



On the status of early Eucricetodontinae (Muroidea, Rodentia) with a special focus on the *Atavocricetodon* vs *Eucricetodon* issue: morphometrical and microstructural aspects

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ABSTRACT

Among the flourishing Muroidea, the Eucricetodontinae constitute the most diversified subfamily of the Eurasian Palaeogene. Early representatives, such as *Atavocricetodon* and *Eucricetodon*, are notably characterized by their simple and primitive dental morphology. As a result, it appears very difficult to discriminate these genera according to their dental morphology, and that is emphasized by their imprecise diagnosis. Here, we aim at challenging the taxonomic validity of *Atavocricetodon*, frequently considered as a grade of *Eucricetodon*. We chose to investigate the outline of first upper molars for four species of *Atavocricetodon* and seven of *Eucricetodon*, to avoid confusions made by their occlusal dental characters. The outline analysis involves samples of ten molars, and was realized by using Elliptic Fourier Transforms. Incisor enamel microstructures were investigated as well in four species, because this dental character appears highly useful in rodents to solve taxonomic issues. Results revealed that if a significant difference exists between the

RESUMEN

Entre los florecientes Muroidea, los Eucricetodontinae constituyen la subfamilia más diversificada del Paleógeno euroasiático. Sus representantes tempranos, tales como *Atavocricetodon* y *Eucricetodon*, se caracterizan notablemente por su morfología dental simple y primitiva. Como resultado, parece muy difícil discriminar estos géneros en relación con su morfología dental, y eso queda enfatizado por su imprecisa diagnosis. Aquí, pretendemos desafiar la validez taxonómica de *Atavocricetodon*, frecuentemente considerado como un grado de *Eucricetodon*. Para evitar las confusiones debidas a sus caracteres dentales oclusales, elegimos investigar el contorno de los primeros molares superiores de cuatro especies de *Atavocricetodon* y siete de *Eucricetodon*. El análisis del contorno implica muestras de diez molares, y fue realizado por medio de Transformaciones Elípticas de Fourier. Las microestructuras del esmalte de los incisivos fueron investigadas también en cuatro especies porque este carácter dental parece muy útil para la resolución de cuestiones

global dental shape of *Atavocricetodon* and *Eucricetodon*, outline morphospaces of the considered species generally overlap as displayed by the multivariate analysis and the hierarchical clustering. This is partly explained by the high intrageneric shape variation, which might correspond to different Oligocene lineages of Eucricetodontinae. Such variation is also due to *Atavocricetodon paaliense*, which could rather belong to another genus, the pseudocricetontine *Kerosinia*. More generally, there is no discrete character or real apomorphy which permits to distinguish these genera, because incisor enamel microstructure patterns are highly variable and a few types are shared by both genera. *Atavocricetodon* cannot thus be retained neither as a genus, nor as a morphosubgenus of *Eucricetodon*. Further studies, including much more fossil material, are needed to accurately identify the various lineages of *Eucricetodon* and to potentially define new genera on a fair basis.

Keywords: Rodents, molar, Palaeogene, outline analysis, enamel microstructure.

taxonómicas en roedores. Los resultados revelaron que, aunque existen diferencias significativas entre la forma dental global de *Atavocricetodon* y *Eucricetodon*, los morfoespacios del contorno de las especies consideradas generalmente solapan tanto en ordenaciones multivariantes como en agrupaciones jerárquicas. Esto se explica parcialmente por la elevada variabilidad intragenérica en forma, la cual podría corresponder a diferentes linajes oligocenos de Eucricetodontinae. Tal variación también es debida a *Atavocricetodon paaliense*, el cual podría pertenecer a otro género, el pseudocricetontino *Kerosinia*. Más generalmente, no existe un carácter discreto o apomorfía real que permita distinguir estos géneros, porque los patrones de microestructura del esmalte de los incisivos son altamente variables y unos pocos tipos son compartidos por ambos géneros. *Atavocricetodon* no puede ser, por tanto, retenido ni como género ni como subgénero de *Eucricetodon*. Estudios adicionales, incluyendo mucho más material fósil, son necesarios para identificar adecuadamente los distintos linajes de *Eucricetodon* y potencialmente definir nuevos géneros.

Palabras clave: Roedores, molar, Paleógeno, análisis de contorno, microestructura del esmalte.

1. INTRODUCTION

Muroid rodents currently represent the most flourishing mammal superfamily (310 genera, 1517 species; Musser & Carleton, 2005). During the Palaeogene, the extinct Eucricetodontinae subfamily was the most diversified group of Muroidea. This Eurasian group is of great interest because it consists of widespread and generalist species which could be at the origin of most of current taxa, such as Eumuroidea (e.g., rats, mice, hamsters, voles; Lazzari *et al.*, 2008). To date, early representatives encompass at least the four following genera: *Eocricetodon* Wang, 2007, *Oxynocricetodon* Wang, 2007, *Atavocricetodon* Freudenthal, 1996, and *Eucricetodon* (Thaler, 1966).

Eocricetodon and *Oxynocricetodon* were strict Late Eocene Chinese genera (Wang, 2007). The Eurasian radiation of Eucricetodontinae really started from the Oligocene with the appearance of both *Atavocricetodon* and *Eucricetodon*. However, *Eucricetodon* was not found in Europe before the Late Oligocene (Vianey-Liaud, 1972). This episode roughly coincides with the disappearance of *Atavocricetodon* in Eurasia. The last record of *Eucricetodon* is European, and dates from the Early Miocene (Hugueney, 1999). All these early forms present a simple and bunodont dental morphology, which can be considered as plesiomorphic. This observation represents the main issue for discriminating these genera between themselves and to find true apomorphies.

Originally, these genera were synonymized with

Eucricetodon (Thaler, 1966). Thaler (1966) first erected *Eucricetodon* as a subgenus of *Cricetodon* Schaub, 1925 to differentiate some Oligocene-Miocene lineages from exclusive Miocene species, considered as highly derived. He did not propose diagnosis for *Eucricetodon*, saying that it consisted of a heterogeneous group. Vianey-Liaud (1972) gave one of the first diagnoses for the genus *Eucricetodon*, including six species: *E. atavus*, *E. huberi*, *E. quercyi* = *E. dubius*, *E. praecursor*, *E. collatus*, and *E. huerzeleri*, this latter considered to be separated from other species. On the basis of additional material and characters (e.g., incisor enamel ornamentation), Comte (1985) proposed to bring *E. huerzeleri* closer to the “*atavus-collatus* group”, while he considered *E. dubius* as a probable immigrant in Europe. Then, Freudenthal (1996) decided to separate the Early Oligocene European “*atavus*-group” from the homogeneous “*collatus*-group”, the “*huerzeleri*-group” and the “*dubius*-group” to erect the genus *Atavocricetodon*, on the basis of four new species described from the Lower Oligocene of Spain (Olalla 4A, Teruel). More recently, de Bruijn *et al.* (2003) doubted about the validity of *Atavocricetodon* saying that it is rather an evolutionary grade of *Eucricetodon*. The most recent definitions of *Atavocricetodon* and *Eucricetodon* are of Freudenthal (1996) and Dienemann (1987), respectively:

- Diagnosis of *Atavocricetodon*: “*Eucricetodontinae* of very small to medium size, with relatively low-crowned cheek teeth, with thin enamel, relatively small cusps, and long crests. Lower molars with or without hypoconid hind

arm. M_1 with protoconid hind arm frequently connected to the metaconid. Upper molars generally with a posterior protolophule (= protolophule II, see Gomes Rodrigues *et al.*, 2010) and an anterior metalophule (= metaloph connected to the anterior arm of hypocone). M^1 generally without a complete anterolophule. Old entoloph (= mure) on M^3 frequently present, or even complete, neo-entoloph (= endoloph) fully developed.”

- Emended diagnosis of *Eucricetodon* (translated from German): “Mostly middle-sized cricetids with bunodont enamel pattern. The predominantly voluminous main-cusps are usually not very accentuated and proceed on broad bases. The slim valleys are constricted by often massively protruding ridges.”

The diagnosis of *Atavocricetodon* relies on the frequency of morphological characters of the occlusal dental surface, while *Eucricetodon* was defined according to its overall dental morphology (outline, global relief,...), and both clearly emphasize two ways of thinking. Since *Atavocricetodon* was created, this diagnosis has never been emended. Most of the characters cited are applicable to *Eucricetodon*, and none of them constitute apomorphy. The diagnosis of *Eucricetodon* has not been emended since the split with *Atavocricetodon*, either. The most obvious difference between them could be the smaller size of *Atavocricetodon* (de Bruijn *et al.*, 2003). The enamel microstructure of lower incisors also provided crucial data on both genera. Kalthoff (2000, 2006) showed that *Atavocricetodon* and *Eucricetodon* species have different three-dimensional arrangements of enamel (i.e., schmelzmuster). They respectively display uniserial type 1 and 4. The type 1 is primitive as respect to type 4, because it was present in stem Muroidea (Koenigswald & Kalthoff, 2007), and that could corroborate the grade assumption concerning *Atavocricetodon*. The type 4 could correspond to an autapomorphic character, since it is only known in *Eucricetodon*. However, the debate still exists given that the enamel of only a few species was investigated, especially during the Early Oligocene. Such examples again show the difficulty of discriminating taxonomic units on the basis of obvious and invariant criterions.

Gomes Rodrigues *et al.* (2010) also discussed the validity of *Eocricetodon* and *Oxynocricetodon*. The first genus appears monophyletic, but it does not display any discrete character, which could discriminate it from *Atavocricetodon*, except a complete anterolophule on M^1 . The second one is paraphyletic, stem group of *Atavocricetodon*, but it differs in preserving a protolophule I on M^1 , a characteristic of basal Muroidea. Given the paucity of material concerning these Late Eocene genera, it seems difficult to more accurately investigate them at that time. At the opposite, *Atavocricetodon* and *Eucricetodon* are widely represented according to the high number of species and dental material available. As

a result, we proposed here to study the global dental shape of different Eurasian species involving both genera, by means of outline analysis excluding the traditional listing of dental characters, to investigate the incisor enamel microstructure, and to discuss the taxonomical validity of *Atavocricetodon*.

2. MATERIAL AND METHODS

2.1. Outline analysis

Dental materials are housed in the collections of Vertebrate Paleontology of the University of Montpellier 2 (UM2, France) and of the Institute of Vertebrate Paleontology and Paleoanthropology of Beijing (IVPP, China; Table 1). The *Atavocricetodon* samples include three European species (*A. atavus*, *A. aff. nanus* and *A. cf. huberi*), and the Asian *A. paaliense*. Surprisingly, this latter species presents a lophodont pattern, as well as a strong and wide prelobe on M^1 as Pseudocricetodontinae. For this reason, *Pseudocricetodon montalbanensis* was added to draw comparisons with this species. Seven species of *Eucricetodon* were investigated. Four European species were considered (*E. huerzeleri*, *E. dubius*, *E. hesperius*, *E. aquitanicus*), in addition to the three Asian (*E. bagus*, *E. asiaticus*, *E. jilantaiensis*). The wide spectrum of species for each genus, although not exhaustive, reflects their important Eurasian diversity through the Oligo-Miocene period (Fig. 1, Table 1).

The dental nomenclature used here follows the rodents' nomenclature defined by Wood & Wilson (1936), slightly modified by Gomes Rodrigues *et al.* (2012). M^n and M_n respectively refer to the n^{th} upper and n^{th} lower molars. Each sample consists of ten M^1 , except for *A. paaliense* for which only seven teeth are available. Overall tooth shapes were investigated by using an outline analysis. By registering the relative size and position of each cusp, the outline analysis represents a suitable method to study the overall shape of the tooth. Fourier methods, notably Elliptic Fourier Transform (EFT), allow the description of complex outlines approximating them by a sum of trigonometric functions of decreasing wavelength (i.e., harmonics; Fig. 2). The x and y coordinates of 64 points equally spaced along the dental outline were calculated to quantitatively describe the shape of M^1 . We applied EFTs to these data using EFAwin software (Ferson *et al.*, 1985), extracting Fourier coefficients from the original outline and normalizing these shape variables. This method considers the separate Fourier decomposition of the incremental change in the x and y coordinates as a function of the cumulative length along the outline (Kuhl & Giardina, 1982). For EFT, any harmonic n yields four Fourier coefficients: A_n and B_n for x , and C_n and D_n for y , which all contribute to describe the initial outline. We retained the

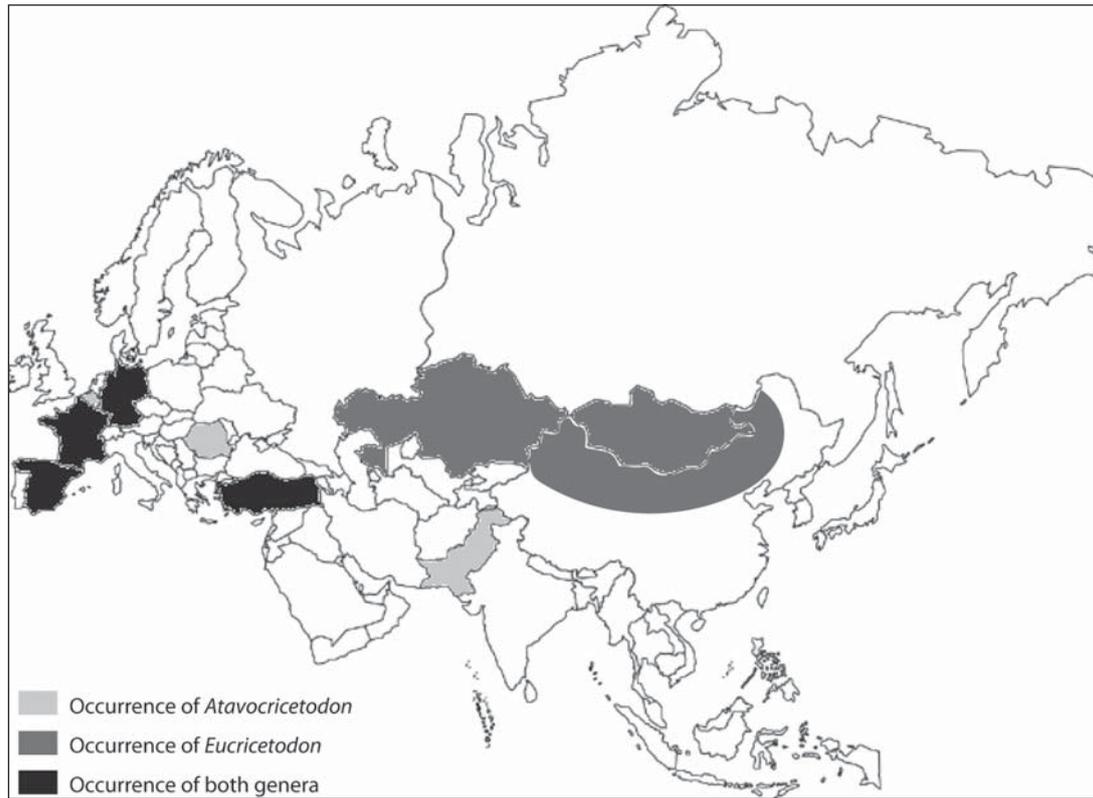


Figure 1. Map of Eurasia showing the main Oligo-Miocene areas where *Atavocricetodon* and *Eucricetodon* specimens were unearthed.

Table 1. Data concerning each species of *Eucricetodon* and *Atavacricetodon* investigated, in addition to *Pseudocricetodon montalbanensis* (N: number of specimens).

Species	N	Age	Country	Locality	Collection
<i>Atavocricetodon</i> aff. <i>nanus</i> Freudenthal, 1996	10	Early Oligocene (MP22)	France (Quercy)	Cavalé	UM2
<i>Atavocricetodon atavus</i> (Misonne, 1957)	10	Early Oligocene (MP23)	France (Quercy)	Itardies	UM2
<i>Atavocricetodon paaliense</i> Marivaux <i>et al.</i> , 1999	7	Early Oligocene	Pakistan (Bugti Hills)	Paali Nala C ₂	UM2
<i>Atavocricetodon</i> cf. <i>huberi</i> (Schaub, 1925)	10	Late Oligocene (MP25)	France (Quercy)	Belgarric 1	UM2
<i>Eucricetodon huerzeleri</i> Vianey-Liaud, 1972	10	Late Oligocene (MP26)	France (Quercy)	Mas de Pauffié	UM2
<i>Eucricetodon dubius</i> (Schaub, 1925)	10	Late Oligocene (MP28)	France (Quercy)	Pech Desse	UM2
<i>Eucricetodon asiaticus</i> (Matthew & Granger, 1923)	10	early Late Oligocene	China (Inner Mongolia)	UTL4 (Ulantatal)	IVPP
<i>Eucricetodon jilantaiensis</i> Gomes Rodrigues <i>et al.</i> , 2012	10	early Late Oligocene	China (Inner Mongolia)	UTL4 (Ulantatal)	IVPP
<i>Eucricetodon bagus</i> Gomes Rodrigues <i>et al.</i> , 2012	10	early Late Oligocene	China (Inner Mongolia)	UTL4 (Ulantatal)	IVPP
<i>Eucricetodon hesperius</i> Engesser, 1985	10	Early Miocene (MN1)	France (Lot-et-Garonne)	Paulhiac	UM2
<i>Eucricetodon aquitanicus</i> Baudelot & de Bonis, 1968	10	Early Miocene (MN3)	France (Hérault)	Bouzigues	UM2
<i>Pseudocricetodon</i> <i>montalbanensis</i> Thaler, 1969	10	Early Oligocene (MP23)	France (Quercy)	Itardies	UM2

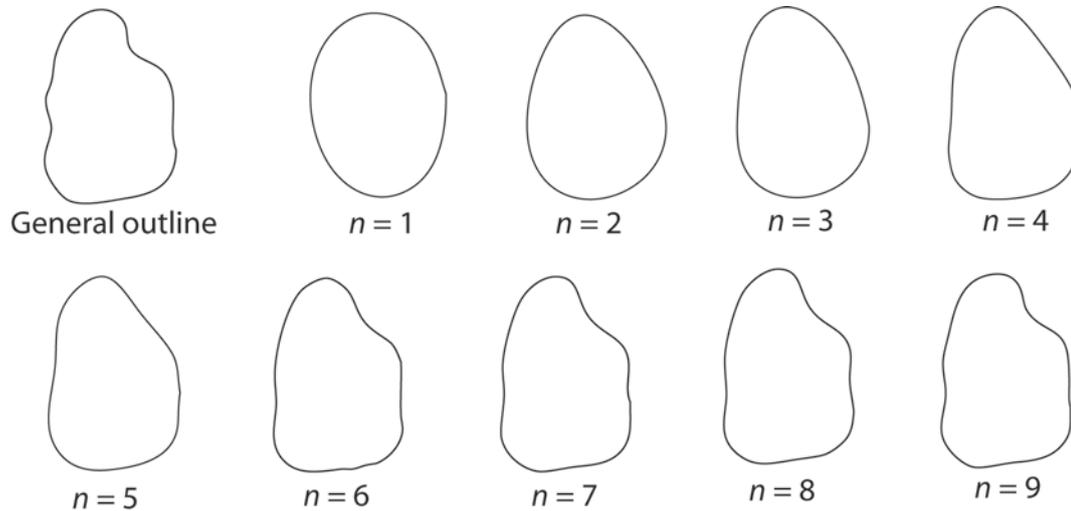


Figure 2. Description of M^1 outline (e.g., *E. asiaticus*) according to the sum of n harmonics.

first eight harmonics for the M^1 , which represents the best compromise between measurement error and information content for these muroid molars (Renaud *et al.*, 1996). However, the four coefficients of the first harmonic ($A1-D1$) were not included in the subsequent analyses, given that they are poorly discriminant and constitute background noise after the standardization step (size and orientation; Crampton, 1995; Renaud *et al.*, 1996).

A principal component analysis (PCA) was performed to evaluate the morphospace of each species. Variables were represented by the 28 coefficients of each harmonics previously selected for M^1 . A multivariate analysis of variations (Manova) allowed researching a potential significant difference between the global morphospaces of *Eucricetodon* and *Atavocricetodon*. This analysis was coupled to a nested Manova to test the intrageneric variations in a same genus. Pairwise multicomparisons tests were also used to assess the differences between other taxa, such as *A. paaliense* and *P. montalbanensis*. Both tests included the coordinates of the first ten axes of the PCA for which the sum met 95 % of the total variation. These data were previously rank transformed since they did not fulfill the required parameters (i.e., normality, homoscedasticity of variances) for such statistical tests (Conover & Iman, 1981). A phenogram was computed as well by using an UPGMA analysis involving a Euclidian distance matrix calculated from the harmonic coefficients.

2.2. Incisor enamel microstructure

Four species were investigated here to complement the Kalthoff's sampling (2006), which already included *A. atavus*, *E. dubius*, *E. gerandianus*, and *E. infralactorensis*. Our samples encompass a French specimen of *A. atavus*,

one specimen of *A. aff. nanus* from the Lower Oligocene, two specimens of *A. cf. huberi* and two specimens of *E. huerzeleri* from the Upper Oligocene, also used for the outline analysis. Asian species could not be investigated here.

Small pieces of lower incisor were imbedded in epoxy resin. This resin was grinded and polished to obtain a smooth transverse section of the incisor. About 5 seconds of etching with HCl 4 % was necessary to make the enamel details visible. The enamel microstructures was then examined and digitized with a scanning electron microscope at different magnification (x 100 to x 5,000). They were described according to the nomenclature of Koenigswald & Sander (1997).

3. RESULTS

3.1. Outline analysis

The first two axes of the PCA represent respectively 30.68 % and 18.64 % of the total variance, while the third represent 15.33 % (Fig. 3). Along the first axis, the shape variation mainly concerns the disto-labial border, which forms an acute angle on the negative side and a right angle on the positive side, and also the prelobe which has a tendency to broaden toward the positive side. On the second component, the length/width ratio mainly varies, that is reflected by a compacted molar on the negative side and a slender one on the positive side. Finally, the particularity of the third axis relies on teeth having an elongated prelobe on one side and compacted teeth with a shorter prelobe on the other side. More generally, outlines of most *Atavocricetodon* and *Eucricetodon* species overlap. Specimens of *E. jilantaiensis* tend to marginalize because

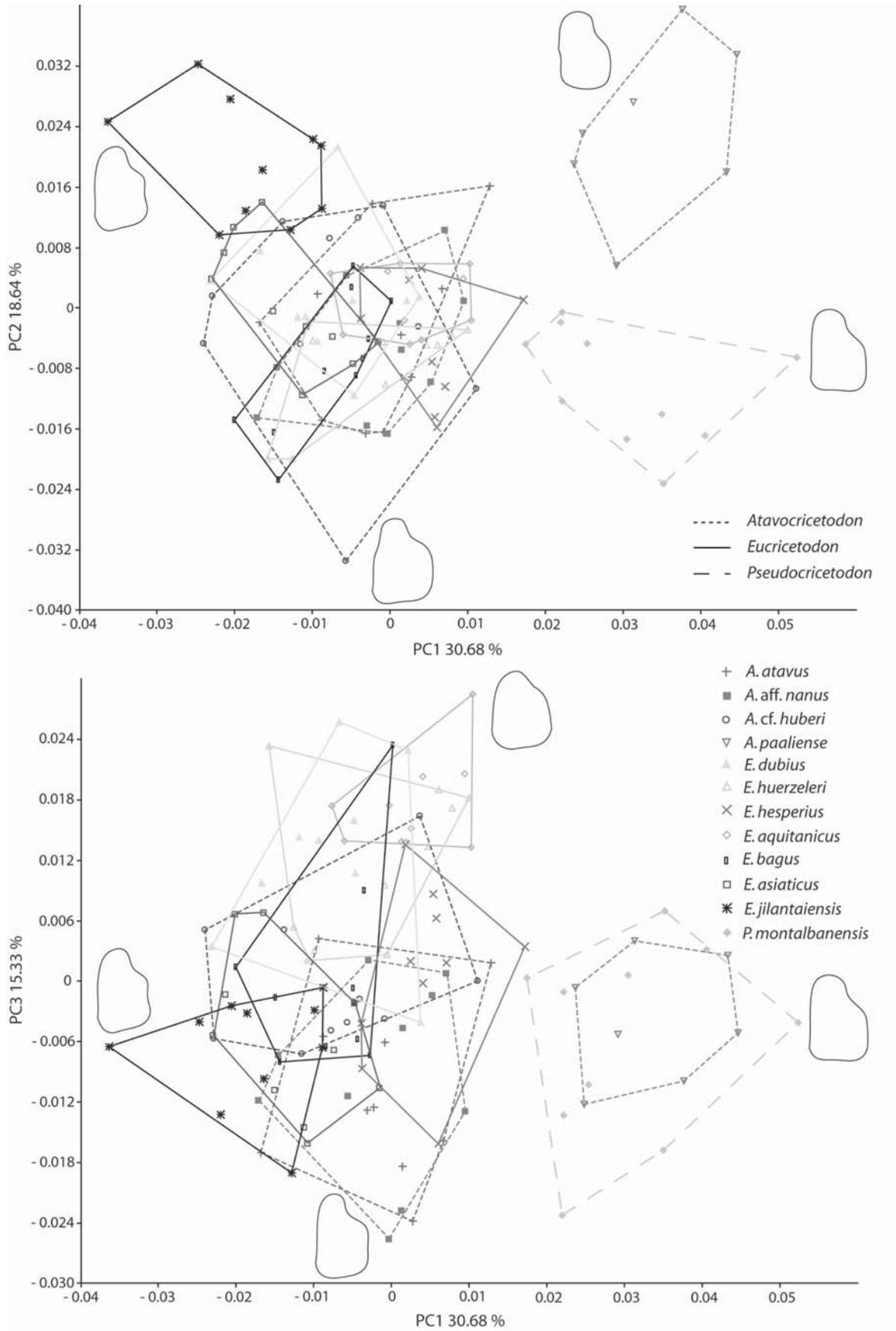


Figure 3. Graphs of the principal component analysis (PCA) realized on the first eight harmonics describing the M¹ outline for each species.

of their strongly slender teeth (axis 2); nonetheless, they present some affinities with *A. asiaticus*. This trend can also be observed in *E. aquitanicus*, which shows compacted teeth with a short prelobe (axis 3). Outlines of *A. paaliense* strongly differ from other *Atavocricetodon* in having slender teeth (axis 2), a broad prelobe and a more quadrate distal shape (axis 1). They are close to *P. montalbanensis* notably on the components 1 and 3, and only their length/width ratio appears distinct (axis 2).

The Manova reveals that there are significant differences between each genus, and also between species within *Atavocricetodon* and *Eucricetodon* according to the nested Manova (Table 2a). The only insignificant difference observed concerns *A. paaliense* and *P. montalbanensis*, according to the conservative Bonferroni test (Table 2b).

Four groups are clearly differentiated on the phenogram (Fig. 4). The first one included *P. montalbanensis* and *A. paaliense*, which, although distant, are opposed to other Eucricetodontinae. Two species from Ulantatal, *E. asiaticus* and *E. jilantaiensis* are gathered. A third geographical heterogenous group encompasses *E. aquitanicus*, *E. bagus* and *E. huerzeleri*. The last group is European and consists of *A. atavus* and *A. aff. nanus* on one side, and of *E. hesperius*, *A. cf. huberi*, and *E. dubius* on the other side.

Table 2. a) Results of the Manova and nested Manova realized on the first ten PCA coordinates involving each species clustered by genus (except *P. montalbanensis*; significant difference at $\alpha=0.05$, df: degree of freedom). b) Results of Hotelling's (above the diagonal) and Bonferroni (below the diagonal) pairwise comparisons tests. * means results with or without *A. paaliense*.

a)	df	F	p
Species (Genus)	99	198.230	<0.001
Species	11	6.251	<0.001

b)	<i>Atavocricetodon</i>	<i>Eucricetodon</i>	<i>A. paaliense</i>	<i>Pseudocricetodon</i>
<i>Atavocricetodon</i>		<0.001*	<0.001	<0.001*
<i>Eucricetodon</i>	<0.001*		<0.001	<0.001
<i>A. paaliense</i>	<0.001	<0.001		0.015
<i>Pseudocricetodon</i>	<0.001*	<0.001	0.092	

3.2. Incisor enamel microstructure

The specimen of *A. atavus* from Itardies shows an enamel thickness of about 25 μm and includes two distinct layers: a *portio externa* (PE) and a thicker *portio interna* (PI). The PE is arranged in parallel prism of crystallites

characterizing the radial enamel (Fig. 5a). The PI consists in uniserial enamel defined by one layer of prisms decussating and thus appearing as Hunter-Schreger bands (HSB; Fig. 5b). The HSB are obliquely and transversally oriented from the enamel-dentine junction (edj), and include prism-parallel interprismatic matrix (IPM). This schmelzmuster corresponds to the type 1 (Fig. 5c), and the overall structure is similar to the investigated specimen of *A. atavus* from Hoogbutsel (Kalthoff, 2000). The enamel microstructures of *A. aff. nanus* (Fig. 5d) and *E. huerzeleri* (Fig. 5e) are type 1 as well with a relatively thicker PE, while their enamel thickness is about 40 and 60 μm , respectively. Conversely, the incisor microstructure of both specimens of *A. cf. huberi* (Fig. 5f) is more complex and corresponds to type 8. The enamel thickness is about 80 μm . The PE is highly reduced compared to PI, and includes both radial and tangential enamel. The PI consists of longitudinal HSB with prism-parallel IPM and rectangular IPM in the part close to edj.

4. DISCUSSION

Early eucricetodontines constitute the simplest forms from a morphological viewpoint, due to their bunodont patterns and their primitive cricetid plan (i.e., without accessory cusp and loph). Despite such shared characters, their global shapes are extremely variable whatever the genus. Therefore, the present outline analysis did not permit to clearly define morphotypes or evolutionary stages. Significant differences exist between dental outlines of *Atavocricetodon* and *Eucricetodon*, but according to the PCA they are minor given the overlapping of morphospaces. That can be considered as the result of a non-negligible interspecific (i.e., intrageneric) variation in view of the results of the nested Manova. Dental shape is notably linked to the own evolutionary history of these taxa and it is not strictly correlated to their occlusal morphology.

That is partly expressed by the phenogram. For instance, the Asian *E. asiaticus* and *E. jilantaiensis* are sister species (Vianey-Liaud *et al.*, 2011), they have a close dental shape, while they present a primitive and derived dental pattern respectively (e.g., proverse vs retroverse distal lophs on upper molars; Gomes Rodrigues *et al.*, 2012). Similarly, *E. aquitanicus*, *E. bagus* and *E. huerzeleri*, which come from different Eurasian areas, have different ages and different dental morphologies, but they display close dental shape. If *A. atavus* and *A. aff. nanus* as early *Atavocricetodon* species are grouped together, the Late Oligocene *A. aff. huberi* and *E. dubius* have comparable shape, even if they do not belong to the same genus. All these observations join the thought of Dienemann (1987) who already argued that the impossibility of finding diagnostic characters for

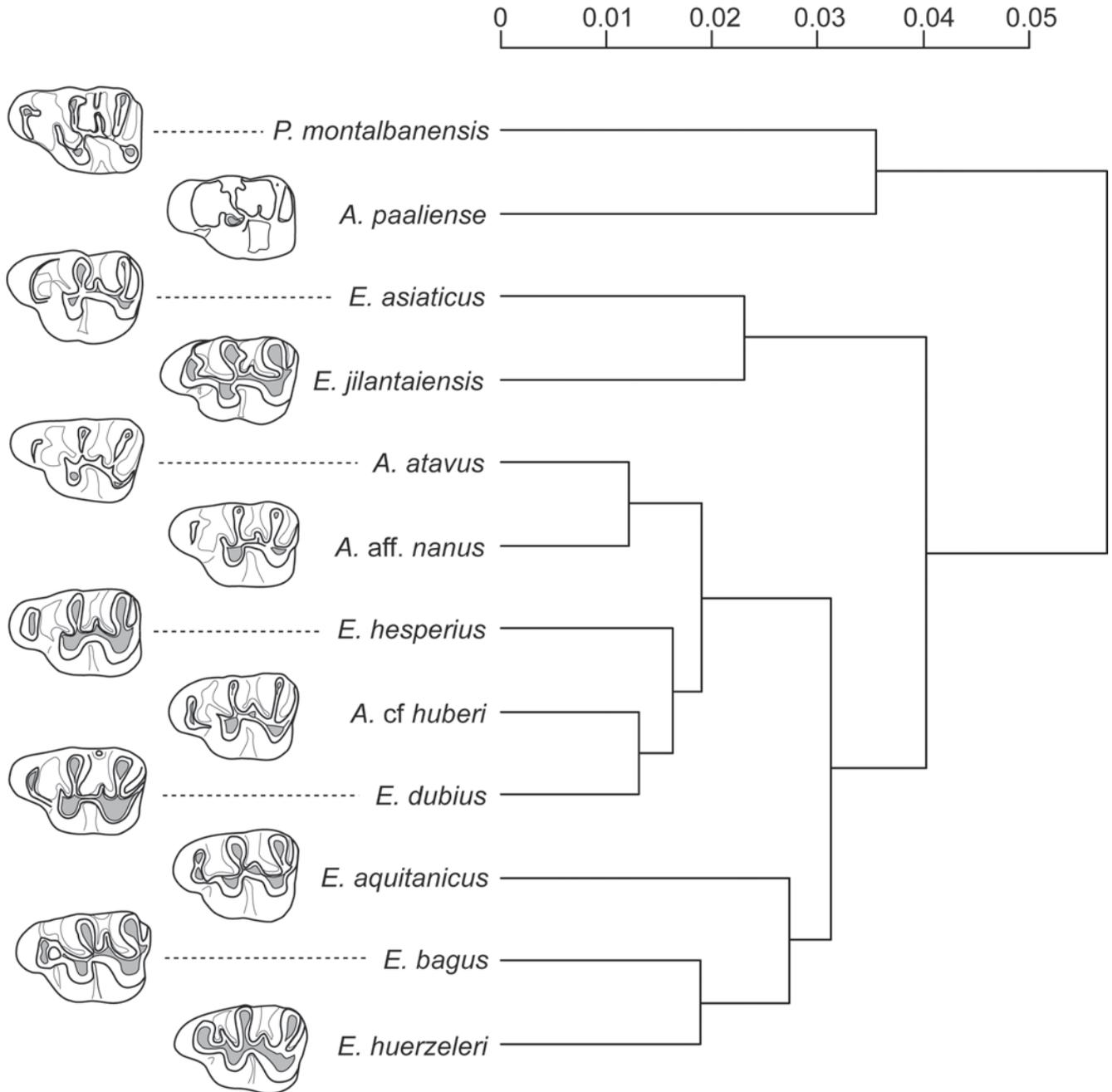


Figure 4. Phenogram of an UPGMA analysis involving a Euclidian distance matrix calculated from the first eight harmonic coefficients, and including left M¹ diagrams (not to scale).

Eucricetodon s.l. (i.e., *sensus* Thaler, 1966), and thus indirectly for *Atavocricetodon*, relies on the fact it is a long-term genus having a vast shape variation, which covers numerous evolutionary stages.

Apart from these observations, the case of *A. paaliense* appears directly linked to the Pseudocricetodontinae, whose stem species have close dental morphologies with respect to Eucricetodontinae that could explain the confusion. This species has a pseudocricetodontine-like shape, in being slender and in having a broad prelobe,

as *Pseudocricetodon nawabi* Marivaux *et al.*, 1999, the only other muroid found in the same locality (Paali Nala C₂, Bugti Hills, Pakistan, Lower Oligocene; Marivaux *et al.*, 1999). However, *A. paaliense* displays much more affinities with another Pseudocricetodontinae, *Kerosinia variabilis* Unay-Bayraktar, 1989, a Turkish species from late Early Oligocene sites. In addition of being small, both taxa present a central mure and an endomesostyle on upper molars, a frequently complete protolophule I on M¹, a weak lingual cingulum on M², similar lower molars with a

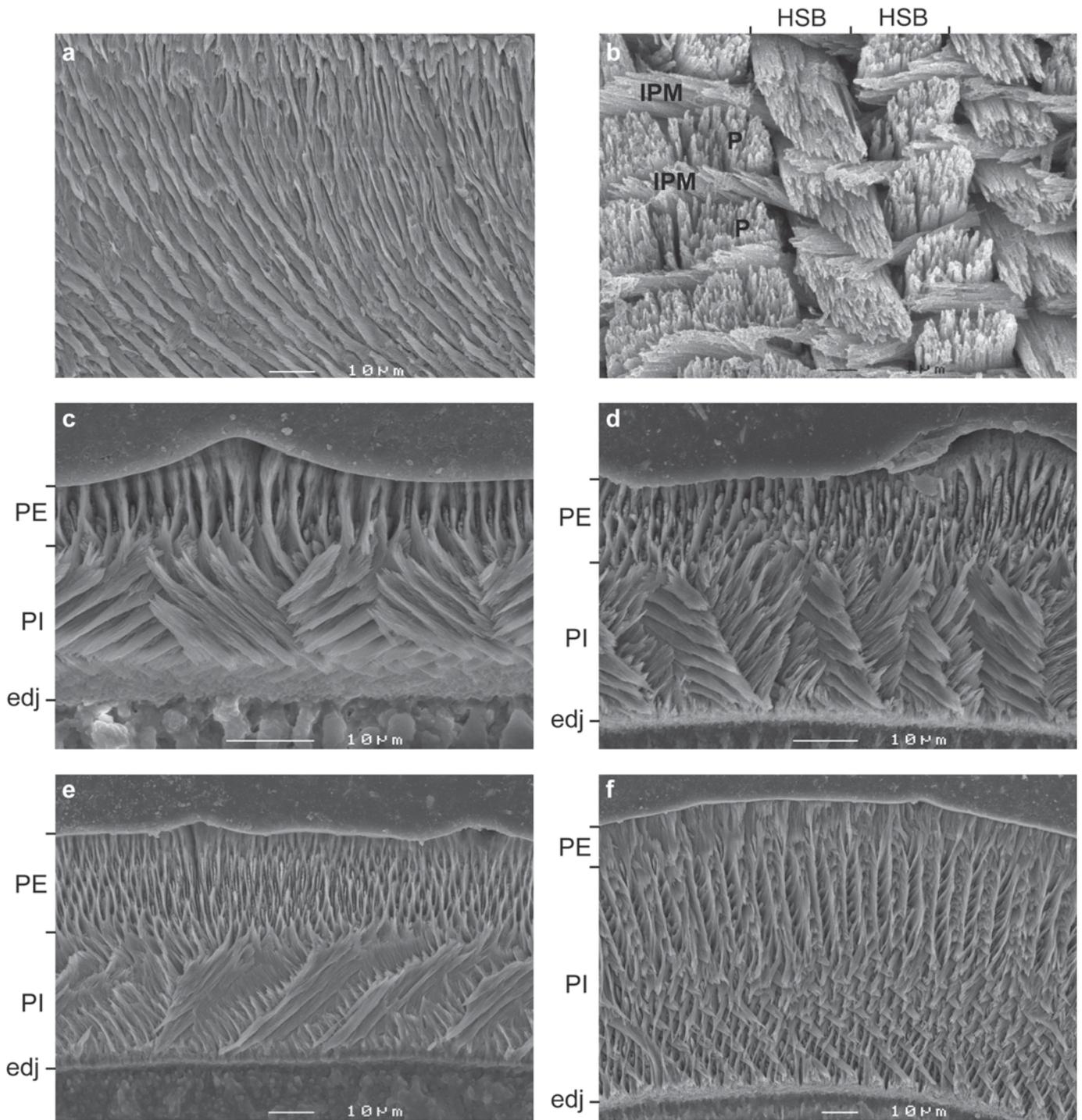


Figure 5. SEM photographs of incisor enamel microstructures. **a)** radial enamel; **b)** uniserial enamel; **c)** *Atavocricetodon atavus* (ITD-53, type 1); **d)** *Atavocricetodon* aff. *nanus* (CAV-701, type 1); **e)** *Eucricetodon huerzeleri* (MPF, type 1); **f)** *Atavocricetodon* cf. *huberi* (Bell-1, type 8). P: prism, IPM: interprismatic matrix, HSB: Hunter-Schreger bands, PE: *portio externa*, PI: *portio interna*, edj: enamel-dentine junction.

complete anterolophulid on M_1 , a metalophulid II reaching the top of the metaconid, a mesolophid short and slightly twinned to absent, and a strong anterolophid on M_2 (Unay-Bayraktar, 1989). From these results, *A. paaliense* likely belongs to *Kerosinia*. This example once again underscores the lack of discrete characters defining *Atavocricetodon*, and the resulting misinterpretations.

More generally, the species attributed to *Atavocricetodon* have a small size as Eocene genera. If this character is specific to this genus, it cannot represent a diagnostic character, and moreover their particularity is not exclusive among *Eucricetodontinae*. For instance, the Asian species *E. bagus* and *E. youngi* have similar size range. If *Atavocricetodon* could also present the practical advantage of forming a morpho-subgenus of *Eucricetodon* (according to de Bruijn *et al.*, 2003) comprising all small and primitive European *Eucricetodontinae*, the taxonomic status (genus or subgenus) still remain hard to distinguish, and there is no evidence that a species is more related to *Atavocricetodon* than to *Eucricetodon*. Nor it is question of a specific stratigraphic range (i.e., “chronogenus”) because there was still *Atavocricetodon* species in Europe, such as *A. huberi*, when *Eucricetodon* appeared during the Late Oligocene (Vianey-Liaud, 1972; Comte, 1985).

Since the last decade (Kalthoff, 2006), the enamel microstructure of lower incisors was assumed as the only one discrete character which could clearly differentiate *Atavocricetodon* from *Eucricetodon* species. Our results do not support this hypothesis, and suggest this character could convergently evolve in the diverse group or lineages of *Atavocricetodon* and *Eucricetodon*. Thus, first *Atavocricetodon*, such as *A. atavus* and *A. aff. nanus*, displays a primitive enamel (type 1), while surprisingly, the more recent one, *A. cf. huberi*, have a highly derived enamel which is convergent to *Pseudocricetodontinae* (e.g., *Pseudocricetodon*, *Heterocricetodon*; type 8, Kalthoff, 2006). Similarly, one of the oldest European *Eucricetodon*, *E. huerzeleri*, has a primitive schmelzmuster (type 1), while the more recent species (e.g., *E. dubius*) have slightly more complex microstructure (type 4). As a result, it is impossible to use this character in the definition of both genera, faced to such a microstructural variability.

If the alpha taxonomy of extinct forms is not an easy task for many reasons, especially as regards to rodents (see Vianey-Liaud *et al.*, 2011), defining a higher-level taxon implies other matters frequently challenged by phylogenetical studies. It can be assumed that *Atavocricetodon* species, as *A. atavus* for some European species, give rise to many *Eucricetodon* lineages, like those of *E. collatus* and *E. huerzeleri* (Comte, 1985). This is notably supported by the incisor enamel schmelzmuster of this latter species (type 1) shared with most *Atavocricetodon* species. In this way, retaining a paraphyletic genus (i.e., *Atavocricetodon*) would also mean that *Eucricetodon* has to be now regarded as a polyphyletic genus. Consequently,

there is no obvious reason, even pragmatical, to keep *Atavocricetodon* as a genus or even a subgenus. As far as we know, the more accurate definition of *Eucricetodon s.l.* was given by Vianey-liaud (1972). Nonetheless, it clearly appears that *Eucricetodon* involves a very high amount of species from different area and with a wide range of dental morphologies (cf. Dienemann, 1987), which represent various lineages and most probably different genera still undefined. More materials, including skulls necessary to notably investigate the evolution of infraorbital foramina (Vianey-Liaud, 1974) and others morphological items are crucial to try to definitely clarify these longstanding issues.

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