# The porcupine *Hystrix suevica* Schlosser, 1884 from the Lower Turolian of Crevillente 2 (Spain)

### Plinio Montoya

Montoya, P. The porcupine *Hystrix suevica* Schlosser, 1884 from the Lower Turolian of Crevillente 2 (Spain). — Scripta Geol., 103: 135-149, 7 figs., Leiden, April 1993.

The fossil record of the genus *Hystrix* is rather scarce, and little is known about its origin. Its presence in Crevillente 2, a well-dated Lower Turolian (MN11) Spanish locality, is an important fact because, from a stratigraphic point of view, it is one of the oldest references of this genus.

The comparative study of the remains from Crevillente 2 reveals the presence of a small species, *Hystrix suevica*, which lived in Europe from Middle Aragonian to Early Turolian time. In most recent revisions of the genus *Hystrix*, this species has not been taken into account. *H. suevica* shows undeniable morphological affinities with *H. primigenia*. The latter was a large-sized *Hystrix*, which spread over Europe from Middle Turolian to Late Pliocene time, reaching Africa at the end of the Turolian.

The geographic distribution patterns of the family Hystricidae allow to relate its regression in Europe with the progressive climatic cooling, which started c. 2.5 Ma ago.

P. Montoya, Departament de Geologia (Area de Paleontologia), Facultat de Biologia, Universitat de València, Dr. Moliner 50, E-46100 Burjassot, Spain.

Key words: Hystrix, Late Miocene, Spain.

135
137
139
143
146
147

## Introduction

The Lower Turolian locality of Crevillente 2 (de Bruijn et al., 1975; Alcalá et al., 1987) is situated on the territory of Crevillente (Province of Alicante, Spain).

Geologically, this area belongs to the Segura-Vinalopó Basin. From this area a great number of micromammal sites, all of Turolian age, have been described (Montenat, 1973, 1977; de Bruijn et al., 1975; Freudenthal et al., 1991a).

Crevillente 2 is the oldest of these sites and the only one with a relatively rich macromammal assemblage. The vertebrate fauna list, from Alcalá & Montoya (1989-1990), Freudenthal et al. (1991b), Montoya et al. (in press), and personal communications by Freudenthal and Martín-Suárez, is established as follows:

Amphibians: Rana perezi.

Reptilians: Eusuchia indet., Anguidae indet., Ophisaurus sp., Lacerta sp., Dracaenosaurus sp., Vipera sp., cf. Naja sp., Cheirogaster sp., Testudo sp. Birds: Anatidae indet.

Mammals: Occitanomys sondaari, Parapodemus lugdunensis, Huerzelerimys vireti, Hispanomys peralensis, Neocricetodon occidentalis, Eliomys truci, Muscardinus sp., Heteroxerus sp., Hystrix suevica, Desmanella sp., Prolagus sp., Indarctos atticus, Mustelidae indet., Plioviverrops guerini, cf. Adcrocuta sp., Amphimachairodus giganteus, Paramachairodus ogygia, Microstonyx major, Dorcatherium naui, Eostyloceros aff. pierensis, Cervidae indet., Birgerbohlinia schaubi, Tragoportax gaudryi, Hipparion mediterraneum, Dicerorhinus schleiermacheri, Deinotherium giganteum, Tetralophodon longirostris.

The micromammals of this locality have been studied by de Bruijn et al. (1975) and Freudenthal et al. (1991b), the macromammals by Montenat & Crusafont (1970), Alcalá et al. (1987), Alberdi & Montoya (1988), Cerdeño (1988), Azanza (1989), Montoya & Morales (1991), and van der Made et al. (1992).

So, Crevillente 2 is one of the few Lower Turolian sites with an abundant fauna of both micro- and macromammal species. Therefore, in most recent reviews of the continental biochronology of the Mediterranean Neogene, Crevillente 2 is considered as the reference locality for zone MN11 (Mein, 1990; de Bruijn et al., 1992).

In a previous paper, concerning the taphonomy of this bonebed (Montoya, 1990), porcupine activity had been noted, clearly proven by the presence of bone and dental remains with gnawed edges, common marks caused by porcupine incisives. So, *Hystrix* was considered as one factor more of observed bioturbation in the fossil assemblage.

In this paper, *Hystrix* remains from Crevillente 2 are described and compared. The studied material consists of two partial dental series and an isolated tooth fragment. No postcranial elements, that might be assigned to *Hystrix* have been found up till now. A paleobiogeographic historical interpretation of the family Hystricidae is proposed.

### Acknowledgements

I am grateful to Esteban José Sánchez and Jordi Guillem for their help in the elaboration of the text, and to Matthijs Freudenthal and Jorge Morales for their critical review of it. Dolores Soria and Salvador Moyà have provided me with useful data on several aspects related to this paper.

## Taxonomy

Order RODENTIA Bowdich, 1821 Family HYSTRICIDAE Burnett, 1830 Genus Hystrix Linnaeus, 1758

Hystrix suevica Schlosser, 1884

1884 Hystrix suevica n. sp. — Schlosser, p. 46, pl. 7, fig. 27 1902 Hystrix suevica Schlosser — Schlosser, p. 138, pl. 1, figs. 10, 11, 15, 24. 1970 Hystrix cf. H. suevica Schlosser — Bachmayer & Wilson, p. 579.

Type locality — Häder (Germany).

Age — Aragonian (MN5).

Other localities — Salmendingen (MN10?), Kohfidisch (MN10), Crevillente 2 (MN11).

*Diagnosis* — Small-sized *Hystrix*; moderately brachyodont teeth with individualized roots; four well-developed synclines in  $M^2$  and  $M^3$ ; synclinid I in the lower dentition not individualized and very little developed; the labial sinusid of  $P_4$  does not reach the crown base.

*Material* — CR2-A16:  $M^2$  sin., CR2-M220:  $M^3$  sin., CR2-926: lower left series with P<sub>4</sub>-M<sub>2</sub>, CR2-460: indeterminate molar fragment. The specimens are deposited in the collections of the 'Museu Paleontològic Municipal de València' (Spain).

*Description* — Although the specimens CR2-A16 and CR2-M220 were found isolated, they are thought to belong to the same individual since their contact facets join perfectly, and they show a similar degree of wear. Finding isolated remains belonging



Fig. 1. Nomenclature of the Hystricidae molars; a: hypothetical upper molar; b: hypothetical lower molar. I to IV: synclines I to IV; I' to IV': synclinids I to IV; A: anterior side; LA: labial side; s: lingual sinus; sd: labial sinusid.





to the same individual is quite frequent in Crevillente 2 (Montoya, 1990). The descriptions are based on the nomenclature followed by Agustí et al. (1987) (Fig. 1).

### Upper dentition (Fig. 2a)

 $M^2$  (CR2-A16) — Tooth with a circular outline; height from the crown base to the wear surface 5 mm; part of the anterior wall is absent; the tooth has three closed roots: two of them in labial position and a lingual one; four labially open synclines; syncline I joined to the lingual sinus, dividing the tooth in two parts; synclines II and III are split, leaving two enamel islets.

 $M^3$  (CR2-M220) — Tooth with an egg-shaped outline; anterior part broader than the posterior one; degree of wear like in  $M^2$ ; presumably closed roots: an anterolingual one, a posterior one and a less-developed labial one; an almost closed syncline I and a labially open syncline II; the two synclines meet with the lingual sinus, resulting in a three-zoned tooth; a small enamel column divides syncline II in two parts; synclines III and IV are closed and divided into five enamel islets.

#### *Lower dentition (Fig. 2b, c)*

 $P_4$  (CR2-926) — Unworn long tooth, divided into two by the synclinids II and III; posterior part broader than the anterior one; in the labial wall the sinusid does not reach the base of the crown.

 $M_1$  (CR2-926) — Long and quadrangular tooth; height from the crown base to the wear surface 5 mm; the anterior wall and part of the labial wall are absent; broken but presumably closed roots; there are only three synclinids, number one being absent or fused to synclinid II; the latter is opened to the lingual side and shows a trilobed morphology; in the labial area exists an extended enamel islet derived from synclinid II or III; the synclinid III is lingually open and shows a lobed morphology; the synclinid IV is lobed and lingually closed; due to damage of the tooth it is not clear whether synclinid IV joins the labial sinusid or not.

 $M_2$  (CR2-926) — General shape similar to  $M_1$ ; height from the crown base to the wear surface 5.5 mm; presumably closed roots; synclinid I is absent; a lingually open and markedly lobed synclinid II; synclinids III and IV are very similar: they both are open and possess an internal isolated enamel column.

## Discussion

Nowadays, the family Hystricidae, of uncertain origin and systematic position (Denys, 1987; Jaeger, 1988), consists of four genera with eleven species, three in Africa and eight in Asia (Novak & Paradiso, 1983). The African species *Hystrix cristata* also lives in Italy, where it was probably introduced by man. The genus *Hystrix* includes all porcupine fossil remains from the Neogene and Quaternary of Europe.

The dental morphology of this genus changes with the attrition, specially in the first stages of abrasion (van Weers, 1990). Besides, the fossil record of *Hystrix* is relatively scarce. These two facts explain the tendency of species splitting in literature. For instance, the number of enamel islets has often been used as a criterion to define a certain species, but the fact of the matter is that this number changes with the degree of wear.

Starting with the papers by Sulimski (1960) and Koliadimou & Koufos (1991), the number of fossil species has been reduced considerably. The present status of our knowledge about the genus *Hystrix* throughout the Neogene and Quaternary in Europe can be schematically drawn as follows:

During Turolian and Pliocene times a big-sized species, *Hystrix primigenia* (Wagner, 1848), was present in a wide geographic realm. In the Pleistocene this species was replaced by the smaller *Hystrix major* Gervais, 1859.

As far as dental morphology is concerned, these species had different developments of synclinid I in the lower molars: reduced in *H. primigenia* and well-developed in *H. major* (Agustí et al., 1987; Bonis et al., 1992).

Another — poorly known — species, smaller than the former ones, *Hystrix* suevica Schlosser, 1884, has been found in some Aragonian and Vallesian sites of Central Europe.

Finally, there is a controversial species, Hystrix refossa from the sites of Perrier

(Gervais, 1848-1852) and St. Vallier (Viret, 1954), synonymous with *H. major* according to Koliadimou & Koufos (1991).

These three species have been taken into account in order to establish the specific determination of the Crevillente 2 remains.

The fossil dental elements described in this paper clearly differ from those assigned to *H. major*, which shows a greater size (Table 1, Fig. 3), and a well-developed synclinid I in the lower molars (Fig. 4).

The poorly developed synclinid I of the lower molars is a character, that the material from Crevillente 2 and *H. primigenia* have in common (Fig. 4). However, there are obvious differences in size (Table 1, Fig. 3) and in some other morphological features.

In the  $M_1$  and  $M_2$  from Crevillente 2 synclinid I is very poorly developed, perhaps fused with synclinid II. Synclinids III and IV are more complex in the  $M_2$ from Crevillente than in *H. primigenia*, due to the presence of internal pillars. On the other hand, in the here-described  $P_4$  the labial sinusid does not reach the base of the crown (Fig. 2c), while this does occur in *H. primigenia* from Weze and Layna (Sulimski, 1960; Agustí et al., 1987).

In both the  $M^2$  and  $M^3$  from Crevillente 2 there exists a well-developed syncline I, fused with the lingual sinus. This feature has not been observed among figured specimens in the literature, and it seems to be a peculiar trait of the Spanish *Hystrix* (Fig. 5).

	H. suevica			B. primigenia				H. major				B. cristata	
	CR2	SAL	кон	min.	mean	max.	n	min.	mean	<b>ma</b> I.	n	min.	max.
P <sup>4</sup> L B		8.1 7.3	7.9 7.9	11.0	11.95 12.08	13.2 13.8	9 9	8.9	10.56 9.02	11.5	5 5	8.5 8.0	10.5 9.0
M <sup>1</sup> L B		7.4 7.7	6.7 7.3	8.9 9.4	10.15	11 <u>2</u> 12.6	9 9	9.0 8.3	9.65 9.15	10.3 10.0	2 2	7.2 7.0	8.0 9.0
м <sup>2</sup> L В	7.8 >7.7		7.1 6.4	9.3 9.8	10.17	11.0 12.4	13 13		10.5		1 1	7.4 7.0	9.0 9.0
M <sup>3</sup> L B	7.9 7.2		6.8 6.9	8.8 8.2	9.41 9.05	10.0 10.0	8 8	9.4 8.0	9.66 8.03	10.0	3 3	6.6 6.0	8.5 8.0
P4L B H	8.9 7.1 9.0			10.7 9.3	11.93 10.08	12.7 10.8	6 6	9.3 7.2	11.27 8.96 11.1	13.0 9.9	7 7 1	7.8 7.0	10.5 8.0
M <sub>1</sub> L B	 6.9			10.3	11.18	11.8	6 6	10.0 8.5	10.64 8.78	11.1 9.1	5 5	7.8 7.0	8.5 8.0
M <sub>2</sub> 1. B	7.8 6.7			9.5 8.6	10.91 9.89	11.7 11.2	8 8	9.5 7.0	10.50 8.66	11.2 9.2	6 6	8.7 7.8	10.0 9.5
м <sub>3</sub> L в				9.3 7.9	10.10 8.54	10.8 8.9	5 5	9.0 7.0	9.75 8.02	10.4 8.6	4	8.2 7.5	9.5 9.0

Table 1. Teeth measurements (in mm) of *Hystrix suevica* from Crevillente 2, Salmendingen (Schlosser, 1902) and Kohfidisch (Bachmayer & Wilson, 1970), compared with those of *H. primigenia*, *H. major* and *H. cristata* (= *H. etrusca*); data from Sulimski (1960), Agustí et al. (1987), Sen & Kovatchev (1987), Koliadimou & Koufos (1991), and Bonis et al. (1992). B: breadth; H: height; L: length; max.: maximum value; mean: mean value; min.: minimum value; n: number of elements.



Fig. 3. Length-width diagrams of the teeth of *H. suevica*, *H. primigenia* and *H. major*. The minimum and maximum values of *H. cristata* are also represented. Source of data as in Table 1.



Fig. 4. Morphology of the M<sub>2</sub> of some Hystricidae; a: *H. suevica* from Crevillente 2; b: *H. primigenia* from Pikermi (Gaudry, 1862-1867); c: *H. primigenia* from Serrat d'en Vacquer (Depéret, 1890-1892); d: *H. primigenia* from Villarroue (Agustí et al. 1087); c: *H. primigenia* from Kalimanci (San &

d: *H. primigenia* from Villarroya (Agustí et al., 1987); e: *H. primigenia* from Kalimanci (Sen & Kovatchev, 1987); f: *H. sivalensis* from the Siwaliks (Stehlin & Schaub, 1950); g: *H. major* from Venta Micena 2 (Agustí et al., 1987); h: *H. major* from Gerakarou 1 (Koliadimou & Koufos, 1991); i: recent *H. cristata* (Vertebrates collection of the Museo Nacional de Ciencias Naturales, Madrid). The figures have been drawn at different scales.

Finally, there is a high biometric agreement between *H. suevica* from the European Aragonian and Vallesian and the studied material from Crevillente 2. Unfortunately, the dental elements found in this site are not equivalent to those of *H. suevica* figured in other papers; therefore, a proper morphological comparison is not possible. Nevertheless, the  $M^1$  from Salmendingen (Schlosser, 1902) possess four well-developed synclines, like the  $M^2$  from Crevillente, both teeth showing a similar outline and a very similar enamel pattern (Fig. 5a, b). The Early Turolian Spanish *Hystrix* must be ascribed to *Hystrix suevica* Schlosser, 1884, specially because of the great biometric similarity between the dental remains found in Crevillente 2 and those from Salmendingen (Schlosser, 1902) and Kohfidish (Bachmayer & Wilson, 1970) (Table 1, Fig. 3). The fossil teeth described in this paper add new information to the knowledge of this species, which has hardly been taken into account in most of the recent papers on European fossil *Hystrix*.

*Hystrix suevica* was defined by Schlosser (1884) on the basis of a tooth found in the German site of Häder. Besides, some material from the localities of



Fig. 5. Morphology of the upper molars of some Hystricidae; a:  $M^1$  of *H. suevica* from Salmendingen (Schlosser, 1902); b:  $M^2$  of *H. suevica* from Crevillente 2; c:  $M^2$  of *H. primigenia* from Layna (Agustí et al., 1987); d:  $M^2$  of *H. primigenia* from Pikermi (Gaudry, 1862-1867); e:  $M^2$  of *H. primigenia* from Weze (Sulimski, 1960); f:  $M^2$  of recent *H. cristata* (Vertebrates collection of the Museo Nacional de Ciencias Naturales, Madrid). The figures have been drawn at different scales; the figures 'c' and 'e' are drawn reversed.

Salmendingen (Schlosser, 1902) and Kohfidish (Bachmayer & Wilson, 1970) is also known.

The site of Häder is dated as Aragonian (MN5) and the Austrian locality of Kohfidisch is dated as Late Vallesian (MN10) (Mein, 1990; de Bruijn et al., 1992). With regard to Salmendingen (Germany), its exact age has not been determined, although *Dryopithecus* and *Dipoides problematicus* simultaneously appear in the fossil assemblage (Schlosser, 1902). *Dryopithecus* is a genus restricted to the Late Aragonian and Vallesian, from MN8 to MN10 (Moyà, pers. comm.), while *D. problematicus* is a beaver known from Early Turolian to Early Pliocene. Therefore, Salmendingen can probably be dated as Late Vallesian (MN10).

# Biogeographic history of the family Hystricidae

The origin of the family Hystricidae is not yet clear (Jaeger, 1988), and we can say the same about the genus *Hystrix*. Its poor representation in the fossil record can be considered as one of the reasons for this situation. Therefore, it is very dificult to establish the phylogeny and biogeographic history of this lineage. We can only point out some general ideas about this question.

The oldest *Hystrix* known seems to be the one from the Middle Aragonian (MN5) German site of Häder, where *H. suevica* was present (Schlosser, 1884). This species has not been recorded from Upper Aragonian beds, but it has been found in



Fig. 6. Stratigraphic distribution of European Hystrix species.

two Central European Vallesian localities: Salmendingen (Schlosser, 1902), and Kohfidish (Bachmayer & Wilson, 1970). The discovery of this species in Crevillente 2 extends its geographic range to Western Europe and confirms its presence during Early Turolian times (Figs. 6, 7).

So there existed a small *Hystrix* species in Europe during the Middle and Late Miocene, morphologically related to *H. primigenia*. Probably, *H. suevica* can be considered as the ancestor of the latter, big-sized, Mio-Pliocene porcupine species.

*Hystrix primigenia*, which spread widely over Europe, has a long and wellknown time range from Middle Turolian (MN12) to Late Pliocene (MN16-17) (Fig. 6), and perhaps it is also present in the Early Turolian (Bonis et al., 1992). This species is well documented in the following localities: Pikermi (Wagner, 1848; Gaudry, 1862), Ditiko 3 (Bonis et al., 1992), Taraklia (Sulimski, 1960), Kalimanci (Sen & Kovatchev, 1987), Weze (Sulimski, 1960), Serrat d'en Vacquer (Depéret, 1890-1892), Villalba Alta (Adrover, 1986), Layna and Villarroya (Agustí et al., 1987) (Fig. 7). Besides, it has been cited in the faunal lists of several other European sites of this age.

Hystrix major appeared at the Neogene-Quaternary boundary. It was a bigsized porcupine, that replaced *H. primigenia* in the European Pleistocene, and spread over, at least, Southern Europe (Fig. 6 and 7). It is cited, sometimes as *Hystrix etrusca*, from the following sites: Ratoneau (Gervais, 1859), Valdarno (Bosco, 1898), Montréjeau (Harle, 1910), Vallonet (Chaline, 1972), Venta Micena 2, Fuentenueva 2 and Atapuerca (Agustí et al., 1987), and recently in Gerakarou 1 (Koliadimou & Koufos, 1991).

It would appear that during the European Late Miocene and Early Pliocene the family Hystricidae had a wide geographic range. Both *H. suevica* and *H. primigenia* are cited from Central and Southern Europe. E.g. *H. primigenia* is present in the Upper Ruscinian (MN15) of Weze (Poland), the last recorded porcupine presence in



Fig. 7. Geographic distribution of the European fossil porcupines. 1: Venta Micena 2 and Fuentenueva 2; 2: Crevillente 2; 3: Villalba Alta; 4: Villarroya and Layna; 5: Atapuerca; 6: Montréjeau; 7: Serrat d'en Vacquer (Roussillon); 8: Ratoneau; 9: Vallonet; 10: Valdarno; 11: Häder and Salmendingen; 12: Kohfidisch; 13: Weze; 14: Taraklia; 15: Kalimanci; 16: Ditiko 3; 17: Alifakas; 18: Gerakarou 1; 19: Pikermi and Halmyropotamos; 20: Samos; 21: Çoban Pinar; 22: Menacer.

Central Europe. But starting from this age, the entire record of this family during the Late Pliocene (*H. primigenia*) and the Pleistocene (*H. major*) is restricted to Southern Europe (Fig. 7). These distribution patterns can be related to the progressive climatic cooling detected from c. 2.5 Ma onwards, with the onset of the Northern Hemisphere glaciation (Rea & Schrader, 1985; Loubere, 1988). This climatic deterioration, occurring in the Middle-Late Pleistocene, may be the cause of the extinction of the family in Europe. The subsequent return of warm-temperate climatic conditions allowed *H. cristata*, presumably introduced by man, to live at present times in Sicily and the southern part of the Apennine Peninsula.

In the Asiatic fossil record, the family Hystricidae appears in the Lower

Siwaliks (Chinji Level) which correspond, in a wide sense, to the Aragonian. The family is represented there by *Sivacanthion complicatus* (Colbert, 1935), a very small-sized species with a more complex enamel pattern than *Hystrix*.

*H. primigenia* has been cited from the Turkish Turolian site of Çoban Pinar (Özansoy, 1965).

In the Pliocene of Hasnot in the Middle Siwaliks appears *Hystrix sivalensis* (Black, 1972), very similar to the European *H. primigenia* (Sulimski, 1960). They are contemporaneous and presumably closely related species.

In the Upper Siwaliks (Pleistocene) *Hystrix* cf. *H. leucurus* is recorded (Black, 1972), while in the Pleistocene site of Sangiran (Java) *Hystrix gigantea* has been described (van Weers, 1985).

In the African fossil record, the first appearance of the family Hystricidae is simultaneously recorded at Lukeino, at c. 6.5 Ma (Pickford, 1975; Lavocat, 1978) and at Menacer (Arambourg, 1959; Thomas & Petter, 1986), which is dated as Late Turolian or MN13 (Mein, 1990). The material from Menacer, classified by Arambourg (op. cit.) as *Hystrix* sp., shows great morphological and biometrical similarities with *H. primigenia*, and can be included in the latter species. This means, that this typically European species probably reached Africa in the Late Turolian (MN13).

During the Pliocene, the family Hystricidae is already diversified. In Laetoli three species have been found: *Hystrix leakeyi*, *Hystrix* cf. *makapanensis* and *Xenohystrix crassidens* (Denys, 1987). *H. makapanensis* is also recorded at the Pliocene sites of Omo and Makapansgat, and at the Pliocene-Pleistocene locality of Olduvai 1. *X. crassidens* also appears at Makapansgat and at the Pliocene site of Hadar (Denys, 1987).

## Conclusions

The most primitive species of the genus Hystrix are found in Europe.

The discovery of *Hystrix* remains at the Lower Turolian Spanish site of Crevillente 2 allows us a better knowledge of the phylogenetic affinities of *H. suevica*. Its known stratigraphic and geographic range have been widened too.

This small species is the only European representative of the genus from Middle Aragonian to Early Turolian. Probably *H. suevica* was the ancestor of the bigsized *H. primigenia*, which is present in European faunal assemblages from Middle Turolian to Late Pliocene, when it becomes extinct. Both species show a large time range. Finally, *H. primigenia* was replaced by *H. major*, present in the southern European Pleistocene.

The increasingly well-developed synclinid I of the lower molars is a remarkable evolutionary event in European Hystricidae. *H. suevica* lacks an individualized synclinid I, *H. primigenia* shows a poorly developed one, and *H. major* is characterized by a distinct and well-developed synclinid I.

Among these three European species, *H. primigenia* shows a wider geographic range, spreading over Southern and Central Europe, from Spain to Turkey, and Northern Africa. On the contrary, *H. major* has only been cited from Meridional

Europe. The observed reduction of the geographic range of the Hystricidae from Pliocene to Pleistocene can be related to the progressive cooling of the European climate.

In spite of the relative incompleteness of the Hystricidae fossil record, it can be said that the family has been represented in Europe by a small number of species, all along its stratigraphic record.

Things have been different in other geographic areas. For example, in Africa, after the immigration of H. primigenia in the Late Miocene, the family Hystricidae is diversified, with several species from the Pliocene to the present time. On the other hand, in Asia this diversification seems to have occurred during the Pleistocene.

### References

- Adrover, R., 1986. Nuevas faunas de roedores en el Mio-Plioceno continental de la región de Teruel (España). Interés bioestratigráfico y paleoecológico. — Inst. Estud. Turolenses (CSIC), Teruel: 1-423.
- Agustí, J., S. Arbiol & E. Martín Suárez, 1987. Roedores y lagomorfos (Mammalia) del Pleistoceno inferior de Venta Micena (depresión de Guadix-Baza, Granada). — Paleont. Evol., Mem. Esp. 1: 95-107.
- Alberdi, M.T. & P. Montoya, 1988. *Hipparion mediterraneum* Roth & Wagner, 1855 (Perissodactyla, Mammalia) del yacimiento del Turoliense inferior de Crevillente (Alicante, España). — Mediterránea, Geol., 7: 107-143.
- Alcalá, L., B. Azanza, E. Cerdeño, M. Iñesta, J.R. Juan, P. Montoya, P. Mora & J. Morales, 1987. Nuevos datos sobre los macromamíferos turolienses de Crevillente (Alicante). — Geogaceta, 3: 24-27.
- Alcalá, L. & P. Montoya, 1989-1990. Las faunas de macromamíferos del Turoliense inferior español.
  Paleont. Evol., 23: 111-119.
- Arambourg, C., 1959. Vertébrés continentaux du Miocène supérieur de l'Afrique du Nord. Publ. Serv. Carte Géol. Algérie, N.S., 4: 1-161, 18 pls.
- Azanza, B., 1989. Los Cervidae (Artiodactyla, Mammalia) del Mioceno de las cuencas del Duero, Tajo, Calatayud-Teruel y Levante. — Doctor's Thesis Univ. Zaragoza: 1-387, 33 pls.
- Bachmayer, F. & R.W. Wilson, 1970. Small mammals (Insectivora, Chiroptera, Lagomorpha, Rodentia) from the Kohfidisch fissures of Burgenland, Austria. — Ann. Naturhist. Mus. Wien, 74: 533-587.
- Black, C.C., 1972. Review of fossil rodents from the Neogene Siwalik beds of India and Pakistan. Palaeontology, 15, 2: 238-266.
- Bonis, L. de, G. Bouvrain, D. Geraads & G.D. Koufos, 1992. A skull of *Hystrix primigenia* from the late Miocene of Macedonia (Greece). N. Jb. Geol. Paläont., Mh., 1992, 2: 75-87.
- Bosco, C., 1898. Hystrix etrusca n. sp. Paleont. Ital., 4: 141-153.
- Bruijn, H. de, R. Daams, G. Daxner-Höck, V. Fahlbusch, L. Ginsburg, P. Mein & J. Morales, 1992. Report of the RCMNS working group on fossil mammals, Reisensburg 1990. — Newsl. Stratigr., 26, 2/3: 65-118.
- Bruijn, H. de, P. Mein, C. Montenat & A. van de Weerd, 1975. Corrélations entre les gisements de rongeurs et les formations marines du Miocène terminal d'Espagne méridional (Provinces d'Alicante et de Murcia). — Proc. Kon. Ned. Akad. Wetensch., B, 78, 4: 1-32, 4 pl.
- Cerdeño, E., 1988. Revisión de la sistemática de los Rinocerontes del Neógeno de España. Doctor's Thesis Univ. Complut. Madrid: 1-429, 51 pls.
- Chaline, J., 1972. Les rongeurs du Pleistocène moyen et supérieur de France (Systématique, Biostratigraphie, Paléoclimatologie). — Cah. Paléont. CNRS: 1-410.

- Colbert, E.H., 1935. Siwalik Mammals in the American Museum of Natural History. Trans. Amer. Phil. Soc., N.S., 26: 1-401.
- Denys, C., 1987. Fossil rodents (other than Pedetidae) from Laetoli. In M.D. Leakey & J.M. Harris (eds). Laetoli, a Pliocene site in northern Tanzania. Clarendon Press, Oxford: 118-170.

Depéret, C., 1890-1892. Les animaux pliocènes du Roussillon. - Mém. Soc. Géol. France, 3: 1-194.

Freudenthal, M., J.I. Lacomba & E. Martín Suárez, 1991b. The Cricetidae (Mammalia, Rodentia) from the late Miocene of Crevillente (prov. Alicante, Spain). — Scripta Geol., 96: 9-46, 5 pls.

Freudenthal, M., J.I. Lacomba, E. Martín Suárez & J.A. Peña, 1991a. The marine and continental Upper Miocene of Crevillente (Alicante, Spain). Scripta Geol., 96: 1-8.

Gaudry, A., 1862-1867. Animaux fossiles et Géologie de l'Attique. Libr. Soc. Géol. France: 1-474, 75 pls, 1 map.

Gervais, P., 1848-1852. Zoologie et Paléontologie françaises. — A. Bertand, Paris, 3 vols.

- Gervais, P., 1859. Sur une espèce de Porc-Epic fossile dans les brèches osseuses de l'île Ratoneau, près Marseille. C.R. Acad. Sc. Paris, 49: 511.
- Harle, E., 1910. Porc-épic Quaternaire des environs de Montréjeau (Haute-Garonne). Bull. Soc. Géol. France, 4, 10: 740-744.
- Jaeger, J.-J., 1988. Rodent phylogeny: new data and old problems. In: M.J. Benton (ed.), The Phylogeny and Classification of the Tetrapods, Vol. 2: Mammals. — Systematics Assoc. Spec. Vol., 35B: 177-199.
- Koliadimou, K. & G.D. Koufos, 1991. The Hystricidae from the Pleistocene of Macedonia (Greece) and a review of the European representatives of the family. — Bull. Geol. Soc. Greece, 25, 2 (Proc. V Congr. Geol. Soc. Greece, Athinai, 1990): 453-471.
- Lavocat, R., 1978. Rodentia and Lagomorpha. In: V.J. Maglio & H.B.S. Cooke (eds). Evolution of African Mammals. --- Harvard Univ. Press, Cambridge (MS): 69-89.
- Loubere, P., 1988. Gradual Late Pliocene onset of glaciation: a deep-sea record from the Northeast Atlantic. Palaeogeogr., Palaeoclimatol., Palaeoecol., 63: 327-334.
- Made, J. van der, P. Montoya & L. Alcalá, 1992. *Microstonyx* (Suidae, Mammalia) from the Upper Miocene of Spain. Géobios, 25, 3: 395-413.
- Mein, P., 1990. Updating of MN zones. In: E.H. Lindsay et al. (eds). European Neogene Mammal Chronology. — Plenum Press, New York : 73-90.
- Montenat, C., 1973. Les Formations Néogènes et Quaternaires du Levant Espagnol (Provinces d'Alicante et de Murcia). Thèse Sc. Univ. Orsay-Paris-Sud: 1-1170.
- Montenat, C., 1977. Les bassins néogènes du Levant d'Alicante et de Murcia. Doc. Lab. Géol. Fac. Sci. Lyon, 69: 1-345.
- Montenat, C. & M. Crusafont, 1970. Découverte de Mammifères dans le Néogène et le Pléistocène du Levant espagnol (Provinces d'Alicante et de Murcia). — C. R. Acad. Sci. Paris, 270: 2434-2437.
- Montoya, P., 1990. Primeros datos sobre la tafonomía de Crevillente-2. Com. Reunión Tafonomía Fosilización, Madrid, 1990: 237-244
- Montoya, P., D. Belló, F. Robles, F. Ruiz-Sánchez & C. Santisteban, in press. Análisis paleoambiental del Neógeno continental del área de Crevillente. Inst. Cult. Juan Gil-Albert, Alicante.
- Montoya, P. & J. Morales, 1991. Birgerbohlinia schaubi Crusafont, 1952 (Giraffidae, Mammalia) del Turoliense inferior de Crevillente-2 (Alicante, España). Filogenia e historia biogeográfica de la subfamilia Sivatheriinae. — Bull. Mus. natl. Hist. nat. Paris, 13, 3-4: 177-200.
- Novak, R.M. & J.L. Paradiso, 1983. Walker's Mammals of the World. J. Hopkins Univ. Press, Baltimore-London, II: 569-1362.
- Özansoy, F., 1965. Etude des gisements continentaux et des Mammifères du Cénozoique de Turquie. — Mém. Soc. Géol. France, 44: 1-92.
- Pickford, M., 1975. Late Miocene sediments and fossils from the Northern Kenya Rift Valley. Nature, 256: 279-284.
- Rea, D.K. & H. Schrader, 1985. Late Pliocene onset of glaciation: ice-rafting and diatom stratigraphy of North Pacific DSDP cores. --- Palaeogeogr., Palaeoclimatol., Palaeoecol., 49: 313-325.

- Schlosser, M., 1884. Die Nager des europäischen Tertiärs nebst Betrachtungen über die Organisation und die geschichtliche Entwicklung der Nager überhaupt. — Palaeontographica, A, 31, 3, 7: 19-162, pls 5-12.
- Schlosser, M., 1902. Beiträge zur Kenntnis der Säugethierreste aus den süddeutschen Bohnerzen. Geol. Paläont. Abh., n.F., 5, 3: 115-258, pls 6-10.
- Sen, S. & D.B. Kovatchev, 1987. The porcupine Hystrix primigenia (Wagner) from the Late Miocene of Bulgaria. — Proc. Kon. Ned. Akad. Wetensch., B, 90, 4: 317-323.
- Stehlin, H.G. & S. Schaub, 1950. Die Trigonodontie der simplicidentaten Nager. Schweiz. Pal. Abh., 67: 1-385.
- Sulimski, A., 1960. *Hystrix primigenia* (Wagner) in the Pliocene fauna from Weze. Acta Palaeont. Polonica, 5, 3: 319-336, 2 pls.
- Thomas, H. & G. Petter, 1986. Révision de la faune de mammifères du Miocène supérieur de Menacer (ex-Marceau), Algérie: discussion sur l'âge du gisement. --- Géobios, 19, 3: 357-373.
- Viret, M.J., 1954. Le loess à bancs durcis de Saint-Vallier (Drome), et sa faune de mammifères Villafranchiens. Nouv. Arch. Mus. Hist. Nat. Lyon, 4: 1-188.
- Wagner, A., 1848. Urweltliche Saugethierreste aus Griechenland. Abh. Bayer. Akad. Wiss., 5: 333-378.
- Weers, D.J. van, 1985. *Hystrix gigantea*, a new fossil porcupine species from Java (Rodentia: Hystricidae). — Senckenberg. Lethaea, 66, 1/2: 111-119.
- Weers, D.J. van, 1990. Dimensions and occlusal patterns in molars of Hystrix brachyura Linnaeus, 1758 (Mammalia, Rodentia) in a system of wear categories. — Bijdragen Dierkunde, 60, 2: 121-134.

Manuscript received 2 February 1993.