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General Palaeontology, Systematics, Evolution (Vertebrate Palaeontology)

New *Pseudaelurus* and *Styriofelis* remains (Carnivora: Felidae) from the Middle Miocene of Abocador de Can Mata (Vallès-Penedès Basin)*Nouveaux restes de Pseudaelurus et Styriofelis (Carnivora : Felidae) du Miocène moyen de l'Abocador de Can Mata (Bassin de Vallès-Penedès)*Josep M. Robles^{a,b}, Joan Madurell-Malapeira^a, Juan Abella^c, Cheyenn Rotgers^{a,b},
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ABSTRACT

New remains of felid jaws and teeth are described from several localities of the local stratigraphic series of Abocador de Can Mata (ca. 11.9 to 11.6 Ma, Middle Miocene; Vallès-Penedès Basin, Catalonia, Spain). Three different taxa are identified: *Styriofelis turtauensis*, *Pseudaelurus romieviensis* and *Pseudaelurus quadridentatus*. The described remains of *P. romieviensis* enable extending considerably the chronological range of this species in the Iberian Peninsula, in agreement with its record in the rest of Europe. Moreover, it is shown for the first time that *P. romieviensis* may possess a p2. The presence of this tooth therefore does not constitute a valid diagnostic feature to distinguish *P. romieviensis* from *P. quadridentatus*.

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R É S U M É

De nouveaux restes dentaires et mandibulaires de Félinés provenant de la série stratigraphique de l'Abocador de Can Mata (de 11,9 à 11,6 Ma, Miocène moyen ; bassin de Vallès-Penedès, Catalogne, Espagne) sont décrits. Trois taxons différents sont déterminés : *Styriofelis turtauensis*, *Pseudaelurus romieviensis* et *Pseudaelurus quadridentatus*. Les restes décrits de *P. romieviensis* permettent d'élargir considérablement le cadre chronologique de la présence de cette espèce dans la péninsule Ibérique, en accord avec sa représentation dans le reste de l'Europe. De plus, il est montré pour la première fois que *P. romieviensis* peut posséder une p2. La présence de cette dent ne constitue donc pas un caractère diagnostique valide permettant de distinguer *P. romieviensis* de *P. quadridentatus*.

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1. Introduction

The genus *Pseudaelurus* Gervais, 1850 (Carnivora: Felidae: Felinae), as understood in the traditional, broad sense (*Pseudaelurus* s.l.; see review in Werdelin et al., 2010) includes several species distributed across Europe (Ginsburg, 1999; Rothwell, 2003), North America (Rothwell, 2003) and, to a lesser extent, Asia (Rothwell, 2003), but not in Africa (Werdelin and Peigné, 2010) except for very scarce material from Saudi Arabia (Thomas et al., 1982). It should be taken into account, however, that *Pseudaelurus* s.l. is a clearly paraphyletic grouping (a grade instead of a clade), from which both the Felinae and the Machairodontinae evolved (Werdelin et al., 2010). The North American species of “*Pseudaelurus*” (see review in Rothwell, 2003) might have independently evolved there from a *Proailurus*-like ancestor, and in any case they do not seem to be ancestral to the subsequent radiations of either conical-toothed or saber-toothed cats (Werdelin et al., 2010).

In Europe, four species have been traditionally recognized (Heizmann, 1973; Ginsburg, 1983, 1999; Rothwell, 2003; Werdelin et al., 2010); they are, from smaller to larger size (see Rothwell, 2003, for further details on the nomenclatural history of the species names): *P. turnauensis* (Hoernes, 1882) (type locality: Göriach, Austria, MN5), including *P. transitorius* Depéret, 1892 (type locality: La Grive-Saint-Alban, MN7+8) as its junior subjective synonym (Beaumont, 1961; Rothwell, 2003; Werdelin et al., 2010); *P. lorteti* Gaillard, 1899 (type locality: La Grive-Saint-Alban, France, MN7+8); *P. romieviensis* (Roman and Viret, 1934) (type locality: La Romieu, France, MN4); and *P. quadridentatus* (Blainville, 1843) (type locality: Sansan, France, MN6), which is the type species of the genus and includes *P. marini* Villalta Comella and Crusafont-Pairó, 1943 (type locality: els Hostalets de Pierola) as its junior subjective synonym (Ginsburg et al., 1981).

The above-mentioned taxonomic scheme for European species of *Pseudaelurus* is untenable in the light of current phylogenetic views (Salesa et al., 2012; Turner et al., 2011; Werdelin et al., 2010;), according to which *P. quadridentatus* would lie at the origin of the true saber-toothed cats (subfamily Machairodontinae), whereas *P. lorteti* and *P. turnauensis* would be at the base of the conical-toothed cats (subfamilies Pantherinae and Felinae). For this reason, based on the more sabertooth-like features of *P. quadridentatus* (Beaumont, 1978), several authors (Beaumont, 1964, 1978; Ginsburg, 2002; Salesa et al., 2012) have favored the splitting of the European species of “*Pseudaelurus*” into several genera or subgenera. *Schizailurus* Viret, 1951 has been therefore employed at least for the two smaller species, *P. lorteti* (type species) and *P. turnauensis*, usually at the subgenus rank (Beaumont, 1961, 1978; Crusafont et al., 1955; Petter, 1976; Viret, 1951) but sometimes elevated to the genus level (Beaumont, 1964). However, as noted by Ginsburg (2002; see also Salesa et al., 2012; Werdelin et al., 2010), *Schizailurus* is an objective junior synonym of *Miopanthera* Kretzoi, 1938 (type species *P. lorteti*). Ginsburg (2002) therefore recognized a taxonomically valid, monotypic subgenus *Miopanthera*,

while classifying *P. turnauensis* into another monotypic subgenus, *Styriofelis* Kretzoi, 1929, both originally erected as distinct genera. However, given the similarities between their respective types species, our recommendation is to consider *Miopanthera* as a subjective junior synonym of *Styriofelis* (Salesa et al., 2011, 2012; Werdelin et al., 2010), including both *S. lorteti* and *S. turnauensis*. Most recently, a new species, *Styriofelis vallesiensis* Salesa et al., 2012 from the MN10 of Spain was erected (Salesa et al., 2012). According to Ginsburg (2002), *P. romieviensis* should be maintained in the genus *Pseudaelurus*, given its ancestral status with regard to *P. quadridentatus* (Heizmann, 1973; Ginsburg, 2002). Such classification is provisionally followed here, although it should be taken into account that the phylogenetic status of *P. romieviensis* is uncertain, because the available material is scarce and fragmentary (Koufos, 2008, 2011; Salesa et al., 2012; Werdelin et al., 2010;).

The European genus *Styriofelis* was first represented by *S. turnauensis* (Werdelin et al., 2010), and its first appearance datum usually attributed to the MN3 (Werdelin et al., 2010), although in the Iberian Peninsula it has been already cited from the MN2 (Alcalá et al., 1990; see also

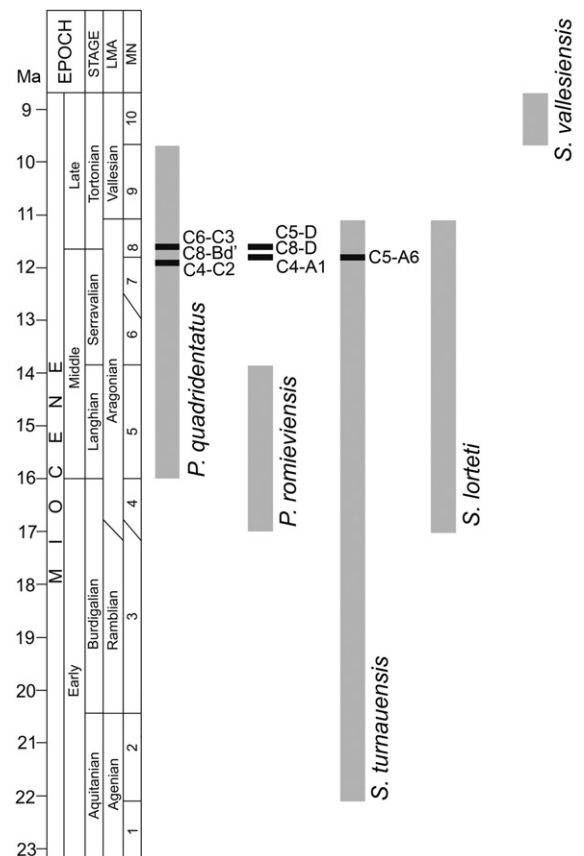


Fig. 1. Stratigraphic chart of *Pseudaelurus* spp. and *Styriofelis* spp. in the Iberian Peninsula. Gray lines correspond to previously known ranges (see main text for references).

Fig. 1. Répartition stratigraphique de *Pseudaelurus* spp. et *Styriofelis* spp. dans la péninsule Ibérique. Les lignes grises correspondent aux répartitions connues précédemment (voir le texte principal pour les références).

our Fig. 1 and the Discussion for further details). In the MN4, both *S. lorteti* and the two species of *Pseudaelurus* are recorded. *Styriofelis lorteti* and *P. romieviensis* became extinct toward the end of the Middle Miocene (ca. 11.6 Ma), *S. turnauensis* and *P. quadridentatus* survived until the MN9 (Werdelin et al., 2010), and *S. turnauensis* was replaced by *S. vallesiensis* in the MN10 (Salesa et al., 2012). The previously known Iberian chronostratigraphic record of these taxa agrees with that in Europe, except that occurrences of *P. romieviensis* are very scarce and restricted to the MN4 and MN5 (Discussion). In this paper, we describe the unpublished remains of *Pseudaelurus* and *Styriofelis* from the Late Aragonian local stratigraphic series of Abocador de Can Mata, which had been preliminarily attributed to *Pseudaelurus* sp. (Alba et al., 2006b, 2009; Casanovas-Vilar et al., 2008) or *P. cf. quadridentatus* and *P. cf. turnauensis* by Alba et al. (2007).

2. Age and geological background

The fossil remains described in this paper come from several ACM localities (Alba et al., 2006a, 2006b, 2009, 2011), situated in the Vallès-Penedès Basin (NE Iberian Peninsula; Fig. 2). This basin is a NNE-SSW-oriented half-graben bordered by the Littoral and Pre-littoral

Catalan Coastal Ranges, which was generated by the rifting of the NW Mediterranean region during the Neogene (Bartrina et al., 1992; Cabrera et al., 1991, 2004; Gibert and Casanovas-Vilar, 2011; Roca and Guimerà, 1992). Besides some Early and Middle Miocene shallow marine and transitional sequences, most of the basin infill consists of distal-marginal alluvial fan sediments with a rich fossil record of Early, late Middle and Late Miocene terrestrial vertebrates (Agustí et al., 1985; Casanovas-Vilar et al., 2011c).

The ACM localities are situated in the area of els Hostalets de Pierola, which is characterized by thick Middle to Late Miocene alluvial sequences that were deposited in the distal-to-marginal, inter-fan zones of the coalescing alluvial fan systems of els Hostalets de Pierola and Olesa (Moyà-Solà et al., 2009a). The age of the more than 250 paleontological localities from the 250-m-thick ACM series can be accurately estimated on the basis of lithostratigraphic, magnetostratigraphic and biostratigraphic correlation (Alba et al., 2009, 2011; Casanovas-Vilar et al., 2011a; Moyà-Solà et al., 2009a), corresponding to the MN7 and MN8 sensu Mein and Ginsburg (2002). In particular, the ACM series spans from ca. 12.5 to 11.4 Ma (Casanovas-Vilar et al., 2011a), and estimated interpolated ages can be provided for the several localities and most isolated remains on the basis of average local sedimentation rates for each

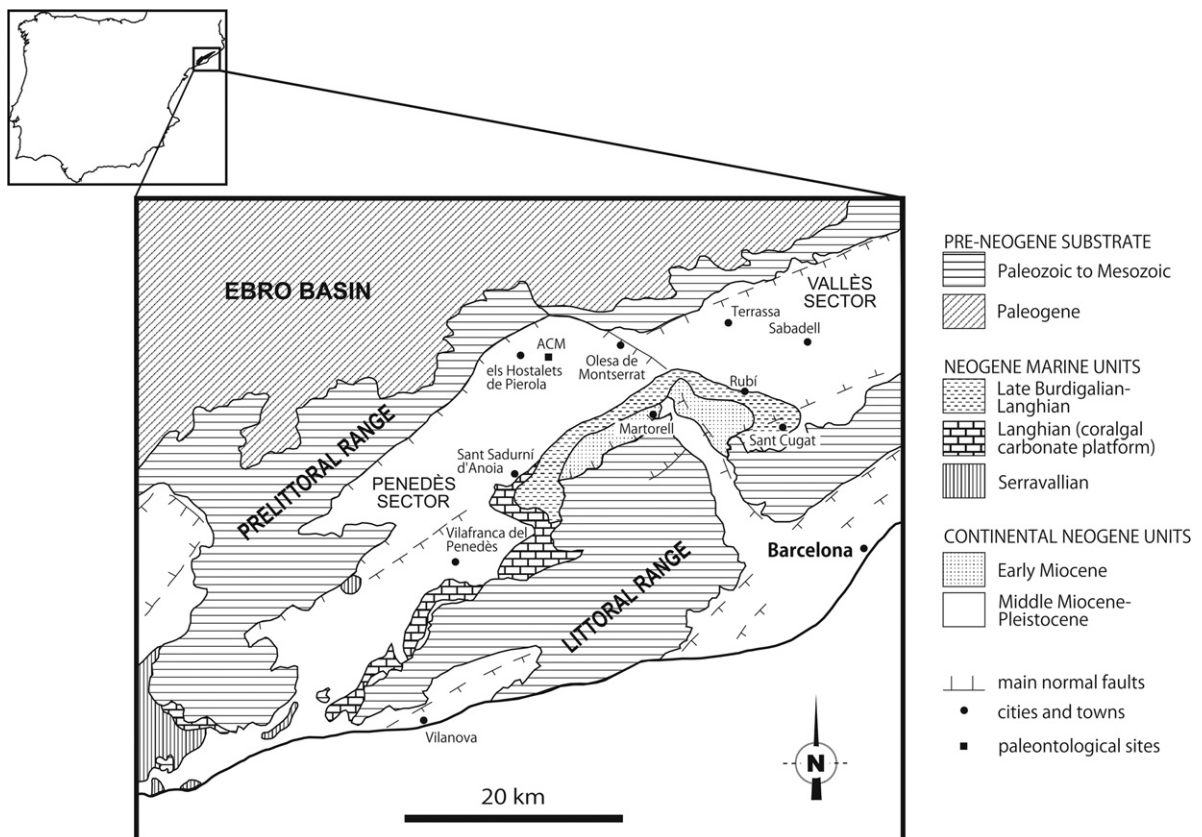


Fig. 2. Schematic geological map of the Vallès-Penedès Basin, showing the main geological units as well as the location of Abocador de Can Mata (ACM, black square). Modified from an original kindly provided by Isaac Casanovas-Vilar.

Fig. 2. Carte géologique schématique du bassin de Vallès-Penedès, montrant les principales unités géologiques, ainsi que la localisation de l'Abocador de Can Mata (ACM, carré noir). Modifié à partir d'un original aimablement fourni par Isaac Casanovas-Vilar.

subchron. The oldest ACM localities with felid remains are correlated to subchron C5r.3r; they include: C4-C2 (11.9 Ma, MN7 or MN8), C4-A1 (11.8 Ma, MN8), and C5-A6 (11.8 Ma, MN8). The remaining localities are correlated to subchron C5r.2n, including: C6-C3 and C8-Bd' (11.6 Ma, MN8). The several isolated felid remains from ACM sub-sectors C5-C and C8-B described in this paper are also correlated to the latter subchron, with an estimated age of 11.6 Ma (MN8).

3. Material and methods

3.1. Abbreviations

Measurements: L: mesiodistal length; B: buccolingual breadth.

Institutions and fossil collections: ICP: Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona; IPS: collections from the ICP.

Fossil sites: ACM: local stratigraphic series of Abocador de Can Mata; C4: Cell 4; C5: Cell 5; C6: Cell 6; C8: Cell 8.

3.2. Studied material and comparative sample

The fossil remains described in this paper (Figs. 3 and 4) are housed at the ICP. The comparative sample includes fossil remains from other European localities, on the basis of data taken from the literature.

3.3. Nomenclature and measurements

Dental nomenclature follows Salesa et al. (2012). Standard dental measurements (L and B) were measured (in mm) from the original specimens described in this paper, or taken from the literature for the comparative sample.

4. Systematic paleontology

Order: CARNIVORA Bowdich, 1821
 Suborder: FELIFORMIA Kretzoi, 1945
 Family: FELIDAE Fischer, 1817
 Subfamily: FELINAE Fischer, 1817
 Genus *Styriofelis* Kretzoi, 1929
Styriofelis turnauensis (Hoernes, 1882)
 (Fig. 4Y–D')

Referred material: IPS41970, left mandibular fragment with m1 from ACM/C5-A6 (Fig. 4B'–D'); IPS42169, right m1 from ACM/C5-A6 (Y–A'). See dental measurements in Table 1.

Description and measurements: The mandibular corpus of IPS41970 is low and buccolingually inflated. It preserves the beginning of the masseteric fossa under the protoconid of the carnassial. The m1 of the two available specimens displays two main cusps: the paraconid, which is mesially curved; and the protoconid, which is distally curved, slightly higher and mesiodistally wider than the paraconid, and separated from the latter by a distinct buccal notch and a deep lingual valley. There is also

a small but distinct cuspid, the metaconid, at the distalmost portion of the crown, being separated from the protoconid by a shallow groove.

Remarks: On the basis of m1 size, *S. turnauensis* can be readily distinguished from the larger *Pseudaelurus* species as well as from the smaller *Styriofelis vallesiensis* (Gaillard, 1899; Heizmann, 1973; Rothwell, 2001; see also our Fig. 5C; Villalta Comella and Crusafont-Pairó, 1943). In this regard, *S. lorteti* reaches larger sizes than *S. turnauensis*, but both species largely overlap so that no secure attribution to the latter species is warranted based on the small size of the described material from ACM alone. The ACM material, however, can be confidently attributed to *S. turnauensis* on the basis of m1 talonid, which like in *S. vallesiensis* is less developed than in *S. lorteti* (see Discussion for further details). The lack of m2 in IPS41970 further supports this attribution, since this tooth is variably present in *S. lorteti* (compare Ginsburg, 2002, fig. 18a and pl. 2 fig. 1a,b, with Heizmann, 1973, pl. 4, fig. 2a).

Genus *Pseudaelurus* Gervais, 1850

Pseudaelurus romieviensis (Roman and Viret, 1934)
 (Figs. 3A–F, V–X, 4V–X, 3A–F)

Referred material: IPS29690, left C1 from ACM/C4-A1 (Fig. 4A–C); IPS29832, right C1 from ACM/C4-A1 (Fig. 4D–F); IPS41973, right partial hemimandible with c1-p4 from ACM/C5-C (Fig. 3D–F); IPS42063, left partial hemimandible with c1-m1 from ACM/C5-C (Fig. 3A–C), and presumably from the same individual as IPS41973, since they were found in close spatial association; IPS60891, right p4 from ACM/C8-B (Fig. 4V–X). See dental measurements in Table 1.

Description and measurements: Only two upper canines are available from the upper dentition. IPS29832 is only worn along the mesial edge of the crown, whereas IPS29690 also displays some apical and distal wear. The crown and root are uniformly curved in buccal/distal view, with the former being slightly higher than the root (buccal crown height of 28.5 mm vs. root height of 37.2 mm in IPS29832, and preserved buccal height of 27.4 mm vs. root height of 31.1 mm in IPS29690). The crown displays an elliptical occlusal contour that is buccolingually compressed (breadth/length index of 57–58%). The lingual side of the crown is rather flat, whereas the buccal one displays a more markedly convex occlusal contour. A distal crest with no crenulations can be discerned in both specimens from tip to base of the crown, whereas the mesial crest is worn away.

The mandibular corpus displays a constant depth along the whole dental arcade, and displays a high and straight symphysis. There are two mental foramina, at the level of the p2 and the p3. The ramus is high and displays a very deep masseteric fossa, which extends anteriorly just below m1 mid-length. The condyloid process is buccolingually broad and posteriorly curved, being shorter than the angular process, which is slightly curved mesiolingually. On the lingual side of the angular process, a thin crest runs in a mesiodistal direction from the mid-length of the masseteric fossa to the end of the angular process.

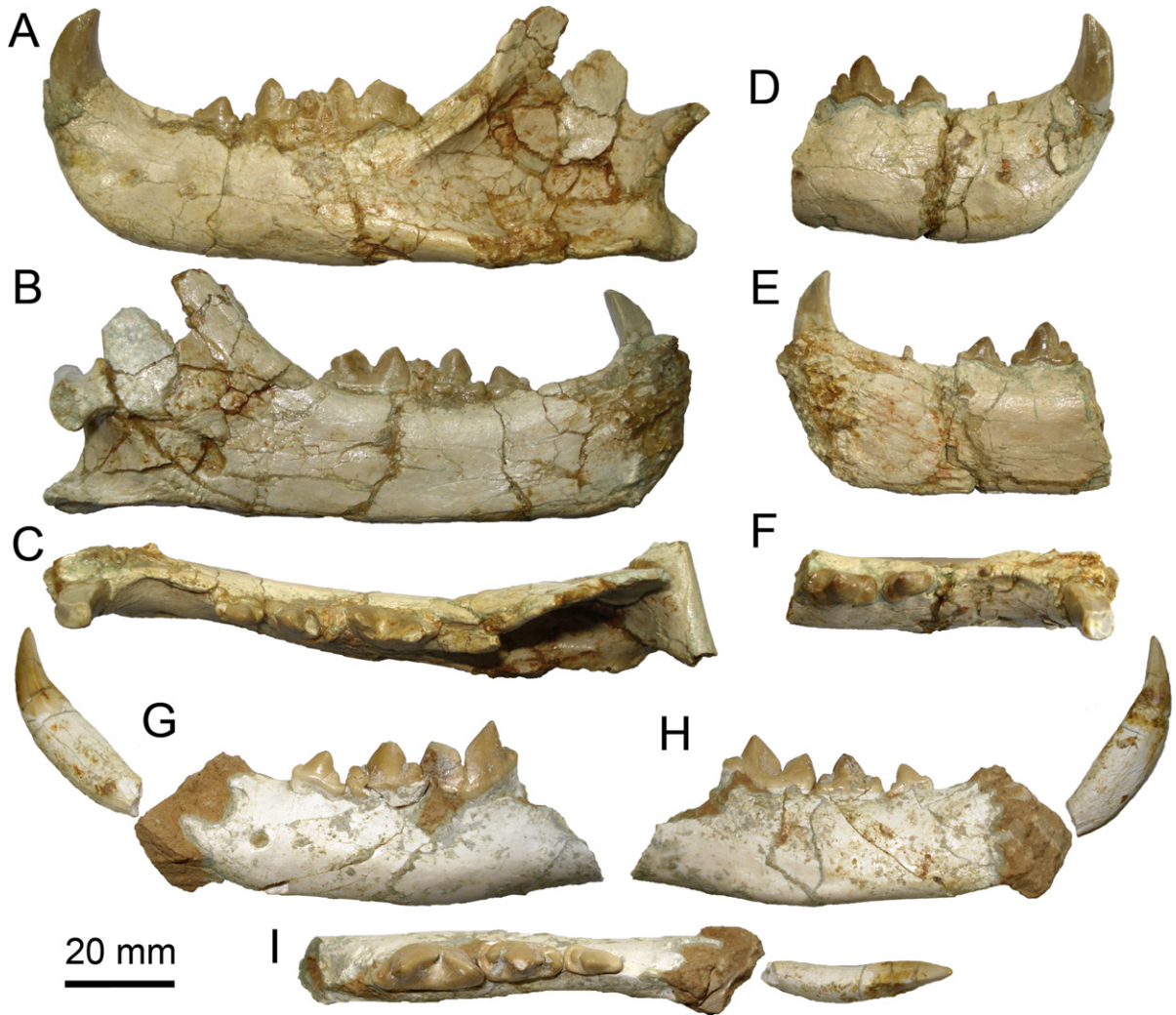


Fig. 3. Mandibular remains of *Pseudaelurus romieviensis* (A–F) and *Pseudaelurus quadridentatus* (G–I) from ACM. A–C: left partial hemimandible with c1-m1 IPS42063: A: buccal view; B: lingual view; C: occlusal view. D–F: right partial hemimandible with c1-p4 IPS41973: D: buccal view; E: lingual view; F: occlusal view. G–I: left partial hemimandible with c1-m1 IPS60892c: G: buccal view; H: lingual view; I: occlusal view.

Fig. 3. Restes mandibulaires de *Pseudaelurus romieviensis* (A–F) et *Pseudaelurus quadridentatus* (G–I) de l'ACM : A–C : hémimandibule gauche partielle avec c1-m1 IPS42063 : A : vue buccale ; B : vue linguale ; C : vue occlusale. D–F : hémimandibule droite partielle avec c1-p4 IPS41973 : D : vue buccale ; E : vue linguale ; F : vue occlusale. G–I : hémimandibule gauche partielle avec c1-m1 IPS60892c : G : vue buccale ; H : vue linguale ; I : vue occlusale.

With regard to the lower dentition, no lower incisors are preserved. The c1 crowns are quite worn (preserved buccal height 14.1 mm in IPS41973 and 15.3 mm in IPS42063). It displays a fine crest with no crenulations along its mesial portion, whereas dental wear can be observed on the distal side (so that no distal crest can be discerned). The two available specimens further display a contact facet with the i3 on the basalmost, mesial side of the crown. A uniradicated and unicuspid p2 is present in IPS41973, whereas IPS42063 also displays the p2 alveolus but the crown is missing. The p2 crown is much smaller than those of the remaining postcanine teeth. The p2 is separated from the c1 by a long diastema (14.2 mm in IPS41973 and 12.7 mm in IPS42063), and from the p3 by a shorter one (8.3 mm and 5.4 mm, respectively). The p3 displays three cuspid,

linked to each other by a fine cristid; the main cuspid (protoconid), situated at about mid-crown length, is higher than the remaining ones and displays an appreciable backward tilt; the mesial accessory cuspid is situated close to the crown base, whereas the distal accessory cuspid is situated on the middle of the talonid basin, which is lingually expanded and displays a faint distal cingulid close to the crown base. The also tricuspid p4 is larger than the p3 and displays a more asymmetric profile in buccal view (the protoconid is more distally inclined). The protoconid, situated at about mid-crown length, is the largest and most conspicuous cuspid. The mesially accessory cuspid is small but nevertheless distinct, being separated from the protoconid by a conspicuous notch. The distal accessory cuspid, in turn, is separated from the protoconid by a

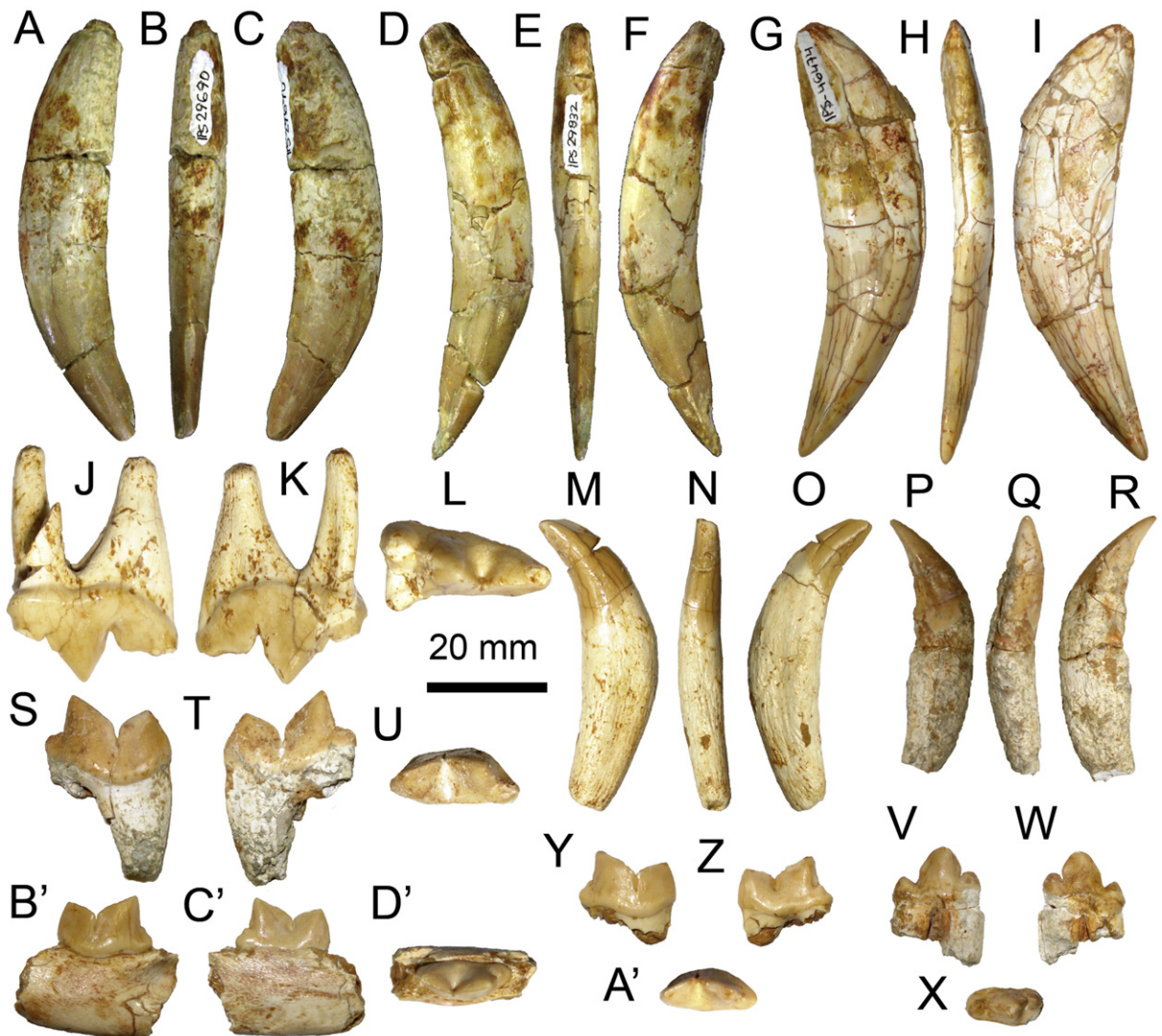


Fig. 4. Isolated dental remains of *Pseudaelurus romieviensis* (A–F, V–X), *Pseudaelurus quadridentatus* (G–U), and *Styriofelis turnauensis* (Y–D’): A–C: left C1 IPS29690: A: buccal view; B: distal view; C: lingual view. D–F: right C1 IPS29832: D: buccal view; E: distal view; F: lingual view. G–H: right C1 IPS46474: G: buccal view; H: distal view; I: lingual view. J–L: left P4 IPS54968: J: buccal view; K: lingual view; L: occlusal view. M–O: right c1 IPS50940: M: buccal view; N: distal view; O: lingual view. P–R: right c1 IPS60892a: P: buccal view; Q: distal view; R: lingual view. S–U: right m1 IPS60892b: S: buccal view; T: lingual view; U: occlusal view. V–X: right p4 IPS60891: V: buccal view; W: lingual view; X: occlusal view. Y–A’: right m1 IPS42169: Y: buccal view; Z: lingual view; A’: occlusal view. B’–D’: left mandibular fragment with m1 IPS41970: B’: buccal view; C’: lingual view; D’: occlusal view.

Fig. 4. Restes dentaires isolés de *Pseudaelurus romieviensis* (A–F, V–X), *Pseudaelurus quadridentatus* (G–U) et *Styriofelis turnauensis* (Y–D’): A–C: C1 gauche IPS29690: A: vue buccale; B: vue distale; C: vue linguale. D–F: C1 droite IPS29832: D: vue buccale; E: vue distale; F: vue linguale. G–H: C1 droite IPS46474: G: vue buccale; H: vue distale; I: vue linguale. J–L: P4 gauche IPS54968: J: vue buccale; K: vue linguale; L: vue occlusale. M–O: c1 droite IPS50940: M: vue buccale; N: vue distale; O: vue linguale. P–R: c1 droite IPS60892a: P: vue buccale; Q: vue distale; R: vue linguale. S–U: m1 droite IPS60892b: S: vue buccale; T: vue linguale; U: vue occlusale. V–X: p4 droite IPS60891: V: vue buccale; W: vue linguale; X: vue occlusale. Y–A’: m1 droite IPS42169: Y: vue buccale; Z: vue linguale; A’: vue occlusale. B’–D’: fragment mandibulaire gauche avec m1 IPS41970: B’: vue buccale; C’: vue linguale; D’: vue occlusale.

buccal groove, and like in the p3 it is included within the talonid basin (although slightly towards the buccal side). Like in the preceding premolar, the talonid is lingually expanded and displays a better-developed distal cingulid close to crown base. The carnassial (m1) is larger than the remaining lower cheek teeth and displays an even more asymmetric profile in buccal view. This tooth bears two main trigonid cusps (paraconid and protoconid) as well as a small but distinct metaconid at the distal end of the

crown. The paraconid is obliquely-oriented towards lingual and separated from the protoconid by a broad buccal notch and a deep lingual valley. The partially-preserved protoconid (the apex is lacking) is distally situated, curved, and higher and mesiodistally longer than the paraconid, further begin separated from the talonid by a shallow buccal groove. No m2 is present.

Remarks: The isolated upper canines attributed to *P. romieviensis* fit well the measurements of two specimens

Table 1Dental measurements of *Pseudaelurus* spp. and *Styriofelis turnauensis* from ACM localities.**Tableau 1**Mesures dentaires de *Pseudaelurus* spp. et *Styriofelis turnauensis* des localités de l'ACM.

Taxon	Site	Age (Ma)	Catalogue No.	Tooth	L	B
<i>Styriofelis turnauensis</i>	ACM/C5-A6	11.8 (MN8)	IPS41970	l m1	11.3	4.9
<i>Styriofelis turnauensis</i>	ACM/C5-A6	11.8 (MN8)	IPS42169	r m1	11.3	5.1
<i>Pseudaelurus romieviensis</i>	ACM/C4-A1	11.8 (MN8)	IPS29690	l C1	13.2	7.7
<i>Pseudaelurus romieviensis</i>	ACM/C4-A1	11.8 (MN8)	IPS29832	r C1	13.3	7.6
<i>Pseudaelurus romieviensis</i>	ACM/C5-C	11.6 (MN8)	IPS41973	r c1	7.4	7.7
<i>Pseudaelurus romieviensis</i>	ACM/C5-C	11.6 (MN8)	IPS41973	r p2	2.0	1.3
<i>Pseudaelurus romieviensis</i>	ACM/C5-C	11.6 (MN8)	IPS41973	r p3	9.5	4.8
<i>Pseudaelurus romieviensis</i>	ACM/C5-C	11.6 (MN8)	IPS41973	r p4	12.8	6.3
<i>Pseudaelurus romieviensis</i>	ACM/C5-C	11.6 (MN8)	IPS42063	l c1	7.8	9.1
<i>Pseudaelurus romieviensis</i>	ACM/C5-C	11.6 (MN8)	IPS42063	l p3	9.1	5.1
<i>Pseudaelurus romieviensis</i>	ACM/C5-C	11.6 (MN8)	IPS42063	l p4	12.8	6.3
<i>Pseudaelurus romieviensis</i>	ACM/C5-C	11.6 (MN8)	IPS42063	l m1	16.3	7.5
<i>Pseudaelurus romieviensis</i>	ACM/C8-B	11.6 (MN8)	IPS60891	r p4	13.8	6.3
<i>Pseudaelurus quadridentatus</i>	ACM/C4-C2	11.9 (MN7 or MN8)	IPS46474	r C1	15.2	6.5
<i>Pseudaelurus quadridentatus</i>	ACM/C6-C3	11.6 (MN8)	IPS50940	r c1	9.1	7.1
<i>Pseudaelurus quadridentatus</i>	ACM/C6-C3	11.6 (MN8)	IPS54968	l P4	22.4	10.5
<i>Pseudaelurus quadridentatus</i>	ACM/C8-Bd'	11.6 (MN8)	IPS60892a	r c1	9.0	6.5
<i>Pseudaelurus quadridentatus</i>	ACM/C8-Bd'	11.6 (MN8)	IPS60892b	r m1	18.0	7.8
<i>Pseudaelurus quadridentatus</i>	ACM/C8-Bd'	11.6 (MN8)	IPS60892c	l c1	9.1	6.6
<i>Pseudaelurus quadridentatus</i>	ACM/C8-Bd'	11.6 (MN8)	IPS60892c	l p3	9.7	4.8
<i>Pseudaelurus quadridentatus</i>	ACM/C8-Bd'	11.6 (MN8)	IPS60892c	l p4	13.9	6.7
<i>Pseudaelurus quadridentatus</i>	ACM/C8-Bd'	11.6 (MN8)	IPS60892c	l m1	18.0	7.9

B: buccolingual breadth; L: mesiodistal length; r: right; l: left.

of *P. romieviensis* from France (Ginsburg, 2002; see also our Fig. 5D), except for the fact that the ACM specimens are slightly more buccolingually compressed than those from France (breadth/length index 63–68%; Ginsburg, 2002). In contrast, the ACM C1 attributed to *P. romieviensis* are much smaller than those of *P. quadridentatus* from Spain (Ginsburg et al., 1981; see also our Fig. 5D), which are moreover much more buccolingually compressed (breadth/length index of 43–45%). An isolated upper canine from the MN9 of Sinap locality 12 (Turkey) was attributed to *P. quadridentatus* by Viranta and Werdelin (2003), but its proportions fit better with those of *P. romieviensis* (breadth/length index 63%).

With regard to the lower dentognathic material of *P. romieviensis* from ACM, it can be distinguished mainly from *P. quadridentatus* by the presence of a distinct and better-individualized metaconid on the m1 (Ginsburg et al., 1981; Roman and Viret, 1934; Salesa et al., 2012). The ACM material attributed to *P. romieviensis* can be further distinguished from *P. quadridentatus* by the somewhat smaller dental size (Heizmann, 1973; Roman and Viret, 1934; Rothwell, 2001), being in contrast larger than *Styriofelis* spp. (Gaillard, 1899; Heizmann, 1973; Rothwell, 2001; Salesa et al., 2012; see also Figs. 5B–D).

In the original diagnosis of this species, Roman and Viret (1934, p. 19) argued that, besides its smaller dental size, *P. romieviensis* also clearly differs from *P. quadridentatus* by the relatively slender mandibular corpus of the former. In fact, the holotype from La Romieu has a mandibular robusticity index (corpus height behind the m1/mesiodistal length of the m1 \times 100) of 127.2%, which matches the figures computed for other material assigned to the same species, such as Baigneaux-en-Beauce (131.3%; data taken from Ginsburg, 2002) and IPS42063 from ACM (142.4%).

In contrast, the material assigned to *P. quadridentatus* displays higher robusticity values: 163.3% for Sansan and 156.1% for La Grive-Saint-Alban (data taken from Gaillard, 1899; Ginsburg, 1961). Roman and Viret (1934, p. 19) further argued that *P. romieviensis* displays a p4 proportionally shorter than the m1, whereas the opposite condition is shown by the mandible of *P. quadridentatus* from Sansan. The holotype from La Romieu has an index of p4/m1 mesiodistal length of 76.7%, which is similar to the values displayed by the specimen of *P. romieviensis* from Baigneaux-en-Beauce (74.7%; data taken from Ginsburg, 2002) and IPS42063 from ACM (78.5%). In contrast, the material traditionally assigned to *P. quadridentatus* from Sansan, La Grive and Steinheim displays higher values (87.6%, 89.2% and 88.4%, respectively; data taken from Gaillard, 1899; Ginsburg, 1961; Heizmann, 1973).

More recently, Heizmann (1973) pointed out that the main diagnostic features of *P. romieviensis* would be the lack of p1 and p2, as well as the presence of a well-developed anterior accessory cuspid in the p4, according to specimens from La Romieu (MN4) and Baigneaux-en-Beauce (MN5). Koufos (2008), following Heizmann's (1973) criteria, further assigned a mandible from Antonios (Greece, MN4-MN5) to *P. romieviensis*. The ACM mandible IPS60892, attributed here to *P. romieviensis*, shows for the first time the presence of a p2 in this species. Moreover, this specimen displays a less developed anterior accessory cuspid in the p4, resembling the condition displayed by the mandible SO-6417 from Baigneaux-en-Beauce (Ginsburg, 2002, p. 131, fig. 19). Such differences are merely attributable to intraspecific variation, which is still insufficiently known due to the scarce record of this species.

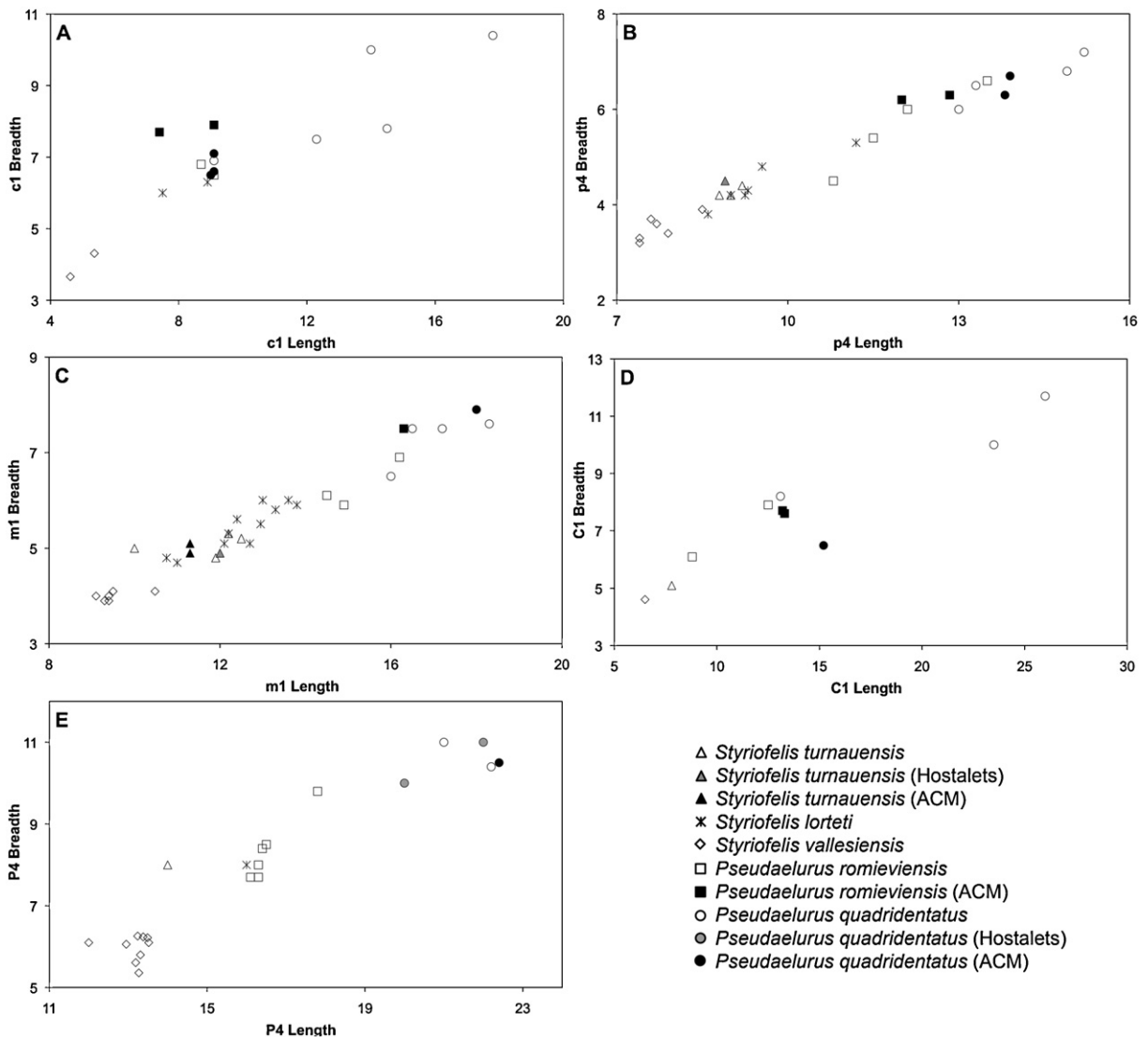


Fig. 5. Dental proportions of *Pseudaelurus* and *Styriofelis* from ACM, compared to other European localities: **A**, c1; **B**, p4; **C**, m1; **D**, C1; **E**, P4. Comparative data for *S. turnauensis* are from Vieux Collonges (Mein, 1958), Göriach (Thenius, 1949), La Grive-Saint-Alban (Gaillard, 1899; Ginsburg, 2002), Can Vila (Crusafont-Pairó, 1952; Villalta Comella and Crusafont-Pairó, 1943) and Sinap Formation (Viranta and Werdelin, 2003); for *S. lorteti*, from Artenay and Chilleurs-aux-Boix (Ginsburg, 2002), La Grive-Saint-Alban (Gaillard, 1899; Ginsburg, 1961) and Steinheim (Heizmann, 1973); for *S. vallesiensis*, from Batallones (Salesa et al., 2012); for *P. romieviensis*, from La Romieu (Roman and Viret, 1934), Vieux-Collonges (Mein, 1958, identified as *P. aff. quadridentatus*), Baigneaux-en-Beauce and Aérotrain (Ginsburg, 2002) and Antonios (Koufos, 2008); and for *P. quadridentatus*, from Göriach (Thenius, 1949), La Grive-Saint-Alban (Gaillard, 1899; Ginsburg, 1961), Steinheim (Heizmann, 1973), Hostalets Inferior (Villalta Comella and Crusafont-Pairó, 1943), Los Valles de Fuentidueña (Ginsburg et al., 1981), and Sinap Formation (Viranta and Werdelin, 2003).

Fig. 5. Proportions dentaires de *Pseudaelurus* et *Styriofelis* de l'ACM, comparées à d'autres localités européennes: **A**, c1; **B**, p4; **C**, m1; **D**, C1; **E**, P4. Les données de comparaison pour *S. turnauensis* proviennent de Vieux Collonges (Mein, 1958), Göriach (Thenius, 1949), La Grive-Saint-Alban (Gaillard, 1899; Ginsburg, 2002), Can Vila (Crusafont-Pairó, 1952; Villalta Comella et Crusafont-Pairó, 1943) et Sinap Formation (Viranta et Werdelin, 2003); pour *S. lorteti*, d'Artenay et Chilleurs-aux-Boix (Ginsburg, 2002), La Grive-Saint-Alban (Gaillard, 1899; Ginsburg, 1961) et Steinheim (Heizmann, 1973); pour *S. vallesiensis*, de Batallones (Salesa et al., 2012); pour *P. romieviensis*, de La Romieu (Roman et Viret, 1934), de Vieux-Collonges (Mein, 1958, identifié comme *P. aff. quadridentatus*), Baigneaux-en-Beauce et Aérotrain (Ginsburg, 2002) et Antonios (Koufos, 2008); et pour *P. quadridentatus*, de Göriach (Thenius, 1949), La Grive-Saint-Alban (Gaillard, 1899; Ginsburg, 1961), Steinheim (Heizmann, 1973), Hostalets Inferior (Villalta Comella et Crusafont-Pairó, 1943), Los Valles de Fuentidueña (Ginsburg et al., 1981), et Sinap Formation (Viranta et Werdelin, 2003).

Pseudaelurus quadridentatus (Blainville, 1843)
(Figs. 3G–I, P–R, 4G–O, S–U)

Referred material: IPS46474, right C1 from ACM/C4-C2 (Fig. 4G–I); IPS54968, left P4 from ACM/C6-C3

(Fig. 4J–L); IPS50940, right c1 from ACM/C6-C3 (Fig. 4M–O); IPS60892, left partial mandible with the p2 alveolus and the p3–m1 series (IPS60892c; Fig. 3G–I), associated isolated right c1 (IPS60892a; Fig. 3P–R) and isolated right m1 (IPS60892b; Fig. 4S–U) from a single individual from C8-Bd'. See dental measurements in Table 1.

Description: Regarding the upper dentition, only an isolated canine and a carnassial are available. The C1 is unworn, and although it is partially crushed at the basal level of the crown and most of the root, the overall shape of the tooth can be adequately evaluated and reliable crown measurements can be taken. In buccal/lingual view, this canine displays a somewhat concave distal contour and a more markedly convex mesial profile, the crown being slightly shorter (buccal crown height 31.9 mm) than the root (33.2 mm in length). The lingual crown aspect is quite flattened, whereas the buccal one is more convex, and the crown displays a buccolingually quite compressed occlusal profile (breadth/length index 43%). Two (mesial and distal) fine crests with no crenulations can be discerned from apex to cervix. The P4 displays three roots and a triangular occlusal profile with four main cusps. The protocone, quite worn and situated on the mesiolingual corner of the crown, is linked to the paracone (located at about the middle of the crown) by a fine crest of distobuccal direction. The paracone is the highest and better-individualized cusp. On the mesiobuccal corner of the crown, there is also a partially-worn unicuspid parastyle, which is linked to the paracone by a fine distolingual crest. The distal crown portion bears an elongated, somewhat sinuous and mesiodistally-aligned crest that corresponds to the metastyle, which ends at the distal end of the crown (where it is somewhat worn). The latter is separated from the paracone by a deep carnassial notch on the lingual side and by a similarly-deep but much broader valley on the buccal side.

The mandibular corpus is uniformly shallow along the whole dental arcade, and the symphysis is low, subvertical and with a straight profile. There are two mental foramina, at the level of the p2 and the p3. No lower incisors are preserved. The canine crowns are unworn (preserved buccal height 18.7 mm in IPS60892a and 18.3 mm IPS60892c) except for a contact facet against the i3 at the cervix, and display a fine crest without crenulations from tip to base on the lingual side. An alveolus for the p2 is present distally from the c1, being separated from the latter by a 5.4 mm-long diastema and from the p3 by a shorter diastema of 3.4 mm. The p3 displays three cusps, the main one (protoconid) being situated at about mid-crown length and being clearly higher than the remaining ones. The mesial accessory cuspid is situated close to crown base, whereas the distal accessory cuspid is located slightly toward the buccal side of the talonid. The latter is lingually expanded and displays a weakly-developed distal cingulid close to the crown base. The p4 is longer, broader and higher than the p3, with a conspicuous protoconid that is similarly located at about mid-crown length, and two accessory cusps. The mesial one is small but distinct, being separated from the protoconid by a groove. The similarly-sized distal accessory cuspid, in turn, is separated from the protoconid by a notch and is more clearly situated on the buccal portion of the talonid than in the p3. As in the latter, the talonid is lingually expanded and displays a weakly-developed but distinct distal cingulid close to the base of the crown. The carnassial (m1), larger than the remaining postcanine teeth, displays two main cusps: the obliquely-oriented paraconid and the distally-curved protoconid. In buccal view, the paraconid is well developed both in length and

height, so that the protoconid is only slightly more protruding than the former, from which it is separated by a narrow buccal notch and a deep lingual valley. The talonid, shorter and much lower than the trigonid, bears no well-individualized distal cuspid. There is no m2.

Remarks: The attribution of the described material from ACM to *P. quadridentatus* is justified by dental size, since the dentition of this species is larger than that of both *P. romieviensis* and *Styriofelis* spp. (Heizmann, 1973; Rothwell, 2001; see also our Fig. 5). Thus, although there is some overlap regarding m1 (Fig. 5C) and c1 (Fig. 5A), the size of both the P4 (Fig. 5E) and the p4 (Fig. 5B) enables a clear-cut distinction of *P. quadridentatus*—the c1 IPS50940 is attributed to *P. quadridentatus* because it falls very close in dental size and proportions to IPS60892a, which is associated to lower cheek teeth. Moreover, an attribution of the above-mentioned mandibular remains from ACM to *P. quadridentatus* is further confirmed by the morphology of the lower cheek teeth (more similar to *Styriofelis* spp.), including the shorter m1 talonid with a lesser-developed distal cuspid, as well as the lower-crowned and more inflated premolars, compared to *P. romieviensis* (Ginsburg, 1961, p. 141; Heizmann, 1973, p. 49, fig. 15). The morphology of the lower carnassials attributed to *P. quadridentatus* seems extremely variable on the basis of previously published material (Gaillard, 1899, pl. I, fig. 7; Ginsburg, 1961, pl. XII, fig. 4; Viret, 1951, pl. II, fig. 3). In particular, the reduction of the talonid and the absence of a distinct metaconid would be characteristic of *P. quadridentatus*, whereas the relative height and mesiodistal length between the paraconid and protoconid would be too variable to serve as a reliable taxonomic criterion. With regard to mandibular proportions, it is not possible to estimate the mandibular robusticity of IPS60892, because the corpus is broken behind the m1. The p4/m1 length index for IPS60892 (77.8%) is however closer to the values usually reported for *P. romieviensis* than to those of *P. quadridentatus* (see the remarks section for *P. romieviensis* above).

Finally, in spite of being smaller than the upper canines of *P. quadridentatus* previously reported from Spain (Ginsburg et al., 1981; see also our Fig. 5D), the isolated C1 from ACM/C4-C2 is attributed to *P. quadridentatus* instead of *P. romieviensis* based on the somewhat larger size and especially the more buccolingually compressed occlusal profile of the former (breadth/length index of 43%, compared to 57–58% in the ACM specimens of *P. romieviensis*; see also the remarks regarding the latter species).

5. Discussion

5.1. Taxonomic attribution

Three different felid species are recorded at the ACM local stratigraphic series. The genus *Styriofelis* is recorded by a single species, *S. turnauensis*, which is identified from two lower carnassials mainly on the basis of dental size—smaller than in *Pseudaelurus* spp. and, with some overlap, than in *S. lorteti* (Gaillard, 1899), but larger than in *S. vallesiensis* (Salesa et al., 2012). This species attribution is further confirmed by the reduced development of the m1 talonid (including a short talonid relative to the

trigonid, as well as a reduced albeit distinct distal cuspid) compared to other felines (Crusafont-Pairó, 1952; Gaillard, 1899; Thenius, 1949; Villalta Comella and Crusafont-Pairó, 1943), including both *S. lorteti* and *Pseudaelurus* species. The reduced development of the m1 talonid is one of the various plesiomorphic dental characteristics shared by *S. turnauensis* and the younger species *S. vallesiensis* from the Vallesian and *Pristifelis attica* (Wagner, 1857) from the Turolian (Salesa et al., 2012). Other primitive features shared by these taxa, such as the robust P3 and the better-developed P4 paracone (Salesa et al., 2012) cannot be evaluated in the ACM material.

The genus *Pseudaelurus* is represented by more abundant remains at the ACM series, being attributed to either *P. romieviensis* or *P. quadridentatus*. The material attributed to the former of these species generally fits well its original diagnosis by Roman and Viret (1934; see also Heizmann, 1973), according to which *P. romieviensis* would be intermediate in size between *S. lorteti* and *P. quadridentatus*, being further characterized by short and high lower premolars, as well as by a lower carnassial with a well-developed talonid. The ACM remains, however, document for the first time the retention of a p2 in *P. romieviensis*; Heizmann (1973) included the lack of p2 in the diagnosis of this species, but the ACM material indicates that this feature is variable and hence does not serve as a taxonomic criterion to distinguish *P. romieviensis* from *P. quadridentatus*. Furthermore, the ACM material indicates that the development of the anterior accessory cuspid of the p4 is also variable in this taxon—thus contrasting with previous descriptions for this species (Heizmann, 1973; Koufos, 2008; Roman and Viret, 1934). In turn, the presence of *P. quadridentatus* among the ACM material is clearly justified by the larger dental size of this taxon as compared to *P. romieviensis*, as well as on the basis of several occlusal details—lesser-developed m1 talonid without a distinct metaconid, as well as lower-crowned and more inflated lower premolars, as compared to *P. romieviensis* (Ginsburg, 1961; Heizmann, 1973; Roman and Viret, 1934).

5.2. The chronostratigraphic range of *Styriofelis* and *Pseudaelurus* in the Iberian Peninsula

Some of the previous citations of *Pseudaelurus* sp. from the Iberian Peninsula could belong to either *Pseudaelurus* or *Styriofelis*; they include those from the MN5 of Somosaguas (Hernández Fernández et al., 2006; Salesa and Morales, 2000) and La Retama (Fraile et al., 1997; Morales et al., 1993), as well as those from the MN9 of Ballestar (Crusafont-Pairó and Golpe-Posse, 1974; Golpe-Posse, 1974, 1981). With these exceptions, the remaining published citations of *Pseudaelurus* s.l. from Iberia can be identified to the species level, thereby permitting us to compare the previously known chronostratigraphic ranges of the various species with the age of the new citations from ACM.

With regard to the genus *Styriofelis*, in the Iberian Peninsula it is represented by three different species. *S. lorteti* is restricted to the Aragonian, being recorded from the MN4 of Sant Mamet (Crusafont and Truyols, 1954; Crusafont et al., 1955) and Quinta do Pombeiro (Antunes, 1959, 2000),

the MN5 of Moratines (Alberdi et al., 1984; Fraile et al., 1997; Morales and Soria, 1985; Peláez-Campomanes et al., 2003), Puente de Vallecas (Alberdi et al., 1984; Fraile et al., 1997; Morales and Soria, 1985; Peláez-Campomanes et al., 2003), Tarazona de Aragón (Astibia, 1987; Fortelius, 2012; identified as *P. cf. lorteti* by Fraile et al., 1997), Torrijos (Fortelius, 2012; identified as *P. cf. lorteti* by Fraile et al., 1997, and as *P. quadridentatus* by Aguirre et al., 1982 and Alberdi et al., 1984) and Chelas 1 (Antunes, 2000), the MN6 of La Barranca (Peigné et al., 2006) and Paracuellos 3 (Alberdi et al., 1984; Fraile et al., 1997; Morales and Soria, 1985; Peláez-Campomanes et al., 2003), and the MN7 + 8 of Toril 3A (Álvarez Sierra et al., 2003; Azanza et al., 2004). The lack of material of this species in the ACM, of course, might be attributable to insufficient sampling (given the amount of fossil remains recovered from the ACM, the small available sample of *Styriofelis* and *Pseudaelurus* indicates that these felids were quite rare). Nevertheless, this fact agrees well with the previous record of *S. lorteti* in the Vallès-Penedès Basin, which is restricted to the MN4 of Sant Mamet (Crusafont et al., 1955). Fraile et al. (1997) reported the presence of *S. lorteti* in both Hostalets de Pierola Inferior (MN7 + 8) and Superior (MN9), but the only previous citations (and available material) of *Styriofelis* from the area of els Hostalets correspond in fact to the MN7 of Can Vila (see below).

S. turnauensis, in contrast, is more frequently recorded than the preceding species within the Vallès-Penedès Basin. In the Iberian Peninsula as a whole, *S. turnauensis* is recorded from the MN2 of Loranca 1 and M (cited as *P. transitorius* by Alcalá et al., 1990 and Fraile et al., 1997), the MN3 of Sant Andreu de la Barca (Agustí and Galobart, 1998), Costa Blanca 1 (Fortelius, 2012), Horta da Tripas (Antunes, 1959, 2000), and Ágredda (Fraile et al., 1997, identified as *P. transitorius*), the MN3 or MN4 of Quinta do Narigaõ/Cristo Rei (Antunes, 2000), the MN4 of Can Canals and El Canyet (Fortelius, 2012), Artesilla (Fraile et al., 1997), and Quinta do Pombeiro/Quinta das Pedreiras (Antunes, 2000), the MN4? of La Vinya Vella in Esparreguera (Crusafont and Truyols, 1954; Crusafont et al., 1955; Golpe-Posse, 1974), the MN5 of Chelas 1 (Antunes, 2000), the MN7 of Can Vila (Crusafont-Pairó, 1952; Crusafont and Truyols, 1954; Villalta Comella and Crusafont-Pairó, 1943), the MN8 or MN9 of Castell de Barberà (Petter, 1976), and the MN9? of Serra d'en Camero in Sabadell (Crusafont-Pairó, 1952; Crusafont and Truyols, 1954). Previously, thus, *S. turnauensis* had been reported from several Vallès-Penedès localities, ranging from the MN3 to the MN8 and, probably, the Earliest Vallesian (MN9), and therefore the recognition of this taxon at the ACM agrees well with the chronostratigraphic range previously known for this species in this basin. Finally, an attribution to *S. turnauensis* agrees with the fact that the recently-described species, *S. vallesiensis*, is restricted to the MN10 of Batallones 1 and 3 (Salesa et al., 2012).

The Iberian records of the genus *Pseudaelurus*, in turn, mostly correspond to *P. quadridentatus*, which is recorded from the MN5 of Montejo de la Vega (Fraile et al., 1997; Mazo et al., 1998, 1999), Puente de Vallecas (Peláez-Campomanes et al., 2003) and Paracuellos 3 and 5 (Alberdi et al., 1984; Fraile et al., 1997; Morales and Soria, 1985;

Peláez-Campomanes et al., 2003), the MN6 of Manchones (Petter, 1976), Alhambra-Túneles (Peláez-Campomanes et al., 2003), Arroyo del Val (Fraile et al., 1997; Peigné et al., 2006) and La Barranca (Peigné et al., 2006), the MN8 of Can Mata 1 (Crusafont-Pairó and Villalta, 1951; Crusafont and Truyols, 1954; Villalta Comella and Crusafont-Pairó, 1943; cited as *P. marini* by Agustí et al., 1985, and also in part by Golpe-Posse, 1974), the MN7 + 8 of Hostalets Inferior indeterminate (Fraile et al., 1997; cited as *P. marini* by Crusafont and Truyols, 1954; Crusafont-Pairó and Villalta, 1951; Villalta Comella and Crusafont-Pairó, 1943), the MN8 or MN9 of Castell de Barberà (Petter, 1976), and the MN9 of Los Valles de Fuentidueña (Fraile et al., 1997; Ginsburg et al., 1981; identified as *P. turnauensis* by Crusafont-Pairó and Ginsburg, 1973, and as *Pseudaelurus* sp. by Golpe-Posse, 1974). Therefore, the presence of *P. quadridentatus* at the MN8 of the ACM fits well with the previously known range of this species in the Iberian Peninsula (and elsewhere in Europe, e.g. Werdelin et al., 2010).

In contrast, only a few citations of *P. romieviensis* are available from the Iberian Peninsula, being recorded from the MN4 of Els Casots (Casanovas-Vilar et al., 2011b) and the MN5 of Chelas 1 (Antunes, 2000)—the remains from the MN4 of Buñol, attributed to *P. quadridentatus* (Belinchón and Morales, 1989; Fraile et al., 1997), might alternatively correspond to *P. romieviensis* on the basis of the small size of the m1—so this locality has not been incorporated in Fig. 5. The identification of *P. romieviensis* in the MN8 of ACM considerably extends the range of this taxon in Iberia (up to 11.6 Ma), approximately coinciding with the last appearance datum of this taxon elsewhere in Europe (Werdelin et al., 2010).

6. Summary and conclusions

New felid dentognathic remains from several localities of the local stratigraphic series of Abocador de Can Mata (MN7 and MN8, late Middle Miocene), in the area of els Hostalets de Pierola (Vallès-Penedès Basin, Catalonia, Spain), are described and attributed to three different species: *S. turnauensis*, *P. romieviensis*, and *P. quadridentatus* (Felidae: Felinae). The remains of *P. romieviensis* enable us to ascertain that, like *P. quadridentatus*, this species variably retained the p2, which cannot be therefore employed as a taxonomic criterion to distinguish these two species. The identification of *P. romieviensis* among the ACM material considerably extends the range of this species in the Iberian Peninsula, in agreement with the reported range for this species in the rest of Europe.

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