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RESEARCH

Dental disorders and mandibular trauma: the last stand of the Miocene gymnure *Galerix stehlini* (Mammalia, Erinaceidae)

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Abstract

Dental disorders regularly occur in mammals. However, their identification and interpretation in the fossil record are extremely rare. Here, I report cases of dental disorders in fossils of insectivoran mammals in the permanent dentition of the endemic gymnure *Galerix stehlini* from La Grive-Saint-Alban (Middle Miocene, France). A supernumerary dental alveolus and several second lower premolars showing a varying degree of double-tooth anomaly (including root subdivision) are described for the first time in the fossil record of the Erinaceidae. These malformations are common in the material, suggesting an issue affecting a significant proportion of the time-averaged population. This pattern is interpreted as the result of reduced population size associated with habitat fragmentation. In addition, I report the first observation of dental anomalies in extant gymnures. Non-deleterious dental disorders are common in modern gymnures, especially hypodontia. Given the frequent parallel evolution toward mandibular shortening in erinaceid lineages, premolar hypodontia is interpreted as a repeatedly selected "anomaly". Finally, a mandibular trauma identified in *G. stehlini* is described and interpreted as bite marks produced by the upper incisors of a medium-sized galericine, probably *Parasorex socialis*. The reconstructed bite is consistent with threat-related gaping behavior observed in extant gymnures. Overall, these results suggest that the ecomorphotype of *Galerix* was relatively unsuccessful by the end of the Middle Miocene.

Keywords Dental development · Erinaceidae · Eulipotyphla · La Grive-Saint-Alban · Mandibular lesion · Middle Miocene · Palaeopathology

Introduction

Dental anomalies are relatively common in mammals (Chemisquy and Martin 2016; Bartosiewicz 2021), but given the usual paucity of paleontological material, their recognition and study in the fossil record are often challenging. Recent advances in the description and analysis of mammalian dental paleopathology (e.g., Ogden 2007; Towle 2017; Böhmer and Rössner 2018; Prieto et al. 2020; Esquivel et al. 2021; Salesa et al. 2024) have highlighted two key observations. First, the failure to recognise pathologies systematically can lead to the establishment of spurious taxa, such as the Middle Miocene lagomorph "*Heterolagus albaredae*" (now included in *Lagopsis penai*; see Crusafont et al. 1954; Moncunill-Solé et al. 2019) and the Pleistocene proboscidean "*Cryptomastodon martini*" (now included in *Stegodon trigonocephalus*; see Van Essen et al. 2006). Second, once anomalies become frequent within an assemblage, they can serve as diagnostic features, as in the case of the supernumerary M4 of the recent erinaceid *Mesechinus wangi* (Ai et al. 2018). The broader implication is that dental pathologies are part of intraspecific variability and therefore contribute to the morphological evolution of populations (Riga et al. 2013; Drehmer et al. 2015; Jentzsch et al. 2020; Esquivel et al. 2021; Love et al. 2022), even when that variability includes deleterious traits (Canguilhem 1966). Accordingly, the study of dental disorders is particularly important for understanding the effects of genetic, developmental, and environmental factors on dental formation and, ultimately, on evolutionary processes.

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During a comparative study of the extensive paleontological collection of Claude-Bernard University (Lyon, France), I discovered recurrent dental pathologies of the gymnure *Galerix stehlini* (Mammalia, Erinaceidae), in its type locality, namely the fissure fillings of La Grive-Saint-Alban (Middle Miocene; France). Dental paleopathologies have not previously been described in erinaceid fossils, and skeletal or dental anomalies in extant and extinct gymnures (subfamily Galericinae) are essentially unknown. This study aims to fill this gap. In addition, *Galerix stehlini* is only recorded from La Grive-Saint-Alban and has received little attention; the last detailed work on the species, including illustrated specimens, dates back to Viret (1938). This manuscript therefore also updates the original diagnosis of Gaillard (1929), provides modern imagery to make the distinctive features of *G. stehlini* more accessible, and proposes an ecological reconstruction to explain the frequent occurrence of pathologies in this species.

Materials and methods

The material described here comprises five mandibles and four isolated lower premolars. Additional specimens, including all dental elements of *G. stehlini*, were also examined to emend the diagnosis of the species. All specimens were collected from La Grive-Saint-Alban (Millat quarry, 45° 35’ 56” N, 5° 12’ 57” E), France, during several expeditions led by Pierre Mein. The material was identified through direct comparison with the collections of Claude-Bernard University, Lyon (UCBL).

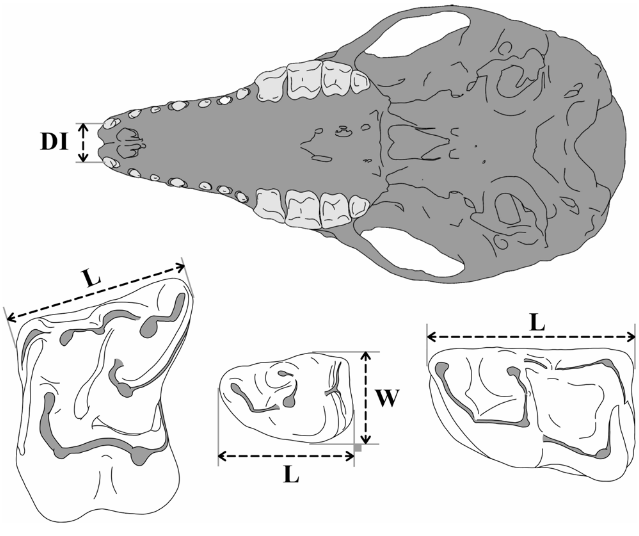

Fig. 1 Measurement protocol used to calculate the distance between the anteriormost margin of I1 (DI, illustrated on cranium of *Hylomys suillus*), the length of the upper molars (lower left, illustrated on a M1 of *Parasorex voesendorfensis*), the length and width of the lower premolars (lower middle, illustrated on a p4 of *Parasorex voesendorfensis*), and the length of the lower molars (lower right, illustrated on a m1 of *Parasorex voesendorfensis*). Image modified from Cailleux et al. (2023)

Lower and upper case letters indicate lower and upper dentition, respectively. Abbreviations are used for incisors (i), canines (c), premolars (p), molars (m), and deciduous teeth (d). Length (L) and width (W) measurements were taken twice, averaged, and reported in millimeters (mm). Measurements were obtained using a digital measuring microscope with a mechanical stage and digital measuring clocks. The measurement protocol follows Prieto and Rummel (2009). Length measurements follow the labial margin on upper molars and the lingual margin on lower molars (Fig. 1). On lower premolars, length follows the central anteroposterior axis and is perpendicular to width. Dental terminology follows Cailleux et al. (2023: Fig. 2). All specimens are figured in left orientation to facilitate future comparisons; right specimens were reversed and are indicated in the figures by an underlined letter. All material is housed in the Paleontological collection of the University Claude Bernard, Lyon 1 (UCBL), France.

To investigate the surface modification observed in one mandibular specimen, dental measurements were taken from extant adult erinaceids housed at the Naturalis Biodiversity Center (NBC), Leiden, the Netherlands (including figured specimens marked ZMA, from the former Zoological Museum of Amsterdam); the Slovak National Museum, Natural History Museum (SNM-NHM), Bratislava, Slovakia; the Department of Biology of Comenius University (UK); and the National Museum of Natural History (MNHN), Paris, France. These data were used to calculate the allometric relationship between the length of m2 (m2L) and the distance from the anteriormost margin of I1 (DI; Fig. 1) in extant gymnures (excluding *Echinosorex gymnura*) and hedgehogs. Online Resource 1 provides several dental measurements (M1L, M2L, p4L, m1L, m2L, m3L, DI) and identifies dentognathic anomalies, if present.

Geological and paleontological setting

La Grive-Saint-Alban is a complex of siderolitic, clay-filled karstic fissures that has been known since the nineteenth century for its abundance of paleontological remains (Jourdan 1861; Depéret 1892; Gaillard 1899; Viret 1951). The history and geological context of these fissures were described in detail by Mein and Ginsburg (2002). The site is among the richest Miocene localities in terms of both material and diversity. The fissures from La Grive-Saint-Alban are diachronic, meaning that they were not filled simultaneously. Consequently, fissures M (Millat quarry) and L3 (Lechartier

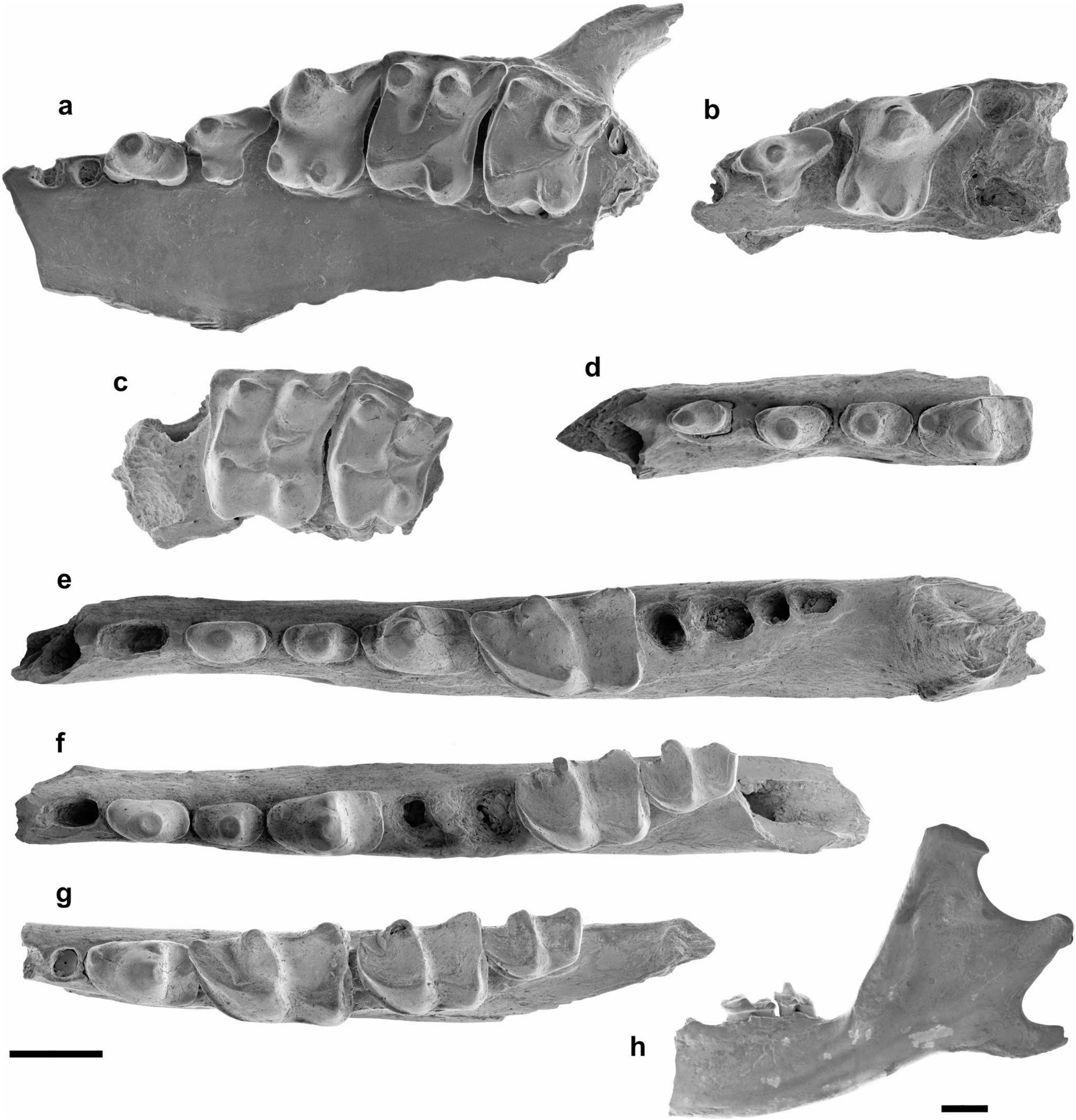

Fig. 2 SEM images of *Galerix stehlini* from La Grive-Saint-Alban, fissure M. **a**. UCBL-FSL 217946, left maxillary with P2-M2; **b**. UCBL-FSL 217947, left maxillary with P3-4; **c**. UCBL-FSL 217948, right maxillary with M1-2; **d**. UCBL-FSL 217949, left hemimandible with p1-4; **e**. UCBL-FSL 217950, left hemimandible with p2-m1; **f**. UCBL-FSL 217951, right hemimandible with p2-4, m2-3; **g**. UCBL-FSL 217952, left hemimandible with p4-m3; **h**. UCBL-FSL 217964, posterior portion of right hemimandible with m2-3 in labial view. Scale bars equal 2 mm

quarry, third fissure) have been considered reference faunas for MN7 and MN8 (Mammal Neogene Unit), respectively (Mein and Ginsburg 2002), which are often merged into a single unit.

The high vertebrate diversity within each fissure at La Grive-Saint-Alban is partly a result of the taphonomic and sedimentological characteristics of fissure-fill assemblages. The individuals found in each fissure did not accumulate contemporaneously but instead accumulated over an extended period of time (Kidwell and Flessa 1995). Such deposits reflect longer and more complex formation processes than those of open-air sites (Bolliger 1997) and may include multi-layered infillings (e.g., Maridet et al. 2000). Fissures and caves infilling can span tens to hundreds of thousands of years (e.g., Farrand and McMhon 1997; Hearty et al. 2004; Constantin et al. 2014). This time-averaged nature of the fossil populations is particularly important for paleopathological studies, as recurrent diseases observed in fissure-fill deposits are more likely to reflect long-term processes rather than momentary crises.

La Grive-Saint-Alban has yielded a large number of new and endemic species. Among them, the erinaceid *Galerix stehlini* (Fig. 2) was originally described by Gaillard (1929) from an unknown fissure. It is now known from numerous specimens from fissure M and from a few specimens from fissure L7 (Lechartier quarry, seventh fissure). Mein and Ginsburg (2002) also reported its presence in fissure L3, although no material from that fissure has yet been formally described. In fissure M, *G. stehlini* is the second most abundant gymnure species, the most abundant one being *Parasorex socialis*.

Galerix stehlini belongs to the Galericinae, a subfamily of Erinaceidae (order Eulipotyphla or Lipotyphla; see discussion in Asher and Helgen 2010), which today is restricted to Southeast Asia (Corbet 1988; Jenkins and Robinson 2002) but was widely distributed from Europe to Africa and North America during the Neogene (Butler 1984; Van den Hoek Ostende 2001; Zijlstra and Flynn 2015). In Europe, Miocene representatives mostly belonged to the Galericini, an extinct tribe comprising at least seven genera (*Tetracus*, *Galerix*, *Riddleria*, *Schizogalerix*, *Parasorex*, *Apulogalerix*, and *Deinogalerix*). This group is characterized by pronounced morphological diversity and a wide range of dietary habits (Van den Hoek Ostende 2001, 2003; Masini and Fanfani 2013). Within this tribe, *Galerix* is a relatively unspecialized and diverse genus that declined in abundance during the late Middle Miocene. The last surviving species were *Galerix rutlandae* in South Asia (Zijlstra and Flynn 2015), *Galerix exilis* from Spain and Germany (De Jong 1988; Prieto et al. 2011), and *Galerix stehlini*, the latter being a large-sized species considered to be a descendant of the Early Miocene species *Galerix aurelianensis* (Ziegler 2000).

In Galericini, the second lower premolar is an elongated, simple, two-rooted tooth bearing a single cuspid in a slightly anterior position, sometimes accompanied by a short posterior cingulum or at least a weak posterior shoulder (Fig. 2d-f). The diagnostic dental traits – mainly the p4 morphology and p2/p3 ratio – of *Galerix stehlini* allowed the identification of nine right mandibles and ten left mandibles with nonpathological p2 in the collection from fissure M assembled by Pierre Mein. In addition, three mandibles with p2 and four isolated p2s showing varying degrees of double-tooth anomaly were identified.

Systematic palaeontology

Order Eulipotyphla Waddell, Okada and Hasegawa, 1999
Family Erinaceidae Fischer, 1814
Subfamily Galericinae Pomel, 1848
Tribe Galericini Pomel, 1848
Genus *Galerix* Pomel, 1848
Type species: *Viverra exilis* (de Blainville, 1839).

Galerix stehlini Gaillard, 1929
Figures 2, 3, 4 and 5.

Holotype: Right mandible with c-m3, MDC Lgr 184; figured in Gaillard (1929: Fig. 1, p. 46); La Grive-Saint-Alban, unknown fissure. The holotype is housed at the Musée des Confluences (MDC), France.

Localities: La Grive-Saint-Alban, France; fissures M, L7 and L3.

Age: Late Middle Miocene, MN7/8.

Diagnosis (emended): *Galerix stehlini* differs from other members of its genus by the following combination of characters: large size, weak development of P3 (the lingual extension is narrow and bears only a small protocone), protocone-metaconule connection always present on M1 and M2 (on 203 M1 and 155 M2), bulbous hypocone weakly connected to the protocone-metaconule crest on M1 and M2, subtriangular M3 with a prominent paracone, small p3, and usually with a reduction of the metaconid on p4. The species is further characterized by a short postmetaconule crest on M1 (in 199 of 200 specimens) and M2 (in 145 of 150 specimens).

Material: Three right mandibles, two left mandibles, one right p2, and three left p2 (UCBL-FSL 217955–217963) (Table 1).

Comparative material: Ten right mandibles and eleven left mandibles. Comparative measurements are available in Table 1.

Description: UCBL-FSL 217955 is a right mandible bearing the unworn p2 and p3 and a broken p4 (Fig. 3a). The alveoli of c and p1, and the anterior alveolus of m1 are preserved. The second lower premolar is inflated and elongated. This tooth consists of two rounded parts, each bearing a cuspid of similar shape and height. The posterior part is longer than the anterior and bears a weak posterior cingulid. The anteriormost part is simple and shows a slight lingual orientation. The two cuspids are separated from each other at half their height. The anterior part of the tooth has

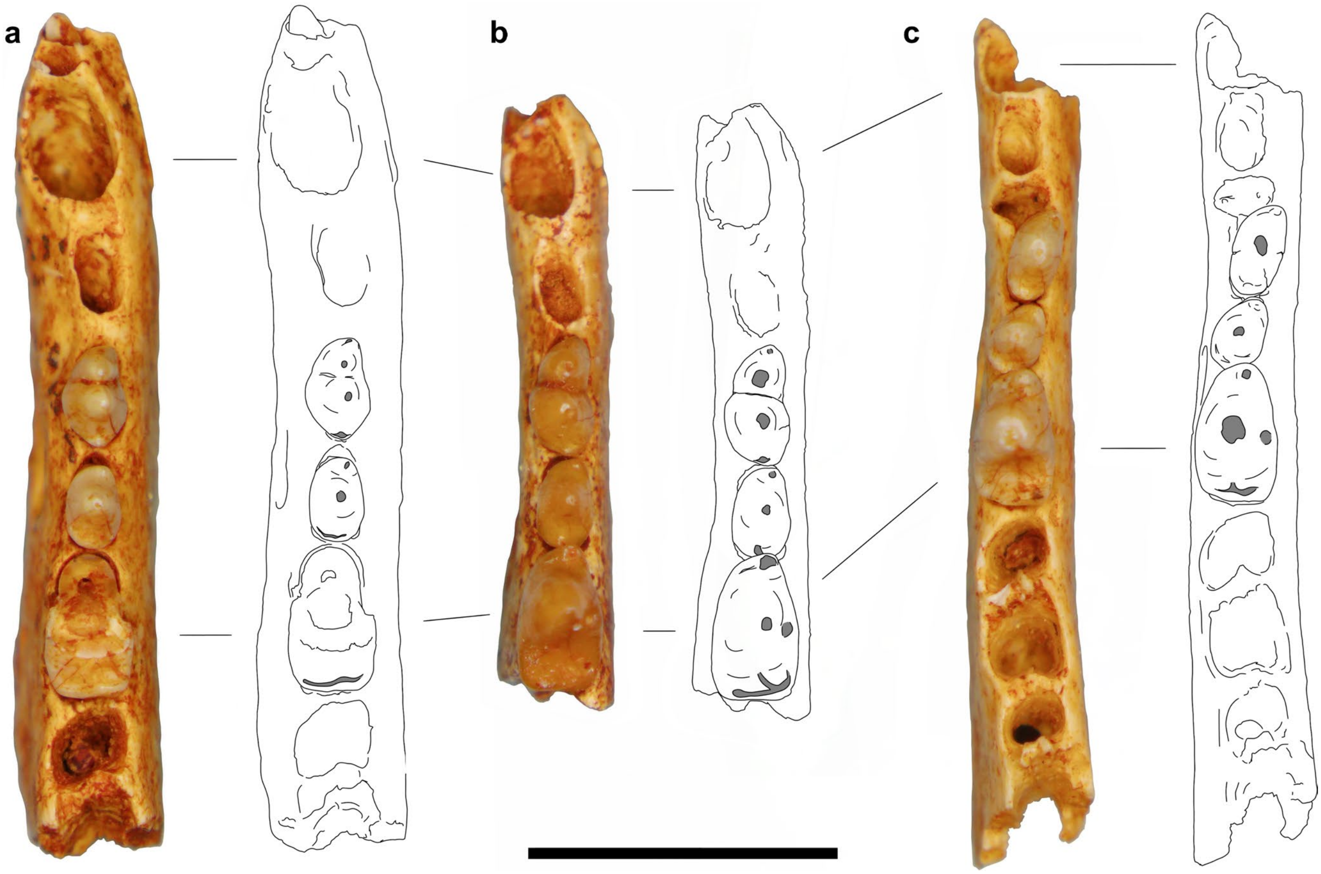

Fig. 3 Photographs (left) and line illustrations (right) of left hemimandibles of *Galerix stehlini* with pathological dental elements. **a**. UCBL-FSL 217955, right hemimandible with p2-4; **b**. UCBL-FSL 217956, left hemimandible with p2-4; **c**. UCBL-FSL 217962, left hemimandible with p2-4. Lines indicate the position of the lower canine and p4. The right specimen, indicated by the underlined letter (**a**), is shown in left orientation

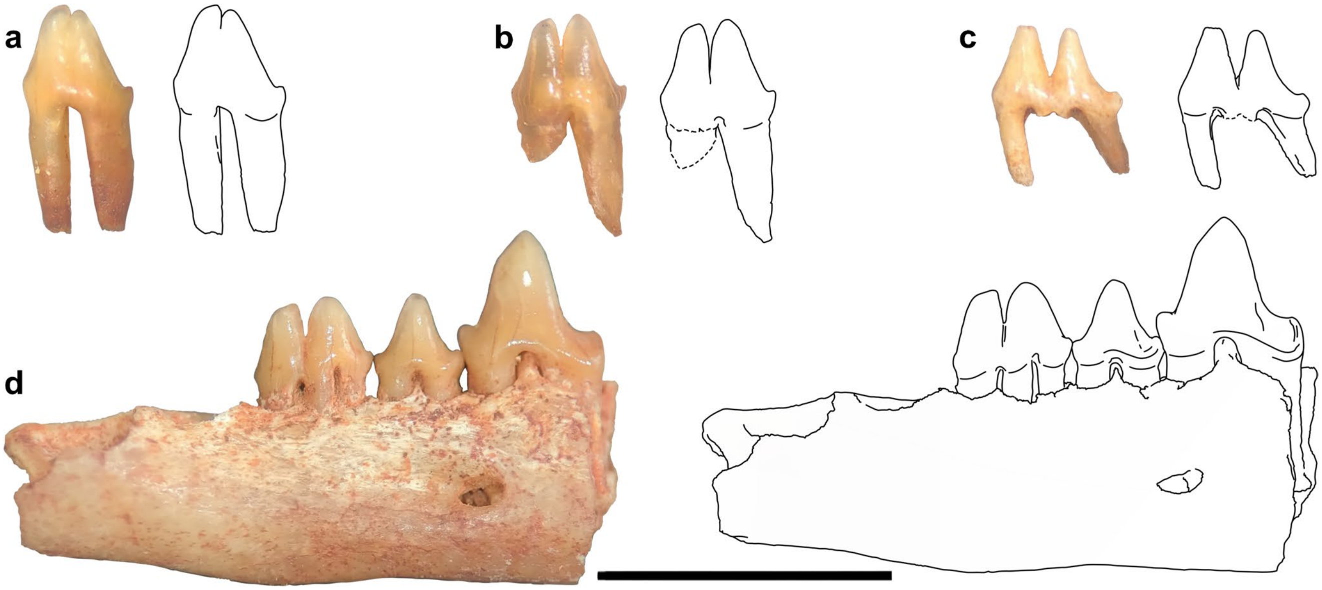

Fig. 4 Dentognathic specimens of *Galerix stehlini* showing pathological p2, with interpretation line drawings. **a**. UCBL-FSL 217961, left p2; **b**. UCBL-FSL 217960, left p2; **c**. UCBL-FSL 217958, right p2; **d**. UCBL-FSL 217956, left hemimandible with p2-4. The right specimen, indicated by the underlined letter (**c**), is shown in left orientation

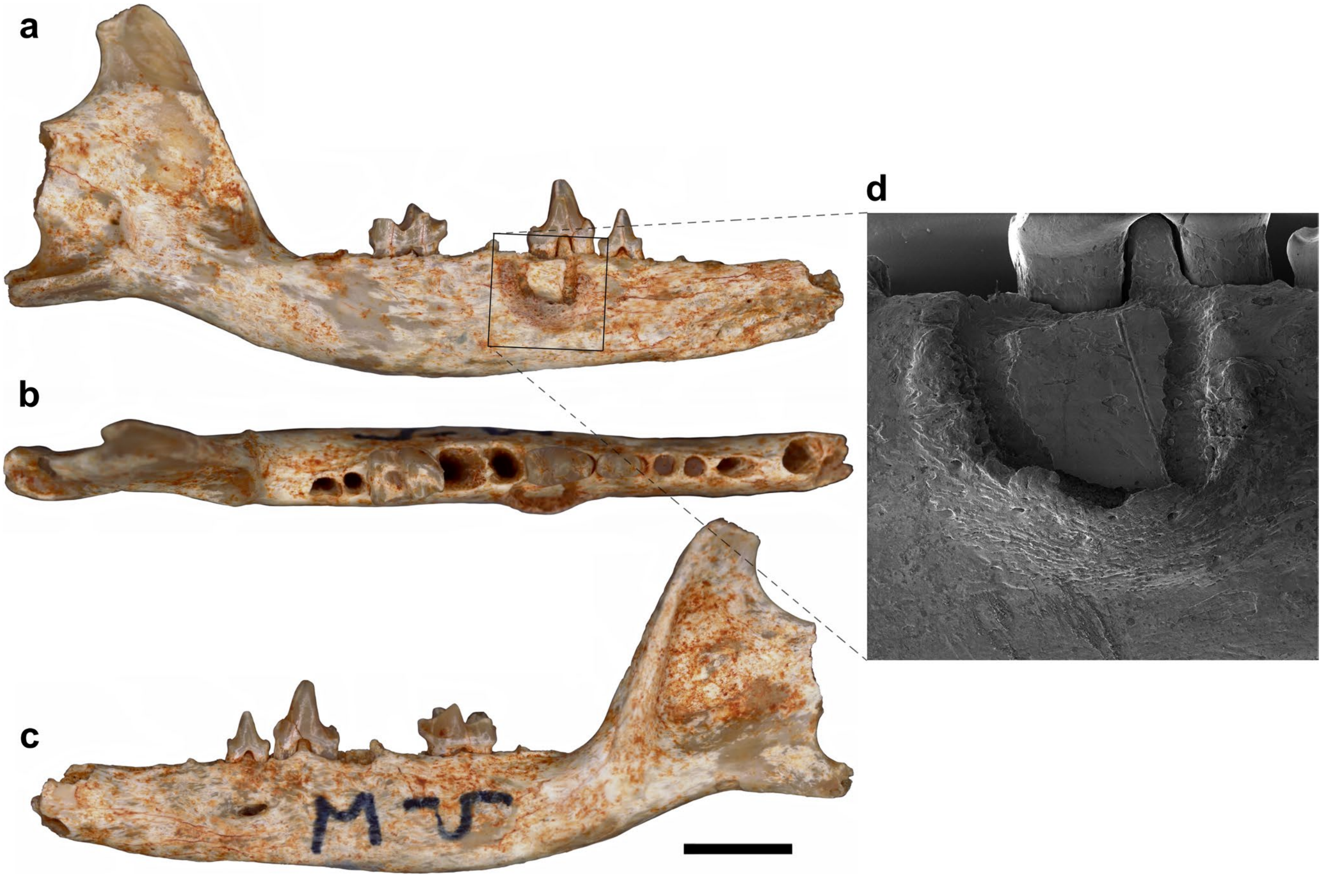

Fig. 5 Mandibular lesion in *Galerix stehlini*, UCBL-FSL 217963. Right hemimandible with p3-4 and m2 in lingual (**a**), occlusal (**b**), and labial (**c**) views; **d**. SEM image of the damaged area. Images are reversed

Table 1 Measurements of pathological and non-pathological specimens of *Galerix stehlini*, La Grive-Saint-Alban, MN7/8

	p1		p2		p3		p4	
	L	W	L	W	L	W	L	W
Comparative material (mean)	1.05–1.35 (1.20); *N* = 2	0.63–0.65 (0.64); *N* = 2	1.50–1.78 (1.66); *N* = 15	0.86–1.00 (0.94); *N* = 15	1.40–1.68 (1.55); *N* = 15	0.82–1.05 (0.94); *N* = 15	2.34–2.65 (2.49); *N* = 13	1.36–1.59 (1.48); *N* = 13
UCBL-FSL 217955			1.71	1.10	1.39	0.91		1.47
UCBL-FSL 217956			2.04	1.12	1.55	0.96	2.47	1.46
UCBL-FSL 217957			1.83	1.00	1.46	0.87	2.31	1.37
UCBL-FSL 217958			2.07	0.86				
UCBL-FSL 217959			1.77	1.06				
UCBL-FSL 217960			1.79	1.16				
UCBL-FSL 217961			1.71	0.96				
UCBL-FSL 217962			1.66	0.88	1.31	0.87	2.36	1.43

a single root. From the labial side, only a large posterior root is visible, but from the lingual side, two short posterior roots are clearly present, indicating an additional root (radix entomolaris).

UCBL-FSL 217956 is a left mandible with unworn p2, p3, and p4 (Figs. 3b and 4d). The alveoli of p1 and c are preserved. The anomalous p2 is similar in occlusal morphology and root pattern to that of UCBL-FSL 21795, except that the two cuspids are separated from each other below half their height. The posterior part is slightly labially oriented in the occlusal view, whereas the anterior part shows a weak lingual orientation. Both the length and width of p2 exceed those of non-pathological specimens (Table 1). The mandibular corpus is lower in height than in all other specimens.

UCBL-FSL 217957 is a right mandible with p2, p3, and p4. The alveoli of p1 and c are present, and all teeth are slightly worn. The anomalous p2 has a more developed anterior part than in UCBL-FSL 217955 and UCBL-FSL 217956, and the asymmetry is less pronounced. The posterior part of p2 is still longer than the anterior part. The two cuspids are fused at their bases. Only two roots are present, the posterior being broader than the anterior.

UCBL-FSL 217958 is a left p2 representing the most extreme expression of the double-tooth phenomenon in the sample (Fig. 4c). The two parts are nearly isolated and of similar dimensions. The cuspids are distinct and of equal height. Only the anterior and posterior roots are preserved, but a broken median root is clearly distinguishable. This third root emerges from the posterior margin of the anterior part and the anterior margin of the posterior part. It is unclear whether this root was divided. Although the width of the specimen falls within the range of variability of the species, the length of UCBL-FSL 217958 is a clear outlier.

UCBL-FSL 217959 is a left p2 with two partially fused cuspids and a narrow posterior cingulid. The anterior part has an oblique orientation. The two similar cuspids are separated by more than half their height. There are two roots, but the posterior one is irregular and enlarged lingually. On the labial side, a small spine is present between the roots.

UCBL-FSL 217960 is an inflated left p2 with an occlusal pattern similar to that of UCBL-FSL 217955 (Fig. 4b). The posterior part of the premolar is more developed. The two fused cuspids are separated by more than half their height. Two regular and robust roots are present.

UCBL-FSL 217961 is an almost non-pathological right p2 (Fig. 4a). Only one large cuspid is present, but with a slightly divided tip. A median constriction is visible on both sides of the cuspid. No other differences from non-pathological p2 are observed.

UCBL-FSL 217962 is a left mandible with p2, p3, and p4 (Fig. 3c). The single alveolus of the p1 is visible just anterior to the partially preserved alveolus of the lower canine. A supernumerary alveolus, wider than long and with a clear buccolingual orientation, is present posterior to p1 and almost in contact with p2. The p2 shows no clear anomaly in shape. It is anterolabially compressed and obliquely oriented towards the lingual side. The nonpathological p3 is also slightly compressed and similarly oriented. The p4 shows no pathology or modification of its usual orientation. The paraconid is low and small; the protoconid is high and conical; the metaconid is absent; and the posterior talon is broad with a thin posterior ridge.

UCBL-FSL 217963 is an almost complete right mandible with p3, p4, and m2 (Fig. 5). No dental anomalies are present. Beneath p4, two moderately deep and nearly parallel grooves are visible, merging at mid-height of the mandible (approximately 2.20 mm below the occlusal plane). The anterior groove is 0.40 mm wide, and the posterior one is 0.32 mm wide. Their minimum distance from each other is 1.50 mm in occlusal view, and the distance from the center of the grooves is 1.84 mm. In the lower external part of the lesion, the bone is more porous, producing a buccal enlargement of the mandible.

Clinical identification of dental paleopathologies

A wide range of dental pathologies has been documented in mammals (e.g., Verstraete et al. 1996; Kawada et al. 2006, 2011; Jogahara et al. 2008; Küchler et al. 2008; Ogden 2007; Uslu et al. 2009; Chemisquy and Martin 2016; Fiorenza and Kullmer 2016; Towle 2017; Towle and Irish 2020; Jentzsch et al. 2020; Rabenstein and Stiefel 2022; Voyta et al. 2024). These include anomalies in tooth number (e.g., hypodontia, supernumerary teeth), eruption disorders (e.g., impaction, ectopic eruption), calcification defects (e.g., taurodontism, hypoplasia), and morphological anomalies (e.g., microdontia, dens invaginatus). Based on studies of domesticated mammals and *Homo sapiens*, malformed teeth occur more frequently in the anterior dentition and deciduous dentitions (Verstraete et al. 1996; Aguiló et al. 1999; Rajab and Hamdan 2002; Türkaslan et al. 2007; Ozcan et al. 2016; Bartosiewicz 2021; Okabe 2024). In the present sample, the three specimens exhibiting such a pathology (UCBL-FSL 217955, 217956, 217957) belong to adult individuals, as indicated by the morphology of p3 and p4, which are easily distinguished from the more complex dp3 and the diagonally elongated dp4 of *Galerix*.

Most of the specimens described here (UCBL-FSL 217955 to 217961; Figs. 3a-b and 4a-d) fall within the category of malformations commonly referred to as double-tooth anomalies (e.g., Aguiló et al. 1999; Knežević et al. 2002; Drehmer et al. 2015; Chen et al. 2023), which are characterized by a complete or partial duplication of a dental element. Such anomalies typically result in malocclusion and malalignment, as observed in cases of complete duplication (i.e., supernumerary teeth; e.g., Fiorenza and Kullmer 2016). This can strongly affect overall dental configuration, as in specimens UCBL-FSL 217956 and UCBL-FSL 217962 (Fig. 3b-c). Double-tooth anomalies reflect either fusion or gemination, two processes that are difficult to distinguish (Carvalho et al. 1998; Aydinbelge et al. 2017) due to the lack of a standardized terminology (see Türkaslan et al. 2007).

Specimen UCBL-FSL 217962 displays an additional alveolus between the p1 and the canine (Fig. 3c). This could correspond either to a supernumerary adult premolar or to a persistent deciduous premolar. The latter hypothesis can be rejected for several reasons. First, there is no evidence that Galericini possess “dp1” or “dp2”; only dp3 and dp4 have been reported in the literature alongside p3 and p4 (e.g., Ziegler 1983, Mein and Ginsburg 2002, Cailleux et al. 2026). More generally, it remains unclear whether p1 and p2 in adults of the tribe Galericini are successional teeth (with or without a deciduous precursor) or whether they instead represent retained deciduous teeth, as this pattern is not homogeneous across mammalian groups (see McKay et al. 2022). Furthermore, given the lack of available space in the dental row of both juvenile and adult individuals, persistence of a deciduous premolar alongside the adult premolar would be less likely than in species with a dental diastema. Finally, the hypothesis of a persistent dp1 does not explain the abnormal transverse orientation of the alveolus. The most parsimonious hypothesis is that specimen UCBL-FSL 217962 possessed a supernumerary premolar that erupted simultaneously with p2. The absence of the tooth itself prevents determination of whether this represents a duplicated p1 or an asymmetrically split p2, although the size of the alveolus better matches the former.

Identification of dental pathologies in extant gymnures

Dental anomalies have been reported in living hedgehogs (e.g., Brockie 1964), but none have previously been documented in gymnures. As detailed in Online Resource 1, 15 of the 64 adult gymnure specimens (all from Naturalis) exhibit dental anomalies, including hypodontia, persistence of deciduous incisors, misaligned teeth, and dental displacement. Mandibles with fewer deciduous lower premolars (dp1 or dp2) are common among unmeasured juvenile specimens, but it is often unclear whether these teeth are absent or unerupted. Among the 64 adult skulls and mandibles, four lack one P1, one lacks both left and right P1s, one lacks one P2, two lack one p1, and one lacks both right p1 and p2. Mild hypodontia is therefore the most common dentognathic anomaly in the sample (14.1%). In contrast, dentognathic anomalies are far less common in erinaceines: only two *Erinaceus* specimens (3.2% of the Erinaceinae material) lack one of the anteriormost premolar (p3).

In the comparative material, three individuals (4.7% of adult specimens) originally identified as *Hylomys suillus* display a doubled p2. Two specimens show malformed, incompletely duplicated p2 (BE 6824–23941; BE 6824–23977), in which the anterior part lacks a talon, and the posterior part lacks an anterior cingulid. In BE 6824–23914, the doubled p2s are fully separated (Fig. 6). Partial and complete duplication of p2 is therefore also present in modern gymnures. All three specimens were collected at Tjiborni (near Bandung, West Java) in 1932. Among the 20 insular specimens (measured and unmeasured) of *H. suillus* from this specific collection (BE 6814–23911 to BE 6814–23979), adult mandibular specimens exhibiting two (hypodontia; BE 6814–23912), three (hypodontia; BE 6824–23970), four (e.g., BE 6824–23974), and five (complete duplication; e.g., BE 6824–23914) lower premolars in a single hemimandible have been identified.

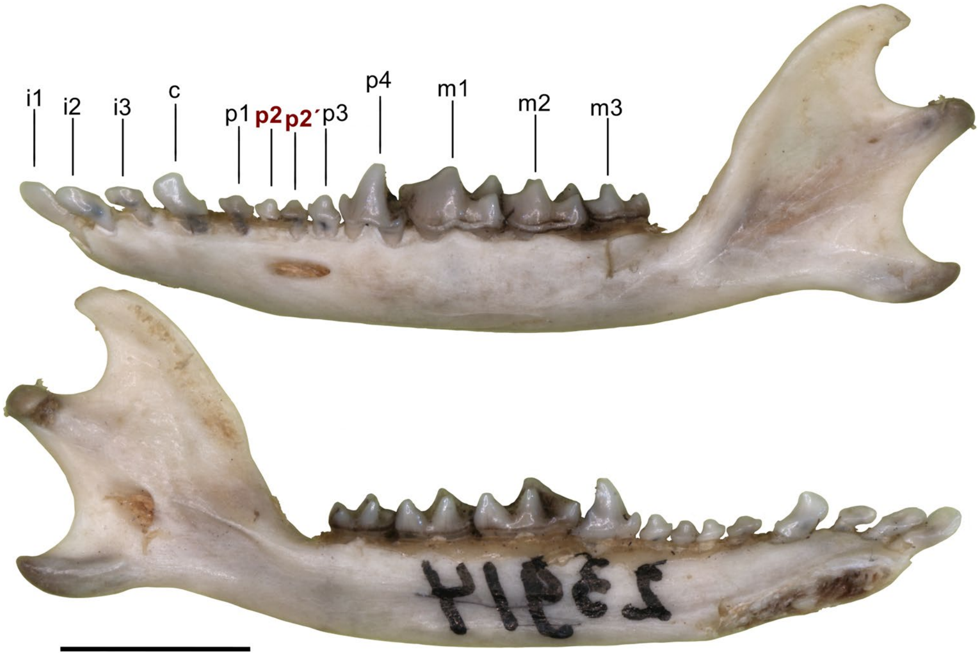

Fig. 6 Case of doubled p2 in a right mandible of *Hylomys suillus*, in labial (above) and lingual (below) views; BE 6824–23914, female, captured at Tjiborni, West Java, on 15 August 1932. Images are reversed

Identification and interpretation of a mandibular trauma (UCBL-FSL 217963)

The modification of the mandibular surface in specimen UCBL-FSL 217963 (Fig. 5) does not correspond to any known disease or pathology in hedgehogs (e.g., Savarin 2014; Lennox and Miwa 2016) and is therefore interpreted as a mechanical trauma resulting from a single event. There is no evidence for taphonomic alteration. The porous, spongy appearance of the superficial bone surrounding the lesion suggests an incomplete healing process, without formation of a fully developed bony callus. The presence of an abscess is suspected.

The two parallel lesions, whose spacing corresponds closely to the distance between the mandibular margin and p4, support the hypothesis of a bite delivered from above by two elements, most likely upper incisors. Bite marks of this type have been documented in small mammal bones (e.g., Mészáros 2014), but their interpretation in the fossil record remains particularly challenging (see Sera et al. 2009; Bennàsar et al. 2015; Furió 2017). At least, the deep, narrow, and well-separated grooves are inconsistent with the dental morphology of Rodentia, Heterosoricidae, or Desmanini. A bite from canines is unlikely, excluding other Talpidae. In Soricidae, the upper incisors are in contact, which would produce much narrower marks. The dimensions of the lesions are also inconsistent with small-bodied species of this family. At La Grive-Saint-Alban, medium-sized insectivores with elongated, caniniforms, and separated upper incisors occur only among adult erinaceids. Both galericines and erinaceines exhibit a similar pattern with elongated, slightly convergent I1. However, erinaceins possess much thicker incisors than galericines, as shown in the fossil record of *Atelerix* (Santana et al. 2010) and *Postpalerinaceus* (Crusafont and Villalta 1947), compared with *Parasorex* (Mein and Ginsburg 2002: fig. 22b) and *Lantanotherium* (see Cailleux et al. 2020: fig. 3o-p). The narrowness of the marks tends to exclude the Erinaceinae.

The fossil record of the Erinaceidae family, like that of most vertebrates, consists largely of isolated and fragmentary remains, making direct comparison with complete anterior skulls impossible. I therefore use allometric relationships (e.g., Legendre 1989; Gingerich and Smith 2025) to estimate the distance between the I1s and the length of the m2. The use of the m2 is justified by the significant, moderate to strong positive correlation found between m2L and DI in modern gymnures (Pearson's correlation test, $N=39$, cor = 0.605, p-value < 0.0001) and hedgehogs (Pearson's correlation test, $N=50$, cor = 0.496, p-value < 0.001). Also, m2 are morphologically conservative and are more frequent in the fossils. The allometric equations are $m2L = 1.1461\ \ln(DI) + 3.218$ for hedgehogs ($R^2 = 0.337$), and $m2L = 0.5957\ \ln(DI) + 1.8699$ for gymnures ($R^2 = 0.3633$).

Using this relationship, the estimated m2L for an erinaceine with DI = 1.835 is approximately 3.91 mm (Fig. 7), a value reached by the large species *Atelerix depereti* (data from Mein and Ginsburg 2002). Examination of the UCBL material, however, shows that the upper incisors of this species are far too wide to fit the bite marks. The estimated m2L for galericines, 2.23 mm, is smaller

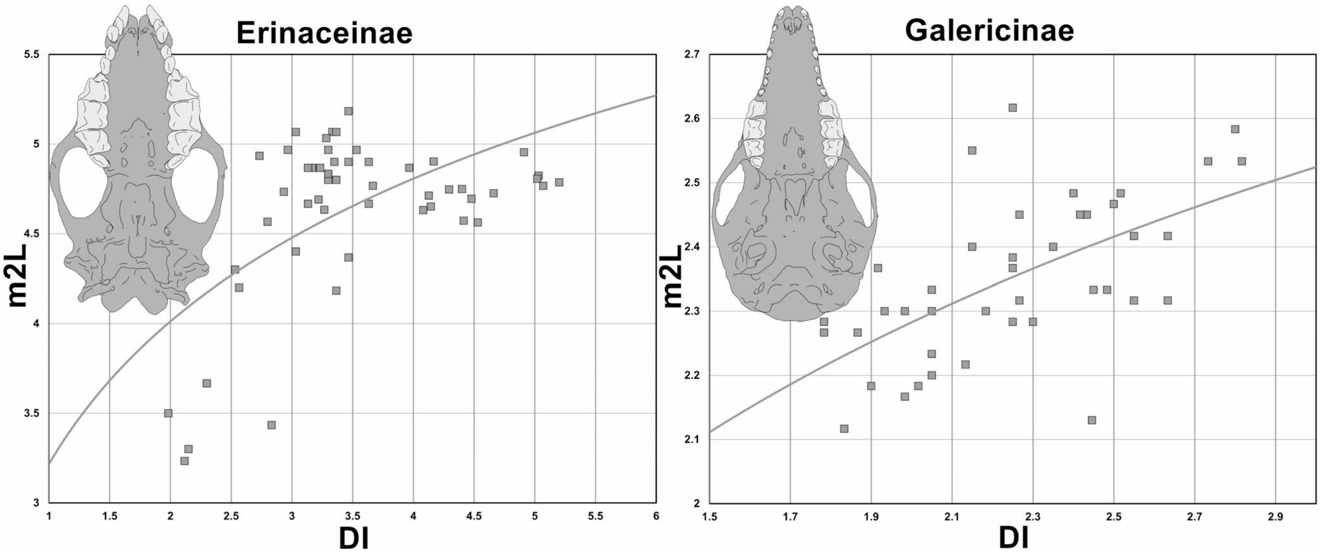

Fig. 7 Allometric relationship between the anterior distance of I1 (DI) and the length of m2 (m2L) in extant Erinaceinae ($N=50$) and Galericinae species other than *Echinosorex gymnura* ($N=39$), with logarithmic trend line

than that of *Lantanotherium robustum* and *L. sabinae* (data extracted from Mein and Ginsburg 2002). *Galerix stehlini* approaches the estimate but remains slightly larger (m2L: 2.50–2.97; *N*=7, fissure M; personal data). Finally, the variability of the m2L of *Parasorex socialis* (m2L: 2.26–2.89; *N*=220, fissure M; personal data) best matches the estimated length. I therefore considered *Parasorex socialis* the most likely candidate.

Discussion

Dental paleopathology in insectivores

Double-tooth anomalies have been identified in several mammalian groups (e.g., Drehmer et al. 2015; Martin and Chemisquy 2018; Irish 2024) and, to date, have been reported only rarely in extant insectivore specimens (e.g., in Talpidae, Kawada et al. 2006). However, I discovered Reumer (1984) illustrated a p4 of *Blarinoides mariae* (plate 26, fig. 9) from Osztramos 7 (Hungary; Pliocene) and an upper antemolar of a Soricidae (plate 24, fig. 9) from Csarnóta 2 (Hungary; Pliocene) that both display a double-tooth anomaly. Given the rarity of these anomalies, it is likely that strong modification of an isolated dental element greatly reduces the probability of its identification in the fossil record.

Previous literature has not firmly reported dental anomalies in erinaceid fossils. A special mention must be made of Wang et al. (2025), who recently described an M1 of Erinaceinae from the Early Miocene of Gusheng, Linxia Basin, China. This specimen (Wang et al. 2025: fig. 4.A) bears a small cusp on a posterolingual cingular crest – a feature previously unknown in the family. Following direct observation, the question remains as to whether this structure represents a dental pathology or is diagnostic of a new erinaceine taxon. These two possibilities are not mutually exclusive. Once again, dental anomalies are an inherent part of species variability and evolution.

Specimen UCBL-FSL 217962 (Fig. 3c) supports the presence of a supernumerary premolar, not previously documented in the fossil record of the Erinaceidae. Cases of supernumerary teeth have been reported in many mammalian groups, including primates (e.g., Schwartz 1984; Fioranza and Kullmer, 2016), rodents (e.g. Angelici and Luiselli 1999; Prieto et al. 2020), bats (e.g., López-Aguirre 2014; Esquivel-Melo et al. 2017; Esquivel et al. 2021), and non-erinaceid insectivores (Hall 1940; Stein 1962; Poduschka and Podu 1983; Kawada et al. 2006, 2011; Asahara et al. 2012; Okabe et al. 2021; Okabe, 2024). In recent erinaceids, a supernumerary tooth has been described in one specimen of *Erinaceus roumanicus*, in which a gymnure-like M3 is present between the M2 and M3 on both dental rows (Éhik 1928). Supernumerary teeth and double premolars also occur in *Erinaceus europaeus* (Brockie 1964; Ruprecht 1965), and the presence of a supernumerary molar (M4) is a diagnostic character of *Mesechinus wangi* (Ai et al. 2018). These anomalies commonly result in mechanical compression and changes in premolar orientation (Fig. 3). Slight changes in the orientation of lower premolars are also evident in non-pathological specimens of *Galerix*, such as a p3 of *G. uenayae* from the Early Miocene of Keseköy, Turkey (Van den Hoek Ostende 1992: plate IV. 1), and a p3 of *G. exilis* from the Middle Miocene of Sansan, France (Baudelot 1972: fig. 73).

Etiology and rarity of dental pathologies

The recognition of a supernumerary alveolus and the presence of several misaligned double-tooth with subdivided roots in the specimens from La Grive-Saint-Alban suggest a fusion process rather than gemination. However, the supernumerary alveolus does not match the morphology of the p2, which may imply two distinct disorders in the same dental region, although double-tooth anomalies do not necessarily imply a complete duplication of the dental element (e.g., Kawada et al. 2006). I therefore interpret the double-tooth anomalies as representing variable and incomplete duplication of the p2 dental germ during different stages of development, or a variably expressed fusion of two already duplicated dental germs. The supernumerary premolar is interpreted as derived from complete duplication of the p1 dental germ, or possibly from a complete but unequal split of the p2 dental germ.

Fusion of two teeth may result from mechanical pressure associated with space in the mandible (Aydinbelge et al. 2017), a condition often favored by growth retardation or a shortened jaw development (Bartosiewicz 2021). However, this explanation better accounts for fusion in deciduous teeth and does not fit the anatomy of the three mandibles examined here (UCBL-FSL 217955, 217956, 217957). Environmental influences and genetic predispositions have otherwise been proposed as causal factors (Knežević et al. 2002; Kawada et al. 2006; Chen et al. 2023), as in other types of dental anomalies (e.g., Martin 2013; Chemisquy and Martin 2016; Towle 2017; Esquivel et al. 2021).

In his discussion of dental pathology, Brockie (1964) argued that insular isolation promoted the spread of pathologies in the small populations of *Erinaceus europaeus*. In the entire dentition, Brockie identified no dental pathologies in a continental European population (*N*=30), whereas 16.7% of individuals from the British mainland population had dental pathologies (*N*=24), and 50.7% of the New Zealand population showed dental pathologies ($N=77$), the latter had been introduced from Britain. These results are consistent with those of Ruprecht (1965). Among the recent adult Erinaceinae examined here (Online Resource 1), mainly from continental populations, only three individuals out of 62 showed any dentognathic pathology. The observations of Brockie (1964) are also consistent with the data of Asahara et al. (2012) from continental populations of the talpid *Mogera wogura*, in which dental pathologies (including double teeth and supernumerary premolars) were more frequently observed in peripheral populations.

Among adults erinaceids, few specimens show a reduced number of elements in the antemolar dentition, i.e., hypodontia. This has already been documented in some insectivore populations (e.g., Kawada et al. 2006) and in mammalian lineages showing progressive mandibular shortening (Bartosiewicz 2021). Apparent hypodentia may in some cases be confused with unerupted teeth, which do rarely occur in erinaceid (e.g., Asher and Olbricht 2009; Online Resource 1). In extant gymnures, mild hypodontia is particularly frequent (see Results). However, assessing the frequency of hypodontia in fossils of Erinaceidae is extremely difficult because dental elements are often isolated, and preserved mandibles are rare.

The high frequency of dental anomalies in the anterior dentition, both in fossils and in recent adult material, suggests greater morphological plasticity and fewer deleterious effects on survival in this region than in the molar region. Consequently, extreme caution is required when using the reduction of the antemolar dentition in small samples as a diagnostic character, even though it has been used to erect new species of Galericini (Mein and Suárez 1993; Masini and Fanfani 2013) and *Lantanotherium* (Mein and Ginsburg 2002; Cailleux et al. 2020). Given the parallel trend toward mandibular shortening in numerous erinaceid lineages and the relatively common occurrence of mild hypodontia in this group, premolar hypodontia may have held evolutionary advantages leading to the permanent loss of an element.

Because p2s are not diagnostic at the species level, they are not reliable indicators for estimating the frequency of anomalies; mandibular elements are required. In the material from La Grive-Saint-Alban fissure M stored at UCBL, 22 mandibles with p2 were attributed to *Galerix stehlini* (based on p4 morphology and the p2/p3 ratio), including three with anomalous p2s and one with a supernumerary alveolus between p1 and p2. Dental disorders therefore occur in 18.2% of the sample. In the absence of obvious methodological or taphonomic bias affecting pathological and non-pathological mandibles, such a high frequency of anomalies in the same dental region and in adult individuals is difficult to explain without involving genetic and/or environmental factors within the time-averaged population. Repeated dental pathologies within a fissure-fill assemblage reflect long-term constraints. Moreover, individuals exhibiting such dental anomalies likely also displayed other skeletal or soft-tissue abnormalities (after Bartosiewicz 2021; Love et al. 2022).

The case of *Galerix stehlini* may be related to other dental paleopathologies documented at La Grive-Saint-Alban by Mein (1986). These were found in the most common species at the locality, including the rodent *Megacricetodon gregarius*. The aberrant material attributed to this species includes a first lower molar (from fissure L7) with two additional median cuspids and an almost divided posterior root (Mein 1986: fig. 10), corresponding to a double-tooth anomaly. However, these previously described pathologies are extremely rare and therefore do not mirror the pattern observed in *Galerix stehlini.*

Bite marks: a behavioral reconstruction

Bite marks have been widely studied in the vertebrate paleontological literature and are documented in numerous taphonomic contexts (e.g., Erickson and Olson 1996; Aiglstorfer et al. 2019; Collareta et al. 2019; Benoit et al. 2021; Godfrey et al. 2025). The presence of bite marks deep within the oral cavity is inconsistent with scavenging behavior, a possibility further ruled out by the likely presence of an incompletely formed bony callus. Bite marks on skulls are typically associated with predation or social biting. Predation is unlikely because the most probable responsible taxon, *Parasorex socialis*, is smaller than *Galerix stehlini* and shows no tendency to vertebrate carnivory. Van den Hoek Ostende (2001) even argued that *Parasorex*, together with *Schizogalerix*, evolved dental adaptations towards a more herbivorous diet.

The bite marks observed in UCBL-FSL 217963 are consistent with intraspecific behavior in extant gymnure. As described by Gould (1978), opening the mouth in *Echinosorex* functions as a threat display when the animal is cornered and during encounters with conspecifics. “Gaping was the most common component of close contact behaviors” (Gould 1978: p. 19). This includes cases in which an individual passes its lower jaw between the dentition of another individual. Bites directly in the mouth have been recorded several times during mutual gaping, providing a plausible behavioral model for the trauma found in a lower jaw (Fig. 8). Grouping two *Echinosorex* in the same cage often resulted in individuals showing bleeding gums, a typical consequence of mouth bites (Gould 1978: p. 16, 19). Interestingly, bites are accompanied by head rotation, which may explain the slightly asymmetrical shape of the mandibular injury (Fig. 5d).

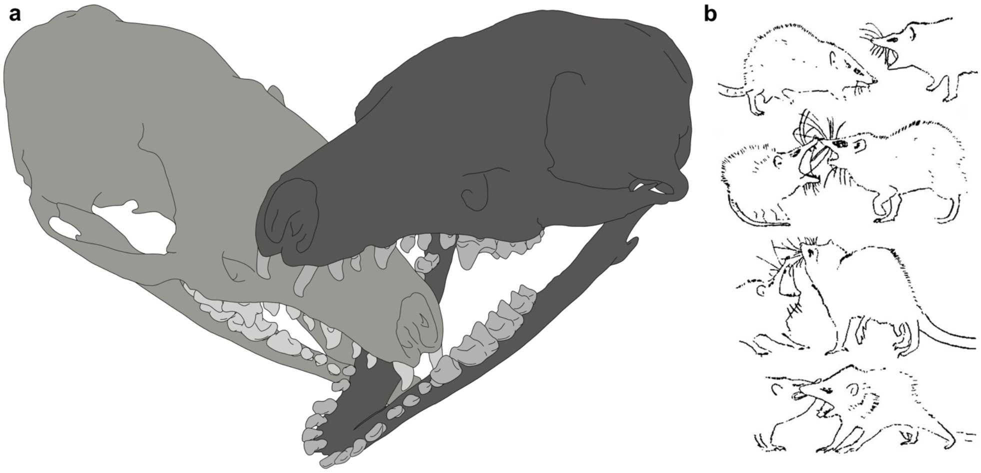

Fig. 8 Interpretation of the bite marks observed in UCBL-FSL 217963. **a**. skeletal model based on modern specimens of *Hylomys maxi* (right, ZMA 6822−3896; left, ZMA 6822−4484). **b**. example of territorial behavior in *Echinosorex gymnura* (reconstructed from different encounters, modified from Gould 1978)

Because few studies have focused on gymnures, threat-related gaping behavior has so far only been recorded in *Echinosorex* (Gould, 1978) and *Hylomys* (Ruedi et al., 1994), although it is common in vertebrates more generally (e.g., Roberts et al. 1967; Gese 2001; Lappin et al. 2006). Given that the dimensions of the bite marks better match *Parasorex socialis* than *Galerix stehlini* as the responsible species, both taxa likely used gaping behavior, including punctal mouth bites and head rotation, during intra- and interspecies encounters.

Beyond isolated lesions: paleoenvironmental and evolutionary interpretation

As in clinical medicine, the significance of pathologies lies not only in the disease itself, but also in the biological and paleoenvironmental context in which it occurred. The genus *Galerix* reached its highest diversity around the Early/Middle Miocene transition (ca. 17 Ma), during the Miocene Climatic Optimum (MCO), a period characterized in Europe by overall warmer and wetter conditions (Costeur and Legendre 2008; Furió et al. 2018). This interval was followed by a decrease in mean temperatures and the establishment of drier climates (Böhme 2003; Domingo et al. 2012; Menéndez et al. 2017). In addition to *Galerix stehlini*, two other *Galerix* species persisted after this interval: *G. rutlandae* in southern Asia and *G. exilis* in western Europe. Both were progressively replaced by *Parasorex* and *Schizogalerix* by the end of the Middle Miocene (Zijlstra and Flynn 2015; Cailleux et al. 2026). Thus, environmental conditions during the late Middle Miocene were no longer sufficient to sustain a *Galerix*-like eco-morphotype. The last occurrences of the invertivorous (species feeding mainly on insects and other small invertebrates) *Galerix* (cf.) *exilis* are characterized by a high morphological variability (De Jong 1988; Prieto et al. 2011; Cailleux et al. 2026). By contrast, *Parasorex* and *Schizogalerix* are considered to be less invertivorous and more cold-tolerant (Van den Hoek Ostende 2001; Klietmann 2013). As the dental morphology of *Galerix stehlini* is very similar to that of *Galerix exilis*, their contemporaneous extinction seems to be the result of a common cause.

The area around La Grive-Saint-Alban remained humid during the late Middle Miocene, with evidence even suggesting a local increase in humidity, possibly related to the Rhodanian sea channel (Van Dam 2006; Maridet et al. 2000; Hugueney et al. 2012). The insectivores also support a humid local environment, at least for fissure M, contrasting strongly with reconstructions for central Spain during the same period (e.g., Daams et al. 1988; Menéndez et al. 2017). The faunal pattern at La Grive-Saint-Alban, characterized by extremely high diversity dominated by humidity-adapted species, supports the idea that this diversity hotspot lay at the periphery of a humid ecosystem, as formulated by Madern and Van den Hoek Ostende (2015). The southward expansion of this ecosystem may explain the high mammalian diversity in the late Aragonian of the Vallès-Penedès Basin (Casanovas-Vilar et al. 2016), and this interpretation is consistent with the recent reconstruction of Casanovas-Vilar et al. (2026). While the presence of multiple biomes likely contributed to high regional diversity, it may also have constrained taxa adapted to narrow ecological niches.

I propose that the pathologies observed in *Galerix stehlini* were a direct consequence of habitat fragmentation, progressively reducing population size in a manner analogous to Brockie's (1964) insular introduction hypothesis. This interpretation is consistent with the findings of Kawada et al. (2006), Martin (2007), and Chemisquy and Martin (2016). The spread of dental anomalies is likely the result of a long-term, environmentally driven genetic bottleneck, as fixation of mutations is favored in small, fragmented populations (Lynch et al. 1995; Higgins and Lynch 2001). Comparable increases in pathology have been recorded in mammals before extinction, such as in the carnivores *Smilodon* and *Aenocyon* described by Schmökel et al. (2023). These authors highlighted the role of inbreeding in the frequency of skeletal disease, a process that is known to diminish the possibility of adaptation (inbreeding depression; see Stoffel et al. 2021). In addition, the high number of co-occurring erinaceid species likely intensified ecological competition and territoriality. This context is consistent with the first plausible evidence of aggressive encounters between two different gymnure species.

Dental peculiarities often classified as pathologies can serve as diagnostic traits or convergent features and may act as strong temporal markers. Like *Galerix* cf. *exilis* from Hammerschmiede (Prieto et al. 2011), *Galerix stehlini* from La Grive-Saint-Alban represents a striking example of increased dental morphological diversity, functional or not, preceding species extinction.

Conclusion

The nine specimens described here, attributed to the gymnure *Galerix stehlini*, document the first fossil occurrences of supernumerary premolars and double-tooth anomalies in the Erinaceidae. Extensive comparisons also identified similar anomalies in extant gymnures. Dental anomalies are common in the material from La Grive-Saint-Alban and may reflect a small effective population size for *Galerix stehlini*, possibly driven by prolonged habitat fragmentation. This study complements previous taxonomic and biostratigraphic work supporting the decline of the *Galerix* ecomorphotype during the late Middle Miocene.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10914-026-09822-6.

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Data availability All data underlying the findings of this study are available within this article and in the Online Resource 1, which can be accessed via the Figshare repository at DOI: https://doi.org/10.6084/m9.figshare.30273418.

Declarations

Competing interests The author declares no competing interests.

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