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RESEARCH ARTICLE



Revised taxonomy and ecology of the Late Miocene Erinaceinae (Eulipotyphla, Mammalia) from Kohfidisch, Austria

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ABSTRACT

The scarcity of Miocene material attributed to Erinaceinae (Erinaceidae, Eulipotyphla) is a major limitation to the understanding of the whole fossil history of this subfamily. The present study describes the Late Miocene (MN11) hedgehogs of Kohfidisch (eastern Austria) based on a new material attributed to *Postpalerinaceus* cf. *vireti*, *Atelerix* cf. *steensmai* and *Atelerix* sp. Additionally, we support the presence of *Atelerix* cf. *steensmai* in the MN12 Moldovan locality of Čimišlija. Our findings confirm a pan-European diversity pattern in the Turolian, characterised by the spread of a few large erinacein forms showing a wide dietary spectrum. This pattern coincides with the establishment of marked seasonality and periods of drought in Europe. Based on actualistic observations, we hypothesise that durophagous dietary behaviour was a key survival strategy for Erinaceinae which had to rely on hard-bodied 'fallback' food. The selection of this behaviour likely contributed to the success and wide range of habitats of modern hedgehogs.

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Introduction

The fossil record of the Erinaceinae (Eulipotyphla, Erinaceidae) represents a major challenge for taxonomists. Fossil hedgehogs have received relatively little attention due to the difficulty of distinguishing species based on isolated dental remains and their usual rarity in small mammal assemblages (Van Dam et al., 2020; Ziegler 2005a). Furthermore, the main diagnostic characteristics of genera are located on the cranium (Gould, 2001), the preservation of which is even more uncommon.

The Middle to Late Miocene is a critical period in the history of European erinaceins, characterised by the last occurrences of the genera *Mioechinus* and *Postpalerinaceus* (Crusafont & Villalta, 1947; Butler, 1948; Ziegler 2005a, 2005b), and the advent of the modern genera *Erinaceus* and *Atelerix*. This apparent diversity masks an important morphological and morphometric dental overlap between taxa, resulting in a considerable quantity of material with uncertain specific and generic attribution. In fact, only type species can be clearly assigned to their respective genera. Even then, the blurred distinction between *Mioechinus*

and *Atelerix*, if both genera are indeed distinct, makes any statement about the generic diversity of the Miocene Erinaceinae tentative (see Butler, 1948; Mein & Ginsburg, 2002, Ziegler 2005a; Van Dam et al., 2020).

In this context, fissure fillings are of particular interest due to their high degree of preservation, both in terms of numbers and in completeness of the material (e.g. Mein & Ginsburg, 2002; Ziegler, 2005a). Of particular interest for the study of Late Miocene eulipotyphlans are the fissure fillings of Kohfidisch (Austria; Figure 1), which yielded rich and abundant material of insectivores initially described in detail by Bachmayer and Wilson (1970, 1978, 1980, 1990). These assemblages include the type material of *Schizogalerix zapfei*, *Petenyia dubia*, *Paenelimnoecus repenningi* and *Crusafontina kormosi*. The limited material attributed to Erinaceinae was insufficient for taxonomic determination. Moreover, at the time of publication our knowledge on fossil eulipotyphlans was still quite limited and major advances have been made over the last decades. In this study, we present additional material of Erinaceinae from the Kohfidisch fissures, shedding light on the diversity and palaeoecology of Late Miocene Central European Erinaceidae.

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Figure 1. Map of Europe showing the record of *Postpalerinaceus* (cf.) *vireti* (black squares) and *Atelerix* (cf.) *steensmai* (white circle), including the location of the studied locality of Kohfidisch (star) and the stratigraphic position of the locality relative to other Austrian assemblages (following Daxner-Höck et al., 2016; created with the software TimeScale Creator [v. 8.0, <https://timescalecreator.org/>]). (A) Cerro de los batallones (Van den Hoek Ostende & Furió, 2005); (B) Teruel basin (Van Dam et al., 2020); (C) Crevillente 2 (Van den Hoek Ostende & Furió, 2005); (D) Vallès-Penedès basin (Van den Hoek Ostende & Furió, 2005); (E) Lo foursnas 1993 (Mein, 1999); (F) Montredon (Mein, 1999); (G) Lissieu (Mein, 1999); (H) Dionay (Mein, 1999); (I) Soblay (Mein, 1999); (J) Schernham (Ziegler, 2006; this work); (K) Kohfidisch (this work); (L) Čimišljica (this work).

Material and methods

The Kohfidisch fissure filling system is situated in the Austrian part of the Danube Basin (eastern Austria; Figure 1). Since 1955, the Museum of Natural History of Vienna (NHMV) has conducted numerous official excavations at the site, resulting in one of the largest Miocene collections of small mammals in Europe (Bachmayer & Wilson, 1990). The geological setting of the locality is described by Bachmayer & Zapfe (1969) and Daxner-Höck et al. (2024). Daxner-Höck et al. (2024) also provided a detailed map of the locality. The material described here comes mainly from the third fissure (III, III unten, III oben), with additional specimens from the fissures I and II. We also consider six specimens whose exact provenance is unknown.

This work includes the material mentioned in the works of F. Bachmayer and R. W. Wilson, which consists of two upper molars and a broken mandible (in Bachmayer & Wilson, 1970), a second upper molar (in Bachmayer & Wilson, 1978), and an upper molar and a broken mandible (in Bachmayer & Wilson, 1980). This material had been classified under the name ? *Erinaceus* sp. (see Bachmayer & Wilson, 1980; Ziegler 2005a), a qualifier often used for limited samples of large Erinaceinae. The published collection is here extended with 38 specimens, discovered in unsorted material from the NHMW.

We follow the measurement protocol of Prieto & Rummel (2009) and the dental terminology of Cailleux

et al. (2023). Measurements were taken twice using a calibrated micrometre eyepiece on a Leica MZ75 stereomicroscope. They were then averaged and reported in millimetres (mm). Considering the numerous different protocols used for measuring the upper molars of Erinaceidae (Engesser, 1980; Rich, 1981; Doukas, 1986; De Jong, 1988, Mein & Suarez 1993; Prieto & Rummel, 2009; Van Dam et al., 2020), metric comparisons are mainly based on lower dental elements, when possible. All specimens described are housed at the Natural History Museum of Vienna, Austria.

Body mass estimation is based on the corrected allometric equation of Legendre (1989) for insectivora: $\text{Log}Y = \text{Log}(b) + k\text{Log}(X)$, where X is the product of the length and width, k is the slope, and $\text{Log}(b)$ is the intercept of the regression line. The 95% confidence interval is provided with $k = 1.8040$ and $\text{Log}(b) = 1.2430$ for the lower boundary and $k = 1.8860$ and $\text{Log}(b) = 1.3849$ for the upper boundary, as used by Cailleux et al. (2020) for Miocene Erinaceidae. This method has been applied to modern erinacein specimens (*Atelerix albiventris*, *A. algirus*, *Paraechinus aethiopicus*, *Hemiechinus auritus*, *Erinaceus europaeus*) housed at the zoological collection of the Naturalis Biodiversity Center, the Netherlands, and the estimated bodymass is consistent with the known body mass of these species. These estimates, including the comparative measurements of m1 and new cranial measurements of the holotype of *Postpalerinaceus vireti*, are provided in supplemental material.

List of abbreviations

H, height; L, length; W, width; W1, anterior width; W2, posterior width.

List of institutions

NHMV, Natural History Museum of Vienna, Austria.

Systematic palaeontology

Order **Eulipotyphla** Waddell, Okada and Hasegawa, 1999

Family **Erinaceidae** Fischer, 1814

Subfamily **Erinaceinae** Fischer, 1814

Genus **Postpalerinaceus** Crusafont & Villalta, 1947

Type species

Postpalerinaceus vireti Crusafont & Villalta, 1947.

Other referred species

P. intermedius (Gaillard, 1899); '*P.* *cingulatus*' Ziegler, 2005a.

Postpalerinaceus cf. vireti Crusafont & Villalta, 1947

Figures 2 and 3(A–B, E, G–H), Table 1

1970 - *Erinaceus?* spec. – Bachmayer & Wilson, p. 35.

1978 - *?Erinaceus* sp. – Bachmayer & Wilson, p. 136.

1980 - *?Erinaceus* sp. (pro parte). – Bachmayer & Wilson, p. 360.

2005 - *Erinaceus?* sp. (pro parte). – Ziegler & Daxner-Höck, p. 21.

Diagnosis

See Crusafont & Villalta, 1947.

Stratigraphic range

The type locality is Can Trullàs 1 (Viladecavalls), Spain, MN10. Various other occurrences are known from the Upper Miocene of western (Crusafont-Pairó and Gibert-Clos 1974; Mein, 1999, Antunes & Mazo, 1983; Van den Hoek Ostende et al., 2012; Van Dam et al., 2020) and Central Europe (Ziegler, 2006; this paper).

Referred specimens

From Kohfidisch I:one M2 (NHMW 2022/0016/0022); one edentulous mandible (NHMW 2022/0016/0003).

From Kohfidisch II:two M2 (NHMW 2022/0016/0023–0024); one m2 (NHMW 2022/0016/0010).

From Kohfidisch III:one P2 (NHMW 2022/0016/0028); two P4 (NHMW 2022/0016/0017–0018); two M1 (NHMW 2022/0016/0020–0021); one M2 (NHMW 2022/0016/0025); one broken mandible with m1, m2 and m3 (NHMW 2022/0016/0005); one broken mandible with m2 (NHMW 2022/0016/0008); one

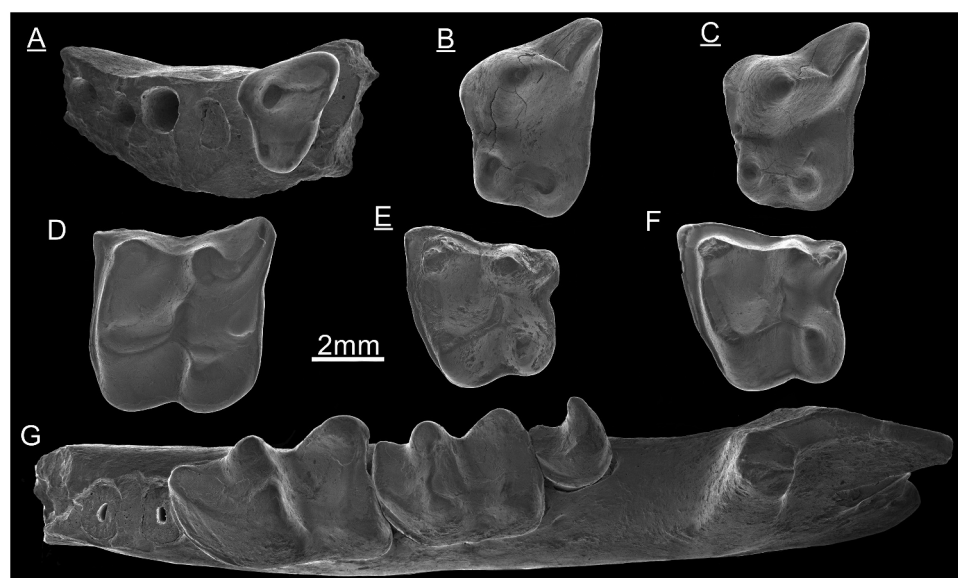


Figure 2. SEM pictures of *Postpalerinaceus cf. vireti* from Kohfidisch. **A:** Fragment of right maxillary with P3, NHMW 2022/0016/0016, indeterminate fissure; **B:** Right P4, NHMW 2022/0016/0017, fissure III; **C:** Right P4, NHMW 2022/0016/0018, fissure III; **D:** Left M1, NHMW 2022/0016/0019, indeterminate fissure; **E:** Right M2, NHMW 2022/0016/0022, fissure I; **F:** Left M2, NHMW 2022/0016/0025, fissure III; **G:** Broken left mandible with m1-m3, NHMW 2022/0016/0005, fissure III. Scale: 2 mm.

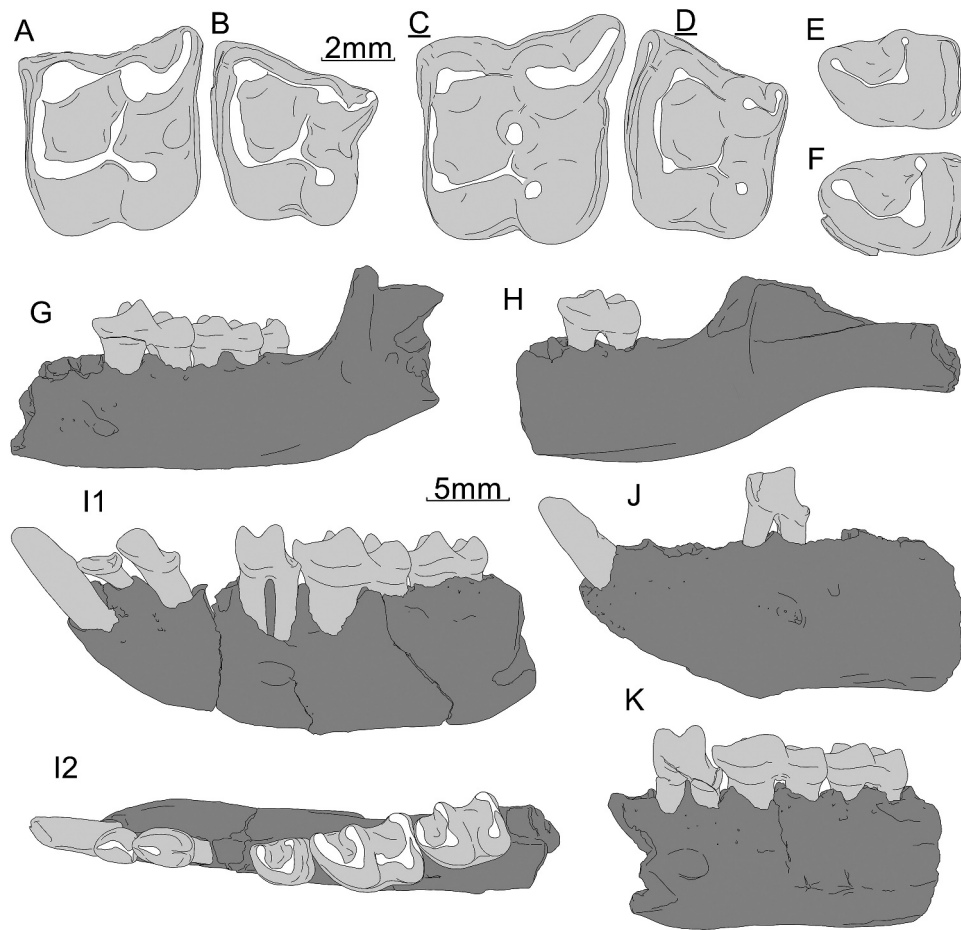


Figure 3. *Postpalerinaceus* cf. *vireti* from Kohfidisch (**A-B, E, G-H**), *Atelerix* cf. *steensmai* from Kohfidisch (**C-D, F, J-K**) and *Atelerix* cf. *steensmai* from Čimišlija (**I**). **A**: Left M1, NHMW 2022/0016/0019, indeterminate fissure; **B**: Left M2, NHMW 2022/0016/0025, fissure III; **C**: Right M1, NHMW 2022/0014/0010, fissure III; **D**: Right M2, NHMW 2022/0014/0011, fissure III; **E**: Left p4, NHMW 2022/0016/0027, fissure III; **F**: Left p4, NHMW 2022/0014/0004 (detail), fissure III; **G**: Broken left mandible with m1-m3, labial view, NHMW 2022/0016/0005, fissure III; **H**: Broken left mandible with m2, labial view, NHMW 2022/0016/0004, fissure III; **I**: Broken left mandible with i2-c, p4-m2, labial (**I1**) and occlusal (**I2**) views, collection TSU-Čimišlija-1/1 (unnumbered specimen); **J**: Broken left mandible with i2, p4, labial view, NHMW 2022/0014/0003, fissure III; **K**: Broken left mandible with p4-m2, labial view, NHMW 2022/0014/0004, indeterminate fissure. Scales: 2mm (**A-F**) and 5mm (**G-K**).

Table 1. Measurements (in mm) of *Postpalerinaceus* cf. *vireti* from Kohfidisch (MN11), Austria.

	P2		P3		P4			M1			M2			p4	
	L	W	L	W	L	W1	W2	L	W1	W2	L	W1	W2	L	W
N	1	1	1	1	2	2	2	2	3	2	4	4	4	2	2
Min					4.45	4.34	5.09	4.73	4.87	5.48	4.13	4.44	3.62	3.89	2.74
Max					4.58	4.39	5.52	5.13	5.26	5.69	4.75	4.88	4.29	3.96	2.85
Mean	2.59	1.99	2.74	2.70	4.52	4.37	5.31	4.94	5.06	5.59	4.50	4.73	3.94	3.93	2.80
m1		m2		m3		Mandible									
	L	W1	W2	L	W1	W2	L	W	H (under p4)					H (under m2)	
N	2	3	3	8	8	8	3	3	1					5	
Min	5.65	3.25	3.60	4.59	2.97	2.92	2.42	1.87						6.69	
Max	6.16	3.81	4.11	5.12	3.48	3.45	2.54	2.08						7.12	
Mean	5.91	3.54	3.79	4.88	3.29	3.32	2.49	1.96	6.58					6.96	

fragment of mandible with m3 (NHMW 2022/0016/0026); one edentulous mandible (NHMW 2022/0016/

0006); three p4 (NHMW 2022/0014/0006–0007, NHMW 2022/0016/0027); two m1 (NHMW 2022/

0016/0007–0008, NHMW 2022/0016/0029); four m2 (NHMW 2022/0016/0011–0014); two m2 (NHMW 2022/0016/0015).

From Kohfidisch, indeterminate fissure: one broken maxillary with P3 (NHMW 2022/0016/0016); one M1 (NHMW 2022/0016/0019); two edentulous broken mandibles (NHMW 2022/0016/0001–0002); one m2 (NHMW 2022/0016/0009).

Body mass estimate

C.a. 1.25 kg, based on UU-2059 (0.82–1.22 kg) from Masia del Barbo 2B (MN10; Van Dam et al., 2020) and NHMW 2022/0016/0007 (1.19–1.77 kg) from Kohfidisch (MN11; this work). The greatest skull length (64.4 mm) and the breadth of the braincase (28.9 mm) measured on the holotype of *P. vireti* from Can Trullàs 1 exceed or only slightly overlap the known size variability of the largest recent erinaceine species *Erinaceus europaeus*, *E. roumanicus* and *E. concolor* (see Ruprecht, 1972; Kryštufek, 2002, for comparisons). This is in line with the slightly larger body mass estimate of the fossil species (supplemental material).

Description

The maxillary fragment (NHMW 2022/0016/0016; Figure 2(A)) contains one P3 and four anterior alveoli. The configuration of the two most posterior alveoli indicates the presence of a double-rooted P2. The two anterior alveoli are not complete but show a similar morphology. They are interpreted as belonging to a double-rooted canine. Above the posterolabial root of P3 an invagination starts that is interpreted as the entrance to the infraorbital foramen.

The P2 is a broad and robust element with two posteriorly oriented roots. A narrow anterior cingulum is present. The main cusp is elongated anteroposteriorly and bears a strong posterior crest. This crest reaches a well-developed cuspule at the posterolabial corner. The posterolingual area is low and enlarged and partially enclosed by a straight lingual cingular crest. The P3 is a three-rooted premolar with a subtriangular outline (Figure 2(A)). A posterior crest emerges from the apex of the broad paracone and joins a low style that is incorporated into a posterolabial cingulum. The lingual extension is well developed and has a functional basin. The small protocone is labially connected to the anterolabial cingulum. A short but wide cingulum is present at the posterior margin of the lingual extension; an incipient protuberance is noticeable at the most lingual margin, between the posterior cingulum and the protocone. The P4 is a robust and rectangular premolar

(Figure 2(B–C)). The anterior and posterior margins are nearly parallel. In the occlusal view, the labial margin is straight in one specimen and concave in another. The paracone is massive and conical. From it emerges posteriorly a broad and sharp, two-segmented ridge. The protocone is an anteroposteriorly compressed cusp; its blunt labial crest joins the anterolabial cingulum. The conical hypocone is the lowest cusp and is connected to the base of the protocone by a straight and sharp ridge. In one specimen (NHMW 2022/0016/0018; Figure 2(C)), a crest-like accessory cusp is present near the labial flank of the hypocone.

The M1 is a square molar with a reduced metastylar region (Figure 2(D)). The anterior width is only slightly less than the posterior width. The metacone is as strong as the paracone and both are connected to their base by a low and straight ectoloph. A small parastyle is attached to the paracone. The paracone and protocone are connected by a broad loph with no discernible protoconule. The massive hypocone is connected to the protocone by a curved loph and to the posterior cingulum by a low posthypocrista. The posthypocrista, fused to the posterior cingulum, surrounds a relatively deep basin. The two molar basins are separated by a well-developed metaconule, which is connected to the protocone-hypocone loph by a short and robust crest. The M2 is longer than it is wide. The paracone and metacone are connected by a low, straight ridge. The parastyle is incorporated into a broad anterior and labial cingulum that runs from below the paracone to below the metacone. The metacone is slightly elongated anteroposteriorly. The postmetacrista is short and turns labially to join the metastyle. There is a thick paracone-protocone loph. A robust crest starts from the protocone and incorporates a blade-like metaconule. In two out of three specimens (NHMW 2022/0016/0023; NHMW 2022/0016/0025, Figure 2(F)), this crest ends at the lingual base of the metacone. The hypocone is weakly connected to this protocone-metaconule loph. A short but broad concave cingulum is present between the hypocone area and the metastyle.

The mandible has a straight corpus with similar heights below the p4 and below the m3. The dentition anterior to p4 is unknown. The posterolingual end of the mandibular symphysis is found below the p3. There is no constriction of the mandible between the m3 and the ramus. The masseteric fossa is well defined by the strong anterior profile of the ascending ramus. The angle of the ramus in NHMW 2022/0016/0005 (Figure 3(A)) is 76° (based on the method of Butler (1948): fig. 20). The angular process is elongated and slightly curved, but the mandibular condyle seems rather high (based on NHMW 2022/0016/0004,

Figure 3(B)). There is a single and marked mandibular foramen between the posterior root of p4 and the anterior root of m1.

The p4 is subtriangular (Figure 3(E)). The paraconid is conical and only slightly lower than the protoconid. The paralophid has a distinct notch. The small metaconid reaches half the height of the protoconid. The talonid is simple in morphology: broad and anteroposteriorly compressed. One specimen (NHMW 2022/0014/0007) is not completely formed and lacks roots and a fully developed talonid. On m1, the paraconid is well developed, although lower than the protoconid and metaconid (Figure 2(G)). It is connected to the protoconid by a slightly curved paralophid. The protoconid and metaconid are joined by a low loph. The entoconid is the strongest cuspid of the talonid: it reaches the level of the metaconid. It is labiolingually compressed and bears a thin entocristid. The hypoconid is subtriangular in cross section and is connected to the trigonid wall by a low oblique cristid. The postcingulid is in contact with the postcristid. A narrow but continuous labial cingulid is present. The m2 differs from m1 by the shape of the paralophid, which is strongly anteriorly compressed. The paraconid is integrated into the paralophid (Figure 3(G)). In the talonid, the entocoid is lower than on m1, and the hypoconid is not in a more labial position than the protoconid. The m3 is oval-shaped and has a single, elongated root. The paraconid is integrated into the low and curved paralophid. The protoconid and the metaconid are similar in shape. There is no connection between these two cuspids despite their proximity. A short anterolabial cingulid is present.

Remarks

The described material represents a large-sized species with advanced dental features. The combination of a large size, anteroposteriorly compressed P3 and P4, a squared M1, a M2 without metaconule, a moderately strong metaconid on p4 and a rather high angle of the ascending ramus precludes an attribution to an *Amphechinus* species (see Baudelot, 1972; Bi, 2000; Viret, 1938). The reduction of the snout in our material, as indicated by the compressed upper premolars, rule out an attribution to *Mioechinus oeningensis* and the small '*M. tobieni*' (see Butler, 1948; Engesser, 1980). The dimensions of our material, as shown in Table 1, exceed those of '*Postpalerinaceus*' *cingulatus* (Ziegler, 2005b), *Atelerix rhodanicus*, and *A. depereti* (Mein & Ginsburg, 2002) while falling below those of *A. steensmai* (Van Dam et al., 2020).

The specimens display certain similarities with *Mioechinus* sp., as described from Petersbuch (Ziegler, 2005a), and *Postpalerinaceus intermedius* from Sansan

and La Grive-Saint-Alban (Baudelot, 1972; Mein & Ginsburg, 2002). These two Middle Miocene taxa are identical in size and differences almost exclusively concern the cranial region (Ziegler, 2005a). However, our P4 and M1 are clearly distinct from these two species. The P4, in which the parastyle is strongly reduced, the protocone is massive, and the lingual area is short (Figure 2(B–C)), is of a morphotype attested in the type material of *P. vireti* (Crusafont & Villalta, 1947). It is also attested in cf. *Postpalerinaceus* from Cañada 12 (Van den Hoek Ostende et al., 2012), the material of which has been reattributed to *P. cf. vireti* by Van Dam et al. (2020). *Postpalerinaceus intermedius* displays a less advanced type, still showing a parastyle and an extended posterolabial margin (Mein & Ginsburg, 2002: fig. 9). In a similar way, the P3 of *P. intermedius* (Mein & Ginsburg, 2002: fig. 8) is less anteroposteriorly compressed than in *P. cf. vireti* (Figure 2(A)), suggesting a lesser reduction of the snout. However, it should be noted that a great variation is found in the dimensions of the P3 in *Postpalerinaceus*, with our specimen being intermediate in size between the holotype of *P. vireti* (L = 2.18, W = 2.22; M. Furió, personal observation) and the material from Can Llobateres (Crusafont-Pairó & Gibert Clois, 1974). Regarding the smaller Vallesian '*P. cingulatus*', no upper premolar have been described from Rudabánya (Ziegler, 2005b). Whereas *P. vireti* seems to be the first erinacein displaying this P4 morphotype in Europe, it is worth noting that a similar type occurs in several lineages of modern hedgehogs (see Bai et al., 2022), differing only by the less bulbous lingual cusps, a feature already attested in the latest Miocene *Erinaceus samsonowiczii* (Doukas et al., 1995). The reduction of the metastyle area on M1, as shown in Figure 2(D), has also been observed in the single erinaceine species from Schernham (Austria, MN10), which is a locality both geographically and stratigraphically close to Kohfidisch (Figure 1). This M1 has been attributed to '? *Postpalerinaceus vireti*' by Ziegler (2006). So far, this morphology has not been described in the material from Can Llobateres (Crusafont-Pairó & Gibert Clois, 1974). After direct comparison, it is evident that the material from Kohfidisch and Schernham belong to a single species, sharing strong affinities with *Postpalerinaceus vireti*. The single large I2 from Krásno (Slovakia, MN11; Cailleux et al., 2023), identified as cf. *Postpalerinaceus* sp., may represent the same species as well. It appears that the measurements of the lower molars from Kohfidisch (Table 1) are also consistent with those of *P. vireti* and *P. cf. vireti* from Spain, as reported by Van Dam et al. (2020). The dimensions of the P2, P4 and M1 match those of the holotype of *P. vireti* (M. Furió, personal observation).

Consequently, and taking into account the peculiar outline of the M1, the specimens from Kohfidisch and Schernham are classified as *Postpalerinaceus* cf. *vireti*. It is clear that this taxon shows a large morphometric and morphological variability (see Crusafont & Villalta, 1947; Crusafont-Pairó & Gibert Clols, 1974; Van Dam et al., 2020), especially in the P3, M1 and M2.

Genus *Atelerix* Pomel, 1848

Type species

Atelerix albiventris (Wagner, 1841).

Other referred species

Atelerix frontalis (Smith, 1831); *Atelerix algirus* (Lereboullet, 1842); *Atelerix sclateri* Anderson, 1895; *Atelerix depereti* Mein & Ginsburg, 2002; *Atelerix rhodanicus* Mein & Ginsburg, 2002; *Atelerix steensmai* Van Dam et al., 2020.

Diagnosis

See Frost et al., 1991.

Atelerix cf. *steensmai* Van Dam et al., 2020

Figures 3(C–D, F, J–K) and 4, Table 2

1980 - ?*Erinaceus* sp. (pro parte). – Bachmayer & Wilson, p. 360, pl. 3: fig. 14.

2005 - *Erinaceus*? sp. (pro parte). – Ziegler & Daxner-Höck, p. 21.

Diagnosis

See Van Dam et al., 2020.

Stratigraphic range

The type-locality is Masada del Valle 2, Spain, Local Zone L, MN12. *Atelerix steensmai* is also described from Masada Ruea (MN12), Spain (Van Dam et al., 2020).

Referred specimens

From Kohfidisch III: one M1 (NHMW 2022/0014/0010); one M2 (NHMW 2022/0014/0011); one mandible with i1 and p4 (NHMW 2022/0014/0003); one i3 (NHMW 2022/0014/0012); one p3 (NHMW 2022/0014/0005); one m1 (NHMW 2022/0014/0008).

From Kohfidisch, indeterminate fissure: one edentulous mandible (NHMW 2022/0014/0001); one mandible with p4, m1 and m2 (NHMW 2022/0014/0004).

Body mass estimate

C.a. 1.69 kg, based on NHMW 2022/0014/0004 (1.45–2.20 kg) from Kohfidisch (MN11; this work) and on the unnumbered mandible (1.25–1.88 kg) from the collection TSU-Čimišlija-1/1 (MN12; Rzebik-Kowalska & Lungu, 2009; this work).

Description

The subrectangular M1 is wider than it is long, as shown in Figure 4(A). In the occlusal view, there is a constriction about half-way between the lingual and

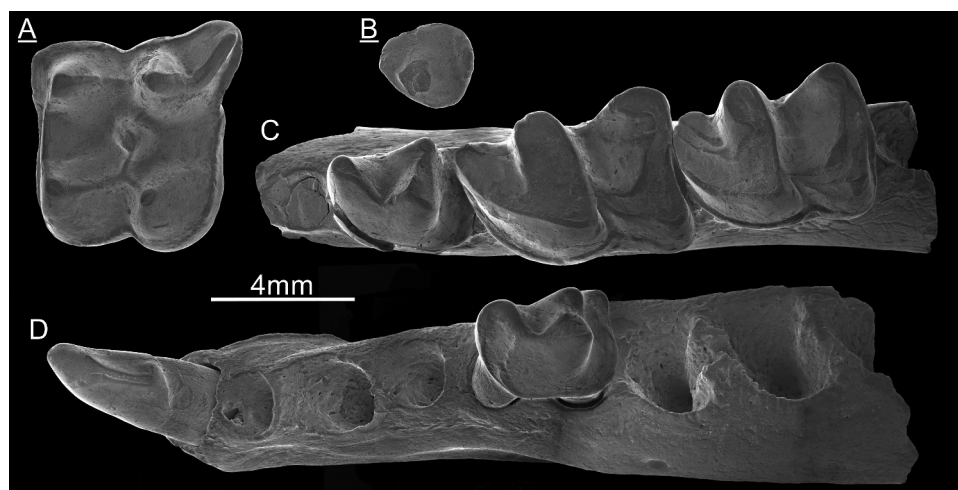


Figure 4. SEM pictures of *Atelerix* cf. *steensmai* from Kohfidisch. **A:** Right M1, NHMW 2022/0014/0010, fissure III; **B:** Right p3, NHMW 2022/0014/0005, fissure III; **C:** Broken left mandible with p4-m2, NHMW 2022/0014/0004, indeterminate fissure; **D:** Broken left mandible with i1 and p4, NHMW 2022/0014/0003, fissure III. Scale: 4mm.

labial margins. The conical metacone is connected to a low and wide metastyle by a curved postmetacrista. The paracone is connected to the base of the metacone by a thin postparacrista. The massive protocone is connected to the paracone by a high, two-segmented paraloph. There is no distinct parastyle, but a broad cingulum runs along the entire anterior and labial margins. The protocone-hypocone-metaconule loph is low and rather narrow. The metaconule is strong and connected to the protocone-hypocone crest. There is a thin premetaconule crest. A thick but short lingual cingulum is present. There is a thin oblique posthypocrista which terminates freely without joining the posterior margin. The posterior cingular crest runs along the entire posterior margin; in its central part, the posterior margin is low-crowned. The M2 is a strong, almost square-shaped element with the exception of the slightly extended parastylar area (Figure 3(D)). The metacone is conical and connected to a strongly compressed, blade-like metastyle. There is a narrow but deep incision at the base of these two structures. The paracone is triangular in the cross-section. The parastyle is strong and connects to the broad anterior and labial cingulums. The ectoloph is low and straight. There is no protoconule on the thick paracone-protocone connection. The protocone-hypocone-metaconule connection is low and thin. The metaconule is indistinguishable from the labiolingual ridge, which reaches the base of the metacone. The cingulums are thick and straight. The labial cingulum ends before the metacone.

As shown in Figure 3(J–K), the mandible has a straight, massive corpus. It becomes thicker below the p4, where the oblique mandibular symphysis ends. The alveole of the lower canine is larger than the alveole of i3 and the alveole of p3. A short diastema is found between the roots of p3 and p4 in one of the two adult mandibles (NHMW 2022/0014/0003, Figure 4(D)). The mental foramen is placed below the posterior root of p4. In one specimen (NHMW 2022/0014/0003, Figure 3(J)), there is also a small secondary foramen below the anterior root of the m1.

The i2 is a projected, high-crowned incisor with an oval outline (Figure 3(I)). A thin posterior cristid is present, running from the main cusp to the posterolingual base of the tooth. The i3 has an oval-shaped outline and a flattened surface. The single cusp at the centre of the tooth is contained within a thick mesocristid that turns labially on the posterior surface. It becomes thinner before touching the posterolabial corner. A well-developed posterior cingular crest is present. The single root is oblique and located posteriorly. In the occlusal view, the p3 has a slightly almond-shaped contour with an asymmetrical configuration (Figure 4(B)). The main

cusp has a slightly labial position. A low anterior ridge descends from this cusp. A distinct posterior cuspule is present, which is not connected to the main cusp but included in a posterior cingulid that continues to the middle part of the lingual margin. The single posteriorly placed root is slightly obliquely directed. The p4 is a massive tooth with a broad trigonid (Figure 4(C–D)). The paraconid is as high as the protoconid. There is a deep notch on the paralophid. The tip of the metaconid is barely independent; it is three-quarters as high as the protoconid. The trigonid basin is just a slope. The talonid is simple in morphology with a complete posterior cingulid. A weak labial cingulid is present.

The m1 has a trigonid and a talonid of similar length (Figure 4(C)). The trigonid is broad, with a curved paralophid, a subtriangular protoconid in cross section and a strong, conical metaconid. The metaconid is positioned slightly more anteriorly than the protoconid. The talonid has a labiolingually compressed entoconid. The hypoconid is weaker than the entoconid and in a more labial position than the protoconid. It is connected to the trigonid wall by an irregular and slightly curved oblique cristid. The postcingulid is in contact with the postcristid. The labial cingulid is continuous and thick. The anterior root is massive. The m2 (Figure 4(C)) differs from m1 by the compressed trigonid, resulting in a more curved paralophid, the presence of a short hook-shaped ridge starting from the paraconid and partially closing the trigonid basin, the less labially positioned hypoconid, and the straighter oblique cristid. The postcingulid is narrow and is not in contact with the postcristid.

Remarks

The dentition of the second species of Erinaceinae described here is surprisingly massive. Although some dental elements (Table 2) are found in the size range of *Postpalerinaceus* (cf.) *vireti*, the combination of a huge size and a strongly bunodont dentition is characteristic for *Atelerix steensmai*. The asymmetry of p3 is not a configuration observed in *Postpalerinaceus intermedius* (based on Mein & Ginsburg, 2002) and is unknown in *Mioechinus* (based on Butler, 1948; Ziegler, 2005a). It is identified in *Erinaceus* and *Atelerix*. Our p3 is distinct from modern species by the combination of a broad outline and a distinct anterior crest. With the exception of size, the p3 of Kohfidisch is very similar to that of *Atelerix* aff. *depereti* from the Teruel and Calatayud-Montálban Basins (Van Dam et al. (2020): fig. 2f). The type material of *A. steensmai* shows a less rounded posterolingual margin, but this character is subject to variation in *Atelerix albiventris* (F. Cailleux, personal

Table 2. Measurements (in mm) of *Atelerix cf. steensmai* from Kohfidisch (MN11), Austria.

	M1			M2			i2		i3		p3		p4	
	L	W1	W2	L	W1	W2	L	W	L	W	L	W	L	W
N	1	1	1	1	1	1	2	2	1	1	1	1	2	2
Min							2.47	2.32					4.05	2.85
Max							3.93	2.99					4.06	2.94
Mean	5.92	5.85	6.56	4.26	5.15	4.38	3.21	2.66	2.39	2.01	2.58	2.31	4.06	2.90
	m1			m2			Mandible							
	L	W1	W2	L	W1	W2	H (under p4)				H (under m2)			
N	1	2	2	1	1	1	2				2			
Min		3.98	4.26				8.88				8.60			
Max		3.99	4.49				9.46				8.87			
Mean	6.30	3.99	4.38	5.56	3.77	3.95	9.18				8.74			

observation). Our p4 matches the evolutionary stage of *Atelerix depereti*. However, they show a higher paraconid, as in *Mioechinus* sp. from Petersbuch 18 (Ziegler (2005a): fig. 4a). The bulbous cusps, high paraconid and moderately high metaconid differ from the configuration of *Postpalerinaceus vireti*. In '*P. cingulatus*', the p4 has a lower paraconid and a stronger labial cingulid (Ziegler, 2005b). The M2 of the latter species, although clearly smaller, share with our specimen the absence of metaconule and the robust cingulum.

The similarities observed with *Atelerix depereti* tend to support a similar generic assignment (as did Van Dam et al., 2020). However, both *A. depereti* and *A. aff. depereti* also show noticeable dental similarities with the late Middle Miocene *Mioechinus oeningensis* (Butler, 1948) and *Mioechinus* sp. from Petersbuch (Ziegler, 2005a). Based mainly on cranial features, Mein and Ginsburg (2002) included *Mioechinus* within *Atelerix* in the original description of *A. depereti*. A decision in this matter would require a thorough study of the record of these forms as well as of recent material of *Atelerix*. In fact, the presence of true *Atelerix* in the Middle and Late Miocene of Europe is still hypothetical.

The overall robustness of the mandible and the stronger angular outline of the mandible below p3/p4 are found in old individuals of *Erinaceus* and *Atelerix* (e.g. Flynn & Wu, 2017; Karataş et al., 2007; Mein & Ginsburg, 2002; Popov, 2004; Sulimski, 1959, 1962; Voyta, 2017). A comparable condition is observed in *Erinaceus samsonowiczi* from the Late Miocene of Maramena (F. Cailleux, personal observation) and in specimens of *Atelerix depereti* (Mein and Ginsburg (2002): plate 1, fig. 4 vs fig. 5), although in the latter species the mandible is less thick below the p4. In other extinct and extant genera (e.g. *Amphexinus*, *Hemiechinus*, *Paraechinus*, *Mesechinus*), the mandible is more gracile and has a more curved lower border in lateral view (e.g. Ai et al., 2018; Karataş et al., 2007; Viret, 1938).

The two mandibles of *Atelerix cf. steensmai* from Kohfidisch are the thickest ever recorded in a Neogene erinacein. These mandibles are even thicker than those of *Amphexinus gigas* from the Oligocene of Mongolia (Lopatin, 2002) and *Erinaceus olgae* from the late Pleistocene of China (Li et al., 2013; Flynn et al., 2017). The dental material is also one of the largest in terms of global dimensions, slightly exceeding the size of the Middle Miocene '*Amphexinus*' *robinsoni* (Gibert, 1975). *Atelerix cf. steensmai* differs from this species by the wider M1, the M2 with better developed cingulum and no metaconule, the proportionally larger p4 and presence of a labial cingulid on p4. The material of *Atelerix cf. steensmai* from Kohfidisch is also larger than any extant species of Erinaceinae in terms of mandibular thickness, dental dimensions and, by extension, body mass (supplemental material).

In the Neogene of Europe, only two mandibles are known that reach the size of the Kohfidisch material. These remains originate from the MN12 Moldovan locality of Čimišlija (Figure 1) and were assigned to '? *Erinaceus* sp'. by Rzebik-Kowalska & Lungu (2009). A direct comparison with this material was not possible, but from the palaeontological collection of the University Lyon 1 (UCBL) we retrieved a cast of a mandible (Figure 3(I)) that was figured by Rzebik-Kowalska and Lungu (2009): fig. 5c, collection TSU-Čimišlija-1/1). The cast contains an i3 (figured in Rzebik-Kowalska & Lungu, 2009: fig. 5b, figured as an isolated i2) and a canine still in position (identified but not figured). No significant morphological or morphometric differences are found between the material from Kohfidisch (Figure 3(J–K)) and the one from Čimišlija (Figure 3(I)). The specimens from Čimišlija are therefore also attributed to *Atelerix cf. steensmai*.

The type material of *Atelerix steensmai* consists of a few completely isolated specimens that show minor differences from our material. These differences are as follows: a better developed lingual cingulum on M1; a less posterior position of the 'metaconular' ridge and

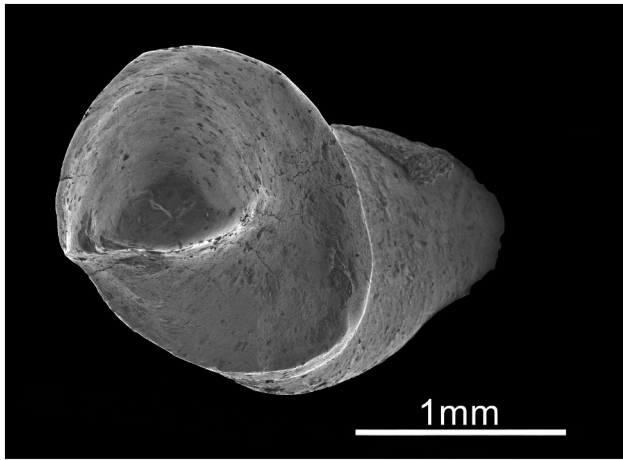


Figure 5. SEM pictures of *Atelerix* sp. from Kohfidisch. Right I2 (reversed), NHMW 2022/0015/0001, fissure III. Scale: 1 mm.

a less compressed metacone on M2; a still distinguishable entocristid on m2. The entocristid is completely absent on both the type material and the m2 from Čimišlija. The latter feature is known to be variable in *Erinaceus samsonwiczii* from Maramena, where the talonid is labially open on one out of two m1 and three out of five m2 (F. Cailleux, personal observation). All in all, the morphology of the M1-M2 supports that *Atelerix* cf. *steensmai* from MN11 of Kohfidisch is slightly less bunodont and therefore less derived than the MN12 type locality of Masada del Valle 2. This is consistent with the hypothesis of Van Dam et al. (2020) that *A. steensmai* evolved from the smaller and more generalist *A. aff. depereti*.

Atelerix sp.

Figure 5

Referred specimens

From Kohfidisch I: two fragments of edentulous mandibles (NHMW 2022/0017/0001: H below m2 = 5.69; NHMW 2022/0017/0002: H below m2 = 5.92).

From Kohfidisch III: one I2 (NHMW 2022/0015/0001: L = 1.44, W = 1.53), two DP2/P2 (NHMW 2022/0015/0002: L = 2.27, W = 1.69; NHMW 2022/0015/0003: L = 2.36; W = 1.75).

Description

The I2 has one posterolingually oriented root. The high cusp is positioned anterolabially and is slightly compressed transversely. The labial wall of the cusp is relatively short, while the posterolingual part of the

enamel extends in a lower position. As shown in Figure 5, the small posterolabial shoulder is bordered by a continuous cingulum. The DP2/P2 has a rounded outline. The main cusp is in a central position and has no anterior ridge. The anterior cingulum is well developed. Its middle part is elevated. The posterior crest is oblique and reaches the posterolabial margin as a low bulge. The posterolingual talon is variable in shape, resulting in a subangular outline in one specimen (NHMW 2022/0015/0002), and an outline with a small lingual extension in another (NHMW 2022/0015/0003). The two elongated roots are partially fused, with a separation still visible on the lingual and labial sides. In NHMW 2022/0015/0002, only the proximal part of the roots are fused.

The mandible has a rather strong and regular corpus. The single elongated alveole of the m3 is found posteriorly of the subrectangular alveoli of the m2. The mental foramen is located below the posterior alveole of the p4.

Remarks

Within the assemblages from Kohfidisch, these few specimens stand out by their smaller size and features. The compressed, elevated structure of the I2 rules out *Postpalerinaceus* and is more typical of *Atelerix*. The I2 of *Atelerix steensmai* is significantly larger than that of our specimen (L = 2.40; Van Dam et al., 2020) and has a massive base. Our specimen exhibits strong metric and morphological similarities with *Atelerix* aff. *depereti* from the Teruel Basin (Van Dam et al., 2020) and Krásno (Cailleux et al., 2023); after direct comparison, the only difference with the latter is the slightly broader posterolingual extension. The dimensions of our specimen are similar to those of *Atelerix depereti* from its type locality (Mein & Ginsburg, 2002). A morphological proximity is also found with the I2 of *A. rhodanicus* (Mein & Ginsburg, 2002), although this species is smaller.

The rounded P2 with an anterior cingulum and partially fused roots is also typical of *Atelerix* (based on Cailleux et al., 2023; Mein & Ginsburg, 2002; Van Dam et al., 2020); Our specimens differ from *Postpalerinaceus* cf. *vireti* by their slightly smaller size and the partly fused roots. The dimensions of the P2 fit within the variability range of *Atelerix* aff. *depereti* from the Teruel Basin (Van Dam et al., 2020). They also fit the upper size variability of *A. depereti* from La Grive Saint-Alban, but only in length (Mein & Ginsburg, 2002). Our P2 differs from that of *Atelerix* aff. *depereti* from Krásno (Cailleux et al., 2023) by its stronger cusp, and from *Atelerix depereti* from La Grive Saint-Alban (Mein &

Rodentia			Eulipotyphla
Dipodidae			Dimylidae
Eozapus intermedius		Sciuridae	<i>Plesiodimylus chantrei</i>
Eomyidae		<i>Miopetaurista</i> sp.	Erinaceidae
Eomyops catalaunicus		<i>Neopetes hoeckarum</i>	<i>Postpalerinaceus</i> cf. <i>vireti</i>
Keramidomys ermannorum		<i>Pliopetes hungaricus</i>	<i>Atelerix</i> cf. <i>steensmai</i>
Gliridae		<i>Pliopetaurista bressana</i>	<i>Atelerix</i> sp.
Glirulus lissiensis		<i>Spermophilinus</i> aff. <i>bredai</i>	<i>Schizogalerix zapfei</i>
Glis minor		family incertae sedis	<i>Lantanothereum</i> cf. <i>sanmigueli</i>
Graphiurops austriacus		<i>Epimeriones austriacus</i>	Soricidae
Muscardinus pliocaenicus			<i>Crusafontina kormosi</i>
Myomimus dehmi	Lagomorpha		<i>Petenya dubia</i>
Vasseuromys pannonicus		Prolagidae	<i>Paenelimnoecus repenningi</i>
Hystriidae		<i>Prolagus</i> sp.	'Neomyine?' sp'.
Hystrix parvae			Talpidae
Muridae			<i>Archaeodesmana vinea</i>
Apodemus lugdunensis	Chiroptera		<i>Desmanella rietscheli</i>
Collimys primus		Megadermatidae	<i>Storchia biradicata</i>
<i>Ischymomys</i> sp.		<i>Megaderma vireti</i>	<i>Talpa gilothi</i>
Kowalskia fahluschi		Rhinolophidae	
Kowalskia skofleki		<i>Rhinolophus delphinensis</i>	
Progonomys woelferi		<i>Rhinolophus grivensis</i>	
Prospalax petteri		Vespertilionidae	
Castoridae		<i>Myotis</i> sp.	
<i>Chalicomys jaeqeri</i>			

The two mandibles are attributed to an Erinaceinae based on their relatively large dimensions, the thickness of the mandible and the single alveole of m3. The two mandibles are significantly smaller than the material attributed to *Postpalerinaceus* cf. *vireti* and *Atelerix* cf. *steensmai*. Therefore, they are tentatively attributed to the same (unnamed) species.

Diversity and biogeography

With respect to Late Miocene insectivores of Europe, the extremely high diversity in Kohfidisch is only exceeded by that of Schernham (Austria, MN10). Both localities support the key role of the North Alpine Foreland Basin and the northwestern Pannonian Basin in the preservation of a rich eulipotyphlan community in the Vallesian and earliest

Erinaceinae are rare in Late Miocene deposits (e.g. Cailleux et al., 2023; Engesser, 1980; Rzebik-Kowalska & Lungu, 2009) leading to the erection of species based on limited material (e.g. Ziegler, 2005b) and to ambiguous identifications (e.g. Mein, 1999; Ménouret & Mein, 2008). For example, a large Erinaceinae from the Czech MN10 locality of Suchomasty was provisionally identified as *Erinaceus samsonowiczi* by Fejfar & Sabol (2005) but the presence of this latest Late Miocene to Pliocene taxon (Doukas et al., 1995; Sulimski, 1959, 1962) in the Vallesian is unlikely. Similarly, the presence of *Amphexhinus* in the Ukrainian MN9 locality of Grytsiv (Nesin & Topachevsky, 1999) is considered doubtful. *Amphexhinus* has been used as a wastebasket taxon for Erinaceinae so that the generic assignment of most Miocene *Amphexhinus* species is actually questionable.

The Erinaceinae fauna from Kohfidisch is remarkably similar to the one identified in the early Turolian of Spain (Van Dam et al., 2020; Van den Hoek Ostende & Furió, 2005; Van den Hoek Ostende et al., 2012), characterised by a large *Postpalerinaceus* (cf.) *vireti*, a massive *Atelerix* (cf.) *steensmai*, and a medium-sized *Atelerix*. Assemblages from the Late Miocene of Austria (Ziegler, 2006) and from Slovakia (Cailleux et al., 2023) are consistent with this diversity pattern as well. In addition, the identification of *Atelerix* cf. *steensmai* in the Turolian of Čimišlija (Moldova, MN12) possibly suggests an even more eastern presence of this pattern. As mentioned by Van Dam et al. (2020), this European homogeneity probably lasted until the MN13, as indicated by the last occurrence of the European *Atelerix* branch (La Gloria 5, Spain; Van Dam et al., 2020) and the first unambiguous record of the modern genus *Erinaceus* in Europe (Maramena, Greece; Doukas et al., 1995). The tentative identification of *Erinaceus* (Sen, 2001) in the Turolian of Afghanistan may indicate a central Asian origin for the genus.

Paleoenvironment and paleoecology

The present study confirms the previously observed trend towards dental robustness (e.g. molarisation) and large size in European erinacein lineages during the Late Miocene (Van Dam et al., 2020). The differences in robustness between the mandibles of *Postpalerinaceus* cf. *vireti* and *Atelerix* cf. *steensmai* in Kohfidisch suggest two different degrees of adaptation to durophagy. Van Dam et al. (2020) suggest that the bunodont molars and crested upper canine of *A. steensmai* are efficient for crushing and cracking, respectively. The thick median crest of i3, the strong roots on lower molars, the massive, molarized p4, the high mandibles and the strong, oblique mandibular symphysis from Kohfidisch represent the same dietary signal, i.e. a clear adaptation towards hard-object feeding. *Postpalerinaceus* shows fewer of these adaptive features and may have included more vertebrate prey into its diet (see Van Dam et al., 2020).

Modern Erinaceinae species feed on a wide range of items, including invertebrates (e.g. beetles, slugs and snails, crustaceans, worms), vertebrates (birds, reptiles, amphibians and small mammals), eggs and fruits (Corbet 1988; Gillies, 1989; Jones & Norbury, 2011; Mouhoub-Sayah et al., 2018; Murdoch et al., 2006; Wroot, 1984). Most hedgehogs are not opportunistic and favour the consumption of nutrient-rich, soft-bodied invertebrates, such as earthworms, slugs and larvae. They show marked differences in consumed prey depending on their seasonal availability and also

show age-related dietary changes, with old individuals being more specialised than young individuals (based on *Erinaceus*; Dickman, 1988).

Soft-bodied invertebrates are rare in the diet of hedgehogs originally living or introduced in more arid areas. In dryland habitats, Jones and Norbury (2011) note a high presence of earwigs in the diet of *Erinaceus*, despite their low-energy content. This is also the case in areas of low humidity or in seasonal periods of low rainfall (Wroot, 1984). Jones & Norbury (2011, p. 49) hypothesised that ‘earwigs [...] represent a good “fallback” food source when drier conditions mean that soft-bodied prey are less abundant’. A similar statement is made for ants, which are largely consumed by *Atelerix* (see Mouhoub-Sayah et al., 2018) and *Paraechinus* in summer (see Kaddouri, 2021). The point here is that, in modern Erinaceinae, the non-preferred food consists almost exclusively of hard-bodied prey. At the same time, it is well documented that fallback foods play a more important role in shaping food-processing structures than preferred foods (e.g. Laden & Wrangham, 2005; Marshall & Wrangham, 2007). Therefore, we hypothesise that durophagous dietary behaviour (i.e. hard-object feeding) was a key survival strategy for Erinaceinae that had to rely on fallback food.

The selection of large-sized Erinaceinae in the Late Miocene may be related to an increase of prey-size. Such a relation is known to occur in Eulipotyphla (see review of McNab, 2010). In our case, this may have accompanied the dietary shift towards hard-bodied invertebrates, as larger size likely favours the consumption of beetles and reduces biomechanical stress. Other possible explanations include the long-term availability of the same trophic niche and the impact of a summer-dry climate. The latter parameter has been analysed by Kryštufek et al. (2009) through the morphometric variability of *E. roumanicus* and reveals a strong negative correlation between size and precipitation: ‘For an animal that remains active throughout the year but faces fluctuations in seasonal availability in resources, the seasonality hypothesis predicts and increase in size’ (Boyce, 1978) (Kryštufek et al., 2009: p. 303). This adds to several studies suggesting that environmental seasonality may select for larger body size, although this is a highly multifactorial and much debated topic (e.g. Fuller et al., 2021; Lindstedt & Boyce, 1985; McNab, 2010; Millar & Hickling, 1990). In small mammals, mass loss has been documented in species that do not go into torpor (Dehnel’s phenomenon; see McNab, 2010). Modern Erinaceinae use a different strategy, as there is a minimum mass requirement (‘critical mass’) for hedgehog survival during the torpor season (Gillies, 1989; Rasmussen et al., 2019).

In the early Turolian, the presence of the large-sized European Erinaceinae coincides with a time of change in mammal communities, associated with the progressive establishment of seasonality and the spread of drier climates in Europe (Franzen & Storch, 1999; Spassov et al. 2006; Van Dam et al., 2023). These changes were already well attested in southwestern Europe during the Vallesian (e.g. Casanovas-Vilar et al., 2014; Van Dam, 2006), where the oldest occurrences of the large-sized *Postpalerinaceus vireti* are found. In the Iberian Peninsula, the large Vallesian and early Turolian Erinaceinae do not seem to show the latitudinal faunal pattern (see Furió & Agustí, 2017; Furió et al., 2011) and coastal-inland faunal differences (see Madern et al., 2018) observed for most insectivores, the European diversity of which greatly suffers during the Turolian. Cases of dietary shifts towards durophagy during the Turolian have also been documented in other mammal lineages and interpreted as the consequence of landscape opening and aridification (e.g. Thiery et al., 2021). The shrew lineage *Crusafontina-Amblycoptus* shows a similar adaptation during the Turolian, which is also accompanied by an increase in size (Van Dam, 2004). Another consequence of aridification is the extinction of the durophagous, humid-dependent Dimylidae family, abundant in Vallesian assemblages but lastly recorded in the earliest Turolian of central Europe (Cailleux et al., 2023). It is likely that the relative success of erinaceins and anourosoricins was favoured by the niche left vacant by the dimylids. All things considered, it is clear that the largely spread Turolian Erinaceinae were living in a period of relatively low resources (although summers appeared to be less dry during MN12; Van Dam et al., 2023). Therefore, durophagy could have been selected in this group because of a more frequent reliance on fallback food throughout the year.

In summary: (1) hard-bodied invertivory is advantageous during periods of low precipitation; (2) in Erinaceinae, large size seems to be due to increasing prey size and/or seasonal variation; (3) the emergence and spread of a few large, hard-bodied, invertivorous omnivore species (sensu Reuter et al., 2023) during the Late Miocene coincided with the establishment of marked seasonality and periods of drought in Europe. This suggests that the history of Erinaceinae was influenced by environmental changes during the Miocene, notably at the end of the Middle Miocene and during the Late Miocene. Size and morphological adaptations similar to those of the Late Miocene European species likely accompanied and favoured physiological/behavioral adaptations observed in modern species. These are in particular the development of seasonal

reproduction (e.g. Alagaili et al., 2017), nocturnal habits (e.g. Corbet, 1988; Fuller et al., 2021; Gillies, 1989) and prolonged seasonal torpor (e.g. Dmi'el & Schwarz, 1984), with hedgehog quills being a possible pre-adaptation for the selection of the latter (see Gillies, 1989). If the mandibular periosteal growth lines (e.g. Haigh et al., 2014) are preserved in fossil material, they may provide further evidence of hibernation. In any case, these adaptations provide a convenient explanation for the ability of present-day hedgehogs to face harsh environments (Bai et al., 2022; Corbet, 1988) – from temperate regions with marked seasonality to deserts – unlike most eulipotyphlans.

Conclusion

The relatively abundant Erinaceinae material from the early Turolian of Kohfidisch, attributed here to *Postpalerinaceus cf. vireti*, *Atelerix cf. steensmai* and *Atelerix sp.*, confirms earlier observations on trends towards large size and dental robustness during the Late Miocene. The few, widely distributed European species show a broadening of their dietary spectrum compared to more ancestral Miocene species as a response to environmental and climatic change. The selection for a more durophagous diet seems to be a direct consequence of a marked dry season, implying a greater reliance on fallback food (i.e. hard-object feeding). This selection pattern provides a convenient explanation for the broad range of habitats occupied by modern hedgehog lineages, including arid and semi-arid environments.

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Data availability statement

All data underlying the findings of this study are available within this article and in the supplementary material, which can be accessed via the Figshare repository at DOI: 10.6084/m9.figshare.29290754.

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