



New data on *Paenelimnoecus* from the middle Miocene of Spain support the shrew subfamily Allosoricinae

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***Limnoecus truyolsi* was long considered an enigmatic shrew. Additional material from the Calatayud-Montalbán Basin (Spain) shows it to be referable to the genus *Paenelimnoecus*. The species represents an intermediate form between *P. micromorphus* and *P. crouzeli*. This lineage confirms the separate development of the “soricine” p4, and thus supports the Allosoricinae as a separate subfamily.**

Introduction

Baudelot (1972) erected the genus *Paenelimnoecus* for a small shrew, *P. crouzeli*, from the French locality of Sansan (Neogene Mammal Zone MN 6). She placed the genus in the Limnoecinae, an American subfamily of shrews, which are characterized by a reduced entoconid on lower molars. The presence of this subfamily in the European record had already been suggested by Doben-Florin (1964), who described *Limnoecus micromorphus* from the locality of Wintershof-West (Germany, MN 3). Other finds were also included in this American genus, such as *Limnoecus truyolsi* Gibert, 1975, and *Limnoecus* sp. (Ziegler and Fahlbusch 1986). Engesser (1979), however, argued that none of the European taxa could be assigned to the Limnoecinae. A year later, he described two *Paenelimnoecus* finds in his overview of the insectivores from Turkey (Engesser 1980), assigning the genus to the Soricinae. Reumer (1984) concurred with this subfamily assignment, and placed it into the tribe Allosoricini, which had earlier been proposed by Fejfar (1966) as a subfamily. Reumer (1984) transferred two more species to *Paenelimnoecus*, *Petenyiella? repenningi* Bachmayer and Wilson, 1970 and *Pachyura pannonica* Kormos, 1934. Ziegler (1989) transferred *Limnoecus micromorphus* to the genus, and argued that *Paenelimnoecus* was best placed in the Crocidosoricinae.

The difficulties of assigning *Paenelimnoecus* to a subfamily were mainly caused by the morphology of the p4, which plays an important role in the taxonomy of the Soricidae. The problem is that the oldest representative of *Paenelimnoecus*, *P. micromorphus*, retains p4 with a Y-shaped wear facet, as is found in Crocidosoricinae. Younger species are characterized by a reduced posterolingual arm, resulting in a p4 with a labial crest and a posterolingual basin, as found in Soricinae. Reumer (1992) resolved this situation by resurrecting the Allosoricinae, assuming that the development of the p4 in this subfamily paralleled the evolution of the Soricinae. Reumer (1992) also in-

cluded the finds of Ziegler and Fahlbusch (1986), described as *Limnoecus* sp., in the genus *Paenelimnoecus*.

In his description of *Paenelimnoecus obtusus* from China, Storch (1995) classified the genus as Soricinae incertae sedis. Ziegler (2003) also preferred to place *Paenelimnoecus* in the Soricinae. Jin and Kawamura (1997) described a second species from China, *P. chinensis*.

Fejfar et al. (2006) suggested that *Paenelimnoecus* developed separately from *Allosorex*, and was better classified in a subfamily of its own, Paenelimnoecinae.

Apart from the matter of the subfamilial assignment, one loose end remained. All European species previously assigned to *Limnoecus* were transferred to *Paenelimnoecus*, with the exception of *L. truyolsi*. Ziegler (1989) considered it unlikely that “*Limnoecus*” *truyolsi* is referable to *Paenelimnoecus*. Reumer (1994: 354), also putting the genus name in quotation marks, considered the species of “uncertain taxonomic affiliation”. Furió et al. (2007) suggested that it could be an intermediate form linking the Crocidosoricinae with the Soricinae, if not already a Soricinae itself, but indicated that further research was needed.

The type locality of *L. truyolsi*, Villafeliche 4 (which was designated 4B, after a lower level at the same site was sampled), is in the Calatayud-Montalbán Basin (Spain). Gibert (1975b) listed the presence of the species in the nearby localities of Valdemoros 3B and Las Planas 4A. Since its description, the Calatayud-Montalbán Basin has become one of the best-sampled areas for micromammal fossils in the world (e.g., Daams et al. 1999), and includes the type sections for both the Ramblian and the Aragonian continental stages. Allosoricine finds from the basin are rare, but given the proximity to the type locality of *Limnoecus truyolsi*, any additional specimens could help elucidate the affinities of this puzzling species.

The material reported herein was collected in the Calatayud-Montalbán Basin (Spain) between 1975 and 1997 by Spanish/Dutch expeditions teams in varying compositions, involving the Universidad Complutense de Madrid, Museo Nacional de Ciencias Naturales-CSIC (Madrid), Utrecht University and Naturalis (Leiden). All localities are situated in the Villafeliche area (Aragonian type area), except for Moratilla 2, which is in the Calamocha area (Ramblian type area) (Fig. 1). The material from Vargas 1 and Villafeliche 4A is stored at RGM, that from San Marcos, Moratilla 2, Vargas 7 and Valdemoros 6B at MNCN, and the type specimen from Villafeliche 4B at ICP. The photo-

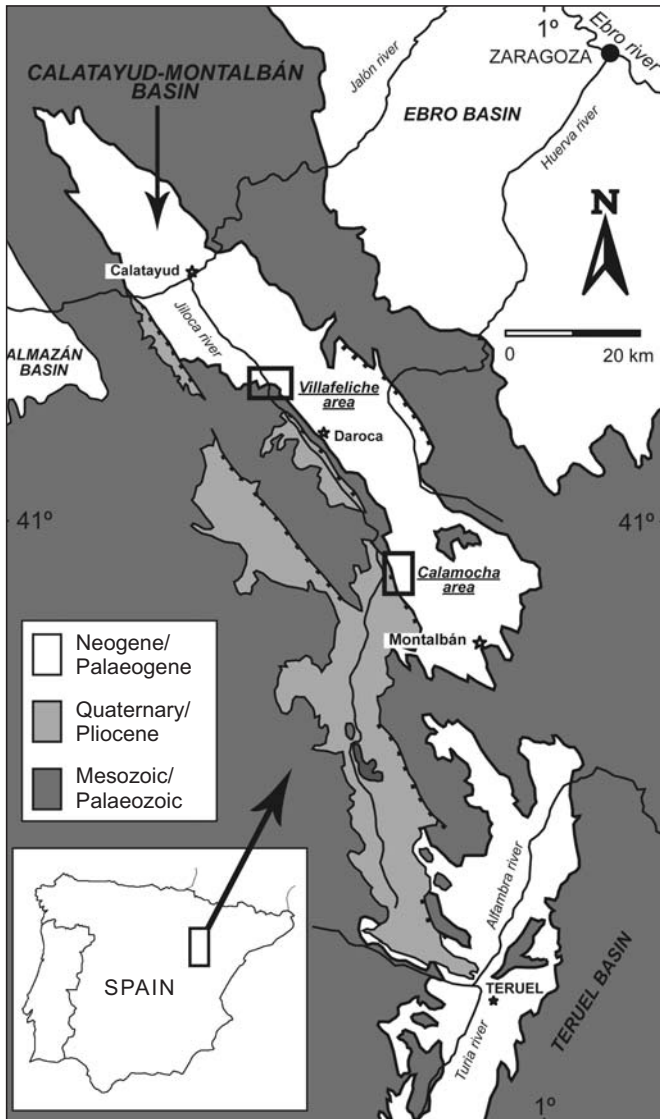


Fig. 1. Location of the Calatayud-Montalbán Basin in Spain and synthetic geology of the region. Areas for studied localities (Villafeliche area and Calamocha area) are indicated with square marks. Modified after Álvarez Sierra et al. (2003).

graphs of specimens (Fig. 2) were made on the Environmental Scanning Electron Microscope FEI Quanta 200 in environmental mode at the MNCN. In order to facilitate comparison, all specimens have been figured as left ones and at the same scale; hence, Fig. 2B and Fig. 2D are reversed.

Measurements follow Reumer (1984), and are given in millimetres. The three measurements for lower molars are length, trigonid width and talonid width, respectively. Also following Reumer (1984) the degree of posterior emargination of the M1 and M2 is determined by the so-called PE-ratio, and classified according to his categories. The local biozones (and their correlation to the MN zonation) and numerical ages assigned for the faunas are after Daams et al. (1999).

Institutional abbreviations.—ICP, Institut Català de Paleontologia (formerly IPS), Barcelona, Spain; MNCN, Museo Nacional

de Ciencias Naturales, Madrid, Spain (the temporary numbers for the MNCN collections consist of the locality acronym followed by "T" and specimen number); RGM, Naturalis, Leiden, The Netherlands.

Systematic palaeontology

Soricomorpha Gregory, 1910

Soricidae Fischer von Waldheim, 1817

Allosoricinae Fejfar, 1966

Genus *Paenelimnoecus* Baudelot, 1972

Paenelimnoecus truyolsi (Gibert, 1975)

Material and measurements.—See Table 1.

Description.—Only the material from the largest assemblage, Moratilla 2, has been described in detail. The p4 has been described separately, since this element is only known from the holotype (Villafeliche 4B).

M2 is known by one specimen. The molar is only somewhat wider than long; the posterior emargination is moderate ($PE = 0.17$). The labial margin is undulating. The largest part of the molar is occupied by the labial cusps, which cover more than two-thirds of the occlusal surface. The protocone is rather small. The hypocone is reduced to a low ridge, completely fused with the posterior ridge that borders the molar at the back. The paracone is somewhat lower and smaller than the metacone. The mesostyle is undivided. There is a strong cingulum along the posterior arm of the metacone. The tips of the labial cusps show sign of discoloration.

The first lower molar is known by two specimens. The trigonid is somewhat longer and narrower than the talonid. The paralophid is long, the protolophid rather short. The trigonid basin is wide. The oblique cristid ends at the middle of the protolophid. The entoconid is low and positioned clearly in front of the posterolingual corner of the molar. It is completely fused with the entocristid, which ends high against the metaconid. The hypolophid is short and slopes abruptly down just short of the posterolingual corner of the m1. The anterior cingulum is strong. The straight labial cingulum and posterior cingulum are somewhat less developed. The lingual cingulum is connected to the hypolophid by a faint ridge. This cingulum is poorly developed in one specimen, well developed in the other.

The second lower molar is represented by four specimens. The trigonid is as long as or shorter than the talonid, and has the same width. The paralophid is only somewhat longer than the protolophid. The oblique cristid ends against the middle of the protolophid. The entoconid is somewhat lower than in the m1, and unlike in the first molar the entocristid retains the same height throughout. The hypolophid slopes down just short of the posterolingual corner of the molar, continuing as a faint ridge connected to the lingual cingulum. The cingulum is well developed to strong on all sides of the m2.

The m3 is known by two specimens. The trigonid strongly resembles that of the m2. The talonid is much reduced, particularly in the posterolingual area. The only structures remaining

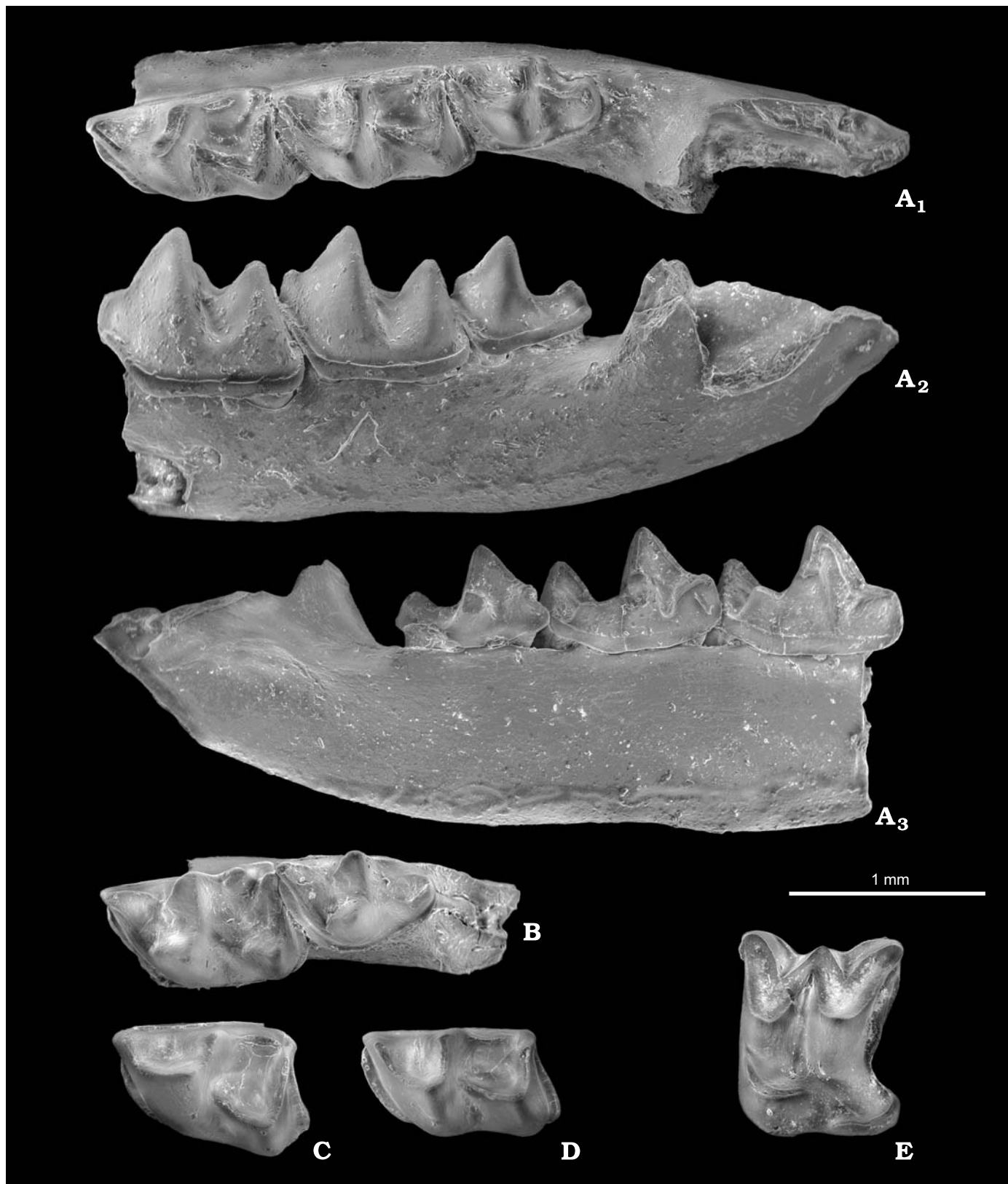


Fig. 2. Allosoricin shrew *Paenelimoecus truyolsi* (Gibert, 1975). **A.** Left mandible with m1, m2, m3 (MNCN Mo2 I 46) from middle Miocene locality Moratilla 2, Spain, in occlusal (A₁), labial (A₂), and lingual (A₃) views. **B.** Right mandible with m2, m3 (RGM 410431) from middle Miocene locality Villafeliche 4A, Spain, in occlusal view (reversed). **C.** Im1 (MNCN VA6B I 5) from middle Miocene locality Valdemoros 6B, Spain, in occlusal view. **D.** rm2 (RGM 410298) from middle Miocene locality Vargas 1A, Spain, in occlusal view (reversed). **E.** IM2 (MNCN Mo2 I 56) from middle Miocene locality Moratilla 2, Spain, in occlusal view.

Table 1. Measurements of *Paenelimnoecus truyolsi*.

Zone	Locality	Specimen number	Figure	Element	Measurements
Zone Dd	Valdemoros 6B	MNCN VA6B I 5	Fig. 2C	lm1	1.09 × 0.60 × 0.58
Zone Dc	Villafeliche 4A	RGM 410431	Fig. 2B	right mandible with m2, m3	1.08 × 0.66 × 0.66; 0.84 × 0.56 × 0.42
		IPS 9007 (holotype)		right mandible with p4, m1, m2	0.61 × 0.50; 1.03 × 0.60 × 0.66; 0.96 × 0.63 × 0.64
	Vargas 7	MNCN VR7 I 31		right mandible with m1	1.00 × 0.55 × 0.62
		MNCN VR7 I 32		right mandible with m2, m3	1.05 × 0.62 × 0.64; 0.82 × 0.49 × 0.43
Zone Db	Moratilla 2	MNCN Mo2 I 44		right mandible with m1, m2	1.09 × 0.62 × 0.69; 1.03 × 0.69 × 0.69
		MNCN Mo2 I 45		right mandible with m1 (broken), m2	1.02 × 0.64 × 0.69
		MNCN Mo2 I 46	Fig. 2A ₁ –A ₃	left mandible with m1, m2, m3 (damaged)	1.06 × 0.58 × 0.62; 0.99 × 0.68 × 0.68
		MNCN Mo2 I 47		left mandible with m2, m3	1.05 × 0.62 × 0.66; 0.86 × 0.51 × 0.47
		MNCN Mo2 I 56	Fig. 2E	IM2	0.89 × 1.12
Zone C	Vargas 1A	RGM 410298	Fig. 2D	lm2	1.03 × 0.65 × 0.73
Zone B	San Marcos	MNCN SAM I 83		rm1	1.13 × 0.63 × 0.65

are the hypoconid and the oblique cristid, which ends against the middle of the protoconid-metaconid crest. The cingulum is strong on the anterior and labial sides, somewhat less developed on the lingual side.

The p4 (from Villafeliche 4B) is asymmetrical, the lingual side being shorter than the labial side. The main cusp only shows a single, short posteriorly-directed crest, which deviates labially near its end. The premolar has one root.

The material from the other localities shows no major differences with the Moratilla 2 assemblage. On the m1 from Valdemoros 6B, the hypolophid is curved and ends behind the entoconid, which appears to be more reduced than in the other assemblages. The San Marcos m1, in contrast, shows a straight hypolophid, which ends closer to the posterolingual corner than in the younger localities.

Discussion

The morphology of the new finds agrees well with that of *Limnoecus truyolsi* Gibert, 1975 (type locality Villafeliche 4B). None of the lower elements, which are fossilised dark reddish brown to black, show any signs of pigmentation, but the M2 from Moratilla 2, which is much lighter in colour, does show a discoloration at the tips of the cusps. All the measured elements are somewhat larger than the values originally indicated in Gibert (1975a). Re-examination of the holotype showed that this must have been a result of difference in measuring techniques, as our new measurements for the type are similar to those of the other material.

Limnoecus truyolsi has been considered a problematic species. Ziegler (1989) argued against including it in *Paenelimnoecus*, based on the clear presence of an entoconid in the illustration of the holotype (Gibert 1975: pl. 2: 1). Indeed, a reduced entoconid is present in our material, but its development seems

comparable to that of the entoconid/entocristid in the photographs in Ziegler's article (Ziegler 1989: pl. 5: 4, 5). Besides, even the much younger *P. repenningi* (Bachmayer and Wilson, 1970) still retains remnants of an entoconid. The M2 from Moratilla 2 also closely resembles the one assigned to *Paenelimnoecus* by Ziegler (1989: pl. 5: 6). Therefore we think that "*L. truyolsi*" is indeed referable to *Paenelimnoecus*.

Placing the Spanish species in *Paenelimnoecus* raises the question as to whether it can be distinguished as a separate species, or should be considered synonymous with any of the other species. Two species come into consideration, the somewhat older *P. micromorphus* (Doben Florin, 1964) (known from MN 3 and MN 4 in southern Germany), and the somewhat younger *P. crouzeli* (Baudelot, 1972) (type locality Sansan, France, MN 6). The latter, like all younger species in the genus, has completely lost the entoconid and entocristid. *Paenelimnoecus micromorphus* and *P. truyolsi* are very close indeed. The main difference is the p4, which in *P. micromorphus* still has the "crocidorsicine" morphology, with a V-shaped wear facet, whereas in *P. truyolsi* the lingual arm has reduced, leaving a "soricine" morphology, as is also found in *P. crouzeli*. Another difference in the p4 according to the description of *P. micromorphus* and the examination of the holotype of *P. truyolsi* is that the latter has only one root, whereas two roots are present in *P. micromorphus*. Baudelot (1972) described the p4 of *P. crouzeli* as having one root. Ziegler (1989) assumed this was a mistake, pointing out that the specimen from Sansan figured by Engesser (1980: fig. 74c) clearly has an alveolus for the anterior root of the p4. Later descriptions of *P. crouzeli* from fissure filling in southern Germany revealed that a tiny anterior root is indeed present (Ziegler 2003).

Another matter of uncertainty is the presence or absence of original pigmentation. Gibert (1975a) indicated that the molars of *P. truyolsi* are pigmented, as Baudelot (1972) did for *P. crouzeli*. An original pigmentation for *P. crouzeli* was considered doubtful

by Engesser (1979), who found no trace of pigmentation in seven specimens from the type locality Sansan in the Basel Museum. The Moratilla 2 assemblage shows that it is indeed possible to have pigmentation preserved in one specimen, whereas it cannot be detected in the others (unfortunately, the type material was coated for SEM-photography by Gibert (1975a), so its original pigmentation could not be ascertained). Furthermore, Ziegler (2003) found pigmentation in the *P. crouzeli* material from Petersbuch 6 (Germany, MN 7/8), but not in the material from any of the other fissure fillings. This shows once more that the presence/absence of pigmentation in fossil soricid molars is difficult to judge. The absence of such pigmentation cannot be taken as absence in the living animal. The presence of discoloration in part of the material can be seen as an indication of original pigmentation, but here too, one needs to be careful. Considering the many indications that species of *Paenelimnoecus* had an original pigmentation, we assume that such pigmentation was indeed present.

Although the differences with *Paenelimnoecus micromorphus* are small, for the moment it is best to retain *P. truyolsi* as a separate species. Having already developed a *P. crouzeli*-like p4, while retaining a small entoconid/entocristid complex, it forms a perfect intermediate between *P. micromorphus* and *P. crouzeli*, both in morphology and stratigraphic occurrence. Finding the strongest reduction of the entoconid/entocristid in our youngest occurrence fits well with the trend, although no conclusions can be drawn based on a single specimen only. The absence of an anterior root on p4 in the holotype of *P. truyolsi*, present in *P. micromorphus* and *P. crouzeli* is problematic, but more material is needed to assess the variability in this character.

Closing the gap between *Paenelimnoecus micromorphus* and *P. crouzeli* strengthens the allocation to a separate subfamily Allosoricinae, as suggested by Reumer (1992). The ongoing reduction of the entoconid-entocristid complex in combination with a shift from a crocidosoricine to a soricine type p4 is well documented. We concur with Ziegler (2003) that the reduction of the entoconid is certainly not limited to the Allosoricinae. However, his suggestion to place *Paenelimnoecus* in the Soricinae would imply that that subfamily is polyphyletic, the soricine p4 also being developed separately within the genus *Paenelimnoecus*.

The subfamily Paenelimnoecinae is based on the assumption that the middle Miocene “*Sorex*”*gracilidens* Viret and Zapfe, 1951 is closely related to the Pliocene genus *Allosorex*, thus representing a lineage separate from *Paenelimnoecus* (Fejfar et al. 2006). The middle Miocene shrew shows a similar carnassial adaptation as *Allosorex*, that is, an elongated paralophid on the m1. However, other than that there is little to suggest a relationship between these taxa that are separated by millions of years, “*S.*”*gracilidens* still having a crocidosoricine p4 and retaining the entoconids and entocristids. We therefore prefer a more conservative classification, placing both *Paenelimnoecus* and *Allosorex* in the Allosoricinae. Should they be shown not to represent a single clade, the clear roots in the Crocidosoricinae would be better expressed by placing *Paenelimnoecus* in a separate tribe within that subfamily, rather than creating a monotypic subfamily for it.

The allosoricine record in the Calatayud-Montalbán Basin is quite patchy. The oldest find of *Paenelimnoecus* are from San

Marco (Zone B, 16.70 Mya) and Vargas 1A (Zone C, 16.14 Mya). Most other finds are from Zone D. From oldest to youngest these are Moratilla 2 (Zone Db, 15.81 Mya), Villafeliche 4A and Villafeliche 4B (Zone Dc, 15.51 and 15.50 Mya, respectively), Valdemoros 3B (Zone Dc, 14.85 Mya), Vargas 7 (Zone Dc, 14.84 Mya), and Valdemoros 6B (Zone Dd, 14.40 Mya). Gibert (1975b) also mentioned the presence in Las Planas 4A (Zone E, 13.96). At first sight this record resembles that of another shrew taxon, the Anourosoricini, in the Spanish upper Miocene of the Teruel Basin (Van Dam 2004). The latter pattern was explained as being climatically controlled, the shrews only entering the Iberian Peninsula when conditions were favourable.

The explanation for the patchiness in the case of the allosoricine record from the Calatayud-Montalbán Basin, however, is probably more mundane. First of all, one has to consider that insectivores over all are pretty rare. In this particular timeframe, they constitute less than 5% of the overall fauna, and the chances of finding *Paenelimnoecus* are already slim to begin with. Moreover, although some localities were washed using a mesh size of 0.5 mm, the mesh size was changed to 0.7 mm when no small rodents were expected (Daams and Freudenthal 1988). Since no Eomyidae are present in Zone D, most of the localities from this zone were washed with the larger mesh size, and isolated molars of small shrews may have been lost. In this context, it is noteworthy that, except for the m2 from Valdemoros 6B, all of the specimens of *Paenelimnoecus* were preserved in mandible fragments. Nevertheless, the presence of single molars only in the very large assemblages from San Marcos and Vargas 1 (N Mm1/Mm2 > 2000), suggests that Allosoricinae were indeed rare in the Villafeliche area. The high number of specimens found in the much smaller assemblage from Moratilla 2 can be considered as a sign of differences in the palaeoenvironment between the Villafeliche and Calamocha areas. Given the small distance (~25 km) between the sections (Fig. 1), this suggests a rather patchy landscape during the early middle Miocene.

Acknowledgements

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