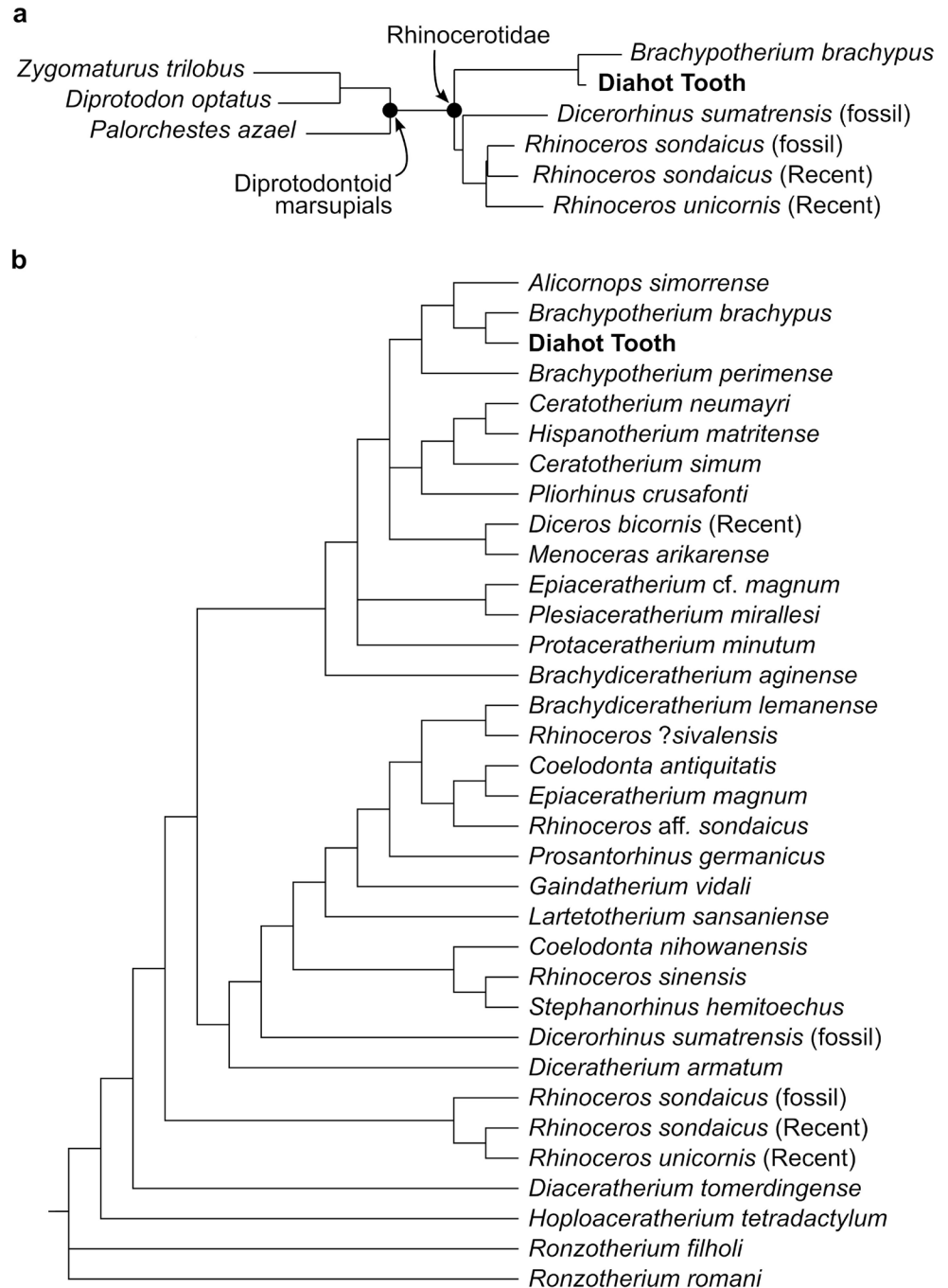
parastyle constriction [-13^0] with *Alicornops simorrense*, while *Brachypotherium perimense* and these three taxa have a labial cingulum [-20^0] but neither a protocone [22^3] nor a protoloph [6^3]. Moreover, the Diahot Tooth has no unique character states that might represent autapomorphies. However, five features distinguish the Diahot Tooth from DP1s of *Brachypotherium brachypus* in the matrix: the absence of the protoloph [6^3] (usually absent in *(B) brachypus* [6^2]), the convex ectoloph [10^3] (usually convex in *B. brachypus* [-10^2]), the absence of the paracone fold [14^0] (usually present in *B. brachypus* [14^2]), the absence of the protocone [22^3] (usually absent in *B. brachypus* [22^2]), and the presence of the crista [26^3] (usually absent in *B. brachypus* [26^1], notably in worn teeth). Nevertheless, all of these five features are sometimes observed in *Brachypotherium brachypus*, and so their presence in the Diahot Tooth does not rule out its referral to this taxon.

Discussion and conclusion

The eroded aspect of the Diahot Tooth is compatible with a fluvial or estuarine depositional context. Its dark color matches fluvial/estuarine/marine Mn-rich settings. The striations running vertically on the labial surface of the enamel unambiguously resemble the vertical decussation observed in rhinocerotoids, specifically rhinocerotids (Bertrand 1986; Rich et al. 1987). The fact that they run transversely all over the occlusal surface of the enamel rules out assignment of the Diahot Tooth to a marsupial (Koenigswald 2000) but also to extinct South American astrapotheres (Rensberger and Pfretzschner 1992) and pyrotheres (Hirayama and Suzuki 2020).

The Diahot Tooth is assignable to *Brachypotherium brachypus*

Distance (UPGMA) and maximum parsimony analyses retrieve the same result: the Diahot Tooth is more similar to the DP1 of rhinocerotids than to the P3 of diprotodontoid marsupials (Fig. 4). Among rhinocerotids, it has closer resemblances to the DP1 of *Brachypotherium brachypus* than to that of any other rhinocerotid. Interestingly, the five characters seemingly distinguishing the Diahot Tooth and *B. brachypus* are variable in *B. brachypus* (presence/absence of the protoloph, the paracone fold, the protocone, and the crista; outline of the ectoloph), and each character state observed in the Diahot Tooth falls within the range of variability seen in DP1s of *B. brachypus*. In other words, no aspect of the preserved morphology of the Diahot Tooth appears to rule out its taxonomic assignment to *Brachypotherium brachypus*, as proposed – without detailed justification – by Antoine (2012). Accordingly, *Zygomaturus diahotensis* Guérin, Winslow, Piboule & Faure, 1981 is considered here a junior synonym of *Brachypotherium brachypus* (Lartet, 1837). The large and heavy-bodied *Brachypotherium brachypus*, with an estimated body mass of ~2000 kg, is a conspicuous element of late Early to early Late Miocene localities of Europe and the eastern Mediterranean (Heissig 1976; Antoine 2002; Becker and Tissier 2020; Antoine et al. in press), and more than a half of its occurrences are in France (Cerdeño 1993; Antoine et al. 2000; Geraads et al. 2021). This species has never been documented or reported in South or Southeast Asia, but two other species from this region, with still larger dimensions, are assigned to *Brachypotherium*: the latest Oligocene to earliest Miocene *B. gajense* from Pakistan, and the late Early to Late Miocene *B. perimense* from the Indian Subcontinent and Thailand (Heissig 1972; Antoine et al. 2013; Sizov et al. 2024). Deciduous P1s of the latter species have some similarities

with the Diahot Tooth but are nevertheless quite distinct and far less similar to it than *B. brachypus* (Fig. 4b-c).

How could a Miocene rhinocerotid tooth from Western Eurasia get to New Caledonia?

Given the regional geodynamical context (Maurizot and Campbell 2020), the unambiguous assignment of the Diahot Tooth to the Western Eurasian Miocene teleoceratine rhinocerotid *Brachypotherium brachypus*: (1) removes support for the hypothesis of a biogeographical connection between Australia and New Caledonia during Pliocene–Pleistocene times; (2) rules out the hypothesis of this taxon being naturally present on the island, whatever timing and dispersal patterns might be invoked for it; and (3) makes it highly unlikely that it was brought to the island during the first wave of human colonization, ~3500 year BP (Carson 2008). On the other hand, and following Antoine's (2012) hypothesis, the Diahot Tooth could have been brought to New Caledonia as a result of European colonization during the 19th century. A wave of European colonization started around 1850 when the island became a French colony, with a sandalwood rush attracting settlers of all geographic origins (Merle 2020). In 1864, French transportation law was enacted and all French-born convicts were "transported" to New Caledonia; there was a particularly large deportation of convicts from the repression of the *Commune de Paris* to New Caledonia in 1872 (Merle 2020). Filhol (1876) recognized in 1875 what would become known as the Diahot Tooth in the collection of Etienne Bonsignorio (an assistant commissioner of the French Navy) as a specimen that had been excavated by gold miners, and he noted the possibility that it could have been brought by sailors or explorers, without giving this much credence (see also Rich et al. 1987: p. 777).

How, then, could a tooth belonging to a Western Eurasian Miocene rhinocerotid get to New Caledonia? Interestingly, *Brachypotherium brachypus* is particularly abundant in France, and more specifically in Miocene localities from the Loire basin, notably in the coastal coquina-rich beds of the "Faluns Sea", which preserve mixed terrestrial mammalian remains and marine fossils (Cerdeño 1993; Antoine et al. 2000; Ginsburg 2001; Gagnaison et al. 2009). Specimens of *B. brachypus* from this site have the same external aspect and preservation (dark to black patina, naturally-eroded surface, broken roots) as the Diahot Tooth. Most museum paleontological collections from France have fossil specimens from the "Faluns Sea", and it seems likely that many more remains have been collected and stored in private collections. Even if there is no way of proving it, our hypothesis is that this tooth was carried as an amulet or a trinket by a settler, a convict, or a naval or prison officer from the

Loire Basin, was then lost in the Diahot area, and subsequently rediscovered. This hypothesis was favored by the late Leonard Ginsburg, who long had it in his office at the Muséum National d'Histoire Naturelle, in Paris. In fact, in 1998, he tested one of us (POA) by presenting him with the "Diahot Tooth", isolated from its pedestal. POA proposed at first sight that this tooth was a *Brachypotherium brachypus* specimen from the "Faluns Sea". The hole through the roots led POA to deduce that this fossil specimen had been made into a pendant, hence the version briefly presented in Antoine (2012). However, it is impossible to know whether this perforation was especially made for the pedestal or whether it predates this. Europeans were very few at that time in the Diahot region, and that population mostly consisted of gold- and nickel-seeking miners. Local historiographers and archeologists agree that French colonization at this period resulted in the presence on the island of numerous surprising and non-native items, such as ostrich eggs (Louis Lagarde, pers. comm., 2023). Available evidence suggests to us that the Diahot Tooth is another example of this. This hypothesis might be testable using trace element analysis of rare earth elements (REE; Suarez et al. 2010; Knutsen and Oerlemans 2020), in order to compare the REE spectrum of the Diahot Tooth to those of "Faluns Sea" and Diahot River-sourced sediments. However, the Diahot Tooth is a patrimonial treasure and, as such, may only be investigated through non-invasive methods.

Appendix 1

1. Occlusal outline, shape: (0) triangular; (1) tear-shaped; (2) comma-like; (3) pentagonal.
2. Occlusal outline, proportion: (0) W/L < 1; (1) W/L > 1.
3. Enamel aspect: (0) striated; (1) corrugated; (2) striated and corrugated.
4. Crown height: (0) low (brachydont; H/L < 1); (1) high (hypsodont; H/L > 1).
5. Cement: (0) absent; (1) present.
6. Protoloph: (0) present; (1) more often or equally present; (2) more often absent; (3) absent.
7. Protoloph: as high as the metaloph/hypocone; (1) lower than the metaloph/hypocone.
8. Protoloph: (0) continuous; (1) split in two parts.
9. Metaloph, orientation: (0) mesolingually directed; (1) transverse; (2) distolingually directed.
10. Ectoloph: (0) straight; (1) more or equally often straight; (2) more often convex; (3) convex.
11. Parastyle: (0) present; (1) absent.
12. Parastyle, orientation: (0) sagittal; (1) curved lingually.
13. Parastyle constriction: (0) present; (1) absent.

14. Paracone fold: (0) absent; (1) more or equally often absent; (2) more often present; (3) present.
15. Metacone fold: (0) absent/weak; (1) more or equally often absent; (2) more often strongly marked; (3) strongly marked.
16. Prefossette: (0) present; (1) absent.
17. Lingual cingulum: (0) present; (1) more or equally often present; (2) more often absent; (3) absent.
18. Lingual cingulum: (0) continuous; (1) interrupted.
19. Hypocone: (0) present; (1) absent.
20. Labial cingulum: (0) present; (1) more or equally often present; (2) more often absent; (3) absent.
21. Labial cingulum: (0) continuous; (1) interrupted.
22. Protocone: (0) present; (1) more or equally often present; (2) more often absent; (3) absent.
23. Protocone-Hypocone: (0) equally developed; (1) protocone < hypocone.
24. Median valley: (0) open lingually; (1) more or equally often open lingually; (2) more often closed lingually; (3) closed lingually (lingual wall).
25. Crochet: (0) absent; (1) more or equally often absent; (2) more often present; (3) present.
26. Crista: (0) absent (1) more or equally often absent; (2) more often present; (3) present.
27. Secondary enamel foldings: (0) absent; (1) present.
28. Postfossette (on worn teeth): (0) narrow; (1) wide.
29. Postfossette: (0) as deep as the median valley; (1) shallower than the median valley.

Declarations

Competing interests The authors declare no competing interests.

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