

Riddleria atecensis nov. gen. nov. sp., a peculiar erinaceid (Erinaceomorpha, Mammalia) from the Lower Miocene of Spain

by

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Zusammenfassung

Es wird eine neue erinaceide Gattung und Art, *Riddleria atecensis* gen. nov. sp. nov. aus dem Unterem Miozän Spaniens, der Lokalität Ateca III (Becken von Calatayud-Teruel, Zaragoza Provinz; MN 3) beschrieben. Die außerordentliche Morphologie der Backenzähne kann als eine Adaption an einer eher carnivore Ernährung interpretiert werden. *Riddleria* wird vorläufig den Galericinae zugeordnet.

Summary

A new genus and species of erinaceid, *Riddleria atecensis* gen. nov. sp. nov. is described from the Lower Miocene locality of Ateca III (Calatayud-Teruel Basin, Province of Zaragoza, Spain; MN 3). The aberrant molar morphology of the species is considered an adaptation to a more carnivorous diet. *Riddleria* is tentatively placed in the Galericinae.

1. Introduction

Erinaceids are a quite common in the European Miocene micromammal faunas. However, mostly Galericinae (moonrats or gymnures) are found and more specifically members of the tribe Galericipini (*Galerix*, *Parasorex*, *Schizogalerix*). The other gymnure genus from the European Miocene, *Lanthanotherium* is far more rare, as are the members of the subfamily Erinaceinae (spiny hedgehogs). Although 10 species of the subfamily have been described from the Miocene of Europe, the fossil record is scanty. ENGESSER (1980) remarked that the fossil representatives of this subfamily are badly in need of revision, a remark that still holds true today. Nevertheless,

the subfamily had a short period in which they were the only erinaceids in Europe, since no gymnures have so far been found in the lowermost part of the Miocene (MN1-2; ZIEGLER, 1999).

In this paper we describe a new genus and species of erinaceid from the Lower Miocene of Spain. In the collections of the Institute of Earth Sciences peculiar erinaceid molars from the locality of Ateca III (MN 3, Province of Zaragoza, Spain) were found. Unearthed in the early 1960's, it had hitherto escaped notice. GIBERT (1974), who worked on this collection and described a shrew from Ateca III, made no mention of Erinaceidae from that locality. The only mention made of an erinaceid in Ateca III is by LOPEZ MARTINEZ (1989) who listed "*Galerix exilis*" for that locality.

2. Material and methods

The locality Ateca III was discovered and excavated by Hans de Bruijn and Thijs Freudenthal during campaigns in 1960-1963 in the Calatayud-Teruel basin (province of Zaragoza, Spain). The locality lies at the northwestern edge of the basin, several kilometres west of the town of Calatayud. As was usual in those days, a relatively small sample was taken by modern standards. DE BRUIJN (1967) remarked that the sediment yielded about one molar per kilogram of sediment, and since he described 221 molars, this would suggest a sample of about 250 kilograms. The material is stored under locality number code 51 in the Institute of Earth Sciences, Utrecht University.

The erinaceid material from Ateca III consists of a mandible fragment, two unicuspid premolars, a damaged m1, two trigonids of the m1, one damaged m2 in a mandible fragment, one trigonid of an m2, one m3, a trigonid of the m3, two P3, a partial P4, one M1, one M2, one M3, and various fragments.

The terminology for parts of molars follows ENGESSER (1980). Measurements were taken at right angles using an Leitz measuring microscope. The measurements are given in mm.

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3. Systematic palaeontology

Class Mammalia

Ordo Erinaceomorpha GREGORY, 1910

Familia Erinaceidae FISCHER VON WALDHEIM, 1817

Subfamilia Galericinae POMEL, 1848

Riddleria nov. gen.

Derivatio nominis: The genus is named after “The Riddler”, an adversary of Batman in both the comic books and the motion pictures. The name was chosen since the peculiar molar morphology presented many riddles.

Diagnosis: Middle-sized erinaceids with high cusps connected by sharp ridges. The posterior cingulum of the m1 and m2 is thick and is connected to the posterior arm of the entoconid. The P3 has a lingual flange bearing a well-developed protocone. In occlusal view the outline of the M1 is irregular with clear concave indentations on all sides. The protoconule of the M1 and M2 is well developed. The metaconule is positioned closely to the metacone and possesses a posterior arm. The anterior and posterior cingulums of the M1 and M2 are wide. The M1 and M2 are only slightly wider than they are long.

Differential diagnosis: The irregular outline of the upper molars and the strong cingular development make *Riddleria* readily recognisable from other Erinaceidae. The presence of a posterior arm of the metaconule is shared with the Galericipini but not found in other Miocene erinaceids. In contrast to the known Galericipini the upper molars are not much wider than they are long.

Type species: *Riddleria atecensis* nov. gen. nov. sp.

Riddleria atecensis nov. gen. nov. sp.

Derivatio nominis: The species is named after its type locality Ateca III.

Diagnosis and differential diagnosis: see genus.

Type locality: Ateca III, Province of Zaragoza, Spain; Upper Ramblian, Local Biozone A, MN 3.

Geographic and stratigraphic distribution: *Riddleria atecensis* is thus far known from its type locality only.

Holotype: M1 sin., 51. 82. (Plate 1, Fig. 2 a,b)

Paratypes: m1 dext., 51.1051 (Pl. 1, Fig. 8); m2 dext., 51.1054 (Pl. 1, Fig. 7); m3 51.1505 (Pl. 1, fig. 6); P3 dext., 51.1018 (Pl. 1, fig. 5); M2 sin., 51. 81 (Plate 1, Fig. 3 a,b); partial P4 sin., 51. 84 (Plate 1, Fig. 1 a,b).

Measurements: m3 = 1,96 x 1,31 x 1,05; P3 = 1,89 x 1,41; M1 = 2,76 x 3,24; M2 = 2,37 x 2,63.

Description

Mandible. Only two fragments of the ramus horizontalis have been preserved, one of which holding the m2 described below. The fragments show little diagnostic features, but clearly indicate that the lower jaw must have been stout and relatively high.

m1. No complete m1 has been preserved. The most complete specimen is damaged lingually, missing the lingual side of the hypoconid and the protoconid. Apart from this specimen, the collection contains one well-preserved trigonid. The description is based on these two specimens.

The trigonid is shorter than the talonid. The protoconid, metaconid, and entoconid are high cusps of about the same height. The protoconid is the largest cusp. Its two arms steep down and connect to the labial arm of the metaconid and the paralophid, respectively. The metaconid lies anterolingually to the protoconid, making the trigonid slightly askew. The metaconid is well developed. Its lingual face is rounded. The labial arm of this cusp steeps down and connects to the posterior arm of the protoconid. There is a deep notch in the posterior flank of the trigonid where the two arms meet. The paralophid is low. In the unworn trigonid, the paraconid is discernible as a conical cusp at the end of the paralophid, directly in front of the metaconid. In the more worn damaged molar, it is more or less incorporated in the paralophid. The trigonid basin is narrow. The hypoconid is clearly lower than the entoconid. It has a triangular wear facet. The oblique cristid ends against the posterior flank of the protoconid, close to the labial side. The posterior arm of the hypoconid ends against the flank of the posterior arm of the entoconid, near the point where the latter connects to the posterior cingulum. The entoconid is crescent-shaped. The posterolingual flank is rounded. A faint ridge slopes down over the anterior face of the cusp, ending near the base of the metaconid. The posterior arm of the entoconid is much better developed and connects to the thick posterior cingulum. A well-developed anterior cingulum runs from the base of the paraconid to the base of the protoconid.

m2. The only available specimen is damaged, lacking the area near the entoconid. The trigonid is somewhat shorter than the talonid. The protoconid is the largest cusp. Its short anterior and posterior arms steep down and connect to the paralophid and the labial arm of the metaconid, respectively. The hind flank of the protoconid is slightly curved posterolabially. The conical metaconid is as high as the protoconid and is well developed. Its labial arm steeps down and connects to the posterior arm of the protoconid. Thus, there is a deep notch between the protoconid and metaconid. The paralophid is low and curved. It reaches up to the lingual side of the m2. The paraconid is completely incorporated in this ridge. The trigonid valley is narrow. The hypoconid is large but low, reaching up to the level of the paralophid. The oblique cristid is weak. It is directed anterolingually and ends against the posterior flank of the protoconid off the tip of that cusp. The talonid basin is large and shallow. The anterior cingulum is well developed and runs from the base of the paraconid to the base of the protoconid. Only a fragment of the posterior cingulum has been preserved. This shows that this cingulum was -very- wide.

m3. The trigonid is longer and wider than the talonid. The metaconid is the highest and largest cusp. It is conical with a weak labial arm connecting to the posterior arm of the protoconid. The protoconid is clearly lower and somewhat

smaller than the metaconid. Its posterior arm slopes down slightly; the notch between protoconid and metaconid is much less pronounced than in the m1 and m2. The anterior arm connects to the paralophid, which is low and strongly curved. The paraconid is completely incorporated in this ridge. The trigonid valley is rather wide.

The entoconid is clearly higher than the hypoconid. On our, somewhat abraded, specimen, it has a crescent-shaped wear surface. The anterior face of the entoconid is rounded. The wear surface of the hypoconid is triangular. The oblique cristid is a faint ridge that is directed forward from the hypoconid and connects to the posterior flank of the protoconid. The hypoconid and entoconid seem not to be connected to one another. The only cingulum is the very weak anterior cingulum.

P3. The premolar is hook-shaped, with a large lingual flange in the front part of the premolar. The paracone is the largest cusp. Its tip lies just in front of the middle of the P3. The paracone is conical, with a very faint posterocrista. Near the base this ridge becomes somewhat more pronounced and runs straight to the back of the premolar. In front of the paracone lies a large flange, which does not bear any cuspules. The protocone lies on the lingual flange off the front of the paracone. It is a small, conical cusp. A very slight and short ridge runs backwards from the base of the protocone, bordering the lingual flange.

P4. Only the labial part of the P4, consisting of the parastyle and paracone has been preserved. The parastyle is low and protrudes slightly. The paracone is very high. Its tip lies close to the front of the molar. The anterior face is rounded. The posterocrista is sharp. It runs quite steep to just beyond the middle of the premolar. There it bends at an angle of about 135 degrees and retains about the same height till it reaches the posterolabial corner of the P4. A well-developed posterior cingulum runs along the flank of this second part of the posterocrista. This cingulum is thickest near its end.

M1. The outline of the occlusal surface is irregular, with all four sides being concave. The six cusps are connected by very high and sharp ridges. The protocone is the largest cusp. Its anterior arm ends low against the anterolingual side of the paracone. The well-developed protoconule is incorporated in the anterior arm of the protocone, forming a large, backwards directed bulge just lingually of the paracone. The posterior arm of the protocone is directed towards the posterolabial corner of the molars. Just lingually of the metaconule it curves, at the same time becoming somewhat lower and ends high against the anterolabial flank of the hypocone. The hypocone is a large, conical cusp. It has a slightly elliptical circumference with the length axis running parallel to the first part of the posterior arm of the protocone.

The metaconule is crescent-shaped. It is as high as the protoconule and the hypocone. Its short anterior arm ends low against the anterolingual side of the metacone. Its posterior arm runs parallel to the flank of the metacone and ends against the posterior cingulum. A very short ridge connects the anterolingual side of the metaconule to the posterior arm of the protocone, just below the point where

it start to bend in the direction of the hypocone.

The parastyle is large and protrudes sharply. It is connected to the base of the paracone by a ridge. The paracone is as high as the protocone. Its anterior side is rounded. A sharp, straight posterocrista steeply down from the tip and connects to the mesostyle, which is undivided. The metacone is somewhat larger than the paracone. It is connected to the mesostyle by a short, curved ridge that ends low against the anterior face of the cusp. A sharp posterocrista runs steeply from the tip backwards. Then it bends sharply to the labial side and retains the same height till it reaches the posterolabial corner of the molar. This second part of the posterocrista is about twice as long as the part before the bend.

A very thick anterior cingulum runs from the base of the protocone to the anterolingual side of the paracone, below the point where the anterior arm of the protocone connects to the paracone. An equally strong posterior cingulum runs from the posterolabial side of the hypocone to the posterolabial corner of the molar, following the contours of the posterior emargination. A somewhat weaker cingulum runs along the labial side of the metacone and two short cingulums are found between the protocone and the hypocone, and the lingual side of the parastyle and the paracone, respectively.

M2. Like the M1, the M2 has an irregular outline, but the lingual and posterior emarginations are less marked and the labial side is only slightly concave. The protocone is the largest cusp. Its anterior arm ends against the anterior side of the paracone. The protoconule is a marked, backwards directed bulge in this arm just lingually of the paracone. The posterior arm of the protocone runs straight to about halfway the M2, where it bends and steepens to end low against the hypocone. The hypocone is a large, conical cusp with a circular circumference.

The metaconule is crescent-shaped. It is somewhat lower than the protoconule and hypocone. Its anterior arm is short and ends against the base of the metacone. The posterior arm is about twice as long as the anterior arm and ends just short of the metacone. A short, curved ridge connects the anterolingual side of the metacone to the posterior arm of the protocone at the point where it bends in the direction of the hypocone.

The parastyle is very well developed, but does not protrude as strongly as in the M1. It is long and ridge-shaped, connected by a short transverse ridge to the base of the paracone. The configuration of the two labial cusps is similar to that of the M1. In contrast to the M1, the paracone and metacone are of equal size. The posterior arm of the metacone is shorter than in the M1 and curves more gently.

The anterior cingulum forms a thin bulge in the outline. It starts halfway the anterior flank of the protocone, becoming quickly thicker and then narrower again to end against the parastyle. The posterior cingulum is narrow as it starts at the base of the hypocone. As it reaches the posterior emargination it becomes well developed and continues to the posterolabial corner of the M2. There are no other cingulums.

M3. The outline of the occlusal surface is triangular. The protocone is the largest cusp. Its prominent anterior arm connects to the base of the paracone. The posterior arm is much less developed and connects to the metacone. The paracone is conical and relatively high. The metacone is smaller. From its tip one weak ridge runs to the base of the paracone, a second connects to the posterior arm of the protocone. The parastyle is well developed and is connected to the paracone by a short ridge. The anterior cingulum is strong near the parastyle, but quickly became more narrow as it ends against the anterior flank of the protocone. There is a short and narrow posterior cingulum halfway between the protocone and the metacone.

4. Discussion

Little material of *Riddleria atecensis* was recovered. The P4 fragment and upper molars are all unworn and all are from the left side. This, in combination with the very small sample size, makes it probable that these elements belonged to one individual.

The morphology of *Riddleria atecensis* is so aberrant, that it was not immediately recognised as an erinaceid. The strongly undulating outline of the M1 and M2 are at first sight reminiscent of *Plesiosorex*. However, the M1 and M2 lack the accessory cuspules outside the paracone and metacone. Furthermore, the M1 of *Plesiosorex* is characterised by being very wide relative to its length, a feature not found in *Riddleria*.

Another feature in which *Riddleria* is unlike other erinaceids, are the very high and sharp ridges connecting the various cusps. The omnivorous life style of most hedgehogs is reflected in have rather blunt cusps and dito ridges connecting them. The very high ridges and low valleys between them of the *Riddleria* molars suggest a cutting specialisation and therefore seem to indicate a more carnivorous diet.

Two subfamilies are recognised within the Erinaceidae, the Erinaceinae or spiny hedgehogs and the Galericinae or gymnures. The primary characters to distinguish between the two subfamilies are found in the p4 and the M3 (BUTLER, 1948). The M3 found would identify the species as a galericine, since it bears a metacone. A metacone lacks in the reduced M3 of the Erinaceinae. However, the M3 cannot be assigned with absolute certainty to *Riddleria*, since it is morphologically and metrically indistinguishable from that of a *Galerix* species that was present in the same area at the same time (van den HOEK OSTENDE, in prep.). Therefore, even though we believe that it belongs to the same individual as the other upper molars, its assignment to the new species is a tentative one.

The m3 found has a clear talonid. In Erinaceinae the talonid is usually absent or at the most strongly reduced. A mix-up with *Galerix*, as with the M3, is not possible with the lower last molar. In *Galerix* the posterior side of the talonid is formed by a fusion of the posterior arms of the hypoconid and entoconid. In the m3 of *Riddleria*, these arms do not meet. Thus, the morphology of the m3

seems to warrant a classification in the Galericinae. This is confirmed by the morphology of the M2. In Erinaceinae the labial side of this cusp is usually slanted, the posterior side of the molar being clearly narrower than the anterior side. In the Galericinae the posterior side of the M2 is also narrower, but here we see a more labial placement of the hypocone and a rather straight labial outline. Comparison with illustrations in literature shows that this character generally holds true, with two exceptions. The erinaceine ? *Amphechinus* sp. 2 from Petersbuch 2 (Germany, MN 4) illustrated by ZIEGLER (1990; pl. 3. Fig. 11) has a straight labial side and the galericine *Neurogymnurus* sp. from Kilçak 3A (Anatolia, MN 1) figured by van den HOEK OSTENDE (1992; fig. 3) has a clearly slanted labial side. Notably, both these taxons were identified on the basis of the M2 only, and thus the correctness of the identifications is open to doubt. The M2 of *Riddleria* has a straight labial outline, as we would expect in a galericine.

Riddleria is of a similar size as the coeval *Galerix* species from Daroca-Calatayud area, its molars being somewhat longer, but narrower. Comparison with the dimensions of the molars of recent Galericinae from ZIEGLER (1983) shows that *R. atecensis* falls in the same size category of the Mindanao gymnure, *Podogymnura truei*. This inhabitant of the mountainous rain forests of Mindanao (Philippines) can reach a body length up to 15 cm.

As mentioned before, the morphology of the molars suggests a deviation of the usual omnivorous diet of the hedgehog family. With the hypoconid of the m1 entering the deep trigon basin of the M1, the sharp anterior arm of the protocone in combination with the protoconule would provide a strong slicing action along the anterior flank with the high posterior flank of the trigonid. The posterior flank of the talonid, mainly consisting of the entoconid and thick posterior cingulum, slices along the posterior arm of the protocone and the metaconule. Simultaneously the protoconid of the m2 would drop into the area left open by the posterior emargination, with the paraconid entering the narrow area between the hypocone and metaconule. The strong emphasis on slicing action suggests a carnivorous life-style, certainly if one takes into account the large labial blade of the P4, which would provide additional shearing action along the paralophid of the m1. This life-style may well account for the resemblance to *Plesiosorex*. ZIEGLER (1999) remarked on that genus: "Its carnivore-like dentition enabled *Plesiosorex* to feed on insects, other arthropods and even small vertebrates." *Riddleria* probably had a similar diet, although its smaller size would limit the number of vertebrate preys it could take on.

Considering *Riddleria* best placed in the Galericinae raises an interesting question about its ancestry, since the fossil record from Central Europe suggests that this subfamily was absent in the earliest part of the Neogene (ZIEGLER, 1999). The gymnures re-enter Europe near the MN 2-MN 3 transition, when *Galerix* migrates into the area, presumably from Anatolia (van den HOEK OSTENDE, 2001b). First of all it has to be noted that very little is known about the MN 1-MN 2 record of insectivores from Spain. So possibly, in contrast to Central Europe, Oligocene galericines may

have continued to survive in this area. If not, *Galerix* would make the likeliest ancestor, since it was the only Galericinae present in the area at the time. This would explain why *Riddleria* shares the posterior arm of the metaconule with the Galericipini and also account for the presumed similarity of the morphology of the M3. The P3 with a well-developed protocone also resembles the type usually found in *Galerix*. The transition to a dentition suitable for a more carnivorous diet would be obtained by a lateral compression of the upper molars and a heightening of the cusps and connecting ridges. Notably, van den HOEK OSTENDE (2001a) found an exactly opposite trend in the genus *Schizogalerix*, suggesting that the widening of the upper molars in this genus was indicative of a more herbivorous diet. If *Riddleria* is derived from *Galerix*, it would have to be included in the tribe Galericipini on phylogenetical grounds, despite not having the wide, rectangular upper molars considered characteristic for the tribe. It would take a full revision of the Eurasian Miocene erinaceids to verify or falsify this taxonomical position. Pending such an undertaking, classifying *Riddleria* as a Galericipini seems to be the best solution for the time being.

5. Acknowledgements

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PLATE 1*Riddleria atecensis* nov. gen. nov. sp. from Ateca III

Fig. 1 fragm. P4 sin. (51.84, Institute of Earth Sciences, Utrecht University); paratype a. occlusal view; b. labial view.

Fig. 2. M1 sin. (51.82, Institute of Earth Sciences, Utrecht University); holotype a. occlusal view; b. labial view.

Fig. 3 M2. sin. (51.81, Institute of Earth Sciences, Utrecht University); paratype a. occlusal view; b. labial view.

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Fig. 4. M3. sin. a. occlusal view; b. labial view.

PLATE 1

