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Editors' choice

New dental elements of the oldest proviverrine mammal from the early Eocene of Southern France support possible African origin of the subfamily

FLORÉAL SOLÉ, THIERRY SMITH, RODOLPHE TABUCE, and BERNARD MARANDAT



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Here we describe and illustrate specimens of hyaenodont mammals from two early Eocene localities of Southern France: Fournes (Minervois) and Fordones (Corbières). Some of these specimens were previously described as cf. *Hyracolestes* sp. (Cimolesta, Sarcodontidae), a taxon only known from Asia, but new arguments allow their referring to the small proviverrine hyaenodont *Parvagula palulae* which was previously only recorded in Palette (Provence). The material notably includes the oldest p4 ever recorded for the European endemic subfamily Proviverrinae. This new material shows that, by the beginning of the early Eocene, proviverrines already displayed their typical combination of dental features characterized by the presence of a large paraconid and entoconid on p4. The comparison between the earliest European proviverrines and sinopines (a mostly North American radiation) supports the divergence of the two subfamilies by this time. Moreover, the early proviverrines are morphologically similar to the African hyaenodont *Tinerhodon* (late Paleocene). Consequently, the history of the European proviverrines is likely rooted in Africa. Finally, the new specimens support a similar age for the localities of Palette and Fordones, and a younger age for Fournes. Due to the ages of these localities *Parvagula palulae* must be regarded as the oldest proviverrine.

Key words: Hyaenodonta, Proviverrinae, Eocene, Europe, France, Fournes, Fordones.

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Introduction

For a long time, the Proviverrinae have been considered as a primitive stem-group of hyaenodonts (Polly 1996). Solé (2013) recently reviewed the early hyaenodonts and redefined the Proviverrinae, which are monophyletic, and defined two new subfamilies, the Sinopinae and Arfiinae. Although the two former subfamilies first occurred in Europe—they are notably recorded in the earliest Eocene (MP7 reference-level) localities of Dormaal and Erquelinnes (Belgium), and Le Quesnoy (France) (Smith and Smith 2001; Missiaen et al. 2013; Solé et al. 2013) (Fig. 1), they mainly radiated in North America during Wasatchian and Bridgerian NALMAs (North American Land Mammal Ages) (Gingerich and Deutsch 1989; Gunnell 1998; Zack 2011). In contrast to these hyaenodonts, the proviverrines diversified in Europe (Solé et al. 2014a).

The oldest proviverrines were of small size and restricted to the Southern European (= Mesogean) Province during the early Eocene (Solé et al. 2014a). Two species are presently recorded in the early Eocene of Provence: *Eoproviverra eisenmanni* (Godinot, 1981) from Rians (Var, France) and *Parvagula palulae* Lange-Badré in Godinot et al., 1987 from Palette (Bouches-du-Rhône, France; Fig. 1). *Eoproviverra eisenmanni* is represented by one m2, one m3, one fragmentary mandible bearing broken m2 and m3, one M1 and one M2. *Parvagula palulae* is represented by one mandible bearing p2, p3, p4, m1, and alveoli for p1, m2 and m3; unfortunately the enamel of the teeth has been worn out, which obscures the features of the species, notably the features of the p4 and m1, which are diagnostic for the proviverrines (Solé 2013). Due to this fragmentary fossil record, the origin of proviverrines is poorly known.

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The fossils here described are from the early Eocene French localities of Fournes (Minervois) and Fordones (Corbières) (Fig. 1). The mammals, almost thirty species, have been described by Marandat (1991). These two localities were considered to be close in age, despite their few shared mammalian species; nonetheless, Marandat (1991) envisaged that Fournes could be slightly younger than Fordones. Fordones is considered to be close in age to Palette, while Fournes is probably close to Rians, these relative ages have been also proposed by Marandat et al. (2012). All these localities are, however, younger than the Belgian MP7 reference-locality of Dormaal as very recently demonstrated by Yans et al. (2014b) based on bio- and chemostratigraphy; the latter authors even hypothesized that the Clot could be 1 million years younger than Dormaal.

No hyaenodont was described from the localities of the Corbières and Minervois before the present study; *Eoproviverra* and *Parvagula* are actually only known in Provence.

Institutional abbreviations.—IRSNB M, Institut Royal des Sciences Naturelles de Belgique, Palaeontological Mammal Collections, Brussels, Belgium; MNHN.F.RI, Muséum National d'Histoire Naturelle, Rians Collection, Paris, France; UM/FDN, University of Montpellier 2, Fordones Collection, Montpellier, France; UM/FNR, University of Montpellier 2, Fournes Collection, Montpellier, France; UM/PAT, University of Montpellier 2, Palette Collection, Montpellier, France; PSS, Mongolian Academy of Sciences, Institute of Geology, Palaeontology and Stratigraphy Section, Ulan Baator, Mongolia; ZIN, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia.

Other abbreviations.—DD, dentary depth; L, length; W, width.

Geological setting, material, and methods

The geological settings of Fournes and Fordones localities and their respective mammalian faunas have been extensively described and discussed by Marandat (1991). The fossils from these localities and those from Palette are housed in the collections of the University of Montpellier 2.

The measurements (length × width in mm) follow Gingerich and Deutsch (1989).

Systematic palaeontology

Class Mammalia Linnaeus, 1758

Infraclass Placentalia Owen, 1837

Grand order Ferae Linnaeus, 1758

Order Hyaenodonta Van Valen, 1967

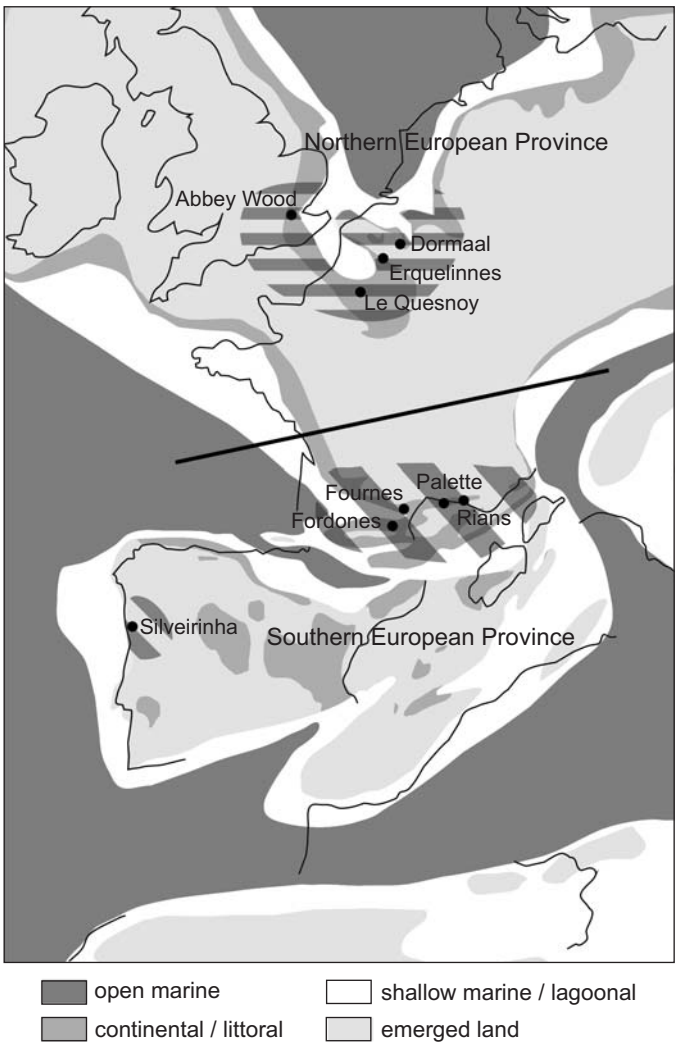


Fig. 1. Eocene palaeogeographic map showing the possible localisation of Rians, Palette, Fournes, Fordones, and Le Quesnoy (France), Dormaal and Erquelinnes (Belgium), Silveirinha (Portugal), and Abbey Wood (England). The earliest proviverrines are restricted to the Southern European Province, while the sinopines are mainly located in the Northern European Province. Redrawn from Marandat et al. (2012: fig. 1).

Family Proviverrinae Schlosser, 1886 sensu Solé 2013

Genus *Parvagula* Lange-Badré in Godinot et al., 1987

Type species: *Parvagula palulae* Lange-Badré in Godinot et al., 1987; Palette, early Eocene; Provence, Bouches-du-Rhône, France.

Parvagula palulae Lange-Badré in Godinot et al., 1987

Figs. 2–5.

Holotype: UM/PAT 4, right dentary bearing p2–m1, and alveoli for p1, and m2–3.

Type locality: Palette, Provence, Bouches-du-Rhône, France.

Type horizon: Early Eocene.

Material.—UM/FNR 51, right m1?; UM/FNR 52, left trigonid of m1?; UM/FNR 53, right fragmentary dentary bearing

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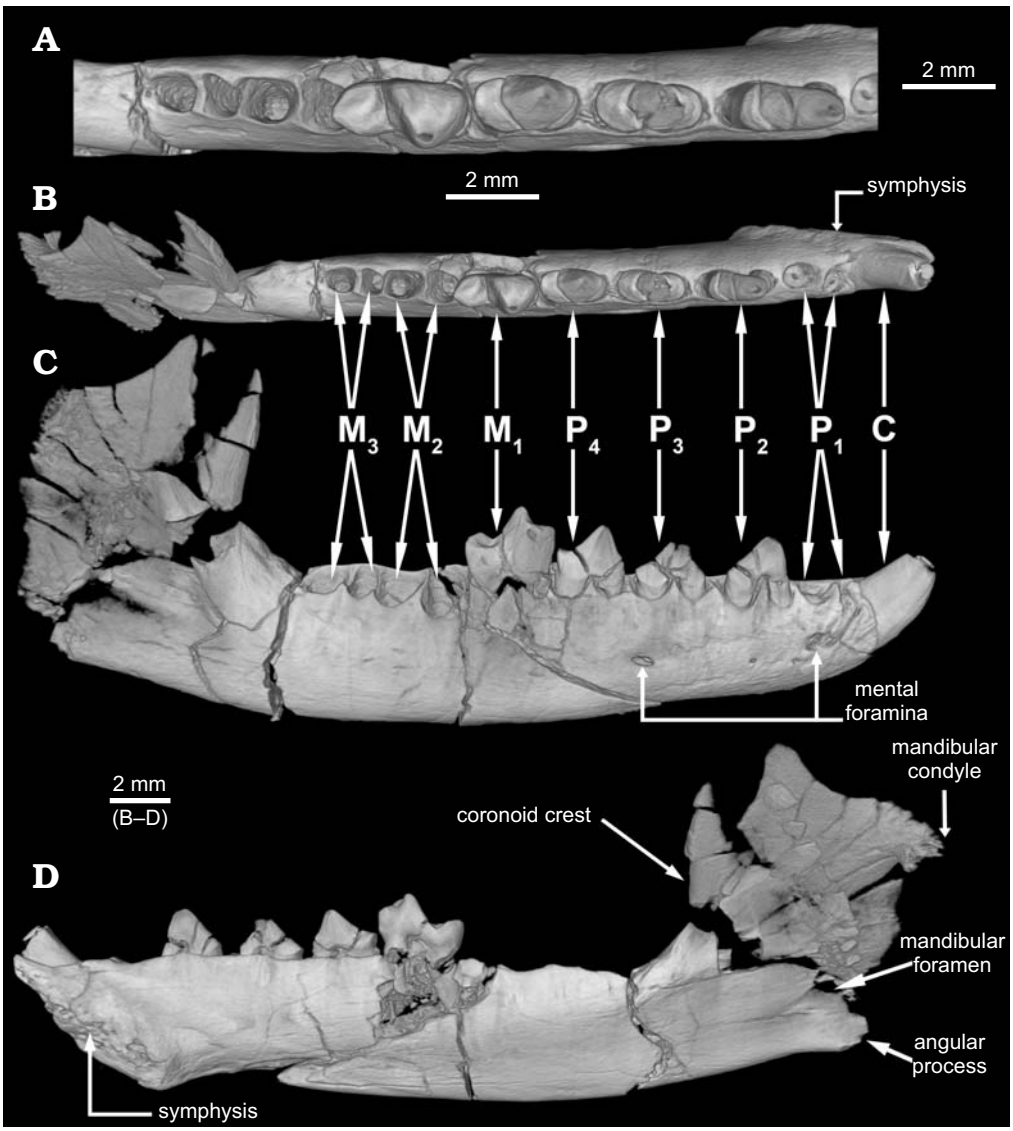


Fig. 2. CT-scan reconstructions of proviverrine mammal *Parvagula palulae* Lange-Badré in Godinot et al., 1987 from Palette, France, early Eocene; UM/PAT 4, holotype, dentary bearing p2–m1, and alveoli for p1, and m2–3. Occlusal close-up (**A**), occlusal (**B**), labial (**C**), and lingual (**D**) views.

p4; early Eocene; Fournes, Minervois, Hérault, France; UM/FDN 153, left trigonid of m1?; early Eocene; Fordones, Corbières, Aude, France.

Emended diagnosis (modified from Godinot et al. 1987).—Small proviverrine characterized by the presence of a deep dentary and symphysis; four two-rooted and closely spaced premolars; p4 with large paraconid and entoconid; molars with short and wide talonid and lingually closed postfossid, large and bulbous entoconid, paraconid poorly developed, and a m3 smaller than m2.

Measurements.—UM/PAT 4: p1, 1.9*×0.8*; p2, 2.3×1.1; p3, 2.4×1.3; p4, 2.5×1.4; m1, 3.0×1.5; m2, 2.7*×1.15*; m3, 2.1*×1.07*; DD, 4.5. Asterisked measurements are based on alveoli. UM/FNR 53: p4, 2.97×1.27; DD, 4.0. UM/FNR 51: m1?, 3.19×2.2.

Description.—The dentary (Fig. 2) found in Palette (UM/PAT 4, holotype) is deep and displays an important dorso-ventrally elongated symphysis; the latter structure extends below the anterior root of p2. Two mental foramina are present respectively below the p1 and p3. The coronoid crest is clearly vertical. The angular process is dorsally located compared to the body of the dentary; there is a concavity anteriorly to the process. The Computed Tomography (CT) reconstruction of UM/PAT 4 suggests that the mandibular condyle, which is unpreserved on the specimen, is dorsal to the tooth row. Based on the reconstruction, we also identified the mandibular foramina. The morphology of the ascending ramus is reminiscent of that described for *Boritia duffaudi* from the early Eocene of La Borie (Aude, France) (Solé et al. 2014a).

The four premolars, which are all two-rooted, are closely located each other along the dentary on UM/PAT 4. The p2, p3 and p4 are symmetric in lateral view. Unfortunately, the premolars are strongly worn (Fig. 2), as is the sole molar (m1): we can, however, note that the talonid is short and wide and there is a large entoconid (Fig. 2). The m3 is clearly shorter than the m1 and m2 (Fig. 2A).

Three specimens have been collected at Fournes: one complete p4, one complete m1, and one trigonid of m1, while only one trigonid of m1 has been found in Fordones.

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The p4 (UM/FNR 53) is almost symmetric in lateral view (Fig. $3A_1$, A_2). The paraconid is clearly individualized. The protoconid is elongated mesio-distally. The talonid is relatively wide. Only two cusps are present on the talonid: the hypoconid and the entoconid. The hypoconid is high and larger than the entoconid; the latter is well developed and is lingually located. There is no crest joining the two cusps. There is only a weak postcingulid on the labial side of the tooth.

UM/FNR 51 (m1?) is almost complete: only the apex of the paraconid is broken (Fig. $3D_1$–D_3); UM/FNR 52, however, provides additional information on the paraconid (Fig. $3C_1$–C_3). The trigonid is twice as high as the talonid. The paraconid is short and slightly mesially shifted. Moreover, it is distinctly lower than the metaconid and protoconid. The metaconid is robust, lower than the protoconid and its apex is tilted lingually. The talonid, which is short, displays a wide postfossid and bears distinct cusps. The latter are distally located. The hypoconulid appears slightly higher than the hypoconid and entoconid, but the apex of the hypoconid is broken. The entoconid is cuspate and bulbous. The postfossid is enclosed lingually and the distance between the bases of metaconid and entoconid is short. The cristid obliqua is clearly oblique and climbs on the distal wall of the trigonid towards the protocristid notch. Only a precingulid is visible along the mesiolabial part of the paraconid.

The morphology of the only known specimen from Fordones (UM/FDN 153) (Fig. $3B_1$–B_3) fits with that of UM/FNR 51 and UM/FNR 52. However, UM/FDN 153 is slightly smaller than the specimens from Fournes. Moreover, as noted by Marandat (1991), the lingual opening of the prefossid on UM/FDN 153 is slightly higher located; this is a primitive condition.

The specimens UM/FNR 51 and UM/FNR 52 from Fournes are considered as possible m1 despite the fact that they are larger than the m1 present on UM/PAT 4, we indeed consider that the fossils from Fournes are younger than those from Palette (see below). However, it is worth keeping in mind that the variability is poorly known for the species due to its weak fossil record.

We estimated, after the methodology proposed by Morlo (1999), that *Parvagula palulae* probably weights close to 60 g at most.

Remarks.—The lower molars described above (UM/FNR 51, UM/FNR 52, UM/FDN 153) have been described by Marandat (1991) as cf. *Hyracolestes* sp. The small mammal *Hyracolestes* has been originally described as a primitive creodont by Matthew and Granger (1925). However, it is still a poorly known taxon, based only on very sparse material. Therefore, it has had a confusing taxonomic history. Based on similarities with *Sarcodon*, Lopatin and Kondrashov (2004) referred this genus to the Sarcodontinae within the micropternodontid soricomorphs, which are insectivorous mammals with well-expressed carnivorous adaptations. Missiaen and Smith (2008) elevated Sarcodontinae to family rank, but rather considered them as members of Cimolesta, with uncertain ordinal affinities based on the presence of only two molars, the absence of hypoconal shelf on P4 and M2, and a different stratigraphic distribution.

Marandat's (1991) hypothesis was supported by the close morphological resemblance between the French fossils and a fossil (PSS 20-124) from Tsagan Khushu (Mongolia, Ypresian) referred to cf. *Hyracolestes* sp. by Russell and Dashzeveg (1986). The similarities between the French and Mongolian specimens are actually striking (see below). However, the similarities with specimens undoubtedly referred to *Hyracolestes* are less supported. The French and Mongolian specimens differ from *Hyracolestes* by the absence of transversal alignment of the talonid cusps, the less mesially shifted paraconid, the lingual closing of the postfossid, and the presence of a precingulid.

Lange-Badré in Godinot et al. (1987) created a new genus and new species for a dentary found in Palette: *Parvagula palulae*. Solé (2013) referred this taxon to the Proviverrinae; these hyaenodonts are endemic to Europe. The three lower molars from Fournes and Fordones are morphologically similar to that of *Parvagula palulae*; they share with the molar of UM/PAT 4 the trigonid morphology characterized by a low paraconid, the short talonid, the circular alignment of the talonid cusps, and the presence of a precingulid.

The p4 from Fournes (UM/FNR 53) is also similar both in size and morphology to that of the holotype of *Parvagula palulae*. The p4 of UM/PAT 4 is, however, more oval in occlusal view than that of FNR 53, and the apex of the protoconid is slightly more mesially located. These features are similar to the p4 of *Tinerhodon* (late Paleocene of Morocco) (see Gheerbrant et al. 2006: fig. 6a); the differences between the p4 from Palette and Fournes could be due to an older age of the fossil from Palette compared to that from Fournes (see below). The specimen from Fournes, which is less worn than that from Palette, also differs from the latter by the presence of a paraconid and by the presence of an entoconid. The presence of a space between the p3 and p4 on UM/PAT 4 implies that a paraconid was possibly present on p4. Based on personal observations of the p4 talonid of UM/PAT 4, Solé (2013) coded in his matrix the presence of the entoconid. He observed a small but worn crest on the lingual part of the talonid that could result from the presence of an entoconid. Despite a slightly more derived morphology, UM/FNR 53 does not really differ from the p4 present on UM/PAT 4. These features, such as the presence of paraconid and entoconid, are important because the morphology of the p4 is important for distinguishing the Proviverrinae from other subfamilies (see below).

The sole other early proviverrine recorded from the lowermost Eocene is *Eoproviverra eisenmanni* from Rians (Godinot 1981; Solé et al. 2014a; Fig. 4). However, the wear of the teeth of UM/PAT 4 prevented detailed comparisons with *Eoproviverra*; this comparison is important because the specimens from Rians and Palette are the oldest proviverrine fossils. The specimens from Fordones and Fournes now allow a comparison between the two proviverrine species,

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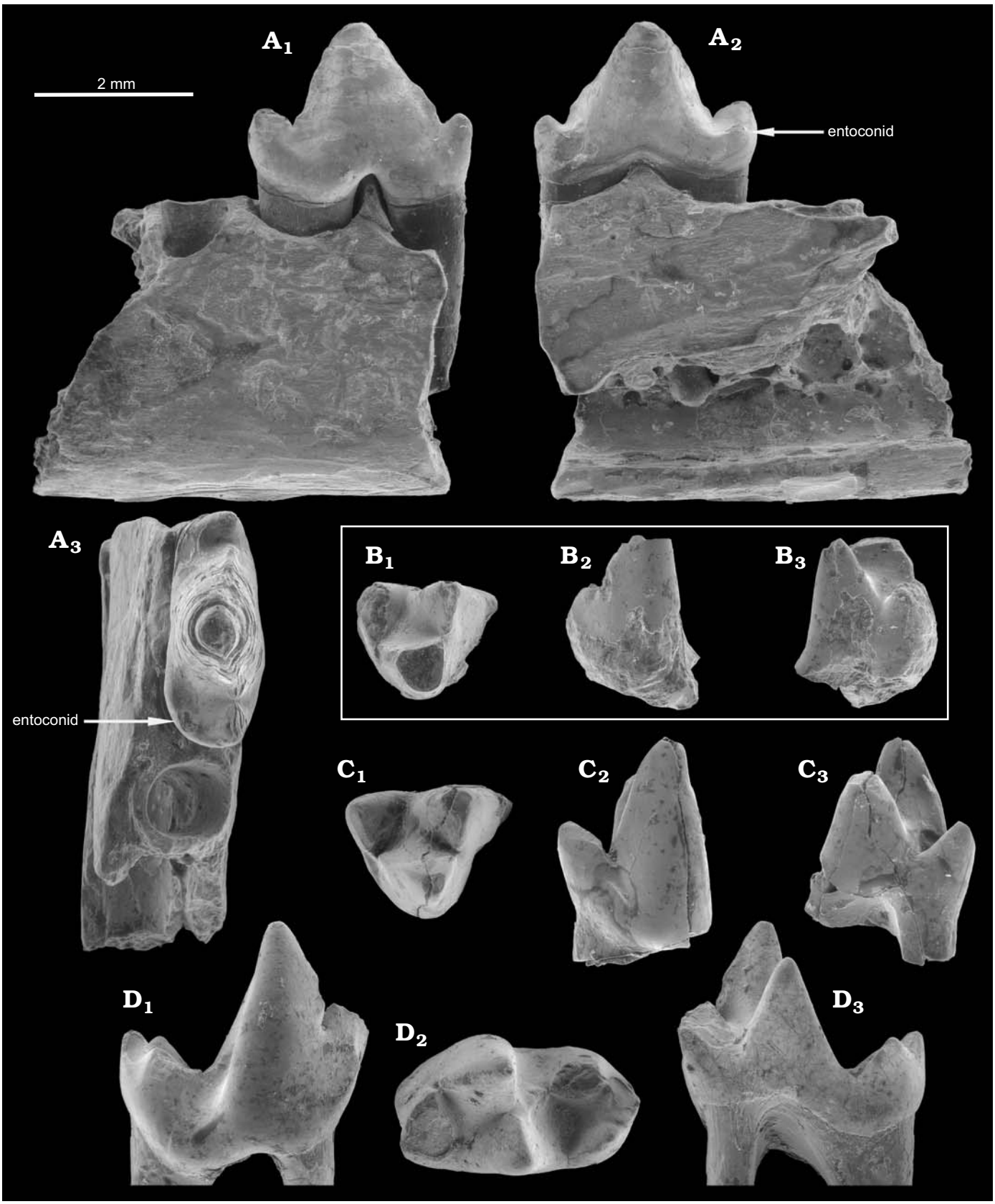


Fig. 3. Proviverrine mammal *Parvagula palulae* Lange-Badré in Godinot et al., 1987 from Fournes (A, C, D) and Fordones (B), France, early Eocene. **A**. UM/FNR 53, right fragmentary dentary bearing p4; labial (A_1), lingual (A_2), and occlusal (A_3) views. **B**. UM/FDN 153, left trigonid of m1?; occlusal (B_1), labial (B_2), and lingual (B_3) views. **C**. UM/FNR 52, left trigonid of m1?; occlusal (C_1), labial (C_2), and lingual (C_3) views. **D**. UM/FNR 51, right m1?; labial (D_1), occlusal (D_2), and lingual (D_3) views. The frame distinguishes the sole specimen from Fordones.

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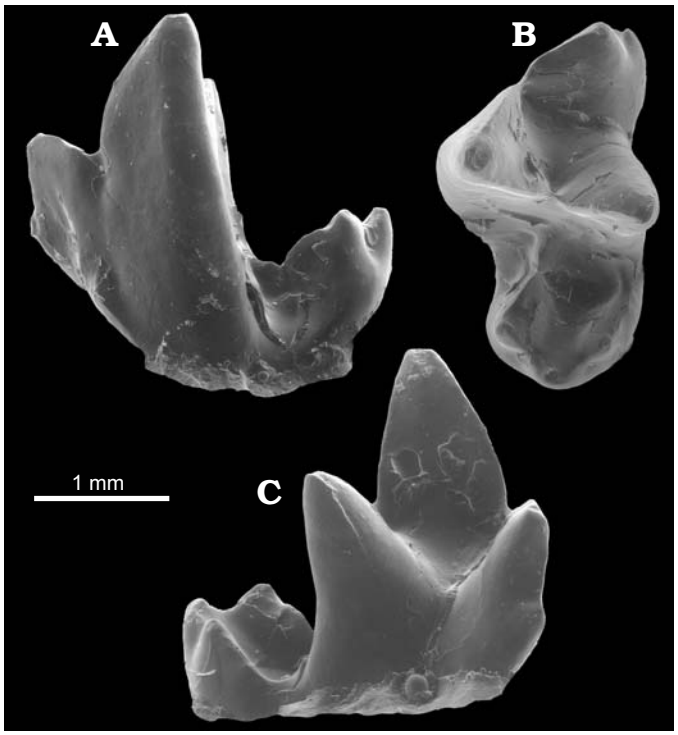


Fig. 4. Proviverrine mammal *Eoproviverra eisenmanni* Godinot, 1981 from early Eocene, Rians, France; MNHN.F.RI 400, left m2; labial (**A**), occlusal (**B**), and lingual (**C**) views.

although the comparison can be made only on the base of the lower molars.

The lower molars of the two proviverrine taxa display large and well individualized entoconid; this feature clearly distinguishes them from the molars of sinopines from Dormaal and Le Quesnoy (*Prototomus* and *Galecyon*) (Fig. 5). The presence of a large entoconid is also a feature of *Arfia*, which is also recorded in Dormaal, Erquelinnes, and Le Quesnoy (Smith and Smith 2001; Missiaen et al. 2013; Solé et al. 2013), but the two proviverrines differ from *Arfia* (Arfiinae) by a narrower talonid, less developed cingulids and smooth enamel.

The molars from Fournes and Fordones are distinguished from those of *Eoproviverra* by a less mesially shifted paraconid, a shorter paracristid, a lingually closed postfossid, and a shorter but wider talonid and postfossid (Figs. 3, 4). As a result, the molars of *Parvagula* appear less secant (e.g., less developed paraconid) but more robust (e.g., wider postfossid) than those of *Eoproviverra*. These differences add to the distinction of the two taxa and their generic distinction thus should be maintained.

The p4 of *Eoproviverra* is presently unknown: only its upper and lower molars have been found (Godinot 1981). Consequently, the p4 present on UM/FNR 53 could be that of *Eoproviverra*. However, the p4 of UM/FNR 53 is slightly larger than the molars of *Eoproviverra* (from Godinot 1981: MNHN.F.RI400, m2, 2.8×1.7; MNHN.F.RI204, m1, 2.1×0.8; m2, 2.4×1.6; MNHN.F.RI203, m3, 2.5×1.6). Moreover, because *Parvagula* is already recorded in Fournes, the reference of UM/FNR 53 to *Parvagula* is the most parsimonious hypothesis.

Finally, it is worth mentioning that the overall robustness of the molars and the close spacing of the premolars recall that of early Eocene genera *Morlodon* Solé, 2013 and *Boritia* Solé, Falconnet, and Laurent, 2014, which are possibly related to durophagous *Matthodon*. This would indicate that the development of the peculiar durophagy of *Matthodon* may have developed early in the history of the proviverrines. However, these relationships cannot be definitively established based on the currently available material.

Stratigraphic and geographic range.—Early Eocene; Palette (Provence, Bouches-du-Rhône), Fournes (Minervois, Hérault) and Fordones (Corbières, Aude), France.

Discussion

Origin of the Proviverrinae and the early radiation of the Hyaenodonta.—As indicated above, the Proviverrinae is a monophyletic subfamily of Hyaenodonta, that is endemic to Europe (Solé 2013; Solé et al. 2014a). The proviverrines seem to have been confronted with a lesser competition than their North American relatives (sinopines and arfiines); indeed, Morlo et al. (2010) evidenced that the Lutetian sinopines and arfiines are ecologically much less diverse than the Lutetian proviverrines. The radiation of the proviverrines was notably favoured by the rapid disappearance from Europe of the Oxyaenodonta; the sinopines and arfiines and the largest carnivoraforms such as *Vassacyon* and *Dormaalocyon* (Solé et al. 2011, 2013, 2014a; Solé 2014). As a result, the proviverrines adapted to numerous ecological niches, for instance, *Quercytherium* was even considered as a possible molluscivorous taxon (Morlo 1999). However, the oldest proviverrines such as *Eoproviverra* and *Parvagula* are poorly known.

The p4 displays characters that distinguish the proviverrines and sinopines (Solé 2013). However, prior to this study, the sole p4 known for the oldest proviverrines was the worn tooth present on UM/PAT 4. The p4 from Fournes thus provides crucial new information. The features that distinguish the two subfamilies are the presence of an individualized paraconid and of a large entoconid (Fig. 5); the first structure is very small in sinopines, while the second is absent (Fig. 5); the absence of the entoconid on p4 is possibly a derived feature (Solé 2013). Consequently, the p4 discovered in Fournes shows that *Parvagula* already displays the features that distinguish the proviverrines from the sinopines recorded in Northern Europe such as *Galecyon morloi* and *Prototomus minimus* (Fig. 5): the p4 of the earliest proviverrines was already distinct from that of the earliest Eocene sinopines.

The proviverrines are also distinguished from the sinopines by a larger and more bulbous entoconid on lower molars; the entoconid is crestiform and tends to be reduced among sinopines, Solé (2013) envisaged that it is a derived feature. This distinction is clearly visible when comparing

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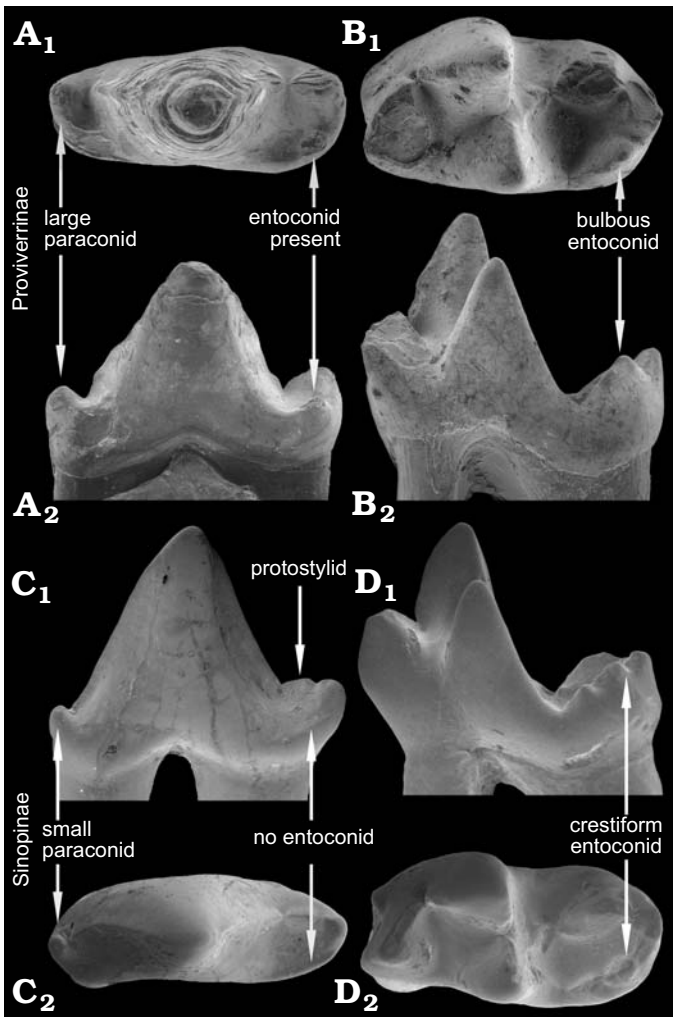


Fig. 5. Comparison of the p4 (A, C) and m1 (B, D) of the early Eocene Proviverrinae and Sinopinae. **A**, **B**. *Parvagula palulae* Lange-Badré in Godinot et al., 1987 from Fournes, France. **A**. UM/FNR 53, right p4; occlusal (A_1) and lingual (A_2) views. **B**. UM/FNR 51, right m1; occlusal (B_1) and lingual (B_2) views. **C**, **D**. *Prototomus minimus* Smith and Smith, 2001 from Dormaal, Belgium. **C**. IRSNB M1286, right p4; lingual (C_1) and occlusal (C_2) views. **D**. IRSNB M1287, left m1; lingual (D_1) and occlusal (D_2) views, reversed. Not to scale.

the lower molars of the earliest representatives of Proviverrinae and Sinopinae (Fig. 5).

Following Morlo and Gunnell (2003) and Morlo and Habersetzer (1999), Solé (2013) also indicated that the oldest proviverrines were characterized by the presence of a two-rooted p1, whereas the sinopines have a single-rooted one. UM/PAT 4 (Fig. 2A) from Palette supports this distinction. The two-rooted p1 is possibly a derived feature (Solé 2013).

As a conclusion, the dentition of the early proviverrines and sinopines are clearly different. The dissimilarity between the proviverrines and sinopines suggests that the two subfamilies diverged prior to the Paleocene–Eocene boundary and is in accord with a Paleocene radiation of the Hyaenodonta as proposed by Solé et al. (2009).

The morphology of the p4 and lower molars of *Parvagula* closely matches that known in *Tinerhodon* from the late Paleocene of Morocco in possessing a distinct entoconid on p4 and a bulbous entoconid on molars. The p4 of *Parvagula*, however, differs from that of *Tinerhodon* in having a larger paraconid (a synapomorphic feature of Proviverrinae) and the absence of the protostylid. The protostylid is present in early sinopines (Fig. $5C_1$) (see Gheerbrant et al. 2006: fig. 7) and is probably a primitive structure among hyaenodonts (Solé 2013). The lower molars of *Parvagula* differ from those of *Tinerhodon* in having a lingually close postfossid and a wider and shorter talonid. It is important to note that *Tinerhodon* is both older and more primitive than *Parvagula*. However, despite these differences, the teeth of *Parvagula* are overall more similar to late Paleocene *Tinerhodon* than to those of the contemporaneous sinopines from Europe. However, *Tinerhodon* cannot be considered as a true proviverrine because it does not display the enlargement of the paraconid of the p4, which is a distinguishing feature of the subfamily (Solé 2013). Moreover, this genus has been often found as the most basal hyaenodont in phylogenetic analyses (Solé 2013; Solé et al. 2014b).

A sister-group relationship between Proviverrinae and *Tinerhodon* has never been found by the cladistics analyses that focused on the relationships within Hyaenodonta (Solé 2013; Solé et al. 2014b; Rana et al. 2015). One can note, however, that the relationships within hyaenodonts are particularly unstable. This is notably obvious for the higher level relationships (Fig. $6A_1$, B_1, C_1). This lack of resolution is possibly caused by the isolation of hyaenodont faunas on different continents during the early Eocene, the convergences in the dentition (e.g., simplification of the carnassial teeth), and the lack of non-dental material for several hyaenodont groups (Solé 2013; Rana et al. 2015).

Anyway, the close morphological resemblance between the material from Palette, Fournes, and Fordones with that from the Ouarzazate Basin is particularly striking. These new data also allow us to revisit the problem of the geographic origin of the Proviverrinae and Sinopinae. Three hypotheses concerning the origins of Hyaenodonta have been proposed, Fig. $6B_1$–B_3 summarizes the hypotheses and their resulting dispersals:

(i) Emmanuel Gheerbrant (Gheerbrant 1995; Gheerbrant et al. 2006) and FS (Solé 2013; Solé and Smith 2013; Solé et al. 2009, 2014b), following Philip D. Gingerich (Gingerich 1989; Gingerich and Deutsch 1989), have proposed an African origin for the hyaenodonts (Fig. $6A_1$, A_2). This hypothesis is based on a combination of a very early record for the family in the middle Paleocene of Africa (Kocsis et al. 2014; Yans et al. 2014a) and a relatively high diversity of early and middle Eocene African hyaenodonts (Solé et al. 2014b).

(ii) An Asian origin for Hyaenodonta has been suggested by several authors (Beard 1998; Meng et al. 1998; Rana et al. 2015) (Fig. $6B_1$, B_2). This hypothesis is supported by a late Paleocene occurrence of Limnocyoninae in Inner Mongolia, China (Meng et al. 1998). Moreover, its supporters related this hypothesis with the Asian origin of other taxa such as Artiodactyla, Euprimates, and Perissodactyla that appeared

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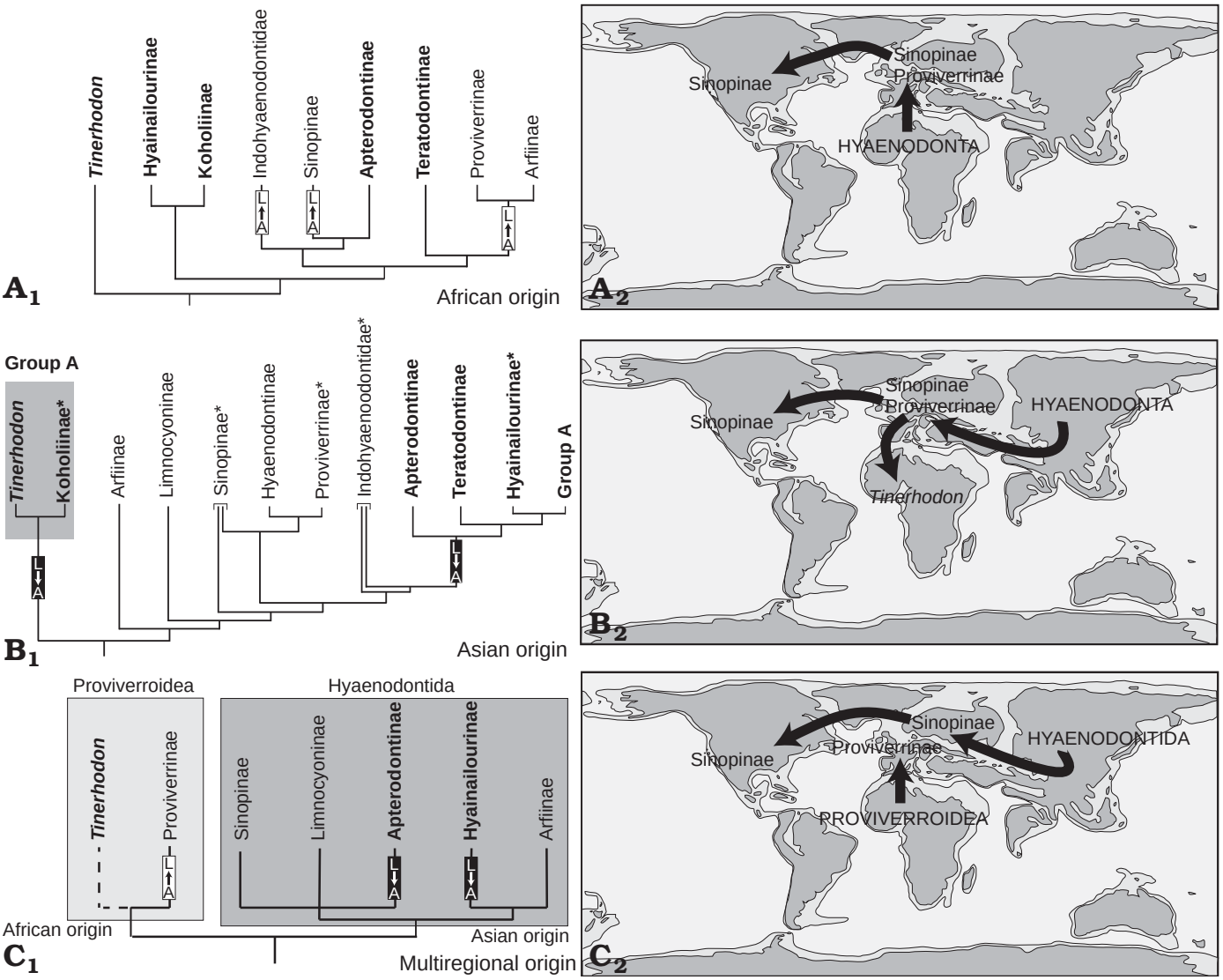


Fig. 6. Comparison of phylogenetic trees and of the three hypotheses of hyaenodont origin and dispersals with focus on the Sinopinae and Proviverrinae. **A**. African origin with subsequent dispersals of the Sinopinae and Proviverrinae into Europe, and of the Sinopinae from Europe to North America. A_1. The phylogenetic tree based on the cladistics analysis of Solé et al. (2014b). A_2. Faunal dispersals during the early Eocene based on the hypothesis of an African origin for the Hyaenodonta. **B**. Asian origin with subsequent dispersals of Sinopinae and Proviverrinae into Europe, and of *Tinerhodon* from Europe to Africa. B_1. The phylogenetic tree based on the cladistics analysis of Rana et al. (in press); the position of the Group A is variable—we represent only two of the four possible positions: the basal position implies two dispersal events from Laurasia to Africa, while the more inclusive position implies one single event. B_2. Faunal dispersals around the Paleocene–Eocene transition based on the hypothesis of an Asian origin for the Hyaenodonta. **C**. Multiregional origin with subsequent dispersals of the Sinopinae from Asia to North America through Europe, and of the Proviverrinae from Africa to Europe. C_1. The phylogenetic tree based on the abstract of Morlo et al. (2010). C_2. Faunal dispersals during the early Eocene based on the hypotheses of an Asian origin for the Sinopinae (Hyaenodontida) and of an African one for the Proviverrinae (Proviverroidea). The phylogeny of Rana et al. (in press) is, however, consistent with either an African or an Asian origin for the Hyaenodonta; only the Asian origin is discussed here; the position of *Tinerhodon* in C_1 is our hypothesis because this taxon is not discussed by Morlo et al. (2010). Abbreviations: A, Africa; L, Laurasia. Bolded, taxa that mainly radiated in Africa; asterisks, paraphyletic subfamilies in Rana et al. (in press). A_2–C_2 are adapted from Ron Blakey, Eocene, http://www2.nau.edu/rcb7/050Marect.jpg.

in North America and Europe also in the beginning of the early Eocene, i.e., the East of Eden hypothesis of Beard (1998).

(iii) Morlo et al. (2009) have proposed a multiregional origin (Fig. 6C_1, C_2). This hypothesis, which is not supported by a cladistics analysis, implies that two distinct groups of Hyaenodonta originated in different landmasses: the Proviverroidea (Proviverrinae and *Tinerhodon*) and Hyaenodontida (Sinopinae, Limnocyoninae) appeared respectively in Africa and Asia. It does not imply a diphyletism of the Hyaenodonta but rather recognizes a wide distribution of this group very early in its history and before its diversification (i.e., before the Paleocene–Eocene boundary).

If the proviverrines and African *Tinerhodon* are not found as sister-groups in the cladistics analyses, a morphological similarity between the dentition of the proviverrines and African *Tinerhodon* makes, however, biogeographic sense.

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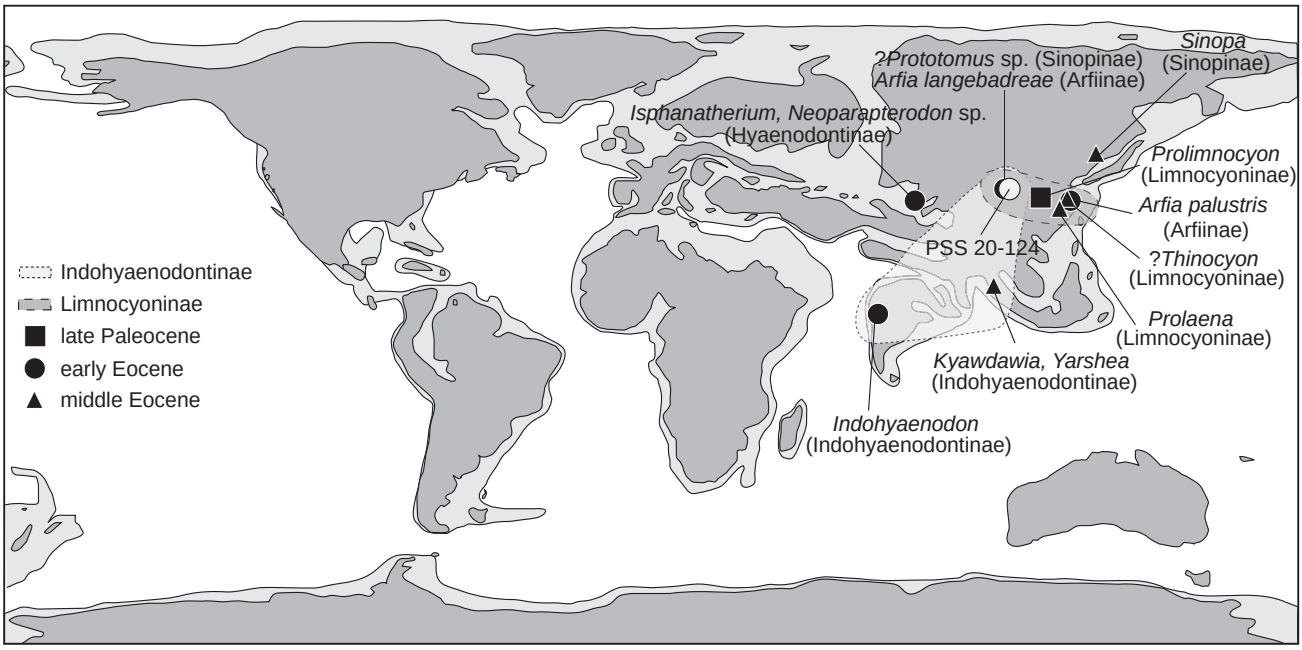


Fig. 7. Geographic localisation of the Asian hyaenodonts mentioned in the text, and distributions of the Limnocyoninae and Indohyaenodontinae. Both the geographic distributions of the Limnocyoninae and Indohyaenodontinae include the Mongolian specimen PSS 20-124. Adapted from Ron Blakey, Eocene, http://www2.nau.edu/rcb7/050Marect.jpg.

This supports faunal interchanges between Europe and Africa around the Paleocene–Eocene boundary as hypothesized by Gheerbrant and Rage (2006) based on several mammalian groups. The primitive morphology of *Tinerhodon* when compared to the proviverrines disagrees with the hypothesis of an Asian origin (Figs. 6B). The similarity between the African genus and the endemic European subfamily better agrees with either the African (Fig. 6A) or multiregional origin (Fig. 6C).

A comparison between the p4 of *Prototomus minimus* (stem sinopine) with that of both *Parvagula* (stem proviverrine) and *Tinerhodon* provides interesting features for discriminating between the two concurrent hypotheses. The p4s of *Prototomus minimus* and *Tinerhodon* share the presence of a protostylid and a low paraconid, but the former differs from the latter by the absence of an entoconid. The p4 of *Prototomus minimus* species thus appears partially similar to that of *Tinerhodon*, as is the p4 of *Parvagula*, but for different features. As a consequence, the p4 of *Tinerhodon* corresponds to a combination of the features visible on the p4 of both the sinopines and proviverrines, and represents a very pertinent morphological ancestor to the two subfamilies. This observation strengthen supports for an African origin not only of the Proviverrinae but also of Hyaenodonta (Fig. 6B).

Stratigraphic implications of *Parvagula* for the biochronology of the early Eocene Southern Europe localities.— Marandat et al. (2012) recently reviewed the biochronological sequence for the earliest Eocene mammalian sites of Southern Europe. The sequence they established is the following from oldest to youngest: (i) Silveirinha (Portugal), (ii) Fordones/Palette/Le Clot, and (iii) Rians/Fournes. Do the proviverrines support this sequence?

Fordones could be close in age to Palette (Marandat 1991; Marandat et al. 2012). Six of the eighteen mammalian species identified in the former locality are actually present or have closely related representatives in the latter one. The specimen UM/FDN 153 here presented allows recognizing a seventh species (*Parvagula palulae*).

The fossils from Fournes are distinctly larger than the holotype recorded in Palette. As discussed above, the former are also slightly more derived than the latter. These observations support a younger age of Fournes compared to Palette. Concerning the correlation between Fordones and Fournes, the specimen from Fordones (UM/FDN 153) is smaller and more primitive (see above) than those from Fournes. These observations agree with an older age for Fordones compared to Fournes. Consequently, the fossils here presented support the sequence of mammalian sites established by Marandat et al. (2012).

A comparison with Rians based on hyaenodonts is presently impossible because only *Eoproviverra* is present here. This genus probably belongs to a different lineage than *Parvagula*; *Eoproviverra* is characterized by more secant structures and does not show the typical reduction of the talonid observed in *Parvagula*. The sequence proposed by Marandat et al. (2012) implies that the two genera may have been contemporaneous: the proviverrines thus were diversified in Southern Europe during the early Eocene. Moreover, their diverging dental specializations indicate that the two taxa were probably separated prior to Rians/Fournes level.

The lower molar from Tsagan Khushu (Mongolia, Ypresian): an intriguing specimen.—As indicated above, Marandat (1991) originally referred UM/FNR 51, UM/FNR 52,

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and UM/FDN 153 as cf. *Hyracolestes* sp. based on similarities with a lower molar (PSS 20-124) from Tsagan Khushu (Mongolia, Ypresian) referred as cf. *Hyracolestes* sp. by Russell and Dashzeveg (1986). We, however, demonstrated above that the French specimens actually correspond to molars of proviverrine hyaenodonts.

The Mongolian specimen differs from the lower molars of *Hyracolestes* by a smaller metaconid, the mesio-distal elongation of the talonid, the presence of well-developed pre- and postcingulid, and the lingual closing of the postfossid. As a result, PSS 20-124 cannot be referred to *Hyracolestes*; Lopatin and Kondrashov (2004), who recently published the description of sarcodontines from Tsagan Khushu, have a similar opinion. The previously listed differences are shared with the lower molars of the proviverrines discussed in the present paper; moreover, several other shared features can be listed: the presence of a carnassial notch on the proto- and paracristid, a large and high paraconid, and a narrow talonid. Moreover, PSS 20-124 (L = 2.6; W = 1.5) is close in size to the molars of *Eoproviverra* and *Parvagula*.

The Mongolian locality shares with Palette and Le Clot the presence of the condylarth *Lessnessina*: *L. praecipuus* is recorded in Palette and Le Clot, while *L. khushuensis* is known from Tsagan Khushu (Marandat et al. 2012). As a result, the presence of a proviverrine in the Mongolian locality is not unexpected. PSS 20-124 however differs from the oldest European proviverrines by the presence of a postcingulid and the reduction of the entoconid, which is crestiform. As noted by Russell and Dashzeveg (1986), the postcingulid even nearly meets the precingulid.

The sole Paleocene hyaenodont in Asia is *Prolimnocyon chowi* from Bayan Ulan (Mongolia) (Meng et al. 1998; Fig. 7); it corresponds to a limnocyonine, a subfamily that is characterized by the strong reduction or loss of M3/m3. The Asian hyaenodonts are more diverse in the early Eocene: *Indohyaenodon* from Vastan Lignite Mine (Gujarat, India) (Bajpai et al. 2009; Rana et al. 2015); *Arfia palustris* from Wutu Basin (Shandong, China) (= "*Anthracoxyaena*" *palustris* Tong and Wang, 2006; reassigned to *Arfia* [Solé et al. 2013]); *Isphanatherium* and *Neoparapterodon* sp. from Andarak-2 locality (Fergana Basin, Kyrgystan) (Lavrov and Averianov 1998); and *Arfia langebadreae* and ?*Prototomus* sp. from Tsagan Khushu (Lavrov and Lopatin 2004) (Fig. 7).

Comparisons with ?*Prototomus* sp. from Tsagan Khushu is presently impossible because the specimens correspond to a toothless dentary and a maxillary bearing only a labial fragment of M2. PSS 20-124 shares with the two Asian *Arfia* species the presence of buccal cingulids, but it differs from the former by a distinctly narrower talonid, a less bulbous entoconid and the absence of crenulated enamel; the Mongolian specimen thus does not represent an arfiine.

It is difficult to compare PSS 20-124 with specimens of *Isphanatherium* and *Neoparapterodon* as those genera are only known from upper teeth. Nevertheless, *Isphanatherium* and *Neoparapterodon* display very secant specializations such as the reduction of the protocone, features not found in association with labial cingulids like those of PSS 20-124. We thus think that PSS 20-124 cannot be assigned to any of these taxa.

Among the hyaenodonts present in the early Paleogene of Asia, the reduction of the entoconid is found in the limnocyonines (Morlo and Gunnell 2003) and indohyaenodontines (Solé et al. 2014b; Rana et al. 2015). The presence of postcingulids is common among indohyaenodontines (*Indohyaenodon*, *Kyawdawia*, and *Yarshea*). However, the latter are considered to be geographically restricted to South and Southeast Asia (Solé et al. 2014b). If PSS 20-124 corresponds to the lower molar of an indohyaenodontine, it would represent the northernmost occurrence of this subfamily (Fig. 7).

Another relevant comparison is with the peculiar limnocyonine *Thereutherium* from the Rupelian (Oligocene; Mammal Paleogene, MP23–MP25) of Europe. This limnocyonine is interesting because it displays both labial cingulids and a reduction of the entoconid (Lange-Badré 1979). Lange-Badré (1979, 1995) hypothesized that this peculiar genus may have evolved in Asia and dispersed from this area to Europe during the Rupelian. However, the origin of this genus is presently unknown because no related or ancestral taxon is known in the fossil record. Lange-Badré (1995) highlighted that the limnocyonines seem to have been present in Asia during the entire Eocene, but that their evolution is only poorly studied due to the lack of fossils. Only *Prolaena* from Hetaoyuan Formation (Henan Province, middle Eocene) and ?*Thinocyon sichowensis* from Guanzhuang Formation (Shandong Province, middle Eocene) (Fig. 7) are tentatively referred to Limnocyoninae at the present time (see Morlo and Gunnell 2003 for a discussion concerning the systematic position of these limnocyonines). One can remark that the locality where PSS 20-124 has been found is closer to those of the Asian limnocyonines than to those of the indohyaenodontines (Fig. 7). In conclusion, PSS 20-124 is possibly related to the Indohyaenodontinae or to the Limnocyoninae rather than to the Proviverrinae.

Conclusions

New elements for the proviverrine hyaenodont *Parvagula palulae* from the early Eocene of Southern France illustrate the morphological differences between the sinopines and proviverrines and support the faunal differences between Northern and Southern Europe previously documented (Marandat 1997; Marandat et al. 2012). Moreover, the similarities of the early Eocene French proviverrines to the African genus *Tinerhodon* support the hypothesis of a northward extension of this group around the Paleocene–Eocene boundary. This northward dispersal of the proviverrines expanded during the early Eocene; they probably dispersed into the Paris Basin during a time of faunal turnover (between 55 and 52 Myr) (Solé et al. 2014a). This dispersal is correlative with the reduction of the geographic range of Sinopinae, which thus was mainly confined to North America, except for a late middle Eocene dispersal into Asia (Morlo et al. 2014).

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