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Systematic revision of Mio-Pliocene Ctenodactylidae (Mammalia, Rodentia) from the Indian subcontinent

RAQUEL LÓPEZ ANTOÑANZAS & SEVKET SEN

Key words: Ctenodactylidae, *Sayimys*, systematics, Mio-Pliocene, Indian subcontinent

ABSTRACT

Ctenodactylids are common elements of Early-Middle Miocene mammal faunas of the Indian subcontinent, West Asia, and North Africa. They are of great interest for biostratigraphical correlations and palaeogeographical relationships between these areas. The study of new ctenodactylid remains from Early-Middle Miocene localities of Saudi Arabia, Turkey, and Chios Island has revealed that the systematics of the Early-Middle Miocene ctenodactylids from the Indian subcontinent are problematic. Seven species belonging to two genera have been recognized so far in the Indo-Pakistani Mio-Pliocene: *Prosayimys flynni* BASKIN 1996, *Sayimys minor* DE BRUIJN et al. 1981, *Sayimys intermedius* (SEN & THOMAS 1979), *Sayimys sivalensis* (HINTON 1933), *Sayimys chinjiensis* BASKIN 1996, *Sayimys perplexus* WOOD 1937, and *Sayimys badauni* VASISHAT 1985. We consider that, at best, only five ctenodactylid species are recognizable in the Mio-Pliocene of the Indian subcontinent: *Prosayimys flynni* BASKIN 1996, *Sayimys baskini* nov. sp., *Sayimys intermedius* (SEN & THOMAS 1979), *Sayimys sivalensis* (HINTON 1933), and perhaps *Sayimys badauni* VASISHAT 1985.

RESUME

Les Ctenodactylidae représentent une composante importante des faunes de mammifères du Miocène inférieur et moyen du sous-continent indien, du Proche-Orient et d'Afrique du Nord. Ils présentent un grand intérêt d'un point de vue biostratigraphique et paléogéographique. L'étude de nouveaux spécimens de cténodactylidés provenant d'Arabie saoudite, de Turquie et de l'île de Chio a révélé combien la systématique des cténodactylidés du Miocène inférieur à moyen du sous-continent indien est problématique. Sept espèces distribuées en deux genres ont été reconnues dans le Mio-Pliocène indo-pakistanaïse: *Prosayimys flynni* BASKIN 1996, *Sayimys minor* DE BRUIJN et al. 1981, *Sayimys intermedius* (SEN & THOMAS 1979), *Sayimys sivalensis* (HINTON 1933), *Sayimys chinjiensis* BASKIN 1996, *Sayimys perplexus* WOOD 1937 et *Sayimys badauni* VASISHAT 1985. Nous reconnaissons seulement cinq espèces au maximum, dans le Mio-Pliocène du sous-continent indien: *Prosayimys flynni* BASKIN 1996, *Sayimys baskini* nov. sp., *Sayimys intermedius* (SEN & THOMAS 1979), *Sayimys sivalensis* (HINTON 1933) et peut-être *Sayimys badauni* VASISHAT 1985.

Introduction

Ctenodactylid rodents (gundi rats) were present in eastern and central Asia since Late Eocene times, but they did not spread out to the Indian subcontinent and farther west prior to the Early-Middle Miocene. They are considered excellent tools for palaeoenvironmental reconstructions (indicators of arid environments), but they are also of importance from biochronological and palaeobiogeographical points of view. However, the use of ctenodactylid representatives in interregional correlation of Cenozoic continental deposits requires a sound systematic background. Yet, on the occasion of the study of new ctenodactylid dental material from Saudi Arabia (López-Antoñanzas & Sen, in press a), Turkey, and Greece conducted by the authors, a number of seriously problematic points has been brought to the fore regarding, in particular, the systematics of South Asian Mio-Pliocene ctenodactylids, as remarked already by some authors (e.g. Munthe 1980, p. 22–23; Wang 1997, p.

62). The situation has considerably improved thanks to the work of Baskin (1996), but a comprehensive systematic revision of Mio-Pliocene ctenodactylid of the *Sayimys* group from the Indian subcontinent is still needed.

The aim of this paper is therefore to provide a systematic revision of all the ctenodactylid species recorded so far in the Mio-Pliocene of the Indian subcontinent that could serve as a necessary basis for future biochronological and phylogenetic work on ctenodactylids.

Systematic review

Prosayimys flynni BASKIN 1996

Holotype. – Z113/295, left m3.

Repository institution. – All the *Prosayimys flynni* material is currently housed at the Peabody Museum of Archaeology

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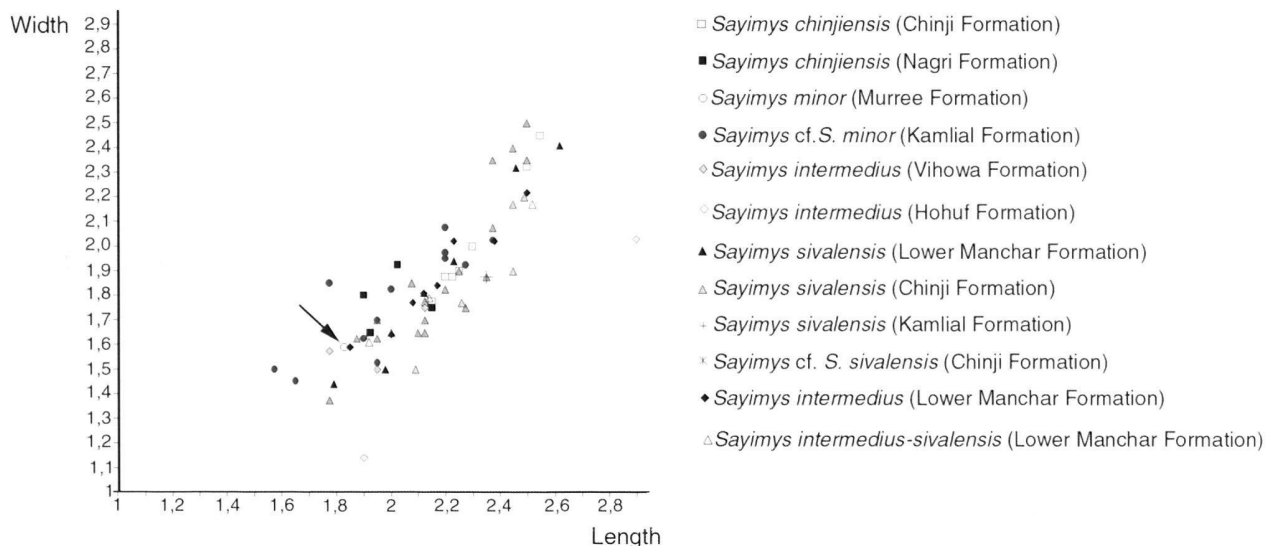


Fig. 1. Variation in the length and width of the m1-2 of various species of *Sayimys*. The arrow pinpoints *Sayimys minor* DE BRUIJN et al. 1981 from the Murree Formation of Pakistan.

and Ethnology (Harvard University, Cambridge, USA). It will be returned to Pakistan and deposited at the Natural History Museum in Islamabad (L. Flynn, pers. com. 2002).

Type-locality. – Z113, Zinda Pir Dome, Pakistan.

Type-horizon. – Dalana section, Chitarwata Formation.

Age. – Early Miocene (MN 3).

Emended diagnosis. – d4 and lower molars having a metalophulid II, upper molars having a long paraflexus.

Discussion. – *Prosayimys flynni* is known so far only from the Chitarwata Formation in Pakistan (Baskin 1996). The synonymy of *Prosayimys* and *Sayimys* has been lately suggested by Kordikova & de Bruijn (2001, p. 398). According to Baskin (1996), the main diagnostic character of the genus *Prosayimys* is the presence of a metalophulid II in the lower deciduous and permanent molars. However, the presence of the metalophulid II in the deciduous molars is also a character retained by all species of *Sayimys* except the most derived ones such as *Sayimys intermedius* and *Sayimys sivalensis*. In addition, the metalophulid II is also present in the m2s of *Sayimys obliquidens*. In other respects the teeth of *Prosayimys flynni* are comparable to those of other species of *Sayimys*. However, the invalidity of the former genus is not substantiated by the results of a recent analysis of ctenodactylin relationships in which *Prosayimys flynni* nests basal to all other species of the ingroup (López-Antoñanzas & Sen, in press a). Therefore, *Prosayimys* can legitimately be considered a genus distinct from *Sayimys*.

Sayimys intermedius SEN & THOMAS 1979

1981 *Sayimys minor* DE BRUIJN et al. 1981 (*partim*), p. 89, Pl. 3, Fig. 2

Holotype. – AJ 545, left mandible with d4-m2.

Repository institution. – National Heritage Museum, Riyadh

(Saudi Arabia).

Type-locality. – Al Jadidah (Saudi Arabia).

Type-horizon. – Hofuf Formation.

Age. – Middle Miocene (MN 5).

Other localities. – Banda Daud Shah, Sind, Zinda Pir Dome, and Potwar Plateau (Pakistan); Paşalar (Turkey); Al Jadidah and Tayma (Saudi Arabia), and Thymiana (Chios Island, Greece) (see discussion).

Emended diagnosis. – d4 lacking metalophulid II and having the anteroconid isolated, p4 having posterolophid, lower molars with mesoflexid and metaflexid extending almost equally far labially, P4 having an anteroloph connecting to the protocone and longer than the posteroloph that joins the protoloph, upper molars with a paraflexus and metaflexus well developed.

Sayimys minor DE BRUIJN et al. 1981

Holotype. – H- GSP 116/313, right m1-2 (de Bruijn et al. 1981: Pl. 3, Fig. 2).

Repository institution. – Geological Survey of Pakistan, Quetta (Pakistan).

Type-locality. – H- GSP 116, near Banda Daud Shah (Pakistan).

Type-horizon. – Murree Formation (Lower Miocene).

Age. – Early Miocene (MN 3).

Remarks. – The holotype (H- GSP 116/313) of *Sayimys minor* DE BRUIJN et al. 1981 is a m1-2. The topotypic sample of *Sayimys minor* consists only of four teeth. De Bruijn et al. (1981) mentioned four characters on the holotype and only specimen of m1-2 of *Sayimys minor*. Three of them (the protoconid and the metaconid forming a transverse blade, the mesoflexid and the metaflexid transverse and reaching equally

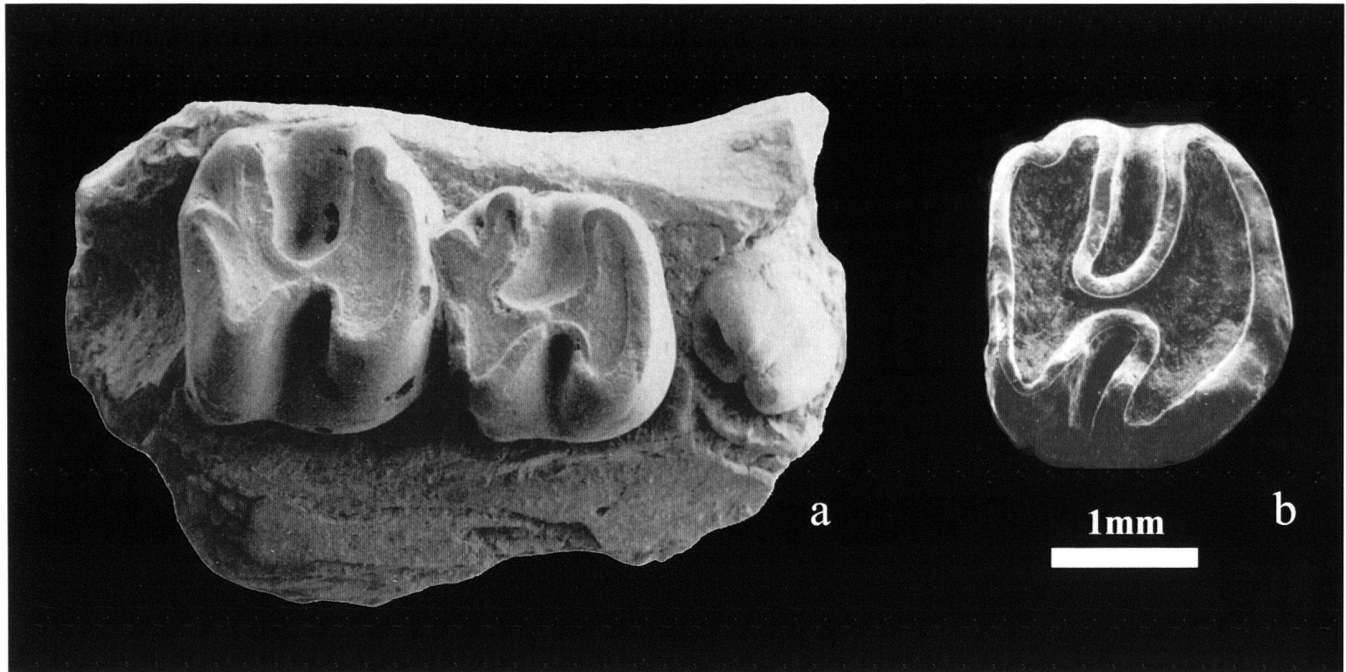


Fig. 2. a. right P4-M2 (Y747/48143, occlusal view) of *Sayimys* cf. *Sayimys minor* (after Baskin 1996). b. right M1-2 (occlusal view) of *Sayimys minor* DE BRUIJN et al. 1981 (after de Bruijn et al. 1981).

far labially, and the transverse hypolophid opposing the hypoflexid) are also present in *Sayimys intermedius* (Sen & Thomas 1979; de Bruijn et al. 1989; Baskin 1996) (Pl. 1 Figs. a-d). The last character noted by de Bruijn et al. (1981) i.e., the posterolophid constricted just before reaching the triangular wear surface of the hypoconid, can be also observed in some specimens of *Sayimys intermedius* (Sen & Thomas 1979; de Bruijn et al. 1989, Pl. 1, Fig. 8 & Pl. 2, Fig. 9, 13). De Bruijn et al. (1981) argued that one of the two differences between these two species rests on the size difference (the other one being the presence of a metalophulid II in the d4, as mentioned below). It may be therefore useful to address biometrically the question of their possible dimensional discrimination.

The measurements given by de Bruijn et al. (1981) for the m1-2 of *Sayimys minor* are 1.83 x 1.59 mm. Baskin (pers. com. 2002) kindly provided extensive measurements of the specimens of Ctenodactylidae from Pakistan he studied (Baskin 1996). A size comparison has been carried out on the basis of this compilation (Fig. 1). The measurements of *Sayimys* cf. *Sayimys intermedius* are only slightly larger than those of *Sayimys minor*. Furthermore, it should be noted that GSP 45121, the smallest specimen of *Sayimys* cf. *Sayimys intermedius* from the locality Z120 of the early Middle Miocene of the Vihova Formation of Pakistan, with a measurement of 1.78 x 1.58 mm, is smaller than the holotype of *Sayimys minor* (Baskin 1996). In addition, the holotype of *Sayimys intermedius* (Sen & Thomas 1979) is only slightly longer but much narrower than the holotype of *Sayimys minor*.

With regard to the paratypic upper molars found in the Murree Formation (de Bruijn et al. 1981, Pl. 3, Fig. 1, 4) (Fig. 2, b), they possibly belong to another taxon. The M1-2 is a very worn tooth in which the paraflexus is lacking. According to Baskin (1996), this tooth may be referred to as *Sayimys* cf. *Sayimys intermedius* because of its dimension, within the size range of *Sayimys* cf. *Sayimys intermedius*, and because it is bigger than *Sayimys* cf. *Sayimys minor* from the Kamliyal Formation (Fig. 2, a-b). Actually, the size of this tooth is not only within the size range of the M1-2 of *Sayimys* cf. *Sayimys intermedius*, but also within that of the M1-2 of *Sayimys sivalensis* (Fig. 3). As mentioned above, the morphology of the holotype of *Sayimys minor* (de Bruijn et al. 1981) is very similar to *Sayimys intermedius* (Sen & Thomas 1979; de Bruijn et al. 1989; Baskin 1996). Therefore, the M1-2 described by de Bruijn et al. (1981) may indeed pertain to *Sayimys* cf. *Sayimys intermedius*, but not merely because of its size. Thus, this tooth is a very worn one in which the paraflexus has been obliterated, whereas the metaflexus is still present. This pattern of dental wear may correspond to the last stage of wear described by de Bruijn (1989) in *Sayimys intermedius*. However, the absence of paraflexus in the M1-2 from the Murree Formation (de Bruijn et al. 1981, Pl. 3, Fig. 4) is a feature of *Sayimys sivalensis* (Hinton 1933; Munthe 1980; de Bruijn 1989; Baskin 1996), inclusive of *Sayimys perplexus* (Vasishat 1978, 1985) and *Sayimys chinjiensis* (Baskin 1996), and *Sayimys badauni* (Vasishat 1985) (see below). Although, there is little doubt that this single isolated tooth does not pertain to *Sayimys minor*, it cannot

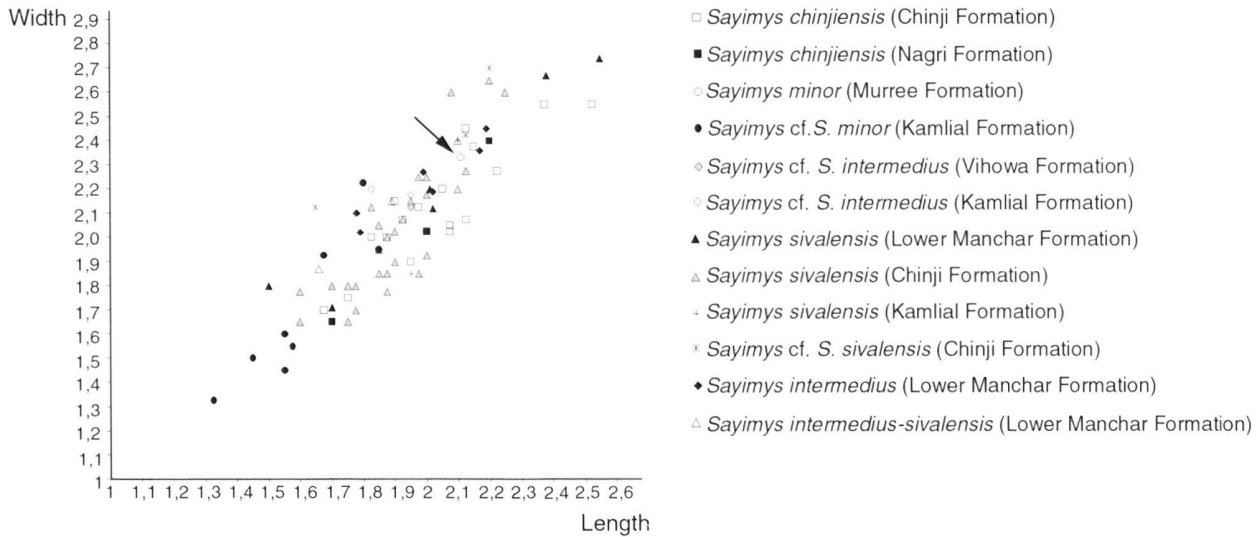


Fig. 3. Variation in the length and width of the M1-2 of various species of *Sayimys*. The arrow pinpoints *Sayimys minor* DE BRUIJN et al. 1981 from the Murree Formation of Pakistan.

be decided if it is a very worn tooth of *Sayimys intermedius* or *Sayimys sivalensis* until more material from the same formation is available. The paratypic m3 of *Sayimys minor* differs from that of *Sayimys* cf. *Sayimys intermedius* (Baskin 1996) and *Sayimys sivalensis* (Wessels et al. 1982, Pl. 4, Fig. 1; Munthe 1980, Fig. 8F; de Bruijn et al. 1989, Pl. 4, Fig. 9–10) in having a much shorter mesoflexid. *Sayimys sivalensis* has also a much shallower metastridium on both m2 and m3 than *Sayimys minor* (Baskin 1996). The morphology of the m3 of *Sayimys minor* is similar to that of *Sayimys* cf. *Sayimys minor* as described by Baskin (1996). The size of the m3 of *Sayimys minor* (de Bruijn et al. 1981) is within the size range provided by Baskin (1996) for *Sayimys* cf. *Sayimys intermedius*, *Sayimys sivalensis*, and *Sayimys* cf. *Sayimys minor* (Fig. 4). Judging by the morphology and the size of this tooth, it probably belongs to the same taxon as that referred to as *Sayimys* cf. *Sayimys minor* by Baskin (1996). The paratypic d4 (de Bruijn et al. 1981, Pl. 3, Fig. 3) is damaged, so that the morphology of the anteroconid is unknown. However, it is possible to observe the metalophulid II. The d4 dental pattern is similar to that described by Baskin (1996, Fig. 4F) for *Sayimys* cf. *Sayimys minor*, but it is very different from the remaining species of the genus *Sayimys*. In both *Sayimys minor* and *Sayimys* cf. *Sayimys minor*, the hypolophid is transverse and situated opposite to the hypoflexid, the protoconid is slightly bigger than the hypoconid, the mesoflexid and the metaflexid are not anteriorly directed and they have a metalophulid II. Only the width of the d4 of *Sayimys minor* could be measured and it is nearly the same as that provided by Baskin (1996, pers. com. 2002) for *Sayimys* cf. *Sayimys minor*. Therefore, to judge by its size and morphology, this tooth, as the m3, probably belongs to the same taxon as that referred to as *Sayimys* cf. *Sayimys minor* by Baskin (1996).

The name-bearing type of *Sayimys minor*, m1-2 H- GSP 116/313, cannot be differentiated from an equivalent tooth of *Sayimys intermedius*. This specimen shows, in particular, a transverse hypolophid and the mesoflexid and metaflexid almost equal in length. This combination of characters in the m1-2 is possibly autapomorphic and can, thus, be considered as diagnostic of *Sayimys intermedius*. As a consequence, the name-bearing type of *Sayimys minor*, H- GSP 116/313 is reallocated to *Sayimys intermedius*. Therefore, the nominal taxon *Sayimys minor* should be considered as a junior synonym of the taxon name *Sayimys intermedius*. *Sayimys minor* DE BRUIJN et al. 1981 is invalid (cf. International Commission on Zoological Nomenclature 1999: Chapter 6).

This was previously suggested by Wang (1997, p. 62) who, however, overlooked the fact that the d4 and m3 described by de Bruijn et al. (1981) as paratypic specimens of *Sayimys minor* do not actually belong to the species represented by the holotype. These teeth, as well as those from the localities Y721 and Y747 of the Kamlial Formation (Potwar Plateau, Pakistan) referred to as *Sayimys* cf. *Sayimys minor* by Baskin (1996), attest the presence of a new ctenodactylid species:

Sayimys baskini nov. sp.

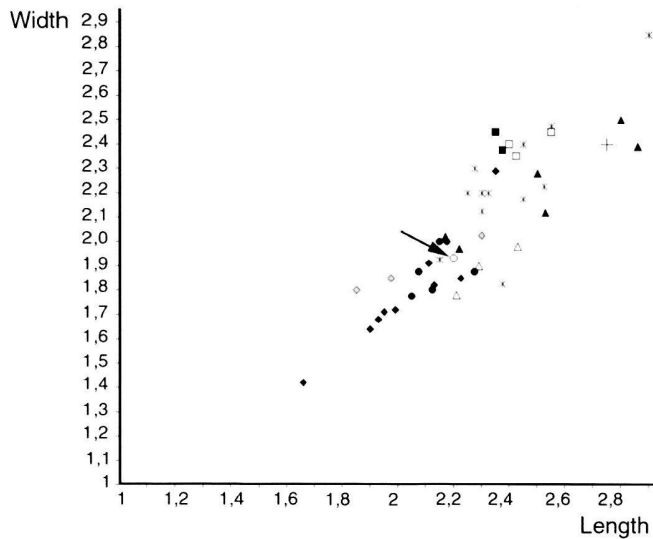
1981 *Sayimys minor* DE BRUIJN et al. (*partim*), p. 89, Pl. 3, Fig. 1, 3

1996 *Sayimys* cf. *Sayimys minor* DE BRUIJN et al.; Baskin, p. 16, Fig. 4

Derivatio nominis. – In honour of Dr. Jon A. Baskin, who has described most of the material of this species known to date.

Holotype. – GSP Y747/48125, right P4 (Baskin 1996, Figs. 4a).

Repository institution. – Geological Survey of Pakistan, Quetta (Pakistan).



- *Sayimys chinjiensis* (Chinji Formation)
- *Sayimys chinjiensis* (Nagri Formation)
- *Sayimys minor* (Murree Formation)
- *Sayimys* cf. *S. minor* (Kamlial Formation)
- ◇ *Sayimys* cf. *S. intermedius* (Vihowa Formation)
- ◆ *Sayimys* cf. *S. intermedius* (Kamlial Formation)
- ▲ *Sayimys sivalensis* (Lower Manchar Formation)
- + *Sayimys sivalensis* (Kamlial Formation)
- × *Sayimys* cf. *S. sivalensis* (Chinji Formation)
- ◆ *Sayimys intermedius* (Lower Manchar Formation)
- △ *Sayimys intermedius-sivalensis* (Lower Manchar Formation)

Fig. 4. Variation in the length and width of the m3 of various species of *Sayimys*. The arrow pinpoints *Sayimys minor* DE BRUIJN et al. 1981 from the Murree Formation of Pakistan.

Paratype. – Left d4: GSP 22000; right d4: GSP 48113; left p4: GSP 21998, 48118, and 48121; right p4: GSP 48119 and 48120; left mandible fragment with m1-2 and alveolus for p4: GSP 48136; left m1-2: GSP 21999, 48115, 48116, 48134, and 48135; right m1-2: GSP 48127, 48128, 48131, 48132, 48137, 48139, and 48140; left m3: GSP 33077, 48141, and 48142; right m3: GSP 33078, 48117, 48133, and 48138; fragmentary right maxilla with D4: GSP 48144; left P4: GSP 21997 and 48122; right P4: GSP 48123 to 48126; fragmentary right maxilla with P4-M2: GSP 48143; left M1-2 GSP 48112 and 48146; right M1-2: GSP 48114, 48147 to 48153, 48155, and 48156; left M3: GSP 48157.

Type-locality. – Y747, Potwar Plateau, Pakistan.

Type-horizon. – Kamlial Formation.

Other localities. – Banda Daud Shah.

Age. – Early Miocene (MN 4).

Diagnosis. – Ctenodactylidae with a P4 characterized by being single rooted, but with a groove on the anterior side, having the protocone slightly larger than the paracone, having a short posteroloph that connects lingually with the protoloph and lacking the anteroloph.

Remarks. – For a detailed description of the material from the type locality, as well as that from Y721, see Baskin (1996). As noted above, among the specimens attributed by de Bruijn et al. (1981) to *Sayimys minor*, the d4 and the m3 should also belong to this species.

Sayimys sivalensis (HINTON 1933)

1933 *Pectinator sivalensis* HINTON, p. 622

1937 *Sayimys perplexus* WOOD, p. 73–76, Figs. 6, 14

1977 *Africanomys sivalensis* (WOOD), p. 129–130, Figs. 2J, 3G, 3L

1996 *Sayimys chinjiensis* BASKIN p. 30–35, Fig. 7)

1985 ? *Sayimys badauni* VASISHAT, p. 113–118, Pl. 24–25

Type-specimen. – GSI D284, left mandibular fragment with m2-m3.

Repository institution. – University of Bristol, Bristol (United Kingdom).

Type-locality. – Near Chinji village (Pakistan).

Type-horizon. – Chinji Formation.

Other localities. – Sind and Potwar Plateau (Pakistan); Ramnagar and Haritalyangar (India) (see discussion).

Age. – Middle Miocene (? MN 7).

Emended diagnosis. – d4 lacking metalophulid II and having the anteroconid connected to the protoconid-metaconid complex by an anterolophulid, p4 lacking posterolophid, lower molars having an oblique hypolophid, P4 having the paracone fused to the protocone and vestigial anteroloph and posteroloph, having paraflexus and metaflexus either very few developed or absent on the upper molars.

Sayimys chinjiensis BASKIN 1996

Holotype. – Y434/45186, left mandible fragment with p4-m1.

Repository institution. – Currently housed at the Peabody Museum of Archaeology and Ethnology (Harvard University, Cambridge, USA). It should eventually be returned to Pakistan and would be deposited at the Natural History Museum in Islamabad (L. Flynn, pers. com. 2002).

Type-locality. – Y434, Potwar Plateau (Pakistan).

Type-horizon. – Chinji Formation.

Age. – Middle Miocene (MN 8).

Remarks. – Baskin (1996) argued that *Sayimys chinjiensis* is more derived than *Sayimys sivalensis* because of the greater height of the crown, the extension of the masseteric crest to below the P4, and in having upper molars almost always lack-

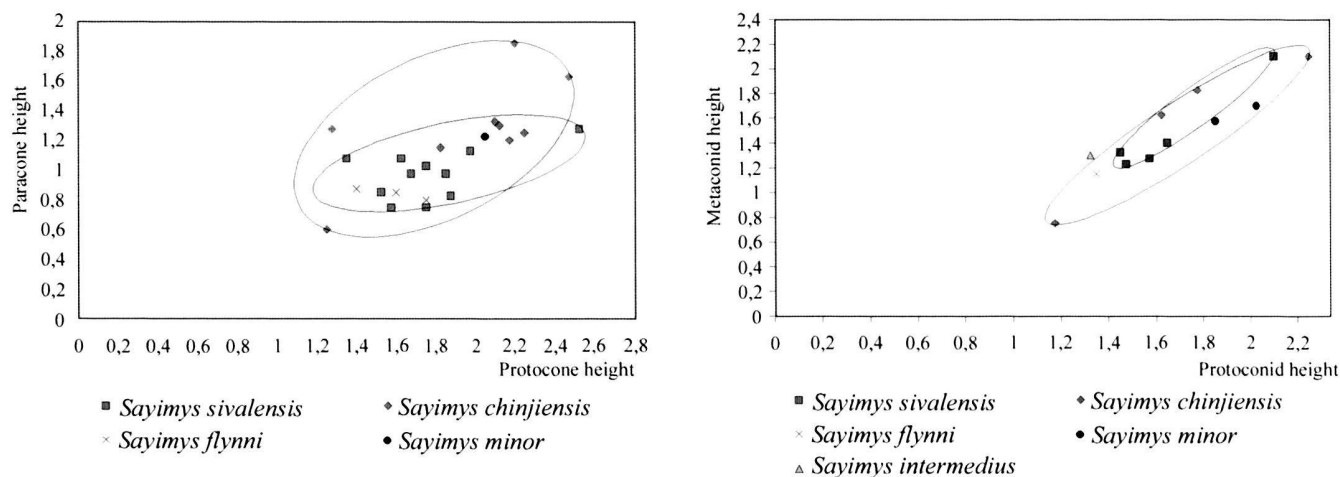


Fig. 5. A- Protocone and paracone heights in various little worn *Sayimys* M1-2. B- Protoconid and metaconid heights in various little worn *Sayimys* m3. Grey areas indicate the overlap of the assumed range of variation in the crown height in *Sayimys sivalensis* and *Sayimys chinjiensis*.

ing a paraflexus. Baskin (pers. com. 2002) kindly provided us with the complete measurements of the Pakistani material he studied. Based on these data, an analysis of the crown height in several *Sayimys* species has been carried out (Figs. 5A and 5B). In the M1-2 (Fig. 5A) and in the m3 (Fig. 5B) the assumed range of variation of the crown height in *Sayimys chinjiensis* widely overlaps that of *Sayimys sivalensis*. Consequently, both taxa can hardly be differentiated in this respect. With regards to the paraflexus, it is generally almost obliterated in *Sayimys sivalensis* and some upper molars of this species (e.g., Y682/21865 (Baskin 1996, Fig. 6D)) even lack it. In addition, according to de Bruijn et al. (1989), a moderate wear produces the fusion of the anteroloph with the protoloph in *Sayimys intermedius*. When the wear increases the metaloph and posteroloph fuse too. Thus, the presence or absence of the paraflexus appears rather a result of the degree of wear and, therefore, it should not be considered as an appropriate character to differentiate between these two species.

Finally, the extension of the masseteric crest is a character the variability of which has not been, and cannot be so far, properly appraised in view of the fact that the *Sayimys* species known from southern and western Asia are mainly based on isolated teeth. For the same reason, if valid, it would however be a quite useless character to distinguish between *Sayimys chinjiensis* and *Sayimys sivalensis*. In conclusion, it clearly appears best to consider *Sayimys chinjiensis* BASKIN 1996 a junior synonym of *Sayimys sivalensis* (HINTON 1933).

Sayimys perplexus (WOOD 1937)

Holotype. – Y.P.M. 13800, left mandible fragment with p4-m3.

Repository institution. – Yale Peabody Museum, New Haven (United States).

Type-locality. – Nagri Zone, East of Haritalyangar (India).

Type-horizon. – Nagri Formation.

Age. – Late Miocene (? MN 10).

Remarks. – The synonymy of *Sayimys perplexus* Wood, 1937 and *Sayimys sivalensis* (HINTON 1933) was suggested by Munthe (1980) and accepted by de Bruijn et al. (1981) and Wang (1997) whereas it has been rejected by de Bruijn et al. (1989) and Baskin (1996). *Sayimys perplexus* is known from a very small sample. On the contrary, *Sayimys sivalensis* is known from numerous specimens revealing a high dimensional and morphological dental variability (Munthe 1980). Black (1972) argued that *Sayimys perplexus* is larger than *Sayimys sivalensis*, that its hypolophid is less transverse, and that the metaconid and entoconid are less closely appressed in the type of *Sayimys perplexus* than in *Sayimys sivalensis*. Actually, the specimens of *Sayimys perplexus* plot within the size range of *Sayimys sivalensis* available to Munthe (1980). In addition, these former specimens show a hypolophid whose the obliquity varies significantly. Finally, in some specimens studied by Munthe, the metaconid and entoconid are widely separated. It thus appears that the characters once considered diagnostic for *Sayimys perplexus* are invalid: a diagnosis of *Sayimys perplexus* appears impossible. Therefore, we agree with Munthe (1980) in considering *Sayimys perplexus* (WOOD 1937) a junior synonym of *Sayimys sivalensis* (HINTON 1933).

Sayimys badauni VASISHAT 1985

Holotype. – PUA 74-70, left mandibular fragment with p4-m2 and i1 (Vasishat 1985: Pl. 24).

Repository institution. – Panjab University, Chandigarh (India).

Type-locality. – Northeast of Badaun village, Bilaspur district (India).

Type-horizon. – Tatrot Formation.

Age. – Pliocene (? MN 15).

Emended diagnosis. – The largest species of *Sayimys*, lower molars having an oblique hypolophid, P4 having the paracone fused to the protocone and vestigial anteroloph and posteroloph, upper molars lacking the paraflexus and the metaflexus.

Remarks. – PUA 74-70, the holotype of this species (Vasishat 1985, Pl. 24) is a left lower jaw with p4-m2 and i1. It comes from the Tatrot Formation (Upper Siwaliks, India). This was the first occurrence of the genus *Sayimys* in Pliocene sediments. The illustrations presented by Vasishat (1985) are not fully satisfactory, but the morphology of *Sayimys badauni* soundly recalls that of *Sayimys sivalensis*. For instance, in the first lower molars of both taxa, the mesoflexid and the metaflexid extend equally far labially whereas in the second molar, the mesoflexid extends farther labially. As in *Sayimys sivalensis*, the dental pattern of the P4 of *Sayimys badauni* seems to be symmetrical, with the paracone fused with the protocone and with an anteroloph and a posteroloph hardly recognizable. With respect to the upper molars, both species display a pattern of wear consisting in two lophs. Therefore, even if *Sayimys badauni* is larger than *Sayimys sivalensis*, the validity of the former taxon name should not be taken for granted.

Discussion and conclusion

We consider that only five ctenodactylid species are recognizable in the Mio-Pliocene of the Indian subcontinent: *Prosayimys flynni*, *Sayimys baskini* nov. sp., *Sayimys intermedius*, *Sayimys sivalensis*, and *Sayimys badauni*. This represents a lesser systematic diversity than previously believed (seven species).

The oldest Miocene ctenodactylid from the Indian subcontinent is *Prosayimys flynni*. As noted above, a recent cladistic analysis has confirmed the opinion of Baskin (1996) according to which *Prosayimys flynni* is more primitive than all the species of *Sayimys* (López-Antoñanzas & Sen, in press a). *Prosayimys flynni* is restricted to the Lower Miocene (MN 3) of the Chitarwata Formation (Zinda Pir Dome, Pakistan).

Sayimys baskini nov. sp. is known in Pakistan (Banda Daud Shah and Potwar Plateau) in the Lower Miocene (MN 3-MN 4) of the Murree and Kamli Formation (de Bruijn 1981; Baskin 1996).

Sayimys intermedius has been recorded in Pakistan from the Murree Formation at Banda Daud Shah (as *Sayimys minor*: de Bruijn et al. 1981), from the Lower Manchar Formation (Sind) at the localities H-GSP 81.06, H-GSP 81.07, and H-GSP 81.14a (de Bruijn et al. 1989), from the Vihowa Formation of the Zinda Pir Dome (as *Sayimys* cf. *Sayimys intermedius*: Baskin 1996), and from the Kamli Formation of the Potwar Plateau (as *Sayimys* cf. *Sayimys intermedius*: Baskin 1996). *Sayimys* cf. *Sayimys intermedius* is mentioned in the Turkish locality of Paşalar (Flynn & Jacobs 1990; Peláez-Campomanes & Daams 2002). In Saudi Arabia, *Sayimys inter-*

medius is known in the Hofuf Formation at Al Jadidah (Sen & Thomas 1979) and at the locality of Tayma (López-Antoñanzas & Sen, in press a). Preliminary results suggesting the presence of *Sayimys* cf. *Sayimys intermedius* in the Dam Formation of Saudi Arabia (Thomas et al. 1982) have proven inaccurate. A detailed study of this ctenodactylid material has revealed that it pertains in fact to a new species, which is older and more primitive than *Sayimys intermedius* (López-Antoñanzas & Sen, in press a). *Sayimys* cf. *Sayimys intermedius* is definitely in the Keramaria Formation at the Thymiana locality of the Greek island of Chios (López-Antoñanzas & Sen, in press b). *Sayimys intermedius* has also been cited in the Hatzeva Formation of the Rotem Basin of Israel (Goldsmith et al. 1982; Tchernov et al. 1987; Savage 1990; Wood and Goldsmith, 1998), but this cannot be attested until a thorough description and determination is available. The presence of *Sayimys intermedius* in the Marada Formation of Lybia has been also suggested (de Bruijn 1999, p. 264). Nevertheless, the same material has been referred to *Africanomys* sp. (Savage 1990; Baskin 1996) and to a new species of *Sayimys* (Wessels et al., in press). In any case, there is no doubt that it is not *Sayimys intermedius*, notably because of the presence of a metalophulid II and the absence of a distinct anteroconid on the d4. The biostratigraphical distribution of *Sayimys intermedius* is probably Lower-Middle Miocene (MN 3-MN6).

Sayimys sivalensis sensu stricto might represent the more plesiomorphic populations of an anagenetic lineage of which the specimens referred to as *Sayimys chinjiensis* by Baskin (1996) would have derived. Interestingly enough, a continuum *Sayimys sivalensis-perplexus* (Black 1972; Flynn et al. 1990), with *Sayimys chinjiensis* as an intermediate form, is suspected (Baskin 1996, p. 42–43). However, such an evolutionary lineage cannot be formalized to serve as a tool of relative dating. In effect, as shown by such an important sample as that of Munthe (1980), *Sayimys sivalensis* is highly variable in characters thought to be of significance for systematic discrimination from *Sayimys chinjiensis* and *Sayimys perplexus*. There is no suite of sites of different ages that have yielded large samples of *Sayimys* that have homogeneous population. Therefore, statistically supported timely evolutionary tendencies from *Sayimys sivalensis* to *Sayimys chinjiensis* to *Sayimys perplexus* have not been demonstrated. In this condition, the above-expressed conclusion considering, at least provisionally, *Sayimys chinjiensis* BASKIN 1996 and *Sayimys perplexus* WOOD 1937 two junior synonyms of *Sayimys sivalensis* (HINTON 1933) is the most rigorous one.

Sayimys sivalensis has been collected in Pakistan from the upper part of the Lower Manchar Formation (Sind) at the localities H-GSP 82.24 and H-GSP 82.27 (de Bruijn et al. 1989), from the upper part of the Kamli Formation (Potwar Plateau) at the localities Y642 and Y682 (Baskin 1996), and from many sites of the lower part of the Chinji Formation in the Potwar Plateau (Hinton 1933; Hussain et al. 1977; Munthe 1980; Dehm et al. 1982; Wessels et al. 1982; Baskin 1996). It is also known from India, from the Chinji Formation at Ramna-

gar (Vasishat 1985) and from the Nagri Formation in the Haritalyangan area (in this latter only as *Sayimys perplexus* (Wood 1937; Prasad 1970; Vasishat 1978, 1985)). The stratigraphical range of this species is Middle-Upper Miocene (MN 5-MN 10).

The validity of the taxon *Sayimys baudauni* (VASISHAT 1985) should not be taken for granted. This species might be the last one of the putative evolutionary lineage originating in *Sayimys sivalensis* (see above). *Sayimys badauni* has been only recorded in the Pliocene (? MN 15) Tatrot Formation of the Badaun village area, Bilaspur district (India).

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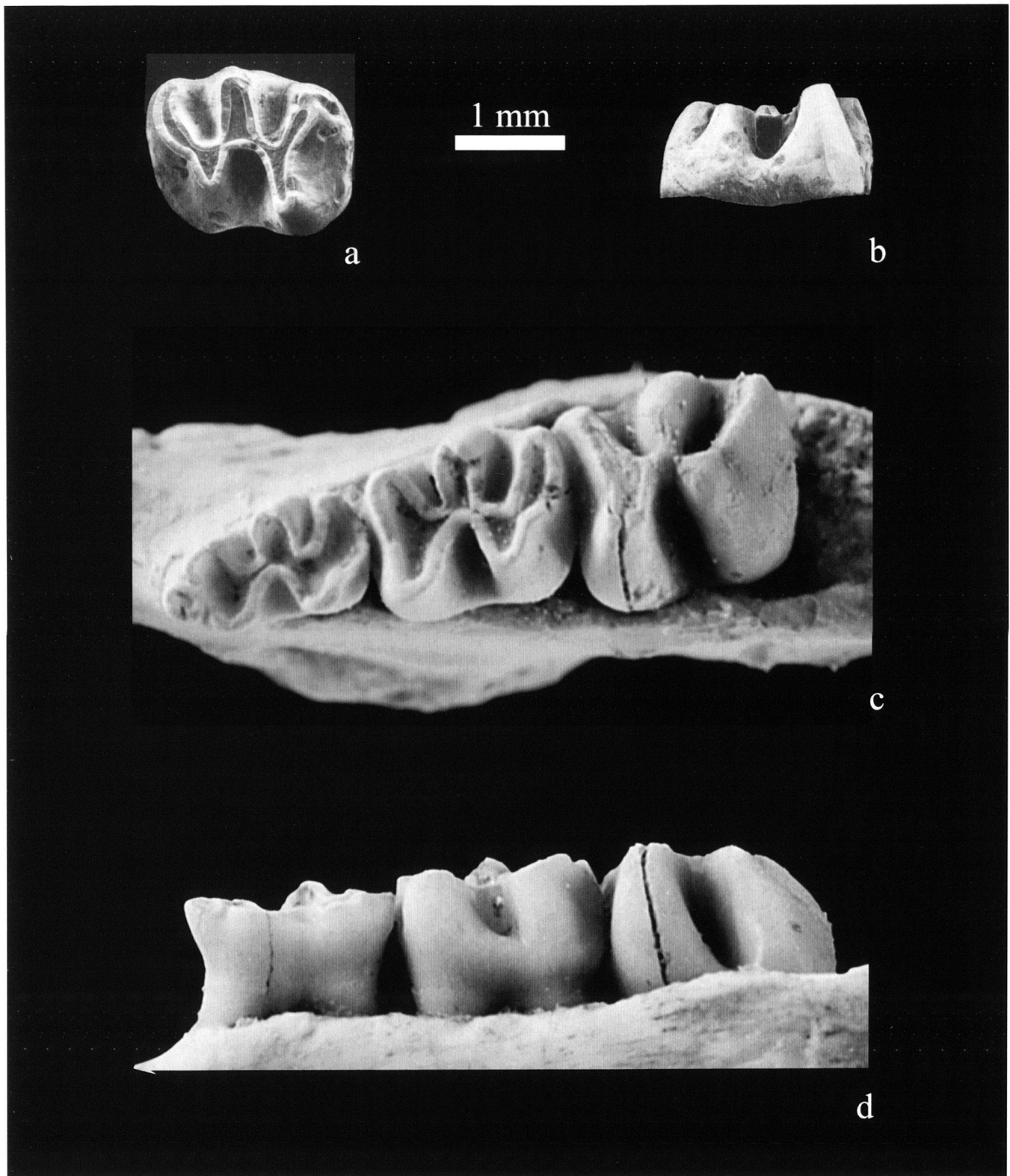


Plate 1. **a.** right m1-2 (occlusal view) of the holotype of "*Sayimys minor*" DE BRUIJN et al. 1981 (after de Bruijn et al. 1981). **b.** right m1-2 (lateral view) of the holotype of "*Sayimys minor*" DE BRUIJN et al. 1981 (after de Bruijn et al. 1981). **c.** left mandible with dp4-m2 (AJ 545, occlusal view) of the holotype of *Sayimys intermedius* SEN & THOMAS 1979 **d.** left mandible with dp4-m2 (AJ 545, lateral view) of the holotype of *Sayimys intermedius* SEN & THOMAS 1979.

