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Martin Pickford, Pierre Mein

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Nuevos Pedetidae (Rodentia: Mammalia) del Mio-Plioceno de Africa

M. Pickford¹, P. Mein²

ABSTRACT

Pedetidae, or springhares, are represented by a single extant genus (Pedetes) and five extinct ones (Parapedetes, Megapedetes, Propedetes, Rusingapedetes and Oldrichpedetes) of which the latter two are new. The fossil record of pedetids tends to be scanty, but remains have been found in Southern Africa, East Africa, the Maghreb, the Arabian Peninsula, Turkey and Greece. Most of the localities have yielded only a few isolated teeth. We here describe some of the abundant fossil material from Namibia and Kenya, which throws a great deal of light on the family.

Key words: Spring hares, Rodentia, Neogene, Africa, Europe, systematics, biogeography

RESUMEN

Los Pedetidae o liebres saltadoras están representados por un solo género actual (Pedetes) y 5 extintos (Parapedetes, Megapedetes, Propedetes, Rusigapedetes y Oldrichpedetes, estos dos últimos son nuevos). El registro fósil de los pedetidos es escaso, pero restos fósiles han sido encontrados en Sudáfrica, África del Este, Magreb, Península Arábiga, Turquía y Grecia. La mayoría de las localidades sólo han suministrado unos pocos dientes aislados. En el presente trabajo describimos parte del abundante material fósil procedente de Namibia y Kenia, que arroja nueva luz al conocimiento de la familia.

Palabras Clave: Liebres saltadoras, Rodentia, Neógeno, África, Europa, sistemática, biogeografía

Introduction

Springhares or Pedetidae are an African family of superficially kangaroo-like rodents characterised by hystricomorphy (enlarged infraorbital foramen) combined with a sciurognathic mandible, by the bilophodont cheek teeth and the special adaptation for bipedal saltatorial locomotion. They should not be confused with other bilophodont rodents such as Diatomys from Thailand, as was already highlighted by Leonard Ginsburg and one of the authors (Mein & Ginsburg, 1997) who erected the family Diatomyidae for it. This paper is dedicated to the memory of Leonard Ginsburg.

There is a single extant genus Pedetes represented by two species, Pedetes capensis in South Africa, and Pedetes surdaster in East Africa (Fig. 1) (the latter is often considered to be a synonym of the former, the position adopted in this paper). Three extinct genera have been described, Parapedetes Stromer, 1922, Megapedetes MacInnes, 1957, and Propedetes Mein & Pickford, 2008. Of these only Propedetes is closely related to the extant genus. We here describe two new genera and species of the family.

Parapedetes is known from only one locality, Elisabethfeld, Sperrgebiet, Namibia, an Early Miocene site aged ca 20-21 Ma. Hopwood (1929) recorded its presence at Langental, but the specimen he mentioned is more properly attributed to Propedetes efeldensis. Parapedetes namaquensis was a small, extremely hypsodont spring hare, and only

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aged individuals developed roots in the cheek teeth and secreted some cementum. In adults the two lophs are connected longitudinally. There is a mesoflexus in the upper teeth and a hypoflexid in lower cheek teeth. Unworn teeth in the samples collected by the Namibia Palaeontology Expedition reveal that Parapedetes exhibit two flexi and two stria of very unequal dimensions, the shallower flexus soon disappearing with even a small degree of wear.

Megapedetes was first described from Songhor, Kenya, an Early Miocene site aged ca 20 Ma. The teeth are not hypsodont but semi-hypsodont. The crown height is roughly equivalent to the length of the tooth. At Arrisdrift, in deposits aged ca 17.5 Ma two species of Megapedetes were described by Mein & Senut (2003) M. gariepensis, which is relatively common, and M. pickfordi, which is rarer. The latter is here attributed to the new genus Oldrichpedetes. The cheek teeth of M. gariepensis are 10% smaller than those of M. pentadactylus (the type species from East Africa) and the molar crowns are slightly more hypsodont, the hypsodonty index H/L (height / length) being 1.3 in lower teeth and 1.5 in upper teeth. In occlusal view the anterior lophid of p/4 is narrower and shows an elongated longitudinal groove on its distal wall. The posterior lophid of m/3 is more transversely developed and among the mandibles collected, one specimen (GSN AD 214’99) exhibits a supernumary tooth (m/4) the first time that such a dental abnormality has been described in Pedetidae.

The genus Megapedetes is represented at a number of other localities in East Africa, North Africa, the Arabian Peninsula, Turkey and Greece (Fig. 1). In the last three countries the fossils have been attributed to Megapedetes aegaeus (Sen, 1977).

Oldrichpedetes brigitteae nov. gen. nov. sp. from Zebra Hill, Namib-Naukluft Park, Namibia, is the smallest pedetid known. It is represented by an isolated m/1 in which the mesostriid is considerably taller than the hypostrid and the hypsodonty index is 2.4. Oldrichpedetes pickfordi from Arrisdrift is known by six teeth. The hypsodonty index is 1.9 and there is a difference in height of the mesostriid and hypostrid of 1.3 mm, making it intermediate between Megapedetes and Propedetes. The last record of the genus Oldrichpedetes is from the Early Pliocene of Tunisia (Batik & Fejfar, 1990).

Rusingapedetes nov. gen. is currently known only from Rusinga Island, Kenya, from deposits aged about 17.8 Ma. Previously, isolated teeth of this genus were attributed to a small, un-named species of Megapedetes (Lavocat, 1973) but now that a complete skull is known it is clear that it represents an undescribed genus of pedetid.

In the aeolianites of Rooilepel and related sites in the Spergebiet, Namibia, there are abundant teeth, jaws and damaged skulls, and occasional articulated skeletons, attributed to the genus Propedetes, first described from Elisabethfeld (Mein & Pickford, 2008). The post-cranial bones indicate that it was well adapted to saltatorial locomotion. The type species, Propedetes efeldensis, is about the same size as Parapedetes namaquensis, and is equally hypsodont. Cementum may appear at the base of the mesostria in senile individuals, when short roots are developed. The mesostria(id) is considerably taller than the hypostria(id). In Parapedetes, the opposite is the case, the hypostria(id) being considerably taller than the mesostria(id). In Megapedetes and Oldrichpedetes, the mesostria(id) and hypostria(id) are about the same height as each other.

In Propedetes the lower p/4 is less hypsodont than the molars and its morphology is different. In contrast to Parapedetes, and similar to Pedetes, some of the teeth of Propedetes are strongly curved, especially the P4/ which is concave anteriorly, and
Table 1.— List of fossil pedetid localities (with latitude and longitude according to Google Earth) and taxa arranged by country. Where necessary the species names have been updated from the original names mentioned in the literature. Several new species of *Propedetes* occur in Namibia, and will be described in a forthcoming paper.

<table>
<thead>
<tr>
<th>South Africa</th>
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<th>EASTERN AFRICA</th>
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<td><strong>SOUTHERN AFRICA</strong></td>
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<td><strong>KENYA</strong></td>
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<td>Kramkleeg (30°17’05.8”S: 16°17’24.0”E) <em>Pedetes cf capensis</em> (this paper).</td>
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<td>Fort Ternan (0°13’10.6”S: 35°20’22.7”E) <em>Megapedetes cf pentadactylus</em> (Denys &amp; Jaeger, 1992).</td>
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<td>Sterkfontein (26°01’02”S: 27°44’24.7”E) <em>Pedetes cf capensis</em> (Brain, 1993).</td>
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<td>Gamble’s Cave (0°39’S: 36°13’E) <em>Pedetes</em> sp. (Hopwood, 1931).</td>
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<td>Swartkrans (26°01’02”S: 27°44’24.7”E) <em>Pedetes cf capensis</em> (this paper).</td>
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<td>Isinya (1°41’01.4”S: 26°51’10.2”E) <em>Pedetes capensis</em> (Brugal &amp; Denys, 1989).</td>
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<td>Namibia</td>
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<td>Kalodirr (3°19’01.8”N: 35°44’51”E) <em>?Megapedetes aegaeus</em> (Winkler, 1992).</td>
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<td>Arrisdrift (28°28’32.8”S: 16°42’23.2”E) <em>Megapedetes gariepensis, Oldrichpedetes</em> pickfordi (Mein &amp; Senut, 2003).</td>
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<td>Kimrun (0°43’58.8”N: 36°53’32”E) <em>Megapedetes aegaeus</em> (Ishida &amp; Ishida, 1982).</td>
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<td>Awasib (25°18’19”S: 15°38’57”E) <em>Pedetes cf gracilis</em> (this paper).</td>
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<td>Lainyamok (1°48’05.8”S: 36°12’31.9”E) <em>Pedetes</em> sp. (Potts &amp; Deino, 1995).</td>
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<td>Berg Auksa (19°30’57.5”S: 18°15’10.5”E) <em>Propedetes laetoliensis, Pedetes cf capensis</em> (this paper).</td>
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<td>Legetet (0°08’40.2”S: 35°15’24.5”E) <em>Megapedetes pentadactylus</em> (Pickford, 1986).</td>
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<td>Bushman Hill (west of) (25°08’00.4”S: 15°44’28.9”E) <em>Pedetes gracilis</em> (this paper).</td>
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<td>Lakeino (0°45’12.7”N: 35°52’29.9”E) OCO Bar 602’02, lower incisor, <em>Propedes</em> sp. (Mein &amp; Pickford, 2006).</td>
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<td>Daberass Dune near inselberg (28°08’35”S: 16°39’40”E) <em>Pedetes gracilis</em> (this paper).</td>
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<td>Maboko (0°09’40.1”S: 34°36’26.7”E) <em>Megapedetes gariepensis</em> (Winkler, 1992).</td>
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<td>Ekuma (18°37’06.9”S: 16°00’59.1”E) <em>Propedetes laetoliensis</em> (Pickford et al., 2009).</td>
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<td>Magare Beach (0°20’56.4”S: 34°16’26.1”E) <em>Megapedetes</em> (Pickford, 1986).</td>
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<td>Elisabethfied (26°58’52.5”S: 15°15’57.1”E) <em>Parapedetes namaquensis</em> (Stromer, 1922, 1926) <em>Propedetes efeldensis</em> (Mein &amp; Pickford, 2008).</td>
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<td>Meswa Bridge (0°08’09.3”S: 35°12’18.6”E) <em>Oldrichpedetes praecursor</em> (Winkler, 1992).</td>
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<td>GP Pan North (28°29’47.3”S: 16°32’14.7”E) <em>Propedes cf laetoliensis</em> (this paper).</td>
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<td>Mfwangano (Makira, Walangani and Hiwegi Formations) (0°27’37.3”S: 34°03’40.1”E) <em>Megapedetes pentadactylus</em> (Pickford, 1986).</td>
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<td>Harasi (19°34’02”E: 17°48’19.3”E) <em>Propedes</em> sp. nov. (Mein et al., 2000).</td>
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<td>Ombo (0°04’04.8”S: 34°33’50.7”E) <em>Megapedetes</em> small sp. (Pickford, 1986).</td>
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<td>Karingarab (28°12’15”S: 16°21’30”E) <em>Propedes laetoliensis</em> (this paper).</td>
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<td>Rusinga (Wayondo and Hiwegi Formations) (0°24’27.7”S: 34°12’39.5”E) <em>Megapedetes pentadactylus, Rusingapedetes tsukikawai</em> gen. et sp. nov., (Lavocat, 1973; MacInnes, 1957; Pickford, 1986; this paper).</td>
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<td>Langenthal (27°24’27.9”S: 15°24’27.9”E) <em>Propedes efeldensis</em> (Hopwood, 1929; Mein &amp; Pickford, 2008).</td>
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<td>Songhor (0°02’06.5”S: 35°12’34.6”E) <em>Megapedetes pentadactylus</em> (Lavocat, 1973; MacInnes, 1957; Pickford, 1986).</td>
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<td>Rooilepel (28°17’56.4”S: 16°35’01”E) <em>Propedes efeldensis, Propedes</em> sp. nov., <em>Propedes laetoliensis</em> (Corbett, 1989; this paper).</td>
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<td><strong>UGANDA</strong></td>
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<td>Tree Pan (25°54’40.6”S: 15°56’09.9”E) <em>Pedetes cf gracilis</em> (this paper).</td>
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<td>Moroto II (2°40’22.1”N: 34°42’54.6”E) <em>Megapedetes gariepensis</em> (Mein &amp; Pickford, 2006).</td>
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<td>Tsachab (24°30’14.4”S: 15°43’01.4”E) <em>Pedetes laetoliensis, Pedetes cf capensis</em> (this paper).</td>
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<td>Napak I (2°06’02.4”N: 34°11’27.1”E) <em>Megapedetes pentadactylus</em> (Lavocat, 1973; MacInnes, 1962).</td>
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<td>Zebra Hill (23°37’40.2”S: 15°38’42.7”E) <em>Oldrichpedetes brigitteae</em> gen. et sp. nov. (this paper).</td>
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<td>Napak IV (2°07’03.6”N: 34°11’17”E) <em>Megapedetes pentadactylus</em> (MacInnes, 1962).</td>
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<td><strong>BOTSWANA</strong></td>
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<td>Napak V (2°06’43.7”N: 34°11’15.6”E) <em>Megapedetes pentadactylus</em> (MacInnes, 1962).</td>
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<td>Koanaka N (20°08’38.3”S: 21°12’33.9”E) <em>Pedetes capensis</em> (this paper).</td>
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<td>Bukwa (1°17’06.3”N: 34°47’04.9”E) <em>Megapedetes pentadactylus</em> (Walker, 1969).</td>
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<td>Koanaka W (20°09’31.5”S: 21°11’40.1”E) <em>Pedetes capensis</em> (this paper).</td>
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<td><strong>TANZANIA</strong></td>
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<td><strong>ZIMBABWE</strong></td>
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<td>Eyasi (3°32’31.6”S: 35°14’32.7”E) <em>Pedetes capensis</em> (Dietrich, 1939).</td>
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<td>Bulawayo (20°10’10.5”S: 28°40’58.8”E) <em>Pedetes capensis</em> (Zeally, 1916).</td>
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<td>Laetoli (3°13’10”S: 35°10’17”E) <em>Propedes laetoliensis</em> (Davies, 1987; Dietrich, 1942).</td>
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<td>Olduvai (2°56’58.9”S: 35°14’32.7”E) <em>Pedetes</em> sp. Peninj (2°19’14.1”S: 35°53’5.4”E) <em>Pedetes</em> sp.</td>
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the m/3 which is concave buccally and posteriorly. In this genus the determination of isolated teeth follows the same rules as for *Megapedetes*.

Broken teeth from Rooilepel show a strange undulation at the base of the flexus creating a central isthmus (Fig. 4). It is not possible to observe this structure in complete teeth. This formation is present in all the broken teeth examined, but unfortunately we have not been able to see it in other species. Abundant specimens of *Propedetes* have been found associated with struthious eggshells which permit them to be correlated to the biochronological time scale, from which their ages can be estimated (paper in preparation). The main horizons are the *Tsondabornis minor* level (21-18 Ma) from which *Parapedetes namaquensis*, *Megapedetes aegaeus* (Thomas *et al.*., 1982).

### Israel


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**NORTHERN AFRICA AND ARABIA**

**Morocco**


**Tunisia**

Ech Chouachi (35°33′45″N: 9°32′21.7″E) MN 14, *Oldrichpedetes fejfarii* gen. et sp. nov. (Batik & Fejfar, 1990).

**United Arab Emirates**


**Israel**


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**EUROPE**

**Turkey**

Bayraktepe (37°01′28″N: 36°46′01″E) MN 7/8, *Megapedetes aegaeus* (Sen, 1977).

**Greece**

Chios (38°18′35.3″N: 26°08′43.7″E) MN 5, *?Megapedetes pentadactylyus* (Tobien, 1968; Sen, 1977).

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<table>
<thead>
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<td>Ech Chouachi (35°33′45″N: 9°32′21.7″E) MN 14, <em>Oldrichpedetes fejfarii</em> gen. et sp. nov. (Batik &amp; Fejfar, 1990).</td>
<td>Chios (38°18′35.3″N: 26°08′43.7″E) MN 5, <em>?Megapedetes pentadactylyus</em> (Tobien, 1968; Sen, 1977).</td>
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</table>

Pedetes is characterised by rootless cheek teeth and a molariform p/4. The hypsodonty of the P4/ increased rapidly with the passage of geological time. In the extant form this tooth is inclined along the premaxillary bone. In *Pedetes gracilis* from Taung, South Africa (Middle Pliocene), the P4/ was less curved and more upright. In Namibia the same extinct species has been collected at Bushman Hill, Daberis Dune (near the inselberg) and Tree Pan. Fossils of the extant species, *Pedetes capensis* have been found in Namibia at Tsauchab and at other sites in South Africa and Botswana (Table 1).

In *Pedetes* the existence of a second flexus in the cheek teeth was demonstrated by Wood (1962, 1965) but for an inexplicable reason, lateral views of young *Pedetes* teeth have never been illustrated. The mesostria (and striids) are so tall that they encompass the entire height of the tooth and cementum occurs in the resulting canal, even in juvenile individuals.

**Nomenclature of the teeth of Pedetidae**

The cheek teeth of pedetids are comprised of two lophs (lophids) separated by a median transverse valley (Fig. 2, 3, 4). On the buccal and lingual surfaces the valley is expressed as notches or deep...
grooves, which, following the nomenclature of Stirton (1935) are called the hypostria(striid) and mesostria(striid). The hypostria(striid) (s) is always narrower than the mesostria(striid) (S). The first loph(id) is always more developed mesio-distally than the second loph(id) on the hypostria(striid) side. The determination of isolated teeth of Propedetes is thus done as follows (Fig. 2, 3, 4):

With the stria(id) oriented vertically and the occlusal surface upwards
1. the anterior loph (id) is longer than the distal one (black arrows in figure 3).
2. upper cheek teeth have a higher distal loph than the mesial one; lower cheek teeth have a lower distal lophid than the mesial one.

Because of the simple bilophodont structure of the cheek teeth it is not easy to determine the meristic position of isolated specimens. In occlusal view the two lophs are more convergent on one side which results in a narrower flexus (hypoflexus) (s) which is lingual in upper teeth and buccal in lower teeth (hypoflexid). On the other side of the crown, the flexus (mesoflexus) is antero-posteriorly longer (S).

In summary, the discrimination of pedetid teeth is based, first and foremost, on the different heights of the mesostria(id) and hypostria(id) in the intermediate molars (M1/ and M2/, m/1 and m/2), secondly, on the maximum ratio of height over length (H/L) which represents the hypsodonty, and thirdly, on the crown area (length x breadth), and in Propedetes on the measure S-s.
Abbreviations


Previous literature

Pedetid fossils have been reported on many occasions, yet a complete listing of the available samples has not previously been compiled. The following table and figures (Table 1, Fig. 5, 6) provide a list of localities and taxa gleaned from the literature as well as of undescribed material collected by the authors. Some of the fossils mentioned in the literature could not be studied, either due to the fact that the material has been lost since being published, or because its current whereabouts are unknown.

Systematic descriptions

Order Rodentia Bowdich, 1821
Family Pedetidae Gray, 1825
Subfamily Pedetinae Gray, 1825
Genus Rusingapedetes nov.
Type species: Rusingapedetes tsujikawai nov.
Diagnosis: Small pedetid with brachyodont cheek teeth, from ventral to dorsal the anterior margin of orbit slopes strongly mesially.
Derivatio nominis: The genus name refers to the type locality, Rusinga, Kenya.
Species Rusingapedetes tsujikawai nov.
Holotype: KNM RU 14355, skull with deeply worn cheek dentition (Fig. 7, 8, 10).
Paratypes: KNM RU 2347, left p/4, KNM RU 2348, left m1; KNM RU 2349, lower molar (Lavocat, 1973, pp. 197-198, pl. 28, fig. 10) (Fig. 9).
Type locality: R1, Rusinga Island, Kenya.
Age: Early Miocene, ca 17.8 Ma.
Diagnosis: Small size, strongly brachyodont cheek teeth, M3/ not reduced.
Fig. 6.—Stratigraphic position and approximate ages of fossil Pedetidae localities.
Derivatio nominis: The species name is in honour of Dr Hiroshi Tsujikawa who kindly provided information valuable for this study.

Description: The holotype skull of *Rusingapedetes tsujikawai* represents a senile individual with heavily worn cheek teeth (Fig. 7, 8, 10). The skull has been slightly distorted by post-mortem processes, it is ca 5 cm long, and ca 3.5 cm at its broadest measured across the zygomatic arches. The cheek tooth row is 10.6 mm long and consists of only three teeth on each side, which we interpret to be the M1/ to M3/, although the anterior tooth is less worn than the two teeth behind it suggesting that the teeth may instead be the P4/ to M2/. There is no sign of alveoli behind the distal teeth but there may be a resorbed alveolus in front of the anterior one on the left side. Further preparation or scanning is required to resolve the uncertainty.

The skull possesses many characteristics of pedetids (skulls are known for *Pedetes capensis*, *Parapedetes namaquensis*, *Megapedetes pentadactylus* and *Propedetes laetoliensis*) (Fig. 10). The rounded extensions of the supra-tympanic part of the auditory bullae are vast, and encroach onto the dorso-lateral aspect of the skull at the rear, where they are separated from each other by the inter-parietal and supra-occipital (Fig. 7). The incisors are opisthodont and rectangular in section, the skull is hystricomorph, the dorsal surface of the brain case is broad with no sign of a sagittal crest, the nasals are large and overhang the upper incisors, and the external auditory meatus is roughly at mid-height of the rear of the skull.

The specimen differs from the skull of *Pedetes* and *Propedetes* by its smaller dimensions, by the forwardly sloping margin of the infraorbital margin (upright in *Pedetes*, *Megapedetes*, *Parapedetes* and *Propedetes*) and the upper incisors diverge more rapidly as they curve upwards and backwards into the premaxilla. The posterior choanae in the fossil extend anteriorly between the M2/s as in *Pedetes*; in *Propedetes* they reach even further forwards to the M1/s (Davies, 1987, fig. 6-28).

*Rusingapedetes* differs from *Megapedetes* by its much smaller dimensions, the anteriorly sloping mesial-distally broader orbital margin. *Rusingapedetes* differs from *Parapedetes* by its greater dimensions, by its forwardly sloping infraorbital margin, and by its brachydont cheek teeth endowed with roots, and by the loss of P4/ in aged individuals.

The orbit in *Rusingapedetes* seems to be small relative to the dimensions of the skull compared to those of *Pedetes*, *Megapedetes*, *Parapedetes* and *Propedetes*. This suggests that it may

Fig. 7.—Holotype skull of *Rusingapedetes tsujikawai* nov. gen. nov. sp. KNM RU 14355, A) dorsal, B) palatal, C) anterior, D) right lateral, E) posterior and F) left lateral views (scale 10 mm).

Fig. 8.—Stereo occlusal image of the palate of KNM RU 14355, holotype of *Rusingapedetes tsujikawai* nov. gen. nov. sp. (scale 10 mm).
have been more diurnal than the other taxa. The first is an obligatory nocturnal animal and the others may have been the same.

There are only three cheek teeth preserved in each maxilla in the skull, which we interpret to be the three molars (Table 2). There is a hint of the presence of a resorbed alveolus in front of M1, which needs to be verified by further preparation of the specimen. The teeth in the holotype skull are deeply worn. There is a prominent mesoflexus on the buccal side of M1 and M2, but M3 is worn so deeply that no sign of the mesoflexus is left. If there were a hypoflexus, then it has been worn away in all the teeth. A superficial glance at the teeth gives the false impression that they are somewhat like those of bathyergids.

Genus **Oldrichpedetes** nov.

*Type species:* *Megapedetes* pickfordi Mein & Senut, 2003

*Diagnosis:* Pedetidae of medium size, cheek teeth with straight columnar crowns, stria and striids oriented as in *Mega-

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Tooth</th>
<th>MDL</th>
<th>blm</th>
<th>Bld</th>
</tr>
</thead>
<tbody>
<tr>
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<td>3.50</td>
<td>-</td>
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<tr>
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<td>2.63</td>
<td>-</td>
</tr>
<tr>
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<td>3.40</td>
<td>3.40</td>
<td>-</td>
</tr>
<tr>
<td>KNM RU 14355</td>
<td>M2 right</td>
<td>2.85</td>
<td>3.60</td>
<td>-</td>
</tr>
<tr>
<td>KNM RU 14355</td>
<td>M3 left</td>
<td>2.80</td>
<td>3.20</td>
<td>2.20</td>
</tr>
<tr>
<td>KNM RU 14355</td>
<td>M3 right</td>
<td>3.00</td>
<td>2.90</td>
<td>-</td>
</tr>
</tbody>
</table>

Fig. 9.—Teeth of *Rusingapedetes tsujikawai* nov. gen. nov. sp. The specimens on the left, A) KNM RU 2348, left m/1, occlusal view, and B) KNM RU 2347, left p/4, occlusal view, were described by Lavocat (1973) but their current whereabouts are unknown. The teeth to the right, C) are of the holotype, KNM RU 14355.

Fig. 10.—Comparison of lateral views of the skulls of fossil and extant pedetids. A – *Parapedetes namaquensis*, B – *Rusingapedetes tsujikawai* nov. gen. nov. sp., C – *Propedetes laetoliensis*, D – *Pedetes capensis*, E – *Megapedetes pentadactylus*. Note the orientation of the anterior margin of the orbit (scale – 5 cm).
Oldrichpedetes, short strid(s) lingual in upper teeth, buccal on lower teeth, roots coalescent and can be long in senile teeth. Crown height increased with the passage of geological time but the difference in length of the strids and stria remained weak.

*Oldrichpedetes* differs from the much larger *Megapedetes* by its greater hypsodonty, the ratio H/L being greater than 1 (in non-senile teeth). *Oldrichpedetes* differs from *Parapedetes* by its greater dimensions and by the inverted heights of the strids. *Oldrichpedetes* differs from *Propedetes* by its straight columnar crowns, not only in buccal and lingual views, but also in mesial and distal views. In *Propedetes* the molars are laterally curved.

**Derivatio nominis:** The genus name honours Oldrich Fejfar and acknowledges his contribution to the understanding of European and African fossil micromammals.

**Included species:**

- *Oldrichpedetes pickfordi* (Mein & Senut, 2003), MN 5, ca 17.5 Ma, Arrisdrift, Namibia.

- *Oldrichpedetes fejfari* sp. nov. MN 14, Ech Chouachi, Tunisia. *Oldrichpedetes brigitteae*, sp. nov. ca 18-19 Ma, Zebra Hill, Namibia. *Oldrichpedetes praecursor*, sp. nov. ca 22.5 Ma, Meswa Bridge, Kenya.

**Species *Oldrichpedetes pickfordi* (Mein & Senut, 2003)**

- **Holotype:** GSN AD 715°99, right P4/ (Mein & Senut, 2003, pl. 2, fig. A)

- **Paratypes:** GSN AD 583°94, left m/2 (Mein & Senut, 2003, pl.1 fig. 6); GSN AD 273b°96, left m/2 (Mein & Senut, 2003, pl. 1, fig. 5).

- **Referred material:** GSN AD 14°99, left M3/; GSN AD 583°94, right m/1; GSN AD 536°95, right m/2.

- **Type locality:** Arrisdrift, Namibia, basal Middle Miocene (MN 4) ca 17-17.5 Ma. Original diagnosis. See Mein & Senut, 2003, p. 166.

- **Emended diagnosis:** m/3 with reduced posterior loph.

- **Complement to original description:** Among the various species of *Oldrichpedetes*, *O. pickfordi* is the best represented with 6 teeth. AD 414°00 is here interpreted to be a left m/1 of *Megapedetes gariepensis* because its dimensions are greater than those of other specimens of *O. pickfordi*, and the root is recurved towards the front.

The upper dentition is represented by two teeth (Table 3). The P4/, GSN AD 715°99 (the holotype) has weak basal elongation and the occlusal surface of the crown is very oblique with respect to the column of the tooth. In 2003 the left M3/ was originally attributed to *Megapedetes gariepensis*, but its dimensions are too small for it to belong to this taxon. In Pedetidae, the M3/ and m/3 usually have similar lengths. The description of the specimen remains valid. The tooth is deeply worn, the hypoflexus has disappeared, and the mesoflexus has been transformed into a fossette. Nevertheless the apparent hypsodonty is strong (H/L is ca 1.5) and the single root is curved towards the rear.

The lower dentition is known by three m/1–m/2s and an m/3. The distinction between m/1 and m/2 is based on the fact that m/2 is shorter than m/1. The maximal breadth is at the rear in m/1 and in the front in the m/2. This is why GSN AD 273b°96 is a left m/1, and GSN AD 583b°94 is a right m/1, whereas GSN AD 583a°94 and GSN AD 273b°96 are left m/2s.

In the 2003 publication, no m/3 was identified. It appears that GSN AD 405°99, initially thought to be a right M1/ is in reality a left m/3, because the posterior loph is lower and shorter than the anterior one.

**Species *Oldrichpedetes fejfari* nov.**

- **Holotype:** Left m/1, Charles University, Prague.

- **Type locality:** Black lacustrine clay with ferruginous nodules south of Ech Chouachi, Central Tunisia (Batik & Fejfar, 1990).

- **Age:** Early Pliocene age (MN 14) based on the associated murids (*Saidomys, Tectonomys, Hansdebruijnia* — reidentified from Batik & Fejfar, 1990).

- **Description:** Largest and most hypsodont species of *Oldrichpedetes*, in which the buccal and lingual stria/strids are equally tall.

- **Derivatio nominis:** The species name is in honour of Oldrich Fejfar and his extensive studies of Old World micromammals.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Tooth</th>
<th>MDL</th>
<th>Blm</th>
<th>bld</th>
<th>H</th>
<th>S</th>
<th>S</th>
<th>H-s/L</th>
<th>H-S/L</th>
<th>S-s</th>
<th>H/L</th>
</tr>
</thead>
<tbody>
<tr>
<td>GSN AD 583°94</td>
<td>m/1 right</td>
<td>2.73</td>
<td>3.13</td>
<td>3.05</td>
<td>3.85</td>
<td>1.53</td>
<td>0.66</td>
<td>1.20</td>
<td>0.80</td>
<td>0.87</td>
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<tr>
<td>GSN AD 273b°96</td>
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<td>3.00</td>
<td>2.65</td>
<td>3.78</td>
<td>1.53</td>
<td>1.10</td>
<td>1.00</td>
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<td>0.43</td>
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<td>GSN AD 583a°94</td>
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<td>2.80</td>
<td>2.80</td>
<td>4.88</td>
<td>3.25</td>
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<td>0.80</td>
<td>0.99</td>
<td>1.30</td>
</tr>
<tr>
<td>GSN AD 405°99</td>
<td>M1/ right</td>
<td>2.90</td>
<td>2.72</td>
<td>2.95</td>
<td>4.00</td>
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<td>0.60</td>
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<td>0.90</td>
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<td>1.30</td>
<td>0.90</td>
<td>1.02</td>
<td>1.30</td>
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</tbody>
</table>

**Table 3.** Measurements (in mm) of the teeth of *Oldrichpedetes pickfordi* (Mein & Senut, 2003).
3.55 and 3.57 and the basal breadths 4.51 and 4.57, which are close, indicating that the tooth is most likely an m/1.

The tooth is juvenile because it had not completed growing, the occlusal dimensions being considerably less than the basal ones. It is noted that with growth the breadth increases faster than the length. In the original description of the specimen (Batik & Fejfar, 1990) the authors inverted the front and back in the occlusal view. Recall that in all pedetids, when the stria(id) is oriented vertically, the occlusal surface of the upper cheek teeth rises towards the rear, whereas in lower teeth it descends to the rear. The stria and striids subdivide the crown into two lophs, of which the anterior one is longer than the posterior one (both upper and lower molars). Despite its marked hypsodonty, the crown of the Ech Chouachi pedetid molar is columnar and straight.

### Species Oldrichpedetes brigitteae nov.

*Holotype:* GSN ZH 1’95, left m/1 or m/2.

*Type locality:* Zebra Hill, Namib-Naukluft Park, Namib Desert, Namibia.


**Diagnosis:** Smallest known species of Pedetidae, buccal striid relatively tall, lingual striid recurved distally towards its base. The specimen has a single root.

**Derivatio nominis:** The species name is in honour of Brigitte Senut, co-leader of the Namibia Palaeontology Expedition.

**Description:** The presence of anterior and posterior contact facets indicates that the tooth is an m/1 or an m/2 (Fig. 12, Table 5). The largest loph is also the tallest (even though the difference in height is not very great) which indicates that it is a right tooth. The presence of a single root apically suggests coalescence of the root or taurodonty, also present in *Parapedetes namaquensis*, but it cannot belong to this species on account of the much greater hypsodonty and curved columns of the latter species. In *Oldrichpedetes brigitteae*, the ratio H/L is 2.55.

### Species Oldrichpedetes praecursor nov.

*Holotype:* KNM ME 10525, left M3/ from Meswa Bridge, Kenya. Type locality. Meswa Bridge, Kenya.

*Age:* Early Miocene age, ca 22.5 Ma (= MN 2).

**Diagnosis:** Extremely small pedetid, transverse lophs incomplete in unworn teeth, extremely brachyodont.
Derivatio nominis: The species name refers to the primitive morphology of the type specimen and its possible role as an ancestor of later species in the genus.

Differential diagnosis: Differs from other species of *Oldrichpedetes* by its smaller dimensions, and its more brachyodont cheek teeth.

Description: The type specimen is a left M3/ comprising three cusps separated by narrow grooves, forming two lophs (Winkler, 1992) (Fig. 13, Table 6). The anterior loph is the widest part of the tooth. There is a narrowing between the loph and the protocone, marked on the mesial surface of the tooth as a narrow groove which would disappear with slight wear. There is also a narrowing on the posterior loph marked by a stronger posterior groove. The posterior loph is slightly oblique towards the rear and is shorter than the anterior loph. The enamel is relatively thick. There is an anterior contact facet towards the lingual side of the tooth. The roots are coalescent near the cervix, but are separated at their apices. The ratio H/L is 0.85.

Discussion

The four species of *Oldrichpedetes* are distinguished from each other on the basis of dimensions of cheek teeth and their hypsodonty. The difference in height of the stria(id) does not change much through the geological record, unlike the genus *Pro-*

Table 5.—Measurements (in mm) of the teeth of *Oldrichpedetes brigitteae* nov. gen. nov. sp.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Tooth</th>
<th>MDL</th>
<th>blm</th>
<th>bld</th>
<th>H</th>
<th>S</th>
<th>s</th>
<th>H-s/L</th>
<th>H-S/L</th>
<th>S-s</th>
<th>H/L</th>
</tr>
</thead>
<tbody>
<tr>
<td>GSN ZH 1’95</td>
<td>m/1 or m/2 left</td>
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<td>2.14</td>
<td>2.17</td>
<td>5.77</td>
<td>3.55</td>
<td>1.28</td>
<td>0</td>
<td>0</td>
<td>2.27</td>
<td>2.55</td>
</tr>
</tbody>
</table>

Table 6.—Measurements (in mm) of the teeth of *Oldrichpedetes praecursor* nov. gen. nov. sp.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Tooth</th>
<th>MDL</th>
<th>blm</th>
<th>bld</th>
<th>H</th>
<th>H/L</th>
</tr>
</thead>
<tbody>
<tr>
<td>KNM ME 10525</td>
<td>M3/</td>
<td>2.50</td>
<td>2.90</td>
<td>2.30</td>
<td>2.14</td>
<td>0.85</td>
</tr>
</tbody>
</table>

Fig. 12.—GSN ZH 1’95, left m/1 or m/2, holotype of *Oldrichpedetes brigitteae* from Zebra Hill, Namib-Naukluft Park, Namibia, A1) occlusal, A2) radicular, A3) buccal, A4) mesial, A5) lingual A6) distal views (scale - 1 mm).

Fig. 13.—KNM ME 10525, holotype left M3/ of *Oldrichpedetes praecursor*, nov. gen. nov. sp. from Measa Bridge, Kenya, A) occlusal, B) buccal, C) mesial, D1) distal, D2) distal oblique, and E) oblique lingual views (scale – 1 mm).
pedetes in which the dimension S-s increases steadily from ca 21 Ma to 3.5 Ma.

**Biogeography**

Pedetids are currently found only in the equatorial and austral zones of Africa (MacDonald, 2001) but it has been known for half a century that the family spread far northwards into the Arabian Peninsula, the Maghreb and even to southern Europe (Fig. 14) (Tobien, 1968).

An interesting point about the greater latitudinal range that the family had during the Miocene and Pliocene than it does today is that the septentrional records coincide with periods during which proto-Ethiopian faunas and floras spread northwards into mid-latitude Eurasia (MN 4, MN 5, MN 9 and MN 14). These were periods during which southern Europe was more tropical than it is today, with mammals such as tapirs appearing in the fossil record of Europe for example. During other periods, when mid-latitude Eurasia was under boreal palaeoclimatic conditions, plants and animals adapted to tropical environments disappeared from most of Europe as the boundary zone between the proto-Ethiopian and proto-Palaearctic Realms withdrew equator-wards (Fig. 14). As such the pedetids provide confirmation of the patterns of Mio-Pliocene faunal change summarised by Pickford & Morales (1994).

From time to time the faunal resemblance between East Africa and Spain was high, at other times low (diagram modified from Pickford &

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Fig. 14.—Northwards migration of Pedetidae during the Miocene (arrows marked 1 to 4) accords reasonably well with the movements of other mammals and plants during the period.
Morales, 1994) reflecting latitudinal shifts in the position of the boundary between the proto-Ethiopian and proto-Palaearctic Zoogeographic Realms.

Conclusions

Fossils collected during the past two decades in Namibia and elsewhere in Africa have revealed that the rodent family Pedetidae is more diverse than previously thought. Until 2008, only three genera had been reported in the literature. Pedetes (the extant genus), Parapedetes (known from a single site in Namibia) and Megapedetes (widespread in equatorial East African Early and Middle Miocene sites, and reported from North Africa, the Arabian Peninsula and southern Europe. Recently the genus Propedes was described, and this paper erects two new genera, Rasingapedetes and Oldrichpedetes, bringing to five the diversity of the family at the generic level. Both Propedes and Oldrichpedetes comprise several species which evolved rapidly in terms of hypsodonty, such that they are of potential use for biochronology. Propedes in particular is likely the ancestral lineage from which the extant genus Pedetes emerged during the Pliocene, the transition from the former to the latter being defined in the main by the non-development of roots in the cheek teeth in the latter.

Pedetids throw light on the biogeographic and palaeoclimatic relations of North Africa, the Arabian Peninsula and parts of Southern Europe during certain periods of the Miocene and Pliocene, revealing the establishment of tropical to subtropical regimes in mid-latitude Eurasia from time to time.

ACKNOWLEDGEMENTS


Gray J.E. (1825). Outline of an attempt at the disposition of the Mammalia into tribes and families with a list of the genera apparently appertaining to each tribe. Annals of Philosophy, New Series, 2, 10: 337-344.


References


Gray J.E. (1825). Outline of an attempt at the disposition of the Mammalia into tribes and families with a list of the genera apparently appertaining to each tribe. Annals of Philosophy, New Series, 2, 10: 337-344.


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