

A brief review of Agenian rhinocerotids in Western Europe

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Abstract The Agenian is the earliest Neogene European Land Mammal Age. It encompasses the mammalian zones MN1 (23.03–22.7 Ma) and MN2 (22.7–20.0 Ma) and roughly coincides with the Aquitanian standard age. Agenian mammalian assemblages from Western Europe encompass a mixture of rhinocerotid taxa of Oligocene affinities and of Miocene newcomers, mostly recorded in France, Germany, Switzerland, and to a lesser extent, Spain. Rhinocerotidae are documented by seven species referred to five genera (*Pleuroceros pleuroceros*, *Protaceratherium minutum*, *Plesiaceratherium aquitanicum*, *Mesaceratherium paulhiacense*, *Diaceratherium lemanense*, *D. asphaltense*, and *D. aginense*), further attesting to a low suprageneric diversity. Their systematics, morphology, ecology, stratigraphical and geographical ranges are detailed in the present article. Occurrences and geographical ranges of all seven rhinocerotid species are illustrated on palaeogeographical maps of the circum-Mediterranean region at 23 Ma (MN1) and 21 Ma (MN2). The richest Agenian localities (Paulhiac, MN1; Laugnac, MN2) record a specific diversity similar to that of Orleanian rhinocerotid assemblages, with up to five/six associated species. All Agenian rhinocerotid species from Western Europe are

endemic to the concerned region, which is consistent with the complete geographic isolation of Western Europe by earliest Miocene times. However, all five genera are documented by twin species in coeval localities of South and Central Asia, which implies (1) vicariant speciation events by latest Oligocene times and (2) the existence of intermittent pathways for terrestrial megamammals such as rhinocerotids during the concerned interval.

Keywords Perissodactyla · Systematics · Biochronology · Palaeogeographical maps · Fossil record · Early Miocene

1 Introduction

The Agenian is the earliest Neogene European Land Mammal Age (ELMA). It encompasses the mammalian zones MN1 [23.03–22.7 Ma] and MN2 [22.7–20.0 Ma] (Mein 1975, 1999; Bruijn et al. 1992; Rögl 1999; Gradstein et al. 2004) and roughly coincides with the Aquitanian standard age (23.03–20.43 Ma; Rögl 1999; Steininger and Wessely 2000; Gradstein et al. 2004). Agenian land mammal assemblages contrast with the Late Oligocene assemblages (Arvernian ELMA) at Western European scale, primarily because many faunal elements became extinct at the Oligocene–Miocene transition or earlier, such as theridomyid rodents, hyracodontid and amynodontid rhinocerotoids, lophiomerycid ruminants, or anthracotheriine anthracotheriids (Prothero and Schoch 1989; Bruijn et al. 1992; BiochroM'97 1997; Huguency 1997; Erfurt and Métais 2007; Lihoreau and Ducrocq 2007; Métais and Vislobokova 2007).

The Agenian period predates the Orleanian ELMA (~Burdigalian and Early Langhian standard ages) that

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was a period of intense faunal interchanges between Europe, Asia, and Africa, partly related to the Proboscidean Datum Events (e.g., Antoine et al. 1997; Mein 1999; Becker et al. 2009; Sen 2013). Accordingly, Western European Agenian faunas lack later African and Asian immigrants such as primates, proboscideans, equid perissodactyls, listriodontine suoids, bovid and tragulid ruminants (Ginsburg 1990; Bruijn et al. 1992; Antoine et al. 1997, 2000, 2010, 2013; Orliac et al. 2006).

Rhinocerotidae were conspicuous elements of post-Eocene mammal faunas in Western Europe (e.g., Cuvier 1822; Duvernoy 1853; Osborn 1900; Roman 1912, 1924; Répelin 1917; Wood 1927; Guérin 1980; Cerdeño 1992, 1998; Antoine et al. 2000, 2003a; Becker 2003; Becker et al. 2009, 2010, 2013; Ménouret and Guérin 2009). Their alpha-diversity reached a climax by Early Miocene times, with five species or more co-occurring in various Agenian and Orleanian localities (Prothero and Schoch 1989; Cerdeño 1998; Heissig 1999; Antoine and Welcomme 2000; Antoine et al. 2000, 2010; Prothero 2005).

Agenian assemblages from Western Europe encompass a mixture of rhinocerotid taxa of Palaeogene affinities and of Miocene newcomers, the systematics and general characteristics of which (morphology, ecology, stratigraphical and geographical ranges) will be discussed hereunder.

2 Materials and methods

Western Europe is here considered as the landmass located south of Scandinavia and west of Poland, Czech Republic, Austria, Slovenia, and Croatia.

The suprageneric systematics within Rhinocerotidae follows the arrangement proposed by Antoine et al. (2010) and Becker et al. (2013).

Occurrences mentioned in the next section were either controlled by direct observation of the concerned specimens or based on bibliographical sources (e.g., Répelin 1917; Richard 1948; Bonis 1973; Brunet et al. 1987; Duranthon 1991; Cerdeño 1992; Heissig 1999; Becker 2003; Antoine et al. 2006; Becker et al. 2009, 2010, 2013).

The biochronological framework is basically that of Engesser and Mödden (1997), Gradstein et al. (2004), and Berger et al. (2005b).

The maximum geographical range illustrated for each Agenian rhinocerotid species (Figs. 1, 2) is mapped on earliest Miocene palaeogeographical reconstructions of Western Europe, by means of the Ocean Drilling Stratigraphic Network (ODSN) palaeomaps (www.ods.de/ods/services/paleomap/paleomap.html).

Fig. 1 Geographical range of non-teleoceratine Rhinocerotidae in the Agenian of Western Europe (23–20 Ma). **a–b**, *Pleuroceros pleuroceros* (Duvernoy, 1853) during the MN1 biozone (**a**) and the MN2 biozone (**b**). **c–d**, *Protaceratherium minutum* (Cuvier, 1822) during the MN1 biozone (**c**) and the MN2 biozone (**d**). **e–f**, *Plesiaceratherium aquitanicum* (Répelin, 1917) during the MN1 biozone (**e**) and the MN2 biozone (**f**). **g–h**, *Mesaceratherium paulhiacense* (Richard, 1937) during the MN1 biozone (**g**) and the MN2 biozone (**h**). Marine areas and landmasses appear in blue and yellow, respectively. Occurrences are indicated by red circles. Palaeogeographical maps at 23 Ma (MN1) and 21 Ma (MN2) are modified from Rögl (1999), Costeur et al. (2012), and <http://www.ods.de/ods/services/paleomap/paleomap.html>

3 Western European Agenian Rhinocerotidae

The Agenian rhinocerotid record for Western Europe is mostly documented in France, Germany, Switzerland, and to a lesser extent, Spain (Figs. 1, 2). To our knowledge, there is no rhinocerotid record for the concerned interval in Portugal (Antunes and Ginsburg 1983, 2000), Great Britain, Belgium, the Netherlands, Luxemburg, Czech Republic, Italy, or Austria, the territory of which is mostly covered by tidal- and/or marine-dominated sediments by Agenian times (Figs. 1, 2; Steininger and Wessely 2000; Becker et al. 2010; Costeur et al. 2012).

3.1 Systematic palaeontology

Order Perissodactyla Owen, 1848

Superfamily Rhinoceroidea Gray, 1821

Family Rhinocerotidae Gray, 1821

Subfamily Rhinocerotinae Gray, 1821

Unnamed clade

Pleuroceros Roger, 1898

Pleuroceros pleuroceros (Duvernoy, 1853)
(Figs. 1a–b, 3)

Menoceras zitteli (Schlosser, 1902)

Stratigraphical range. (?MP29/30) + MN1–MN2 (Hugueney 1997; Antoine et al. 2010; Becker et al. 2013).

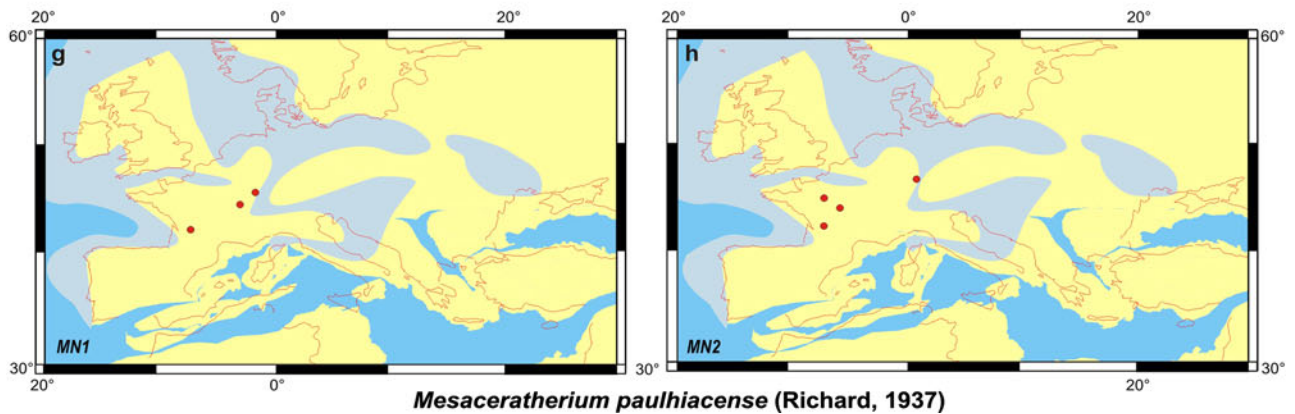
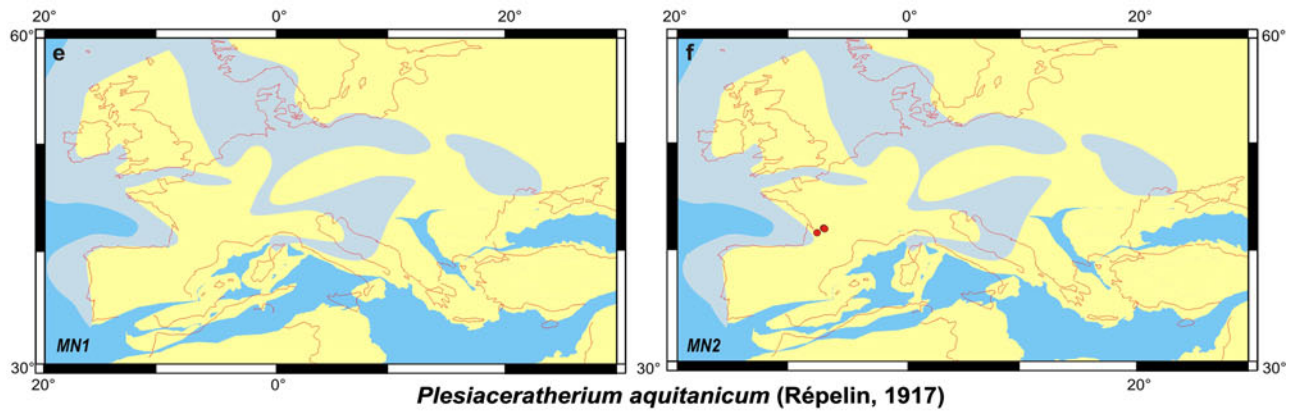
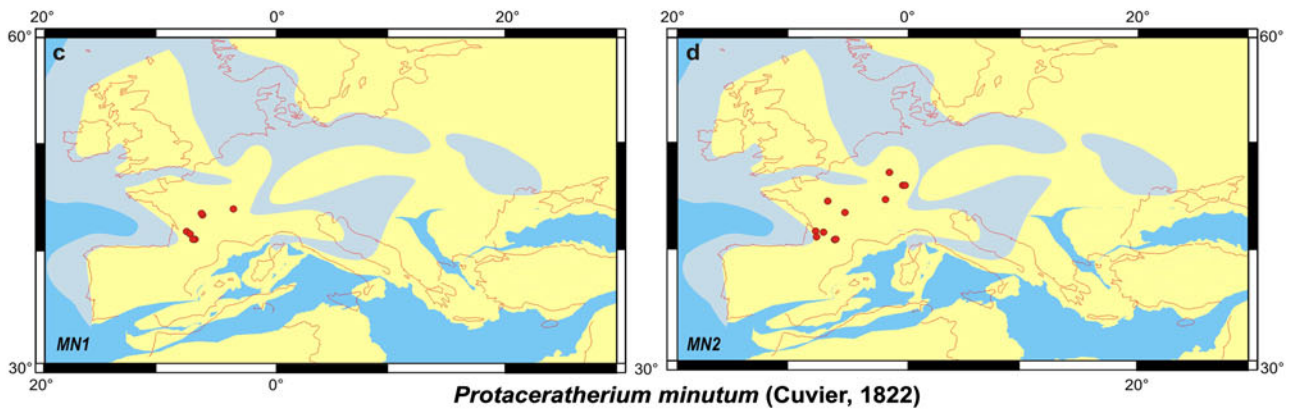
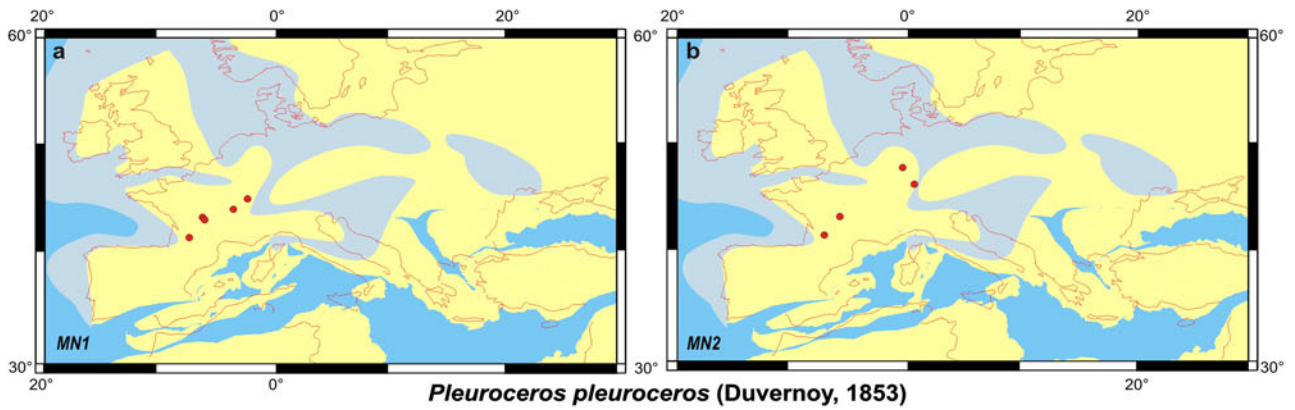
Agenian occurrences.

France: Gannat, MN1 (type locality); Paulhiac, MN1; Pyrimont-Challonges, MN1; Saulcet, MN1; Laugnac, MN2; Montaignu-le-Blin, MN2; (Duvernoy 1853; Lavocat 1951; Bonis 1973; Hugueney 1997; Ginsburg and Bulot 2000; Ménouret and Guérin 2009; Antoine et al. 2010; Becker et al. 2013)

Germany: Flörsheim, MN2; Pappenheim, MN2 (Schlosser 1902; Heissig 1999; Ménouret and Guérin 2009)

Switzerland: Wischberg, MN1 (Schaub and Hürzeler 1948; Heissig 1999; Becker 2003)

Pleuroceros pleuroceros is the type species of *Pleuroceros* Roger, 1898, otherwise documented by a coeval



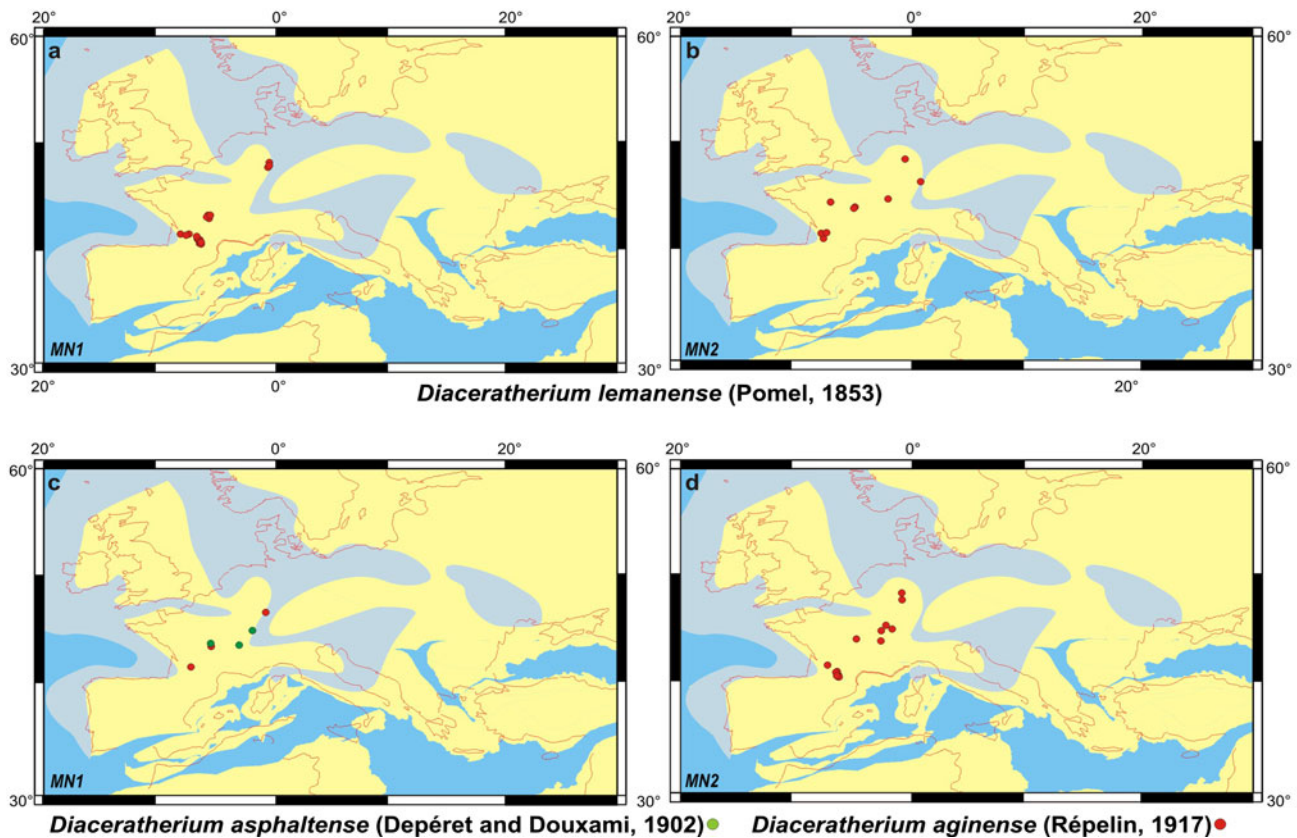


Fig. 2 Geographical range of teleoceratine Rhinocerotidae in the Agenian of Western Europe (23–20 Ma). **a–b** *Diaceratherium lemanense* (Pomel, 1853) during the MN1 biozone (**a**) and the MN2 biozone (**b**). All the occurrences from Toulouse, SW France, are represented by a single circle. **c** *Diaceratherium asphaltense* (Depéret and Douxami, 1902) and *D. aginense* (Répelin, 1917) during the MN1 biozone. **d** *Diaceratherium aginense* (Répelin, 1917) during the MN2

biozone. All the occurrences from the *Molasse grise de Lausanne* Formation, W Switzerland, are represented by a single circle. Marine areas and landmasses appear in blue and yellow, respectively. Occurrences are indicated by red circles (except for *D. asphaltense*: green circles). Palaeogeographical maps at 23 Ma (MN1) and 21 Ma (MN2) are modified from Rögl (1999), Costeur et al. (2012), and <http://www.odsn.de/odsn/services/paleomap/paleomap.html>

species, *Pleuroceros blanfordi* (Lydekker, 1884) from South Asia (Antoine et al. 2010). *Pleuroceros pleuroceros* is a small to medium-sized rhino, mediportal and quite short-limbed, with a three-toed manus and a pair of nasal horns (Fig. 3). Somewhat similar paired nasal horns occur in the North American elasmotheriine rhinocerotids *Diceratherium* Marsh, 1875 (Oligocene–Miocene) and *Menoceras* Troxell, 1921 (Early Miocene), but they were acquired independently in the latter genera (Heissig 1989, 1999; Antoine et al. 2010). Given its dental morphology (brachydonty) and limb proportions, *P. pleuroceros* was most likely a browser and a forest dweller. A subjective junior synonym of *P. pleuroceros* is *Menoceras zitteli* (Schlosser, 1902), the type locality of which is Pappenheim, Germany (MN2; Schlosser 1902; Heissig 1999).

Pleuroceros pleuroceros is generally considered as restricted to the Agenian ELMA (Antoine et al. 2010), but Hugué (1997) recognised it in the lowest levels of Billy (MP29–30), in central France. This would represent the earliest (and only ante-Miocene) occurrence of the



Fig. 3 Head-and-shoulders life reconstruction of the early diverging pair-horned rhinocerotine *Pleuroceros pleuroceros* (Duvernoy, 1853), from the Arvernian-Agenian of Western Europe (shoulder height: ca. 1.0 m; body mass: ca. 500 kg). Sketch by P.-O. Antoine

concerned taxon. Given the palaeogeography of Western Europe during Agenian times (Fig. 1), such an early

occurrence is compatible with a latest Oligocene vicariant event between South Asian and Western European *Pleuroceros*, leading to the *P. pleuroceros*–*P. blanfordi* split.

Protaceratherium Abel, 1910

Protaceratherium minutum (Cuvier, 1822)

(Fig. 1c–d)

Ceratorhinus tagicus Roman, 1907

Stratigraphical range. MP30-base MN4 (e.g., Antoine and Duranthon 1997; Antoine et al. 2000, 2006; Becker et al. 2013)

Agenian occurrences.

France: Beaupuy, MN1; Billy, MN1; Moissac-La Madeleine, MN1; Moissac-Saint-Laurent, MN1 (type locality); Moissac-Saint-Martin, MN1; Paulhiac, MN1; Pechbonnieu, MN1; Pyrimont-Challonges, MN1; Saulcet, MN1; Toulouse Ginestous, MN1; Barbotan-les-Thermes, MN2; Cintegabelle, MN2; Cintegabelle Montalivet, MN2; Gans, MN2; Gibel, MN2; Issus, MN2; Laugnac, MN2; Montaigu-le-Blin, MN2; Nicot, MN2; Pouvourville, MN2; Selles-sur-Cher, MN2; (Noulet 1861; Roman 1912, 1924; Richard 1948; Astre 1959; Bonis 1973; Ginsburg and Huguenev 1980; Duranthon 1991; Huguenev 1997; Heissig 1999; Ginsburg et al. 1991; Steininger et al. 1996; Antoine and Duranthon 1997; Ginsburg and Bulot 2000; Antoine et al. 2011; Becker et al. 2013)

Germany: Budenheim, MN2; Ulm-Westtangente, MN2 (Roman 1912, 1924; Bruijn et al. 1992; Cerdeño 1992; Heissig 1999; Uhlig 1999; Costeur et al. 2012)

Spain: Valquemado, MN2; Loranca del Campo, MN2 (Cerdeño 1989, 1992; Bruijn et al. 1992; Antoine and Duranthon 1997; Antunes and Ginsburg 2000; Ménouret and Guérin 2009)

Switzerland: La Chaux, MN2 (Schaub and Hürzeler 1948; Bruijn et al. 1992; Cerdeño 1992; Engesser and Mödden 1997; Becker 2003; Becker et al. 2009)

Protaceratherium minutum (Cuvier, 1822) is the type species of *Protaceratherium* Abel, 1910, an extinct genus which includes small and slender hornless stem rhinocerotids with tapir-like dimensions and habits (cursorial browser-forest dweller; Antoine 2002). Up to now, *Protaceratherium* was considered as comprising also another Western European species, “*Acerotherium albigense* Roman, 1912”, from the Oligocene (e.g., Roman 1912; Lihoreau et al. 2009), and sharing similar dimensions and proportions—but no synapomorphy—with *P. minutum* (Becker et al. 2013). Based on a formal phylogenetic analysis performed by Becker et al. (2013), the former species now typifies a new genus restricted to the Oligocene epoch.

P. minutum was very abundant throughout the Agenian interval in Western Europe (Fig. 1c–d). In particular, Roman (1924) described a subcomplete skeleton from Budenheim, Germany (MN2). Close relatives of *P.*

minutum (namely *P. cf. minutum* and *P. sp.*) were recognised in Toulouse-Borderouge (lower level) and in Coderet, respectively; these two coeval French localities are referred to the latest Oligocene reference level (MP30; Huguenev 1997; Antoine et al. 2006). This species survived well into the Orleanian ELMA, notably in France; its last occurrences are Artenay and Béon 2 (base MN4; e.g., Antoine et al. 2000).

Plesiaceratherium Young, 1937

Plesiaceratherium aquitanicum (Répelin, 1917)

(Fig. 1e–f)

Stratigraphical range. MN2–MN3 (Ginsburg and Bulot 2000; Sanisidro 2011)

Agenian occurrences.

France: Barbotan-les-Thermes, MN2; Laugnac, MN2; Nicot, MN2 (type locality) (Répelin 1917; Ginsburg et al. 1991; Antoine et al. 2000; Ginsburg and Bulot 2000).

Plesiaceratherium encompasses large hornless rhinocerotids, with much elongated nasals, long but robust limb bones, a four-toed manus, and interpreted as forest dwellers (Yan and Heissig 1986; Antoine 2002). This genus is well documented in Eurasia throughout the Early and early Middle Miocene, with various occurrences in China, South Asia, and Europe (Fig. 1e–f; e.g., Young 1937; Yan and Heissig 1986; Antoine et al. 2000, 2010; Peter 2002). The earliest representatives of this genus are *P. naricum*, from the earliest Miocene of Pakistan (~MN1–MN2, ~23–20 Ma; Antoine et al. 2010, 2013) and *P. aquitanicum*. *Plesiaceratherium aquitanicum* is mostly documented by teeth, typical of a large-sized browser, tentatively interpreted as a forest dweller (Répelin 1917; Ginsburg et al. 1991). The latest record of *P. aquitanicum* consists of two fragmentary teeth in the Early Orleanian locality of Estrepouy, in SW France (MN3; Sanisidro 2011).

Mesaceratherium paulhiacense (Richard, 1937)

(Fig. 1g–h)

pro parte Mesaceratherium gaimersheimense Heissig, 1969

Stratigraphical range. MP30–MN2

Agenian occurrences.

France: Paulhiac, MN1 (type locality); Pyrimont-Challonges, MN1; Laugnac, MN2; Montaigu-le-Blin, MN2; Selles-sur-Cher, MN2 (Richard 1948; Astre 1959; Heissig 1969; Bonis 1973; Duranthon 1991; Huguenev 1997; Ginsburg and Bulot 2000; Antoine et al. 2006, 2010; Ménouret and Guérin 2009)

Germany: Ulm-Westtangente, MN2 (Costeur et al. 2012)

Switzerland: Wischberg, MN1 (Schaub and Hürzeler 1948; pers. obs.)

Mesaceratherium paulhiacense was a medium-sized to large stem rhinocerotine, with long and slender limbs, as documented in Laugnac (Bonis 1973). The manus was four-toed, with extremely slender and elongated metapodials—among the slenderest ones among ceratomorph perissodactyls—, pointing to a cursorial locomotion (Bonis 1973). *Mesaceratherium paulhiacense* was probably hornless but cranial remains are virtually unknown so far (Antoine et al. 2010). This taxon is interpreted as a browser and open woodland dweller. The species *Mesaceratherium paulhiacense* is sometimes included in the genus *Alicornops* Ginsburg and Guérin, 1979, typified by *A. simorreense* (Lartet, 1851) from the Middle and Late Miocene of Eurasia (e.g., Heissig 1999; Heissig and Fejfar 2007). However, several recent parsimony analyses demonstrated that both genera were monophyletic and phylogenetically remote, *Mesaceratherium* (slender-limbed) and *Alicornops* (short-limbed) being part of stem Rhinocerotinae and of Aceratheriini, respectively (Antoine et al. 2003b, 2010; Becker et al. 2013).

Even if it is usually considered as a marker of the Agenian ELMA, *M. paulhiacense* was found in association with the theridomyid rodent *Issiodoromys bransatensis* in Toulouse Borderouge, SW France (middle level; Antoine et al. 2006). Hence the concerned locality dates back to the MP30, which makes it record the earliest *M. paulhiacense*; the latest local occurrence of *M. paulhiacense* is Tuhofice, Czech Republic (MN3; “*Aceratherium* (*Alicornops*) aff. *paulhiacense*”; Heissig and Fejfar 2007).

Tribe Rhinocerotini Owen, 1845

Subtribe Teleoceratina Hay, 1902

Genus *Diaceratherium* Dietrich, 1931

(Fig. 2)

Diaceratherium includes early diverging teleoceratine rhinocerotids ranging from the Late Oligocene up to the Early Miocene in Eurasia (e.g., Cerdeño 1993; Boada-Saña et al. 2008; Becker et al. 2009; Antoine et al. 2013). Although its earliest unambiguous representative (*D. lamilloquense* Michel, 1987 [in Brunet et al. 1987]) has rather slender limbs, later species of *Diaceratherium* get more and more short-legged (“brachypod”, with hippo-like proportions), which is particularly marked in *D. aurelianense* (Nouel, 1866), from the Orleanian of Western Europe. From the Late Oligocene up to the late Early Miocene, the representatives of *Diaceratherium* were generalist browsers that likely shifted from a *Dicerorhinus*-like ecology, in dense forested environments, to a hippo-like lifestyle, living in swampy areas and wetlands, close to riverine grasslands.

Diaceratherium is by far the commonest rhinocerotid genus in the Agenian of Western Europe (Fig. 2). It is mentioned in most localities referred to the MN1 and MN2 (see below).

This genus is also the only one to be documented by at least two species during the concerned interval: *D. lemanense* and *D. aginense* were long supposed to coincide with successive chronospecies (e.g., Répelin 1917; Brunet et al. 1987; Duranthon 1991; Martinez 1997; Marivaux 1999; Becker et al. 2009; Ménouret and Guérin 2009), being part of the Late Oligocene-Early Miocene anagenetic lineage (*D. massiliae* Ménouret and Guérin, 2009 [MP26]–*D. lamilloquense* (MP29)–*D. lemanense* (MN1)–*D. aginense* (MN2)–*D. aurelianense* (MN3-base MN4)). However, the generic attribution of *D. massiliae* remains doubtful by several non-*Diaceratherium* morphological features (e.g., humerus bearing a low fossa olecrani and a diablo-like trochlea of the distal articulation) and the co-occurrence of *D. lemanense* and of *D. aginense* is now attested in several Agenian localities from France and Switzerland, referred to both the MN1 and the MN2 (Fig. 2a–d; Boada-Saña et al. 2008; Becker et al. 2010). This would be consistent with niche-and-resource partitioning between *D. lemanense* and *D. aginense*, as it occurs during Pleistocene and Holocene times with the co-generic Asian rhinoceroses *Rhinoceros unicornis* Linnaeus, 1758 and *R. sondaicus* Desmarest, 1822 (Antoine 2012).

Diaceratherium lemanense (Pomel, 1853)

(Fig. 2a–b)

Stratigraphical range. MN1–MN2

Agenian occurrences.

France: Bazas, MN1; Bézac, MN1; Cagnac, MN1; Casteljaloux-Balade, MN1; Gannat, MN1 (type locality); Ginestous, MN1; Grenade-sur-Garonne, MN1; Labastide-Beauvoir, MN1; Pechbonnieu, MN1; Lamothe-Capdeville, MN1; La Roche-Blanche-Gergovie, MN1; Paulhiac, MN1; Pech David, MN1; Randan, MN1; Saint-Loup Cammas, MN1; Saint-Michel-du-Touch, MN1; Saulcet, MN1; Saverdun, MN1; Toulouse Borderouge (upper level), MN1; Toulouse Embouchure, MN1; Cindré, MN1/2; Barbotanles-Thermes, MN2; Gans, MN2; Laugnac, MN2; Montagu-le-Blin, MN2; Selles-sur-Cher, MN2 (Pomel 1853; Duvernoy 1853; Roman 1912; Richard 1948; Lavocat 1951; Astre 1959; Bonis 1973; Ginsburg and Huguenev 1980; Brunet et al. 1987; Duranthon 1991; Ginsburg et al. 1991; Huguenev 1997; Huguenev et al. 1999; Ginsburg and Bulot 2000; Antoine et al. 2006; Bentaleb et al. 2006; Boada-Saña et al. 2008; Becker et al. 2009, 2010)

Germany: Finthen, MN1; Oppenheim, MN1; Weisenau, MN1; Budenheim, MN2; Ulm-Michelsberg, MN2 (Roman 1924; Dietrich 1931; Tobien 1980; Becker et al. 2009)

Switzerland: Engehalde, MN2; Eschenbach, MN2 (Ooster and Fischer-Ooster 1871; Stehlin 1914; Becker et al. 2009, 2010)

Diaceratherium lemanense is known by various skulls from the earliest Miocene of France, Germany, and Switzerland (e.g., Pomel 1853; Lavocat 1951; Becker et al. 2009). In particular, the type locality of *D. lemanense*, Gannat (central France, MN1), yielded a complete skeleton in the mid-1800 s (Pomel 1853). New excavations led by the Rhinopolis Association in the last decades unearthed associated cranial and postcranial elements from dozens of individuals and allowed the reconstruction of complete composite skeletons, confirming a *Rhinoceros*-like general appearance. Accordingly, *D. lemanense* is interpreted as a medium-sized and mediportal bushland dweller, browser in the transitional zone between forest and grassland.

In our opinion, the right pes from La Roche Blanche-Gergovie (France, MN1), referred to as *Mesaceratherium paulhiacense* by Hugueney et al. (1999), belongs unambiguously to *D. lemanense*, as attested by several morphological features on the astragalus (calcaneal and fibular facets), calcaneus (twisted tuber calcanei), cuboid (posteromedial facet distinct from the proximal facet), and MtIII (proximal margin sigmoid).

The earliest remains of *D. lemanense* slightly predate the Miocene epoch, as they were recognised in the latest Oligocene of France, in both Billy (lower level, MP29-30; Hugueney 1997) and Toulouse Borderouge (middle level, MP30; Antoine et al. 2006) and possibly in Thézels (MP30; Brunet et al. 1987), as well as of Germany in Rott bei Bonn (MP 30; von Koenigswald et al. 1992; Mörs 2002). *Diaceratherium lemanense* mainly occurs in localities referred to the MN1, but it was also recognised in Late Agenian localities (MN2), such as Gans, Montaigu-le-Blin, Barbotan-les-Thermes, and Cindré (France), Budenheim and Ulm-Michelsberg, in Germany (Becker et al. 2009), or Eschenbach and Engehalde, in Switzerland (Fig. 2; Becker et al. 2009, 2010).

Diaceratherium asphaltense (Depéret and Douxami, 1902) (Fig. 2c)

Stratigraphical range. MN1

Agenian occurrences.

France: Pymont-Challonges, MN1; Saulcet, MN1 (Depéret and Douxami 1902; Hugueney 1997; Heissig 1999; Becker et al. 2009; Ménouret and Guérin 2009).

Switzerland: Wischberg, MN1 (Schaub and Hürzeler 1948; Becker et al. 2009)

Diaceratherium asphaltense was named by Depéret and Douxami (1902), based on associated remains including a skull, from Pymont-Challonges (MN1). The concerned skull has nasal bumps, testifying to the

presence of two small paired nasal horns in the corresponding individual. Nasal horns occur more or less frequently in various taxa of—usually hornless—teleoceratine rhinocerotids such as *Teleoceras* (a single horn; Mead 2000) or *Diaceratherium aurelianense* (paired horn bosses; undescribed specimen from Béon 2, Montréal-du-Gers (Bulot et al. 2009), stored in the *Muséum de Toulouse*). Most representatives of *Diaceratherium* are hornless, as is usual in teleoceratine Rhinocerotinae (e.g., Antoine 2002). This feature is perhaps a dimorphic trait, as observed in *Teleoceras* (Mihlbachler 2005). A large amount of morphological features of *D. asphaltense* (type material and referred material from Wischberg and Saulcet) was recently shown to be shared with *Diaceratherium aginense* (Boada-Saña 2008). If confirmed through a more comprehensive phylogenetic analysis (i.e. at Teleoceratina scale), this statement is likely to imply a synonymy between “*Diceratherium asphaltense* Depéret and Douxami, 1902” and “*Teleoceras aginense* (Répelin, 1917)”, the former having priority over the latter following the International Commission on Zoological Nomenclature (1999). This potential synonymy led us to illustrate the geographical range of both taxa in a single map (Fig. 2c): both the stratigraphical and geographical ranges of *D. asphaltense* (MN1; southeast quarter of France and Switzerland) fall within that of *D. aginense*. Given its general morphology, and likewise *D. aginense*, *D. asphaltense* can be interpreted as a medium- to large-sized graviportal rhinocerotid, inhabitant of swampy areas and wetlands, close to riverine grasslands.

Diaceratherium aginense (Répelin, 1917) (Fig. 2c–d)

Diaceratherium tomerdingense Dietrich, 1931

Stratigraphical range. MN1–MN2

Agenian occurrences.

France: Gannat, MN1; Paulhiac, MN1; Auterive, MN2; Beaupuy, MN2; Calmont Saint-Cernin, MN2; Cintegabelle, MN2; Grépiac, MN2; Laugnac, MN2 (type locality); Montaigu-le-Blin, MN2; Toulouse Pouvourville, MN2; Venerque, MN2 (Duvernoy 1853; Pomel 1853; Roman 1912; Répelin 1917; Lavocat 1951; Bonis 1973; Brunet et al. 1987; Duranthon 1991; Hugueney 1997; Ginsburg 2000; Ginsburg and Bulot 2000; Boada-Saña et al. 2008; Becker et al. 2009, 2010)

Germany: Tomerdingen, MN1; Budenheim, MN2; Hessler, MN2 (Roman 1924; Tobien 1980; Heissig 1999; Becker et al. 2009)

Switzerland: Engehalde, MN2; La Chaux, MN2; set of Swiss localities of the *Molasse grise de Lausanne* Formation (Béthusy, Chemin des Falaises, Haut du Calvaire, Maupas, Morrens, Moulin d’Assens, Rovéraz, Le Tunnel),

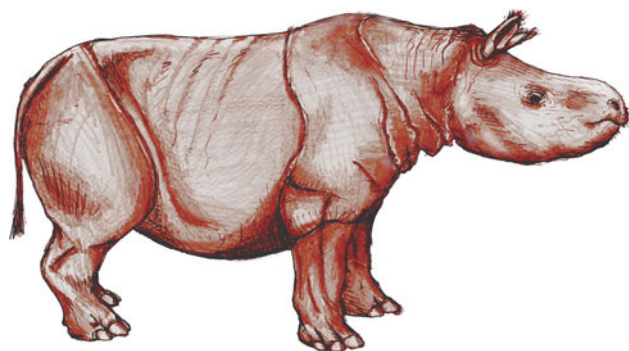


Fig. 4 Tentative life reconstruction of the teleoceratine rhinocerotine *Diaceratherium aginense* (Répelin, 1917), from the Agenian of Western Europe (shoulder height: ca. 1.3 m; body mass: ca. 1,500 kg). Sketch by P.-O. Antoine

MN2; Tavannes, MN2 (Engesser and Mödden 1997; Becker 2003; Becker et al. 2009, 2010; Mennecart 2012)

Diaceratherium aginense was first described by Répelin (1917), based on splendid associated cranial and postcranial remains from Laugnac (MN2). We propose a life reconstruction of this taxon, based on the concerned elements (Fig. 4). *D. aginense* is likely to be a junior synonym of *D. asphaltense* (see above).

D. aginense was long considered as a marker of the MN2 biozone, but its occurrence has been notably attested in both Paulhiac and Gannat localities, which yielded the most diversified MN1 mammal faunas from France (Boada-Saña 2008; Boada-Saña et al. 2008; Becker et al. 2010). No Orleanian occurrence is documented so far for *D. aginense*. Accordingly, *D. aginense* is a marker for the Agenian ELMA as a whole (MN1-MN2).

4 Discussion

At Western European scale, Agenian rhinocerotid alpha-diversity ([six or] seven species) is far from being as high as it was during the Orleanian (around 15 species; Prothero and Schoch 1989; Cerdeño 1998; Antoine et al. 1997, 2000). However, some Agenian localities, such as Paulhiac (MN1: *Pleuroceros pleuroceros*, *Protaceratherium minutum*, *Mesaceratherium paulhiacense*, *Diaceratherium lemanense*, and *D. aginense*) and Laugnac (MN2: same species plus *Plesiaceratherium aquitanicum*), include up to five/six co-occurring rhinocerotid species, which is comparable to what is observed during the Middle Orleanian (e.g., Montréal-du-Gers; Antoine et al. 2000). Nevertheless, Agenian rhinocerotid assemblages display both low suprageneric diversity (with only stem Rhinocerotinae [*Protaceratherium*, *Pleuroceros*, *Plesiaceratherium*, and *Mesaceratherium*] and Teleoceratina [*Diaceratherium* spp.]) and a high rate of endemism/

Oligocene inheritance at species level, by contrast with the Orleanian ones (Costeur et al. 2012). These Orleanian rhinocerotid faunas combine (1) Asian immigrants referred to Rhinocerotina (*Gaindatherium* Colbert, 1934 and *Lartetotherium* Ginsburg, 1974), Teleoceratina (*Brachypotherium* Roger, 1904 and *Prosantorhinus* Heissig, 1973), and Elasmotheriina (*Hispanotherium* Crusafont and Villalta, 1947) and (2) the last representatives of Late Oligocene/Agenian genera (*Protaceratherium*, *Plesiaceratherium*, and *Diaceratherium*; e.g., Antoine et al. 2000, 2003a).

All Agenian rhinocerotid species from Western Europe (*Pleuroceros pleuroceros*, *Protaceratherium minutum*, *Plesiaceratherium aquitanicum*, *Mesaceratherium paulhiacense*, *Diaceratherium lemanense*, *D. asphaltense*, and *D. aginense*) are endemic to the concerned region, *Plesiaceratherium aquitanicum* being only known in France so far (Fig. 1e–f). This high degree of endemism is not surprising at all, given the complete geographic isolation of Western Europe by earliest Miocene times (Figs. 1, 2). Interestingly, the situation is completely different at genus level, with all five genera being documented by twin species in coeval localities of South and Central Asia (*Pleuroceros blanfordi*, *Protaceratherium* spp., *Plesiaceratherium naricum*, *Mesaceratherium welcommi*, and *Diaceratherium fatehjangense*; e.g., Boada-Saña 2008; Antoine et al. 2010, 2013). Such homotaxic assemblages on both sides of the Transtethyan Trench Corridor/Rhine Graben seaway in the earliest Miocene of Eurasia may imply (1) vicariant speciation events by latest Oligocene times and (2) the existence of intermittent pathways for land megamammals as attested by the locations of Swiss and German Agenian rhinocerotid localities (Figs. 1, 2) and the Aquitanian palaeogeographic maps of the Upper Rhine Graben and the Swiss Molasse Basin (Berger et al. 2005a).

A short worldwide glaciation, recorded at the Oligocene–Miocene transition and designated Mi-1 (Zachos et al. 2001), probably influenced Western European climate, environments, and the concerned biocenoses during the Agenian interval (for review, Costeur et al. 2012). The climate was probably warm-temperate, with a low latitudinal thermal gradient, and “still relatively cold compared to the late Early Miocene context” (Costeur et al. 2012: 196).

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