

Evolutionary history of hoofed mammals during the Oligocene–Miocene transition in Western Europe

Laureline Scherler · Bastien Mennecart ·
Florent Hiard · Damien Becker

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Abstract The biostratigraphy and diversity patterns of terrestrial, hoofed mammals help to understand the transition between the Palaeogene and the Neogene in Western Europe. Three phases are highlighted: (1) the beginning of the Arvernian (Late Oligocene, MP25–27) was characterised by a “stable” faunal composition including the last occurrences of taxa inherited from the Grande Coupure and of newly emerged ones; (2) the latest Arvernian (Late Oligocene, MP28–30) and the Agenian (Early Miocene, MN1–2) saw gradual immigrations leading to progressive replacement of the Arvernian, hoofed mammals towards the establishment of the “classical” Agenian fauna; (3) the beginning of the Orleanian (Early Miocene, MN3–4) coincided with the African–Eurasian faunal interchanges of the Proboscidean Datum Events and led to complete renewal of the Agenian taxa and total disappearance of the last Oligocene survivors. Faunal balances, poly-cohorts and particularly cluster analyses emphasise these three periods and define a temporally

well-framed Oligocene–Miocene transition between MP28 and MN2. This transition started in MP28 with a major immigration event, linked to the arrival in Europe of new ungulate taxa, notably a stem group of “Eupecora” and the small anthracothere *Microbunodon*. Due to its high significance in the reorganisation of European, hoofed-mammal communities, we propose to name it the *Microbunodon* Event. This first step was followed by a phase of extinctions (MP29–30) and later by a phase of regional speciation and diversification (MN1–2). The Oligocene–Miocene faunal transition ended right before the two-phased turnover linked to the Proboscidean Datum Events (MN3–4). Locomotion types of rhinocerotids and ruminants provide new data on the evolution of environments during the Oligocene–Miocene transition and help understand the factors controlling these different phases. Indeed, it appears that the faunal turnovers were primarily directed by migrations, whereas the Agenian transitional phase mainly witnessed speciations.

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L. Scherler (✉)

Section d’archéologie et paléontologie, République et Canton du Jura, Office de la Culture, Hôtel des Halles, 2900 Porrentruy, Switzerland
e-mail: laureline.scherler@net2000.ch

B. Mennecart · F. Hiard

Département des Géosciences, Université de Fribourg, Chemin du Musée 6, 1700 Fribourg, Switzerland

D. Becker

Musée jurassien des sciences naturelles, Route de Fontenais 21, 2900 Porrentruy, Switzerland

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1 Introduction

During the last 25 years, many synthetic works on terrestrial mammals were published (e.g., Schmidt-Kittler 1987; Lindsay et al. 1989; Prothero and Schoch 1989; Aguilar et al. 1997; Rössner and Heissig 1999; Blondel 2001; Prothero and Foss 2007), explaining the evolutionary history of European faunas. They particularly highlighted biotic and abiotic events (e.g., Grande Coupure, Proboscidean Datum Events, Antarctic glaciations, Late Oligocene Warming, Middle Miocene Climatic Optimum) that likely had major impacts

on mammalian communities. Interestingly, most of these books treated independently the Palaeogene and Neogene faunas, but only a few papers specifically discussed the Oligocene/Miocene boundary (MP30-MN1; e.g., Hugueney 1984; Maridet et al. 2007; Costeur and Legendre 2008; Becker et al. 2009). Our study aims to link both periods, from the Late Oligocene to the Early Miocene, to better understand the transition (MP28-MN2) between Palaeogene and Neogene terrestrial mammals.

During the Late Oligocene, various climatic events are recognised (e.g., Antarctic glaciations, Late Oligocene Warming; Zachos et al. 2001; Pekar et al. 2006). To understand the evolutionary history of ungulates during the Oligocene–Miocene transition, it is important to include the last stage of the Palaeogene into the discussion. Indeed, the beginning of the Arvernian (MP25–26), which coincided with the outset of the Late Oligocene Warming (MP26–28; Vianey-Liaud 1991; Zachos et al. 2001), encompassed most of the last occurrences of Grande Coupure heritage taxa before they underwent a progressive faunal change in the latest Oligocene. The end of the Oligocene–Miocene transition is unmistakably demarcated by the migration waves linked to the Proboscidean Datum Events (Van Couvering and Berggren 1977; Antunes 1989; Tassy 1989), which began at the end of the Early Miocene (*Gomphotherium* and *Deinotherium* landbridges linked to the *Brachyodus* and *Creodont* Events, MN3–4, Orleanian; Van der Made 1999). Some authors already directed their research towards the evolution of selected Western European taxa during the Oligocene/Miocene boundary (e.g., Becker et al. 2009 for Rhinocerotidae; Scherler et al. 2011 for Tapiridae), and only Costeur (2005) and Costeur and Legendre (2008) treated the large mammal community as a whole, however without taxonomically reviewing the faunas.

The climatic and environmental context of the Late Oligocene, albeit showing a progressive degradation, remained relatively stable with the domination of temperate to tropical conditions and woodland environments in the northern hemisphere (Janis 1993; Prothero 1994; Becker 2003). The Late Oligocene Warming, primarily documented in the marine record (Zachos et al. 1997, 2001) and further observed in terrestrial environments (Vianey-Liaud 1991), took place between MP26 and MP28. It was followed by a decrease in temperature and humidity (e.g., Berger 1990) that led to the Mi-1 Glaciation Event (base of the Miocene; Pekar et al. 2006). During the Agenian (earliest Miocene), the general conditions remained dry although the environments became more scattered, represented by open landscapes and closed woodlands (Costeur 2005; Costeur et al. 2012). During the Orleanian, the humidity increased again, leading to the appearance of moist and swampy forests (Whybrow and Andrews 2000) and this situation peaked at the Middle Miocene Climatic Optimum (Zachos et al. 2001; Böhme 2003).

Based on a systematic review and an exhaustive literature control of Western European ungulates (Perissodactyla, terrestrial Cetartiodactyla, and Proboscidea), we describe the diversity trends and control factors recorded during the Oligocene–Miocene transition (MP28-MN2). Large mammals have been hypothesised to show an evolutionary inertia (Maridet and Costeur 2010) and better react to migratory events linked to biotic and abiotic changes when compared to small mammals, which evolve more rapidly.

2 Materials and methods

2.1 Distribution of localities

Our dataset originates from a 6-year-long work (2007–2012) of compiling European localities bearing fossils of hoofed mammals from the Early Oligocene to the Middle Miocene. From the initial 400, the present study considers 248 localities biostratigraphically dated from the mammal level MP25 to the mammal biozone MN4 (Online Resources 1 and 2), and assembled into 18 regions of Western Europe (Fig. 1; palaeoprovinces adapted from Costeur 2009). Although we principally focused on large ungulates, most of the studied localities were dated by small mammals. The other localities were correlated using large mammals of high biostratigraphic resolution (e.g., Eschenbach, Bavois, Béthusy).

2.2 Biochronology

The chronostratigraphical framework is based on geological time scales for the Palaeogene (Luterbacher et al. 2004) and Neogene (Steininger 1999; Lourens et al. 2004). Successions and durations of Oligocene mammal levels were established by Luterbacher et al. (2004), whereas mammal biozones for the Early Miocene were correlated by Berger (2011) based on biostratigraphic and magnetostratigraphic data from Mein (1999), Steininger (1999) and Agustí et al. (2001). The period chosen for this study ranges from MP25 to MN4 and encompasses the Arvernian (Late Oligocene, MP25–30), Agenian (Early Miocene, MN1–2), and the earliest Orleanian (Early Miocene, MN3–4) European land mammal ages (ELMA). This timeframe shows the transition from the last fauna with a Grande Coupure heritage to the first migrants linked to the Proboscidean Datum Events (*Brachyodus* and *Creodont* Events; Van der Made 1999).

2.3 Taxonomy

Under the term of ungulates and hoofed mammals, we take into account 24 families of Proboscidea (*Gomphotheriidae*, *Mammutidae*, *Deinotheriidae*), *Perissodactyla* (*Palaeotheriidae*, *Equidae*, *Tapiridae*, *Amyndontidae*, *Hyracodontidae*,

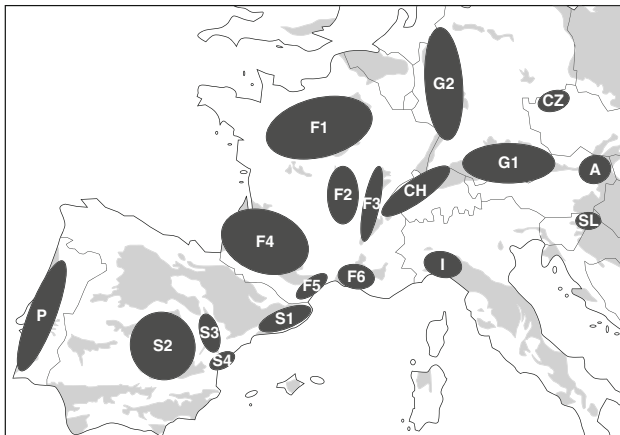


Fig. 1 Geographic positions of the regions of Western Europe (adapted and modified from Costeur 2009) gathering all the localities studied in this paper (see details in Online Resources 1 and 2). **A** Austria, **CH** North Alpine foreland Basin (Swiss Molasse Basin, Switzerland, and Savoy, France), **CZ** Northern Bohemia (Czech Republic), **F1** Paris Basin (France), **F2** Massif Central (France), **F3** Central East (France), **F4** Aquitaine Basin (France), **F5** Languedoc-Roussillon (France), **F6** Provence (France), **G1** Bayern and Baden-Württemberg (Germany), **G2** Bremen, Nordrhein-Westfalen and Rhine Graben (Germany), **I** Liguria (Italy), **P** Portugal, **SL** Pannonian Plain (Slovenia), **S1** Valles Penedes (Spain), **S2** Guadalajara-Madrid (Spain), **S3** Catalayud-Daroca-Teruel (Spain), **S4** Castillon-Valencia (Spain)

Rhinocerotidae, Chalicotheriidae), and terrestrial Cetartiodactyla (Anthracotheriidae, Entelodontidae, Palaeochoeriidae, Suidae, Dichobunidae, Cainotheriidae, Lophiomerycidae, Bachitheriidae, “Gelocidae”, Bovidae, Tragulidae, Cervidae, Palaeomerycidae, Giraffidae), as well as 19 species from undefined families of “Eupecora” (following Mennecart 2012, as highly derived ruminants in having aligned trochleae of the astragals, totally fused metapods, an elongated diastema c-p1/2, a basically elongated upper canine with a weak curve, a compact p4, and that can possess appendages; e.g., *Dremotherium guthi*, *Babameryx engesseri*, *Friburgomeryx wallenriedensis*). Altogether, we consider 127 species gathered in 72 genera (Online Resources 1 and 2). Most of the perissodactyls and terrestrial cetartiodactyls were reviewed by the authors (Becker et al. 2009, 2010, 2013; Scherler 2011; Scherler et al. 2011; Mennecart 2012; Mennecart et al. 2012b; Antoine and Becker 2013). The database was completed with information from the literature (see Online Resource 3 for exhaustive reference list) and the taxonomical attributions were homogenised following the last updates in systematics (e.g., Rössner and Heissig 1999; Prothero and Foss 2007).

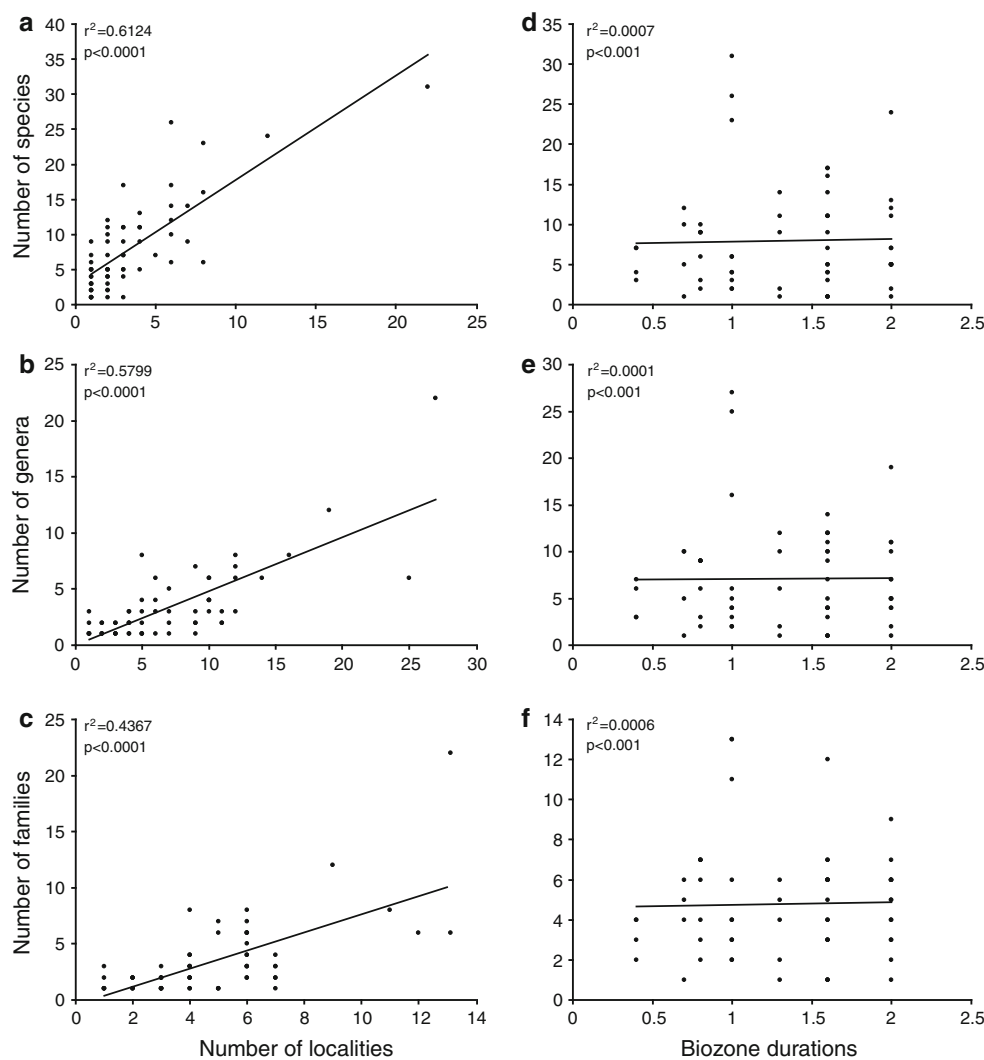
The taxonomical attribution of the postcranial remains of ruminants is mostly based on comparative anatomy and comparison of relative abundances with dental remains. Only a few localities provide associated teeth and bones, allowing direct determinations. However, most of the referred sites yield more than one taxon, sometimes of

roughly similar dimensions, where postcranial and dental elements are not connected. In this case, the taxonomical attribution of the bones are based on the compatibility of their size with the teeth. In the eventuality of similar dimensions, the relative abundance of the identified taxa (based on the dental remains) is associated, within a locality, with that of different morphotypes of bones.

Uncertain generic attributions for some of the considered taxa are expressed with quotation marks (“*Diaceratherium massiliae*”, “*Anthracotherium bumbachense*”, “*Anthracotherium hippoideum*”, “*Amphitragulus quercyi*”, “*Amphitragulus feningrei*”, “*Gelocus quercyi*”), as their phylogenetic relationships at the genus level are still debated. Furthermore, species of Rhinocerotidae and Anthracotheriidae have been synonymised. As for the enigmatic mid-Oligocene “*Diaceratherium massiliae*” Ménouret and Guérin, 2009 recorded in St-André (MP26; Ménouret and Guérin 2009), the same taxon was identified in Bumbach (MP25) based on postcranial elements (DB pers. obs.). However, the generic attribution of the fossils from Bumbach remains doubtful, since no dental remains of diacatheres were observed and the postcranial elements, although rather robust, clearly differ from those of *Diaceratherium* (Antoine and Becker 2013). Besides, a large amount of morphological features of *Diaceratherium asphaltense* are shared with *D. aginense* and *D. tomerdingense* (Boada-Saña et al. 2008). In this paper, *D. aginense* and *D. tomerdingense* are considered as junior synonyms of *D. asphaltense*, as it is suggested by Antoine and Becker (2013), even though these authors propose to perform a more comprehensive phylogenetic analysis first in order to confirm this synonymy.

The genus *Anthracotherium* encompasses all of the anthracotheriine anthracotheres from the Oligocene of Western Europe (Lihoreau and Ducrocq 2007). However, dental remains recorded in several localities (e.g., Bumbach, St-Menoux, Aarwangen) clearly morphologically differ from those of the true *Anthracotherium* (Scherler 2011). The relationship of “*Anthracotherium bumbachense*” and “*A. hippoideum*” with the genus is thus debatable. Furthermore, “*Anthracotherium cuvieri*” and *Anthracotherium valdense* are considered synonym of “*A. hippoideum*” and *A. magnum*, respectively (Scherler 2011). Regarding the ruminants, and in addition to the species of “Eupecora” without defined familial attributions, the clade “Gelocidae” is used as a “useful piece of descriptive nomenclatures” (Janis 1987), even though reassessment of the clade clearly demonstrates the polyphyly of the family (Mennecart et al. 2012a). Recent cladistic analyses proved that “*Gelocus quercyi*” and *Prodremotherium elongatum* are sister group and differ from the true *Gelocus* species in having, for example, more selenodont cusps and a better developed metaconule. Thus, they probably belong to a new tribe, implying that “*Gelocus quercyi*” should not be considered as a *Gelocus* species anymore (BM pers. obs.). Additionally, the relationship

Fig. 2 Relationship between species/genus/family richness with number of localities and biozone/level durations (in Ma) per regions. For each regression the correlation coefficient (r^2) and its significance (p) are provided



between the species of *Amphitragulus* and other genera of ruminants is still unresolved (Jehenne 1985; Blondel 1997; Mennecart et al. 2012b). For this reason, the genus for “*Amphitragulus*” *quercyi* and “*Amphitragulus*” *feningrei* is reported here using quotation marks (Mennecart et al. 2012b).

2.4 Sampling biases

The number of localities differs with regards to the various time intervals and significantly increases through time (from 6 localities during MP26 to 64 during MN4). Similarly, the number of species varies through time (from 11 species during MP27 to 54 during MN4). Based on these observations, the sample effort has been analysed to test the consistency of our interpretations (Fig. 2). There is no correlation ($r^2 < 0.001$; $p < 0.001$) between the number of species/genera/families and the duration of the levels/biozones (Fig. 2d–f). However, the repartition of the species/genera/families per number of localities does not seem to be

totally random (r^2 between 0.43 and 0.62; $p < 0.0001$; Fig. 2a–c). Therefore, our interpretations concentrate on faunal turnovers, balances, and appearances/disappearances, instead of considering raw taxonomic diversity, the latter being considerably controlled by sampling effort.

2.5 Diversity dynamics

The biostratigraphic range of each genus (Fig. 3) is based on its FAD and LAD (first/last appearance data). For the analyses of diversity dynamics, Lazarus taxa (e.g., the tapir *Protapirus* or the bothriodontine anthracothere *Elomeryx*) are considered as continuous through time from their FAD to their LAD. The trends of biodiversity are highlighted by the faunal balance and richness curves and by the survivorship poly-cohorts for each group of taxa. The faunal balance simply shows the difference between the number of originations and extinctions during one level/zone, and the generic/specific richness encompasses the total number of genera/species present during one level/zone. The

individual poly-cohort analysis, or survivorship poly-cohorts, is a standard analytic tool for the investigation of taxa survivorship for a given time span. It allows the visualisation of origination/immigration and extinction/emigration parts during the Oligocene–Miocene transition. In this study, we use the “nested” analyses, for which the survivorship curves simply illustrate the percentage of taxa still existing from an initial taxonomical assemblage until the last appearance of its last representative; these curves show the on-going decay of the assemblage by extinction of its constituent taxa (Escarguel and Legendre 2006). Additionally, the within-family diversification analysis of the whole community is illustrated by cumulated curves of percentage of families showing an increasing, stable, or decreasing specific richness from one biochronological unit to the next (Escarguel and Legendre 2006).

Finally, we performed two cluster analyses based on the Dice and the Jaccard similarity indices (see Sect. 3.2) using the PAST software (Hammer et al. 2001) in order to define the consistency of our palaeocommunities through time. According to Hammer (1999–2012), the Dice index for the absence/presence of data puts more weight on joint occurrences than on mismatches. When comparing two columns (or associations), a match is counted for all taxa with presences in both columns. The Dice index is expressed as $2M/(2M + N)$, where M is the number of matches and N the total number of taxa with presences in only one column. On the other hand, the Jaccard similarity index, highlighting absent/present taxa as well, and expressed as $M/(M + N)$, measures the similarity between samples, which increases the effect of dissimilarity between groups in comparison to the Dice index (Hammer 1999–2012; Arias and Whatley 2005). Accordingly, we constructed the clusters for both the Dice and the Jaccard similarity indices according to two methods: (1) with the “Unweighted Pair-Group Method with Arithmetic mean” (UPGMA), the clusters are joined based on the average distance between all members of both groups, and (2) with the “Single Linkage” or “Nearest Neighbour” method (SINGL), the clusters are joined based on the smallest distance between both groups (Hammer 1999–2012).

2.6 Ecomorphology

Ecomorphologic analyses on rhinocerotids and ruminants are provided in order to determine their locomotion types. The morphology of the postcranial skeleton of ungulates reflects different locomotor adaptations depending on their environmental preferences (e.g., Köhler 1993; Cerdeño and Nieto 1995; Cerdeño 1998). The metapods (distal segments of the limbs) are amongst the best-suited skeletal parts of vertebrates to reflect different adaptive trends (Cerdeño and Nieto 1995). At the same time, these bones are usually well preserved and offer a wide base for comparison.

The locomotion types (cursorial, mediportal, graviportal) of the rhinocerotids are defined from the slenderness of the central metapods (McIII) after calculation of the gracility index (GI; sensu Guérin 1980: transversal diameter of the diaphysis/length of the metapod). Following Becker et al. (2009), the locomotion types for rhinocerotids are defined as cursorial ($GI < 0.250$), mediportal ($GI = 0.250–0.300$) and graviportal ($GI > 0.300$).

Different types of ruminant feet can be recognised according to the characteristics expressed by Köhler (1993). Ruminants from wooded areas, corresponding to Köhler’s morphotype A, show splayed and aligned phalanges, which contribute to a better stability on moist soils. On the contrary, ruminants from open areas (corresponding to Köhler’s morphotype B) have parallel phalanges that prevent dislocation during fast running and bear an inter-phalangeal flexion of the digits, which permit a better absorbency of horizontal shocks (Köhler 1993). These different adaptations entail several differences in the articular surfaces of metapods and phalanges and in marks and furrows for the insertion of ligaments. Furthermore, the elongation of limb bones, particularly the metapods and the proximal phalanges, is a good indicator for corporeality (e.g., Christensen 2002). Moreover, Köhler (1993) reported the occurrence of intermediate forms, more difficult to categorise. In this study, the adaptations on 453 ruminant postcranial remains from 20 European localities were analysed and the specimens were classified into the three different types (A, B, or intermediate).

3 Results

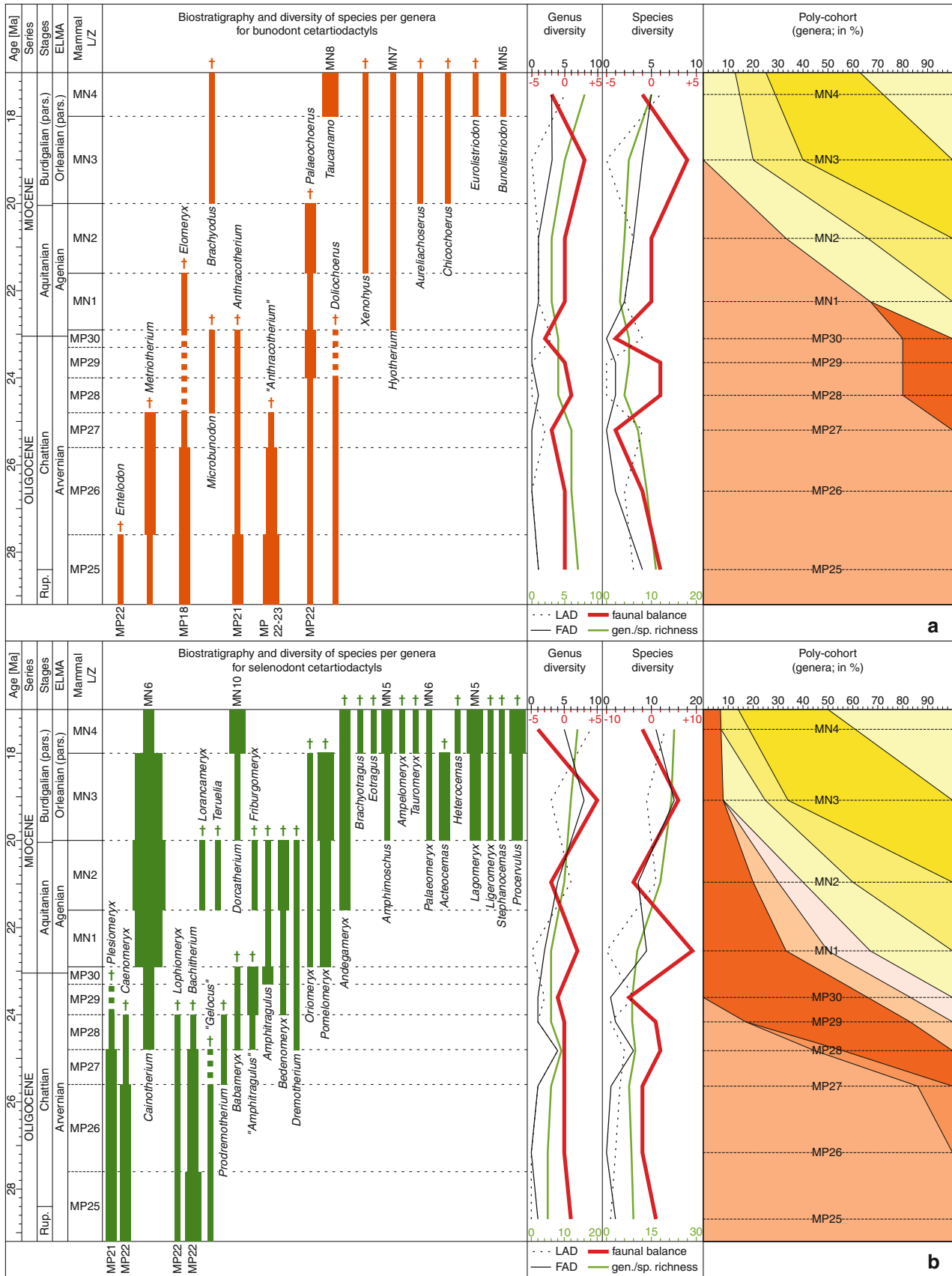
3.1 Evolutionary history of hoofed mammals

The temporal distribution of the studied genera is illustrated in Fig. 3. The detailed database with localities, faunal lists and references is provided as electronic supplementary material (Online Resources 1 and 2).

3.1.1 *Bunodont cetartiodactyls*

Five families are grouped under the expression “bunodont cetartiodactyls” (Fig. 3a), as their dental morphology is mainly characterised by bunodont cheek-teeth: Entelodontidae, Dichobunidae, Anthracotheriidae, Palaeochoeriidae, and Suidae, the two last families being encompassed in the superfamily Suoidea. These families were represented, during the Late Oligocene and the Early Miocene of Western Europe, by 16 genera and 28 species.

Most of the bunodont cetartiodactyls that were present during the Early Oligocene in Europe arrived with the migration waves linked to the Grande Coupure (MP21–22)



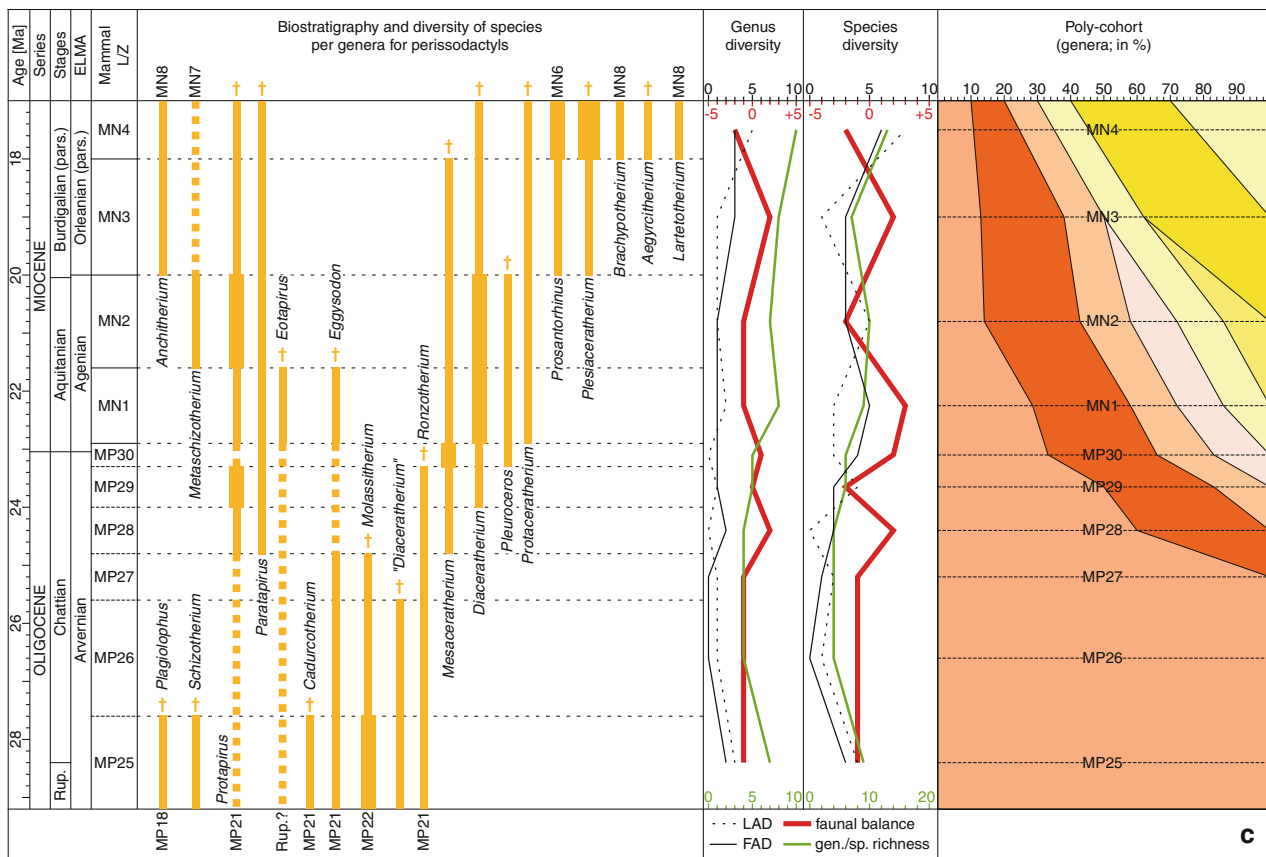


Fig. 3 continued

and disappeared well before the end of the Oligocene: *Entelodon deguilhemi* (Sudre 1995) and *Anthracotherium monsvialense* (Scherler 2011) already in MP25, *Elomeryx crispus* in MP26 (Lihoreau et al. 2007), “*Anthracotherium*” *hippoideum* and *Elomeryx borbonicus* in MP27 (Scherler 2011). The small anthracothere *Microbunodon* had a short-term occurrence in Western Europe from MP28 to MP30 and was represented by a single species, *M. minimum*, recorded in many localities of Austria, France, Germany, and Switzerland (Lihoreau et al. 2004; Scherler 2011). It vanished from this continent at the very end of the Oligocene (MP30), contemporaneously with the

disappearance of the large *Anthracotherium magnum* and the pig *Dolichochoerus quercyi*.

The bothriodontine anthracothere *Elomeryx* is documented shortly after the Oligocene–Miocene boundary, subsequently to a gap in its fossil record since MP28, but was only discovered in three localities of the early Aagenian so far (*Elomeryx minor* in Pyrimont-Challonges, Wischberg, and Urnäsch Tobels, all situated in the North Alpine foreland Basin and dated to the biozone MN1; Scherler 2011). On the opposite, the Palaeochoeridae, also rooted in Europe since the Early Oligocene, were still represented by three species of *Palaeochoerus* (*P. pusillus*, *P. typus* and *P. cf. gergovianus*) in MN1 and MN2 (Hellmund 1992; Scherler 2011). The first Suidae, or true pigs, arrived in Western Europe in MN1 with the small species *Hyotherium meissneri* (Van der Made 2010). Their diversity amplified rapidly with the successive appearances of *Xenohyus venitor* (MN2; Hünermann 1999; Van der Made 2010), *Aureliachoerus aurelianensis* and *Chicochoerus minus* (MN3; Hünermann 1999; Orliac et al. 2006), and *Eurolestriodon tenarezensis* and *Bunolestriodon lockharti* (MN4; Fortelius et al. 1996; Orliac et al. 2006). After a gap in their biostratigraphical record during MN2, the bothriodontine anthracotheres re-colonised briefly on this part of the

◀ **Fig. 3** Temporal ranges of ungulate genera from MP25 (Arvernian) to MN4 (Orleanian) and evolution of the diversity trends (faunal balance, genus/species richness, origination/extinction curves, survivorship poly-cohort [%]) through time. **a** Bunodont cetartiodactyls; **b** Selenodont cetartiodactyls; **c** Perissodactyls (data from Online Resources 1–2). ELMA is for European Land Mammal Ages, and the dashed lines in the Mammal L/Z (Level/Zone) column correspond to the supposed boundaries delimiting the ranges of the Oligocene localities referred to a given European Mammalian Reference Level (according to Luterbacher et al. 2004). The bold dashed lines of the temporal ranges illustrate supposed/uncertain occurrences of a genus. The FAD and LAD of each genus are precised when not comprised in the time spanned (before MP25 or after MN4)

continent through the arrival in MN3 of *Brachyodus onoides* from Africa (Van der Made 1999; Scherler 2011). The occurrence of several species of *Taucanamo* from MN4 onwards (*T. aff. sansaniense*, *T. primum*, *T. grandaevum*) led to the re-establishment of palaeochoeres in Europe (Orliac et al. 2006).

3.1.2 *Selenodont cetartiodactyls*

During the same time interval (MP25 to MN4), the selenodont cetartiodactyls (Fig. 3b) were represented by no less than 60 species gathered in thirty-one genera. This term gathers here nine families: the Cainotheriidae, Lophiomerycidae, Bachitheriidae, “Gelocidae”, Cervidae, Bovidae, Palaeomerycidae, Giraffidae, Tragulidae, as well as the representatives of undefined families of “Eupecora”.

The cainotheres appeared in Europe before the Grande Coupure event (Blondel 2005). Both genera were present in the Early Oligocene and vanished before the end of the Arvernian, with the extinction of *Caenomeryx filholi* in MP28, probably contemporaneous to that of *Plesiomeryx huerzeleri* (Schmidt-Kittler 1987; Blondel 2005). These genera were slightly more diversified at the beginning of the Arvernian, but were progressively replaced by the arrival of *Cainotherium*, first occurring in Western Europe in MP28 with two species (*C. geoffroyi* and *C. commune*). In the Early Agenian, the biodiversity of cainotheres exploded and reached its highest point during MN2, with no less than six contemporaneous species. After a progressive decrease, the history of the genus ended in MN6, during the Middle Miocene (Berthet 2003).

The Ruminantia entered Europe in the earliest Oligocene. However, only three genera are recorded during the beginning of the Arvernian (MP25-26; *Lophiomeryx*, *Bachitherium*, and “*Gelocus*”). Their diversity began to significantly rise in the latest Oligocene (Mennecart 2012; Mennecart et al. 2012a), with the successive appearances of *Prodremotherium elongatum* in MP27, *Babameryx engeseri*, “*Amphitragulus quercyi*” and *Dremotherium guthi* in MP28, *Bedenomeryx milloquensis* and “*Amphitragulus feningrei*” in MP29, and *Amphitragulus primaevus* in MP30 (Jehenne 1987; Mennecart 2012; Mennecart et al. 2012b). During the Agenian, the genera *Oriomeryx* and *Pomelomeryx* arrived in Europe in MN1 (with *O. major*, *P. boulangeri*, and *P. gracilis*), and the mammal level MN2 showed the first (and temporary) record of the Giraffidae (*Lorancameryx pachyostoticus* and *Teruelia adroveri* in Spain), as well as other new occurrences of “Eupecora” (*Friburgomeryx wallenriedensis*, *Bedenomeryx truyolsi*, *Andegameryx andegaviensis*, and *A. laugnacensis*; Gentry et al. 1999; Becker 2003). Most of the abovementioned genera disappeared in MN2 (e.g., *Amphitragulus*, *Dremotherium*, *Bedenomeryx*), and only a few of them survived

until their complete extinction in Europe in MN3 (*Oriomeryx*, *Pomelomeryx*) and MN4 (*Andegameryx*). The first representatives of the Bovidae (*Brachyotragus*, *Eotragus*), Cervidae (e.g., *Acteocemas*, *Lagomeryx*, *Procervulus*), Palaeomerycidae (*Ampelomeryx*, *Tauromeryx*, *Palaeomeryx*), and Tragulidae (*Dorcatherium*) appeared only in MN3 or MN4 in Western Europe (Gentry 1994; Gentry et al. 1999), coming with the first migrations linked to the Proboscidean Datum Events; their diversification increased abruptly as they progressively replaced the Agenian fauna.

3.1.3 *Perissodactyls*

Seven families of perissodactyls (Fig. 3c) are considered in this study: the Tapiridae, Palaeotheriidae, Equidae, Amynodontidae, Hyracodontidae, Rhinocerotidae, and the Chalicotheriidae. They were represented, in Western Europe, by 21 genera and 35 species during the Late Oligocene and the Early Miocene.

Plagiolophus minor was an Eocene relic of the endemic, ante-Grande Coupure, European fauna and was already present at MP18 (Lutetian, Late Eocene), along with other palaeotheres (Brunet and Jehenne 1989). This family flourished before the Grande Coupure event with several species (e.g., *Palaeotherium curtum*, *Plagiolophus major*), but only *Plagiolophus minor* survived after MP20 and until MP25 (Joomun et al. 2010), when its last representatives became extinct (LAD in Le Garouillas, France; Remy 1995).

All other Oligocene perissodactyls were migrant of the Grande Coupure and arrived during the Suevian (Early Oligocene) in Western Europe (Prothero and Schoch 1989; Becker 2009; Scherler et al. 2011). The Amynodontidae, represented by *Cadurcotherium minus*, disappeared at the same time as the Palaeotheriidae (LAD in MP25, Rigal-Jouet and Le Garouillas, France; De Bonis and Brunet 1995). During the same mammal level, the chalicotheres *Schizotherium priscus* appeared for a short time, being recorded in a single French locality (Le Garouillas, France; De Bonis 1995). Interestingly, another sporadic occurrence of this family was documented much later with the species *Metaschizotherium wetzleri*, during the Agenian of Germany (Eggingen-Gemeindesteinbruch and Ulm-Westtangente, MN2; Costeur et al. 2012). The Hyracodontidae, flourishing during the Suevian, were only represented by one species since MP24, *Eggysodon gaudryi*. This species was rare and only recorded in few localities until MP27 (LAD in Aarwangen, Switzerland; Becker 2003). After a gap in its fossil record, this Lazarus taxon reappeared in the locality of Gannat-sommet (MP30/MN1, France) with *Eggysodon pomeli* (Uhlig 1999).

The true rhinoceroses (Rhinocerotidae) were diverse and common during the Oligocene and the Early Miocene. The taxa linked to the Grande Coupure migrants became

extinct during the Arvernian: *Molassitherium delemon-tense* in MP25 (Becker et al. 2013), followed by *Molassitherium albigenense* in MP27 (Bavois, Switzerland, DB pers. obs.) and *Ronzotherium romani* in MP29 (Menecart et al. 2012b). However, successive appearances occurred since the latest Oligocene, with the arrivals of *Mesaceratherium gaimersheimense* in MP28 (Heissig 1969), *Diaceratherium lamilloquense* in MP29 (Brunet et al. 1987), *Pleuroceros pleuroceros* in MP30 (Antoine and Becker 2013), and *Protaceratherium minutum* in MP30/MN1 (Antoine and Becker 2013). Nevertheless, none of these four genera survived long during the Orleanian (LAD already in MN2 (Agenian) for *Pleuroceros*, in MN3 for *Mesaceratherium*, and MN4 for *Diaceratherium* and *Protaceratherium*; Antoine and Becker 2013). At this time, the complete renewal of the rhinocerotid fauna began with the arrival of new taxa recorded in many European localities, such as *Plesiaceratherium aquitanicum* already in MN2 (Antoine and Becker 2013), *Prosantorhinus douvillei* in MN3 (e.g., Chilleurs/Neuville-aux-Bois, France; Antoine et al. 2000), and *Brachypotherium brachypus*, *Aegyrcitherium beonense*, and *Lartetotherium sansaniense* in MN4 (e.g., Baigneaux-en-Beauce, Pellecahus, France; Charneca de Lumiar, Portugal; Antoine et al. 2000). The equid *Anchitherium aurelianense* arrived along with these

new genera. Besides, this taxon is the biostratigraphical marker for the base of biozone MN3 (Mein 1999; Bernor and Armour-Chelu 1999).

According to Cerdeño and Ginsburg (1988) and Scherler et al. (2011), the tapirs were represented during the Early Oligocene by the genus *Protapirus*, which rarely and sporadically occurred in the Suevoian, and mostly in not well-dated localities (mainly in the Quercy Phosphorites, France). This family only began to diversify at the end of the Arvernian and beginning of the Agenian, with the successive appearances of three species of *Protapirus* (*P. bavaricus* in MP27, *P. aginensis* in MP29, and *P. douvillei* in MN1). The genus *Paratapirus*—with the species *P. helvetius*—was already present in the latest Oligocene, but in only two Swiss localities (Othmarsingen and Haslen, MP28–30). *Paratapirus intermedius* colonised several regions of Western Europe throughout the Early Miocene (LAD in MN4), all along with the smaller *Protapirus douvillei*. During the Agenian, two other species locally occurred: *Eotapirus broennimanni* in MN1 in the North Alpine foreland Basin (Pyrimont-Challonges, France, and Wischberg, Switzerland), and *Protapirus cetinensis* in MN2a in Spain (Valquemado, Cetina de Aragón). The primitive tapirs vanished completely from Western Europe by the end of MN4.

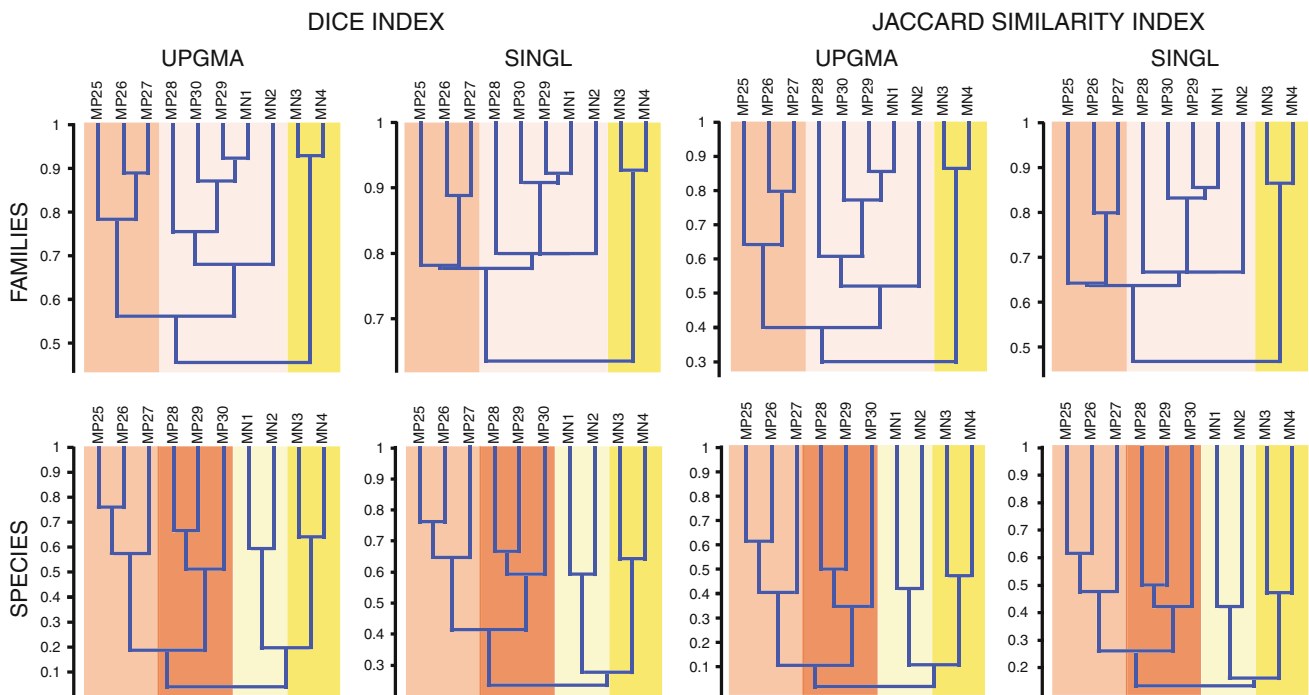


Fig. 4 Dendrograms from cluster analyses on the ungulate assemblages of Western Europe during the time interval MP25 to MN4, at the familial and specific levels. The similarity indices used are the

Dice Index and the Jaccard Similarity Index, and the clustering techniques are the “Unweighted Pair-Group Method with Arithmetic mean” (UPGMA) and the “Single Linkage” (SINGL)



3.1.4 Proboscideans

The first occurrences of proboscideans in Europe (see Online Resource 2 for the detailed localities and

references) are dated to MN3, with the French record of *Zygodolophodon turicensis* in Marsolan and *Gomphotherium* cf. *sylvaticum* in Mauvières (Antoine et al. 1997). In MN4, this group expanded with representatives being recorded in

◀**Fig. 5** Morphological evolution of third metacarpals of European Rhinocerotidae during the Oligocene–Miocene transition (MP25–MN4). Scale bar = 10 cm. The values of the gracility index (GI) are given only when the calculation was possible. The drawings are from DB's personal observations (specimens housed in the Naturhistorisches Museum Basel, NMB, and the Naturhistorisches Museum der Burgergemeinde Bern, NMBE) and from the literature. **1–2:** *Molassitherium delemontense* from (1) Bumbach (MP25, NMBE-D1567) and (2) Puy de Vaur (Late Oligocene; Michel 1983, pl. X.a1); **3–4:** *Ronzootherium romani* from (3) Bumbach (MP25, NMB-Um7) and (4) Le Garouillas (MP25; GI: 0.192; De Bonis and Brunet 1995, fig.4b); **5:** *Molassitherium albigense* from Saint-André (MP26, NMB-Mar354b; GI: 0.174); **6:** “*Diaceratherium*” *massiliae* from Saint-André (MP26; GI: 0.305; Ménouret and Guérin 2009, figs. 13b, 14a, tab. S8); **7:** *Ronzootherium romani* from Rickenbach (MP29; Mennecart et al. 2012b, fig.4); **8–9:** *Diaceratherium lamilloquense* from (8) Rickenbach (MP29; Mennecart et al. 2012b, fig.4) and (9) La Milloque (MP29; GI: 0.281; Brunet 1979, fig. 16d; Michel 1983, fig. 14.b1, pl. Xc1); **10:** *Diaceratherium* aff. *lemanense* from Thézels (MP30; GI: 0.281; Michel 1983, pl. Xb); **11:** *Mesaceratherium paulhiacense* from Paulhiac (MN1; GI: 0.192; De Bonis 1973, fig. 38.1a); **12–13:** *Pleuroceros pleuroceros* from Paulhiac (MN1), (12) GI: 0.272 female (De Bonis 1973, fig. 43.1a) and (13) GI: 0.279 male (De Bonis 1973, fig. 44.1); **14:** *Diaceratherium lemanense* from Gannat (MN1, NMB-Gn39; GI: 0.291); **15–17:** *Diaceratherium asphaltense* from (15–16) Pyrimont (MN1, UCBL-213011 and UCBL-213012; GI: 0.331, respectively) and (17) Saulcet (MN1, MHNG-v4988; GI: 0.327); **18:** *Protaceratherium minutum* from Budenheim (MN2; GI: 0.200; Roman 1924, fig. 13, pl. IV.4); **19:** *Diaceratherium lemanense* from Laugnac (MN2; GI: 0.286; De Bonis 1973, fig. 30.1a); **20:** *Diaceratherium asphaltense* from Laugnac (MN2, NMB-Cg194; GI: 0.343); **21–22:** *Diaceratherium aurelianense* from Artenay (MN4), (21) NMB-So3182; GI: 0.431 and (22) GI: 0.374 (Cerdeño 1993, tab. III, pl. III.4); **23:** *Lartetotherium sansaniense* from Coca (MN6; GI: 0.228; Cerdeño 1986, pl. 2.3a); **24:** *Plesiaceratherium mirallesi* from Pellecahus (MN4; GI: 0.241; Antoine et al. 2000, fig.1.1, tab. 1); **25:** *Brachypotherium brachypus* from Chevilly (MN4; GI: 0.378; Cerdeño 1993, tab. 5, tab. VII, pl. VI.5); **26:** *Prosantorhinus douvillei* from Chevilly (MN4; GI: 0.413; Cerdeño 1996, tab. 5, pl. 19.7)

many French, Spanish or Portuguese localities with the arrival of *Gomphotherium angustidens*, *Archaeobelodon filholi*, and *Prodeinotherium bavaricum* (e.g., La Romieu, Buñol, Quinta das Pedreiras; Göhlich 1999).

3.2 Cluster analyses

The clusters obtained from the Dice and the Jaccard similarity indices are illustrated in Fig. 4. These analyses were run at the familial and specific levels. Four groups are highlighted at the specific level instead of only three at the familial one. However, in both cases, the groups gathering together the periods MP25–27 and MN3–4 are well separated from the other levels/zones. The period MP28–MN2 forms a homogeneous set considering the families only, but two distinct assemblages (MP28–30 separated from MN1–2) arise when the specific level is considered.

3.3 Ecomorphology and locomotion types

3.3.1 Rhinocerotids

With respect to the outline of the third metacarpal in anterior view, Fig. 5 represents the slenderness diversity through time of European Rhinocerotidae from the Late Oligocene to the Early Miocene. The evolution of locomotion types shows a progressive decrease in gracility from the beginning of the Arvernian to the end of the Orleanian.

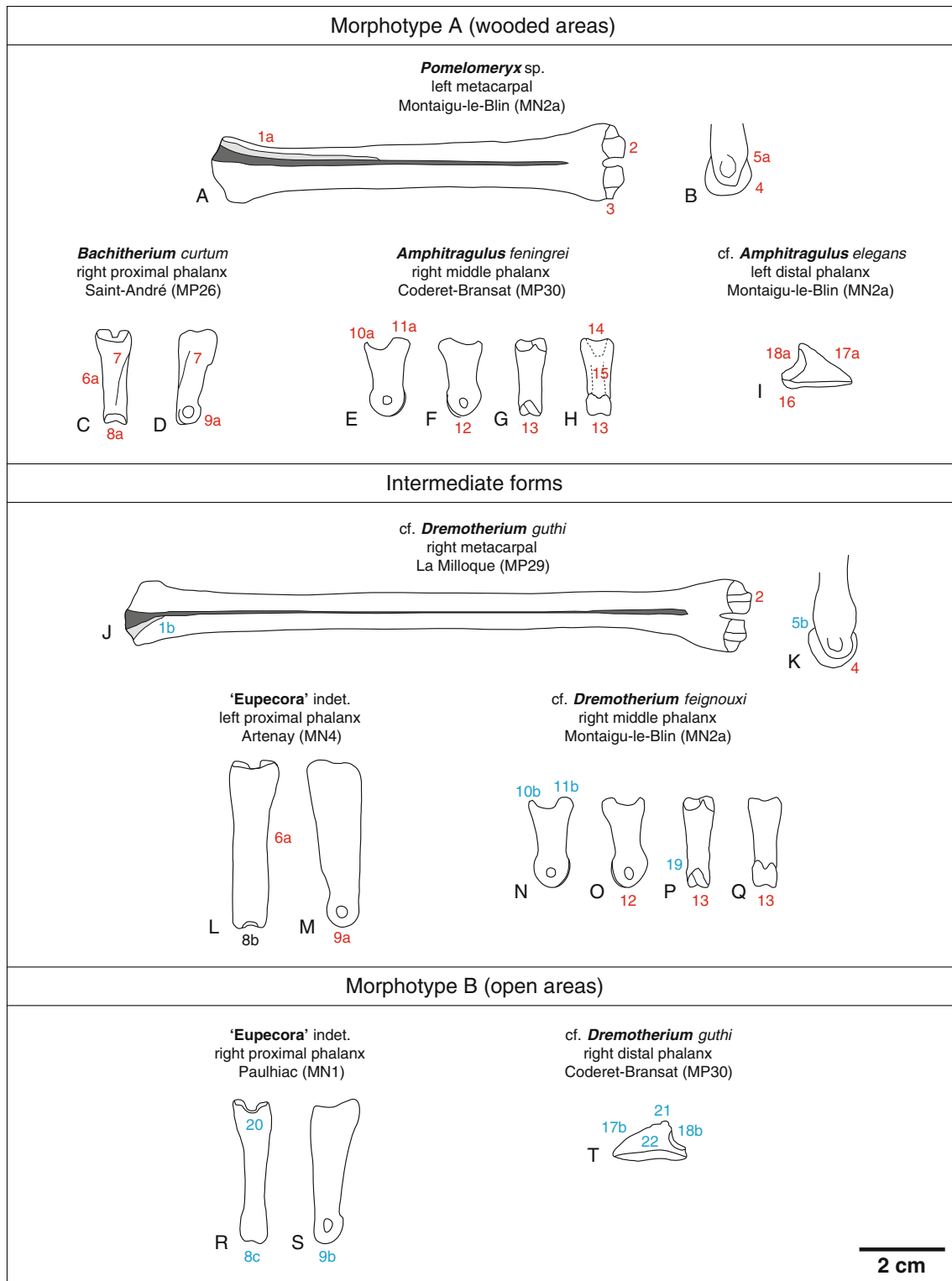
The early European rhinocerotids were mostly cursorial, as determined by the slender metapods of *Ronzootherium* and *Molassitherium* (Fig. 5, sketches 1–5 and 7). The slightly younger *Mesaceratherium* (Fig. 5, sketch 11), from the latest Oligocene (FAD in MP28) to its disappearance in MN4, also shared such a morphology and locomotion type. Additionally, the short-term occurrence of the enigmatic “*Diaceratherium*” *massiliae* (Fig. 5, sketch 6), with broad and short metapods, attested to the presence of graviportal forms during the early Arvernian (MP25–26).

The first mediportal forms appeared during the latest Oligocene (MP29–30) with *Diaceratherium* (*D. lamilloquense* and *D. lemanense*) and *Pleuroceros* (Fig. 5, sketches 8–10, 12–14 and 19) and lasted until the end of the Agenian (MN2). The rhinocerotids of this period were represented by a high diversity of anatomical types, covering all three categories, with the presence of the cursorial *Protaceratherium* (Fig. 5, sketch 18) and the appearance of the graviportal species *D. asphaltense* in MN1 (Fig. 5, sketches 15–17 and 20). The Orleanian was emphasised by the disappearance of the intermediate type, giving way to new taxa like the cursorial *Lartetotherium sansaniense* and *Plesiaceratherium mirallesi* (Fig. 5, sketches 23–24), and the graviportal *D. aurelianense*, *Brachypotherium brachypus* and *Prosantorhinus douvillei* (Fig. 5, sketches 25–26).

3.3.2 Ruminants

Figure 6 illustrates the different morphotypes (A, B, and intermediate forms) as inferred from postcranial bones (metapods and phalanges) of Ruminantia from European localities dated to the Late Oligocene and the Early Miocene; principal ecomorphologic features, as defined by Köhler (1993), are indicated for each fossil.

Fossils from localities dated from MP25 to MP27 present the characteristics of morphotype A: the metapods bear weak and flattened distal articular surfaces and a broad sulcus, and the proximal phalanges (e.g., *Bachitherium curtum* (NMB-Mar440) from St-André, France, MP26; Fig. 6, sketches C–D) are broad with a straight outline of the external side, a well-rounded distal articulation and a strong sulcus for the interosseus tendon. The middle



phalanges are broad and show an elongated post-articular plateau, a short dorsal extensor process and the outline of the distal articular surface, from the internal aspect, is triangular with a distally directed angle. Furthermore, the distal part of a metatarsal bone of "*Gelocus*" *quercyi*

(NMB-UM2292) from Mümliswil-Hardberg (MP26, Switzerland) is transversally inflated with very low and flattened condyles: this morphology corresponds to Köhler's (1993) subtype A2 and is characteristic of small ruminants living in wooded and very humid environments.

◀**Fig. 6** Postcranial remains of Oligocene and Miocene European ruminants, main morphologies. **A–B:** Left metacarpal of *Pomelomeryx* sp. from Montaigu-le-Blin (Naturhistorisches Museum Basel NMB-Ma3796), dorsal view (A), and lateral view of the distal articulation (B); **C–D:** Right proximal phalanx of *Bachitherium curtum* from Saint-André (NMB-Mar440), dorsal (C) and interdigital (D) views; **E–H:** Right middle phalanx of *Amphitragulus feningrei* from Coderet-Bransat (NMB-Cod875), external (E), interdigital (F), dorsal (G), and palmar (H) views; **I:** Left distal phalanx of cf. *Amphitragulus elegans* from Montaigu-le-Blin (NMB-Ma7131), interdigital view; **J–K:** Right metacarpal of cf. *Dremotherium guthi* from La Milloque (NMB-Lm1127), dorsal view (J), and lateral view of the distal articulation (K); **L–M:** Left proximal phalanx of “*Eupecora*” indet. from Artenay (NMB-So6211), dorsal (L) and interdigital (M) views; **N–Q:** Right middle phalanx of cf. *Dremotherium feignouxi* from Montaigu-le-Blin (NMB-Ma4233), external (N), interdigital (O), dorsal (P), and palmar (Q) views; **R–S:** Right proximal phalanx of “*Eupecora*” indet. from Paulhiac (NMB-Pa788), dorsal (R) and interdigital (S) views. **T:** Right distal phalanx of cf. *Dremotherium guthi* from Coderet-Bransat (NMB-Bst10815), interdigital view. Typical features of the postcranial remains corresponding to Köhler’s (1993) morphotypes A (in red) and B (in blue), and to intermediate forms (in black): **1:** Furrow for the Lateral Extensor tendon (light grey), long (a), short (b); **2:** Low articular surface; **3:** Metacarpal inflated in its distal part; **4:** Flattened condyle; **5:** Palmar continuation of the condyle, continual (a), abrupt ending (b); **6:** Outline of the external side, straight (a), concave (b); **7:** Strong sulcus for the Interosseus tendon; **8:** Facet of distal articulation, extended in the dorsal side (a), poorly extended (b), not extended (c); **9:** Outline of the distal articulation, well rounded (a), flattened (b); **10:** Dorsal Extensor process, short (a), elongated (b); **11:** Postarticular plateau, elongated (a), short (b); **12:** Triangular outline of the distal articular surface; **13:** Weak dorsal and palmar extension of the articular surface; **14:** Strong marks for the insertion of the Flexor Digitorum Superficialis; **15:** Sagittal groove; **16:** High wedge for the insertion of the Deep Flexor tendon; **17:** Outline of the dorsal ridge, straight (a), angled (b); **18:** Outline of the articular surface, well rounded (a), forming a plateau (b); **19:** Light compression of the shaft; **20:** Incision for the metapodial condyle; **21:** Protuberance for the Extensor insertion; **22:** Angled interdigital border of the plantar surface. Morphotype A characterises ruminants from wooded areas, whereas morphotype B characterises those from open areas

In addition of depicting a general morphology of type A, the ruminants of the latest Oligocene (from MP28 to MP30) started to exhibit adaptations to a more effective cursoriality compared to their predecessors. The metapods from Pech Desse (MP28, France), La Milloque (MP29, France; e.g., cf. *Dremotherium guthi*, Fig. 6, sketches J–K) and Küttigen (MP30, Switzerland) are elongated and show a V-shaped intertrochlear incision and an abrupt ending of the condyles in the palmar side. Thus, they correspond to an intermediate morphology between Köhler’s (1993) morphotypes A and B. On the other hand, almost all the metapods of the ruminants from Coderet-Bransat (MP30, France) belong to morphotype A, while proximal phalanges are slenderer than the others and show several features of morphotype B. These bones, along with some specimens from La Milloque, bear a weak sulcus for the interosseus tendon, a slightly concave outline of the external side and a lightly flattened distal articulation on the volar side with its facet not visible from the dorsal

aspect. Nearly all the middle phalanges of the latest Oligocene ruminants (e.g., “*Amphitragulus*” *feningrei* from Coderet-Bransat, Fig. 6, sketches E–H) are morphologically characteristic of type A, but some samples from Küttigen and Thézels (MP30, France) bear features of morphotype B, such as a slight transversal compression just before the distal articular surface. Finally, concerning the distal phalanges, most of the specimens from La Milloque and Coderet-Bransat present features from morphotype A, exhibiting a shallow and well-rounded articular surface, a high wedge with a plantar process for the insertion of the deep flexor tendon, and a long and slightly angled dorsal ridge inclined towards the interdigital side. On the other hand, several distal phalanges from Coderet-Bransat (e.g., cf. *Dremotherium guthi*, Fig. 6, sketch T) depict a more angled dorsal ridge, a protuberance for the insertion of the extensor tendon and an articular surface forming a platform, corresponding to type B.

During the Agenian, the ruminants were represented by a wide range of morphological types with plenty of intermediate forms. The metapods from Paulhiac (MN1, France), Saulcet (MN1, France), La Chaux (MN2, Switzerland) and Selles-sur-Cher (MN2, France) hold mixed features from both morphotypes A and B, nonetheless with a dominance of the first one. In Montaigu-le-Blin (MN2, France), the morphology of the metapods range from small ones characteristic of type A (e.g., *Pomelomeryx* sp., Fig. 6, sketches A–B) to more elongated and more slender intermediate forms. The proximal phalanges found in Paulhiac present several morphologies, mostly of intermediate forms. Additionally, a single proximal phalanx (Fig. 6, sketches R–S) shows typical adaptations of morphotype B. It is slender and elongated, with a concave outline of the external side and a flattened distal articular surface. The middle phalanges of Paulhiac, La Chaux, Selles-sur-Cher and Laugnac (MN2, France) are morphologically mainly of type A, but with some features from type B, such as a relatively short post-articular plateau, a weak transversal compression just before the distal articular surface, and a weak sagittal groove. In Montaigu-le-Blin, the middle and distal phalanges range from a pure morphotype A to intermediate forms (e.g., cf. *Dremotherium feignouxi*, Fig. 6, sketches N–Q). In Paulhiac, La Chaux, and Selles-sur-Cher, the distal phalanges exhibit an intermediate morphology, though with a dominance of features from morphotype B.

During MN3 and MN4, the metapods found in Glovelier (MN4, Switzerland) show a morphological diversity of type A, but more intermediate forms are described in Chilleurs-aux-Bois (MN3, France), Artenay (MN4, France) and Langenau (MN4, Germany). The proximal phalanges from Chilleurs-aux-Bois and Artenay (e.g., “*Eupecora*” indet., Fig. 6, sketches L–M) show, as well, intermediate

morphologies, as it is the case for the middle phalanges from Artenay. However, the distal phalanges from both Artenay and Glovelier present morphological features of type A.

4 Discussion

4.1 Biostratigraphy and diversity patterns

Three major diversity trends occurred during the Late Oligocene and the Early Miocene in Western Europe (Fig. 7): (1) the beginning of the Arvernian (Late Oligocene, MP25-27) was characterised by a “stable” faunal composition with the last occurrences of taxa from the Grande Coupure and of newly emerged ones; (2) the latest Arvernian (Late Oligocene, MP28-30) and the Agenian (Early Miocene, MN1-2) was subject to gradual immigrations leading to progressive replacement of the Arvernian, hoofed mammals towards the establishment of the “classical” Agenian fauna; (3) the beginning of the Orleanian (Early Miocene, MN3-4) coincided with the African-Eurasian faunal interchanges of the Proboscidean Datum Events (*Gomphotherium* and *Deinotherium* landbridges/*Brachyodus* and Creodont Events; Van der Made 1999) and led to the complete renewal of the Agenian taxa and the total disappearance of the last Oligocene survivors.

The last representatives (at the specific level) of the ante-Grande Coupure fauna got extinct in MP25 and MP26 with *Plagiolophus minor* and *Elomeryx crispus*, respectively. The former is the last representative of the family Palaeotheriidae, whereas the genus *Elomeryx* persisted until MP27 with *E. borbonicus*. The unexpected occurrence of *E. minor* in MN1 in three localities of the North Alpine foreland Basin remains uncertain because of its doubtful assignment to the genus (LS pers. obs.). The mammal level MP25 experienced the extinction of two families of the Grande Coupure heritage fauna, the Aymnodontidae and the Entelodontidae (Brunet 1979; Becker 2009). The cluster analyses (Fig. 4) characterise well the fauna of the interval MP25-27, which is separated from the others at both the specific and the familial level and which is composed by a homogeneous ungulate community.

The most relevant point within the evolution of diversity of the hoofed mammals was certainly the almost complete, gradual renewal during the Oligocene–Miocene transition, with a first step dated to the mammal level MP28. We interpret this as an immigration phase with the incoming from Asia of the “Eupecora” and the anthracothere *Microbunodon*, and the appearance of the rhinocerotid *Mesaceratherium* (Lihoreau et al. 2004; Heissig 1969; Scherler 2011; Mennecart et al. 2012b). Indeed, *Microbunodon* appeared to stem from the genus *Anthracokeryx*,

which was recorded during the Late Eocene and the Early Oligocene in Southeast Asia, implying an Asian origin for *Microbunodon* and highlighting exchanges between Europe and Asia during the Late Oligocene (Lihoreau et al. 2004). This small anthracothere was, moreover, recorded in the Late Oligocene of Turkey (Lihoreau et al. 2004). Additionally, *Amphitragulus* sp., “*Amphitragulus*” cf. *quercyi* and *Dremotherium* cf. *guthi* were recorded in Asian, Oligocene localities of Mongolia (e.g., Yagan Tolgoi and Taatsiin Gol) and of the Aral Formation in Kazakhstan (Vislobokova 1997; Vislobokova and Daxner-Höck 2002; Devyatkin et al. 2002). Even though “*Amphitragulus*” cf. *quercyi* was probably recorded in latest Oligocene deposits (possibly between MP28 and MP30), an older age (early Late Oligocene) is suggested for the specimen of *Dremotherium* cf. *guthi*, supporting an Asian origin of the “Eupecora” (Vislobokova 1997; Vislobokova and Daxner-Höck 2002).

This MP28 event is particularly marked in the poly-cohort analyses and the faunal balances of the whole ungulates (Fig. 7b), as well as in the cluster analyses (especially at the familial level; Fig. 4) where its taxa association is distinct from the early Arvernian fauna (MP25-27) and from the Orleanian fauna (MN3-4). Furthermore, it coincided with the end of the Late Oligocene Warming (recorded by marine oxygen isotopes; Zachos et al. 2001). Afterwards, progressive faunal changes occurred until MN1 (e.g., appearance of *Diaceratherium lamilloquense* and *Bedenomeryx milloquensis* in MP29, *Pleuroceros pleuroceros* and *Amphitragulus primaevus* in MP30, *Protaceratherium minutum*, *Hyotherium meissneri* and *Oriomeryx major* in MN1). This last biozone (MN1) is marked by a high positive value of the faunal balance at the specific level (Fig. 7b), undoubtedly related to a diversification through regional speciations, according to the fact that, among cluster analyses (Fig. 4), it is characterised by a single group at the familial level and two distinct groups at the specific level for the time interval MP28-MN2. This speciation phase is particularly well observed with the explosion in the number of species of *Cainotherium*. The changes observed from MP29 to MN1 are certainly linked to the aridification and cooling that intensified during the latest Oligocene (Rögl and Steininger 1984; Berger 1990; Szyndlar and Böhme 1993; Rage and Szyndlar 2005; Becker et al. 2009) and can be correlated with the Mi-1 Glaciation event (a major glaciation recorded in Antarctica; Zachos et al. 2001; Pekar et al. 2006).

The fauna inherited from the renewal MP28-MN1 was relatively stable during MN2. The observed changes essentially concern the disappearance of the last Oligocene survivor, *Eggysodon*, and the arrival of the new taxa *Xenohyus*, *Andegameryx*, *Metaschizotherium*, *Friburgomeryx*, *Lorancameryx*, and *Teruelia*. It is worth noting that

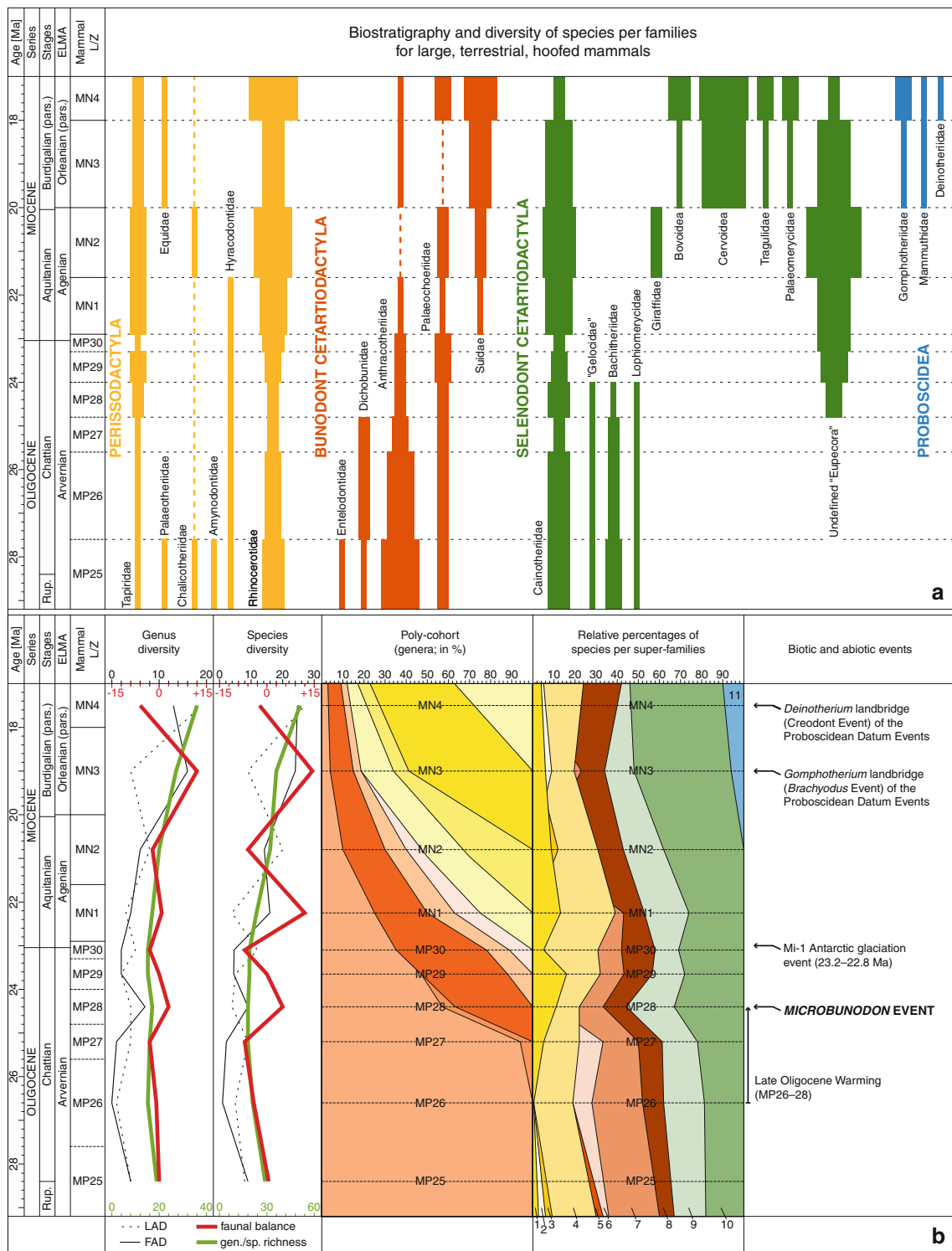


Fig. 7 Temporal ranges (a) of ungulate families from MP25 (Arvernian) to MN4 (Orleanian) and (b) evolution of the diversity trends faunal balance, genus/species richness, origination/extinction curves, survivorship poly-cohort [%], within-super-family diversification through time (data from Online Resources 1–2). Numbers for super-families correspond to: 1, Tapiroidea; 2, Equoidea; 3, Chalicotheroidea; 4, Rhinocerotidae; 5, Entelodontoidea; 6,

Dichobunoidea; 7, Anthracotheroidea; 8, Suidae; 9, Cainotheroidea; 10, Ruminantia; 11, Proboscidea. ELMA is for European Land Mammal Ages, and the dashed lines in the Mammal L/Z (Level/Zone) column correspond to the supposed boundaries delimiting the ranges of the Oligocene localities referred to a given European Mammalian Reference Level (according to Luterbacher et al. 2004). Dashed lines in the temporal ranges of families indicate lack of record

the ungulate community of the Agenian was composed of many taxa documented by twin species in older or coeval localities of South and Central Asia, which suggests the existence of landways for terrestrial taxa (e.g., Vislobokova 1997; Vislobokova and Daxner-Höck 2002; Lihoreau et al. 2004; Marivaux et al. 2004; Antoine and Becker 2013). For example, Marivaux et al. (2004) signalled the occurrence of *Diaceratherium* cf. *lamilloquense* in the Late Oligocene deposits of Thailand and Antoine et al. (2010) assigned numerous fossils from the Early Miocene deposits of the Bugti Hills (Baluchistan, Pakistan) to the species *Pleuroceros branfordi* and *Mesaceratherium welcommi*.

The Orleanian fauna was stressed by the incoming of new African and Asian taxa linked to the Proboscidean Datum Events, which led to the progressive but complete renewal of the ungulate community (e.g., Tassy 1989; Vislobokova 1997; Van der Made 1999; Costeur and Legendre 2008; Becker et al. 2009; Scherler et al. 2011). These new migration waves are well supported by the cluster analyses in showing a strongly separated branch at the familial level for the Orleanian (Fig. 4). It began in MN3 with the *Brachyodus* Event/*Gomphotherium* landbridge (Tassy 1989; Van der Made 1999), which particularly included the occurrence in Western Europe of the first proboscideans *Gomphotherium sylvaticum* and *Zygodon turicensis*, the comeback of the equids with *Anchitherium aurelianense* and the bothriodontine anthracotheres with *Brachyodus onoideus*, and the first representatives of the ruminant families Bovidae, Cervidae, and Palaeomerycidae (Gentry 1994; Göhlich 1999; Bernor and Armour-Chelu 1999; Gentry et al. 1999; Van der Made 1999; Scherler 2011; Mennecart 2012). The second migration wave of the Creodont Event/*Deinotherium* landbridge in MN4 (Tassy 1989; Van der Made 1999) knocked out not only the typical Agenian fauna, but also the last surviving taxa of the latest Oligocene, with the exception of the genus *Cainotherium* (Berthet 2003).

To sum up, the major changes observed amongst the hoofed mammals during the Oligocene–Miocene transition, highlighted by the faunal balances, the poly-cohorts and the cluster analyses, underline a turnover in MP28, a phase of regional speciations and diversifications during the Agenian (MN1–2), and the two-phased turnover of the Proboscidean Datum Events in MN3–4. Additionally, these analyses clearly define the start and end of the Oligocene–Miocene transition as it is considered here (that is to say from MP28 to MN2), the transition being well encompassed between the phase in MP25–27 containing the remnant fauna of Grande Coupure heritage and the migrations linked to the Proboscidean Datum Events in MN3–4.

4.2 Ecology

4.2.1 Rhinocerotids

The distribution of locomotion types for the rhinocerotids seems to be a good proxy for pointing out faunal and environmental changes. As illustrated in Fig. 5, the evolution of rhinocerotids during the Late Oligocene and the Early Miocene can be subdivided in four phases, the same ones that were already defined by the biostratigraphy and diversity patterns (see Sect. 4.1). The early Arvernian fauna (MP25–27) was strongly represented by cursorial rhinocerotids of diverse sizes. Small cursorial forms (such as *Molassitherium*) are considered to have lived in small herds and especially inhabiting forests, whereas larger cursorial types (e.g., *Ronzotherium*) were probably more ubiquitous, living still in small groups, but preferentially in slightly more open habitats with dry and hard soils like in woodlands (Uhlir 1999). The occurrence of the enigmatic, graviportal “*Diaceratherium*” *massiliae* may, additionally, indicate the sporadic establishment of patches of humid environments in MP25–26, before the onset of the Late Oligocene Warming. Indeed, the graviportal rhinocerotids (e.g., *Diaceratherium aurelianense*, *Brachypotherium brachypus*) were characterised by stocky limbs (which was particularly true for the distal segments), a feature interpreted as an adaptation to soft grounds and aquatic environments like swampy habitats within woodlands (Cerdeño and Nieto 1995; Cerdeño 1998; Heissig 1999). However, the shortened limbs of extinct, hippo-like ungulates (including the teleoceratines) are not always clearly indicative of an aquatic lifestyle. An alternate hypothesis states that the reduced limbs can be related to open terrain, to grazing habits, and often to gregarious behaviour (Mihlbachler 2005). Conversely, the Oligocene and Miocene rhinocerotids referred to in this study showed no dental evidence for grazing habits (DB, pers. obs.). Merely a few Orleanian taxa (e.g., *Diaceratherium aurelianense*, *Brachypotherium brachypus*) could have been mixed feeders. Consequently, the graviportal forms included in Fig. 5 are considered as adapted to soft grounds and humid zones, and, additionally, are associated to a gregarious behaviour.

During the late Arvernian (MP28–30), the mediportal type appeared and became common along with the classical, cursorial rhinocerotids. The mediportal forms are supposed to tolerate a wider range of habitats from woodland to grassland, while being possibly better adapted to soft soils (Cerdeño 1998). This co-occurrence may mark a change towards more diverse types of environments, which however remained generally dry (Costeur 2005). Indeed, environmental conditions in the latest Oligocene were rather open and arid, as suggested by the ungulate

assemblage of Rickenbach (MP29, Switzerland) characterising a savannah woodland (Mennecart et al. 2012b).

During the Agenian (MN1-2), the rhinocerotids included a large diversity of sizes and anatomical types, from small cursorial to large graviportal forms, highlighting a wide-range of mosaic environments at the scale of Western Europe. Since MN3 finally, the successive arrivals of new taxa related to the *Gomphotherium* and *Deinotherium* landbridges led to strong intra-familial interactions and to the record of cursorial and graviportal types only. The environments were probably in conformity with the rather closed habitats and the marked seasonality suggested by Costeur (2005) and Becker et al. (2009).

4.2.2 Ruminants

Such as for the Rhinocerotidae, the locomotor adaptations of ruminants are good proxies of their ecological conditions. From MP25 to MP27, the ruminants were mostly adapted to walking on woody, moist soils, reflecting forested habitats. In contrast to the rhinocerotids, there is no indication that some forms could have preferred more open and dry habitats during this period. This is not the case during the late Arvernian (MP28-30): although the forested forms still dominated the fauna, the emergence of several features linked to a better cursoriality suggests the presence of more open habitats. This is the case in Rickenbach for example, from where the ruminant *Dremotherium guthi* was described and defined to be adapted to a wooded savannah environment (Hiard 2010; Mennecart et al. 2012b).

The morphological diversity increased during the Agenian (MN1-2). Similarly to what has been observed with the rhinocerotids, this diversity concurred with a high variety of environments. The emergence of ruminants more adapted to cursoriality, such as those from Paulhiac, Tavannes (Hiard 2010; Mennecart 2012), and Engehalde (Becker et al. 2010; Hiard 2010), revealed more open habitats. On the other hand, the dominance of ruminants of morphotype A and of intermediate forms indicated the presence of more closed habitats (e.g., in Wallenried, Becker et al. 2001, and Montaigu-le-Blin). For the latter locality, the presence of small ruminants with features of subtype A2 (Köhler 1993) indicated a wooded and humid environment around lakes, an interpretation in agreement with Costeur (2005). The morphological diversity during MN3 and MN4 was also high, but slightly less than during the Agenian. Furthermore, the ruminants of this period corresponded more to forested forms.

4.3 Towards the definition of the “*Microbunodon* Event”

Slightly before the Oligocene/Miocene boundary, the Arvernian was marked by an important immigration event in

Western Europe in MP28 (see Sect. 4.1). This event primarily recorded the first appearances in Europe of the genera *Microbunodon* (Anthracotheriidae), *Mesacerattherium* (Rhinocerotidae), *Cainotherium* (Cainotheriidae), and the basal “Eupecora” (defined here as highly derived ruminants, sensu Mennecart 2012; see Sect. 2.3). In accordance to these observations, the origination values of the curves for both genera and species are the highest of the Arvernian and correspond to the only important peak of the faunal balance for this period (Fig. 7b). According to the poly-cohort analyses, new migrants composed 40 % of the ungulate fauna at the level MP28 (Fig. 7b). This immigration can be further observed in other mammal groups, such as the Eomyidae Rodentia, where the genera *Eomyodon* and *Pseudotheridomys* appeared contemporaneously in Europe, probably originating from Asia (Engesser 1999).

Coinciding with the end of the Late Oligocene Warming (Zachos et al. 2001), the event in MP28 corresponded to a change in the structure of the ungulate community, indicating a wooded savannah environment, in contrast with the more forested and wetter environment that occurred before (Legendre 1989; Mennecart et al. 2012b). These ecological interpretations are consistent with the ecomorphological analyses on Rhinocerotidae and Ruminantia (see Sect. 4.2). The level MP28 marked the first step of the major changes that occurred during the Oligocene–Miocene transition. This turnover, with 40 % of new ungulate migrants at MP28, is highly significant. During all the period concerned by our study, the *Gomphotherium* landbridge is the only peak in the faunal balance at the generic level comparable to the one at MP28 (Fig. 7b). Subsequently, the immigration event at MP28 should be considered as a major terrestrial event of the European Palaeogene. Therefore, we propose to name it the “*Microbunodon* Event”, a name that highlights the arrival of this latest Oligocene genus in Europe at this particular time (MP28-30, occurrences in Austria, France, Germany, Switzerland and Turkey; Lihoreau et al. 2004; Scherler 2011).

5 Conclusions

This study describe the ungulate evolution during the Oligocene–Miocene transition, considering the fauna inherited from the Grande Coupure and the migrants of the Proboscidean Datum Events. First of all, the Oligocene fauna was surprisingly stable during most part of the Late Oligocene Warming (until MP27), given that it underwent important changes in temperature conditions. A first turnover occurred in MP28 along with a peak in incoming taxa, marked by a positive excursion of the faunal balance and the formation of a new branch in the cluster analyses at the

familial level, interpreted as an important immigration wave. This happened contemporaneously with the end of the Late Oligocene Warming. The fauna then entered a phase of progressive changes from MP29 to MN2, with a regular decrease of the Oligocene survivors and with the colonisation by the classical Agenian fauna. We particularly observed a strong positive excursion of the faunal balance in MN1, much more marked at the specific than at the generic level. Furthermore, a splitting among the cluster analyses of the MP28-MN2 familial branch is noticed at the specific level. These results are interpreted as a phase of regional diversification through speciations. Indeed, the Agenian ungulate community was composed of many taxa documented by twin species in coeval localities of South and Central Asia, suggesting intermittent, migration pathways of terrestrial, large mammals. In biozone MN2, the stabilisation of the Agenian fauna continued, and, starting in MN3, the ungulate community endured a two-phased turnover characterised by the two migration waves of the Proboscidean Datum Events.

To sum up, the Oligocene–Miocene transition was framed by two turnovers primarily controlled by migrations: the first during MP28, initiating the transition, and the second, related to the Proboscidean Datum Event (MN3–4), terminated it. In between occurred progressive changes and the establishment of the Agenian fauna. Finally, the importance of the immigration event of MP28 leads us to consider it as a benchmark in the European, terrestrial biostratigraphy and we propose to name it the *Microbunodon* Event.

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