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ORIGINAL ARTICLE

INTEGRATIVE ZOOLOGY

A new Late Miocene *Hystrix* (Hystricidae, Rodentia) from Turkey

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Abstract

The Çorakyerler fossil locality in Anatolia reveals unique faunal elements. This study introduces *Hystrix kayae* sp. nov., a new Late Miocene porcupine initially classified as *Hystrix* sp. Yavuz *et al.*, 2018. This finding expands our knowledge of Late Miocene Anatolian porcupines, bringing the total number of known species to three. *H. kayae* sp. nov. is larger than *Hystrix aryanensis* and exhibits greater upper cheek tooth crown height. Its cheek tooth morphology differs from *Hystrix depereti*, and it possesses distinctive U-shaped choanae unlike *Hystrix primigenia*. The Çorakyerler locality may predate sites with *H. aryanensis* and *H. primigenia* but aligns temporally with *Hystrix parvae* localities. This study enhances our understanding of Late Miocene porcupine diversity in Anatolia, emphasizing the importance of Çorakyerler in unraveling the evolutionary history of these fascinating mammals.

Key words: Çorakyerler, *Hystrix*, Late Miocene, paleobiogeography, Turkey

INTRODUCTION

The Çorakyerler fossil site is situated in the fluvial floodplain deposits of the Tuğlu Formation within the Çankırı Basin of north-central Anatolia, Turkey (Sickenberg *et al.* 1975; Kaymakçi *et al.* 2001). Its discovery can be attributed to the collaborative efforts of German and Turkish geologists involved in the "Lignite Deposit Exploration in Turkey" project during the late 1960s. The initial excavations, led by O. Sickenberg and his team, yielded promising results, with a faunal list comprising 13 macro-mammalian taxa, which were subsequently published in 1975 (Sickenberg *et al.* 1975).

In the early 2000s, an exciting discovery of a hominoid added significant importance to the Çorakyerler locality, placing it among the prominent Late Miocene sites in Eurasia (Güleç *et al.* 2007). Subsequent systematic excavations, spearheaded by Ayla Sevim Erol and her team since 2001, have enormously expanded our understanding of the site. Ongoing excavations have resulted in the identification of nearly 5000 fossil mammal remains, primarily comprising ungulates, proboscideans, and carnivores (Kostopoulos *et al.* 2020, 2021; Sevim Erol *et al.* 2020).

Previous biochronological and magnetostratigraphic findings have suggested an early-middle Turolian age for the Çorakyerler fauna (e.g. Köhler 1987; Ünay *et al.* 2006; Güleç *et al.* 2007; Geraads 2013; Kaya *et al.* 2016). However, recent studies by Kostopoulos *et al.* (2020,

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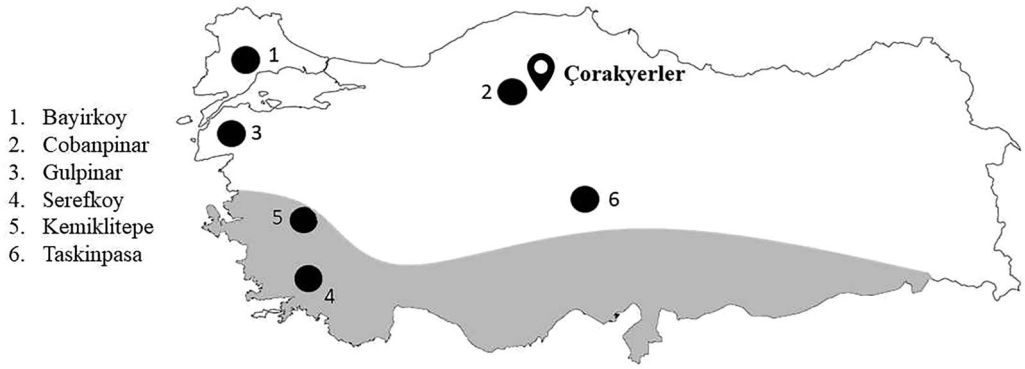


Figure 1 Late Miocene fossil and extant porcupine species distribution in Anatolia. Black dots are *Hystrix* fossil localities; gray area is extant porcupine species (*H. indica*) geography.

2021) and Sevim Erol *et al.* (2020) propose an older age of "late Vallesian-earliest Turolian," which appears to be more compatible with the fauna.

Despite its significance, the micromammal fauna of Çorakyerler has received relatively limited attention in the past. Only one study has investigated the sediments (approximately 10 tons) from which the large mammals were collected during the field seasons of 2001–2002. This study reported the presence of 12 taxa, primarily rodents, including *Hansdebruijnia erksinae*, *Hansdebruijnia* cf. *neutrum*, *Byzantinia pikermiensis*, *B*. aff. *hellenicus*, aff. *Rhinocerodon* sp. by Ünay *et al.* (2006) and Güleç *et al.* (2007), *Allocricetus aylasevimae*, *Cricetidae* gen. *et* sp. indet., *Pseudomeriones latidens*, cf. *Pliospalax* sp., *Protalactaga* aff. *major*, and *Myomimus* sp. (Ünay *et al.* 2006). Subsequently, Tarhan *et al.* (2017) identified the first large rodent in the micromammal assemblage—a well-preserved palate of a medium-sized *Hystrix*. Later, an additional specimen of this taxon was unearthed at the locality during 2019, expanding our understanding of the micromammal fauna at Çorakyerler.

Locating *Hystrix* fossils in the field proved to be an exceptionally challenging task, which hindered our ability to accurately define its paleogeography and phylogeny in this study. Initially, the earliest fossil discoveries of *Hystrix* in Hungary, Austria, Germany, and Spain were tentatively assigned to *Hystrix parvae*, suggesting a Vallesian age (Van Weers & Montoya 1996; Şen & Purabrishemi 2010). However, several studies have consistently proposed that the origin of Hystricidae can be traced back to Southern Asia during the Paleocene (Huchon & Douzery 2001; Van Weers 2005; Rovie-Ryan *et al.* 2017; Azzarà *et al.* 2022). The Old World porcupines (Hystricidae) consist of three genera, which are *Trichys*, *Atherurus* (subfamily Atherurinae), and *Hystrix* (subfamily Hystricinae; Happold 2013). Şen and Purabrishemi (2010) provide a comprehensive overview of Late Miocene *Hystrix* findings in Asia and Asia Minor, highlighting a temporal and spatial gap. Miocene *Hystrix* species generally exhibit low-crowned cheek teeth, with an EH/L ratio not exceeding 1.0 (Van Weers 2005). Van Weers and Rook (2003) and Şen (1999) emphasize a distinct shift in hypsodonty among Hystricidae species during the Turolian.

The Late Miocene porcupine findings in Anatolia are presented in Fig. 1, with the identified species being *Hystrix primigenia* and *Hystrix depereti* in six localities, which are Bayırköy, Şerefköy, Çobanpinar, Kemiklitepe, and Gülpınar (Atalay 1980; Ünay & Bruijn 1984; Şen 1994; Van Weers & Rook 2003). Another porcupine from Taşkınpaşa is described as *Hystrix* sp. (Prieto 2013).

Mori *et al.* (2014) focused on extant *Hystrix* species, shedding light on their herbivorous nature and their role as prey for medium and large predators such as lions, panthers, hyenas, wolves, and foxes. These quilled animals, as observed in both extant and fossil records (Uldis 2012; Więckowski *et al.* 2013; Mori *et al.* 2014; Coppola *et al.* 2020), frequently display a scavenging diet.

Institutional abbreviations: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; IPGM, Institut fur Palaontologie und Historische Geologie, Munich; BSPG, Bavarian State collection for Palaeontologie and Geologie, Munich; MNLP, Museum National, Laboratoire de Paleontologie, Paris; AMNH, American Museum of Natural History, New York.

MATERIALS AND METHODS

The Çorakyerler locality has been the site of excavation for over 30 years, and the majority of the fossil materials are currently housed in the excavation warehouse.

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The porcupine specimens, CO-2481 and CO-3259 (CO for Çorakyerler), studied in this work were discovered during the 2015 summer excavation season.

Dental terminology in this study follows the works of Van Weers (1990), Şen (2001a), Lopatin *et al.* (2003), Van Weers and Rook (2003), and Azzarà *et al.* (2022). Azzarà *et al.* (2022) provide a comprehensive list of these terms in their literature, which serve as the primary reference source for study (Azzarà *et al.* 2022, Online Resource 2). To illustrate the stages of wear in the teeth, we employ the "system of wear classes" originally developed by Van Weers (1990) and Van Weers and Rook (2003). In the figures presented, all teeth are identified as left sides, and reversed specimens are indicated by underlining in the figures. Measurements were taken using an electronic caliper, rounded to the nearest 0.01 mm.

Reconstruction drawings were made possible with the assistant of Ms. NOvia Shin under the direction of K.H. and P.R. NOvia Shin is a professional artist; her works are mainly using water-color, pencil, and art line. The paleoenvironment reconstruction was adapted from various literature published on Çorakyerler fauna (Sevim *et al.* 2001; Güleç *et al.* 2007; Mayda *et al.* 2015; Kaya *et al.* 2016; Kostopoulos *et al.* 2020, 2021). The figures were prepared on Adobe Photoshop CC 2018 and Adobe Illustrator CC 2018 software. Additionally, line drawings were drawn on an actual scale by referring to the original specimens.

The study strictly complied with all existing regulations and no permits were required in this context. Material described in this study was legitimately collected and adheres to the Society of Vertebrate Paleontology's guidelines. Authors are advocates of parachute science in paleontology and are from diverse ethnic and cultural backgrounds. No animals were harmed in the process of this research.

Odontological abbreviations: EH, the Enamel Height measured on the lingual side; EH/L, Enamel Height/Length; L, length corresponding to the maximum values along the longitudinal tooth axe situated in the middle crown height; W, width corresponding to the maximum values along the transverse tooth axe in the middle crown height.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821

Family HYSTRICIDAE Fischer de Waldheim, 1817

Genus *Hystrix* Linnaeus, 1758

Type species. *Hystrix cristata* Linnaeus, 1758.

Hystrix kayae sp. nov. (Fig. 2)

Hystrix sp. Yavuz *et al.*, 2018, pp. 70–75 (figs 1–3).

Etymology

Named in honor of Prof. Tümel Tanju Kaya, who is a leading paleontologist in Turkey.

Holotype

CO-2481, palate, preserving right and left P4-M3, collection of the Çorakyerler excavation warehouse.

Paratype

CO-3259, right maxilla with P4-M2, collection of the Çorakyerler excavation warehouse.

Type locality

Çorakyerler, Türkiye.

Occurrence

Late Vallesian–earliest Turolian of Anatolia.

Measurements

See Table 1.

Diagnosis

Medium sized *Hystrix* with brachydont upper cheek teeth. The three molars are of equal length, with the P4 slightly larger, approximately 20% larger than the molars. The choanae, located at the anterior end, have a U-shaped structure and are positioned at the level of the M2's hypoflexus. The EH/L ratio of the upper molars is nearly identical. The P4 displays an additional groove on its anterior side due to the absence of a parastyle, resulting in a wider parafossetta that transforms into a groove, thus separating the anteroloph from the protocone. On occlusal surface of the M1 and M2, there is a notable connection between anterior mesoflexus and hypoflexus. The occlusal surface of the P4 and M3 is oval in shape, while the M1 and M2 are rectangular.

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Table 1 Measurement of holotype and paratype of *Hystrix kayae* sp. nov

		Hystrix kayae sp. nov.		
		CO-3481		CO-3259
		Holotype		Paratype
		Right (mm)	Left (mm)	Left (mm)
P4	L	11.4	11.3	>8.8
	W	10.8	10.7	>8.9
	EH	10.7	10.6	4.03
	EH/L	0.94	0.94	
M1	L	9.3	9.2	9.35
	W	9.2	9.2	>8.7
	EH	8.2	8.1	>5.13
	EH/L	0.88	0.88	
M2	L	9.5	9.5	9.4
	W	9.3	9.3	8.9
	EH	8.2	8	6.84
	EH/L	0.86	0.84	0.72
M3	L	9.4	9.2	
	W	8.95	8.9	
	EH	8.06	7.43	
	EH/L	0.85	0.8	
P4-M3		40.37	40.12	

Description

The well-preserved palate specimen CO-2481 contains P4-M3 on both sides. The anterior border is preserved till the premaxilla, while the posterior border is preserved up to the end of M3 and the anterior part of the choanae. Laterally, the maxilla is continuous until the zygomaticomaxillary suture. The dorsal aspect of the palate is horizontally broken, revealing the clearly visible nasopharyngeal duct. The specimen anteriorly ends with nasoturbinate and maxilloturbinate, both of which are filled with sediments. In contrast to the well-preserved CO-2481 (holotype), CO-3259 (paratype) only consists of the right maxilla, where its M2 is complete, while the P4 and M1 are broken (Fig. 2).

The occlusal surface of the P4 indicates that its eruption has just begun, and it corresponds to wear class B2. The condition of the M3 suggests that CO-2481 belongs to age class V, while CO-3259, with its more erupted occlusal surface of molars (B5), falls to age class VI according to Van Weers's classification (1990). This information implies that CO-3259 represents an adult individual, while CO-2481 is a subadult.

The choanae exhibit a U-shaped structure anteriorly and terminate at the level of the M2's hypoflexus. The anterior portion of the palate is slightly wider than the posterior side, and the occlusal surface of the teeth gradually turns laterally from the P4 to the M3.

The molars in this specimen exhibit an almost square shape in terms of width and length, while their surfaces are rectangular. The outline of the occlusal surface of the P4 is oval. All teeth are preserved in CO-2841, and its P4 has just begun to erupt, indicating a subadult status. Apart from one on the posteroloph, all cusps of the P4 have recently erupted, and there are four labial synclines. The protocone is strongly separated from the anteroloph by a deep groove, transforming the protocone into an isolated loph. The parastyle is absent and the parafossette is wide. There is a small cusp on antero-mesoflexus, which is connected to the hypoflexus, and divides the occlusal surface of the P4 into two parts. The posterior part of the P4 is significantly longer than the anterior part. The metacone does not have any connections and appears as an isolated structure. The paracone is connected to the anteroloph by protolophule, resulting in a simpler anterior surface compared to the posterior part.

The enamel height (EH) of the P4 is 40% higher on the lingual side as compared to the labial side. The EH of the lingual face measures 10.7 mm and the EH/L ratio is 0.94. These ratios indicate that they are slightly above the brachydont EH/L level observed in rodents. On the lingual side, the hypoflexus extends posteriorly from the occlusal face toward the roots. There are no labial sinus lines reaching the root, and their ends are at the same level. The hypostria measures 4 mm in height and begins at 5.1 mm above the base of the crown.

The molars possess four labial synclines, and the posterior mesoflexus and posterofossette are connected in each molar. Except for the M2 of the paratype, there is a single syncline dividing the occlusal surface into two parts between the anterior mesoflexus, and hypoflexus in all molars. The posterior part is slightly larger than the anterior part. Another notable feature of the molars is the presence of a cusp in the posterior mesoflexus. The M3 is the same length as the M1 and M2 but slightly narrower. The occlusal surface of the M3 is oval, and the hypoflexus is connected to the posterofossette, anterior mesoflexus, and posterior mesoflexus. All molars show a distinct outline of the hypocone. Both Çorakyerler specimens have a similar

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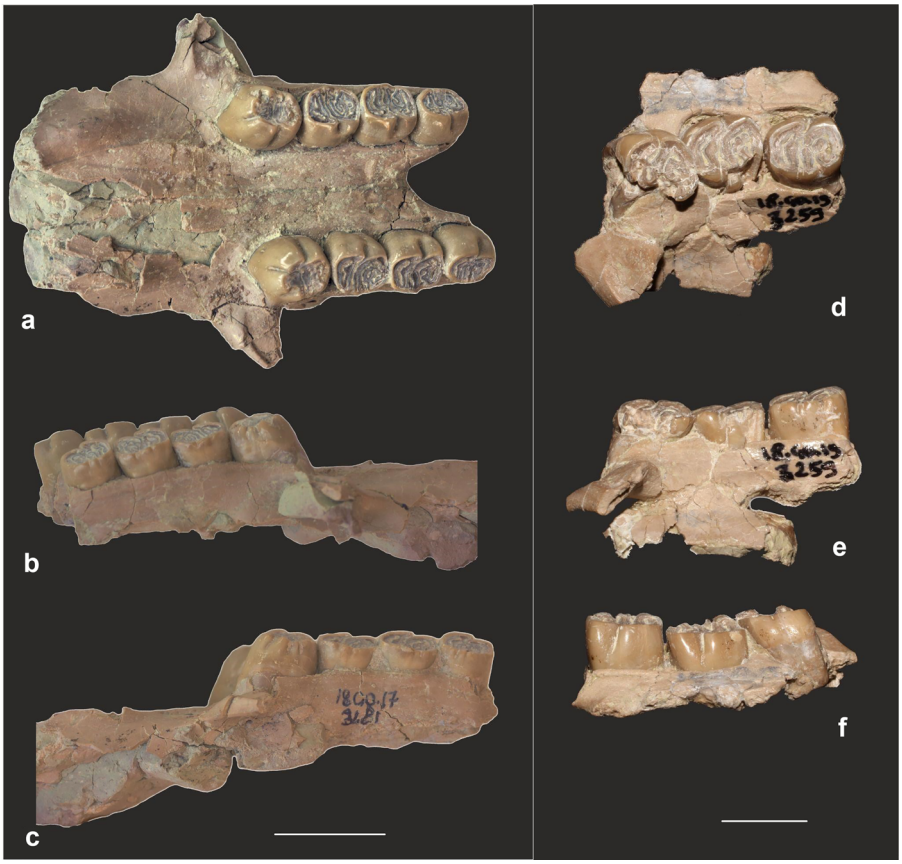


Figure 2 Palate and maxilla of *Hystrix kayae* sp. nov. from Çorakyerler, Turkey. (a–c) CO-2481 (holotype), ventral view (a); lateral views (b,c). d–f, CO-3259 (Paratype), ventral view (D); lateral view (E); medial view (F). Scales for holotype is 20 mm and paratype is 10 mm.

size, although CO-3259 is poorly preserved, with only the M2 being fully measurable.

COMPARISONS AND DISCUSSIONS

The distinguishing features of *Hystrix* species include their occlusal pattern, occlusal outline, enamel height, and the size of cheek teeth, as highlighted by various studies (Van Weers 1990; Şen 2001a,b; Lopatin *et al.* 2003; Van Weers & Rook 2003; Şen & Purabrishemi 2010; Fejfar & Sabol 2022; Azzarà *et al.* 2022). While the occlusal pattern of *Hystrix* species is generally conservative but still informative (Van Weers & Rook 2003; Şen & Purabrishemi 2010), the occlusal outline is commonly used in systematic studies, and size remains the primary tool for distinguishing taxa (Van Weers & Rook 2003; Şen & Purabrishemi 2010; Fejfar & Sabol 2022). Şen (2001a) and Van Weers and Rook (2003) note a shift in hypsodonty between *Hystrix* species during the middle Turolian, with later Miocene species being more hypsodont (e.g. *H. depereti*) during latest Miocene, allowing differentiation of the brachydont *H. kayae* sp. nov. from other Plio-Pleistocene *Hystrix* taxa, which are not discussed in this study.

In Turkey, there are two fossil records of porcupines (*H. primigenia* [Wagner 1848] and *H. depereti* [Şen 2001b]), as well as one extant species (*Hystrix indica*). The Çorakyerler porcupine specimens stand out from *H. parvae* and extant species in term of size and enamel height. In this study, we compare the Çorakyerler specimens with predominantly Late Miocene *Hystrix* species, including *H. aryanensis, H. primigenia, H. depereti, H. brevirostra, H. lufengensis*, and *H. gansuensis*.

Asian forms

H. kayae sp. nov. is compared to four Asian species, which are *H. aryanensis, H. lufengensis, H. brevirostra*,

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Table 2 Turolian *Hystrix* fossil localities in Türkiye

Stage	MN zones	Localities	Species	References
Turolian	MN 11–13	Taşkinpaşa	*Hystrix* sp.	Prieto 2013
	MN 13	Çobanpinar	*H. depereti*	Van Weers & Rook 2003
	MN 12	Bayırköy	*H. primigenia*	Ünay & Bruijn 1984
		Şerefköy	*H. primigenia*	Atalay 1980
	MN 11	Kemiklitepe	*H, primigenia*	Şen 1994
		Gülpınar	*H. primigenia*	Van Weers & Rook 2003
		Çorakyerler	*H. kayae* sp. nov.	This study

and *H. gansuensis*. The large size and short rostrum of *H. brevirostra* make it easily distinguishable from *H. kayae* sp. nov. with its square outline and hypsodont molars (Wang & Qiu 2020, fig. 3; table 2). *H. gansuensis*, on the other hand, exhibits high-crown and small size cheek teeth, contrasting with the specimens from Çorakyerler, and it also has simpler occlusal pattern compared to Çorakyerler (Wang & Qiu 2002, table 1; fig. 1). While the P4-M3 length of *H. lufengensis* is considerably shorter, its molars are slightly wider than those of *H. kayae* sp. nov. Additionally, the occlusal patterns of the molars for both species are distinctly different (Fig. 5) (Wang & Qi 2005, fig. 1A,B1). The P4-M3 lengths of Moloyan and Ivand 1 *H. aryanensis* are also smaller than that of CO-2841 (Table S1, Supporting Information). The size of the P4 in the Çorakyerler specimen is larger than that of *H. aryanensis* and *H. gansuensis*, but smaller than *H. brevirostra* and *H. lufengensis* (Fig. 3).

In the Çorakyerler samples, the size of the P4 is considerably larger than that of *H. aryanensis* and *H. gansuensis* specimens, while the size of its M1/2 is comparable to that of *H. aryanensis* and *H. gansuensis* specimens. Therefore, it can be inferred that *H. kayae* sp. nov. is larger than *H. aryanensis* and *H. gansuensis* (Fig. 3; Table S1, Supporting Information).

According to Fig. 3, *H. lufengensis* and *H. brevirostra* appear to be slightly larger in size than the Çorakyerler samples (Fig. 3; Table S1, Supporting Information).

European forms

The P4-M3 length of CO-2841 measures 40.37 mm, consistent with *H. primigenia* from Taraklia and Dytiko. However, the length of the "*H. depereti"* from Weze is considerably longer than CO-2841. The extant species exhibit relatively smaller P4-M3 lengths compared to the Çorakyerler specimen. The Dytiko-3 *H. primigenia* specimen has the same P4-M3 length as *H. kayae* sp. nov., but its M1 and M2 are 20–30% wider than those of *H. kayae* sp. nov. (Fig. 3). It is similar in size to both the smaller *H. depereti* specimens found in Brisighella, Menacer, and Perpignan, as well as the larger *H. primigenia* specimens found in Dytico, Kemiklitepe, and Pikermi.

The size of the P4 in the Çorakyerler samples is similar to that of the larger *H. primigenia* specimen, while the size of its M1/2 is comparable to that of the smaller *H. primigenia* specimen. This suggests that the P4-M1/2 ratios of the Çorakyerler specimens are greater than those of *H. primigenia* (Fig. 3; Table S1, Supporting Information).

Although some authors specializing in *Hystrix* studies often emphasize tooth height and size as the primary characteristics for differentiating Hystricidae species, it should be noted that there are considerable intraspecific variations in the occlusal pattern of cheek teeth (Van Weers & Rook 2003; Şen & Purabrishemi 2010). Taking the aforementioned discussion into account, we conducted a principal component analysis (PCA) using enamel height and the size of cheek teeth (Fig. 4). The PCA diagram illustrates the distribution of the Çorakyerler porcupine and two other Late Miocene porcupine species, which are holotypes of *H. aryanensis* and *H. primigenia* (Mol 51 and ASII 144, respectively). The PCA diagram reveals a significant difference between *H. kayae* sp. nov. and *H. aryanensis* in terms of size. *H. kayae* sp. nov. exhibits larger molars than *H. aryanensis*, despite having shorter enamel height, even though they are in the same wear stage (Figs 3b,4). The quite worn molars of the holotype of *H. primigenia* show short enamel height. If we disregard this short enamel height, *H. primigenia* can be distinguished from *H. kayae* sp. nov. by its wider molars.

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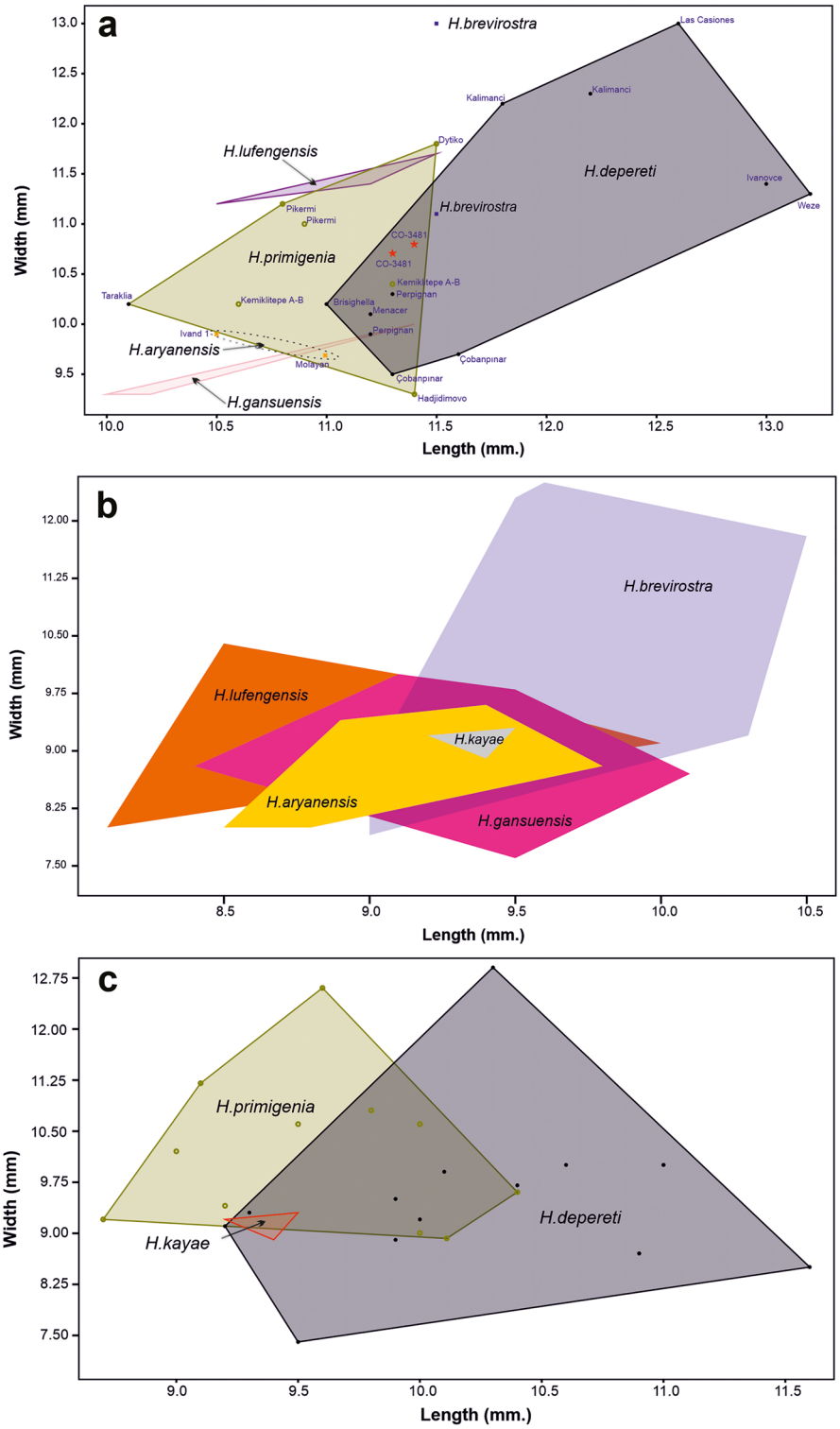


Figure 3 Length–width diagram of P4 (a) and M1/2 (b, c) of the Miocene *Hystrix* species from Asia (a, b) and Europe (a, c). Data source: Sulimski 1960; Van Weers 1990; Şen 1999; Şen 2001a, b; Wang & Qiu 2002; Lopatin *et al.* 2003; Van Weers & Rook 2003; Wang & Qi 2005; Şen & Purabrishemi 2010; Wang & Qiu 2020; Fejfar & Sabol 2022.

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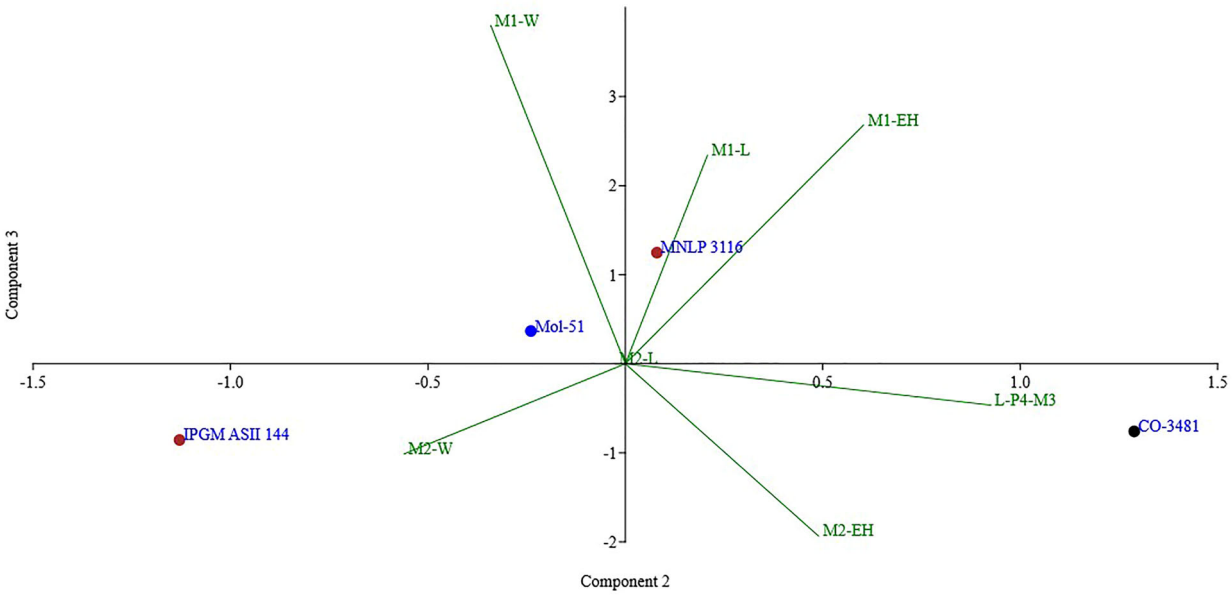


Figure 4 PCA analysis of Çorakyerler porcupine and holotypes of *Hystrix aryanensis* and *H. primigenia*. M1-W, width of M1; M2-W, width of M2; M1-L, length of M1; M2-L, length of M2; M1-EH, enamel height of M1; M2-EH, enamel height of M2; and L-P4-M3, length of P4-M3. Mol 51, *H. aryanensis* from Moloyan; ASII 144 and MNLP 3116, *H. primigenia* from Pikermi.

Morphology

The M1 and M2 occlusal outline of the Çorakyerler porcupine is more rectangular compared to the Moloyan and Ivand-1 *H. aryanensis*. The EH/L ratio of Çorakyerler (0.86) is smaller than that of Moloyan and Ivand-1, which are 0.95 and 1.29, respectively. The most notable differences are observed in the anterolingual groove of P4 and the size of M3 between Çorakyerler and the Moloyan and Ivand-1 specimens. The occlusal outline of the cheek teeth in Çorakyerler specimens is more rectangular compared to all *H. aryanensis* samples (Fig. 5).

The cheek teeth of Çobanpinar and Pikermi specimens exhibit simpler occlusal pattern compared to the Çorakyerler specimens. While the occlusal outline of M1 and M2 in the Samos specimen is similar to Çorakyerler, the oval occlusal outline of its M3 differs from the rectangular outline of the Çorakyerler specimen. According to Van Weers and Rook (2003), the morphology of M3 shows high variability among extant and fossil porcupines compared to other cheek teeth. Therefore, it is not sufficient to classify the Çorakyerler specimens at different systematic levels, but they can be distinguished based on other differential characteristics of the Çorakyerler porcupine. Van Weers and Rook (2003) discussed the Polgardi porcupine collection and concluded that it consists of two species from the same locality. With this information, it is reasonable to assume that Late Miocene Anatolia could have *Hystrix* taxa.

Choanae

Variation in the anterior airways of nasal opening in hominins and mammals are related to cold and dry climates, while posterior airways of the nasal are less variable between species (Van Weers & Rook 2003; Noback *et al.* 2011; Bastir 2019). This indicates that U-shape choanae can serve as differentiating character for *H. kayae* sp. nov. from other species.

H. primigenia (Van Weers & Rook 2003, fig. 3a) and *H. brevirostra* (Wang & Qiu 2020, fig. 3b1,b2) from pikermi and Gansu, respectively, exhibit "V"-shaped choanae located at the end of the M2-M3 connection. *H. depereti* from Samos (Van Weers & Rook 2003, fig. 7C) also has "V"-shaped choanae, but it is situated at the end of the mid M2. Another representation of "V"-shaped choanae is observed in the Hadzhidimivo *H. primigenia*, where it is located at the end of the beginning M3 (Kovachev 2012, fig. 1c). The Çorakyerler specimen is distinguished by its "U"-shaped choanae, which sets it apart from other Turolian porcupines, except for the Weze specimen (Sulimski 1960, plate I.2).

Weze fossils, initially described as *H. primigenia* (Sulimski 1960), and later reclassified and attained to *H.*

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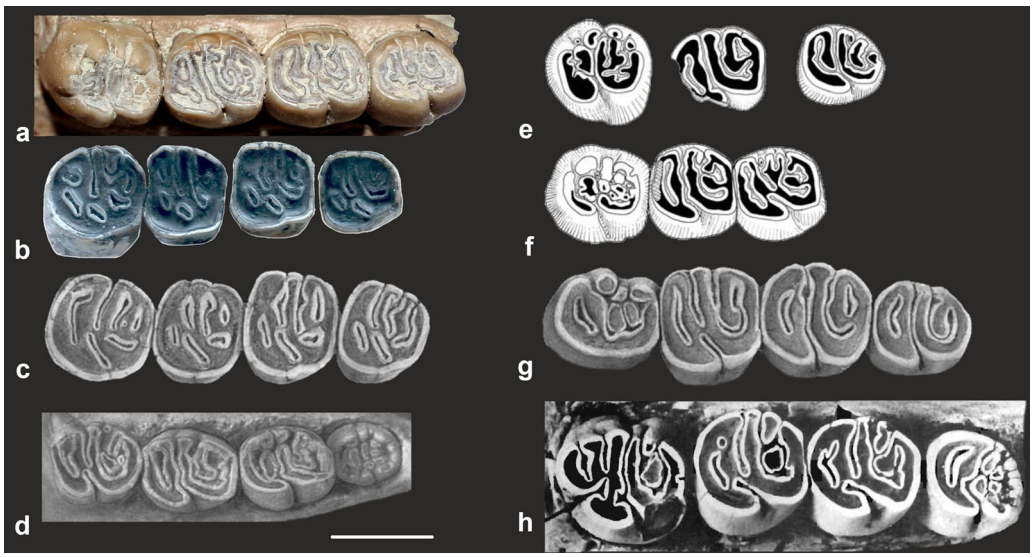


Figure 5 Occlusal pattern comparison of the upper cheek teeth from various *Hystrix* species from Eurasia. a, Holotype of *Hystrix kayae* sp. nov. (CO-3481); b, *H. lufengensis* (IVPP V-14152.1-6) from Lufeng, P. R. China (this study); c, *H. primigenia* (IPGM AS144) from Pikermi, Greece (Van Weers & Rook 2003); d, *H. depereti* (AMNH 20551) from Samos, Greece (Van Weers & Rook 2003); e, *H. aryanensis* from Ivand 1, Iran (Şen & Purabrishemi 2010); f, (Mol 52) from Moloyan, Afghanistan (Şen & Purabrishemi 2010); g, *h. depereti* without catalogue number from Çobanpınar, Turkey (Van Weers & Rook 2003); h, *H. depereti* (Rod. 1) from Weze (Sulimski 1960). All teeth are given as left sides; scale equals to 10 mm.

depereti based on the size and hypsodonty (Van Weers & Rook 2003), also served as a reference for this study. However, it is evident that the Weze collection requires thorough re-examination. Weze and Çorakyerler material shares "U"-shaped choanae and the anterolingual groove of P4, although their occlusal patterns, molar outlines, and sizes are significantly different. The early Pliocene Weze and earliest Turolian Çorakyerler porcupines are clearly different species, but the phylogenetic relationship between *H. kayae* sp. nov. and the Weze specimen may be closer than with other Pliocene *Hystrix* species.

PALEOGEOGRAPHY OF TUROLIAN PORCUPINE IN EURASIA

In Eurasia, there are seven Turolian *Hystrix* species mentioned in the discussion of this study. One of these species is *H. parvae* (Kretzoi 1951). Previously, *H. parvae* was believed to be the oldest known *Hystrix* species recorded in Europe, primarily found in the earliest Turolian (MN11) faunas (Van Weers & Montoya 1996). However, according to Van Weers (2005) and Şen (2001a), *H. parvae* likely migrated to Europe from Asia during the Vallesian stage. It has been considered a specialized *Hystrix* and not a direct ancestor of the Late Miocene forms. *H. parvae* is the smallest *Hystrix* species in Miocene and can be easily distinguished from *H. kayae* sp. nov. based on size (Supporting Information).

Notes on *H. parvae* localities

Apart from the MN 11 localities of Csakvar (Hungary) and Crevillente 2 (Spain) (Van Weers & Montoya 1996; Şen 2001a; Van Weers 2005; NOW 2023), the fissure fillings locality of Salmendingen (Germany) (MN9-11, NOW; MN6-17, this study) and Kohfidisch (Austria) (MN6-11), consisted of mixed faunas, including both Middle-Late Miocene (Kohfidisch) and even Pleistocene (Salmendingen) taxa. Recent studies on large mammals assigned the Çorakyerler fauna to the earliest Turolian (early MN11) (Mayda *et al.* 2015; Kostopoulos *et al.* 2020, 2021), contrary to previous preliminary studies suggesting a younger age (MN11-12, Middle Turolian) (Kaya *et al.* 2016).

The age of Csakvar is quite problematic as it has been recently assigned to MN11 based on micromammal assemblage, although the large mammal fauna includes both Vallesian and Turolian taxa. Crevillente 2 is placed in the Lower Turolian based on micromammal records (*Parapodemus lugdunensis, Valerymys vireti*), which are typical of MN11 (De Bruijn *et al.* 1975). The ages of

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these localities are consistent with Çorakyerler, and therefore, we consider all three localities to be coeval and dated to earliest Turolian. While *H. parvae* and *H. kayae* sp. nov. are undoubtedly different species, this age assignment raises the question of which one represents primitive *Hystrix*.

H. primigenia

The distribution of this species has been widely explained by Alcalá and Montoya (1998), Van Weers and Rook (2003), Lopatin *et al.* (2003), and Şen and Purabrishemi (2010). This large-sized and brachydont porcupine species was recorded in southeastern Europe and Asia Minor between MN11 and MN15. *H. primigenia* can be distinguished from *H. kayae* sp. nov. by its broader and more brachydont molars (Figs 3–5 and Table S1, Supporting Information).

H. aryanensis

A mid-sized *Hystrix* with high crowned cheek teeth has been recorded in Moloyan (Middle Turolian), Afghanistan and Ivand (Late Miocene), Iran (Şen 2001a; Van Weers & Rook 2003; Şen & Purabrishemi 2010). The main differences between *H. aryanensis* and *H. kayae* sp. nov. lie in their size and hypsodonty (Figs 3–5 and Table S1, Supporting Information).

H. depereti

A re-examination of the Perpignan material led to the conclusion that the specimens indeed belong to a new *Hystrix* species, *H. depereti* (Şen 2001b). Comparative restudy of tooth size and crown height in Pikermi and Perpignan porcupines reveals that *H. depereti* is larger than *H. primigenia* in both size and crown height (Şen 2001b; Van Weers & Rook 2003). Following the recognition of this new porcupine species, Van Weers and Rook (2003) assigned specimens from Villastar/Teruel (Spain), Samos (Greece), Çobanpinar (Turkey), Weze (Poland), Brisighella (Italy), Kalimanci (Bulgaria), Menacer (Algeria), and Las Casiones (Spain) to *H. depereti* based on their size and crown height. More recently, another *H. depereti* specimen was reported in Ivanovce (Slovakia) by Fejfar and Sabol (2022), who noted that the distribution area of *H. depereti* is much larger than that of *H. primigenia*. This largest European porcupine species can be easily distinguished from *H. kayae* sp. nov. by its size (Figs 3, 5 and Table S1, Supporting Information).

H. brevirostra

Wang and Qiu (2020) announced the discovery of a new, larger-sized fossil porcupine species from Gansu, China, which they named *H. brevirostra*. This species is characterized by a short rostrum and lower-crowned upper cheek teeth, as well as higher-crowned lower teeth. Its distribution ranges from the Late Miocene to the Early Pliocene (Wang & Qiu 2020). This large Asian porcupine species has a longer P4-M3 series and broader molars compared to *H. kayae* sp. nov. (Table S1, Supporting Information).

H. gansuensis

This porcupine species has been recorded in Gansu and Yunnan, China (Wang & Qiu 2002; Van Weers 2004). Wang and Qiu (2020) noted that *H. gansuensis* can be distinguished from *H. brevirostra* based on its different skull morphology and lower-crowned cheek teeth. This smallest Asian porcupine species easily stands out in terms of size and crown height when compared to *H. kayae* sp. nov. (Table S1, Supporting Information).

H. lufengensis

Wang and Qi (2005) described a new extinct porcupine species, *H. lufengensis*, from Yunnan, China. The mid-sized and primitive *Hystrix* species is estimated to age of the Late Miocene (~6.9–6.2 Ma). It possesses square molars and a shorter P4-M3 series in comparison to *H. kayae* sp. nov. (Fig. 5; Table S1, Supporting Information).

TUROLIAN PORCUPINE OF ANATOLIA

Several studies have been reported on the presence of Late Miocene porcupine species in Anatolia, including two identified species (Ünay & Bruijn 1984; Şen 1994; Atalay 1980; Van Weers & Rook 2003). Additionally, a single molar specimen from Taşkinpaşa (Kayseri) was described as a *Hystrix* sp. (Prieto 2013; Table 2).

Taşkinpaşa

A single tooth specimen housed at the BSPG, has been assigned to *Hystrix* sp. (Prieto 2013), although it exhibits similarities to *H. primigenia*.

Çobanpinar

Van Weers and Rook (2003) were the first to identify *H. depereti* in Anatolia based on eight isolated

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Figure 6 Possible gnaw marks of a porcupine species on a giraffe tibia bone (right) and a proboscid patella (left) from Çorakyerler excavation warehouse.

upper cheek teeth recovered from Çobanpinar (Van Weers & Rook 2003, fig. 6B).

Bayırköy

Ünay and Bruijn (1984) initially reported a porcupine specimen from the late Turolian Bayırköy fauna as *Hystrix* sp. However, Van Weers and Rook (2003) suggested that the material could only be attributed to *H. primigenia*. Measurements of the small cheek teeth (i + p4-m3) were found to be consistent with those of *H. primigenia* (Van Weers & Rook 2003, table 3).

Şerefköy

Atalay (1980), in his study of the Muğla, Yatağan Formation and its faunas, initially identified the specimen from Şerefköy as *Hystrix* sp. and assigned it to *H. primigenia*. Van Weers and Rook (2003) agreed with his description but emphasized similar measurement problems with the Kemiklitepe specimens.

Kemiklitepe

Şen (1994) allocated Kemiklitepe materials from Turkey to *H. primigenia*. Van Weers and Rook (2003) noted some measurement issues, particularly with M3, but attributed it to wear status. However, a re-examination of these specimens is warranted.

Gülpınar

Van Weers and Rook (2003) classified another porcupine specimen from Gülpınar as *H. primigenia*.

H. primigenia specimen from Bayırköy, Gülpınar, and Şerefköy consist of lower cheek teeth, which cannot be directly compared to the upper cheek teeth of the Çorakyerler samples. However, the upper cheek teeth of the Kemiklitepe and Taşkinpaşa samples are suitable for comparison with the Çorakyerler samples. Their sizes and morphology differ significantly from the Çorakyerler samples (Table S1, Supporting Information) (Şen 1994, fig. 1; Prieto 2013, fig. 1).

The Çobanpinar sample exhibits notable differences in size and morphology compared to the Çorakyerler samples (Fig. 5 and Supporting Information). Nevertheless, according to Van Weers and Rook (2003), this specimen is considered an individual of the extinct *H. depereti*.

PALEOENVIRONMENT OF ÇORAKYERLER

According to Roze (2009) and Labanowski (2017), the gnawing behavior of porcupines is believed to occur during summer months (from April to October) due to their need for salt. This theory, supported by gnaw marks on fossils (Fig. 6), suggests that the catastrophic event at Çorakyerler, involving the accumulation of thousands of carcasses, likely took place during summer.

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Table 3 Fauna list of Çorakyerler. Data are taken from Ünay *et al.* 2006; Geraads 2013; Kaya *et al.* 2016; Sevim Erol *et al.* 2016, 2020; Tarhan *et al.* 2017; Kostopoulos *et al.* 2020, 2021

Group	Species	MN range
Suidae	*Hippopotamodon antiquus*	MN 9–11
	Hippopotamodon major	MN 10–13
Giraffidae	*Paleotragus coelophrys*	MN 10–12
	Paleotragus rouneii	MN 10–13
	Samotherium boisseri	MN 11
	Bohlinia attica	MN 10–13
Bovidae	*Criotherium* sp.	MN 10–12
	Oioceros rothi	MN 10–12
	Qurliqnoria corakensis	MN 10–11
	Plesiaddax sp.	MN 9–11
	Gangraia anatolica	MN 10–11
Perissodactyla	*Miodiceros neumayri*	MN 9–11
	Chilotherium sp. (small form)	MN 9–11
	Hipparion depereti	MN 9–11
	Ancylotherium pentelicum	MN 10–13
Carnivora	*Parataxidea maraghana*	MN 11–12
	Machairodus aphanistus	MN 9–11
	Adcrocuta eximia	MN 9–13
	Ictitherium viverrinum	MN 10–12
	Chasmaporthetes sp.	MN 11–17
Rodentia	*Hansdebruijnia erksinae*	MN 10–11
	Pseudomeriones latidens	MN 10–11
	Byzantinia pikermiensis	MN 10–12
Proboscidea	*Coeroloehodon pentelici* (primitive form)	MN 10–12
	Konobelodon sp. (primitive form)	MN 10–11

Figure 7 depicts a vivid reconstruction of a captivating scene along the riverbank during the Late Miocene. The illustration captures the intense prey–predator interaction between *H. kayae* sp. nov., and a formidable saber-tooth cat (*Machairodus* sp.). Adding to the lively tableau, an otter (*Sivaonyx* sp.) can be observed savoring its meal nearby. In the flowing river, partial carcasses of giraffes can be glimpsed, while *H. kayae* sp. nov. is depicted gnawing on the tibia bone of one of these towering creatures. This evocative visual representation offers a glimpse into the dynamic ecosystem and the complex interactions that shaped life in Late Miocene Anatolia.

Van Weers and Rook (2003) observed that in extant porcupines, tooth height and size increase as adaptations to drier habitats and larger ecological and geographical ranges. Considering this, the relatively brachydont *H. kayae* sp. nov. is likely to have adapted to a humid and warm environment, as indicated by recent studies on the paleoecology and paleoenvironment of Çorakyerler (Mayda *et al.* 2015; Kostopoulos *et al.* 2020, 2021). These studies have highlighted the presence of semi-aquatic fauna (e.g. *Sivaonyx*), indicating a humid environment in which *H. kayae* sp. nov. thrived. The Paşalar locality, which yielded Miocene hominoid fossils, includes a *Python* remain to emphasize a comparable environmental signature to that of Çorakyerler, suggesting similar paleoenvironmental conditions (Georgalis *et al.* 2020). Both localities likely developed within a humid, tropical, or sub-tropical paleoecological context but there are no hystricids there.

Çorakyerler is known for its extensive and diverse faunas from the Late Miocene of Anatolia. Along with

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Figure 7 The illustration captures the intense prey–predator interaction between *Hystrix kayae* sp. nov., and a formidable saber-tooth cat (*Machairodus* sp.). Adding to the lively tableau, an otter (*Sivaonyx* sp.) can be observed savoring its meal nearby. In the flowing river, partial carcasses of giraffes can be glimpsed, while *H. kayae* sp. nov. is depicted gnawing on the tibia bone of one of these towering creatures. Reconstruction drawing by NOvia Shin.

its unique hominoid record, the site exhibits a significant presence of bovids, diverse carnivores, and other ungulates (Sevim Erol *et al.* 2016). Sevim Erol *et al.* (2016) revised the fauna list of Çorakyerler, including species such as *Konobelodon* nov. sp., *Lycyaena* sp., *Adcrocuta eximia, Parataxidea maraghana, Sivaonyx* sp., *Samotherium boissieri, Ancylotherium pentelicum*, and *Hipparion depereti*. This revision suggests that the age of Çorakyerler can be assigned to the earliest Turolian (early MN11) (Table 3). However, over 3000 fossil specimens await taxonomic revision, and currently, only a few studies and preliminary results are available (Sevim *et al.* 2001; Güleç *et al.* 2007; Mayda *et al.* 2015; Kaya *et al.* 2016; Kostopoulos *et al.* 2020, 2021). Based on the fauna list derived from these studies, Çorakyerler is believed to represent a well-watered paleoenvironment.

CONCLUSION

Based on the analysis of morphological and biometric data of the Çorakyerler porcupine, a new species within the *Hystrix* genus, *H. kayae* sp. nov. is named. The distinguishing features used to differentiate porcupine species included the occlusal pattern, occlusal outline, enamel height, and size of the cheek teeth. *H. kayae* sp. nov. exhibited a unique occlusal outline and molar pattern, particularly in the distinctive P4 tooth. Furthermore, the enamel height was relatively short, and M3 displayed robustness and was of the same size as M1 and M2. This study contributes to the growing knowledge of Miocene Turkish porcupine by adding a third *Hystrix* species to the list. These identifications of a brachydont porcupine align with previous studies on the paleoenvironment of the Çorakyerler, which characterized the region as a humid and forested habitat.

In summary, the discovery of *H. kayae* sp. nov. and its specific dental characteristics provides valuable insights into the diversity and paleoenvironmental conditions of Miocene porcupines in Turkey. Further research and analysis are necessary to fully understand the evolutionary significance and ecological implications of this new species within the *Hystrix* genus.

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SUPPLEMENTARY MATERIALS

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 Measurements of *Hystrix kayae* sp. nov. upper cheek teeth from Çorakyerler and collected measurements from some other localities.

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