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New data on Mio-Pliocene Sciuridae (Rodentia, Mammalia) from southern Spain

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Abstract

Sciurids are very scarce in the fossil record, especially in the basins of southern Spain. The aim of this paper is to review the Sciuridae record in these basins. The Granada and Guadix basins have yielded specimens of Xerini and Pteromyinae, which represent the largest collection of fossil Sciuridae in southern Spain from the Middle Turolian to the Upper Ruscinian. The new discoveries change the currently known geographical and temporal range of some taxons, since we find the oldest evidence of *Pliopetaurista pliocaenica* in localities from the Late Turolian and of *Heteroxerus mariatheresae* in a locality of the Middle Turolian. Furthermore, we record the first evidence of *Atlantoxerus margaritae* in southern Spain. ***To cite this article: A. García-Alix et al., C. R. Palevol 6 (2007).***

Résumé

Nouvelles données sur les Sciuridae (Rodentia, Mammalia) mio-pliocènes du Sud de l'Espagne. Les Sciuridae fossiles, très rares dans les bassins du Sud de l'Espagne, constituent le sujet de ce travail. Les bassins de Grenade et de Guadix ont livré du matériel de Xerini et Pteromyinae, qui forment la plus grande collection de Sciuridae fossiles du Sud de l'Espagne pour l'intervalle Turolien moyen–Ruscinien supérieur. Les nouvelles découvertes modifient le registre géographique et chronologique de ces taxons. *Pliopetaurista pliocaenica* est maintenant connu au Turolien tardif et *Heteroxerus mariatheresae* au Turolien moyen. Par ailleurs, *Atlantoxerus margaritae* est documenté pour la première fois dans le Sud de l'Espagne. ***Pour citer cet article : A. García-Alix et al., C. R. Palevol 6 (2007).***

Keywords: Mio-Pliocene; Sciuridae; Granada Basin; Guadix basin; Spain

Mots clés : Mio-Pliocène ; Sciuridae ; Bassin de Grenade ; Bassin de Guadix ; Espagne

1. Introduction

This paper describes the Sciuridae from several Mio-Pliocene fossiliferous localities in the continental deposits of the Granada and Guadix basins, intramontane

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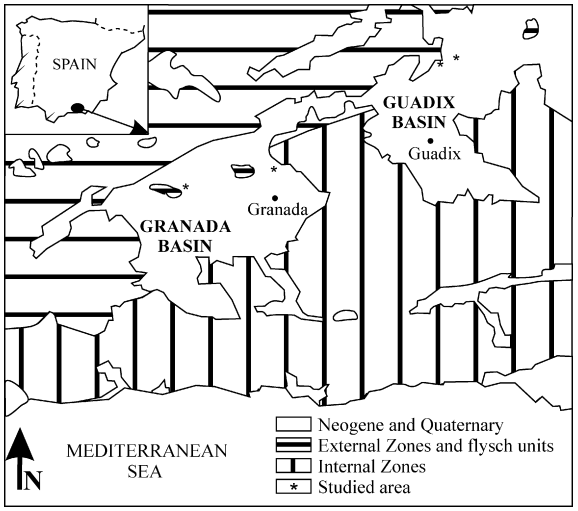

Fig. 1. Geographical and geological situation of Granada and Guadix basins and of the studied sections (after [4]).
Fig. 1. Situation géographique et géologique des bassins de Grenade et de Guadix, et des coupes étudiées (d'après [4]).

basins [4,11,19,20] situated in the central sector of the Betic Cordillera (southern Spain) (Fig. 1). Their Neogene and Quaternary sediments cover the contact between the Internal and External Zones of the Cordillera, and record a marine and continental history [11,14,19]. The marine infilling is Upper Miocene, and the continental phase began in the Latest Tortonian; in this last phase, alluvial, fluvial, and lacustrine systems are evolving in time and space [4,11,14,19,20].

The sections studied in the East of the Granada basin are those of Jun (locality JUN-2B, UTM: 30SVG479199), and Purcal (localities PUR-24A, UTM: 30SVG462219; PUR-25, UTM: 30SVG462219; PUR-4, UTM: 30SVG455217; PUR-13, UTM: 30SVG439217) (Fig. 1). In the western part of the basin, we have the section of Cerro del Águila (locality AGU-1C, UTM: 30SVG201165) (Fig. 1). The locality JUN-2B is Middle Turolian, PUR-24A, PUR-25 and AGU-1C are Upper Turolian, and PUR-4 and PUR-13 are Lower Ruscinian.

The sections studied in the Guadix basin are situated in its central part (Fig. 1). We have studied the sections of Gorafe (code GOR) and Tollo de Chiclana (code TCH), where we have found Ruscinian and Villafranchian localities, but only GOR-1 (Lower Ruscinian; UTM: 30SVG920510) and TCH-1B (Upper Ruscinian; UTM: 30SVG958552) contain fossil Sciuridae.

2. Methodology

The nomenclature used in the descriptions of the teeth of Sciuridae is that of de Bruijn [5] and Cuenca [9]; length and width have been measured as defined by van de Weerd [22] and amended by Reumer and van den Hoek Ostende [18]. In all cases, length and width are perpendicular. The measurements followed by a star are estimates because of the poor preservation state of the teeth.

Measurements were taken with a Wild M7S binocular microscope, equipped with a Sony Magnescale LM12 digital measuring device. The measurement data were processed by a computer program provided by the last author. Measurements are given in units of 1 mm. Photographs were made with the FEI ESEM QUANTA 400 of the 'Centro Andaluz de Medio Ambiente' (Granada, Spain). The specimens are kept in the Departamento de Estratigrafía y Paleontología de la Universidad de Granada, Spain.

3. Systematic palaeontology

Heteroxerus Stehlin and Schaub, 1951 is a medium-sized Xerini. It differs from *Atlantoxerus* Forsyth Major, 1893 mainly because the teeth of *Atlantoxerus* are larger than those of *Heteroxerus* are, and because the lower teeth of *Heteroxerus* usually have an anterior cingulum. *Heteroxerus* can be also distinguished by the absence of a mesostyle (except for some rare specimens of *H. grivensis*), which is usually present in *Atlantoxerus*, except in *A. adroveri*. The species of *Atlantoxerus* have higher crowns and cusps, more rounded conules and wider crests than *Heteroxerus* [9].

The teeth of *Pliopetaurista* Kretzoi, 1962 are large with sinuous crests; rugose surfaces are frequent. The upper teeth have a very well developed metaconule and metaloph and protoloph converge towards the protocone [15].

Order **Rodentia** Bowdich, 1821
Family **Sciuridae** Fischer von Waldheim, 1817
Subfamily **Sciurinae** Fischer von Waldheim, 1817
Genus ***Heteroxerus*** Stehlin and Schaub, 1951
Species ***Heteroxerus mariatheresae*** Adrover, Mein and Moissenet, 1993 (Fig. 2A)
Locality: JUN-2B
Material: 1 M^{1-2}

Description: M^{1-2} (1.83×2.33) with rectangular outline. The parastyle is slightly inflated. There is no mesostyle. Protocone and paracone are connected by the protoloph. There is no protoconule sensu stricto. Metacone and a large metaconule are connected by the metaloph, and the metaconule is in weak contact with the posteroloph. There are three roots.

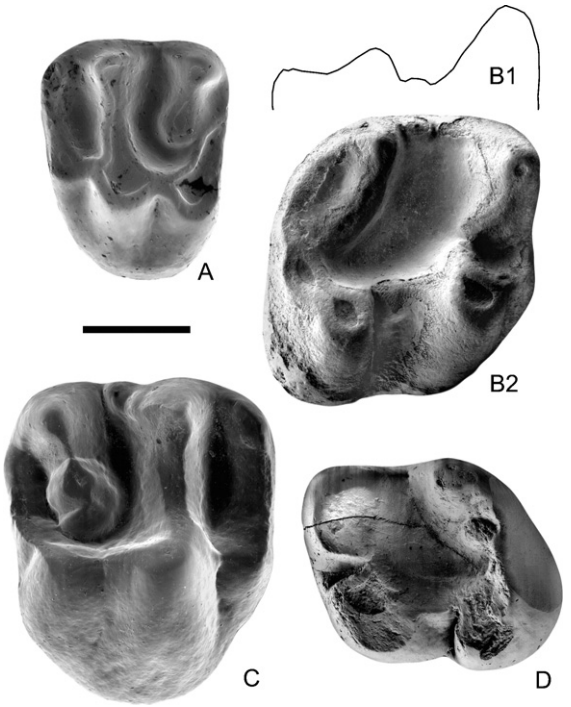

Fig. 2. *Heteroxerus mariatheresae* Adrover, Mein and Moissenet, 1993: **A**, left M^{1-2}, JUN-2B 33; *Atlantoxerus margaritae* Adrover, Mein and Moissenet, 1993: **B**, right M_{1-2}, PUR-13 217: **B1**, lingual view; **B2**, occlusal view; **C**, right M^{1-2}, GOR-1 1; **D**, left P_4, PUR-13 216. Scale bar: 1mm.

Fig. 2. *Heteroxerus mariatheresae* Adrover, Mein et Moissenet, 1993 : **A**, M^{1-2} g., JUN-2B 33 ; *Atlantoxerus margaritae* Adrover, Mein et Moissenet, 1993 : **B**, M_{1-2} d., PUR-13 217 : **B1**, vue linguale ; **B2**, vue occlusale ; **C**, M^{1-2} d., GOR-1 1 ; **D**, P_4 g., PUR-13 216. Échelle : 1 mm.

Discussion: Molars of *Atlantoxerus* are larger than the JUN-2B specimen is, and they usually have a mesostyle, except for *Atlantoxerus adroveri* (de Bruijn and Mein, 1968); however, *A. adroveri* differs from our specimen by its large size and by its outline. *Heteroxerus* is poorly represented since the Vallesian. The $M^{1,2}$ of *Heteroxerus grivensis* (Forsyth Major, 1893), the most similar Vallesian species, has usually a metaconule that is less developed than in our specimen, because the metacone is, in general, larger than the metaconule (in contrast with our specimen). The metaconule is frequently reduced to an inflated end of the metaloph in *H. grivensis*. Our specimen has no mesostyle, which is sometimes present in the M^{1-2} of *H. grivensis*. The parastyle is slightly more developed in our specimen. The outline of our M^{1-2} is more rectangular than that of *H. grivensis*.

Another Vallesian species, *H. molinensis* Lacomba, 1986, is larger than our specimen is, and the anterior contour of its M^{1-2} is different, due to the very lingual position of the anteroconule; that cusp is situated more labially in our M^{1-2}.

The shape and the size of our specimen are within the variation range of *H. mariatheresae* from the Turolian of Teruel (La Gloria-5). It resembles *H. mariatheresae*, among other features, in the degree of development of the metaconule, in the position and development of anteroconule and anteroloph, and in the absence of mesostyle and protoconule. Therefore, it is determined as *Heteroxerus mariatheresae*.

Genus ***Atlantoxerus*** Forsyth Major, 1893

Species ***Atlantoxerus margaritae*** Adrover, Mein and Moissenet, 1993 (Fig. 2B–D)

Localities: Purcal-13 (PUR-13) and Gorafe-1 (GOR-1)

Material: 1 P_4, 1 M_{1-2} and 3 M^{1-2}

Description: In the locality PUR-13, we find:

P_4 (2.49×2.03): Trapezoidal outline, wider posteriorly than anteriorly. Protoconid and metaconid are connected by a posterior metalophid and separated anteriorly by a narrow groove. The posterolophid is in contact with the entoconid, but the short entolophid is not. Two roots.

M_{1-2} (2.68×2.73): Worn and digested specimen. Sub-squared outline. The four main cusps and the hypoconulid are well developed; the mesoconid and the anteroconulid are less developed. The metalophid is continuous and low. There is a small depression enclosed by the anterolophid and the metalophid. There is a vestigial mesostylid. Four roots.

M^{1-2} (2.31×2.96*; 2.46×2.98): Sub-rectangular outline. The four main cusps, the anteroconule and the metaconule are well developed. The anteroconule is labially displaced and not aligned with protocone and hypocone. Metaconule and metacone have the same size. Metaconule and posteroloph are in weak contact. There is no protoconule. The complete posteroloph is parallel to the metaloph. There is a little inflation in the mesostylar crest, forming a reduced mesostyle. Three roots.

Discussion: The M^{1-2} from GOR-1 (2.63×3.15) is very similar to the PUR-13 specimens; it only differs in being a little larger, and having a medium-sized mesostyle.

The studied specimens are larger than those of *Heteroxerus*, *A. cuencae* Aguilar, Calvet and Michaux, 1995, and *A. martini* Aguilar, 2002, and smaller than *Atlantoxerus huvelini* Jaeger, 1977.

The size of the specimens is close to the lower values of *Atlantoxerus tadlae* (Lavocat, 1961) from the Middle Miocene locality of Beni-Mellal [12], but the

mean values are smaller. Our specimens have a complete metalophid in the lower molars, whereas it is interrupted in *A. tadlae*; the posteroloph is weakly connected to the metaconule in our M^{1-2}, and isolated in *A. tadlae.*

Peláez-Campomanes and Aguilar [2,16] considered *Atlantoxerus idubedensis* Cuenca, 1988 to be a synonym of *A. blacki* (de Bruijn, 1967); the teeth of the populations that were ascribed to *A. idubedensis* are smaller than ours. The size of our teeth is close to *A. blacki* (not considering *A. idubedensis*), and *A. rhodius* de Bruijn, Dawson and Mein, 1970. Our lower teeth have a complete metalophid, which forms a closed depression together with anterolophid and anteroconule; the complete metalophid and this closed depression are not present in *A. blacki*. In our material, the valley of the talonid is less developed and the crests are wider than in *A. rhodius*; our P_4 has a metalophid and an entolophid, which are not observed in *A. rhodius*.

Our material resembles most *Atlantoxerus adroveri* and *A. margaritae*. The size of the specimens from PUR-13 is within the upper range of *A. adroveri* from its type locality [8] and of the most abundant samples of this species studied by van de Weerd [22] (Los Mansuetos and Concud-3, among others), except for the length of P_4, which exceeds the values given by van de Weerd [22]. *A. adroveri* from the type locality Los Mansuetos [8] is, in general, smaller than the M^{1-2} from GOR-1; our single specimen is longer than those studied by van de Weerd [22], and its width agrees with the upper range of the M^{1-2} from Teruel [22]. The size of the specimens from PUR-13 and GOR-1 agrees with that of *A. margaritae*. The posterolophid of the P_4 of *A. adroveri* does not join the entoconid [8], so it has a lingually open valley between entoconid, entolophid and posterolophid, whereas in our material, and in the three P_4 of *A. margaritae* from Teruel [1], the posterolophid is in contact with the entoconid, and closes this valley. There is no mesostylid in the M_{1-2} of *A. adroveri* [8], but our specimens and those of *A. margaritae* from Teruel (17 specimens) do have a small one [1]. The metalophid of the M_{1-2} of *A. adroveri* is interrupted [8], so the depression between anterolophid and metalophid is open; in our specimens and in those of *A. margaritae* from Teruel [1], the metalophid is continuous and this depression is closed. Our P_4 and those of *A. margaritae* from Teruel (three specimens) have a reduced and wide entolophid [1]. The upper molars of *A. margaritae* from Teruel [1] and ours have a mesostyle or mesostylar crest, which is absent in *A. adroveri* [8]. The comparison with *A. margaritae* from La Gloria-4 is based on material deposited in the Departamento de Estratigrafía y Paleontología of Granada University. On the basis of these features, we determine our molars as *A. margaritae.*

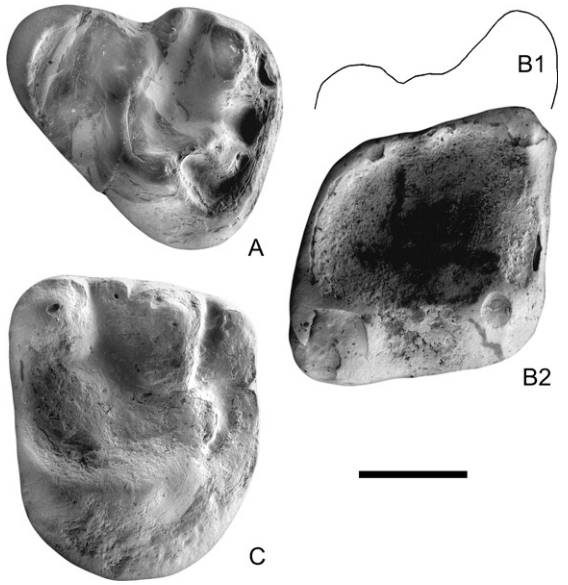

Fig. 3. *Atlantoxerus* cf. *margaritae* Adrover, Mein and Moissenet, 1993: **A**, left D^4, PUR-4 939; **B**, right M_{1-2}, PUR-4 944: **B1**, lingual view; **B2**, occlusal view; **C**, right M^{1-2}, PUR-4 942. Scale bar: 1 mm.

Fig. 3. *Atlantoxerus* cf. *margaritae* Adrover, Mein et Moissenet, 1993 : **A**, D^4 g., PUR-4 939 ; **B**, M_{1-2} d., PUR-4 944 : **B1**, vue linguale ; **B2**, vue occlusale ; **C**, M^{1-2} d., PUR-4 942. Échelle : 1 mm.

Species ***Atlantoxerus* cf. *margaritae*** Adrover, Mein and Moissenet, 1993 (Fig. 3)

Locality: Purcal-4 (PUR-4)

Material: 1 M_{1-2}, 2 D^4, and 2 M^{1-2}

Description of the material from PUR-4: M_{1-2} (2.34×2.70*). One can only recognize the four main cusps and the shallow depression of the talonid, because the specimen is much worn. There is a reduced mesostylid and four roots.

D^4 (2.69×2.26): The parastyle is separated from paracone and protocone by a wide valley. The protocone is large, connected to the paracone by a long protoloph. There is a mesostyle. Metacone and metaconule are separated, or interconnected by a low crest, and each of them is in contact with the posteroloph through a low crest. Roots are not preserved.

M^{1-2} (2.38×2.85; 2.35×2.89*): Subrectangular outline. One specimen is worn, the other one digested. There is a large mesostyle and a large and lingually displaced protoconule. A large metaconule seems to connect with the posteroloph by a low crest. Three roots.

Discussion: Our specimens are larger than those of *Heteroxerus*, *A. cuencae* and *A. martini* are, and smaller than those of *Atlantoxerus tadlae* and *Atlantoxerus huvelini* are.

Atlantoxerus blacki, *A. rhodius* and *A. adroveri* are similar in size to our material; the size of the specimens from PUR-4 is in the lower range of *A. adroveri*; our specimens are similar in size or slightly smaller than those of *A. rhodius*. The populations attributed to *A. idubedensis* by Cuenca, 1988 have smaller teeth than ours. The main differences are found in M^{1-2}: our specimens have a very well developed protoconule, which is displaced forward, whereas, in the other species, it may be reduced or absent, and not displaced forward; our specimens also have a large mesostyle.

The upper molars of *A. margaritae* have the same shape as our specimens (M^{1-2} subrectangular with parallel anterior and posterior borders), a mesostyle, and a large metaconule. The M_{1-2} has a reduced mesostylid too. However, our specimens differ from *A. margaritae*, and from the other species mentioned above, by a very well developed and forward displaced protoconule; moreover, the D^4 from PUR-4 has a more prominent parastyle than in *A. margaritae*. This parastyle is similar to that of the D^4 of *Atlantoxerus* cf. *margaritae* II from Villalba Alta [1]. Our specimens are smaller than those of *A. margaritae* from La Gloria-4 [1], PUR-13 and GOR-1, and similar to those from Orrios-1, Orrios-B, and La Judería [1]. The comparison with *A. margaritae* from La Gloria-4 is based on material deposited in the Departamento de Estratigrafía y Paleontología of the Granada University. The specimens from PUR-4 resemble *A. margaritae*, but the material is scarce and badly preserved; we identify it as *Atlantoxerus* cf. *margaritae*.

Species ***Atlantoxerus*** sp.

Material: 1 D^4 and 1 M^{1-2}

One D^4 from PUR-24A (2.17×2.31) and one not measurable fragment of M^{1-2} from AGU-1C cannot be identified at the species level.

Subfamily **Pteromyinae** Brandt, 1855

Genus ***Pliopetaurista,*** Kretzoi, 1962

Species ***Pliopetaurista pliocaenica*** (Depéret, 1897) (Fig. 4A–E)

Localities: Purcal-24A (PUR-24A), Purcal-25 (PUR-25) and Purcal- 4 (PUR-4).

Material: 1 P_4, 1 M_{1-2}, 1 D^4, 3 M^{1-2} and 1 M^3

Description: In PUR-24A, we have found one M^3 (3.13×2.84). A weak anteroloph connects anterocone with paracone. The parastyle is absent. Paracone and protocone are very well developed. The high protoloph delimits two closed depressions with rugose surface. There is a weak mesostyle. The endoloph has a rugose lingual face and connects anteroconule, protocone, and hypocone. Three roots.

PUR-25 has yielded a non-measurable fragment of M_{1-2}; one may observe the protoconid, mesoconid, hypoconid, part of the entoconid and a large mesoconid. There is no hypoconulid. The bottom of the central depression is rugose. Roots are not preserved.

In PUR-4, we have found one fragment of P_4, one D^4, and two M^{1-2}.

P_4: Only the posterior part is preserved. The bottom of the central depression is rugose. There is a vestigial hypoconulid. The posterolophid is wide. Roots are not preserved.

D^4 (2.54×2.55): Sub-triangular outline. Parastyle and anteroloph are connected. A deep and open valley separates parastyle and protoloph. The large and high protocone is connected with the paracone by a slightly curved protoloph. There are a large mesostyle and a mesostylar crest. The metacone is larger than the metaconule; they are connected by a low and curved crest and their bases connect with the posteroloph. Metaconule and protocone are connected by a low and curved crest. Hypocone and posteroloph are low. Roots are not preserved.

M^{1-2} (2.91×3.14; $2.86 \times$ –) Only one specimen is complete; it has a sub-rectangular outline. The parastyle is connected to the paracone by a low and narrow crest. There is a mesostylar crest with an inflation (mesostyle) joined to the paracone. There is a sinuous protoloph. A low crest connects the large metacone and the metaconule, each of which is connected independently to the posteroloph; the metaconule connects with the protocone too. The hypocone is present. There are two main depressions: one delimited by anteroloph–protoloph, and the other one delimited by metacone–metaconule–protoloph. There are three smaller depressions, delimited by the crests that connect metacone–metaconule–posteroloph. The bottom of these depressions and the lingual face of the molar are rugose. Roots are not preserved.

Discussion: These specimens are characteristic for the subfamily Pteromyinae: large teeth with many sinuous accessory crests that give a labyrinthic appearance. The convergence of the lophs and the very well developed metaconule in the upper teeth are typical features of *Pliopetaurista* [15].

The size of our material is larger than that of other Neogene species of *Pliopetaurista* from Europe: *P. bres-*

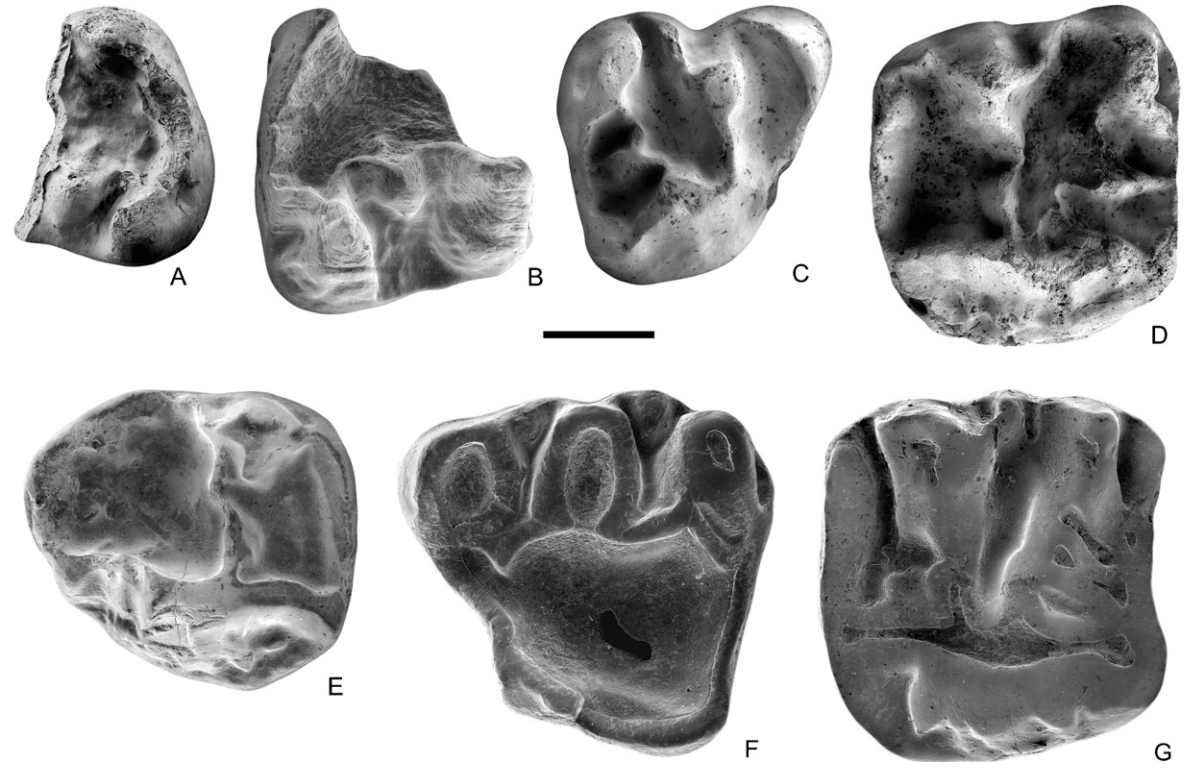

Fig. 4. *Pliopetaurista pliocaenica* (Depéret, 1897): **A**, left P_4, PUR-4 938; **B**, right M_{1-2}, PUR-25 73; **C**, right D^4, PUR-4 941; **D**, left M^{1-2}, PUR-4 945; **E**, right M^3, PUR-24A 117; *Pliopetaurista* cf. *pliocaenica* (Depéret, 1897): **F**, left P^4, TCH-1B 612; **G**, left M^{1-2}, TCH-1B 613. Scale bar: 1 mm.

Fig. 4. *Pliopetaurista pliocaenica* (Depéret, 1897) : **A**, P_4 g., PUR-4 938 ; **B**, M_{1-2} d., PUR-25 73 ; **C**, D^4 d., PUR-4 941 ; **D**, M^{1-2} g., PUR-4 945 ; **E**, M^3 d., PUR-24A 117 ; *Pliopetaurista* cf. *pliocaenica* (Depéret, 1897) : **F**, P^4 g., TCH-1B 612 ; **G**, M^{1-2} g., TCH-1B 613. Échelle : 1 mm.

sana Mein, 1970 from its type locality (Soblay) [15] and from the Austrian locality of Eichkogel [10], *P. dehneli* Sulimski, 1964 from Wèze-1 [21] (type locality), Rebielice Królewskie [3], Hautimagne [15], Maramena [6] and Wèze-2 (personal comparison with specimens in Coll. Mein, Lyon-1 University), *P.* cf. *dehneli* from Podlesice [3] and *P. meini* Black and Kowalski, 1974 from Zalesicki (type locality) [3] (Fig. 5). The record of *P. rugosa* Qui, 1991 from Mongolia is very poor. The upper teeth of *P. rugosa* have no mesostyle, are shorter, wider and their cones are larger than in our material.

In Serrat d'en Vacquer, the type locality of *P. pliocaenica*, no upper teeth are preserved, but we have compared with other populations. The size and the main features of our material agree with *P. pliocaenica* from La Gloria-2, Desvío and Arquillo-3 [1], Wölfersheim [15] and Ivanovce (personal comparison with specimens in Coll. Mein, Lyon-1 University). The M_{1-2} from PUR-25 cannot be measured, but its estimated size is close to *P. pliocaenica's* one.

Although size and morphology are quite variable in the genus *Pliopetaurista*, especially in *P. pliocaenica* [1], some features are more developed in *P. pliocaenica* and less developed or absent in *P. dehneli* (the most similar species in size and morphology to *P. pliocaenica*), like the hypocone, the parastyle, the mesostyle or the mesostylar crest, and the hypoconulid [15]; moreover, the size of *P. pliocaenica* is larger than that of *P. dehneli* [6,15]. Our material shares these characteristics, so we determine it as *P. pliocaenica*.

Species ***Pliopetaurista* cf. *pliocaenica*** (Depéret, 1897) (Fig. 4F–G)

Locality: Tollo de Chiclana-1B (TCH-1B)

Material: 1 D_4, 1 P^4 and 3 M^{1-2}

Description: The specimens are very damaged.

D_4 ($2.33 \times$ –): Digested specimen. High and fused metaconid and protoconid. A curved posterolophid connects entoconid and hypoconid. A reduced mesoconid is present. The degree of wear impedes the observation of entolophid and hypoconulid. Roots are not preserved.

P^4 (3.46×3.29): Worn specimen. The lingual border is shorter than the labial one. A large parastyle that is

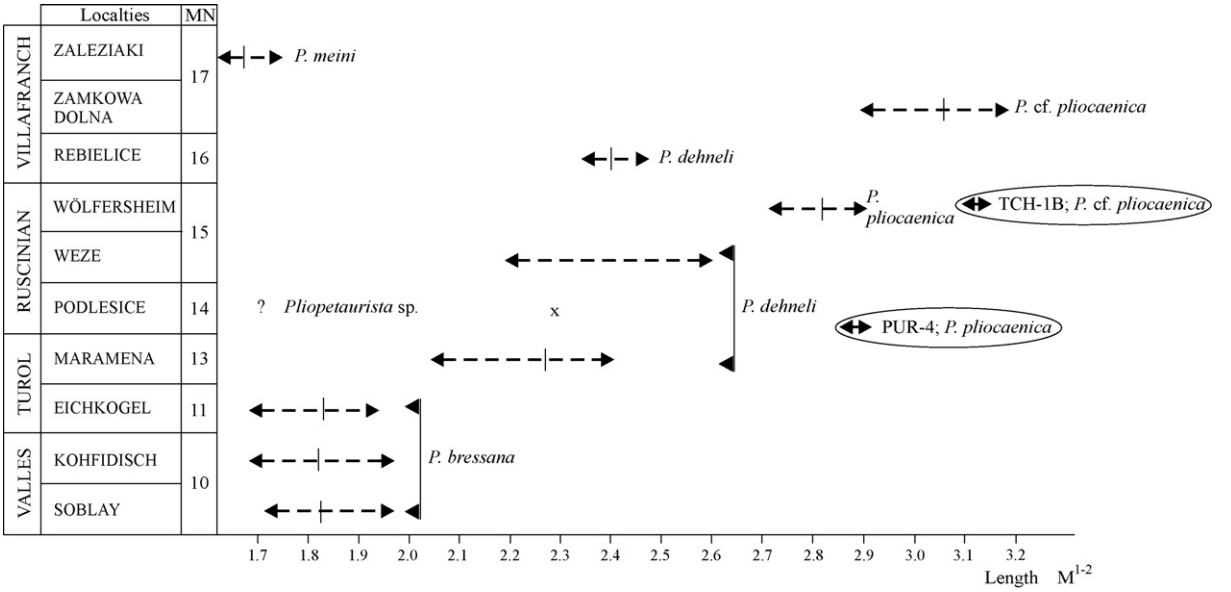

Fig. 5. Size variation of the length of M^{1-2} of different species of *Pliopetaurista* throughout the Neogene. Modified after [6].
Fig. 5. Variation de la longueur de M^{1-2} chez plusieurs espèces de *Pliopetaurista* au Néogène. D'après [6], modifié.

similar in size to the paracone and the metacone protrudes over the outline of the molar. The parastyle has a small postero-labial cusp and a low crest that connects with the paracone. There is a mesostylar crest and a large mesostyle that protrudes over the outline of the molar. Metacone, paracone and posteroloph are connected by broad crests. Due to wear, protocone, hypocone, and metaconule cannot be observed. Three roots.

M^{1-2} (3.09×3.48; 3.15×3.41; $- \times 3.54$): Subrectangular outline. The parastyle is separated from the paracone and much inflated. Large and high paracone and metacone. There is a mesostylar crest with a distinguishable mesostyle that protrudes over the outline of the molar. The metacone is connected with the metaconule and the posteroloph. The large and triangular metaconule is connected with the posteroloph and the protocone by a crest. Hypocone and protocone are large and there is a small anteroconule. The endoloph has a rugose lingual face. The hypocone is present. As in the specimens from PUR-4, there are two main depressions and three smaller ones, but all of them are attenuated due to wear. There are three roots with rugose face.

Discussion: Our specimens are larger than those of other European species of *Pliopetaurista* (*P. bressana*, *P. dehneli*, and *P. meini*). The upper teeth of the Asiatic, *P. rugosa*, are shorter, wider and their cones are larger than in TCH-1B. However, the main difference of the specimens from TCH-1B is the very much developed mesostyle sensu stricto in P^4, and its presence in M^{1-2}. The main features of our material (hypoconulid, large hypocone, large parastyle and mesostyle) are very similar to *P. pliocaenica*. These features are absent or less developed in *P. dehneli*. The main difference with *P. pliocaenica* is that our material is larger; the M^{1-2} from TCH-1B are larger than the ones from Wölfersheim [15], Ivanovce (personal comparison with specimens in Coll. Mein, Lyon-1 University), La Gloria-2, Desvío, Arquillo-3 [1] and PUR-4 (Figs. 5 and 6). On the other hand, their size is similar to that of *P.* cf. *pliocaenica* from Zamkowa Dolna [3] and Escorihuela-B [1] (Figs. 5 and 6).

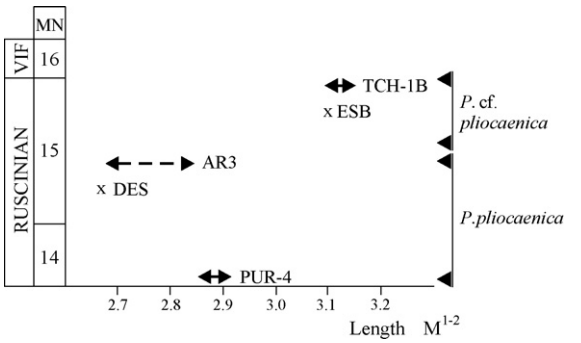

Fig. 6. Size variation of the length of M^{1-2} of different species of *Pliopetaurista* from Spanish localities. DES, Desvío; AR-3, Arquillo-3; ESB, Escorihuela-B [1]. The length of the M^{1-2} from La Gloria-2 [1] is not taken into account, because it is damaged.
Fig. 6. Variation de la longueur de M^{1-2} de plusieurs espèces de *Pliopetaurista* dans les gisements espagnols. DES, Desvío ; AR-3, Arquillo-3 ; ESB, Escorihuela-B [1]. La longueur de la M^{1-2} de La Gloria-2 [1] est omise, puisqu'elle est endommagée.

Table 1
Chronostratigraphic scheme of different species of *Pliopetaurista*. Modified after [6]. *P. pliocaenica* in light grey shading, *P*. cf. *pliocaenica* in dark grey shading
Tableau 1
Schéma chronostratigraphique des différentes espèces de *Pliopetaurista*. D'après [6], modifié. *P. pliocaenica* sur fond gris clair, *P*. cf. *pliocaenica* sur fond gris foncé

	Spain	France	Central Europe	Eastern Mediterranean	Asia
Villafranchian			***P. meini*** ZALEZIAKI ***P.* cf. *pliocaenica*** ZANK. DOLNA		
Ruscinian	***P.* cf. *pliocaenica*** TCH-1B ***P.* cf. *pliocaenica*** ESCORIHUELA B ORRIOS 3 CEMENTERIO ***P. pliocaenica*** ARQUILLO-3 LA GLORIA-2 ***P. pliocaenica*** PUR-4	***P. pliocaenica*** PERPIGNAN ***P. dehneli*** HAUTIMAGNE	***P. pliocaenica*** WÖLFERSHEIM ***P. dehneli*** WEZE ***P. dehneli/P.* sp.** PODLESICE		
Turolian	***P. pliocaenica*** PUR-25/PUR-24A	***P.* cf. *bressana*** MOLLON	***P. bressana*** EICHKOGEL	***P. dehneli*** MARAMENA ***P. bressana*** DÜZYAYLA	***P. rugosa*** ERTEMTE
Vallesian		***P. bressana*** SOBLAY	***P. bressana*** KOHFIDISCH	***P. bressana*** LEFKON	

The M^{1-2} from TCH-1B have a mesostyle sensu stricto that protrudes over the molar outline, clearly more developed than in *P. pliocaenica* from Wölfersheim [15], Arquillo-3 [1] and PUR-4. The single M^{1-2} of *P*. cf. *pliocaenica* from Escorihuela-B [1] also has a mesostyle sensu stricto [1]; these authors noted that the M^{1-2} of *P*. cf. *pliocaenica* from Escorihuela-B and Orrios-3 have an 'isolated mesostyle'; they did not refer to a cusp that is completely isolated from the mesostylar crest, but they referred to an individualized or distinguishable cusp, which may have a connection with the mesostylar crest. We emphasize this point because the figured specimen of M^{1-2} from Orrios-3 [1] has a well-developed mesostyle that may have a connection with the mesostylar crest. These specimens of *P*. cf. *pliocaenica* have a mesostyle sensu stricto, in contrast with the inflated mesostylar crest in the M^{1-2} of *P. pliocaenica*. *Pliopetaurista pliocaenica* from PUR-4, Wölfersheim [15], La Gloria-2, Desvío and Arquillo-3 [1] is older than *P*. cf. *pliocaenica* from TCH-1B and Escorihuela-B [1] (see Table 1). Because of these differences, we determine this material as *Pliopetaurista* cf. *pliocaenica*. The scarce and poorly preserved material does not allow more precision.

4. Remarks about the genera *Heteroxerus* and *Atlantoxerus*

Atlantoxerus and *Heteroxerus* are ground squirrels. The record of these genera in the Turolian (Upper Miocene) is very scarce and discontinuous. In the Lower and Middle Miocene, the record is more complete and some phylogenetic hypotheses have been established [2,9]. *Heteroxerus* is present in Europe since the Late Oligocene [7,9]. *Atlantoxerus* appears in the Iberian

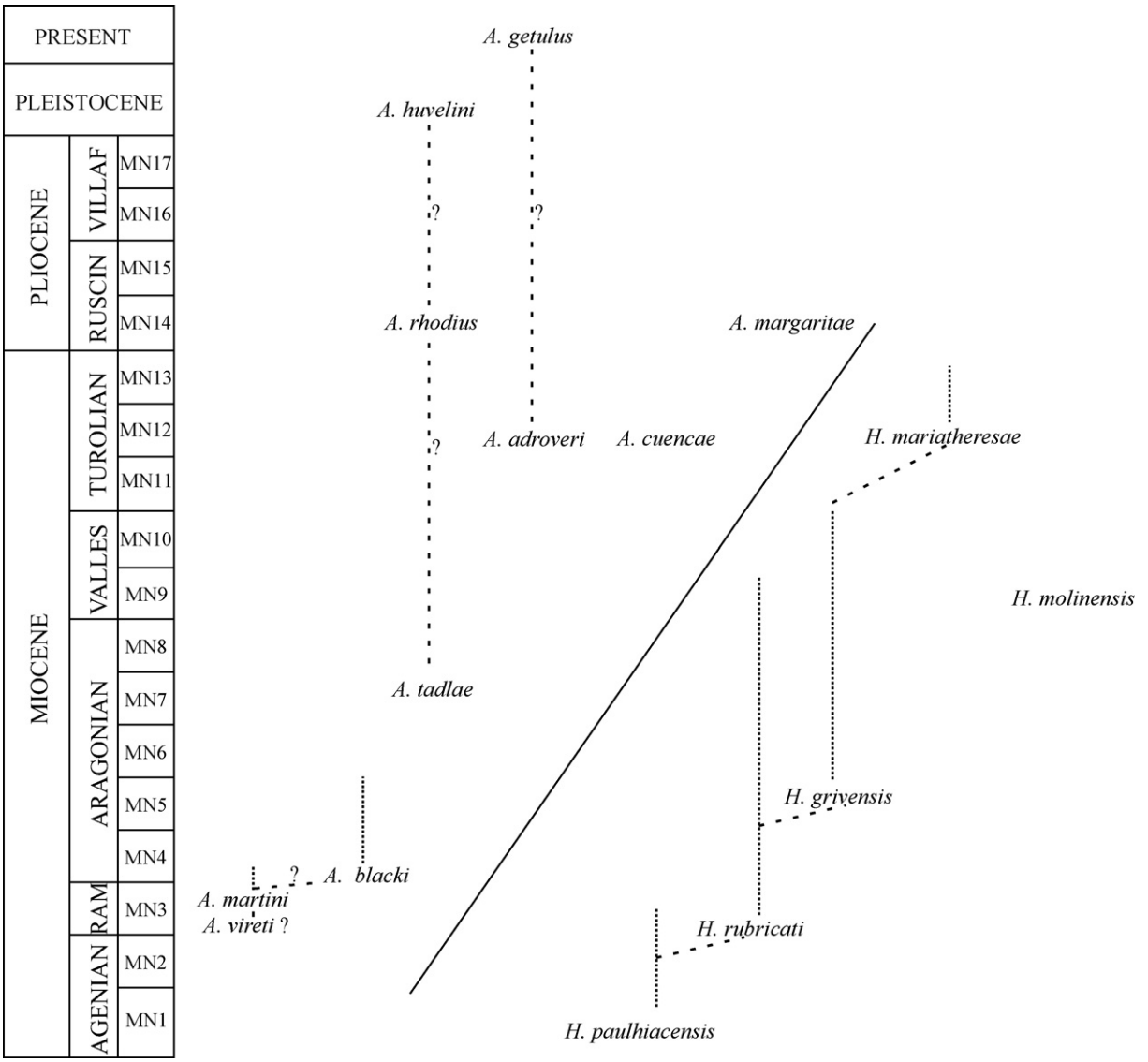

Fig. 7. Phylogenetic scheme of Miocene and Pliocene *Atlantoxerus* and *Heteroxerus* after Jaeger [12], Cuenca [9], Lacomba Andueza [13], Aguilar [2], Adrover et al. [1], and data of this study.
Fig. 7. Schéma phylogénétique des *Atlantoxerus* et *Heteroxerus* miocènes et pliocènes d'après Jaeger [12], Cuenca [9], Lacomba Andueza [13], Aguilar [2], Adrover et al. [1] et les données du présent travail.

Peninsula in the Aragonian (MN4) [2,7,9], but it is present in France in MN3 [2]. The oldest record is from the Agenian of China (MN1) [17]; apparently, it is an immigrant that reaches France before the Iberian Peninsula; however, the absence in Spain in MN2 may be due to a lack of data.

There is an ancestor–descendant relationship between *Heteroxerus paulhiacensis–H. rubricati–H. grivensis* [9], and *H. mariatheresae* from La Gloria-5 (Upper Turolian) is the youngest representative of this lineage [1] (Fig. 7). The specimens from the Granada basin extend the register of *H. mariatheresae* to the end of Middle Turolian.

Heteroxerus vireti and *H. rubricati* were considered synonyms [9], but according to Aguilar [2], *H. vireti* from the French locality of Estrepouy must be classified as *Atlantoxerus vireti*, the predecessor of *A. martini* (Fig. 7). *Atlantoxerus martini* may be the ancestor of *A. blacki* [2], which has no relationship with younger species [12]. *Atlantoxerus idubedensis* and *A. blacki*, as said above, are considered as synonyms [2,16]. *Atlantoxerus tadlae* (Middle Miocene), *A. rhodius* (Mio-Pliocene boundary)

and *A. huvelini* (Lower Pleistocene) are ancestors, and descendants [12] (Fig. 7).

Atlantoxerus margaritae is only known in the Lower Ruscinian of the Teruel [1] and Granada basins; it occupies an indeterminate position in the phylogeny of *Atlantoxerus* [1] (Fig. 7), and it does not seem to be related with *A. adroveri*, because the mesostyle is not present in *A. adroveri*. The phylogenetic relationships of *A. adroveri* are not clear either; it might be related with the extant species, *A. getulus* [12] (Fig. 7), but until now no intermediate record is known.

5. Remarks about the genus *Pliopetaurista*

The genus *Pliopetaurista* belongs to the subfamily Pteromyinae. They are giant flying squirrels, forest dwellers that plane between trees.

Pliopetaurista shows a great variability in size and morphology. There are two lineages that may have a common origin in *Forsythia* or *Pliopetaurista bressana* [3,6]. The first line includes the small forms, which are only known from Poland [6]: *Pliopetaurista* sp. from Podlesice and *P. meini* from Zaleziaki (see Fig. 5). The species of the second line *P. bressana–P. dehneli–P. pliocaenica* show a tendency to size increase [6,15], and have a large geographic distribution [6] (see Figs. 4 and 5). *Pliopetaurista rugosa* from the Upper Turolian of Mongolia represents a central Asiatic branch of this group [6]. In the locality of Podlesice, two species of *Pliopetaurista* coexist: *Pliopetaurista* sp. (small size), and *P. dehneli* (large size) [3] (see Table 1 and Fig. 5).

This scheme is complicated due to the record of *P. pliocaenica* from the Granada Basin, in the localities of PUR-24A, PUR-25 (Upper Turolian) and PUR-4 (Lower Ruscinian), which are contemporaneous with central and eastern European localities containing *P. dehneli* (see Table 1 and Fig. 5). This finding constitutes the oldest record of *Pliopetaurista* in the Iberian Peninsula, and the oldest record of *P. pliocaenica* in Europe; it extends the biogeographic range of the genus to the South of the Iberian Peninsula.

As we said above, the lineage of *P. bressana–P. dehneli–P. pliocaenica* shows an increase of size through time [6,15]. Within *P. pliocaenica*, size increases too, and we find the biggest teeth of *Pliopetaurista* in localities like Escorihuela-B (Teruel, Spain, MN15) [1], TCH-1B (Guadix, Spain, MN15), and Zamkowa Dolna, (Poland, MN17) [3]; these are usually determined as *P.* cf. *pliocaenica*.

The oldest record of a large *Pliopetaurista* is from the Granada Basin (Mio-Pliocene boundary). The mesostyle is more developed in *P. pliocaenica* than in *P. dehneli* [6]. The M^{1-2} of *P. pliocaenica* from PUR-4, Wölfersheim [15], La Gloria-2, Desvío, Arquillo-3 [1], have apparently a less developed mesostyle than those of *P.* cf. *pliocaenica* from Escorihuela-B [1] and TCH-1B. The mesostyle in *P. pliocaenica* is reduced to an inflated mesostylar crest or a protuberance in this crest, whereas in *P.* cf. *pliocaenica* from Escorihuela-B and TCH-1B, it is a well-distinct cusp that protrudes over the outline of the teeth, and may have a connection with the mesostylar crest. There are no references to the mesostyle of *P.* cf. *pliocaenica* from Zamkowa Dolna [3].

We agree with de Bruijn [6] in that the evolution of *P. pliocaenica* towards *P.* cf. *pliocaenica* is marked by size increase. The apparent increase in the development of the mesostyle from the oldest populations of *P. pliocaenica* to the youngest ones of *P.* cf. *pliocaenica* should be corroborated by a more complete record. The new data show that the larger-sized specimens of *Pliopetaurista* are recorded first in Spain (*P. pliocaenica* in PUR-24A, PUR-25 and PUR-4 from the Mio-Pliocene boundary; *P.* cf. *pliocaenica* in Escorihuela-B and TCH-1B from the Upper Ruscinian), and afterwards in the rest of Europe (see Table 1), whereas in contemporaneous central and eastern European localities (see Table 1), *P. dehneli* (in localities from the Mio-Pliocene boundary) and *P. pliocaenica* (in localities of the Latest Ruscinian) are present. Therefore, *P. pliocaenica* and *P.* cf. *pliocaenica* in Central Europe might be immigrants from the Iberian Peninsula.

6. Conclusions

The record of Sciuridae at the Mio-Pliocene boundary is very scarce, and although our material is poor too, it constitutes the most complete record of fossil Sciuridae in the South of Spain, with five species that have never been found before in this area.

The new data extend the record of *H. mariatheresae* to the Middle Turolian and enlarge its geographic range to the South of Spain. The biostratigraphic record of *A. margaritae* is extended to the Lower Ruscinian of the South of Spain, where it coexists with another lineage, which is represented in the Lower Ruscinian locality PUR-4 (*A.* cf. *margaritae*).

The appearance of *P. pliocaenica* at the Mio-Pliocene boundary of the Granada Basin extends the biostratigraphic record of *P. pliocaenica* to the Upper Turolian and Lower Ruscinian; this constitutes the oldest occurrence of the species, and its first record in the South of Spain. *P.* cf. *pliocaenica,* which is larger than *P. pliocaenica*, is recorded in other Upper Ruscinian

localities of Spain. We suppose an emigration of these forms to Central Europe in two waves: one between the Mio-Pliocene boundary and the Late Ruscinian and another one during the Late Ruscinian and/or the Early Villafranchian.

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