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A comprehensive phylogeny of the gundis (Ctenodactylinae, Ctenodactylidae, Rodentia)

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A comprehensive phylogeny of the gundis (Ctenodactylinae, Ctenodactylidae, Rodentia)

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The subfamily Ctenodactylinae is known from the Early Miocene to the present. Today this group comprises five species, restricted to north and east equatorial areas in Africa. However, in Miocene times the ctenodactylines experienced their greatest diversification and widest distribution, from Asia, their land of origin, to Africa, which they entered during the Middle Miocene at the latest. So far 24 species can be referred to this group: *Ctenodactylus gundi*, *C. vali*, *Massoutiera mzabi*, *Felovia vae*, *Pectinator spekei*, *Pellegrinia panormensis*, *Sayimys obliquidens*, *S. baskini*, *S. giganteus*, *S. assarrarensis*, *S. intermedius*, *S. sivalensis*, *Metasayimys curvidens*, *Africanomys pulcher*, *A. major*, *A. minor*, *A. kettarati*, *Irhoudia bohlini*, *I. robinsoni*, *Pireddamys rayi*, *Sardomys dawnsonae*, *S. antoniettae*, *Akzharomys mallos* and *Prosayimys flynni*. A cladistic analysis involving all of the above-mentioned species has been carried out. *P. flynni* emerged as the most basal species of the ingroup. The genus *Sayimys* did not appear monophyletic. This analysis also provided information on the origin not only of the African ctenodactylines, found to be the Indian subcontinent, but also the origin of European ctenodactylines: Asiatic for Sardinian species, African for Sicilian species.

Keywords: Mammalia; systematics; cladistics; Cenozoic; Eurasia; Africa

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Introduction

The Ctenodactylidae Gervais, 1853 (as Ctenodactylina) is a family of rodents with hystricomorphous skulls and sciurognathous lower mandibles. This family comprises four subfamilies: Tataromyinae Lavocat, 1961, Karakoromyinae Wang, 1994, Dystylomyinae Wang, 1994 and Ctenodactylinae Gervais, 1853. The Karakoromyinae and Dystylomyinae went extinct during the Oligocene; the Tataromyinae at the end of the Middle Miocene. The only extant family is Ctenodactylinae, which ranges from Early Miocene to Recent. It includes 22 species distributed in 14 genera. In Miocene, the Ctenodactylinae experienced their greatest diversification and widest distribution, from north-western Africa to north-western India and central China (Fig. 1). The four extant genera (*Pectinator*, *Massoutiera*, *Felovia* and *Ctenodactylus*) are restricted to areas in north and east equatorial Africa (Fig. 1).

Despite their rich evolutionary history, the phylogeny of the Ctenodactylinae has been the focus of very few studies. This is particularly unfortunate because the development of this group is intertwined with major palaeoecological perturbations such as the collision of Afro-Arabia with Eurasia in the Early Miocene and the birth of the Sahara desert in Late Miocene times. This motivated us to provide a substantiated hypothesis of the mutual relationships within Ctenodactylinae using cladistic methods.

Material and methods

The phylogenetic analysis presented below is based on examination of original specimens, casts and data from the literature. We examined the following: skulls of extant *Massoutiera mzabi* (71064, 71149, 71154, 71156, 71157, 71152, 71155, 71150,71158, 71161, 71163, 71164, 71151, 71162, 71159, 37735, 37736, 37737, 37738, 37739 in the MB, and C.G.1960-3741, C.G.1959-93, C.G.1960-3812, C.G.1959-92, C.G.1989-29, C.G.1912-322, C.G.1953-381, C.G.1955-3, C.G.2000-686 in the MNHN), *Felovia vae* (41239, 41242, 4124 in the MB, and CG-1994-612, CG-1994-613, C.G.1995-3157 in the MNHN), *Ctenodactylus gundi* (15515, 15516, 71186, 25640, 37765, 1302, 71177, 71188, 71185, 20721, 2784, 71179, 71181, 71187, 71182 in the MB, and C.G.1963-921, C.G.1975-303, C.G.1975-304, C.G.1975-305, C.G.1975-306, C.G.1975-307, C.G.1975-309, C.G.1975-308, C.G.1975-306, C.G.1975-304, C.G.1905-437, C.G.1991-1298, C.G.1991-1316, C.G.1993-1680, C.G.2007-329 in the MNHN), *C. vali* (C.G.1952-664, C.G.1952-666, C.G.1952-668, C.G.

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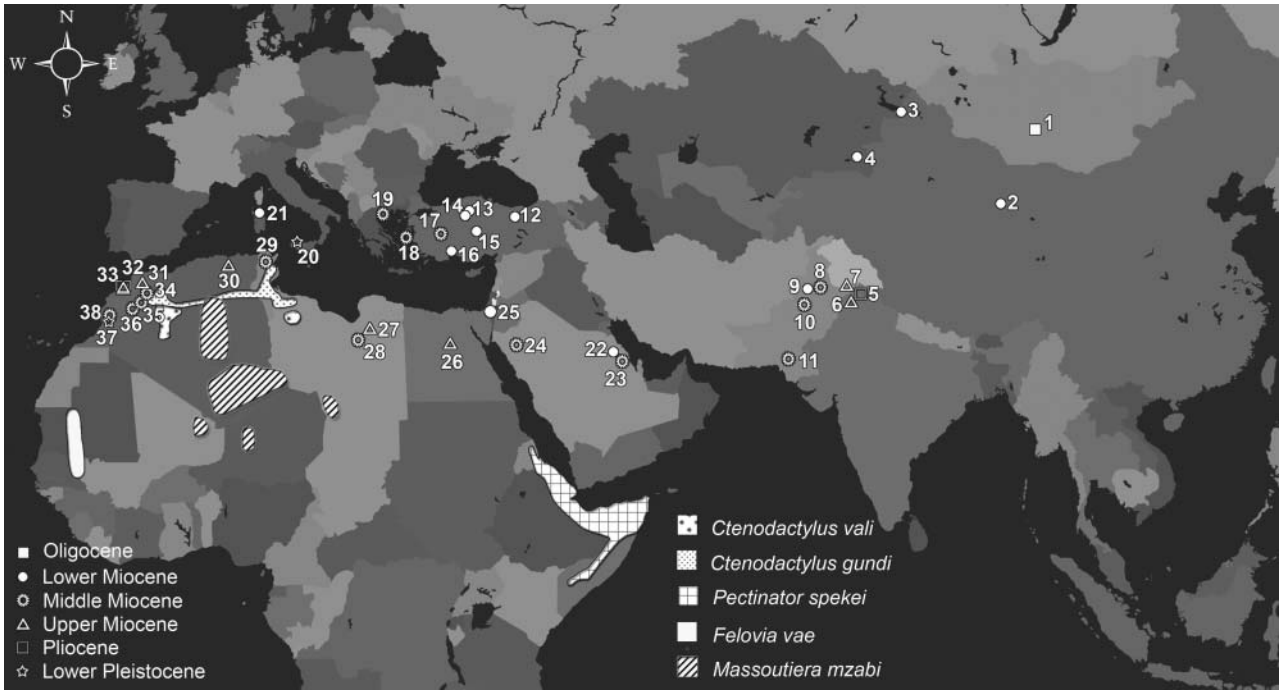

Figure 1. Distribution of the extant Ctenodactylinae (after IUCN data) and fossil localities. **1,** Ulaan Tolgoi (Mongolia); **2,** Tabenbuluk (China); **3,** Batpaksunde (Kazakhstan); **4,** Aktau Mountains (Kazakhstan); **5,** Badaun (India); **6,** Haritalyangar (India); **7,** Ramnagar (India); **8,** Chinji (Pakistan); **9,** Banda Daud Shah (Pakistan); **10,** Zinda Pir Dome (Pakistan); **11,** Sind (Pakistan); **12,** Hórlak (Turkey); **13,** Keseköy (Turkey); **14,** Hijarcik (Turkey); **15,** Çatalarkaç (Turkey); **16,** Mut (Turkey); **17,** Paşalar (Turkey); **18,** Thymiana (Greece); **19,** Antonios (Greece); **20,** Monte Pellegrino (Italy); **21,** Oschiri (Italy); **22,** As-Sarrar (Saudi Arabia); **23,** Al-Jadidah (Saudi Arabia); **24,** Tayma (Saudi Arabia); **25,** Negev (Israel); **26,** Sheikh Abdallah (Egypt); **27,** As Sahabi (Libya); **28,** Jebel Zelten (Libya); **29,** Testour (Tunisia); **30,** Amama (Algeria); **31,** Oued Zra (Morocco); **32,** Ahl al Oughlam (Morocco); **33,** Lissasfa (Casablanca, Morocco); **34,** Jebel Rhassoul (Morocco); **35,** Azdal (Morocco); **36,** Beni-Mellal (Morocco); **37,** Jbel Irhoud (Morocco); **38,** Pataniak (Morocco).

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1951-389, C.G.1953-787 in the MNHN), and *Pectinator spekei* (26563, 71171, 71169, 71153, 37977, A2636, 3935, 71165, 71166, 71167, 71175, 71170, 71172, 71174, 71173 in the MB, and C.G.1895-461, C.G.1895-459, C.G.1895-460, C.G.1986-240, C.G.1978-263, C.G.1978-264, C.G.1978-265, C.G.1978-266, C.G.1978-267, C.G.1981-504, C.G.1960-3744, C.G.1960-3783 in the MNHN); isolated teeth, maxillary fragments and mandible fragments of the following extinct species: *Prosayimys flynni* (casts of Z295, Z307, Z317, Z312, Z308, Z309, Z310, Z311, Z313, Z310, Z316, Z294, Z292, Z287, Z289, Z293, Z290, Z306, Z296, Z291, Z305, Z288, Z303, Z304, Z297 in RLA's personal collection); *Sayimys assarrarensis* from Saudi Arabia (AS21-1001, AS21-1002, AS21-1004, AS21-1005, AS21-1008, AS21-1016 to AS21-1018, AS21-1023 to AS21-1026, AS21-1028, AS8-1000 to AS8-1003 in the MNHN); *S. giganteus* from Turkey (KSK1-100 to KSK1-102; KSK2-100 to KSK2-104; HJ-100 to HJ-108 in the MNHN); *S. intermedius* from Saudi Arabia (TMA 100, TMA 101 in the MNHN) and from Chios Island, Greece (THA91-01 to THA91-03, THA91-10 to THA91-14, THA91-21 to THA91-25, THA91-28 to THA91-31; THA93-26, THA93-27, THA93-04 to THA93-09; THA93-15 to THA93-20, THA93-32 to THA93-36 in the MNHN); *S. chinjiensis* (= *S. sivalensis*) (casts of Y-GSP 634/45186, Y-GSP 634/45183, Y-GSP 634/45187 in RLA's personal collection); *Metasayimys curvidens* (Ben Mel 1357, Ben Mel 1353, Ben Mel 1354, Ben Mel 1371 in the MNHN); and *Africanomys pulcher* (Ben Mel 1356; Ben Mel 1367, Ben Mel 1369 in the MNHN).

First, second and third lower molars are designated as m1, m2 and m3 respectively, and first, second and third upper molars as M1, M2 and M3. Lower and upper permanent premolars are designated as p4 and P4 respectively, and lower and upper deciduous premolars as dp4 and DP4. The terminology used in the tooth descriptions follows the rodent dental terminology of Baskin (1996) with some adjustments (see Fig. 2).

The cladistic analysis involves all extant and fossil species of this subfamily known to date. *Karakoromys* and *Tataromys*, basal ctenodactylid genera according to the phylogenetic analysis of Wang (1997), are selected as outgroup taxa. The data matrix was built under Mesquite 2.6 (Maddison & Maddison 2009) and the analysis was run in PAUP version 4.0b10 (Swofford 2002) using the

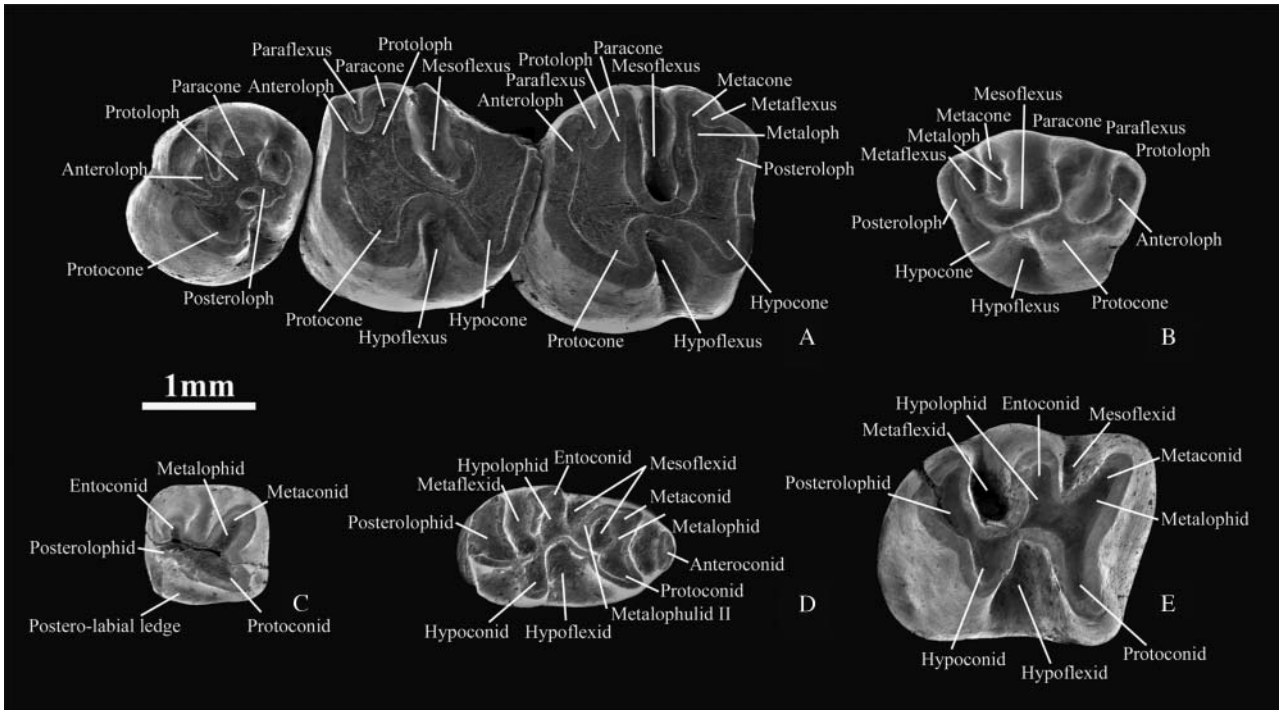

Figure 2. Ctenodactyline dental terminology used in this paper. **A,** left maxilla with P4-M2; **B,** right D4; **C,** right p4; **D,** right dp4; **E,** right m1–2.

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PaupUp graphical interface (Calendini & Martin 2005). Branch support was estimated through two complementary indices: Bremer support and relative Bremer support. Bremer support measures support of a clade as the minimum length of suboptimal trees in which the clade is not fully supported by the data, collapsing in the strict consensus (Bremer 1994). Relative Bremer support expresses support as the percentage of favourable minus contradictory evidence for each clade (Goloboff & Farris 2001). Both support indices were calculated in TNT (Goloboff *et al*. 2008).

Abbreviations

C. BR: Collection of Dr J. Braillon; **C.G**: Catalogue général MNHN; **CM**: Carnegie Museum of Natural History, Pittsburgh, USA; **GSI**, Geological Survey of India, Calcutta, India; **FSO**: Faculté des Sciences d'Oran, Algeria; **Y-GSP**: Yale-Geological Survey of Pakistan, Quetta, Pakistan; **IVAU**: Department of Earth Sciences, Utrecht, Netherlands. **MB**: Museum für Naturkunde der Humboldt-Universität, Berlin, Germany; **MGONM**: Muséum de Géologie Office National des Mines, Tunis, Tunisia; **MNHN**: Muséum national d'Histoire naturelle, Paris, France; **MTA**: Mineral Resources and Exploration, General Directorate, Natural History Museum, Ankara, Turkey; **PMNH**: Pakistan Museum of Natural History, Islamabad, Pakistan; **NHMR**: National Heritage Museum, Riyad, Saudi Arabia; **PMAE**: Peabody Museum of Archaeology and Ethnology, Cambridge, USA; **PMU**: Palaeontological Museum, University of Uppsala, Uppsala, Sweden; **PUA**: Panjab University, Chandigarh, India; **PIN**: Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; **SGM**: Geological Service of Rabat, Morocco; **UB**: Üniversitat Bonn, Bonn, Germany; **UM**: Université des Sciences et Techniques du Languedoc, Montpellier, France; **Z**: Zinda Pir area, Pakistan.

Systematics

Ctenodactylids are distributed in northern and eastern Africa, essentially in desert or semidesert terrain, where they dwell in caves or rocky crevices. As they are found in arid or semiarid climates, vegetation is sparse; they must forage over long distances and are opportunistic in their diet (they eat leaves, stalks, flowers and seeds of almost any plant, but animal food is not known to be eaten). Misonne (1971, pp. 5–6) and Dieterlen (2005, pp. 1536–1537) provided censuses of valid extant species of ctenodactylids (see also Ellerman & Morrison-Scott 1951, pp. 521–522, 1966, pp. 521–522). They concluded that only five species exist at present: *Ctenodactylus gundi*, *C. vali*, *Massoutiera mzabi*, *Felovia vae* and *Pectinator spekei*. This is widely acknowledged by mammalogists so we shall not reconsider their synonymies, which appear very reasonable and are beyond the scope of this paper. The morphology

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of the teeth of the living ctenodactylines was described in detail by Jaeger (1971). Therefore, in this work, we only give a short historical background for these four genera as well as some additional details.

The mention of a possible Pliocene representative of *Pectinator* in Asia (see e.g. McKenna & Bell 1997, p. 190) probably comes from Darlington (1957, p. 392). However, this was based on Hinton (1933) and is, therefore, incorrect (see below). Based on the works of previous authors (Joleaud 1935; Arambourg 1949, 1952; Arambourg & Coque 1958), Le Houérou (1995, p. 60, 1997, p. 629) mentioned the presence of *C. gundi* at the Pliocene locality of Aïn Brimba (Tunisia). However, none of the mentioned publications indicated the presence of *Ctenodactylus* at this locality (see also Coque 1962) so this record appears dubious. Jaeger (1975, p. 7) merely listed Ctenodactylidae indet. at this site. For extrinsic reasons (age), it is more likely that this material belongs to the fossil genus *Irhoudia*. The extant genera have been mentioned as known only from the Holocene (Wood 1977; Novak 1999, p. 1622). However, *Ctenodactylus* spp. has been cited recently from the Upper Pleistocene site of the Grotte des Pigeons (Taforal, Morocco) (Bouzouggar *et al.* 2007). Except for *C. gundi* from Redeyef (Table Sud and Table Redeyef, Gafsa, Tunisia) (Vaufrey 1955, p. 394) and *M. mzabi* from Ti-n-Torha (Tadrart Acacus, Libya) (Gautier & van Neer 1982), no sub-fossil material of the extant genera has been found to date, probably due to a bias in the observational record.

Genus ***Ctenodactylus*** Gray, 1830

Type species. *Ctenodactylus gundi* (Rothman, 1776).

***Ctenodactylus gundi* (Rothman, 1776).** Rothman (1776, p. 339) described the first ctenodactylid as *Mus gundi*, from a specimen coming from the Gharyan area (Libya), about 80 km south-south-west of Tripoli. The brief Latin diagnosis he gave (Fig. 3) can be translated as follows: "Tail short. With all feet tetradactyl. All the body brick-reddish. Ears short, opening large, oval. First teeth excavated, upper teeth truncated, lower teeth pointed. All fingers with nails. Walking on the sole. Of smaller size than the rabbit". The present whereabouts of the original specimen are unknown; it is not in the Naturhistoriska Riksmuseet in Stockholm (U. Johansson, pers. comm., 2010). Thomas (1920) proposed the specimen BMNH 1855.12.24.128 as provisional topotype of *C. gundi*. Gray (1830, p. 11) published the description of what he thought was an arvicolid as *C. massonii*. The two were soon considered as the same species (see Yarrell 1830), the North African gundi. *C. gundi* is found in some parts of Morocco, Algeria, Tunisia and Libya (Fig. 1).

***Ctenodactylus vali* Thomas, 1902.** *C. vali*, the desert gundi, is the latest validly named living ctenodactylid. The holotype specimen (BMNH 1902.11.4.76) is in the Natural History Museum (London). It comes from Wadi Bey (Libya), about 330 km south-east of Tripoli. The species is found in some parts of Morocco, Algeria and Libya (Fig. 1).

M v s *Gundi*, cauda abbreuiata, pedibus omnibus tetradactylis. Corpus totum teſtaceo-rufeſcens. Auriculae truncatae, apertura larga, orata. Dentes primores excauati, ſuperiores truncati, inferiores ſubulati. Digiti omnes unguiculati. Plantae talis inſiſtentes. Magnitudo cuniculi minoris.

Figure 3. Diagnosis of *Mus gundi* provided by G. Rothman (1776).

The specific distinctiveness of *Ctenodactylus vali* with regard to *C. gundi* has been rejected by Ellerman & Morrison-Scott (1951) and some subsequent authors, who considered the former a subspecies of the latter. However, the differences between the two taxa, such as the morphology of the M3, which is L-shaped in *C. gundi* and kidney-shaped in *C. vali*, support specific distinction (George 1982).

Genus ***Massoutiera*** Lataste, 1885

Type species. *Massoutiera mzabi* (Lataste, 1881).

***Massoutiera mzabi* (Lataste, 1881)..** In 1881, Lataste named this species *Ctenodactylus mzabi*, which he allocated to the new genus *Massoutiera* in 1885. The original material came from Ghardaïa (Algeria), about 480 km south of Algiers. The lectotype (Thomas 1919; P. Jenkins, pers. comm. 2010) consists of the skull (BMNH 1919.7.7.1311) and skeleton of the same specimen (BMNH 1957.3.19.2). The Mzab gundi has a large, though discontinuous, geographical range: central and south-western Algeria, eastern Mali, western Niger and north-western Chad (Fig. 1). Its presence was mentioned from the prehistoric (c. 7000 BC) site of Ti-n-Torha (Tadrart Acacus, Libya; Gautier & van Neer 1982; Gautier 1987). The remains, identified on the basis of size and the distribution of extant ctenodactylids (incidentally, they were initially attributed to *Ctenodactylus* sp. in Cassoli & Durante 1974), have been morphologically studied in detail by López-Antoñanzas & Knoll (2010), who proved this assignation correct.

It is unusual to find premolars in the maxillae and mandibles of *Massoutiera*. This is especially true for the p4 to the point that Jaeger (1971, p. 117) was uncertain about its presence in this genus and gave the following dental formula to *Massoutiera*: I 1/1-P 1/?-DP4 1/1-M 3/3). However, specimens housed at the MNHN (C.G. 1989-29, C.G. 1912-322 and C.G. 1953-381) show the lower and upper permanent premolars (Fig. 4A, C). Thus the dental pattern of *Massoutiera* is I 1/1-P 1/1-DP4 1/1-M 3/3. It seems to us that this taxon loses the p4 before the P4

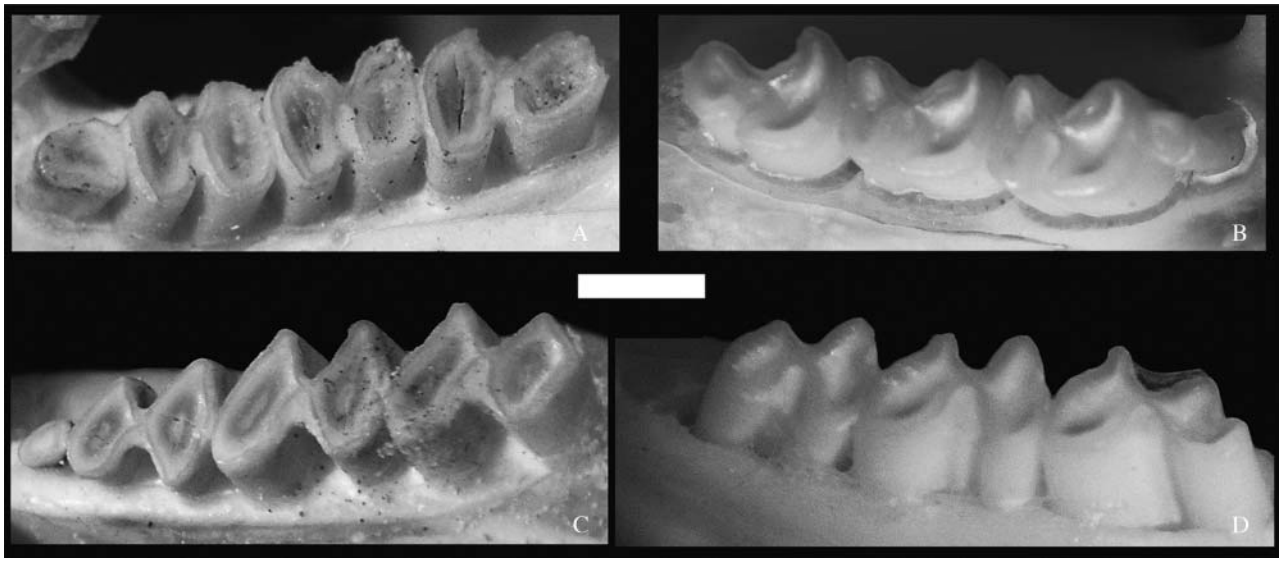

Figure 4. Cheek teeth of *Massoutiera mzabi* and *Felovia vae*. **A,** upper cheek teeth of *M. mzabi* (specimen C.G.1912 no. 322) with P4-M3; **B,** upper cheek teeth of *F. vae* (specimen C.G.1994 no. 613) with P4-M3; **C,** lower cheek teeth of *M. mzabi* (specimen C.G.1912 no. 322) with p4-m3; **D,** lower cheek teeth of *F. vae* (specimen C.G.1994 no. 613) with m1-m3 and socket for the p4. Except for the upper cheek teeth of *F. vae*, all specimens are figured with anterior to left. Scale bar equals 2 mm.

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(e.g. specimens M.B. 71164 and MNHN CG-1960-3741), which could explain the particular paucity of the p4 in *Massoutiera*. We have not seen deciduous premolars in this genus, but according to Jaeger (1971) the DP4 and dp4 are morphologically similar to the molars, but clearly smaller in size. The upper incisors of this taxon are usually smooth, but in some specimens they are very weakly grooved.

Genus ***Felovia*** Lataste, 1886

Type species. *Felovia vae* (Lataste, 1886).

Felovia vae **Lataste, 1886.** The lectotype (Thomas 1919) consists of the skin (BMNH 1919. 7. 7. 3233) and skull (BMNH 1919. 7. 7. 3232) of an adult female. It comes from around Felou (Senegal), about 380 km east-south-east of Dakar. The Felou gundi is confined to western Senegal, eastern Mali and western Mauritania (Fig.1).

Originally described as belonging to *Massoutiera* within the new subgenus *Felovia*, this species resembles *M. mzabi*. However, *Felovia* can be distinguished by its strongly grooved upper incisors, a feature also differentiating it from all remaining living ctenodactylid species. As with *Massoutiera*, the p4 is not usually observed in the mandible of this taxon. Jaeger (1971, p. 117) thought that this tooth was absent. However, some specimens (e.g. specimen number 41239 housed in the MB or MNHN C.G. 1995-3157, C.G. 1994-613) clearly show the sockets for this type of tooth (Fig. 4D). Therefore, the dental pattern of *Felovia* is no doubt the same as that of *Massoutiera*: I 1/1-P 1/1-DP4 1/1-M 3/3 (Fig. 4B, D). *Felovia* and *Massoutiera* are more hypsodont than *Ctenodactylus* and *Pectinator*.

Genus ***Pectinator*** Blyth, 1856

Type species. *Pectinator spekei* Blyth, 1856.

Pectinator spekei **Blyth, 1856.** The original specimen (which is supposed to be in the Indian Museum, Calcutta) was collected in the Laasqoray area (Somalia), about 1040 km north-north-east of Mogadishu. Besides Somalia, the Speke's gundi lives in Ethiopia, Djibouti and Eritrea (Fig. 1), geographically isolated from the other gundis. The dental morphology of this species, with three-lobed lower molars that lack cement filling in their valleys, clearly resembles that of *Sayimys sivalensis* (Fig. 5).

Genus ***Pellegrinia*** De Gregorio, 1887

Type-species. *Pellegrinia panormensis* De Gregorio, 1887.

Pellegrinia panormensis **De Gregorio, 1887.** This species was erected by De Gregorio in 1887 on the basis of dental, cranial and postcranial remains found in Monte Pellegrino (near Palermo, northern Sicily). De Gregorio (1925) described additional material of this species from the same site. Unfortunately, De Gregorio did not designate a type (nor did any later author). The original material is housed in the Museo Geologico G. G. Gemmellaro in Palermo (C. Di Patti, pers. comm. 2010). Jaeger (1971) redescribed this species on the basis of material housed in the collections

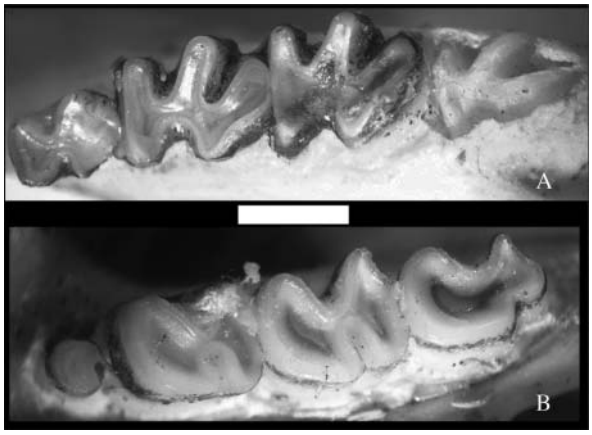

Figure 5. Cheek teeth of *Pectinator spekei* (specimen M.B. 71169). **A,** mandible with dp4-m3; **B,** maxilla with P4-M3. All specimens are figured with anterior to left. Scale bar equals 2 mm.

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of the Naturhistorisches Museum, Basel. In 1972, Thaler published the discovery of *Pellegrinia* at three localities in Monte Pellegrino, which he called Pellegrino-Vetta, Pellegrino-Falde and Pellegrino-Occidentale. The first was the locality from which the material described by De Gregorio (1887) came. The localities of Monte Pellegrino have not been properly dated and are, therefore, a matter of controversy. Most authors considered them Late Pliocene or Early Pleistocene in age (De Gregorio 1887; Jaeger 1971; Thaler 1972; Kotsakis 1986; Azzaroli 1990; Villa 2001; Agnesi *et al.* 2004; Marra 2005). However, they were considered Early or Middle Pliocene in age by Sondaar & Van der Geer (2005).

Genus ***Sayimys*** Wood, 1937

Type species. *Sayimys perplexus* Wood, 1937.

Due to scarcity of fossils or their poor preservation, some records of *Sayimys* cannot be distinguished at species level. Thus, *Sayimys* sp. has been recorded from the Lower Miocene Anatolian localities of Horlak, Çatalarkac and Yapinti (Sümengen *et al.* 1990; De Bruijn 1999; Ünay *et al.* 2001), from the Middle Miocene Greek locality of Antonios (Vasileiadou & Koufos 2005) and from some Middle Miocene Pakistani localities in the Kamlial, Chinji and Manchar formations (De Bruijn *et al.* 1989; Baskin 1996).

Sayimys obliquidens **Bohlin, 1946.** The holotype (T. b. 268 b) of this species (Bohlin 1946, p. 111, fig. 30b, 30b′, 30b″) is a left lower jaw with p4-m3 (the lingual halves of p4 and m1 are missing) housed in the PMU. It comes from an horizon of the Tiejianggou Formation in the Tabenbuluk region (Gansu, China). This horizon is different from the beds in which most of the micromammals were found at Taben-buluk (Bohlin 1946) and its age is controversial. Most authors assign it an Early Miocene age (e.g. Wang *et al.* 2003). However, a recent study of the Tabenbuluk vertebrate localities discovered by Bohlin suggests a possible Middle Miocene age for the strata with remains of *S. obliquidens* (Wang *et al.* 2008). These authors are cautious in this assertion due to the scarcity of associated taxa and the possibility of a mixed fauna therein. In our opinion, the stage of evolution of *S. obliquidens*, which is among the most basal species of the Ctenodactylinae (e.g. for having a metalophulid II on the lower molars), suggests an Early Miocene age.

One d4 considered as an m1 of *Asiazapus ingens* by Lopatin & Zazhigin (2000), but belonging in fact to *Sayimys obliquidens* (López-Antoñanzas & Sen 2004), has been found in the Lower Miocene Akzhar Formation of Batpaksunde (Eastern Kazakhstan). Elsewhere, *Sayimys* aff. *obliquidens* has been recorded in Kazakhstan from the Lower Miocene middle members of the Chul'adyr Formation of the Aktau Mountains (Kordikova & De Bruijn 2001).

Sayimys baskini López-Antoñanzas & Sen, 2003

1981 *Sayimys minor (partim)* De Bruijn et al.
1996 *Sayimys* cf. *minor* Baskin

López-Antoñanzas & Sen (2003) argued that the species *Sayimys minor* De Bruijn *et al*., 1981 from the Lower Miocene Murree Formation of Pakistan is invalid because its holotype (one m1-2) was in fact an m1-2 of *S. intermedius*. It differs from the m1-2s of the early Middle Miocene Kamlial Formation of Pakistan tentatively referred to as *Sayimys* cf. *minor* (Baskin 1996, pl. 1G). Therefore, López-Antoñanzas & Sen (2003) considered the nominal taxon *S. minor* a junior synonym of *S. intermedius*, and coined the new species *S. baskini* for all specimens from the Kamlial Formation, together with two (d4 and m3) out of the four paratypic specimens of *S. minor* from the Murree Formation described by De Bruijn *et al.* (1981). Thus, the holotype of *S. baskini* (Y-GSP 747/48125) is a right P4 (Baskin 1996, fig. 4a) from the Lower Miocene locality Y 747 of the Kamlial Formation of the Potwar Plateau, Pakistan. There is additional material of this taxon from locality Y 721 of the same Formation (Baskin 1996) as well as the specimens from the Lower Miocene Murree Formation in the Banda Daud Shah area in Pakistan (De Bruijn *et al.* 1981).

Sayimys giganteus **López-Antoñanzas, Sen & Saraç, 2004.** López-Antoñanzas *et al.* (2004) erected the new species *Sayimys giganteus* on the basis of some isolated cheek teeth and maxillary fragments from the Lower Miocene (MN3-MN4) Turkish localities of Keseköy and Hişarcik. The holotype (KSK1-100), a fragmentary left maxilla with P4-M1, is housed in the MTA (López-Antoñanzas *et al.* 2004).

Sayimys assarrarensis **López-Antoñanzas & Sen, 2004.** The holotype of this species (AS21–1023), a fragmentary left maxilla with P4-M2, is housed in the MNHN and comes

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from the Lower Miocene locality of As-Sarrar, Saudi Arabia (López-Antoñanzas & Sen 2004).

***Sayimys intermedius* (Sen & Thomas, 1979).** This species was originally described by Sen & Thomas (1979) as *Metasayimys intermedius*. It was later assigned to the genus *Sayimys* (Munthe 1980 and subsequent authors). The holotype (AJ 545) is a fragmentary left mandible with p4-m2 from the Middle Miocene Hofuf Formation, Al Jadidah, Saudi Arabia (Sen & Thomas 1979), which is housed in the NHMR. This species is also recorded from the likely MN5 age site of Tayma, north-western Saudi Arabia (López-Antoñanzas & Sen 2004). Beyond the Arabian peninsula, *Sayimys intermedius* is known in Pakistan from the Lower Miocene Murree Formation at Banda Daud Shah (as *S. minor* [De Bruijn *et al.* 1981]) and from the Middle Miocene Lower Manchar Formation at the Sind localities H-GSP 81.06, H-GSP 81.07, and H-GSP 81.14a (De Bruijn *et al.* 1989). In addition, ctenodactylid teeth from the early Middle Miocene (MN5) locality of Thymiana (Chios Island, Greece), Keramaria Formation, are identified as *S. intermedius*, despite slight differences from the Pakistani and Saudi Arabian representatives of this taxon (López-Antoñanzas *et al.* 2005). Finally, *S. intermedius* has been cited in the Lower Miocene (MN3a) Hatzeva Formation of the Rotem Basin, Israel (Goldsmith *et al.* 1982; Tchernov *et al.* 1987; Savage 1990; Wood & Goldsmith 1998). However, this latter record cannot be confirmed until a thorough description and determination is available. Mein (2003, p. 408) was probably misled by De Bruijn (1999, p. 264) when he cited *S. intermedius* in Jebel Zelten (Libya). Based on the illustrations provided by Wessels *et al.* (2003) and Fejfar & Horáček (2006), it can be affirmed that the Libyan Miocene ctenodactylid is not *S. intermedius*, notably because of the presence of a metalopulid II and the absence of a distinct anteroconid on the dp4. According to Wessels *et al.* (2003, 2008) and Fejfar & Horáček (2006), this material belongs in fact to a new species of *Sayimys*. The biostratigraphical distribution of *S. intermedius* is probably Lower-Middle Miocene (MN 3-MN6).

Sayimys cf. *intermedius* has been recorded in Pakistan from the early Middle Miocene Vihowa Formation of the Zinda Pir Dome and from the early Middle Miocene Kamlial Formation of the Potwar Plateau (Baskin 1996). A single worn and damaged tooth considered as *Sayimys* cf. *intermedius* has been recovered from the Oligocene Ulaan Tolgoi section UTO-A/3 (level D1), Valley of Lakes, Central Mongolia (Schmidt-Kittler *et al.* 2007). *Sayimys* cf. *intermedius* is also mentioned from the Middle Miocene Turkish locality of Paşalar (Flynn & Jacobs 1990; Peláez-Campomanes & Daams 2002).

Sayimys sivalensis (Hinton, 1933).

1937 *Sayimys perplexus* Wood
1996 *Sayimys chinjiensis* Baskin

Hinton (1933) coined this species as *Pectinator sivalensis*, giving a brief description and no illustration. Later, Black (1972) illustrated and described this taxon and transferred it to the genus *Sayimys*. The holotype (GSI D284) is a left dentary fragment with m2 and m3 from the Middle Miocene Chinji Formation, Pakistan (Hinton 1933). Though supposed to be kept in the collections of the University of Bristol, it might have been returned to the GSI (E. Loeffler, pers. comm. 2010).

Sayimys perplexus Wood, 1937 (named as the type species of the genus) is here considered a junior synonym of *S. sivalensis* in agreement with Munthe (1980), Wang (1997) and López-Antoñanzas & Sen (2003). However, this is a case of subjective synonymy; therefore, the genus *Sayimys* should continue to be used (see discussion in Munthe 1980, p. 25). We agree with López-Antoñanzas & Sen (2003) in considering *S. chinjiensis* a junior synonym of *S. sivalensis*.

Sayimys sivalensis (including *S. perplexus* and *S. chinjiensis*) is known in Pakistan from the Middle Miocene Lower Manchar (De Bruijn *et al.* 1989), Kamlial (Baskin 1996), and Chinji formations (Hinton 1933; Hussain *et al.* 1977; Munthe 1980; Dehm *et al.* 1982; Wessels *et al.* 1982; Baskin 1996). It is also known in India, from Ramnagar (Vasishat 1985) and from the Upper Miocene of the Haritalyangar area (as *S. perplexus* Wood 1937; Prasad 1970; Vasishat 1978, 1985). Thus, the biostratigraphical distribution of *S. sivalensis* is probably Middle-Upper Miocene (MN5-MN10).

***Sayimys badauni* Vasishat, 1985.** The holotype of this species (PUA 74-70) is a left lower jaw with p4-m2 and i1, thought to come from the Tatrot Formation, Upper Siwaliks, India (Vasishat 1985, pl. 24). *S. badauni* is the last record of *Sayimys* (c. 3.4 Ma). It was rivalled as a late survivor by the material from As Sahabi (two isolated teeth from P61A and a mandible fragment found by surface prospecting at P34A) in North Africa (Munthe 1982, 1987; Boaz 1996). However, As Sahabi may in fact be Late Miocene rather than Early Pliocene in age (see Agustí 2008; Beyer 2008; Boaz *et al*. 2008). In addition, Baskin (1996, p. 42) pointed out that the ctenodactyline material from As Sahabi would be better referred to *Africanomys*, whereas according to Agustí (2008) it belongs to *Irhoudia*.

The validity of the taxon *Sayimys baudauni* Vasishat, 1985 needs additional study. Its morphology strongly resembles that of *Sayimys sivalensis*, but the illustrations presented by Vasishat (1985) are not fully satisfactory (López-Antoñanzas & Sen 2003). Therefore, this species is not included in our cladistic analysis.

Genus ***Metasayimys*** Lavocat, 1961

1961 *Dubiomys* Lavocat

Type species. *Metasayimys curvidens* Lavocat, 1961.

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Metasayimys curvidens Lavocat, 1961

1953 *Sayimys* Lavocat
1961 *Sayimys jebeli* Lavocat
1961 *Africanomys incertus* (partim) Lavocat
1961 *Africanomys pulcher* (partim) Lavocat
1961 *Dubiomys mellali* Lavocat

Lavocat (1961) based this species on two teeth from the Middle Miocene of Beni-Mellal, Morocco. He designated as holotype the specimen Ben. Mel. 35, which is now housed in the MNHN. Jaeger (1971) synonymized *Africanomys pulcher* (*partim*), *A. incertus* (*partim*), *Sayimys jebeli*, *Metasayimys curvidens* and *Dubiomys mellali*, an action accepted by Wood (1977). However, Jaeger (1971), without explanation, rejected the species *M. curvidens* and created the combination *M. jebeli* to include all the above-mentioned species. Wood (1977) disagreed with this and pointed out that since *M. curvidens* was a valid name for the type species of the genus *Metasayimys*, the rules of zoological nomenclature dictate that it must be the valid species. We agree with Wood (1977) in considering *S. jebeli* a junior synonym of *M. curvidens*.

Additional material from this taxon has been recovered from the Middle Miocene site of Jebel Rhassoul (Benammi 1997, 2006). The presence of *Metasayimys* cf. *jebeli* (= *M*. cf. *curvidens*) from the Middle Miocene locality of Pataniak 6 (Jebel Irhoud, Morocco) has been mentioned by Jaeger (1977). In addition, Benammi (2006) has identified *Metasayimys* aff. *jebeli* (= *M*. aff. *curvidens*) from the Middle Miocene localities of Azdal 1 and 3 (Aït Kandoula, Morocco).

Genus ***Africanomys*** Lavocat, 1961

Type species. *Africanomys pulcher* Lavocat, 1961.

Africanomys pulcher Lavocat, 1961.

1961 *Africanomys incertus* (partim) Lavocat

The holotype of this species (Ben. Mel.1375) is a right DP4 from the Middle Miocene of Beni-Mellal that is housed in the MNHN. Jaeger (1971) synonymized *Africanomys incertus* (*partim*) with *A. pulcher*, an action with which we agree. Additional material of this taxon has been recovered from the Middle Miocene site of Jebel Rhassoul, Morocco (Benammi 1997, 2006). Furthermore, the presence of *Africanomys* cf. *pulcher* has been mentioned by Benammi (2006) from the Middle Miocene localities of Azdal 1 and 3 (Aït Kandoula, Morocco).

Africanomys major **Jaeger, 1977.** This species was defined on the basis of 14 isolated dp4, 28 mandible fragments and 18 maxillary fragments from the Pataniak 6 locality in Jebel Irhoud, Morocco (Jaeger 1977). This locality has been considered Middle Miocene in age (Benammi *et al.* 1996). The holotype (P6-141) is a mandible fragment with p4-m3 housed in the SGM (Jaeger 1977). Additional material from this taxon has been recovered from the Upper Miocene of Sheikh Abdallah, Egypt (Heissig 1982; Wanas *et al.* 2009).

Africanomys minor Jaeger, 1977

1961 *Africanomys* aff. *pulcher* Lavocat in Jaeger 1974

Africanomys minor was coined and described in 1977 by Jaeger on the basis of 60 maxillary fragments, 54 mandibular fragments, 16 isolated dp4 and eight isolated m3 from the Middle Miocene Pataniak 6 locality (Jebel Irhoud, Morocco). The holotype of this species (P6–84) is a mandible fragment with m1-m3, housed at the collections of the SGM (Jaeger 1977). Additional material of this taxon has been recovered from the Upper Miocene of Sheikh Abdallah, Egypt (Heissig 1982), but according to Wanas *et al.* (2009) this material could be *A. kettarati*.

Africanomys kettarati **Jaeger, 1977.** This species was defined on the basis of six isolated teeth from the Upper Miocene Oued Zra locality (Middle Atlas), Morocco. Its holotype (OZ-36) is an isolated M1-M2 housed in the SGM (Jaeger 1977). Additional material from this species has been recovered from the Upper Miocene Bou Hanifia 5, Algeria (Ameur 1984).

Genus ***Irhoudia*** Jaeger, 1971

Type species. *Irhoudia bohlini* Jaeger, 1971.

Remains of *Irhoudia* sp. have been found from the Upper Miocene locality of Amama 1, Algeria (Jaeger 1977) and from the Miocene/Pliocene site of Lissasfa, Casablanca, Morocco (Geraads 1998, 2002). Recently, Agustí (2008) pointed out on the basis of new material recovered from the Late Miocene of As Sahabi that the ctenodactyline remains from this site would pertain in fact to *Irhoudia* and not to *Sayimys* as suggested by Munthe (1982, 1987), but neither description nor photographs of these remains were provided. In addition, Agustí (2008) remarked that these specimens retain a primitive DP4 as is the case in *Africanomys*. This observation is in agreement with the suggestion of Baskin (1996, p. 42), who considered the material from As Sahabi to belong to *Africanomys*. Actually, the As Sahabi ctenodactyline teeth described and figured by Munthe (1987) appear different from those of *Irhoudia* spp. (they are less hypsodont, show a posterobuccal cingulum, their protoconid is not hypertrophied, etc.), which precludes their assignment to this genus.

Irhoudia bohlini **Jaeger, 1971.** This species was described and illustrated by Jaeger (1971) based on some isolated teeth as well as maxillary fragments from the Lower Pleistocene of Jebel Irhoud, Morocco. The holotype is an isolated m1, currently housed in the UM. *Irhoudia* aff. *bohlini* has been described from the Upper Pliocene of Ahl al Oughlam, Casablanca, Morocco (Geraads 1985).

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***Irhoudia robinsoni* Jaeger, 1977.** This species was named on the basis of 34 isolated cheek teeth from the Upper Miocene (c. 7.5 Ma) locality of Amama 2, Algeria (Jaeger, 1977, p. 93). Its holotype, one m1 or m2 (A2–14), is kept in the collections of the FSO.

Genus ***Testouromys*** Robinson & Black, 1973

Type species. *Testouromys solignaci* Robinson & Black, 1973.

***Testouromys solignaci* Robinson & Black, 1973.** This species was named on the basis of a single first upper molar (T-3724) and a broken first lower molar (T-3802) from the Middle Miocene of Testour Beja, Tunisia, currently housed in the MGONM. We agree with De Bruijn *et al.* (1989) in considering this material insufficient to define a new genus and species. The same locality yielded an M3 of a species of *Africanomys*, which is larger and more hypsodont than *A. pulcher* from Beni Mellal according to Robinson & Black (1973). Specimens T-3724 and T-3802 might belong to the genus *Africanomys*. Due to the scarcity of this material and dubious validity of this taxon, we do not take it into account in our phylogenetic analysis.

Genus ***Pireddamys*** De Bruijn & Rümke, 1974

Type species. *Pireddamys rayi* De Bruijn & Rümke, 1974.

***Pireddamys rayi* De Bruijn & Rümke, 1974.** The holotype (O.S. 142) of this taxon, a right mandible with p4-m3 and the incisor, was found at the Lower Miocene Oschiri road cut locality, Sardinia, Italy (De Bruijn & Rümke 1974). The holotype is housed in the IVAU. This species is larger than all other ctenodactylid species except *Sardomys dawnsonae*. It differs from *Sayimys* spp. *Metasayimys* spp. and *Africanomys* spp. not only in its much greater size, but also in having deeply grooved incisors and in the presence of mesolophids on the lower molars. It differs from the species belonging to the genus *Sardomys* in lacking crown cement on the molars.

Genus ***Sardomys*** De Bruijn & Rümke, 1974

Type species. *Sardomys dawnsonae* De Bruijn & Rümke, 1974.

***Sardomys dawnsonae* De Bruijn & Rümke, 1974.** The holotype of this species (O.S.131) is a mandible with dp4-m3 from the Lower Miocene Oschiri road cut locality (De Bruijn & Rümke 1974). The holotype is stored in the IVAU. This species is the largest member of the family known to date. It has semi-hypsodont molars and it differs from all *Prosayimys*, *Sayimys* and *Africanomys* species in having crown cementum in both the lingual and labial folds of the m2 and the m3. The anterior face of the lower incisor is almost flat except for a shallow central longitudinal groove. The upper incisor has a deep central longitudinal groove.

***Sardomys antoniettae* De Bruijn & Rümke, 1974.** The holotype of *Sardomys antoniettae* (O.S. 144), a mandible fragment with p4-m1, was recovered from the Lower Miocene Oschiri road cut locality (De Bruijn & Rümke 1974). The holotype of this species is housed in the collections of the IVAU. *S. antoniettae* is larger than any other fossil ctenodactyline species except for *S. dawnsonae*, which is much larger.

Genus ***Akzharomys*** Shevyreva, 1994

Type-species. *Akzharomys mallos* Shevyreva, 1994.

***Akzharomys mallos* Shevyreva, 1994.** This species was defined by Shevyreva (1994) on the basis of four isolated teeth (one M1, one M2, one m1 and one m3) from the Lower Miocene of the Akzahr Formation (Kazhakstan). The holotype of this taxon (PIN no 3462/724) is a right M2. No additional material from this taxon has been found so far.

Genus ***Prosayimys*** Baskin, 1996

Type species. *Prosayimys flynni* Baskin, 1996.

***Prosayimys flynni* Baskin, 1996.** The holotype of *P. flynni* (Z113/295) comes from the upper part of the Chitarwata Formation in the Dalana section of the Zinda Pir Dome, Pakistan. Its age is constrained to Late Oligocene or possibly earliest Miocene (23 Ma), but cannot be determined definitively by the limited palaeomagnetic evidence (Lindsay *et al.* 2005). The *Prosayimys* material is currently housed at the PMAE. It should eventually be returned to Pakistan and deposited at the PMNH (L. Flynn, pers. comm. 2002).

Phylogenetic analysis

Previous works

George (1979). George (1979) tried to decipher the relationships within the extant ctenodactylids based on their karyotypes. With this end in view, she calculated an index of dissimilarity based on differences in chromosome length and centromere position.

On the basis of George's (1979) dissimilarity indices, we constructed a distance matrix (Appendix 1, which is available via the Supplementary Content on the article's online page) that could be processed in QuickTree (Howe *et al.* 2002) via the Mobyle server (http://mobyle.pasteur.fr/cgi-bin/portal.py). The Newick format tree file generated was visualized in the same platform through Drawtree (Felsenstein 2005). The resulting unrooted phenogram (Fig. 6A) showed the shorter distance between *Pectinator spekei* and

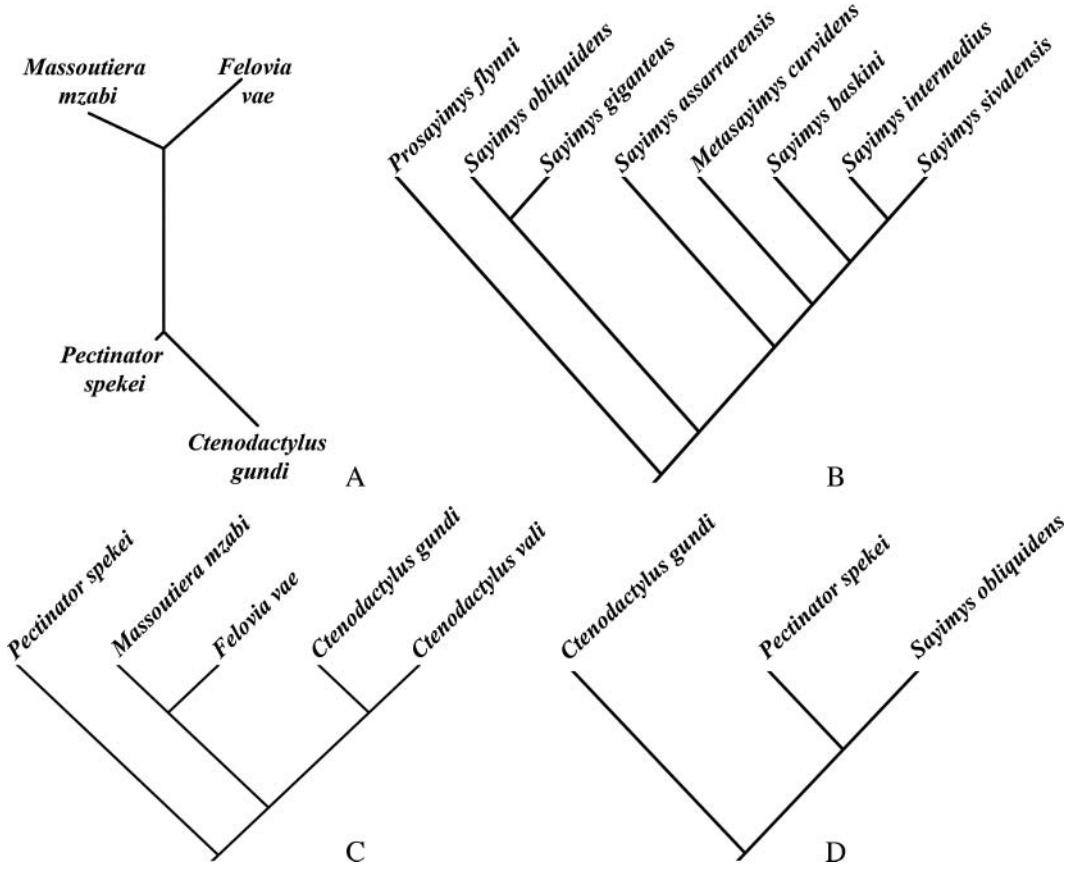

Figure 6. Previous phylogenies. **A,** unrooted phenogram obtained from the dissimilarity indices given by George (1979); **B,** majority rule consensus tree generated by the cladistic analysis of all species of *Sayimys*, *Prosayimys* and *Metasayimys* performed by López-Antoñanzas *et al.*, (2004); **C,** most parsimonious tree found by George (1985) including the five extant species of Ctenodactylinae; **D,** clade of the strict consensus tree generated by the cladistic analysis carried out by Wible *et al.*, (2005) showing the relationships of three ctenodactylines.

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Ctenodactylus gundi. The latter would in fact be closer to *Ctenodactylus vali* than to *Pectinator spekei* according to the George (1979) indices, but this last taxon was not included in the present analysis due to incomplete data. *Massoutiera mzabi* and *Felovia vae* are closer to one another than to the other two taxa. As *F. vae* and *C. gundi* are the farthest apart, the mid-point rooting method gave a phenogram with the following topology: ((*P. spekei*, *C. vali*) (*M. mzabi* and *F. vae*)).

George (1985). George (1985) conducted the first cladistic analysis of ctenodactylids. She included all five extant species and considered 28 characters from a diversity of fields (gross anatomy, physiology, karyotype, behaviour, etc.). She noted that "the decision about the derived apomorphic status or the plesiomorphic status of each character was based on fossil evidence where possible or by comparing the character with its state in other mammals" (George 1985, p. 56) and added that the cladogram was "constructed as a result of decisions (some of them arbitrary) on the status [of these characters]" (George 1985, p. 58).

George (1985) found a single, fully resolved most parsimonious tree in which *Pectinator spekei* is the sister group to a symmetrical clade comprising *Felovia vae* and *Massoutiera mzabi* on one hand and the two *Ctenodactylus* species on the other (Fig. 6C).

López-Antoñanzas *et al.* (2004). In the course of the description of *Sayimys giganteus*, López-Antoñanzas *et al.* (2004) offered a complement to previous work (López-Antoñanzas & Sen 2004) by conducting a cladistic analysis of all valid species of *Sayimys*, *Prosayimys* and *Metasayimys*. A data matrix of 19 characters was processed with PAUP version 3.1.1 (Swofford 1993), using the exhaustive search option, and thereby generated five equally most parsimonious trees whose majority rule consensus solution is shown in Fig. 6B.

Apart from sister-species relationships between *Sayimys obliquidens* and *S. giganteus*, the topology is perfectly asymmetrical from the most basal taxon, *Prosayimys flynni*, to the most derived dyad: (*S. intermedius*, *S. sivalensis*).

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Wible *et al.* (2005). In the course of the study of a new Eocene ctenodactyloid rodent, *Exmus mini*, Wible *et al.* (2005) evaluated through a cladistic analysis the relationships of this species to other ctenodactyloids and of ctenodactyloids to other Eocene rodents. Both dental and cranial characters were considered (the former representing a little less than 40% of the character list). Three ctenodactyline genera were included in the ingroup: *Sayimys*, *Ctenodactylus* and *Pectinator*. The scoring of *Ctenodactylus* was based on *C. gundi*: specimens SSLG Nr. 519 (UB) for incisor enamel characters (from Martin 1992) and CM 45490 and 79249 for all the remaining characters. That of *Sayimys* was based on the specimen of *S. sivalensis* SSLG Nr. 632 (UB) for the two incisor enamel characters (from Martin 1992), but the remaining 102 dental and cranial characters were based on *S. obliquidens* (from Bohlin 1946). Inasmuch as all ctenodactylines are believed to have the same incisor enamel microstructure (multiserial HSB; Martin 1992, 1993, 1995; see also Bohlin 1946, pp. 143–146, pl. 4, figs 1–3), the composite coding of *Sayimys* in Wible *et al.* (2005) is effectively that of *S. obliquidens*.

According to Wible *et al.* (2005), a PAUP* 4.0b10 (Swofford 2002) heuristic running (stepwise-addition) of their matrix, with 13 out of 23 multistate characters ordered, resulted in two most parsimonious trees. The strict consensus of these trees showed resolved relationships of the three ctenodactylines (Fig. 6D), with *Ctenodactylus* as sister-taxon to (*Sayimys*, *Pectinator*).

New analysis

Terminal taxa. The taxonomic units chosen are all the valid species of ctenodactyline rodents (see above), namely *Ctenodactylus gundi*, *C. vali*, *Massoutiera mzabi*, *Felovia vae*, *Pectinator spekei*, *Pellegrinia panormensis*, *Sayimys obliquidens*, *Sayimys baskini*, *Sayimys giganteus*, *Sayimys assarrarensis*, *Sayimys intermedius*, *Sayimys sivalensis*, *Metasayimys curvidens*, *Africanomys pulcher*, *Africanomys major*, *Africanomys minor*, *Africanomys kettarati*, *Irhoudia bohlini*, *I. robinsoni*, *Pireddamys rayi*, *Sardomys dawnsonae*, *Sardomys antoniettae*, *Akzharomys mallos* and *Prosayimys flynni*. They have been entered in the character/taxon matrix (Appendix 2, which is available via the Supplementary Content on the article's online page) in approximate chronostratigraphical order.

Character polarity and rooting. According to the analysis performed by Wang (1997), the subfamily Distylomyinae (*Prodistylomys*, *Distylomys*) is the sister group of the Ctenodactylinae. Therefore, it would seem appropriate to choose one of these two genera as the outgroup of the Ctenodactylinae. However, when Wang (1997) performed her analysis, the distylomyines were very poorly known. Since then, new material has been described which allowed Bi *et al.* (2009) to suggest that these rodents may be closer to the hystricognathous South American *Cephalomys* than to the ctenodactylids. Pending the resolution of the relationships of *Distylomys* and related taxa with the ctenodactylids, it is better to choose another outgroup. Therefore, *Karakoromys decessus* and *Tataromys plicidens* (two non-ctenodactyline ctenodactylid rodents) have been selected instead, to give a direction to the character transformation and an order of reading of the successive branchings of the tree. Based on the results of the phylogenetic analysis of Dashzeveg & Meng (1998) and the fact that the monophyly of the ingroup is not problematic (see e.g. Wang 1997), we have constrained *K. decessus* and *T. plicidens* to form a paraphyletic grouping (with the former species in the basalmost position) with respect to the ingroup.

Characters, character weighting and transformation weighting. A total of 39 phylogenetically informative dental characters have been coded (Appendix 3, which is available via the Supplementary Content on the article's online page). Of these, 19 characters are binary, whereas 20 are multistate. All the latter characters have two derived states. Owing to the lack of a priori information, all characters were unordered and equally weighted (Fitch optimality criterion).

Procedure. The data matrix was built under Mesquite 2.6 (Maddison & Maddison 2009) and the analysis was run in PAUP version 4.0b10 (Swofford 2002) using the PaupUp graphical interface (Calendini & Martin 2005). The relatively high number of terminal taxa and characters precluded exact tree building, so a branch and bound search was performed.

Results. Nine most parsimonious trees were generated with a length of 127 and a relatively high degree of homoplasy (CI = 0.4567 and RI = 0.7305). The strict and semi-strict consensus trees are identical and largely resolved (Fig. 7A) with one polytomy involving *Metasayimys curvidens*, *Africanomys* spp. and the more derived ctenodactylines. The majority-rule consensus tree is completely resolved (Fig. 7B). As some species are known so far from only a few specimens, the influence of intraspecific variation in the scoring of the characters could not be assessed. Bremer and relative Bremer support indices (Goloboff & Farris 2001) for the clades in the analysis are listed on the cladogram in Fig. 7A.

The transformations supporting the topology of this tree (under the ACCTRAN and DELTRAN optimizations) are listed in Table 1. Each internal node is discussed below, beginning from the most inclusive.

Node 49. *Prosayimys flynni* + more derived taxa. This node is supported by seven exclusive synapomorphies both under ACCTRAN and DELTRAN optimizations (metaconid connected to the metalophulid II and to the protoconid, anteroconid present on the dp4, moderate posterolabial ledge on the m1-m2, hypoflexid in front of the

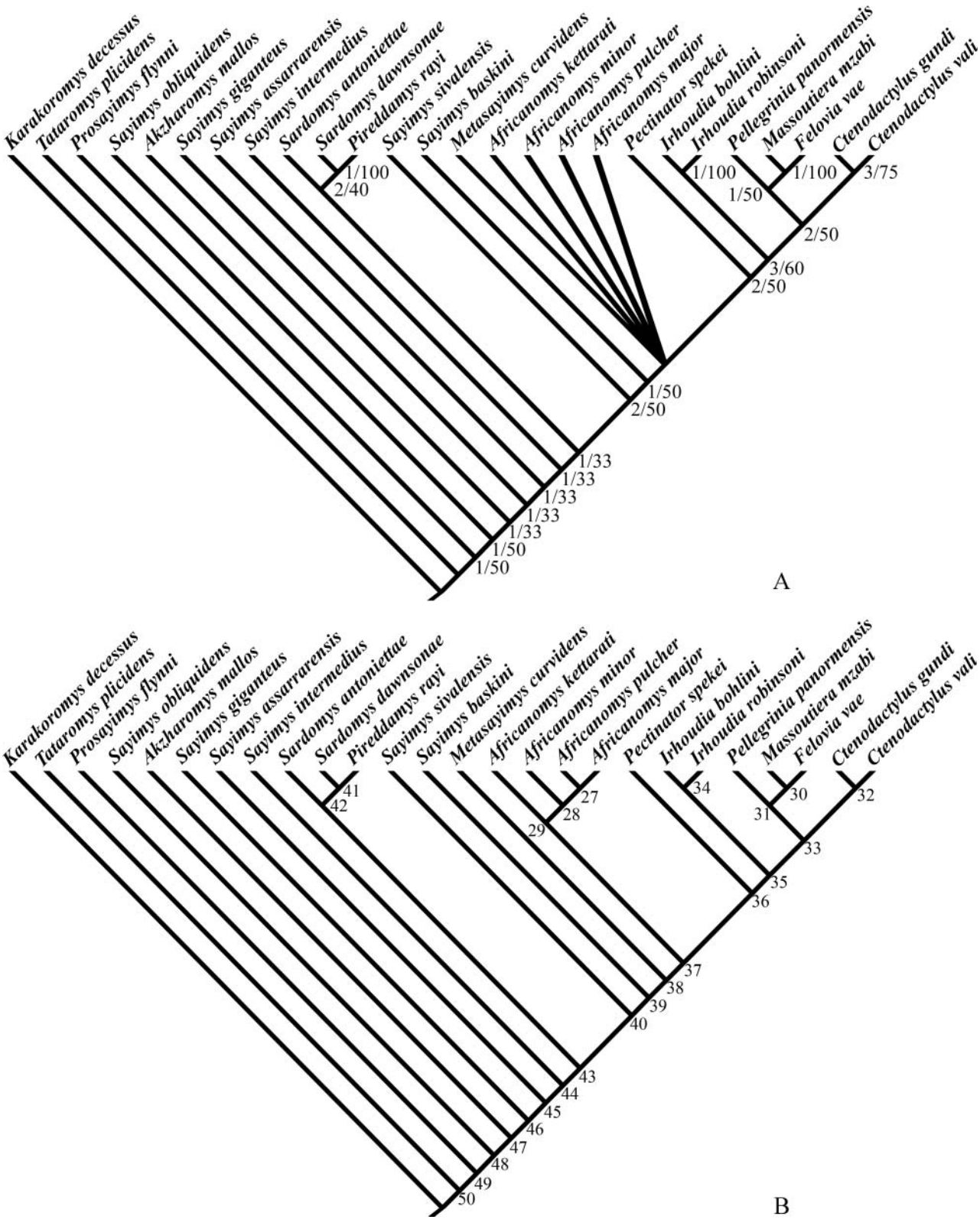

Figure 7. Consensus trees generated by the cladistic analysis of the Ctenodactylinae performed in this paper (matrix in Appendix 3). **A,** strict and semi-strict consensus trees, Bremer and relative Bremer indices are showed at the appropriate nodes; **B,** majority-rule consensus tree, nodes are designed by numbers 49 to 27. The trees have a length of 127 steps, a consistency index (CI) of 0.4567 and a retention index (RI) of 0.7305.

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Table 1. Transformations supporting the topology of the 50% majority rule consensus tree under ACCTRAN and DELTRAN optimizations. Bold indicates exclusive synapomorphies at internal nodes and autapomorphies in terminal ingroup taxa. Italics indicate synapomorphies that change with the optimization.

Node	Acctran	Deltran
Prosayimys flynni	32(0→1)	*10(1→0)*, 32(0→1)
Sayimys obliquidens	9(0→1), 21(1→0), 25(0→1)	9(0→1), 21(1→0), 25(0→1)
Akzharomys mallos	19(1→0)	*1(0→1)*, 19(1→0)
Sayimys giganteus		*1(0→1)*
Sayimys assarrarensis	34(0→1)	34(0→1)
Sayimys intermedius	5(0→1), 6(1→2), 9(0→1), 26(0→2), 32(0→1)	5(0→1), 6(1→2), 9(0→1), 26(0→2), 32(0→1)
Sardomys antoniettae		*1(0→1)*
Sardomys dawnsonae	22(0→1)	22(0→1)
Pireddamys rayi		
Sayimys sivalensis	5(0→1), 6(1→2), 9(0→1), 10(1→0), 31(1→0)	5(0→1), 6(1→2), 9(0→1), 10(1→0), *21(1→0)*, 31(1→0)
Sayimys baskini		*28(0→1)*
Metasayimys curvidens	22(0→1), 27(1→0), *28(1→0)*, 38(0→1), 39(1→0)	22(0→1), 27(1→0), *29(1→2)*, 38(0→1), 39(1→0)
Africanomys kettarati		
Africanomys minor	3(0→1)	3(0→1), *28(0→1)*
Africanomys major	1(0→1), 25(0→1)	1(0→1), 25(0→1), *28(0→1)*
Africanomys pulcher	*28(1→0)*	
Pectinator spekei	21(1→0), 26(0→2), 37(0→1)	21(1→0), 26(0→2), *27(1→2), 28(0→2), 33(1→2)*, 37(0→1)
Irhoudia bohlini	21(1→2), 28(0→1)	21(1→2), 28(0→1)
Irhoudia robinsoni	3(2→1)	3(2→1)
Pellegrinia panormensis	1(1→2), **18(1→2)**, 20(1→0), *21(0→2)*, **25(0→2)**, 33(1→2)	1(1→2), **18(1→2)**, 20(1→0), *21(1→2)*, **25(0→2)**, 33(1→2)
Massoutiera mzabi	**26(0→1)**, 39(1→0)	**26(0→1)**, 39(1→0)
Felovia vae	15(2→1)	15(2→1)
Ctenodactylus gundi		
Ctenodactylus vali		
27	11(2→1), 12(0→1)	11(2→1), 12(0→1)
28		*8(0→1), 23(2→1), 32(2→0)*
29	*8(0→1), 23(2→1), 29(2→1), 32(2→0)*	
30	35(0→1)	*21(1→0)*, 35(0→1)
31	*21(1→0)*, 22(0→1), 38(0→1)	22(0→1), 38(0→1)
32	26(0→2), **37(0→2)**, 39(1→0)	26(0→2), **37(0→2)**, 39(1→0)
33	**2(0→1), 4(0→1)**, 8(0→1), **10(1→2), 15(1→2)**, *33(2→1)*	**2(0→1), 4(0→1)**, 8(0→1), **10(1→2), 15(1→2)**, *27(1→2)*, *28(0→2)*
34	*27(2→1)*, *28(2→0)*, 35(0→1)	*33(1→2)*, 35(0→1)
35	**3(0→2)**, 17(1→0), **18(0→1), 20(0→1), 24(1→0)**	**3(0→2)**, 17(1→0), **18(0→1), 20(0→1), 24(1→0)**
36	1(0→1), 6(1→2), ***27(1→2)***, ***28(1→2)***, 31(1→0), ***33(1→2)***, **36(1→2)**	1(0→1), 6(1→2), *29(1→2)*, 31(1→0), **36(1→2)**
37	5(0→1), **7(1→0)**	5(0→1), **7(1→0)**
38	**11(1→2)**, 14(1→0), 19(1→0), ***29(1→2)***	**11(1→2)**, 14(1→0), 19(1→0)
39	17(0→1), *21(0→1)*, 25(1→0), ***28(0→1)***	17(0→1), 25(1→0)
40	12(1→0), **30(1→0), 32(0→2)**, 33(0→1), **34(0→2)**	12(1→0), **30(1→0), 32(0→2), 33(0→1), 34(0→2)**
41	*1(1→2)*, 3(0→1)	*1(0→2)*, 3(0→1)
42	*1(0→1)*, 15(1→0), 16(1→0), 19(1→0)	15(1→0), 16(1→0), 19(1→0), *21(1→0)*
43	*21(1→0)*, **23(1→2), 39(0→1)**	**23(1→2), 39(0→1)**
44	17(1→0)	17(1→0)
45	*1(1→0)*, 25(0→1)	25(0→1)
46	**16(0→1), 36(0→1)**	*12(0→1)*, **16(0→1)**, ***27(0→1)***, **36(0→1)**
47	*1(0→1)*, *12(0→1)*, 15(0→1), ***27(0→1)***	15(0→1)
48	***10(0→1)***, **13(0→1), 14(0→1)**, 17(0→1)	**13(0→1), 14(0→1)**, 17(0→1)
49	**6(0→1), 7(0→1)**, 11(0→1), **19(0→1), 24(0→1)**, 29(0→1), **30(0→1)**, **31(0→1), 37(1→0)**	**6(0→1), 7(0→1)**, 11(0→1), **19(0→1)**, *23(0→1)*, **24(0→1), 29(0→1)**, **30(0→1), 31(0→1), 37(1→0)**

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hypolophid on the lower molars, well developed anteroloph on the P4, presence of the lingual re-entrant fold on the P4, and deep hypoflexus on the M1-M2) and one more under DELTRAN (reduced P4).

Node 48. *Sayimys obliquidens* + more derived taxa. This node is supported by two exclusive synapomorphies both under ACCTRAN and DELTRAN (Y-shaped p4 and presence of the posterolabial ledge on the p4) and one more under ACCTRAN (transverse hypolophid on the dp4).

Node 47. *Akzharomys mallos* + more derived taxa. This node is supported by one exclusive synapomorphy under ACCTRAN: DP4 with short metaflexus.

Node 46. *Sayimys giganteus* + more derived taxa. This node is supported by two exclusive synapomorphies both under ACCTRAN and DELTRAN (metalophulid II absent on the lower molars and short metaflexus on the M1-M2) and one additional under DELTRAN (short metaflexus on the DP4).

Node 45. *Sayimys assarrarensis* + more derived taxa. This node is based on one ambiguous synapomorphy both under ACCTRAN and DELTRAN (posterolophid bended towards the entoconid on the m1-m2: a parallelism with *S. obliquidens* and *Africanomys major*) and one more under ACCTRAN (small size: a reversal with respect to node 46).

Node 44. *Sayimys intermedius* + more derived taxa. This node is based on one ambiguous synapomorphy: mesoflexid equal or longer than the metaflexid on the lower molars (a reversal with respect to node 48).

Node 43. *Sardomys antoniettae* + *Pireddamys rayi* + *S. dawnsonae* + more derived taxa. This node is based on two exclusive synapomorphies both under ACCTRAN and DELTRAN: length of the m2 smaller than that of the m3 and the M3 with reduced posterior lobe.

Node 42. *Sardomys antoniettae* + *Pireddamys rayi* + *S. dawnsonae*. This node is supported by four ambiguous synapomorphies both under ACCTRAN and DELTRAN: intermediate size, a parallelism with respect to *Africanomys major* and nodes 36 and 47 (only under the ACCTRAN optimization); four-lobed m1-m2 (a reversal with respect to node 47); metalophulid II on the m1-m2 (a reversal with respect to node 46); postero-labial ledge absent on the m1-m2 (a reversal with respect to node 49) and one more under DELTRAN (oblique hypolophid on the m1-m2).

Node 41. *Pireddamys rayi* + *Sardomys dawnsonae*. This node is supported by two ambiguous synapomorphies both under ACCTRAN and DELTRAN: large size (parallelism with *Pellegrinia panormensis*) and semihypsodont teeth (parallelism with *Africanomys minor* and *Irhoudia robinsoni*).

Node 40. *Sayimys sivalensis* + more derived taxa. This node is supported by three exclusive synapomorphies both under ACCTRAN and DELTRAN (anteroloph weak or absent on the P4 (a reversal with respect to node 49), posteroloph weak or absent on the P4, paraflexus absent on the M1-M2) and one additional under DELTRAN (three-lobed M1-M2).

Node 39. *Sayimys baskini* + more derived taxa. This node is supported by one exclusive synapomorphy under ACCTRAN: the presence of a short paraflexus on the DP4.

Node 38. *Metasayimys curvidens* + more derived taxa. This node is supported by two exclusive synapomorphies under ACCTRAN optimization (very reduced p4 and P4) and one under DELTRAN (very reduced p4).

Node 37. *Africanomys kettarati* + *A. minor* + *A. major* + *A. pulcher* + more derived taxa. This node is based on one exclusive synapomorphy both under ACCTRAN and DELTRAN: absence of the anteroconid on the dp4 (a reversal with respect to node 49).

Node 36. *Pectinator spekei* + more derived taxa (crown-group). This node is supported by four exclusive synapomorphies under ACCTRAN (very early disappearance of the metaflexus and paraflexus on the DP4, two-lobed M1-M2 and metaflexus absent on the M1-M2) and one under DELTRAN (metaflexus absent on the M1-M2).

Node 35. *Irhoudia bohlini* + *I. robinsoni* + more derived taxa. This node is based on four exclusive synapomorphies both under ACCTRAN and DELTRAN: hypsodont teeth, short metaflexid, hypertrophy of the protoconid on the m1-m2, and hypoflexid in front of the mesoflexid on the m1-m2 (a reversal with respect to node 49).

Node 34. *Irhoudia bohlini* + *I. robinsoni*. This node is based on three ambiguous synapomorphies under ACCTRAN (DP4 with a short metaflexus (a reversal with respect to node 36), DP4 with a long paraflexus (a reversal), and hypertrophy of the protocone on the M1-M2 (a parallelism with node 30)) and two under DELTRAN (hypertrophy of the protocone on the M1-M2 (a parallelism with node 30) and two-lobed M1-M2 (a parallelism with *Pectinator spekei* and *Pellegrinia panormensis*)).

Node 33. *Ctenodactylus gundi* + *C. vali* + more derived taxa. This node is supported by four exclusive synapomorphies both under ACCTRAN and DELTRAN (ever-growing teeth, reduced dp4, absence of the hypolophid on the dp4, two-lobed m1-m2).

Node 32. *Ctenodactylus gundi* + *C. vali*. This node is based on one exclusive synapomorphy both under ACCTRAN and DELTRAN (absence of the hypoflexus on the M1-M2).

Node 31. *Pellegrinia panormensis* + more derived taxa. This node is based on three ambiguous synapomorphies under ACCTRAN and two under DELTRAN (oblique hypolophid on the m1-m2 (a reversal with respect to node 39), valleys of the m2 and m3 filled with cement (a parallelism with *Metasayimys curvidens* and *Sardomys dawsonae*; only under ACCTRAN), and those of the upper molars as well (a parallelism with *M. curvidens*).

Node 30. *Massoutiera mzabi* + *Felovia vae*. This node is based on one exclusive synapomorphy under both ACCTRAN and DELTRAN (hypertrophied protocone on

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the M1-M2 (a parallelism with the node 34)) and one additional under DELTRAN (oblique hypolophid on the m1-m2 (a parallelism with *Sayimys obliquidens*, *S. sivalensis*, *Pectinator spekei* and node 42)).

Node 29. *Africanomys kettarati* + more derived taxa. This node is based on four ambiguous synapomorphies under ACCTRAN (metaconid located on the anterior edge of the dp4 (a parallelism with node 33), m2 similar in length to the m3 (a reversal with respect to node 43), reduced p4 (a reversal with respect to node 38), and posteroloph longer than the anteroloph on the P4 (a reversal with respect to node 40)).

Node 28. *Africanomys minor* + more derived taxa. This node is based on three ambiguous synapomorphies under DELTRAN (metaconid located on the anterior edge of the dp4 (a parallelism with node 33), m2 similar in length to the m3 (a reversal with respect to node 43), and P4 with the posteroloph longer than the anteroloph (a reversal with respect to node 40)).

Node 27. *Africanomys major* + *A. pulcher*. This node is based on two ambiguous synapomorphies under both ACCTRAN and DELTRAN (a reduced p4 (a reversal with respect to node 38) and the presence of a posterolophid on the p4 (a parallelism with node 47 under ACCTRAN and with node 46 under DELTRAN)).

Discussion

Position of *Prosayimys flynni*

Prosayimys flynni is the most basal species of the ingroup. As suggested by Baskin (1996), López-Antoñanzas & Sen (2004) and López-Antoñanzas *et al.* (2004), this genus can be seen as ancestral to *Sayimys*. Contrary to the opinion of Kordikova & De Bruijn (2001, p. 398), *Prosayimys* should not be considered a synonym of *Sayimys*.

Non-monophyly of the genus *Sayimys*

López-Antoñanzas & Sen (2004) and López-Antoñanzas *et al.* (2004) pointed out that in order to test the monophyly of the genus *Sayimys* a complete phylogenetic analysis involving all the species belonging in Ctenodactylinae had to be performed. One of the most interesting results of the present work is that the genus *Sayimys* does not appear monophyletic.

The earlier studies suggested that *Sayimys giganteus* and *S. obliquidens*, on one hand, and *S. intermedius* and *S. sivalensis*, on the other, were sister-species. The present work does not confirm this topology, but rather advocates sister-group relationships between *S. obliquidens* and the clade composed of *Akzharomys mallos* and more derived ctenodactylines (of which *S. giganteus* is the most basal species). *S. intermedius* nests as the sister-species of the *Sardomys-Pireddamys* clade and more derived ctenodactylines (of which *S. sivalensis* is the most basal species).

Regarding *Sayimys obliquidens*, Jaeger (1971) and De Bruijn *et al.* (1981) advocated that this taxon is morphologically very close to *Metasayimys curvidens*. Jaeger (1971) thought that this species should be reallocated to the genus *Metasayimys*. Robinson & Black (1973) agreed with Jaeger (1971) in considering *S. obliquidens* as close to *Metasayimys* and not belonging to *Sayimys*, but they felt it was 'premature' to assign it to the former genus. In contrast, Wood (1977) agreed with Bohlin (1946) that *S. obliquidens* belonged in *Sayimys*. He thought that this species was closely related to *S. perplexus* (= *S. sivalensis*; see López-Antoñanzas & Sen 2003), but not to *M. curvidens*. De Bruijn *et al.* (1981) suggested that due to the morphological similarity between the Chinese *S. obliquidens* and the African *Metasayimys curvidens*, the African ctenodactylines may have descended from a Central Asiatic form rather than from an ancestor in the Indian subcontinent. However, *S. obliquidens* is far from close (phylogenetically speaking) to *M. curvidens*. Actually, the African ctenodactylines (*M. curvidens* and the more derived species but *Pellegrinia panormensis*) are closely related to the Pakistani *S. sivalensis* and *S. baskini* (see below); therefore, their immediate ancestor is likely to be found in the Indian subcontinent.

In his comprehensive study of the evolution of the ctenodactylids, Wood (1977) suggested that *Sayimys sivalensis* was closer to *Metasayimys* than to *S. obliquidens* and should be placed in the genus *Africanomys*. Munthe (1980) proposed a phylogenetic sequence proceeding from *S. obliquidens* through *S. sivalensis* to *Metasayimys*, and argued in favour of an independent origin for the genus *Africanomys*. De Bruijn *et al.* (1989) and Baskin (1996) advocated that *Metasayimys* had derived from *S. minor* (= *S. baskini*). Our analysis gives *S. sivalensis* a sister-species position to the clade comprising *S. baskini* and the more derived taxa. *S. baskini*, as the sister-species of the clade comprising *M. curvidens* and the more derived taxa, is very close to *Metasayimys.* Therefore, our result is in concordance with De Bruijn *et al.* (1989) and Baskin (1996), but also with Wood (1977) and Munthe (1980), who could not take into account *S. baskini*, which was published later. However, the transfer of *S. sivalensis* to *Africanomys* suggested by Wood (1977) is not justified. More recently, Kumar & Kad (2002, p. 739) suggested that *S. minor* (*S. baskini*) is a plesiomorphic taxon of the lineage leading to *S. sivalensis*, but according to our results the reverse is correct.

The Oschiri ctenodactylines

The Lower Miocene species of ctenodactylines from Sardinia form a clade. The topology of the tree suggests that they may all be best seen as members of a single genus (*Sardomys*). However, due to the scarcity of available material of *S. antoniettae*, its classification in the genus

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Sardomys is open to discussion (De Bruijn & Rümke 1974). If indeed *S. antoniettae* turns out to be morphologically distant from the type-species of the genus (*S. dawsonae*), it could be reallocated to a genus of its own and *Pireddamys* could be saved.

De Bruijn & Rümke (1974) assumed that the ctenodactylids migrated from Asia to Sardinia through Africa, an opinion with which some authors agreed (Azzaroli & Guazone 1979). Wood (1977) advocated that *Sardomys* and *Pireddamys* could have derived from ancestors similar to the Asiatic Oligocene *Karakoromys* and *Tataromys*, and suggested that the ctenodactylids might have reached Sardinia from a source distinct from North Africa. Later, De Bruijn (1999) proposed an Early Oligocene migration from an Asiatic Kakaromyinae (like *Bounomys* or *Euryodontomys*) that reached as far west as Sardinia. Kotsakis & Palombo (2009) did not discard this possibility. To test the relationships of *Sardomys* and *Pireddamys* with kakaromyines, we reran our analysis with *T. plicidens* alone as outgroup (*K. decessus* being added into the ingroup). *K. decessus* appears then as the most basal species of the ingroup, being sister-species of the clade comprising *Prosayimys flynni* and the more derived ctenodactyline taxa. The topology of the majority consensus tree is otherwise similar to that obtained in our original analysis. Therefore, the Oschiri ctenodactylines do not appear to have close relationships with Kakaromyinae. Our analysis hints at an Asiatic origin of the Sardinian species, but a more recent one than postulated by De Bruijn (1999). It is likely that the ancestor of the Sardinian species is to be found in species similar to *Sayimys intermedius* that migrated during the earliest Early Miocene from Asia through the Hellenides, Dinarides, and northern Apennines to reach what would become Sardinia.

The genus *Africanomys*

Another interesting result is the evidence of the monophyletic nature of the genus *Africanomys*, the sister-group of the clade originating from node 36 (the crown-group). According to Wood (1977), *Africanomys* was structurally ancestral to *Metasayimys*, but our results suggest that *M. curvidens* is more basal than *Africanomys* spp.

The crown group

Wood (1977) suggested that *Pectinator spekei* seemed derivable from *Africanomys* and *Metasayimys*, an opinion with which we agree. As defended by some authors (Jaeger 1971; George 1979, 1985), *Pectinator spekei* is the most basal of the living species of Ctenodactylinae. This taxon shares an exclusive common ancestor with the species of the *Ihroudia* clade and the more derived ctenodactylines.

According to De Bruijn & Rümke (1974), *Pellegrinia panormensis* would have been a descendant of the *Sardomys*/*Pireddamys* branch rather than a Pleistocene immigrant from Africa as suggested by other authors (Thaler 1972; De Bruijn 1999; Villa 2001). However, our phylogenetic results are in line with the opinion of the latter authors: the origin of *Pellegrinia panormensis* is most probably African as this species is far from being connected to the other European representatives of the subfamily (i.e. the Oschiri species originating from node 42).

Wood (1977) concluded that *Pellegrinia* was phylogenetically closer to *Felovia* and *Massoutiera* than to *Irhoudia*, which is more basal. This opinion is supported by our results. However, he considered that *Irhoudia* and *Pectinator* derived from an *Africanomys*-*Metasayimys* lineage, and that *Pellegrinia*, *Massoutiera* and *Felovia* came from an independent lineage in which *Sayimys obliquidens* was basal. It turns out that *Pectinator spekei* and *Irhoudia* spp. actually constitute successively closer sister taxa to the clade constituted by *Pellegrinia* and the remaining extant ctenodactylines. *Massoutiera mzabi* and *Felovia vae* are sister species and are closer to *Pellegrinia panormensis* than to the two species of *Ctenodactylus*. The very close relationship between *Massoutiera* and *Felovia* is unsurprising due to their similar morphology. This result is in agreement with the analyses carried out by George (1979, 1985).

Conclusions

The most basal and oldest representative of the subfamily Ctenodactylinae is *Prosayimys flynni* from the Late Oligocene or earliest Miocene of Pakistan. The genus *Sayimys*, considered the most speciose and widely distributed, is non-monophyletic.

The ctenodactylines provide a fine example of long-distance dispersal of rodents consistent with geological evidence indicating the establishment of an Early Miocene corridor between Afro-Arabia and Eurasia (resulting from the collision of the Arabian Peninsula with the Anatolian plate). Even if the ctenodactylines are restricted to Africa at present, their phylogenetic relationships imply that the ancestry of these species is to be found in Asia. This subfamily underwent a wide geographical expansion during Miocene times, reaching Sardinia at the beginning of the Early Miocene and the north of Africa possibly in the Middle Miocene, through the Arabian Peninsula where the record of this subfamily dates as far back as the end of the Early Miocene. The origin of the European ctenodactylines is diverse; the Early Miocene *Sardomys* and '*Pireddamys*' from Sardinian have south-western Asiatic origins, whereas the Sicilian Pleistocene *Pellegrinia* originated from an African ancestor. Interestingly, the ctenodactylines became extinct in Asia during the Pliocene and never returned from Africa.

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