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Hedgehogs (Erinaceidae, Lipotyphla) from the Miocene of Pakistan, with description of a new species of

Galerix

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Abstract Hedgehogs (erinaceid insectivores) are a common element in Miocene small mammal faunas of Pakistan, but little material has been formally described. Here, we report on extensive collections from numerous localities across Pakistan, most from the Potwar Plateau, Punjab, and the Sehwan area in Sind. The dominant erinaceid is *Galerix*, which is also known from Europe, Turkey, and East Africa. We document a new early species of *Galerix*, *G. wesselsae*, in sites from Sehwan, the Zinda Pir Dome, the Potwar Plateau, and Banda Daud Shah ranging in age from about 19 to 14 Ma. This species briefly co-occurs with and is then replaced by the smaller *Galerix rutlandae*, previously based on a few teeth from Daud Khel. *G. rutlandae* is a common element of Chinji Formation faunas through about 11.5 Ma. Scanty material of an apparently new species of *Schizogalerix* succeeds *Galerix*. After 10.2 Ma, no galericines occur in Pakistan, but rare erinaceines are later faunal components.

Keywords Miocene, Pakistan, Siwalik, taxonomy, biogeography, *Galerix*

Introduction

Erinaceidae, a clade that today includes the spiny hedgehogs of Eurasia and Africa and the soft-furred, ratlike gymnures of Southeast Asia, is an important insectivorous component in Miocene faunas of Eurasia (Van den Hoek Ostende 1992, 2001; Van den Hoek Ostende et al. 2005; Ziegler et al. 2007). In Europe and Turkey, most Miocene erinaceids are spiny hedgehogs of the Tribe Galericipini, and are useful for biostratigraphy and paleoecology (Ziegler 2005a; Doukas and Van den Hoek Ostende 2006; Van den Hoek Ostende and Fejfar 2006). Other galericipine records (Butler 1956, 1984, 2010; Gureev 1979; Munthe and West 1980; Bi et al. 1999) are based generally on small samples.

Here, we describe hedgehog teeth, mostly Tribe Galericipini, from a long sequence of Miocene deposits in Pakistan. Some single localities of the Siwalik Group and Manchars Formation yield good samples of hedgehogs representing nearly all tooth loci. Our rich material covers a time period spanning most of the Miocene (~20 to 7 Ma, million years ago), enabling us to track changes over time among the hedgehogs of the small mammal community.

Materials and methods

We use upper and lower case to refer to teeth of the upper and lower jaws, respectively. Dental terminology and measurement protocols generally follow Engesser (1980; our Fig. 1). In the lower jaw, we measured depth below the middle of each tooth on the lingual side. Following Van den Hoek Ostende (1992), shelflike areas at the margins of the teeth, usually at the front and back of premolars, are "flattenings".

Specimens come from a large number of sites and several numbering schemes are used. Most are Yale–Geological Survey of Pakistan (YGSP) specimens from "Y" localities of the Potwar Plateau, Punjab, currently housed at Harvard University. "Z" specimens (and some YGSP teeth) are from "Z" localities of the Zinda Pir Dome, Balochistan. Key material comes from the collections of the Institute of Earth Sciences at the University of Utrecht, including specimens from the Sehwan and Gaj areas of Sind (sites in the form of "Seh 81.14" and "Gaj 83.11"); these specimens use the prefix "H-GSP" (for Howard University–Geological Survey of Pakistan). Some additional material in the Utrecht collection comes from the Banda Daud Shah area in Khyber-Pakhtunkhwa (sites referred to as "CH O", "CH BS", and "CH BS 1978"). Potwar localities generally have paleomagnetic dating control (see Barry et al. 2013) and this frame of reference is used for ages throughout. Specimens are listed by locality with measurements and available paleomagnetic age estimates as Electronic Supplementary Material (ESM1). Relative dimensions for fossils described herein given in Figure 2.

Systematic Paleontology

Order Lipotyphla Haeckel 1866

Family Erinaceidae Fischer 1814

Remarks.—Authorship of this family name is sometimes attributed as "Fischer de Waldheim 1817" (e.g., McKenna and Bell 1997). However, G. Fischer did not acquire his noble title "de Waldheim" until 1835 (Hutterer 2003) and he first published a family level name based on *Erinaceus* in 1814 (Fischer 1814: 144).

Subfamily Galericinae Pomel 1848

Tribe Galericini Pomel 1848

Type genus.—*Galerix* Pomel 1848.

Included genera.—*Deinogalerix* Freudenthal 1972; *Parasorex* von Meyer 1865; *Pseudogalerix* Gaillard 1929 (= *Galerix*); *Schizogalerix* Engesser 1980.

Remarks.—Our concept of the Tribe Galericini derives from Van den Hoek Ostende (2001), and is narrower than that of McKenna and Bell (1997) and Lopatin (2006). The latter arrangements mask substantial distinctions between the living gymnures (Tribe Hylomyini Anderson 1879) and the extinct Galericini. Indeed, there is little evidence that these two groups form a clade (Gould 1995). *Pseudogalerix* is a synonym.

Genus *Galerix* Pomel 1848

Type species.—*Viverra exilis* de Blainville 1840, by subsequent designation (Gervais 1852: 10).

Included species.—*Galerix africanus* Butler 1956; *Galerix aurelianensis* Ziegler 1990; *Schizogalerix iliensis* Kordikova 2000; *Galerix remmertii* Van den Hoek Ostende 2003; *Galerix rutlandae* Munthe and West 1980; *Galerix saratji* Van den Hoek Ostende 1992; *Pseudogalerix stehlini* Gaillard 1929; *Galerix sudrae* Baudelot 1972 (= *Galerix exilis*); *Galerix symeonidisi* Doukas 1986; *Galerix viverroides* Pomel 1848 (= *Galerix exilis*); *Galerix uenayae* Van den Hoek Ostende 1992; *Galerix wesselsae*, new species.

Excluded/doubtful species.—*G. atticus* Rümke 1976 (= *Schizogalerix zapfei*); *G. depereti* Crochet 1986 (= *Parasorex depereti*); *G. ehiki* Kretzoi 1954 (possibly a *Schizogalerix*); *G. hipparionum* Kretzoi 1954 (possibly a *Lantanotherium*); *G. iberica* Mein and Martín Suárez 1993 (= *Parasorex ibericus*); *G. kostakii* Doukas and Van den Hoek Ostende 2006 (= *P. kostakii*); *G. magnus* Pomel 1848; *G. moedlingensis* Rabeder 1973 (= *S. moedlingensis*); *G. paraexilis* Gureev 1979 (= *S. x paraexilis*); *G. sarmaticum* Lungu 1981 (= *S. sarmaticus*); *G. tadzhikistanicus* Gureev 1979; *G. voesendorfensis* Rabeder 1973 (= *S. voesendorfensis*); *G. zapfei* Bachmayer and Wilson 1970 (= *S. zapfei*).

Diagnosis.—See Van den Hoek Ostende (2001).

Remarks.—The grammatical gender of *Galerix* has been treated variously in the literature; for example, Butler (1956) named *Galerix africanus* (masculine), but Mein and Martín Suárez (1993) named *Galerix iberica* (feminine). Pomel (1848) did not give an etymology when naming *Galerix*, but he included *Galerix magnus* (currently unidentifiable), indicating that he treated the name as masculine. The name most likely derives from Greek *gale* "weasel" plus an abbreviated version of Latin *ericus* "hedgehog" (*contra* Palmer 1904, who gave a far-fetched etymology deriving the name from *Hystrix* "porcupine"). *Ericus* is masculine; therefore, in accordance with Article 30 of the International Code of Zoological Nomenclature, *Galerix* is to be treated as masculine. Derived from *Galerix*, *Deinogalerix* and *Schizogalerix* must be masculine (ICZN Article 30.1.1), and Butler's (1980) *Deinogalerix* would be *Deinogalerix intermedius*. Several *Schizogalerix* species names are corrected below.

Our concept of the genus *Galerix* derives mainly from Engesser (1980) and Van den Hoek Ostende (2001), who separated the genera *Schizogalerix* and *Parasorex*, respectively. Doukas and Van den Hoek Ostende (2006) transferred *Schizogalerix iliensis* Kordikova, 2000 to *Galerix* and Prieto et al. (2012) referred *Galerix kostakii* Doukas and Van den Hoek Ostende 2006, to *Parasorex*. The identity of a few species ascribed to *Galerix* remains uncertain. *Galerix magnus* Pomel 1848, was described as a "Tertiary" species as large as the European hedgehog. It probably had only three premolars, the first with only one root. To our knowledge it has never been mentioned except in reiterations of Pomel's original description. No galericine this large being known from France, it may be an erinaceine but must be regarded as a *nomen dubium* unless an identifiable type specimen can be shown to exist. Kretzoi (1954) described *Galerix hipparionum* and *G. ehiki* from Csákvár and Felsőtárkány, respectively, both Miocene of Hungary. *G. hipparionum* was distinguished by the posteriorly displaced metaconid on p4 and the weak talon on P3. A posteriorly displaced metaconid, not usually seen in *Galerix*, is present in *Lantanotherium*, which also has a weak lingual lobe (possibly corresponding to Kretzoi's "talon") on P3. Ziegler (2005b) described a population of *Lantanotherium sanmigueli* from the Hungarian MN 9 site of Rudabánya; the measurements Kretzoi gave for the holotype p4 of *G. hipparionum* (1.8 x 1.2 mm) fall inside the range of variation of the Rudabánya population of *L. sanmigueli*. Possibly *G. hipparionum* is a *Lantanotherium*, but this needs to be confirmed through restudy of the type material. *G. ehiki* was based on better material—a pair of lower jaws, a P4, and an associated M1–3—but described cursorily and not figured. It is said to be somewhat smaller than *G. exilis*, with wider, less square upper molars, a less reduced anterior dentition, and a less molarized P4. Wide, less-square upper molars suggest that this form is a

Schizogalerix, but the anterior dentition is more, not less, reduced in *Schizogalerix* than in *Galerix*. Gureev (1979) described *Galerix paraexilis* from the Late Miocene of Kazakhstan and *G. tadjikistanicus* from the Miocene of Tajikistan. His figure of the former indicates that it is a *Schizogalerix*, as the lingual cusps on m1 are displaced anteriorly and the posterior cingulum appears to be strongly connected to the entoconid. It should be compared to *S. duolebulejinensis*, which has a similarly short talonid on p4 and is close in size. *G. tadjikistanicus*, is based on a jaw fragment bearing p3–m2 with well-developed anterior cuspule on p3, absence of a metaconid on p4, short talonid on p4, and relatively small m2. These distinctive features make the species like a true *Galerix*, but it should be restudied to confirm affinity.

***Galerix wesselsae*, sp. nov.**

Type locality.—Y642, Potwar Plateau, Punjab Province, Pakistan, 15.2 Ma.

Holotype.—YGSP 52202, isolated right M1, slightly worn and complete except for some damage in the parastyle area (Figure 3).

Referred material.—listed in ESM1.

Etymology.—This species is named after Wilma Wessels in honor of her contributions to small mammal paleontology in Pakistan.

Diagnosis.—A species of *Galerix* with the following combination of characters: size small (larger than *G. saratji* and *G. rutlandae*, similar in size to *G. symeonidisi* and *G. uenayae*, smaller than other species in the genus); P3 relatively short and broad, bearing a hypocone; M1 with strong, labially directed metastyle crest; protocone and metaconule on M1 and M2 usually connected; connection between protocone and hypocone on M2 relatively weak; posterior arm of metaconule relatively long, but usually not reaching posterior cingulum; p2 and p3 without anterior cuspule; p4 with metaconid but without paralophid, the conical paraconid being isolated.

Differential diagnosis.—*Galerix wesselsae* differs from all species of *Galerix* except *G. symeonidisi* and *G. iliensis* in the presence of a well-developed hypocone on P3, but differs from all three in that the P3 is relatively shorter and broader and that the protocone-metaconule connection is invariably present (though sometimes weak) on M1 and M2. *Galerix wesselsae* is smaller than both *G. iliensis* and the similar *Parasorex kostakii*. Additionally, it differs from *G. iliensis* in the less well-developed protoconule on the upper molars and from *P. kostakii* in a stronger metastyle crest on M1, the absence of a long posterior arm of the metaconule of M1 and M2 in most specimens, and the weaker protoconule on the upper molars. *Galerix wesselsae* has a stronger, more labially directed metastylar crest

on M1 than does *G. symeonidisi* and the protoconule on M3 is weaker. It differs from *G. uenayae* in having M1 clearly longer than P4; m2 clearly longer than p4; and the metaconid on p4 well-developed. *Galerix wesselsae* differs from *G. rutlandae* in the stronger, more labially directed metastyle crest on M1; less well-developed protocone-hypocone connection on M2; more isolated paraconid on p4; and the absence of the anterior cuspule on p2 and p3.

Distribution.—We record *Galerix wesselsae* from around 19 Ma (Z124, Z122, and Z167) in the Zinda Pir Dome area, 17.8 Ma (Y721, Y747) to 14.1 Ma (Y733) in the Potwar Plateau, and from sites in the Manchar Formation and Banda Daud Shah area, which have not been dated paleomagnetically. *Galerix wesselsae* is the oldest known erinaceid in Pakistan. It is succeeded in the record by the smaller *G. rutlandae*, which appears to co-occur with it in several localities, including the rich sites of Seh 82.24 (Manchar Formation) and Y709 (Potwar Plateau).

Description.—Except for the incisors and lower canine, we identify examples of all tooth positions of *Galerix wesselsae*. However, much material is fragmentary and no single locality preserves all molar positions. The lower jaw is known only from a small fragment bearing m2 (specimen Z572); the bone preserves no distinctive features and not enough of it is preserved to measure the depth of the mandible.

p1 ($n=1$).—The first lower premolar is a small, elliptical, two-rooted tooth. The main cusp is anterior to the middle of the tooth. A small flattening is present anterior to this cusp. A larger flattening is present posteriorly. The posterior face of the tooth is strongly convex and bears a low cingulum.

p2 ($n=3$).—The main cusp is anterior to the middle of these rectangular and elongate teeth. There is no anterior cuspule. A posterior flattening is present, closed by a cingulum at the lingual side of the posterior margin of the tooth. There are two roots.

p3 ($n=2$).—The labial margin is more convex than the lingual margin. The central cusp is anterior to the middle of the tooth. A low crest descends anteriorly from this cusp. Posterolingual to the main cusp, a flattening is bounded by a posterior cingulum.

p4 ($n=9$).—Teeth about triangular in shape in occlusal view. The protoconid, by far the largest cusp, lies labial to the middle of the tooth. A small metaconid is present, slightly posterior to the protoconid in two specimens and directly lingual to it in three. The paraconid, located anterior and slightly lingual to the protoconid, is conical and isolated. It is lower than the metaconid in four specimens and as high in two, but more voluminous. The short talonid bears a posterior cingulum, strongest lingually. A metacristid connects the metaconid to the lingual end of the posterior cingulum in four of eight specimens. There is no median ridge. There are two roots.

m1 ($n=5$).—Most specimens are incomplete. The trigonid is about as long and broad as the talonid. The metaconid and protoconid are equally high and are connected by a crest. The metaconid is slightly anterior to the protoconid. The paralophid descends from the anterolabial corner of the protoconid as a narrow, almost transversely-oriented crest. This crest quickly changes direction and forms a broader, diagonal crest that extends to the anterior edge of the trigonid. The anterior cingulum extends from a point labial to the anterior edge of the tooth to a point anterior to the protoconid; in one specimen, it extends further posteriad towards the hypoconid. Both the hypoconid and the slightly higher entoconid are well-developed, though lower than the trigonid cusps. The cristid obliqua connects the hypoconid to the protoconid and slants slightly lingually. The posterior arm of the hypoconid joins the entoconid. A posterior cingulum connects to the posterior arm of the entoconid (observed in three specimens only). There are two roots.

m2 ($n=10$).—In terms of morphology and root number, *m1* and *m2* generally resemble each other. In *m2*, however, the trigonid is slightly shorter than the talonid, the tooth is smaller overall, and the configuration of the paralophid is different. In *m2*, the paralophid descends from the anterolabial corner of the protoconid as a low crest. The labial portion is broad and oriented diagonally until the anterior edge of the trigonid. There, it turns posteriad as a narrower crest that ends anterolingual to the metaconid. The metacristid is not fully preserved in any *m1*, but in *m2* it runs from the lingual side of the base of the metaconid to the entoconid and is notched slightly posterior to its anterior end. The posterior cingulum is connected to the entoconid in three of the six specimens that preserve enough of the talonid to observe this character.

m1/2 ($n=9$).— Among nine fragmentary specimens not securely identified as either *m1* or *m2*, the posterior cingulum is connected to the entoconid in four.

m3 ($n=5$).—Of the five specimens, much smaller than *m1* or *m2*, two are worn (one missing part of the paraconid) and two only preserve the trigonid. The trigonid is about as long as the talonid, but broader. The metaconid is the highest cusp in the trigonid and is slightly anterior to the protoconid. The metaconid and protoconid are connected by a low crest. The paralophid descends from the anterolabial corner of the protoconid and forms a broad curve at the anterior margin of the trigonid. The paralophid turns slightly posterior at the anterolingual edge of the trigonid, but does not reach the metaconid. An anterior cingulum is present at the labial side of the trigonid. Both the hypoconid and entoconid are well-developed, though lower than the trigonid cusps. The hypoconid is closer to the trigonid than the entoconid is. The entoconid is higher than the hypoconid. The nearly longitudinal cristid oblique connects hypoconid to protoconid. The metacristid runs from the lingual side of the base of the metaconid to the entoconid. A

crest connects the entoconid and hypoconid at the posterior margin of the tooth. There is no posterior cingulum or hypoconulid. There are two roots.

C1 (*n*=2).— High-crowned and with two roots, the tall central cusp is anterior to the middle of the tooth and slightly recurved. The posterior side of the tooth bears a flattening with a small cuspule.

P1 (*n*=2).— The tear-shaped tooth consists of a single large cusp with a posterior flattening; there are two roots.

P2 (*n*=5).—*P2* is larger than *P1* and while the labial side is rounded, the lingual face is almost straight. The main cusp is anterior to the middle of the tooth and a flattening lies posterior to it. There are two roots.

P3 (*n*=7).—Four complete teeth are identified as *P3* of *Galerix wesselsae*, and three fragments preserve only the labial side of the tooth. The complete teeth are generally rectangular in shape and clearly wider than long, except for one relatively longer specimen. A large paracone is present near the anterolabial corner. A metastyle crest extends posteriorly from this cusp and gently turns labially, ending in the posterolabial corner of the tooth. A cingulum extends across the posterior face of the tooth. Two low but distinct cusps, the protocone and hypocone, are present on the lingual side, separated from the paracone by a broad basin. No parastyle is apparent in four of seven specimens. Two specimens are worn, so that the protocone and hypocone are indistinct. *P3* has three roots.

P4 (*n*=14).—Despite the large number of specimens, only one *P4* is complete. One specimen is missing part of the metastyle crest; two lack the parastyle; six preserve only the labial side; and nine only the lingual side. *P4* is relatively broad labiolingually and short anterodistally. The paracone is a large cusp, located slightly anterior to the middle of the labial side of the tooth. A parastyle region is present as a small bulge on the anterolabial side of the tooth. In three specimens, this is only a small flattened area; in three others, a low crest is present at the anterior margin of the parastylar area. A strong metastyle crest descends posteriorly from the paracone. It turns sharply labially and ends in the posterolabial corner of the tooth. A sloping, slightly flattened area is present labial and anterior to the metastyle crest. The lingual side of the tooth bears both a protocone and hypocone. The protocone is larger than the hypocone, but both are much smaller than the paracone. A posterior cingulum extends across the posterior margin of the tooth from the posterior end of the metastyle crest; in one specimen, it continues along the lingual margin to a point between the protocone and hypocone, but in ten it stops anterior to the protocone. There are three roots.

M1 (*n*=9).—This tooth is rectangular in overall shape, with a pronounced metastyle crest directed posterolabially. The four main cusps are arranged in a square. The protocone and metacone are the largest cusps and the hypocone is the smallest main cusp. A crest descends labially from the protocone towards the paracone. No protoconule is

apparent on this crest, but a notch is present slightly lingual to the paracone. The paracone is connected to the labial side of the metacone by a low but continuous mesostyle. Anterior and labial cingula are present. Because the posterolabial corner is not well preserved in any specimen, the condition of the metastyle is unclear. The anterior cingulum ends lingually at the anterior side of the protocone. The posterior arm of the protocone splits into two branches, one leading to the hypocone and the other to the metaconule. The former is stronger in six out of seven specimens. The hypocone is a conical cusp, without a posterior arm. The metaconule is a small, triangular cusp with a short posterior arm that ends at about the level of the bend in the metastyle crest. The metaconule is connected to the metacone by a weak crest. The well-developed metastyle first extends posteriad and then sharply bends labially, ending at the posterolabial corner of the tooth. The labial portion of the metastyle crest points towards the hypocone. The posterior cingulum is present and runs undivided from the posterolabial corner of the tooth to a point posterior to the hypocone. There are three roots, the lingual root deeply grooved on its lingual side.

M2 ($n=10$).—*M2* is generally similar to *M1*, but the metastyle crest is less well-developed and the metacone is shifted a little lingually, so that the main cusps do not form a perfect square. The anterolabial area is preserved in several specimens; the anterior and labial cingula intersect at the anterolabial corner and a crest connects the paracone to the anterior cingulum. In one specimen the posterior arm of the metaconule continues to the posterolabial corner of the tooth and the posterior cingulum; in seven the metaconule has a short posterior arm, as on *M1*. The protocone-metacone connection is stronger than the protocone-hypocone connection; one specimen has no protocone-hypocone connection.

M3 ($n=12$).—*M3* is triangular, with protocone, paracone, and metacone, near the apices of the triangle. A crest descends from the protocone to the paracone. It does not reach the paracone, ending anterolingual to it in two specimens, but does reach the paracone in nine others. The crest is slightly thickened near its labial end in four specimens, but there is no distinct protoconule. Low crests do connect the metacone to both the paracone and the protocone. A low cingulum is present on the posterolingual side of the tooth in five specimens. A strong parastyle at the anterolabial corner of the tooth is connected to the paracone by a low crest. An anterior cingulum descends from the parastyle to a point anterior to the protocone. A root supports each of the main cusps.

Discussion.—Most of the galericine materials from the Zinda Pir Dome area and the lower strata of the Potwar Plateau and Sehwan deposits consists of specimens that are at or beyond the upper end of the size range in our large samples of *Galerix rutlandae* from younger sites in the Potwar Plateau (Fig. 2). We have detected several

morphological differences between *G. rutlandae* and the larger form represented in the older sites, and we believe these differences, together with the difference in size, are sufficient to recognize a new species. The differences between the two species are perceptible across relatively large samples, but subtle enough that the assignment of individual teeth is often debatable (compare our discussion of apparently mixed samples like Seh 82.24, below). This is no different from the situation in Europe, where it is often difficult to assign small samples to any one well-established *Galerix* species.

The assignment of the three complete specimens that we identify as P3s to *Galerix wesselsae* merits discussion, as these teeth are unlike most *Galerix* P3s. However, they are not so different from the P3s of some *Parasorex* and *Schizogalerix* (e.g., Engesser 1980), and P3 in general is a rather variable tooth in galericines (Engesser 2009; Van den Hoek Ostende 1992). These teeth are smaller than P4s that we assign to *G. wesselsae* and lack the strong notch seen in the metastyle crest of P4. The only sympatric mammal these teeth could conceivably belong to would be a second species of erinaceid, but the only such species found in any of the localities the P3s come from are *Galerix rutlandae* (which is known to have a morphologically different P3) and one indeterminate Erinaceidae from Seh 84.26 (see below). The P3s would be quite small for this latter species, and it would be unlikely that the three P3s all represent this rare taxon (known from a single tooth), instead of the more common *Galerix wesselsae*.

We identify a number of isolated specimens as lower anterior premolars (p1–p3) of *Galerix wesselsae* on the basis of similarities to their homologues in other *Galerix* species, such as *G. rutlandae* and *G. uenayae*. If these teeth are identified correctly and representative of their tooth positions, p2 was larger than p3 in *G. wesselsae*, as in most *Galerix* species and unlike in *G. rutlandae*. Although the hypocone on P3 and the frequent presence of a connection between the entoconid and the posterior cingulum on m1–m2 are unusual for *Galerix*, both occur in some species (see *G. rutlandae* below for discussion; *G. symeonidisi* and *G. iliensis* are the only *Galerix* species that consistently have a hypocone on P3). Because the new species also lacks essential diagnostic features of *Parasorex* and *Schizogalerix* (as listed under *Galerix rutlandae*, below), its assignment to *Galerix* is secure.

***Galerix rutlandae* Munthe and West 1980**

Type locality.—H-GSP locality 18, Daud Khel, Punjab, Pakistan. Chinji Formation.

Holotype.—H-GSP 2371, M1.

Referred material.—See Munthe and West (1980), Cheema et al. (1996), ESM1.

Revised diagnosis.—A species of *Galerix* with the following combination of characters: size very small

(comparable to *G. saratji*); hypocone absent on P3; metastyle crest on M1 weak and relatively posteriorly directed; protocone and metaconule on M1 and M2 almost always connected; connection between protocone and hypocone usually strong; metaconule on M1 and M2 usually with a short posterior arm that does not reach the posterolabial corner of the tooth; p1 two-rooted; p2 and p3 with distinct anterior cuspule; p3 larger than p2; p4 with poorly developed metaconid and with the paraconid pressed closely to the protoconid; entoconid always connected to the posterior cingulum in m1 and usually in m2.

Differential diagnosis.—*Galerix rutlandae* is smaller than the European and African species *G. africanus*, *G. aurelianensis*, *G. exilis*, *G. stehlini*, and *G. remmerti* and differs from all in the invariable presence of a connection between the entoconid and the posterior cingulum of m1. *Galerix symeonidisi*, *G. iliensis*, and *G. wesselsae* are larger and possess a strong hypocone on P3. Further differences with *Galerix wesselsae* are discussed under that species. The Early Miocene Turkish species *G. saratji* and *G. uenayae* are most similar to *G. rutlandae*, but in both the p2 is larger than the p3 and both of these teeth lack an anterior cuspule. In addition, *G. uenayae* is larger, with enlarged P4 and p4, and the metaconid on the p4 is weak or absent. In *G. saratji*, the trigonid of p4 is better developed with more separated protoconid and metaconid.

Distribution.—*Galerix rutlandae* occurs in Potwar sites of age 14.3 Ma (Y709) to 11.6 Ma (Y504). It is preceded by *Galerix wesselsae*, with which it co-occurs at a few sites, and followed by *Schizogalerix* sp. A. *Galerix rutlandae* is known from its type locality, Daud Khel (Munthe and West 1980), from Dhok Tahlian (Cheema et al. 1996), and from the Banda Daud Shah, Sehwan, and Gaj areas. Cheema et al. (2000) conferred a molar fragment from Jalalpur (ca. 10–11 Ma) to *G. rutlandae*, but as they note, its assignment is tenuous.

Description.—*Mandible* ($n=7$).—The lower jaw of *Galerix rutlandae* is known only from fragments. Three show that the mental foramen is below the posterior root of p3 and two show that p3 is larger than p2. We refer a fragment preserving a piece of the mandible posterior to m3 to *G. rutlandae*. It is similar to *G. exilis* and distinct from *Schizogalerix* in that the ascending ramus does not rise steeply. The ventral border of the bone turns dorsad below the posterior root of m3.

p1 ($n=8$).—The first lower premolar is an anteroposteriorly elongate tooth. The anterior and posterior ends tend to be lingually displaced. The main cusp is anterior and labial of the middle of the tooth. Anterior to this cusp is a small flattening, which bears a cuspule in two of six specimens, and posteriorly is a larger flattening, bearing a posterior cingulum that is very weak in most specimens, but quite pronounced in one. There are two roots.

p2 (*n*=7).—This tooth is relatively broad and short. The main cusp is near the center of the tooth. A distinct cusplule is present anterior to it. A posterior flattening is present, closed by a short cingulum on the lingual side. There are two roots.

p3 (*n*=15).—The third premolar is somewhat narrower and longer. The main cusp is slightly anterior to the middle of the tooth. An anterior cusplule is present. The posterior cingulum is present along the entire posterior margin of the tooth. There are two roots.

p4 (*n*=30).—The fourth lower premolar is larger and more molariform, with a longer talonid and more complex trigonid (Figure 4). The trigonid is larger than the talonid and dominated by the protoconid. A paraconid is present. It is elongate in shape and diagonal to almost anteroposterior in orientation. The metaconid is small, often appearing as little more than a raising in the lingual flange of the protoconid, but is often about as high as or higher than the paraconid. It is usually directly lingual to the protoconid, but slightly posterior to it in one of 27 specimens. The talonid is present as a low ridge at the back of the tooth, strongest at the lingual side. A low ridge usually connects the metaconid to the talonid at the lingual margin of the tooth. In 9 of 22 specimens, a very low anteroposterior ridge runs anteriad from the posterior cingulum at the center of the talonid.

m1 (*n*=24).—The trigonid is about as long as the talonid, but narrower. The metaconid and protoconid are approximately equally high and are connected by a crest. The metaconid is slightly anterior to the protoconid. The paralophid descends from the anterolabial corner of the protoconid as a narrow, almost transversely oriented crest. This crest quickly changes direction and forms a broader, diagonal crest that extends to the anterior edge of the trigonid, where it forms a rounded cusplule. The anterior cingulum extends from a point labial to this cusplule to a point anterior to the protoconid. In 6 of 16 specimens, the cingulum continues further posteriorly along the labial flank of the protoconid to a point anterolabial to the hypoconid. Both the hypoconid and the higher entoconid are well-developed, though slightly lower than the protoconid and paraconid. The cristid obliqua connects the hypoconid to the protoconid. The metastylid runs from the lingual side of the base of the metaconid to the entoconid. The posterior arm of the hypoconid is connected to the entoconid. A posterior cingulum is present, connected to the posterior arm of the entoconid in all specimens. There is one anterior and one posterior root.

m2 (*n*=32).— Similar in most respects to *m1*, *m2* is slightly smaller, the talonid and trigonid are about equally broad, and the configuration of the trigonid is different. The paralophid descends from the anterolabial corner of the protoconid as a low crest. The labial portion is broad and oriented diagonally toward the anterior edge of the trigonid.

There, it turns posteriad as a narrower crest that ends anterolingual to the metaconid. The labial cingulum continues posterior to the protoconid in 9 of 19 specimens. The posterior cingulum is connected to the entoconid in 12 of 18 specimens.

m1/2 (*n*=9).—In eight of these isolated talonids of *m1* or *m2*, the entoconid is connected to the posterior cingulum.

m3 (*n*=31).—The *m3* is smaller and narrower than the *m1* and *m2*. The trigonid is about as long as the talonid, but broader. The metaconid is the highest cusp in the trigonid. The metaconid and protoconid are connected by a low crest. The paralophid descends from the anterolabial corner of the protoconid and forms a broad curve at the anterior margin of the trigonid. The paraconid is not individually distinguishable on the paralophid. The paralophid turns slightly posterior at the anterolingual edge of the trigonid, but does not reach the metaconid. An anterior cingulum is present at the labial side of the trigonid. Both the hypoconid and higher entoconid are well-developed, though lower than the trigonid cusps. The hypoconid is slightly closer to the trigonid than the entoconid is. The cristid obliqua connects the hypoconid to the protoconid and is almost longitudinally oriented. The metastylid runs from the lingual side of the base of the metaconid to the entoconid. A crest connects the entoconid and hypoconid at the posterior margin of the tooth, but there is no posterior cingulum or hypoconulid. There is one anterior and one posterior root.

Maxilla (*n*=3).—The upper jaw is known only from small fragments. One fragment bearing P3 suggests there may have been a diastema between P2 and P3. Another fragment bears M1 and M2 and shows that the zygomatic arch diverges from the maxilla opposite the paracone of the M2.

C1 (*n*=7).—The double-rooted upper canine is a simple, high-crowned, unicuspid tooth with the tip of the cusp slightly recurved.

P1 (*n*=5).—This is an elliptical tooth with the relatively low main cusp anterior to the midpoint. A flattening is present posteriorly, sometimes with a small cuspule. There are two roots.

P2 (*n*=3).—P2 is similar to P1, but slightly larger. The lingual side is almost straight, while the labial side is rounded.

P3 (*n*=12).—This tooth is quite variable in shape. The largest cusp is the paracone. A parastyle is present anteriorly. A high metastyle crest descends from the tip of the paracone to the posterolabial corner of the tooth. The protocone is the only cusp on the lingual flange of the tooth; it is separated from the paracone by a deep valley. In two of seven specimens, a low crest connects the paracone to the protocone at the anterior end of this valley. The posterior cingulum runs from the posterolabial corner of the tooth along the distal margin to the protocone. There are three

roots.

P4 ($n=22$).—The largest cusp is the paracone. A parastyle is present, but varies in degree of development. A crest descends posteriorly from the paracone and then rises toward the metacone, located on the posterolabial corner of the tooth. This crest displays a clear notch in the middle, where the portions descending from the metacone and paracone meet each other at an almost perpendicular angle. The lingual lobe of the tooth bears two cusps, the protocone and hypocone; the protocone is larger. A valley separates them from the paracone and metacone. A low crest closes the anterior end of the valley. The posterior cingulum runs from the metacone along the distal margin of the tooth to the posterolingual corner, where it forms a small raised area. There are three roots, supporting the protocone–hypocone, parastyle, and metacone.

D3 ($n=1$).—The single *Galerix rutlandae* D3 found is a triangular tooth. The paracone is anterior and labial to the center of the tooth. A parastyle is present anterior to the paracone. A metastyle crest descends posteriorly from the paracone and curves into the posterolabial corner of the tooth. A lingual lobe is present posterior to the paracone. It bears a low cingulum on the lingual margin. No roots are preserved.

D4 ($n=1$).—We found a single deciduous upper fourth premolar. It resembles P4, but is narrower and relatively longer. The parastyle is strong. The metastyle crest is not directed as labially as in P4. The hypocone is small and lingually displaced relative to the protocone. The tooth has roots under the parastyle, metastyle crest, and protocone.

M1 ($n=35$).—This tooth is rectangular in overall shape, with a pronounced posterolabial metastyle crest. The protocone and metacone are the largest cusps. The main cusps are arranged in a square. A crest descends labially from the protocone towards the paracone. A distinct protoconule is evident on this crest in about half of the specimens. The paracone is connected to the metacone by a low but continuous mesostyle. A parastyle is present at the anterolabial corner, connected to the paracone by a low crest. The anterior cingulum extends lingually from the parastyle, and is continuous with labial cingulum. The posterior arm of the protocone splits into two branches, one leading to the hypocone and the other to the metaconule. The protocone-metaconule connection is weak in one of 20 specimens and absent in two. The hypocone is a conical cusp and lacks a posterior arm. The metaconule is a tear-shaped cusplule with a short posterior arm that generally ends at or anterior to the level of the bend in the metastyle crest. However, one of 19 specimens lacks the posterior arm and in another the posterior arm of the metaconule joins, but does not divide the posterior cingulum. The metaconule is connected to the metacone by a weak crest. The metacone is large and connects to a metastyle crest that at first extends posteriorly and then makes a sharp bend labially to the posterolabial corner of

the tooth. A posterior cingulum is present. There are three roots, the lingual root deeply grooved.

M2 ($n=68$).—This molar is similar to the first, but the metastyle crest is much weaker and the metacone is slightly lingual to the paracone, so that the main cusps are arranged in a trapezoid instead of a square. As on M1, the protoconule may or may not be present. The protocone-metaconule connection is present in 51 of 53 specimens. All 51 specimens in which the structure can be observed have a protocone-hypocone connection, but the connection is weak in 10. A short posterior metaconule arm does not reach the posterior cingulum in 36 of 42 specimens, and 6 lack the posterior arm completely. As on M1, the lingual root is deeply grooved.

M3 ($n=43$).—Triangular in overall shape, with cusps (protocone, paracone, and metacone) at each corner. The posterolabial side tends to be shorter than the posterolingual side; the anterior side is longest. The protocone tends to be the largest cusp. Along the margins of the molar, the cusps are connected by low crests; the crest connecting the paracone and protocone tends to be higher. Anterolabial to the paracone, a small parastyle is present, which forms the labial end of an anterior cingulum. The paracone and parastyle are usually connected by a low crest. A posterolingual cingulum is present in 16 of 27 specimens. A root supports each of the three cusps.

Discussion.—The original description (Munthe and West 1980) of *Galerix rutlandae* and all subsequent records were based on scanty material. The samples described here are consistent in morphology and size with the hypodigm of *G. rutlandae*, sharing such features as absence of a hypocone on P3, presence of a protocone-metaconule connection on M1 and M2, a short, relatively posteriorly directed metastyle crest on M1, and a relatively weak metaconid on p4. Munthe and West (1980) show an M2 of *Galerix rutlandae* with the posterior arm of the metaconule bisecting the posterior cingulum, but re-examination of a cast of this specimen shows that the posterior cingulum is in fact continuous, and the posterior arm of the metaconule ends short of the cingulum. Some measurements given by Munthe and West (1980) are outside the range of our samples. Our measurements of casts of the M1 and M2 from the type sample fall well within the range of variation in our samples, possibly reflecting a difference in measuring techniques (unspecified measurement protocol). Munthe and West (1980) gave the length and width of the one M3 they referred to *G. rutlandae* as 1.40x1.28 mm, but *Galerix* M3s are always wider than long. Their figure shows greater width than length, and a cast of this specimen is 1.12x1.50 mm. The 1.32 mm width of an m3 trigonid given by Munthe and West (1980) is well outside the range of variation of our samples and even of the larger *Galerix wesselsae*. Unfortunately, this specimen was not figured and we do not have access to a cast.

Here, we expand the known material of the species by more than an order of magnitude. For this reason, we

characterize the species in detail and provide a revised diagnosis. Although Munthe and West (1980) emphasized the similarity between *Galerix rutlandae* and *G. exilis*, the type species of the genus, Middle Miocene of Europe, our material shows that *G. rutlandae* has a number of distinctive features that set it apart as well-differentiated. Indeed, some of its traits are usually considered characteristic of other galericine genera (Van den Hoek Ostende 2001; Prieto et al. 2012).

For example, the posterior cingulum of m1 and m2 is usually connected to the entoconid in *G. rutlandae*. Although Van den Hoek Ostende (2001) listed the usual presence of this trait as diagnostic of *Schizogalerix*, he noted that it is also seen in some specimens of *G. symeonidisi*, *G. saratji*, and *G. remmerti* (Doukas 1986; Ziegler and Fahlbusch 1986; Van den Hoek Ostende 1992, 2003). Interestingly, the connection is more frequently present in m1 than in m2 in *G. saratji* and *G. remmerti*, matching the condition in the Pakistani *Galerix*. Possibly this trait was variable in early species of *Galerix* and became fixed in later galericines. In *G. rutlandae*, p3 was larger than p2, as shown by the preserved alveoli of several jaw fragments as well as measurements of isolated teeth, although Van den Hoek Ostende (2001) listed a p2 that is larger than or as large as p3 as a diagnostic character of *Galerix*. However, p3 is also larger than p2 in *Galerix exilis* from the type locality of Sansan, France (Engesser 2009). Prieto et al. (2012) questioned the generic assignment of *G. rutlandae* on the basis of the presence of a paralophid on p4. Although the condition of the p4 in this species is distinct from the more typical *Galerix* condition seen in *G. wesselsae*, our material shows that its variable paralophid is not similar to that of *Parasorex*.

Other features of *Galerix rutlandae* are characteristic of *Galerix* and distinguish it from *Parasorex*, *Schizogalerix*, or both: the relatively small width/length ratio of the upper molars, the almost invariable presence of a protocone-metaconule connection and a short posterior arm of the metaconule, the lack of anterior displacement of the lingual cusps of m1 and m2, and the lack of a hypocone on P3. Thus, we continue to assign this species to *Galerix*.

***Galerix*, sp. indet.**

Several assemblages (Seh 82.24 and 81.14, Y709 and Y733, CH O) include specimens with diagnostic features or size that match either *G. rutlandae* or *G. wesselsae*. We interpret these assemblages as sampling sympatric populations of both species, rather than a transitional form between *G. wesselsae* and *G. rutlandae*, because there is an abnormally large amount of variation in size at several sites. For example, site Seh 82.24 contains both one of the largest m1s (specimen 82.24-14) and one of the smallest M2s (specimen 82.24-56) in our entire collection. Also, the older *G. wesselsae* appears to be more derived than *G. rutlandae* in some morphological features, rendering an

ancestor-descendant relationship unlikely. Both species occur at localities Y709 and 733, 14.3-14.0 Ma, and we suspect that all of these sites are of similar age.

The two Pakistani species of *Galerix* are similar enough that it is not possible to securely identify all material from these sites. The smallest specimens are likely *G. rutlandae*, the largest can be referred to *G. wesselsae*, and some specimens have features that enable referral to a species, but others are in a size range of overlap for either or belong to tooth positions in which the species do not differ detectably.

Discussion.—*Seh 82.24.*—This richest site in our sample, with over 60 erinaceid teeth, includes both specimens unambiguously referable to *G. wesselsae* (e.g., P3 with hypocone) and some with features diagnostic of *G. rutlandae* (p3s with anterior cuspule). Overall, *G. rutlandae* appears to be the more common species in this site by a factor of two to one, but a large proportion of the material cannot be identified to species.

We refer the single p1 from this site to *G. wesselsae* because of large size. Among three p3s, we refer two to *G. rutlandae* and one to *G. wesselsae* on the basis of the presence of an anterior cuspule. The latter is also the largest of them. Among the five p4s from the site, one is small and shows the elongate paraconid characteristic of *G. rutlandae*, while two larger ones have a paraconid more reminiscent of *G. wesselsae*. Among six m1, we allocate a virtually complete tooth and an isolated trigonid, both quite large, to *G. wesselsae* and two small trigonids to *G. rutlandae*. The site has yielded seven m2s, none completely preserved. Two small teeth are *G. rutlandae*, a larger is *G. wesselsae*, and four others (three with trigonid only) are *G. sp.* Six specimens represent m3, and the size difference between a complete tooth referable to *G. wesselsae* and another we identify as *G. rutlandae* is striking.

The single P3 from *Seh 82.24* bears a hypocone and is referable to *G. wesselsae*. Two of 8 complete P4 have the labiolingually broader shape characteristic of *G. wesselsae* and two small ones are similar to *G. rutlandae*; identification of the others is left open. The lone M1 fragment from *Seh 82.24* is not identifiable to species level, and a small M1 or M2 fragment is almost certainly *G. rutlandae*. M2 is represented by an impressive 14 specimens. While morphological differences of *G. rutlandae* and *G. wesselsae* M2s are too subtle to be of much help, size differences between the two species are pronounced in this tooth position, and we identify 12 specimens as *G. rutlandae*. Of five M3s from *Seh 82.24*, two are noticeably smaller and relatively broader, and the paracone is narrower when observed in anterior view, so we refer these to *G. rutlandae* and the others to *G. wesselsae*.

CH O.—Four *Galerix* teeth include a small lingual fragment of P3 bearing a single cusp and a posterior cingulum (*CH O 269*), which is definitely not referable to *G. wesselsae*, but also one of the largest M3s found anywhere in

Pakistan (CH O 268), which is likely to be *G. wesselsae*. Of the other two specimens, a large m1 trigonid (CH O 270) is consistent with *G. wesselsae*, but a lingual P4 fragment (CH O 263) bearing two worn cusps is considered *G. rutlandae*.

Y709.—This relatively rich site, with about 30 teeth referable to *G. rutlandae* on the basis of size, includes four quite large teeth likely representing *G. wesselsae*. A large P4 is like the P4 of *G. wesselsae* in shape. A complete M2 is too large for *G. rutlandae* and an M2 fragment appears to be even larger. The single large m1 recovered from Y709 also probably represents *G. wesselsae*.

Y733.—Most of the 20 *Galerix* teeth from this site appear to be *G. rutlandae* on the basis of size and morphology as at Y709, but a very large m1 probably represents *G. wesselsae*.

Seh 81.14.—This site is likely older (Wessels 2009) than the others, and the material is predominantly *G. wesselsae*. One worn and abraded M2, 81.14-4718, stands out because it is substantially smaller than two better-preserved M2s from the same locality, 81.14-4715 and -4716. The protocone is connected to both the metaconule and the hypocone, and the posterior arm of the metaconule is short. The cingula are weak and the parastyle is missing, possibly due to abrasion. We believe this specimen provides evidence for a second smaller species of *Galerix* here.

Genus *Schizogalerix* Engesser 1980

Type species.—*Schizogalerix anatolicus* Engesser 1980, by his original designation.

Included species.—*Schizogalerix duolebulejinensis* Bi et al. 1999; *S. evae* De Bruijn et al., 2006; *S. intermedius* Selänne 2003; *S. macedonicus* Doukas 1995; *S. moedlingensis* (Rabeder 1973); *S. paraexilis* (Gureev 1979); *S. pasalarensis* Engesser 1980; *S. sarmaticus* (Lungu 1981); *S. sinapensis* Sen 1990; *S. voesendorffensis* (Rabeder 1973); *S. zapfei* (Bachmayer and Wilson 1970). Doukas and Van den Hoek Ostende (2006) add *S. iliensis* Kordikova 2000 (= *Galerix iliensis*) and *S. pristinus* Ziegler 2003 (= *Parasorex pristinus*).

Diagnosis.—See Van den Hoek Ostende (2001).

Remark.—Since the genus *Schizogalerix* is masculine (see above) several specific names have been corrected for gender agreement.

***Schizogalerix* sp. A**

Localities.—Y259 (age 10.5 Ma); Y450 (10.2 Ma); Y791 (11.2 Ma); Y76 (11.4 Ma).

Material.—See ESM1, Figure 5.

Description.—*p3* (YGSP 24491).—This tooth is dominated by a large central cusp. A small knob is pressed against

the anterolingual face of the central cusp, but there is no true anterior cuspule. A short talonid is closed labially by a low crest. There are two roots.

p4 (YGSP 24490).—This is a wide tooth, especially posteriorly. The trigonid is dominated by a triangular protoconid. The small metaconid is tightly appressed on the anterolingual side of protoconid. The paraconid is elongate and relatively anteroposteriorly oriented. A paralophid connects the protoconid to the paraconid. The talonid is short, and the posterior cingulum is reduced to a short, low crest posterior to the metaconid.

m2? (YGSP 39487).—Only the talonid of this specimen is preserved. The hypoconid is triangular, with anterior and posterior arms descending from the anterolingual and posterolingual corners. The anterior arm of hypoconid is directed relatively lingually. A small cingulum is present labial to the anterior arm. The posterior arm of the hypoconid joins the posterior arm of the entoconid, which is continuous with the posterior cingulum. The entoconid is much higher than the hypoconid and oriented anteroposteriorly. Its anterior arm continues anteriorly to the front margin of the fragment, which bears a single large root.

P2? (YGSP 39486, YGSP 24459).—Oval-shaped teeth with a large central cusp; posterior to this cusp is a basin closed by a posterior cingulum. Two roots are preserved in YGSP 39486.

P3 (YGSP 49003, YGSP 17255).—In YGSP 49003, the paracone is the largest cusp. Anterior to the paracone is a small basin bordered anteriorly by a cuspule, the parastyle. The labial margin of the tooth is slightly concave. A strong crest descends from the posterior side of the paracone. This crest is slightly curved and reaches the posterolabial corner of the tooth, where a small metacone is present. The lingual lobe of the tooth is missing. No roots are preserved. YGSP 17255 is only a lingual fragment with one root, grooved lingually. The fragment bears two cusps, separated by a valley; the anterior cusp (the protocone) is higher than the posterior one (the hypocone). The lingual margin of the tooth is indented. Posterolabial to the hypocone, the posterior margin of the tooth is smoothly convex.

P4 (YGSP 49004, YGSP 34946).—The paracone is the largest cusp. The labial margin of the tooth is virtually straight. A strong, slightly curved crest descends posteriorly from the paracone towards a posterolabially located metacone. Both the parastyle region and the lingual lobe of the tooth are missing in both specimens. YGSP 49004 preserves a remnant of a root under the metacone and similar remnants are preserved under the paracone and metacone of YGSP 34946.

D3 (YGSP 21833).—This tooth has undergone some enamel loss and breakage. It is roughly rectangular, with a large convex bulge slightly anterior to the midpoint of the lingual margin. The main cusp (paracone) is slightly

anterior to the middle of the tooth. Anterior to it is a slight flattening, forming a parastyle. A bladeliike but relatively low metastyle crest descends posteriorly from the paracone. A root is preserved under the lingual bulge; additional roots appear to have been present under the parastyle and metastyle crest.

M2 (YGSP 24492).—The anterolabial corner is broken off. The tooth is rectangular in overall shape and relatively short and wide. The protocone and metacone are the largest cusps. A crest descends labially from the protocone to the protoconule. The protoconule is only weakly connected to the paracone. An anterior cingulum is present. A low mesostyle descends posteriorly from the paracone; it forms a loop that reaches close to the labial margin of the molar. Breakage makes it difficult to examine the precise condition of the mesostyle, but it appears that it is not or only superficially divided. The posterior arm of the protocone connects to the hypocone, a conical cusp without a posterior arm. The protocone and metaconule are not connected. The metaconule has a short anterolabially oriented arm, which is not connected to the metacone. The posterior arm is long, extending to the posterolabial corner of the tooth and truncating the posterior cingulum. The metacone has an anterolabially oriented arm that forms a low, bulbous cusplule at the posterior side of the mesostyle. Its posterior arm curves labially and slightly anteriorly. One lingual root is preserved.

M1 or M2 (YGSP 39496).—This fragment preserves only the lingual side of a lower molar. The cusps are narrow and spaced far apart. A protocone and protoconule are present, but no anterior cingulum is apparent. There is no connection from the protocone towards the metaconule. The hypocone is smaller than the protocone.

Discussion.—The M2 YGSP 24492 can be assigned to *Schizogalerix* on the basis of the following traits (Van den Hoek Ostende 2001; Engesser 1980): molar short and wide, with width/length ratio of 1.51; no connection between protocone and metaconule; posterior arm of M2 metaconule extends to posterolabial corner of tooth; mesostyle displaced labially ("Schlaufenbildung"). The well-developed protoconule also appears to be characteristic of *Schizogalerix*. The specimen is unfortunately missing part of its anterolabial corner, rendering the condition of the mesostyle uncertain, but it appears that although displaced almost to the labial margin of the tooth, the mesostyle was weakly divided, similar to the situation in the primitive *Schizogalerix* species *S. evae*, *S. pasalarensis*, and *S. voesendorfensis* (Engesser 1980; De Bruijn et al. 2006). The posterior portion of the mesostyle is developed into a cusplule, which distinguishes the tooth from *S. voesendorfensis*, in which the posterior part of the mesostyle is a curved crest and the metacone is closer to the labial margin of the tooth (Engesser 1980; Kälin and Engesser 2001; Prieto et al. 2010). Unlike in *S. pasalarensis*, there is no cingulum labial to the metacone and the posterior part of the

mesostyle reaches the labial margin of the tooth (Engesser, 1980; M2 is unknown in the more primitive *S. evae*). The M2 is medium in size for the genus, comparable to *S. voesendorffensis* among other species (measurements in Engesser 1980; Rzebik-Kowalska and Lungu 2009).

Although incomplete, YGSP 24492 shows traits distinct from those of all other species of *Schizogalerix*; the closest similarities appear to be with the Central European *S. voesendorffensis*. In view of the small available sample from Y259 and similarly aged sites, the attributions of other teeth to the same species as YGSP 24492 must remain tentative (see below). If these teeth are identified correctly, they provide additional characters that are diagnostic of the Pakistani species of *Schizogalerix*, but the samples are too small to exclude the presence of additional galericine species in these sites. In view of the scanty material, this species of *Schizogalerix* is not named here, and we provisionally refer to it as *Schizogalerix* sp. A.

YGSP 24490, a p4, differs from p4s and other lower premolars of *G. rutlandae* in being relatively short and wide, with a talonid that is much wider than the trigonid, and in lacking a distinct metaconid. Although its length is similar to the average for *G. rutlandae*, it is relatively wide. Its general shape resembles that of the p4 of *Schizogalerix*, but the metaconid is usually well-developed in that genus. However, an indistinct metaconid is also seen in several apparently unrelated species of *Galerix* (Van den Hoek Ostende 2001) and even in *Schizogalerix voesendorffensis* (Engesser 1980, fig. 3d). We tentatively refer the tooth to *Schizogalerix* sp. A.

The premolar YGSP 24491 resembles p2s of *Galerix rutlandae*, but is longer and broader and has a less distinct anterior cuspule. It is morphologically similar to anterior premolars of *Schizogalerix*, particularly p3 (Engesser 1980), and is probably referable to *S. sp. A.* Another premolar from Y259, YGSP 39486, resembles the P2 of *G. rutlandae*, but is somewhat broader; it may be a P2 of *Schizogalerix* sp. A. A similar though substantially larger tooth from site Y450, YGSP 24459, may be another *Schizogalerix* P2.

In talonid YGSP 39487, the entoconid is connected to the posterior cingulum. This trait is generally diagnostic of *Schizogalerix* according to Van den Hoek Ostende (2001), but is also seen in some *Galerix symeonidisi*, *G. remmertii*, *G. rutlandae*, and *G. wesselsae* (see discussion above). The specimen is similar in size to specimens of *G. rutlandae*, but differs in a smaller angle between the anterior and posterior arms of the hypoconid, which are almost perpendicular in *G. rutlandae*, but form an acute angle in YGSP 39487. Some species of *Schizogalerix* show a similar morphology, especially in m2 (e.g., *S. pasalarensis*; Engesser 1980). With a width of only 1.48 mm, the specimen is among the narrowest known *Schizogalerix* m1s or m2s (Engesser 1980; De Bruijn et al. 2006; Rzebik-Kowalska and

Lungu 2009; Kälín and Engesser 2001). Unlike derived *Schizogalerix* species such as *S. zapfei*, *S. sinapensis*, and *S. macedonicus*, YGSP 39487 does not show a free-ending posterior arm of the hypoconid (Van den Hoek Ostende 2001); nor does the posterior arm extend into the posterolingual corner of the tooth, as in *S. duolebulejinensis* (see Bi et al. 1999). Since the narrowest m2s of *S. voesendorfensis* are similar in size to YGSP 39487 (Kälín and Engesser 2001; Prieto et al. 2010) and the specimen is morphologically similar to *Schizogalerix*, this specimen is most likely referable to *Schizogalerix* sp. A. Because m2 is appreciably narrower than m1 in *Schizogalerix* (Engesser 1980; Rzebik-Kowalska and Lungu 2009), the specimen is in that case likely an m2.

YGSP 39496 appears to represent the lingual side of the M1 or M2 of an erinaceid. Though fragmentary and apparently abraded, its morphology and size generally match YGSP 24492.

YGSP 49003 is a partial erinaceid P3. Among *Schizogalerix* species, it resembles *Schizogalerix pasalarensis* in its relatively large size, strong parastyle, and concave labial margin.

YGSP 49004 and 34946, labial fragments of P4, preserve few distinctive characters, but their non-concave labial faces appear to resemble *S. voesendorfensis* and *S. duolebulejinensis* (see Engesser 1980; Bi et al. 1999). Both teeth are larger than the largest P4s of *Galerix rutlandae* and more robust than more comparably sized P4s of *Galerix wesselsae*. They differ from both in that the posterolabial bulge is narrower; the posterior and labial margins meet each other at an acute angle, instead of being about perpendicular as in *Galerix*.

YGSP 21833 appears to be a galericine D3. To our knowledge, no D3 of *Schizogalerix* has been described or figured before, although Prieto et al. (2010) listed measurements for a *Schizogalerix voesendorfensis* D3 from Gratkorn, Austria. YGSP 21833 is from site Y76, which is intermediate in age between the last occurrence of *Galerix rutlandae* at site Y504 (11.6 Ma) and the possible occurrence of *Schizogalerix* at site Y791 (11.2 Ma). However, it is unlike the D3 of *Galerix rutlandae* (known from a single specimen) in being more robust, with a more centrally placed paracone and broader parastyle. Thus, we tentatively assign it to *Schizogalerix* sp. A.

Subfamily Erinaceinae Fischer 1814

Erinaceinae A, B, C, gen. et spp. indet. Figure 5

Material.—Site Z122 (19 Ma, M1 fragment YGSP 52204), Y691 (13.1 Ma, m3 YGSP 34899), Y931 (7.3 Ma, m3 YGSP 39462); Banda Daud Shah CH BS 40, ?p4 fragment, Seh 81.14, unnumbered molar talonid.

Description.— **Erinaceinae A:** YGSP 52204 (M1). The lingual side of M1 preserves an anterior cingulum and a crest descending labially from the large protocone, without a clear protoconule. Posterior arm of protocone splits into

two branches leading to metaconule and hypocone, the branch to hypocone weak. A small, conical metaconule is hardly differentiated from protocone-metaconule crest. Metaconule without posterior arm and without labial crest leading to metacone. Posterior cingulum present. Roots not preserved.

Remark. YGSP 52204 differs from *Galerix* in its large size and poorly developed metaconule. It resembles *Parvericius buk* Ziegler et al. 2007, from the Miocene of Mongolia in lacking a distinct protoconule and lingual cingulum and having a metaconule closely pressed against the postprotocrista, but differs in being larger (lingual length 2.4 mm; 1.66 to 1.99 mm in *P. buk*). Although it is closer in size to *Parvericius montanus* and *Parvericius voorhiesi*, the two other species in the genus (M1 length 2.1–2.3 mm and 2.00–2.15 mm, respectively; Rich and Rasmussen 1973; Korth 1992), those species completely lack a metaconule on M1. YGSP 52204 differs from the M1 of *Amphelchinus kreuzae* Munthe and West 1980 in being much smaller and lacking a lingual cingulum. Although Munthe and West (1980) described and figured *A. kreuzae* as having an isolated metaconule, our cast of the only known M1 (H-GSP 2380) shows that the metaconule was in fact connected to the protocone and hypocone by low ridges. Most other species of *Amphelchinus* are also larger. Although the essential diagnostic trait of *Parvericius*, a short lower molar trigonid, cannot be observed, YGSP 52204 may represent *Parvericius* or a closely related taxon.

Erinaceinae B: YGSP 34899 (*m3*). The morphology of this somewhat abraded tooth is typically erinaceine: the talonid is absent and the trigonid is long, with a low paraconid. The adjacent protoconid and metaconid are about equally high, much higher than the paraconid. They are connected by a crest at the posterior margin of the trigonid. The paralophid extends as a low crest anteriorly from the protoconid, across the rounded anterior margin of the tooth, and posteriorly on the anterolingual face, terminating anterior to the metaconid. A continuous cingulum is present on the labial and posterior sides of the tooth. Part of the single root is preserved.

Erinaceinae C: The smaller YGSP 39462 (*m3*), also worn and abraded, is typically erinaceine in appearance. The protoconid and metaconid are higher than the paraconid, but not as high as in YGSP 34899. They are not connected by a crest. The paralophid forms a raised area at the anterior margin, but does not extend as far posterolingually as in YGSP 34899, leaving the paraconid and protoconid well separated. The anterior part of the tooth is relatively broad. A cingulum is present on the labial and posterior sides of the tooth. There is one, non-bifurcated root.

Remark. Compared to the *m3* published as *Amphelchinus kreuzae* (H-GSP 2382, Munthe and West 1980), YGSP 34899 is somewhat longer, lacks a cingulum on the lingual and anterior sides, and has a longer paralophid that does not form a distinct paraconid. The relatively shorter paralophid of YGSP 39462 has a strong paraconid, but this tooth

is distinctive in its incomplete metalophid and broad anterior side. The three m3s probably represent three species, and the M1 YGSP 52204 is too small to be conspecific with any.

Erinaceinae indet. *CH BS 403 (p4)*. The paraconid, about as high but narrower as the protoconid, is separated from the protoconid by a long valley, which descends lingually. The metaconid is much lower than the protoconid, hardly protruding above the valley between the protoconid and paraconid. No talonid is preserved. There is a conical root below the paraconid and there may have been a broader, elliptical root below the protoconid and metaconid. CH BS 403 resembles p4s of some erinaceines (e.g., *Amphechinus major* Ziegler et al. 2007).

Seh 81.14 (m1 or m2 talonid). Its posterior hypoconid arm bends distinctly and connects to the entoconid. A posterior cingulum descends from the point where the entoconid meets the posterior arm of the hypoconid and extends around the hypoconid towards the talonid. This worn fragment, too large for *Galerix*, is broadly similar to erinaceines like *Amphechinus major*.

Erinaceidae, gen. et sp. indet.

Material.—Site Y668, 13.4 Ma, m1 YGSP 24499 (Figure 5); Y634, 12.3 Ma, m3 YGSP 24485 ; Seh 81.14a, m2 H-GSP 81.14a-4293.

YGSP 24499 (m1).—The quite open trigonid is narrower but about as long as the talonid. The protoconid is larger than, but about equally high as the metaconid. The paralophid descends from the protoconid as a straight diagonal line. An anterior cingulum is present labial to the paralophid, extending posteriorly to a point between the protoconid and hypoconid. The talonid cusps are low and the entoconid is not much higher than the hypoconid. The cristid obliqua and the metastylid connect the hypoconid to the protoconid and the entoconid to the metaconid, respectively. The posterior cingulum is weak and not connected to the entoconid. There are two roots, both grooved posteriorly.

H-GSP 81.14a-4293 (m2).—This tooth is abraded and portions of the paraconid and hypoconid are broken off. The trigonid is much shorter than the talonid. The protoconid and metaconid are about equally high and near each other, connected by a slightly notched crest. The paralophid is low. The cristid obliqua and metacristid are transversely oriented and reach the protoconid and metaconid, respectively. The entoconid is a high, voluminous cusp connected to the posterior cingulum. The posterior arm of the hypoconid appears to have been only weakly connected to the entoconid. The tooth has widely spaced anterior and posterior roots.

YGSP 24485 (m3).—Some enamel is missing and part of the posterolingual corner of the tooth is broken away. The trigonid is broader and somewhat longer than the talonid and is quite open. The protoconid is larger than, but

about equally high as the metaconid. The paralophid descends from the protoconid; it is at first oriented transversely, then turns diagonally and continues to the anterior tip of the tooth. A short and weak anterior cingulum lies labial to the paralophid. The talonid is reduced and the cusps are indistinct. The cristid obliqua and the metastylid connect the hypoconid to the protoconid and the entoconid to the metaconid, respectively. There is no posterior cingulum. No roots are preserved.

Discussion.— These specimens may represent three unknown galericines. Although they share a relatively long, narrow shape, low cusps, and similarities to *Hylomys*-like taxa, the m3 seems quite small even for the relatively small m1, and the m2 is large in comparison to either tooth and is much older.

YGSP 24499 differs from *Galerix rutlandae* in its small size especially width, low crown, straight paralophid without a conical paraconid, and weak posterior cingulum. Many of the same characters, especially the weak posterior cingulum and the configuration of the paralophid, differentiate it from other members of the tribe Galericini. Its low crown, strong anterior cingulum, labially placed cristid obliqua, and missing hypoconulid identify it as an erinaceid. All Recent galericines have a stronger posterior cingulum. Miocene *Hylomys engesseri* Mein and Ginsburg 1997 of Li Mae Long, Thailand, the generic allocation of which seems doubtful, has a shorter labial cingulum and the labial margin of m1 is concave between the protoconid and hypoconid. *Lantanotherium* is larger and has a broader m1, with stronger posterior cingulum. Erinaceines are generally larger, have relatively broader teeth, a paralophid that does not descend straight from the protoconid, and a stronger posterior cingulum. Brachyericines have a much longer trigonid. The strongest similarities appear to be to *Lantanotherium* and *Hylomys*.

YGSP 24485 is too small and narrow for a *Galerix rutlandae* m3, the talonid is more reduced, the trigonid more open, and the anterior cingulum is weaker. H-GSP 81.14a-4293 is too narrow and elongate and the trigonid is too short to be referable to *G. wesselsae*. While most other galericines have a broader m3 with a stronger anterior cingulum, *Hylomys engesseri* and *Neotetracus butleri* from Li Mae Long, resemble YGSP 24485, although both species are larger and have a broader m3. H-GSP 81.14a-4293 is most similar to *H. engesseri* in its short trigonid and well-spaced cusps, but the latter apparently has a more lingually located cristid obliqua and a weaker connection between the entoconid and the posterior cingulum. The paralophid continues further lingually in *N. butleri*, and *H. engesseri* lacks a crest connecting the metaconid to the entoconid. (The m3 of Li Mae Long *Thaiagymnura equilateralis* is unknown.)

Discussion

Previous studies

There are few published records of fossil insectivores from Pakistan. Munthe and West (1980) identified a handful of teeth from Daud Khel in the Chinji Formation as *Galerix rutlandae*, *Amphechinus kreuzae*, cf. *Echinosorex* sp., an indeterminate soricid, and an indeterminate talpid. The “talpid”, a fragment of an upper molar, likely represents a treeshrew and we see little resemblance of the three premolars called cf. *Echinosorex* sp. to living *Echinosorex*. Munthe and West (1980) included four teeth (P3, M1, i2, m3) in the hypodigm of *Amphechinus kreuzae*. The labial cingulum, narrow lingual lobe, centrally placed paracone, and weak protocone of P3 suggest a treeshrew. The other specimens, while representing an erinaceine, are questionably allocated as only cranial characters distinguish *Amphechinus* (Ziegler 2005a). Engesser (1980) considered the presence of a metaconule on M1-2 (seen in *Amphechinus kreuzae*) to be characteristic of *Mioechinus*, but this character is inconsistent according to Ziegler (2005a). For now the Daud Khel erinaceine could be referred to as "*Amphechinus*" *kreuzae*.

Cheema et al. (1996) described a few teeth of *Galerix rutlandae* from locality PMNH 8608, also in the Chinji Formation. They saw similarity to *Galerix symeonidisi* Doukas 1986 from the Early Miocene of Greece, but these resemblances are genus level diagnostic characters of *Galerix*. The teeth match *Galerix rutlandae*, except for an unusually broad m3.

Age

The samples from the Potwar Plateau, which represent the majority of the material studied here, have been securely dated on the paleomagnetic timescale of Gradstein et al. (2004) and range in age from 17.8 Ma (Y721, Y747) to 7.3 Ma (Y931). The Zinda Pir Dome area localities Z122, Z124, and Z167 yield erinaceids and occur low in or just below the Vihowa Formation (~19 Ma, Lindsay et al. 2005). Ages of other studied localities are not as well constrained and must be based in part or entirely on faunal correlation. In describing rodents from localities in the Sehwan and Gaj areas (Sind, southern Pakistan), Wessels (2009) estimated site ages through biochronological comparisons with dated assemblages of northern Pakistan. She related older erinaceid sites Seh 81.14a and 84.24 to Z124, on the basis of the presence of *Myocricetodon sivalensis* and multiple species of *Prokanisamys* and *Democricetodon*. Wessels (2009) also listed *Kanisamys indicus* at Seh 81.14a (but not Seh 84.24), which does not appear in the Siwaliks until 17 Ma, suggesting that the Sehwan sites may be younger. Other Sehwan sites (Seh 84.25, 84.26, 82.27, 84.27, and 82.24) appear to be restricted to an interval between the occurrence of abundant murines at

16.3 Ma and the first appearance of *Dakkamys barryi* at 13.5 Ma. We record *Galerix wesselsae* at most of these sites and a mixed sample of *G. rutlandae* and *G. wesselsae* at the youngest site, Seh 82.24. The younger Sind locality Gaj 82.14, dated to about 13 Ma on the basis of similarities to Potwar Chinji Formation faunas, contains *Galerix rutlandae*.

The fauna of Banda Daud Shah, west of the Potwar Plateau, was described by Wessels et al. (1982) and presumed to be about 13 Ma, similar to Gaj 82.14 and Chinji assemblages. The Daud Khel fauna of Hussain et al. (1977, 1979), Munthe (1980), and Munthe and West (1980), is partly undescribed, and its age is not precisely known.

Biogeography and relationships

The galericine fossil record of Pakistan mirrors that of western and central Europe (see Van den Hoek Ostende 2001; Van den Hoek Ostende and Doukas 2003; Prieto et al. 2011) in some important ways. In both areas, *Galerix* first appears in the Early (not earliest) Miocene as an apparent immigrant. Several species of *Galerix*, with broadly successive but overlapping ranges, are followed by more advanced galericines referred to *Schizogalerix* or *Parasorex* in the late Middle or early Late Miocene.

Turkey has a comparably rich and dense Miocene galericine record, but its sequence of galericines is markedly different (Engesser 1980; Van den Hoek Ostende 2001; Van den Hoek Ostende and Doukas 2003; Sel anne 2003; De Bruijn et al. 2006): *Galerix* occurs in the earliest Miocene or even latest Oligocene, *Schizogalerix* is earlier (late Early Miocene Sabuncubeli, correlated to MN 3), and *Galerix* disappears from the record soon afterwards.

The Pakistani record differs from that of Europe in other details. The earliest galericine species in Pakistan is *G. wesselsae*, which first appears around 19 Ma (site Z124). *Galerix* appears penecontemporaneously in Spain (~19.5 Ma; Larraso na et al. 2006) and East Africa (19–20 Ma; Butler 2010; Werdelin 2010). The Spanish *G. remmerti* (Van den Hoek Ostende and Furi o 2005) and Kenyan *G. africanus* are large, primitive species lacking a hypocone on P3. *G. symeonidisi*, morphologically more similar to *G. wesselsae*, appears later in Europe, around 16.8 Ma in Spain (Van der Meulen et al. 2012). In Spain and Germany, this species is soon replaced by the larger *Galerix exilis* (first appearance in Spain at 16.4 Ma), which is thought to be another immigrant (Van den Hoek Ostende and Doukas 2003).

During the Middle Miocene 14.3–14.1 Ma interval on the Potwar Plateau, *Galerix wesselsae* is replaced by *G. rutlandae*, and it is unlikely that the latter is a descendant of the former. If *Galerix rutlandae* is an immigrant in Pakistan, we do not know what its ancestor would be. By the time it appears in Pakistan, *Galerix* is only known from

Europe, and all European *Galerix* species are larger and not especially similar morphologically to *G. rutlandae*. Central Asia may hold clues to this mystery. The stratigraphic range of *G. rutlandae* is shorter than that of *G. wesselsae*, but it coincides with one of the best-sampled intervals in the Siwalik fossil record. The species last appears at 11.6 Ma, close to the last secure occurrence of *Galerix exilis* in Spain at 11.5 Ma (Prieto et al. 2011). *Galerix* is also known from similar-age sites in France and Germany (Mein and Ginsburg 2002; Prieto et al. 2011).

In Pakistan, a species of *Schizogalerix* appears around 11 Ma, securely identified at 10.5 Ma. As far as can be determined from the limited material, the Pakistani *Schizogalerix* is most similar to European *Schizogalerix voesendorfensis*, which first appears in Gratkorn, Austria, at about 12 Ma (Prieto et al. 2010). Galericipines are apparently absent from Pakistan after 10.2 Ma; they survive longer in Turkey and Europe, with the last occurrences in southern Europe in the Pliocene (Crochet 1986; Van den Hoek Ostende 2001; Selänne 2003; Doukas 2005).

One unexpected aspect of the samples described here is the rarity of erinaceines: we found more than 400 teeth of *Galerix*, but only five of erinaceines. In contrast, Munthe and West (1980) found three or four erinaceine teeth in Daud Khel alone, a site that yielded only eight *Galerix* teeth. Erinaceines are often rare in the Miocene (Ziegler, 2000). They are absent in much of the Early Miocene of Turkey and Spain (Van den Hoek Ostende 2001, 2003; Van der Meulen et al. 2012), but become more common in the Miocene of East Africa and Mongolia (Butler 1956; Ziegler et al. 2007). Possibly erinaceines were briefly more abundant in special habitats, and fortuitously represented at Daud Khel, or the paleoenvironment at this site may have been different, perhaps drier than other Siwalik sites, as might be consistent with the absence of tree squirrels but abundant *Sayimys* at Daud Khel (Munthe 1980).

A few other fossils indicate yet different erinaceids: three lower molars from disparate sites suggest the presence of hedgehogs distinctly more gracile than *Galerix*. These may be related to taxa described by Mein and Ginsburg (1997) from Li Mae Long in Thailand, or to the widespread genus *Lantanotherium*, which is known throughout the Holarctic during the Miocene.

Paleoecology

The living gymnures of Southeast Asia are inhabitants of moist forest, and Engesser (1980) therefore postulated a similar ecology for Turkish *Schizogalerix*. However, extant gymnures are morphologically quite different from extinct galericipines and more restricted geographically, so it is plausible that galericipines differed substantially ecologically from living gymnures. Indeed, European *Galerix* species such as *G. remmerti* and *G. exilis* are thought to have preferred a dry environment (Van den Hoek Ostende 2001, 2003; Van den Hoek Ostende and Fejfar 2006).

However, *Galerix symeonidisi* may have preferred a wetter habitat (Van den Hoek Ostende and Doukas 2003) and opinions differ on the ecological preferences of *Parasorex socialis* (Ziegler 2005a; Prieto 2007). Thus, it is prudent to regard the habitat preferences of Pakistani galericines as unknown.

The appearance of *Galerix rutlandae* at about 14.3 Ma coincided with an increase in squirrel diversity and appearance of dormice (Flynn and Wessels 2013), perhaps suggesting that *G. rutlandae* preferred closed, moist habitats. At the time of the final disappearance of galericines in Pakistan, after around 10.2 Ma, C4 grasses first appeared in the Siwaliks, and with a more seasonal climate (Barry et al. 2002). However, other forest-adapted taxa, including treeshrews, lorises, and rhizomyines like *Miorhizomys*, survived another two million years (Flynn 2003). Although woodland taxa persisted on the Late Miocene Siwalik landscape, a trend toward more seasonal conditions coincided with disappearance of the galericines.

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Figure Captions

Figure 1. Nomenclature of structures for upper and lower molars of *Galerix*.

Figure 2. Scatterplots for posterior premolars and molars of fossil erinaceids from Pakistan. Symbols are:

Galerix rutlandae, triangle; *Galerix cf. rutlandae*, diamond;
Galerix wesselsae, cross; *Galerix* sp., square; *Schizogalerix* sp. A, dash
Axes are length (L) and width (W) of teeth, in mm.

Figure 3. Representative cheek teeth of *Galerix wesselsae*. A., left M3 Z568 from Z122; B., right M2 YGSP 48066 from Y747; C., holotype right M1, YGSP52202 from Y642; D., right p4 YGSP 24500 from Y592, in occlusal (above) and latera views; E., left P3 HGSP 84.26-4184; F., left m1 YGSP24542 from Y733 in occlusal and (right) posterior views; G., left m2 in dentary fragment, Z572 from Z122. Scale for all: 1 mm.

Figure 4. Representative cheek teeth of *Galerix rutlandae*. A., left p4 YGSP40025 from Y496, in occlusal (above) and lateral views; B., left M1 YGSP 34925 from Y718 in occlusal and (right) posterior views; C., right m3 YGSP24434 from Y491; D., left M3 YGSP24484 from Y634; E. left M1 YGSP40010 from Y718; F., left P4 YGSP34883 from Y726; left P3 YGSP24454 from Y491; left P3 YGSP24480 from Y634. Scale for all: 1 mm.

Figure 5. A., *Schizogalerix* sp. A, left M2 YGSP24492 from Y259; B. Erinaceinae indet., broken left M1 YGSP52204 from Z122; YGSP 52204; C. *Schizogalerix* sp. A, left p4 YGSP24490 from Y259; D., Erinaceidae indet., left m1 YGSP24499 from Y6668; E., Erinaceinae indet., left m3 YGSP39462 from Y931. Scale for all: 1 mm.