New dental material and redescription of *Agerinia roselli* (Primates, Adapiformes) from Les Saleres (early Eocene, NE Iberian Peninsula)

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ABSTRACT

In this work, new dental material of *Agerinia roselli* from its type locality, Les Saleres (NE Spain), is described. An emended diagnosis of the species is provided, together with a redescription of the entire hypodigm from that locality, which was necessary due to some inaccuracies in previous descriptions. The studied material includes 12 teeth (from P_3 to M_3); the roots of the anterior premolars preserved in a mandible fragment are reported for the first time. Some previously undescribed traits have been identified after the new analysis of this material, such as the P_4 with distinct hypoconid and entoconid and the tiny paraconid on the M_1. A detailed comparison with other cercamoniines has been made. The body mass of *A. roselli*, ranging from 650 to 900 g, has also been estimated.

The presence of a minuscule paraconid in the M_1 is the most reliable criterion for distinguishing this molar from the M_2. This is supported by the complete absence of paraconid in four M_2 preserved in mandible fragments. The trigonid length seems to be less reliable for distinguishing M_1 from M_2, due to its high variability in this species. Concluding, this study updates the knowledge about the dental anatomy of *A. roselli* and demonstrates that it is a valid taxon clearly distinguishable from other cercamoniines.

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INTRODUCTION

The early Eocene recorded an important step in the early diversification of primates. The primate record in Europe at this time is not very abundant, although rather diverse and geographically widespread (e.g., Russell et al., 1967; Godinot, 1978, 1981; Franzen, 1987, 2000a; Marandat, 1991; Estravís, 2000; Smith et al., 2006; Franzen et al., 2009; Gebo et al., 2012, 2015; Hooker, 2012; Marigó et al., 2012, 2014). In the Iberian Peninsula, the first studies of Eocene primates were undertaken in the 1960s (Crusafont-Pairó, 1967). In the last decade, the research team of the Institut Català de Paleontologia Miquel Crusafont (ICP) has restarted the study of the Paleogene primate record from Spain, but focusing on middle and late Eocene sites (Minwer-Barakat et al., 2010, 2012, 2013a, 2013b, 2015a, 2015b), including the definition of several new anchomomyins (Marigó et al., 2010, 2011, 2013) and the first interpretations about their locomotion (Marigó et al., 2016). On the contrary, recent studies of early Eocene primates from the Iberian Peninsula only involve some preliminary studies of Euprimates (Femenias-Gual et al., 2014, 2015) and the description of *Arcius* from Masia de l'Hereuet, the first record of Plesiadapiformes from Spain (Marigó et al., 2012). For this reason, the revision of classical material is essential in order to improve the knowledge of the primates from this time span.

Crusafont-Pairó (1967) first described an early Eocene primate from the Iberian Peninsula, *Agerinia roselli*. Since then, the paucity of material and the lack of detailed descriptions and high quality images have complicated the comparison of this species with other taxa. Moreover, the exact geographic location of the type locality Les Saleres is unknown, preventing the collection of further material. Furthermore, this species and *Donrussellia lusitanica* are the only euprimates determined at the specific level in the early Eocene from the Iberian Peninsula. For all these reasons, the redescription of this species is absolutely necessary.

The species, originally named as *Agerina roselli*, was described on the basis of two mandible fragments with M_2 and M_3, as well as three isolated teeth, either M_1 or M_2 (Crusafont-Pairó, 1967). Later on, Crusafont-Pairó (1973) changed the generic name into *Agerinia*, because the original name was preoccupied by a genus of trilobites. Szalay (1971) gave more accurate descriptions of the material from Les Saleres, including most (but not all) of the remains described by Crusafont-Pairó (1967) and another previously unpublished specimen from the same locality (a mandible fragment with P_3-P_4). Szalay (1971) also provided a first diagnosis for this species, since the original description by Crusafont did not include a proper diagnosis, but only a short description of the material. Crusafont-Pairó and Golpe-Posse (1975) reported a supposed upper molar of *A. roselli* from Les Saleres, but after direct observation of this specimen (IPS-36182), housed in the ICP, it has been proved to belong to an artiodactyl. Therefore, the upper dentition of *A. roselli* remains unknown. *Agerinia* was synonymized with *Periconodon* by Gingerich (1976, 1977), but Szalay and Delson (1979) and Godinot (1988) considered *Agerinia* as a valid genus. Regarding its suprageneric placement, *Agerinia* was tentatively included in the Necrolemuridae by Crusafont-Pairó (1967). However, it was later relocated within the Adapidae by Szalay (1971) and Szalay and Delson (1979), due to its similarities with *Protoadapis, Pelycodus* and *Pronycticebus*. Later, Godinot (1998) included this genus in a new subfamily, Pronycticebinae, within an "incertae sedis" family of Adapiformes. Recent works place *Agerinia* in the subfamily Cercamoniinae (Gebo, 2002; Godinot, 2015).

Recently, during the revision of the classical collection from Les Saleres stored in the ICP, more unpublished dental specimens of *A. roselli* have been found, including three complete and one incomplete lower molars. In this work, a detailed description of all the available dental material of *Agerinia roselli* from Les Saleres is provided for the first time, including both unpublished and previously published specimens, together with accurate measurements and high quality images. It is further presented an emended diagnosis of this species that emphasizes and discusses some morphological features not observed before, such as the roots of the mesial premolars interpreted on the basis of the root fragments preserved in one of the available mandibles. In addition, the body mass of *A. roselli* is estimated based on the size of the M_1 and M_2. Finally, the material of *A. roselli* from Les Saleres is compared with other samples ascribed to *Agerinia*, as well as with other Eurasian adapiformes, thus improving the knowledge about this still poorly known primate genus.

Geographical, Geological, and Biochronological Context

The exact geographic location of Les Saleres, the type locality of *Agerinia roselli*, is unknown. However, Crusafont-Pairó and Rosell-Sanuy (1966) stated that it was close to the small town
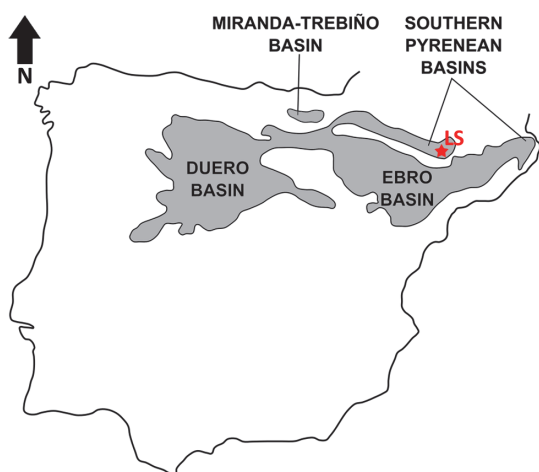
FIGURE 1. Map showing the main Tertiary basins of the Iberian Peninsula with the location of Les Saleres (LS) fossil site (modified from Antunes et al., 1997).

called L'Ametlla del Montsec, in the eastern sector of the Àger valley (La Noguera, Lleida province, NE Spain). Geologically, this fossil site is placed in the Àger sub-basin, within the Southern Pyrenean Basins (Figure 1). The continental Eocene deposits of this sub-basin were first studied by Crusafont-Pairó and Rosell-Sanuy (1966) and later by Rosell-Sanuy and Llompart-Díaz (1988), Checa (1995), and Badiola et al. (2009). Its infill mainly consists of marls, clays and sandstones, with conglomeratic levels in several areas. The sandstones are associated with complex channels of braided rivers, whereas the marls and clays correspond to flood-plain deposits. Scarce and generally dispersed fossil remains of mammals, crocodiles and turtles have been found in these deposits.

Regarding the age of this fossil site, Les Saleres was assigned to the late early Eocene by Crusafont-Pairó (1967) and Szalay (1971). Later, Antunes et al. (1997) provided a faunal list for this locality and ascribed it to the MP10 Mammal Paleogene Reference Level. However, the mammal assemblage listed by Antunes et al. (1997) presents clear inconsistencies. On the one hand, the perissodactyl *Lophiaspis maurettei* is present in other European localities such as Palette (MP7; Godinot et al., 1987), Silveirinha (MP7; Estravís, 2000) and Mutigny (MP8/9; Hooker, 1996), thus suggesting for Les Saleres an age older than MP10. But, on the other hand, other taxa presumably identified in Les Saleres are recorded in much younger localities. This is the case of the artiodactyl *Cebochoerus*, present in middle and late Eocene fossil sites like Eckfeld Maar (MP13),

Robiac (MP16), Fons 4, Sossís (MP17a) or La Débruge (MP18), and the carnivore *Cynodictis*, recognized in even younger localities such as La Débruge and Escamps (MP19) (BiochroM'97, 1997; Franzen, 2004; Minwer-Barakat et al., 2015b, among others). Some of the taxonomic determinations of the material from Les Saleres seem to be incorrect, so the fauna from that site claims for a careful revision and, consequently, the age proposed by Antunes et al. (1997) cannot be considered conclusive. In any case, although a detailed dating cannot be provided, Les Saleres can be confidently assigned to the early Eocene, which is the age of the continental deposits of the Àger sub-basin (Barnolas et al., 2004).

MATERIALS AND METHODS

Studied Material

The studied material includes, first, the specimens from the type locality, Les Saleres, previously described by Crusafont-Pairó (1967) and Szalay (1971) and, second, unpublished dental material from this site. The first sample consists of a left mandible fragment preserving P_3, P_4, and two fragments of roots mesially located with respect to the P_3 (IPS-2543); two right isolated M_1 (IPS-82793; IPS-82816); a left mandible fragment with M_2 and M_3 (IPS-1981, holotype) and a right mandible fragment with M_2 and M_3 (IPS-2541). The unpublished sample includes a left mandible fragment with the distal part of the M_3 and part of the ramus mandibularis (IPS-82790); a right mandible fragment with M_3 (IPS-82795), and one right and one left mandible fragments with M_2 (IPS-82794 and IPS-2542, respectively). One of these two latter specimens probably corresponds to the M_1 or M_2 referred by Crusafont-Pairó (1967) but not included in the work of Szalay (1971), but this cannot be affirmed due to the lack of illustrations of that molar. All the studied material is housed at Institut Català de Paleontologia Miquel Crusafont, ICP (Sabadell, Spain).

Comparative Sample

The material of *Agerinia roselli* from Les Saleres has been compared directly with the specimens of *Agerinia* sp. from Condé-en-Brie (France), *Donrussellia gallica, Pronycticebus gaudryi* and *Protoadapis curvicuspidens,* all housed in the collections of the Muséum National d'Histoire Naturelle (MNHN), Paris. It has also been compared with the material of *Agerinia* cf. *roselli* from Azillanet (France), belonging to the collections of

the Université de Montpellier 2, in loan in the MNHN. It has also been compared with casts of *Periconodon huerzeleri, Donrussellia magna, D. provincialis, Cantius eppsi, Europolemur klatti, Protoadapis ignoratus, Marcgodinotius indicus,* and *Asiadapis cambayensis,* also stored in the MNHN. Finally, comparisons with *Agerinia* sp. from Casa Ramón (Spain), cf. *Agerinia* from Rians (France), *Periconodon* sp. from Eckfeld Maar (Germany), *P. lemoinei, P. jaegeri, Donrussellia lusitanica, D. louisi, D. russelli, Darwinius masillae, Pronycticebus neglectus, Europolemur koenigswaldi, E. dunaifi, E. kelleri, Cantius savagei, Protoadapis angustidens, P. brachyrhynchus, P. weigelti,* and *P. muechelnensis* are based on published data.

Dental nomenclature, Measurements, Micrographs, and Radiographs

The dental nomenclature used follows Szalay and Delson (1979). Measurements have been taken with an optic calliper "Nikon measuroscope 10" connected to a monitor "Nikon SC112", using the criteria described by Marigó et al. (2010). The height of P_3 and P_4 has been measured as the distance between the apex and the crown base observed in lingual view. Micrographs have been taken using the Environmental Scanning Electron Microscope (ESEM) at the Universitat de Barcelona. Body mass has been estimated on the basis of the equations for the M_1 and M_2 of prosimian proposed by Egi et al. (2004). Radiographs have been taken using a constant potential X-ray equipment "Yxlon", with different voltages (50, 55, 60, 65, 70, 75, and 80 kV), at Centre de Restauració de Béns Mobles (Valldoreix, Barcelona).

SYSTEMATIC PALAEONTOLOGY

Order PRIMATES Linnaeus, 1758
Suborder STREPSIRRHINI Geoffroy Saint-Hilaire, 1812
Infraorder ADAPIFORMES Hoffstetter, 1977
Family NOTHARCTIDAE Trouessart, 1879
Subfamily CERCAMONIINAE Gingerich, 1975
Genus *AGERINIA* Crusafont-Pairó, 1973
Agerinia roselli (Crusafont-Pairó, 1967)
Figures 2, 3

Original Diagnosis (Szalay, 1971)

"The adapine adapid *Agerina* differs from all known species of *Protoadapis* in having P_3 and P_4 subequal in height, and in lacking a distinct, anteroposteriorly oriented cristid obliqua on P_4 talonid. Unlike the trigonids of *Protoadapis* or *Pronycticebus,* those of *Agerina* are sealed off lingually by the union of the metaconid mesially and the paracristid distally. Although the paracristid is very low in *Agerina,* this crest invariably extends lingually almost to the limits of the metaconid, whereas in *Pronycticebus* the paracristid extends only midway on M_1 and slightly more lingually on M_2 and M_3. Differences between *Agerina* and *Adapis* are most noticeable in the complete absence of a metastylid on the lower molars of the former. *Agerina* differs from *Caenopithecus* in having a larger metaconid on P_4 and in lacking a metastylid and any traces of an entoconid. Talonid cusps of *Agerina* are generally less bulbous than those of *Caenopithecus. Agerina* differs from *Pelycodus* in lacking the distinct, cuspate paraconid on M_1 and in the generally less bulbous nature of the talonid cusps."

Emended Diagnosis

Medium-size cercamoniine. P_3 and P_4 subequal in height. P_4, with well-developed protoconid, metaconid, and cristid obliqua, distinct paraconid, entoconid, and talonid basin. M_1 with a tiny paraconid; M_2 and M_3 without any trace of paraconid. Trigonid basin closed in all the three lower molars. Protocristid subperpendicular to the lingual and buccal borders in all molars. Short talonid basin with rounded outline in the M_1 and M_2.

Agerinia roselli differs from *Periconodon* in the presence of a marked metaconid in the P_4 and the shorter and broader trigonid in the M_1; it further differs from *Periconodon jaegeri* in the lack of enamel wrinkling. It differs from *Darwinius masillae* in the smaller size and the presence of a tiny paraconid in the M_1. It can be distinguished from *Donrussellia* by the shorter trigonid and the smaller paraconid in the M_1 and by the absence of paraconid in the M_2 and M_3. *Agerinia roselli* differs from *Cantius* in the much smaller size, the less inflated cuspids, the protocristid of the M_1 subperpendicular to the buccal and lingual borders and the lack of paraconid in the M_2 and M_3. It can be distinguished from *Pronycticebus* by the much smaller size; it further differs from *P. gaudryi* in the absence of paraconid in the M_2 and M_3. *Agerinia roselli* differs from *Europolemur* in the smaller size. Besides, it differs from *E. kelleri* in the presence of paraconid in the M_1 and from *E. dunaifi* in the closed and shorter trigonid in the M_1 and M_2. *Agerinia roselli* differs from *Protoadapis* in being smaller, in having P_3 and P_4 similar in height and in the less inflated cuspids in the lower molars. It differs from *Asiadapis cambayensis* in the well-developed metaconid in the P_4 and in having the paraconid smaller in the M_1 and
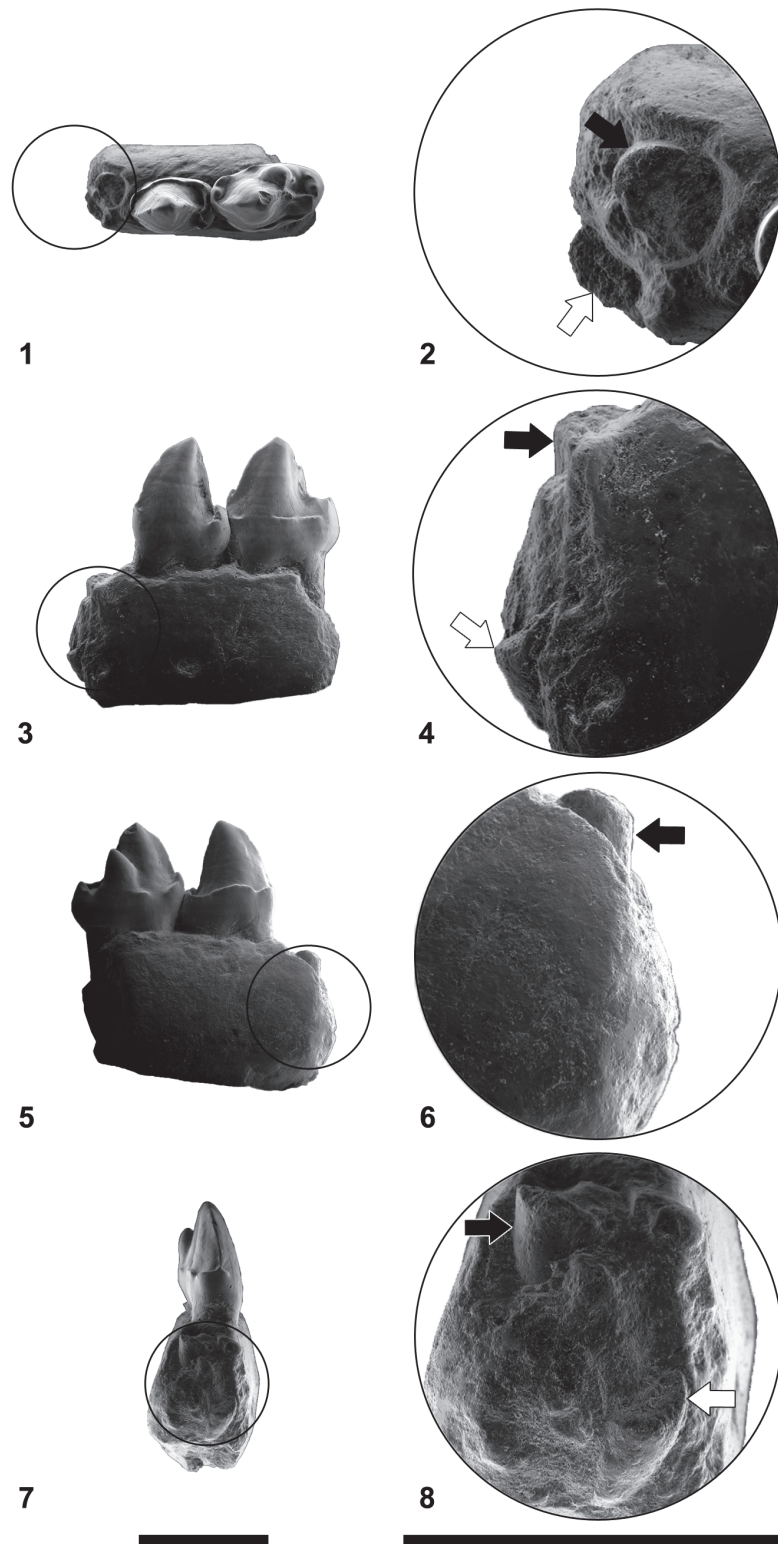
FIGURE 2. *Agerinia roselli* from Les Saleres. IPS-2543, left mandible fragment with P_3 and P_4 in occlusal (**1**), buccal (**3**), lingual (**5**), and mesial (**7**) views; enlarged images of mesial roots of the same specimen in occlusal (**2**), buccal (**4**), lingual (**6**), and mesial (**8**) views; white arrows indicate the position of the most mesial root; black arrows indicate the position of the root immediately mesial with respect to the P_3. Scale bar represents 3 mm in both cases.
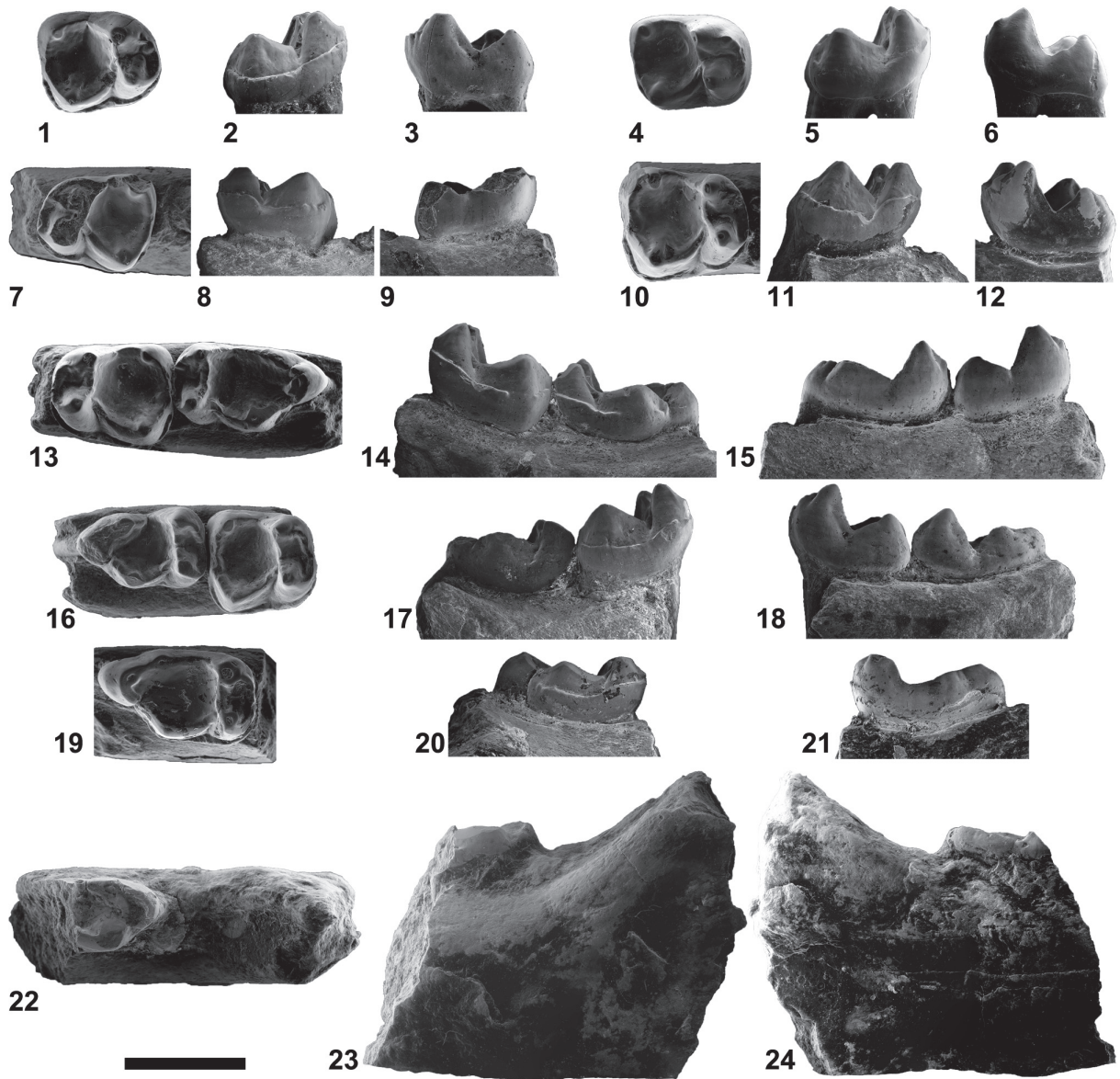
FIGURE 3. *Agerinia roselli* from Les Saleres. IPS-82793, isolated right M_1 in occlusal (**1**), buccal (**2**) and lingual (**3**) views. IPS-82816, isolated right M_1 in occlusal (**4**), buccal (**5**) and lingual (**6**) views. IPS-2542, left mandible fragment with M_2 in occlusal (**7**), buccal (**8**) and lingual (**9**) views. IPS-82794, right mandible fragment with M_2 in occlusal (**10**), buccal (**11**) and lingual (**12**) views. IPS-1981, holotype, left mandible fragment with M_2 and M_3 in occlusal (**13**), buccal (**14**) and lingual (**15**) views. IPS-2541, right mandible fragment with M_2 and M_3 in occlusal (**16**), buccal (**17**) and lingual (**18**) views. IPS-82795, right mandible fragment with M_3 in occlusal (**19**), buccal (**20**) and lingual (**21**) views. IPS-82790, left mandible fragment preserving part of the ramus mandibularis and a fragment of the M_3 in occlusal (**22**), buccal (**23**) and lingual (**24**) views. Scale bar represents 3 mm.

absent in the M_2 and M_3. *Agerinia roselli* can be distinguished from *Marcgodinotius indicus* by its larger size, the presence of a paraconid and the more developed metaconid in the P_4 and the closed trigonid in the M_1.

Description

Mandible. Some morphological traits of the mandible can be observed in specimens IPS-2543 and IPS-82790. The former specimen, bearing P_3 and P_4, also preserves two root fragments of the ante-

rior premolars. There is a root fragment in central position, placed mesially with respect to the P$_3$. In addition, in a more mesial position, the specimen preserves a small fragment of root strongly displaced towards the buccal border of the mandible. The assignation of these roots to single-rooted P$_1$ and P$_2$ or to a double-rooted P$_2$ is further analysed in the discussion. In addition, this mandible shows two mental foramina, oval shaped, and similar in size. The mesial mandibular foramen is located at the level of the root placed immediately mesial to the P$_3$ and the distal mandibular foramen at the level of the distal root of the P$_3$. The specimen IPS-82790 preserves the mesial part of the ramus mandibularis, which is robust and shows a well-marked masseteric fossa.

P$_3$. It is clearly longer than wide. There is no paraconid. At the center of the tooth, there is a high and pointed protoconid with sharp paracristid and protocristid, both mesiodistally oriented. At the end of the protocristid, close to the distobuccal corner of the tooth, there is a small bulge that does not constitute a differentiated cuspid. There is a strong cingulid, starting at the mesial corner, occupying the lingual and distal borders, and reaching the distobuccal bulge. This cingulid encloses a well-differentiated basin on the distolingual part of the tooth. There are two roots.

P$_4$. It is larger than the P$_3$, similar in height and with better developed cuspids. The protoconid is as high as in the P$_3$ and has a sharp paracristid directed mesially; this cristid turns lingually near the base of the crown, reaching a small but distinct paraconid. There is a short cristid directed lingually from the paraconid, restricted to the mesiolingual corner of the tooth. The protoconid connects to the metaconid by a short protocristid, which shows a trigonid notch. The metaconid is well differentiated, inflated, and two-thirds the height of the protoconid. There is no premetacristid. The cristid obliqua reaches the trigonid wall at the level of the trigonid notch. At the distobuccal corner of the tooth, the cristid obliqua thickens, forming a minuscule hypoconid. There is a very short postcristid that connects the hypoconid to the entoconid, which is similar in size to the paraconid, and slightly higher than the hypoconid. There is a short preentocristid, which does not reach the metaconid, so the talonid basin is open lingually. The lingual cingulid is very weak and short, only observed on the middle of the lingual side. The buccal cingulid is also weak; it runs from the buccal base of the paraconid to the buccal base of hypoconid, but it is interrupted at

the level of the protoconid apex. There are two roots.

M$_1$. The two available isolated molars are here attributed to M$_1$ (see discussion for further details). The trigonid is slightly narrower than the talonid; in IPS-82816 this difference is less marked and the outline is more quadrate than in IPS-82793. The paracristid is curved and connects the protoconid to a minuscule paraconid, attached to the mesial side of the metaconid. The trigonid basin is deep and closed. The protoconid is placed in a faintly more mesial position than the metaconid, which is slightly higher. The protocristid, connecting protoconid and metaconid, is nearly straight and almost perpendicular to the lingual and buccal borders of the tooth. The cristid obliqua reaches the trigonid wall faintly buccally with respect to the trigonid notch. The talonid basin is closed, deep, and much longer than the trigonid. The cristid obliqua, postcristid, and preentocristid are slightly curved, thus giving a rounded aspect to the outline of the talonid. The hypoconid is slightly higher and more voluminous than the entoconid, which is placed in a faintly more distal position. A minuscule hypoconulid is observed in specimen IPS-82793. The buccal cingulid is very strong in IPS-82793 and barely marked in IPS-82816; it occupies the entire buccal border, from the mesial base of the protoconid to the distal base of the hypoconid.

M$_2$. The trigonid width is variable: it is very narrow in IPS-1981, somewhat wider in IPS-82794 and in IPS-2542; and only slightly narrower than the talonid in IPS-2541. There is no paraconid. The paracristid surrounds the mesial side of the tooth, continues in a premetacristid and connects to the metaconid, closing a relatively deep trigonid basin. The protoconid and metaconid are similar in height; the former is placed in a slightly more mesial position. The protocristid, almost perpendicular to the buccal and mesial borders, connects the protoconid and metaconid. The cristid obliqua reaches the trigonid wall close to the trigonid notch. The talonid basin is closed, deep, and slightly wider than long. The hypoconid is higher than the entoconid and located in a slightly more mesial position. The postcristid is curved and, mainly at the middle of its length, it has a minuscule hypoconulid in all specimens except for IPS-2542. The buccal cingulid is strong; it runs from the mesial base of the protoconid to the level of the hypoconulid. This cingulid becomes thinner or even almost interrupted at the level of the hypoconid.

M$_3$. There is no trace of paraconid. The paracristid starts at the protoconid, borders the mesial side of

TABLE 1. Teeth measurements (in mm) of *Agerinia roselli* (Crusafont-Pairó, 1967) from Les Saleres.

Catalogue number	Tooth	Length	Width	Height
IPS-2543	P_3	2.27	1.43	2.65
	P_4	2.77	1.70	2.66
IPS-82793	M_1	3.24	2.72	-
IPS-82816	M_1	3.24	2.50	-
IPS-2542	M_2	3.26	2.61	-
IPS-82794	M_2	3.51	3.06	-
IPS-1981	M_2	3.31	2.66	-
	M_3	3.93	2.29	-
IPS-2541	M_2	3.28	2.73	-
	M_3	3.24	2.11	-
IPS-82790	M_3	-	≥1.97	-
IPS-82795	M_3	3.97	2.42	-

the tooth, and continues in a premetacristid that reaches the metaconid, closing the trigonid. The trigonid basin is deep; it is relatively shorter and wider in IPS-2541 and IPS-82795 than in IPS-1981. The protoconid is placed in a slightly more mesial position than the metaconid. The protocristid is nearly perpendicular to the mesial and buccal borders of the tooth, and shows a trigonid notch, more marked in IPS-2541 than in the rest of specimens. The cristid obliqua reaches the trigonid wall at the level of the protoconid, in a more buccal position than in the M_1 and M_2. The talonid basin is deep and longer than wide. The hypoconid is larger than the entoconid and placed in slightly more mesial position. The hypoconulid lobe is broad and well differentiated; it is placed in lingual position, closer to the entoconid than to the hypoconid. The preentocristid connects the entoconid to the metaconid in IPS-82795; IPS-1981 shows a shallow talonid notch close to the metaconid, whereas IPS-2541 and IPS-82790 display a deep talonid notch. The hypocristid is interrupted close to the base of the hypoconulid, showing in all specimens a well-marked notch. The buccal cingulid is strong in IPS-82795, weaker in IPS-1981, and almost not observable in IPS-2541. It starts at the mesial base of the protoconid and reaches the distal base of the hypoconid, being interrupted at the level of the hypoconid apex in IPS-1981. Specimen IPS-82795 shows a very weak mesial cingulid at the base of the metaconid.

Measurements

See Table 1.

Comparisons

Comparisons with other samples attributed to *Agerinia*. The specimens from Les Saleres have been compared with the material from Azillanet (France), assigned to *Agerinia* cf. *roselli* by Godinot (1983, 1998). The latter is larger than *A. roselli*; the difference in size is more evident in M_2 and M_3 than in M_1. Despite the resemblance in overall morphology, some differences can be observed. The M_1 of *Agerinia* cf. *roselli* from Azillanet lacks the minuscule paraconid present in those from Les Saleres. The trigonid is longer in the lower molars of *A.* cf. *roselli* than in those of *A. roselli*, although this difference is more accentuated in the M_1. The cuspids are slightly more bulbous in *A.* cf. *roselli* than in *A. roselli*. The protocristid is more oblique in all the lower molars of *A.* cf. *roselli* than in *A. roselli*. *Agerinia* cf. *roselli* also has the protoconid in a more mesial position than the teeth from Les Saleres. The development of the buccal cingulid is similar in both samples (slightly stronger in the M_3 of *A.* cf. *roselli* from Azillanet).

Differences are obvious with the scarce material of *Agerinia* sp. from Casa Ramón (Peláez-Campomanes, 1995). The main difference is size, with *Agerinia* sp. being clearly smaller than *A. roselli* from Les Saleres. In addition, some morphological differences are observed. The single M_1 from Casa Ramón only preserves the buccal part; it differs from the specimens of *A. roselli* in the shape of the paracristid, which forms an acute angle near the mesiobuccal corner of the tooth in *Agerinia* sp. The M_2 of *Agerinia* sp. from Casa Ramón is relatively longer and narrower than those of *A. roselli*. The paracristid is lower in *Agerinia* sp. from Casa Ramón than in *Agerinia roselli* from Les

Saleres. Finally, the protocristid is slightly more oblique to the buccal and lingual borders in *Agerinia* sp*.* than in *A. roselli.*

The material from Les Saleres has been also compared with the specimens of *Agerinia* sp. from Condé-en-Brie figured by Herbomel and Godinot (2011). The lower molars from this French locality share many similarities with *A. roselli*, but some differences exist that reinforce the idea that they can belong to a new, still undescribed species, as suggested by Herbomel and Godinot (2011). The main difference is size, with *Agerinia* sp. from Condé-en-Brie being clearly larger. The trigonid is longer and narrower in the lower molars from Condé-en-Brie than in those from Les Saleres. In addition, the M_1 of *Agerinia* sp. from Condé-en-Brie differs from the specimens of *A. roselli* in the presence of a large paraconid and in the open trigonid basin, while in *A. roselli* the paraconid is very small and the premetacristid closes completely the trigonid basin. The M_1 from Condé-en-Brie shows slightly wrinkled enamel in the talonid, whereas no specimen from Les Saleres has enamel crenulation. The protocristid is clearly more oblique to the longitudinal axis of the tooth in the lower molars of *Agerinia* sp. than in those of *A. roselli*, especially in its buccal half. Moreover in *A. roselli,* the talonid basin of the M_1 and M_2 is wider than long, whereas in *Agerinia* sp. from Condé en Brie it is longer than wide. In addition, according to the descriptions of Herbomel and Godinot (2011), some M_2 of *Agerinia* sp. from Condé-en-Brie have a very small paraconid, which is absent in the all the M_2 from Les Saleres.

Finally, comparisons with the single M_2 from Rians assigned by Godinot (1983; 1998) to cf. *Agerinia* have been made. It shares some similarities with *A. roselli* such as the broad and deep talonid basin, despite that in RI 410 the talonid is slightly narrower than in *A. roselli*. Nevertheless, they show some clear differences, particularly the presence of a well-developed paraconid in the specimen from Rians. Moreover, the protocristid is more oblique to the lingual and buccal borders in the M_2 from Rians than in *A. roselli*. In addition, the single tooth from Rians shows a marked distolingual expansion that is not observed in the molars from Les Saleres and a slightly less developed buccal cingulid.

In conclusion, *Agerinia roselli* shows several morphological traits that allow distinguishing this species from the others samples assigned to the genus *Agerinia.* Unfortunately, the material from other fossil sites is, in general terms, scarce and poorly preserved, preventing the erection of other species and the interpretation of the phylogenetic relationships between several samples. Probably, the detailed study of the material from Condé en Brie, only preliminarily studied (Herbomel and Godinot, 2011), will shed new light on the evolution of this genus. In addition, further fieldwork is needed to recover more material of this genus.

Comparisons with other Eurasian Notharctidae. *Agerinia* was interpreted by Gingerich (1977) as a synonym of *Periconodon*, but this opinion is not shared by most authorities, who consider *Agerinia* a valid genus (Szalay and Delson, 1979; Godinot, 1983, 1988, 2015; Gebo, 2002). Despite some similarities, the material of *A. roselli* from Les Saleres shows significant differences with *Periconodon* that support the existence of two separated genera. Only the species of *Periconodon* that include lower teeth allow comparison with *A. roselli*. Among them, *Agerinia roselli* is slightly larger than *P. huerzeleri* and similar in size to *P. jaegeri.* The only material of *P. lemoinei* allowing comparisons is the holotype, an M_1 from Grauves described and figured by Gingerich (1977). According to this author, other isolated teeth from this French locality are also assignable to this species, but data about the size and morphology of these specimens are not published. The inclusion of this species in the genus *Periconodon* has been questioned by Godinot (1998). In any case, we have compared with the type of *P. lemoinei*, which is longer than the M_1 of *A. roselli* and similar in width. *Agerinia roselli* also differs from the holotype of *P. lemoinei* in having the trigonid of the M_1 lingually closed. The teeth of *A. roselli* are shorter but wider than those of *Periconodon* sp. from Eckfeld Maar (Franzen, 2004). Morphologically, *Periconodon* differs from *Agerinia* in having a weak metaconid in the P_4, whereas in *Agerinia* this cuspid is well differentiated. In addition, *Periconodon* shows a longer and narrower trigonid in the M_1 than *Agerinia*. Moreover, some M_1 of *Periconodon* lack the small paraconid that is present in those of *Agerinia*. Besides these characters, *A. roselli* clearly differs from *P. jaegeri* because this latter species shows wrinkled enamel and a cristid starting in the metaconid and directed towards the centre of the trigonid that is absent in *A. roselli*.

Darwinius masillae is clearly larger than *Agerinia roselli* and very similar regarding the morphology of the M_1 and M_2 (Franzen et al., 2009): both species have the trigonid shorter and narrower than the talonid, a protocristid almost perpendicular to the buccal and lingual borders, and closed trigonid basins. Despite these similarities, clear differ-

ences are observed, such as the presence of a tiny paraconid in the M_1 of *A. roselli* that is absent in *D. masillae*. In addition, *Darwinius* shows a well-developed metastylid in the M_1, which is absent in *Agerinia*. The buccal cingulid is slightly more marked in *Darwinius* than in *A. roselli*. Regarding the premolars, if the two mesial root fragments of the specimen IPS-2543 correspond to single-rooted P_1 and P_2, *A. roselli* would differ from *D. masillae* in the number of premolars, since this latter lacks a P_1. If, on the contrary, the roots of the specimen from Les Saleres correspond to a double-rooted P_2, *A. roselli* would be also different from *D. masillae*, because the specimen from Messel shows a single-rooted P_2. In both cases, therefore, the premolar arrangement of *D. masillae* would be more derived than that of *A. roselli*.

Donrussellia includes several species described from France (*D. provincialis*, *D. gallica*, *D. magna, D. louisi,* and *D. russelli)* and Portugal (*D. lusitanica*). *Agerinia roselli* is clearly larger than *D. provincialis* from Rians (Godinot, 1978), *D. gallica* from Avenay (Russell et al., 1967), *D. lusitanica* from Silveirinha (Estravís, 2000) and *D. russelli* from Avenay (Gingerich, 1977). On the contrary, it is smaller than *D. louisi* from Avenay (Gingerich, 1977) and *D. magna* from Palette (Godinot et al., 1987). Morphologically, clear differences exist between these two genera; the most remarkable one is the presence of a distinct paraconid in all the three lower molars of *Donrussellia,* whereas there is only a tiny cuspid in the M_1 of *A. roselli*. The trigonid of the M_1 is shorter than the talonid in *A. roselli,* whereas in *Donrusellia* the trigonid is almost as long as the talonid. The trigonid basin in the lower molars of *Donrussellia* is shallow and generally open, whereas in *A. roselli* this basin is always quite deep and closed lingually. Moreover, *D. lusitanica, D. provincialis,* and *D. magna* have a well-developed hypoconulid in M_1 and M_2, whereas in *A. roselli* this cuspid is very reduced or absent. In the cases of *D. russelli* and *D. louisi*, comparisons are only possible with the M_1 due to the scarcity of the available material; in any case, the presence of a large paraconid and a well-developed hypoconulid in both species (Gingerich, 1977) allows a clear distinction from *A. roselli*. In general terms, the buccal cingulid is more marked in *A. roselli* than in *Donrussellia.*

The genus *Cantius* is much larger than *Agerinia*. This genus includes several species recorded from North America and two forms from Europe, *Cantius eppsi* and *Cantius savagei*. The material from Les Saleres has been only compared in detail with the European species. Besides the clear difference in size with both species (Gingerich, 1977; Hooker, 2010), the P_4 of *A. roselli* differs from that of *C. eppsi* in the presence of a distinct entoconid. In addition, the trigonid is broader and shallower in the molars of *C. eppsi* than in those of *Agerinia*, especially in the M_2 and M_3. The most obvious difference is the presence of a very well-developed paraconid in all the lower molars of *C. eppsi* (with the exception of some M_3) and in the M_1 of *C. savagei*, whereas in *A. roselli* only the M_1 displays a very reduced paraconid. In addition, *C. eppsi* and *C. savagei* show more inflated cuspids than *A. roselli*. The protocristid has a more oblique orientation in the M_1 of *C. eppsi* and *C. savagei* than in those of *A. roselli*. Furthermore, in the M_1 of *C. savagei* the talonid basin is shorter than in *A. roselli,* and the cristid obliqua reaches the trigonid wall at the level of the metaconid, whereas in *A. roselli* it reaches the level of the protoconid.

Concerning *Pronycticebus gaudryi* from Mermerlein in France (Grandidier, 1904; Le Gros Clark, 1934; Szalay, 1971), it is slightly larger than *Agerinia roselli*. In both species there is a small paraconid in the P_4, but this premolar is more robust in *P. gaudryi* than in *A. roselli*. *Pronycticebus gaudryi* has a paraconid in all the lower molars, decreasing in size from M_1 to M_3, whereas in *A. roselli* only the M_1 displays a minuscule paraconid. The trigonid basin is shallow, mesiodistally elongated and lingually open in *P. gaudryi* whereas in *A. roselli* it is deep, short and closed; moreover, this basin is clearly narrower in *P. gaudryi*. The cuspids of *P. gaudryi* are slightly more bulbous than those of *A. roselli.* The orientation of the protocristid is one of the main differences between these species: oblique to the buccal and lingual sides in *P. gaudryi* and almost perpendicular to them in *A. roselli*. The cristid obliqua is clearly more curved in *A. roselli* than in *P. gaudryi.* The buccal cingulid is, in general, more marked in *A. roselli* than in *P. gaudryi*. Regarding *Pronycticebus neglectus,* described by Thalmann, Haubold and Martin (1989), this species was later ascribed to the genus *Godinotia* by Franzen (2000b). *Godinotia neglecta* can be clearly distinguished from *Agerinia roselli*, mainly by its notably larger size.

There are four described species of *Europolemur: E. koenigswaldi* and *E. kelleri* from Messel (Franzen, 1987, 2000a), *E. dunaifi* from Bouxwiller (Godinot, 1988), and *E. klatti* from Geiseltal (Thalman, 1994). All of them are clearly larger than *Agerinia roselli*. The presence of paraconid in the molars of *Europolemur* is variable: *E. kelleri* lacks

this cuspid in all the lower molars; *E. koenigswaldi* shows a tiny paraconid in the M_1; *E. dunaifi* shows generally a small paraconid in M_1 but usually lacks this cuspid in the M_2 (in *A. roselli* a tiny paraconid is only observed in the M_1). Moreover, the trigonid is much shorter in *A. roselli* than in *E. dunaifi*, especially in the M_1. In addition, the trigonid is open in the M_1 and M_2 in *E. dunaifi*, whereas it is closed in *A. roselli*. Another clear difference is the orientation of the protocristid, which is more oblique to the buccal and lingual sides in *E. dunaifi*. Furthermore, in the latter species the cristid obliqua reaches the trigonid wall more lingually than in *A. roselli*.

According to Godinot (2015), the genus *Protoadapis* includes the species *P. curvicuspidens, P. ignoratus, P. angustidens, P. (Cercamonius) brachyrhynchus, P. weigelti,* and *P. muechelnensis,* all of them poorly known. These six species are clearly different from *A. roselli,* being much larger and having more inflated cuspids in the lower molars. The P_3 is clearly higher than the P_4 in *Protoadapis*, whereas in *A. roselli* these two premolars are subequal in height. Besides, some *Protoadapis* species like *P. curvicuspidens* have a distinct paraconid in the M_1 and M_2, while in *A. roselli* there is a tiny cuspid only in the M_1. The trigonid basin of *Protoadapis* is larger than in *A. roselli* and sometimes open lingually. The talonid basin is relatively larger and deeper in *A. roselli* than in *Protoadapis.*

There are several similarities between *Asiadapis cambayensis* from Vastan Mine in India (Rose et al., 2007) and *Agerinia roselli*, such as the presence of a small paraconid in the P_4, the broad and short trigonid basin in the M_2 and M_3, or the relatively wide, short, and deep talonid basin of the molars. However, there are significant differences between these species. The premolars of *A. cambayensis* are slightly larger than those of *A. roselli*, especially the P_3. However, the molars are slightly smaller in *A. cambayensis* than in *A. roselli*. The metaconid of the P_4 is well-developed in *A. roselli*, whereas it is absent or small in *A. cambayensis*. Moreover, the P_3 in *A. cambayensis* is higher than the P_4, whereas in *A. roselli* they are similar in height. Regarding the molars, *A. cambayensis* shows a well-marked paraconid in the M_1 and a small cuspid in some M_2 and M_3 (see Rose et al., 2009) whereas in *A. roselli* the paraconid is faint in the M_1 and absent in the M_2 and M_3. The cristid obliqua is curved in *A. roselli* (and therefore the talonid basin has a somewhat rounded outline), and straight in *A. cambayensis*. In general, the buccal cingulid in *A. roselli* is stronger than in *A. cambayensis.*

Marcgodinotius indicus from Vastan Mine (Bajpai et al., 2005) shares some features with *A. roselli* such as a closed and deep trigonid basin in the M_2 and M_3 or a deep talonid basin in all the lower molars. However, they differ in some traits such as the larger size of *A. roselli*. The P_4 of *M. indicus* lacks a paraconid and only one specimen shows a very small metaconid, whereas in *A. roselli* there is a distinct paraconid and a prominent metaconid. In the lower molars, the trigonid is slightly longer in *M. indicus* than in *A. roselli*. The trigonid basin is open lingually in the M_1 of *M. indicus* whereas it is closed in *A. roselli*. Moreover, *M. indicus* shows a small paraconid in some M_1 and M_2, while in *A. roselli* a minuscule paraconid is only present in the M_1. The protocristid in the M_1 and some M_2 of *M. indicus* is slightly more oblique to the lingual and buccal sides than in *A. roselli.* The difference in width between trigonid and talonid is much more marked in *A. roselli* than in *M. indicus.* The cristid obliqua, postcristid, and preentocristid of *A. roselli* are more curved than those of *M. indicus*, and therefore the outline of the talonid basin is more rounded. The buccal cingulid is more marked in *A. roselli* than in *M. indicus.*

Body Mass Estimation

The body mass of *Agerinia roselli* was already estimated by Conroy (1987), who calculated a weight between 376 and 466 g. However, that study was based only on the area of the M_1. A later work by Egi et al. (2004) considered other dental elements for body mass estimation and, in addition, excluded larger-sized primates from the equations, thus making them more suitable for the estimation of body mass in small- and medium-sized fossil primates. Therefore, a new estimation of the body size of *A. roselli* has been developed following this latter work.

According to Egi et al. (2004), the first and second molars are the best elements for body mass estimations in small samples of fossil primates (the correlation coefficient between the area of these dental elements and the body mass is very high in living prosimians: $R=0.971$ for M_1 and $R=0.986$ for M_2). Following these authors, the body mass of *Agerinia roselli* has been estimated based on the area (mesiodistal length x buccolingual width) of the two available M_1 and the four available M_2. Using the M_1 and M_2 prosimian equations of Egi et al. (2004), the body mass of *A. roselli* falls within the range from 650 to 725 g for the M_1 (Fig-
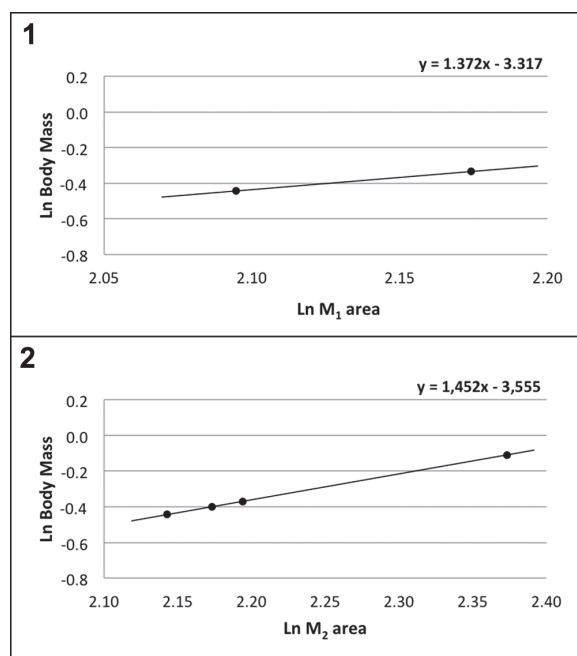
FIGURE 4. Body mass estimate regressions for *Agerinia roselli*. **1**, derived from the area of the M_1; **2**, derived from the area of the M_2. Black dots represent different molars of *A. roselli*. Black line indicates regression based on extant prosimian data from Egi et al. (2004).

ure 4.1) and from 644 to 900 g for the M_2 (Figure 4.2). Therefore, the body mass of *A. roselli* can be estimated to range from 650 to 900 g approximately, similar to that of living strepsirrhines such as the Sunda slow loris (*Nycticebus coucang*) or the Ankarana sportive lemur (*Lepilemur ankaranensis*).

DISCUSSION

The Spanish site Les Saleres, type locality of *Agerinia roselli*, has yielded the most abundant material attributed to this genus up to now, including the previously published material and the new remains described here for the first time. The description of the entire hypodigm has improved the knowledge about the dental anatomy of this species, including some features that have not been observed until now.

One of the most important characters previously undescribed for this species is the presence of two roots mesial with respect to the P_3 observed in the mandible fragment IPS-2543, which could belong to single-rooted P_1 and P_2 or to a double-rooted P_2. Since the presence of four premolars

has previously been interpreted as a primitive character for adapiforms, the fact that *A. roselli* could present single-rooted P_1 and P_2 would represent a solid argument for distinguishing it from other adapiforms such as *Darwinius masillae*. Moreover, the single-rooted P_2 would represent an advanced character in comparison with other cercamoniines such as *Donrussellia, Asiadapis,* or *Pronycticebus gaudryi*, all of them having double-rooted P_2. If this was the case, the P_1 would be markedly shifted towards the buccal side of the mandible, occupying a much more buccal position than the rest of the premolars. Such an arrangement of the premolars has been described in other early primates such as *Teilhardina*, which shows a reduction of the size of the P_1 and a displacement of this premolar towards the buccal side from older to younger species, being this premolar lost in the most recent forms (Smith et al., 2006).

If the two roots correspond to a double-rooted P_2, it would present a very oblique orientation with respect to the mesiodistal axis of the mandible. In this case, it would be similar to other cercamonines like *Mazateronodon endemicus* that has imbricated third and fourth premolars obliquely oriented (Marigó et al., 2010) or *Marcgodinotius indicus*, which shows an oblique double-rooted P_2 (Rose et al., 2009). However, the obliquity of the P_2 would be even more marked in *A. roselli* than in *M. indicus*.

In order to discern between these two possibilities, several radiographs of the specimen IPS-2543 have been made, with different voltages ranging from 50 to 80 kV. The radiograph in which the image is clearer, corresponding to a voltage of 75 kV, is presented in Figure 5. This radiograph clearly shows the roots of P_3 and P_4, which in both cases are long and divergent, but the two mesial roots cannot be distinguished, probably due to the preservation of the specimen. However, the space between the mesial root of the P_3 and the most mesial fragment of root, the end of which is directed backwards and reaches a very low position (Figure 5.2), seems to be not enough to house another root of the same length (as it would be expected if the two fragments of roots correspond to a double-rooted P_2, with two roots divergent and similar in length, like those of the P_3 and P_4). It seems more likely that these fragments correspond to single-rooted P_1 and P_2, with roughly parallel (not divergent) roots, being the former slightly longer than the latter.

In any case, none of these two possibilities can be accepted or refused, and more, well-pre-
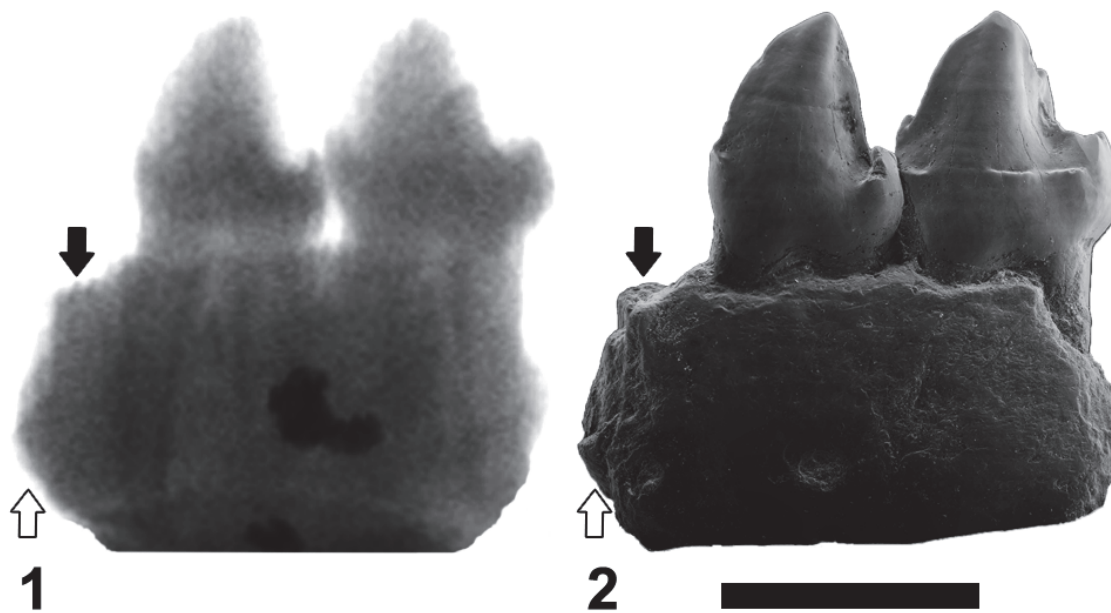
FIGURE 5. Radiograph represented with inverted colours (**1**) and ESEM micrograph (**2**) of the left mandible fragment of *Agerinia roselli* (IPS-2543) in buccal view. White arrows indicate the position of the most mesial root; black arrows indicate the position of the root immediately mesial with respect to the P_3. Scale bars represent 3 mm.

served material will be necessary to confirm the number of premolars of *A. roselli*. However, the presence of single-rooted P_1 and P_2 seem to be more plausible, because if the two roots correspond to a double-rooted P_2, it would present an unusual, extremely oblique orientation, very different to the mesiodistal alignment of P_3 and P_4.

Similarly, the morphology of the P_4 was not correctly described in previous works. The detailed observation of this premolar has led to the description of very small but distinct entoconid and hypoconid and a well-developed cristid obliqua, elements that were not depicted until now. In fact, the lack of a cristid obliqua in the P_4 was one of the criteria listed by Szalay (1971) in his generic diagnosis of *Agerinia*, but, as shown in Figure 2.1, this cristid is clearly distinct in the only known P_4 of *A. roselli*. Summarizing, the P_4 of this species shows better-differentiated cuspids than described by previous authors.

Regarding the lower molars, the redescription of the material from Les Saleres has also highlighted some features that were not described until now. Particularly, according to previous works (Crusafont-Pairó, 1967; Szalay, 1971; Szalay and Delson, 1979; Godinot, 2015) all the lower molars of *Agerinia* were characterized by the complete absence of a paraconid. Nevertheless, the detailed observation of the lower molars of *A. roselli* from Les Saleres has allowed distinguishing a very small paraconid in two specimens (IPS-82816 and 82793), here interpreted as M_1. This interpretation is reinforced by the fact that the specimens IPS-1891, 2541, 2542, and 82794, preserving their original position in the mandible and thus clearly identified as M_2, lack any trace of paraconid. This way, we propose the presence or absence of this small paraconid as the most reliable criterion for differentiating first and second lower molars when they are found isolated. Szalay (1971) used the length of the trigonid to distinguish these two elements, based on the fact that, like in many other primates, the trigonid is progressively shorter from M_1 to M_3. However, we have observed certain variability in the length of the trigonid in the M_2 from Les Saleres. Among the four undoubtedly identified M_2, specimens IPS-2541 and 82794 display a very short and wide trigonid, whereas IPS-1891 and 2542 show a relatively long and narrow basin. Moreover, the presence of a minuscule hypoconulid in some M_1 and M_2 was not noted in the descriptions made by Szalay (1971).

Concerning the phylogenetic affinities of *Agerinia*, Herbomel and Godinot (2011) suggested that it could be very close to *Darwinius* although, as stated by these authors, these interpretations are

tentative and must be tested with more detailed analyses of the teeth of *D. masillae*, as well as with further descriptions of still unpublished material of *Agerinia* from the Paris Basin. Our detailed study of the material of *A. roselli* from Les Saleres confirms the resemblance in overall morphology with *Darwinius*, although clear differences also exist. The scarcity of material of *Agerinia roselli* and, especially, the lack of upper teeth hinder a more precise analysis of the dental morphology of this species. Therefore, further fieldwork allowing the recovery of additional material is necessary for improving the knowledge about this species and clarifying its relationships with other Adapiformes.

CONCLUSIONS

New material of *Agerinia roselli* from its type locality, Les Saleres, has been described. In addition, the sample from this site published by Crusafont-Pairó (1967) and Szalay (1971) has been carefully redescribed, since some inaccuracies were noted in previous studies of this species. This new description is accompanied by more accurate dental measurements and high-resolution images of all the available teeth from Les Saleres. An emended diagnosis is provided, emphasizing some traits such as the P_3 and P_4 subequal in height, the P_4 with well-developed cuspids and crests, lower molars with short talonid basins and protocristid subperpendicular to the lingual and buccal borders, and paraconid very small in the M_1 and absent in the M_2 and M_3. The presence of two root fragments in a mesial position with respect to the P_3 could indicate either the existence of single-rooted P_1 and P_2 or the presence of a very obliquely oriented double-rooted P_2. More material would be necessary to confirm the number of premolars of this species.

Among the most significant characters of *Agerinia roselli*, the minuscule paraconid in the M_1 has been identified in this study for the first time. Indeed, the presence of a distinct paraconid on the M_1 is proposed as the most reliable criterion to discern M_1 from M_2 when they are isolated. Other criteria used for distinguishing M_1 from M_2, particularly the length of the trigonid, have been demonstrated to be less consistent due to the high intraspecific variability. Finally, the body mass estimation made for this species, based on the area of the M_1 and M_2, indicates a weight ranging from 650 to 900 g approximately, similar to that of the extant *Nycticebus coucang* or *Lepilemur ankaranensis* and larger than interpreted in previous studies.

Summarizing, this work delivers new valuable data on the species *Agerinia roselli* and highlights its differences with other Eocene Adapiformes. However, the dental anatomy of this species is still not well known, mainly due to the lack of upper teeth. Further studies, involving new fieldwork and allowing the recovery of additional material, will surely improve the knowledge about this primate, its paleobiology, and its phylogenetic relationships.

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