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A NEW LARGE CTENODACTYLID SPECIES FROM THE  
LOWER MIOCENE OF TURKEY

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RH: LÓPEZ-ANTOÑANZAS ET AL.-NEW LARGE CTENODACTYLID FROM TURKEY

## ABSTRACT

A new species of *Sayimys* (Ctenodactylidae, Mammalia), *Sayimys giganteus* sp. nov., is described from the Early Miocene localities of Keseköy 1, Keseköy 2, and Hisarcik (Turkey). *Sayimys giganteus* sp. nov. differs from other known species of *Sayimys* by its larger size and several plesiomorphies (e.g., metalophulid II on dp4, strong anterolophid and posterolophid on P4, and a long paraflexus and metaflexus on upper molars), but also in the presence of some derived characters. Two species of *Sayimys* are currently recognized in Turkey: *Sayimys* cf. *Sayimys intermedius* (at Pa??alar, Middle Miocene) and *Sayimys giganteus* sp. nov. Based on a cladistic analysis involving all known species of *Sayimys*, *Metasayimys*, and *Prosayimys*, *Sayimys giganteus* sp. nov. emerges as the sister-taxon of *Sayimys obliquidens*.

## INTRODUCTION

During the last two decades, great effort was directed towards collecting and studying small mammal remains from the Tertiary deposits of Turkey. Our knowledge is improving, although several Cenozoic time intervals have not yet been surveyed, and many groups are poorly documented. The occurrence of ctenodactylid rodents in Turkey has been known for almost thirty years since Sickenberg et al. (1975) mentioned the presence of this family at Paşalar, a Middle Miocene locality in northwestern Turkey. Later, the presence of ctenodactylid remains at several other Early to Middle Miocene Turkish localities (Fig. 1) was reported (Flynn and Jacobs, 1990; Sümengen et al., 1990; Bruijn, 1999; Ünay et al., 2001; Peláez-Campomanes, 2002), but still no detailed study is available.

In this paper we describe new ctenodactylid material as a new species and assess the phylogenetic relationships of this taxon. It was collected from the Hisarcik (Hañçili Formation) and Keseköy 1 and Keseköy 2 (Güvem Formation) sites. The former is situated about 3 km southeast of the village of Hisarcik and 50 km south southwest of the town of Çankiri. Its age is possibly latest Early Miocene (MN4). This locality yielded a rich micromammal fauna, which will be described elsewhere. In addition to Ctenodactylidae, preliminary results indicate the presence of *Eumyarion* sp., *Cricetodon* sp., *Democricetodon* sp., *Megacricetodon* sp., *Debruijnia* sp., *Palaeosciurus* sp., *Spermophilinus* sp., *Microdryomys* sp., *Albertona* sp., and Insectivora indet. The other Anatolian locality, Keseköy, is situated about 150 km north northwest of Ankara. It has produced an abundant and diverse fauna, including rodents and insectivores (Theocharopoulos, 2000:86-87). Both Keseköy 1 and Keseköy 2 are considered to be Early Miocene (MN3) in age.

The occurrence of ctenodactylids in Turkish Miocene deposits improves our knowledge of their spatial distribution at this time. It contributes especially to a better understanding of the paleobiogeographic relationships between southern and western Asia and the Arabian Peninsula and northern Africa.

**Acronyms**— **AJ**, Al Jadidah (Saudi Arabia); **GSI**, Geological Survey of India (Calcutta); **GSP**, Geological Survey of Pakistan (Quetta); **H-GSP**, Howard University (Washington DC) -Geological Survey of Pakistan,; **HJ**, Hisarcik, (Turkey); **KSK**, Keseköy (Turkey); **RU**, Rijkuniversiteit Utrecht (Utrecht); **T.b.**, Taben-buluk, (China); **UU**, Uppsala universitet (Uppsala); **ZP**, Zinda Pir Dome (Pakistan).

## SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821

Family CTENODACTYLIDAE Zittel, 1893

Genus *SAYIMYS* Wood, 1937

*SAYIMYS GIGANTEUS* sp. nov.

**Etymology**-Indicative of its great size in comparison with the other species of the genus *Sayimys*.

**Holotype**-KSK1-100 (Fig. 5C, D), a fragmentary left maxilla with P4-M1 housed in Mineral Resources and Exploration, General Directorate, Natural History Museum, Ankara, Turkey.

**Paratype**-KSK1-101 (Fig. 6E, F) and KSK1-102 (Fig. 6I, J), left M2 or M3.

**Type Locality**-Keseköy 1 (Kizilcahamam, Ankara).

**Age**-Early Miocene (MN3).

**Other Localities**-Keseköy 2 (Kizilcahamam, Ankara) and Hisarcik (Çankiri).

**Referred Material from Keseköy 2**-KSK2-104 (Fig. 4B, C), left dp4; KSK2-103 (Fig. 4F), left m3; KSK2-102 (Fig. 4I, J), right DP4; KSK2-101 (Fig. 5A, B), left maxilla fragment with P4-M1; KSK2-100 (Fig. 6G, H) left maxilla fragment with M2-M3.

**Referred Material from Hisarcik**-HJ-107 (Fig. 4A), right dp4; HJ-108 (Fig. 4D, E) right m3; HJ-105 (Fig. 4G), right DP4; HJ-106 (Fig. 4H), left DP4; HJ-100 (Fig. 5E, F), left M1; HJ-101 (Fig. 5G), HJ-102 (Fig. 5H, I), both right M1s; HJ-103 (Fig. 6A, B), HJ-104 (Fig. 6 C, D) right M2 or M3.

**Diagnosis**-*Sayimys* species of large size (Table 1, Figs. 2, 3) with the m3 lacking a constriction in the posterolophid; dp4 with a metalophulid II connecting with the metaconid or nearly reaching it; DP4 with obliterated metaflexus, but with a well developed paraflexus; P4 with a long posteroloph connecting to the paracone and with the anteroloph joining the protocone; upper molars with a paraflexus longer than the metaflexus.

**Differential Diagnosis**-*Sayimys giganteus* differs from *Prosayimys flynni* and *Sayimys obliquidens* primarily in the absence of metalophulid II on the lower molars, in having the metaflexus obliterated in the DP4, and in having the anteroloph shorter and more lingually situated in P4. *Sayimys giganteus* differs from *Sayimys baskini* chiefly in having the metaflexus obliterated in the DP4, an anteroloph in the P4, and the paraflexus well developed in the upper molars. *Sayimys giganteus* principally differs from *Sayimys intermedius*, in possessing a metalophulid II in the dp4 and in having an anteroloph shorter than the posteroloph in the P4. *Sayimys giganteus* is distinct from *Sayimys sivalensis* primarily in having a metalophulid II and an anteroconid isolated in the dp4, the paracone and protocone unfused on P4, a long posteroloph and an anteroloph connected to the protocone on this tooth, and the paraflexus and the metaflexus well developed in the upper molars. *Sayimys giganteus*

is distinct from *Sayimys obliquidens* mainly by the absence of metalophulid II on the lower molars. *Sayimys giganteus* differs from *Sayimys badauni* in having a P4 in which the paracone and the protocone are unfused and the long posteroloph and the anteroloph are connected to the protocone. In addition, the paraflexus and the metaflexus are well developed in the upper molars. *Sayimys giganteus* differs from all described species of *Sayimys*, except *Sayimys badauni* (of comparable size), by its larger size (Figs. 2, 3).

## DESCRIPTION

### **dp4 (HJ-107 and KSK2-104)**

The occlusal outline of the dp4 is elongate and narrow (Fig. 4A, B). The anteroconid is large and isolated. Both specimens have a metalophulid II. In HJ-107 it extends to the metaconid, and through occlusal wear helps form an enamel lake. The other specimen (KSK2-104) is much less worn, and its metalophulid II reaches nearly the base of the metaconid. The mesoflexid is shorter than the metaflexid. The hypolophid is slightly oblique and is situated opposite the hypoflexid. The hypoflexid extends transversely more than the mesoflexid and it is deeper. The postero-labial cingulum is weak on HJ-107 but is strong on KSK2-104.

### **m3 (KSK2-103 and HJ-108)**

Unfortunately, only two badly preserved lower molars are available (KSK2-103 is digested and HJ-108 is broken). The occlusal surface is trapezoidal in outline. The mesoflexid is only visible in the specimen KSK2-103: it is shorter and deeper than the metaflexid. The mesoflexid is less deep than the hypoflexid. The hypolophid is roughly transverse and does not oppose exactly the hypoflexid. The protoconid extends more labially than the hypoconid. A constriction separates the anterior arm of the hypoconid and the posterior arm of the

protoconid. The posterolophid does not constrict before reaching the triangular wear surface of the hypoconid. The cingulum on the postero-labial side is visible only on HJ-108, where it is well developed.

**DP4(KSK2-102, HJ-105, and HJ-106)**

All specimens are heavily worn. The robust anteroloph is confluent with the anterior arm of the protocone. The roughly transverse protoloph connects the paracone and the protocone. Due to the wear, the metaloph is fused with the posteroloph and therefore the metaflexus is obliterated. Only KSK2-102 shows a vestigial metaflexus, which is more affected by the increase of wear than the paraflexus. The mesoflexus appears deeper than the paraflexus and both re-entrants are deeper than the hypoflexus. The hypoflexus is relatively short and narrow.

**P4 (KSK1-100 and KSK2-101)**

The protocone is elongated antero-posteriorly. The posteroloph is longer than the anteroloph. The posteroloph connects labially with the protoloph whereas the anteroloph joins the protocone lingually. KSK2-101 is broken postero-labially, so it is only possible to see the trace left by the posteroloph. The posterior re-entrant fold is deeper than the anterior re-entrant. They almost join, separating the protocone from the paracone.

**M1 (KSK1-100, KSK2-101, HJ-100, HJ-101, and HJ-102)**

The occlusal outline is sub-quadrate. The protocone and hypocone are connected by a straight to slightly oblique endoloph. In all specimens, the paraflexus is longer than the metaflexus, but both are well developed. HJ-100 is unusual in having the paracone isolated from the protoloph. The protoloph connects to the medial or posterior margin of the protocone. The internal area of the hypoflexus is deeper than that of the mesoflexus. The mesoflexus is deeper than the paraflexus, which is deeper than the metaflexus.

**M2 or M3 (HJ-103, HJ-104, KSK1-101, KSK1-102, and KSK2-100)**

KSK2-100 shows that there is no morphological differences between M2 and M3. There are some differences between the M2 or M3 and the smaller M1. Most significantly, the outline of the occlusal surface of the M2 and M3 is more rounded. In addition, the sub-equal protocone and hypocone are connected by a straight endoloph, the protoloph connects to the medial or posterior margin of the protocone, and the mesoflexus is deeper than the paraflexus, which is deeper than the metaflexus. the paraflexus is longer than the metaflexus, but the latter difference is not as marked as in the M1..

## COMPARISONS

### **Comparison with *Prosayimys flynni* Baskin, 1996**

The holotype of this species (Z113/295) comes from the Early Miocene (ca. 20 Ma) Dalana section of the Chitarwata Formation (Zinda Pir Dome, Pakistan). Data provided by Baskin (1996, pers. comm., January, 2002), show that all the Keseköy and Hisarcik teeth are larger than the largest equivalent teeth of *Prosayimys flynni*.

Comparison of the dp4s from Keseköy and Hisarcik with the two equivalent specimens (ZP312, ZP316; Baskin, 1996) of *Prosayimys flynni* is difficult because both specimens of *Prosayimys flynni* are badly worn and broken. However, a metalophulid II is present in *Prosayimys flynni* (Baskin, 1996), as in the Turkish specimens.

In the m3s of *Sayimys giganteus* (KSK2-103 and HJ-108) the mesoflexid is shorter and deeper than the metaflexid. In contrast, the m3s of *Prosayimys flynni* show a mesoflexid and a metaflexid nearly equal in length as well as in depth (Baskin, 1996). Furthermore, the m3s of *Prosayimys flynni* are easily distinguished from those of *Sayimys giganteus* by the presence of a strong metalophulid II. The m3s of *Prosayimys flynni* show a transverse hypolophid as in KSK2-103 and HJ-108. The posterolophid on HJ-108 is not constricted

before reaching the triangular wear surface of the hypoconid whereas on the only m3 figured by Baskin (1996:fig. 3M) the posterolophid is constricted.

The dental pattern of the DP4s from Keseköy and Hisarcik (KSK2-102, HJ-105, and HJ-106) has only a few differences with those of *Prosayimys flynni* (Baskin, 1996). In *Prosayimys flynni* the hypoflexus is shorter and deeper, the metaflexus in the DP4s of *Sayimys giganteus* shortens more quickly with occlusal wear than in *Prosayimys flynni*. However, in both *Prosayimys flynni* and *Sayimys giganteus*, the paraflexus persists to an advanced wear stage.

All the P4s of *Prosayimys flynni* are broken (Baskin, 1996), and only the paracone, not the protocone, is preserved in the P4 (Z113/275) figured by Baskin (1996:fig. 3B). In the P4s from Keseköy, the posteroloph is longer than the anteroloph. Z113/275 appears to have the anteroloph longer than the posteroloph.

The M1-3 of *Prosayimys flynni* and *Sayimys giganteus* seem to be morphologically similar, except for the size, the latter being larger.

### **Comparison with *Sayimys baskini* López-Antoñanzas et Sen, 2003**

The validity of the species *Sayimys minor* from the Murree Formation (Early Miocene) of Pakistan was discussed recently (López-Antoñanzas and Sen, 2003). The holotype of *Sayimys minor* (one m1 or m2) cannot be distinguished from an m1 or m2 of *Sayimys intermedius*. Consequently, the nominal taxon *Sayimys minor* should be considered a junior synonym of *Sayimys intermedius*. Other specimens from the Kamliyal Formation (early Middle Miocene) of Pakistan, tentatively referred to as *Sayimys* cf. *Sayimys minor* (Baskin, 1996), represent a new species, *Sayimys baskini*, to which two (dp4 and m3) of the four paratypic specimens of *Sayimys minor* are reallocated (López-Antoñanzas and Sen, 2003).

The dp4s of *Sayimys baskini* (Bruijn et al., 1981; Baskin, 1996) are much smaller than the dp4s from Keseköy and Hisarcik. The dp4s from Keseköy 1 and Hisarcik have a large and

isolated anteroconid, like GSP 48113 from the Kamlial Formation (Baskin, 1996:fig. 4F, incorrectly mentioned as left in the caption). In both specimens of *Sayimys giganteus*, the metalophulid II is long and connects, or nearly connects, to the metaconid, whereas in GSP 48113, the metalophulid II is short and does not connect with the metaconid. However, in the dp4 (H-GSP 116) from the Murree Formation, a well-developed metalophulid II, comparable to that in HJ-107, is observed (Bruijn et al., 1981). Thus, the length of the metalophulid II seems to be a variable character, at least for *Sayimys baskini*.

The m3s of *Sayimys giganteus* (KSK2-103 and HJ-108) have a transverse hypolophid, whereas that of the only m3 found by Bruijn et al. (1981:pl.3, fig.1) is oblique. The specimens from locality Y747 (Baskin,1996) also have the hypolophid oblique. In those from locality Y721, the hypolophid is nearly transverse. Like the specimens of *Sayimys baskini*, the m3s from Turkey have the mesoflexid shorter than the metaflexid. The specimen HJ-108 is much larger than all the m3s described by Baskin (1996) and the single m3 considered by Bruijn et al. (1981).

There are a few differences between the dental pattern of the DP4s of *Sayimys baskini* (Baskin, 1996:13) and *Sayimys giganteus*. Although no figure of the three specimens (GSP 45374, GSP 33113, and GSP 48144) from the Kamlial Formation has been published, drawings kindly provided by Baskin (pers. comm., January, 2002) show that in these specimens, the paraflexus and the metaflexus are well developed. In the three specimens the paraflexus is longer than the metaflexus. The more worn specimens (GSP 45374 and GSP 48144) show that the paraflexus shortens more quickly with occlusal wear than the metaflexus. In the DP4s of *Sayimys giganteus*, the metaflexus shortens more quickly with occlusal wear than the paraflexus. Thus, in the three Turkish specimens the metaflexus is obliterated while the paraflexus has not suffered any obvious shortening. In *Sayimys baskini*, the hypocone is slightly internal to the protocone whereas in HJ-105 and KSK2-102, it is

slightly external to it. Furthermore, in *Sayimys baskini*, the hypoflexus is short, wide, and shallow, whereas in all the specimens from Keseköy and Hisarcik it is also short and shallow, but narrow. With respect to size, the Turkish DP4s are much bigger than those of *Sayimys baskini*.

The P4s of *Sayimys giganteus* (KSK1-100 and KSK2-101) have a posterolingual protocone and the anteroloph is well developed, but shorter than the posteroloph. In all (except GSP 48126) specimens of *Sayimys baskini* from the Kamlial Formation (locality Y747) (Baskin, 1996), the anteroloph is missing. GSP 48126 is an unerupted specimen, in which the anteroloph would have likely disappeared with light wear (Baskin, 1996). In GSP 48125 (Baskin, 1996:fig. 4A), the posteroloph is much shorter than in the two specimens from Turkey. The P4s from Keseköy are significantly larger than those of *Sayimys baskini* available to Baskin (1996, pers. comm., January, 2002).

The single isolated M1 or M2 from the Murree Formation (Bruijn et al., 1981) does not pertain to *Sayimys baskini* (López-Antoñanzas and Sen, 2003). However, it is not clear whether it is a very worn tooth of *Sayimys intermedius* or a specimen of *Sayimys sivalensis* until more material from the same formation is available. Thus, we compared the M1s from Hisarcik and Keseköy (KSK1-100, KSK2-101, HJ-100, HJ-101, and HJ-102) with the M1-2 from the Kamlial Formation described by Baskin (1996).

Based on one maxilla (Baskin, 1996:pl. 1: fig. F), Baskin (1996:13) argued that the M1 of *Sayimys baskini* is considerably smaller than the M2. This also seems to be true for *Sayimys giganteus*.

Of the 19 M1s or M2s from the Kamlial Formation (localities Y721 and Y747) described by Baskin (1996), only one (GSP 36353) has a paraflexus, which is longer and deeper than the mesoflexus. Baskin (1996) argued that the absence of the paraflexus is, at least in some specimens, real and not the result of occlusal wear. Baskin (1996) also observed

that the metaflexus is lost with moderate wear. In contrast, the M1-M3s of *Sayimys giganteus* have the paraflexus and the metaflexus well developed (the former being longer than the latter). The mesoflexus of *Sayimys giganteus* is as deep and long as in *Sayimys baskini*. In addition to these morphological differences, the specimens from the Turkish localities are characterized by a larger size of all cheek teeth than those of *Sayimys baskini* (Figs. 2, 3).

### **Comparison with *Sayimys intermedius* Sen and Thomas, 1979**

The holotype of this species (AJ 545) is a fragmentary left mandible with p4-m2 from the Middle Miocene Hofuf Formation, Al Jadidah, Saudi Arabia. This species was also recorded at Tayma, north-western Saudi Arabia (López-Antoñanzas and Sen, in press).

*Sayimys intermedius* is also present in Pakistan in the Murree Formation of Banda Daud Shah (as *Sayimys minor*: Bruijn et al., 1981), in the Lower Manchar Formation at localities H-GSP 81.06, H-GSP 81.07, and H-GSP 81.14a (Bruijn et al., 1989), in the Vihowa Formation of the Zinda Pir Dome, and in the Kamlial Formation of the Potwar Plateau (as *Sayimys* cf. *Sayimys intermedius*: Baskin, 1996). *Sayimys* cf. *Sayimys intermedius* was also reported from Paşalar, Turkey (Flynn and Jacobs, 1990; Peláez-Campomanes and Daams, 2002). *Sayimys intermedius* might be present 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 of the available material is published. The presence of *Sayimys intermedius* in the Marada Formation of Libya was also suggested (Bruijn, 1999:264). Nevertheless, the same material was referred to as *Africanomys* sp. (Savage, 1990; Baskin, 1996) and a new species of *Sayimys* (Wessels et al., 2003). 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 dp4. Finally, *Sayimys intermedius* was discovered in the Keramaria Formation of the Greek island of Chios (López-Antoñanzas et al., in press).

The dp4s from Keseköy and Hisarcik (HJ-107 and KSK2-104) are similar to those of *Sayimys intermedius* from the Al Jadidah and Pakistani localities in having an elongated outline. However, the dp4 of *Sayimys giganteus* differs from these in having a strong metalophulid II. HJ-107 and KSK2-104 have an isolated anteroconid, like the dp4s of *Sayimys* cf. *Sayimys intermedius* from the Kamlial Formation (locality Y802: GSP 21862) and from the Vihowa Formation (locality Z120: GSP 36157) figured by Baskin (1996:fig. 5G, H). A few specimens of *Sayimys intermedius* have the anteroconid joined to the protoconid-metacoid complex, without an anterolophulid (as from Al Jadidah, Sen and Thomas, 1979) or through an anterolophulid (some specimens from the Lower Manchar Formation, Bruijn et al., 1989). Unlike the condition in *Sayimys intermedius* and in *Sayimys* cf. *Sayimys intermedius* (Bruijn et al., 1989; Baskin, 1996), in the dp4s of *Sayimys giganteus* the mesoflexid is shorter than the metaflexid, and it is also deeper, or as deep as the metaflexid. In *Sayimys giganteus*, the hypoflexid is larger and deeper than the mesoflexid whereas they have nearly the same size in *Sayimys intermedius* (Sen and Thomas, 1979; Bruijn et al., 1989) and *Sayimys* cf. *Sayimys intermedius* (Baskin, 1996). In GSP 21862, the hypoflexid is even smaller than the mesoflexid (Baskin, 1996:fig. 5G). In HJ-107 and KSK2-104, mesoflexid and metaflexid are not anteriorly directed. This condition is identical in AJ 545 (Sen and Thomas, 1979:fig. 1). On the contrary, in *Sayimys* cf. *Sayimys intermedius* (Baskin, 1996:fig. 5H) and in *Sayimys intermedius* (Bruijn et al., 1989:pl. 1, fig. 9; pl. 2, figs. 10-11), the mesoflexid is more anteriorly directed than the metaflexid. The postero-labial cingulum varies from weak (HJ-107) to well developed (KSK2-104) in *Sayimys giganteus*, whereas in *Sayimys intermedius* and *Sayimys* cf. *Sayimys intermedius* (Bruijn et al., 1989; Baskin, 1996) it is weak or absent. HJ-107 is larger than any specimen of *Sayimys intermedius* and *Sayimys* cf.

*Sayimys intermedius* (Sen and Thomas, 1979; Bruijn et al., 1989; Baskin, 1996, pers. comm., January, 2002).

In comparison with *Sayimys intermedius* and *Sayimys* cf. *Sayimys intermedius* from Pakistan, on the m3 of *Sayimys giganteus* (KSK2-103 and HJ-108) the mesoflexid is shorter and deeper than the metaflexid. In the specimens described as *Sayimys intermedius* and *Sayimys* cf. *Sayimys intermedius*, the hypolophid varies from roughly transverse (Bruijn et al., 1989:pl. 2, fig. 12; Baskin, 1996:fig. 5J) to oblique (Bruijn et al., 1989:pl. 1, figs.10-11; Baskin, 1996:fig. 5K) whereas in KSK2-103 and HJ-108, it is transverse. As in *Sayimys intermedius* and *Sayimys* cf. *Sayimys intermedius*, in HJ-108, the protoconid is somewhat longer than the hypoconid and the posterolophid does not constrict before reaching the triangular wear surface of the hypoconid. Only one specimen of *Sayimys intermedius* figured by Bruijn et al. (1989:pl. 1, fig. 10) shows this constriction.

There are few differences between the dental pattern of the DP4s from Keseköy and Hisarcik and that of *Sayimys intermedius* (Bruijn et al., 1989:pl. 1, figs 4-5; pl. 2, figs 3, 7) and *Sayimys* cf. *Sayimys intermedius* from Y592 of the Kamlial Formation and from Z120 and Z122 of the Vihowa Formation (Baskin, 1996). The main difference is that in *Sayimys giganteus* the metaflexus is more quickly shortened and eventually obliterated with occlusal wear compared to the paraflexus. An obliterated metaflexus was not observed in *Sayimys intermedius* or *Sayimys* cf. *Sayimys intermedius*. With respect to size, the Turkish specimens are bigger than all specimens of *Sayimys intermedius* and *Sayimys* cf. *Sayimys intermedius*.

In the P4s from Keseköy (KSK1-100 and KSK2-101), the protocone extends posterolingually whereas in those of *Sayimys intermedius* (Bruijn et al., 1989:pl. 2, figs. 5-6) and *Sayimys* cf. *Sayimys intermedius* (Z120/45119; Baskin, 1996:fig. 5A), it is situated more or less transversely. KSK1-100 and KSK2-101 have the anteroloph shorter than the posteroloph. In contrast, in *Sayimys intermedius* the anteroloph and posteroloph have nearly the same

length (Bruijn et al., 1989:pl. 2, fig. 5; Baskin, 1996:fig. 5A), the anteroloph is longer than the posteroloph (Bruijn et al., 1989:pl. 2, fig. 6), or the posteroloph is absent (Baskin, 1996:20). As in *Sayimys intermedius* (Bruijn et al., 1989), in *Sayimys giganteus* the posteroloph joins the protoloph and the anteroloph connects to the protocone. In Z120/45119 of *Sayimys* cf. *Sayimys intermedius* (Baskin, 1996:fig. 5A) the anteroloph and posteroloph join the anterior and posterior arms of the protocone, respectively. In this specimen as in KSK1-100 and KSK2-101, the protoloph is almost transverse, whereas in the P4 of *Sayimys intermedius* (Bruijn et al., 1989), it is directed rather obliquely. The P4s of *Sayimys giganteus* have the first labial flexus (anterior) shallower and smaller than the second one (posterior), like those of *Sayimys intermedius* (Bruijn et al., 1989:pl. 2, figs. 5-6). In comparison, Z120/45119 (Baskin, 1996:fig. 5A) has the anterior flexus slightly longer than the posterior flexus.

In the M1s from Keseköy and Hisarcik, as well as in the M1s or M2s of *Sayimys intermedius* (Bruijn et al., 1989), the protocone and slightly smaller hypocone are connected by a straight endoloph. *Sayimys intermedius* has a paraflexus more quickly affected by occlusal wear than the metaflexus and, therefore, that shortens more rapidly (Bruijn et al., 1989:199). With heavy wear, the paraflexus may disappear, but a short metaflexus is still preserved. The metaflexus also persists longer than the paraflexus in *Sayimys* cf. *Sayimys intermedius* (Baskin, 1996:20). All upper molars from Turkey show the metaflexus and paraflexus well developed, therefore it cannot be known whether or not their pattern of wear coincides with the above mentioned one. The M1s of *Sayimys giganteus*, like those of *Sayimys intermedius* (Bruijn et al., 1989), have the paraflexus longer than the metaflexus. The M1s or M2s of *Sayimys* cf. *Sayimys intermedius* (Baskin, 1996) usually have a short paraflexus and metaflexus, except for GSP 45354, which has the paraflexus longer. The anterior side of the teeth is wider than the posterior side, like in *Sayimys intermedius* (Bruijn et al., 1989) and *Sayimys* cf. *Sayimys intermedius* (Baskin, 1996). The M1s or M2s of *Sayimys*

cf. *Sayimys intermedius* (Baskin, 1996) show a mesoflexus nearly as deep as that of the hypoflexus, whereas in the upper molars from Keseköy and Hisarcik, the mesoflexus is shallower than the hypoflexus.

As mentioned above, the M2s or M3s from Keseköy and Hisarcik (HJ-103, HJ-104, KSK1-101, KSK1-102, and KSK2-100) have a more rounded morphology and a larger size than the M1s. These differences are also observed in the M3s of *Sayimys intermedius* (Bruijn et al., 1989) and *Sayimys cf. Sayimys intermedius* (Baskin, 1996). Bruijn et al. (1989) noted that the lengths of the paraflexus and metaflexus show more variation in unworn M3s than in unworn M1s or M2s. Unfortunately, there are no unworn M2s or M3s of *Sayimys giganteus* to test this observation. The M2s and M3s of *Sayimys giganteus* with moderate to heavy occlusal wear also show more variation in the length of the paraflexus and metaflexus than do the M1s. Length of the paraflexus varies from nearly equal that of the metaflexus (see HJ-104, Fig. 6C) to clearly longer than the metaflexus (see KSK1-102, Fig. 6I). Based on the extensive data provided by Bruijn et al. (1989) for *Sayimys intermedius* and, above all, by Baskin (1996, pers. comm., January, 2002) for *Sayimys cf. Sayimys intermedius*, the size of the M3s from Turkey is much greater.

### **Comparison with Sayimys sivalensis (Hinton, 1933)**

The holotype of this species (GSI D284) is a left dentary fragment with m2 and m3 from the Middle Miocene Chinji Formation, Pakistan (Hinton, 1933). López-Antoñanzas and Sen (2003) agreed with Munthe (1980) in considering *Sayimys perplexus* Wood, 1937, a junior synonym of *Sayimys sivalensis*. *Sayimys chinjiensis* Baskin, 1996 is also considered a junior synonym of *Sayimys sivalensis* (López-Antoñanzas and Sen, 2003).

Hence, *Sayimys sivalensis* (including *Sayimys perplexus* and *Sayimys chinjiensis*) is known in Pakistan from the Lower Manchar (Bruijn et al., 1989), Kamliyal (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 the Chinji Formation at Ramnagar (Vasishat, 1985) and from the Nagri Formation in the Haritalyangar area (as *Sayimys perplexus*, Wood 1937; Prasad, 1970; Vasishat, 1978, 1985).

There are two important differences between the dp4s from Keseköy and Hisarcik (HJ-107 and KSK2-104) and almost all dp4s of *Sayimys sivalensis*. The first is the presence in *Sayimys giganteus* of a metalophulid II. The specimen RU 3034 (Bruijn et al., 1989:pl. 4, fig. 7) excepted, *Sayimys sivalensis* appears derived by the loss of the metalophulid II. The second difference is the presence in the Turkish material of an isolated anteroconid. In the dp4s of *Sayimys sivalensis*, the anteroconid is connected to the protoconid-metaconid complex by an anterolophulid situated on the longitudinal axis (Munthe, 1980:fig. 8; Wessels et al., 1982; Bruijn et al., 1989; Baskin, 1996). Another derived feature of *Sayimys sivalensis* is the anteriorly directed mesoflexid; this structure is transverse in the Turkish specimens. The dp4s from Keseköy and Hisarcik have the hypolophid slightly oblique and situated opposite the hypoflexid. In most specimens of *Sayimys sivalensis* the hypolophid is directed obliquely forward and it is continuous with the posterior arm of the protoconid (Munthe, 1980; Wessels et al., 1982; Bruijn et al., 1989; Baskin, 1996).

The poor preservation of the known m3s of *Sayimys giganteus* makes it difficult to evaluate the maximal extension of the metaflexus and mesoflexus. However, in KSK2-103, the mesoflexid is shorter than the metaflexid, as in the m3 of *Sayimys sivalensis* (Black, 1972; Munthe, 1980; Bruijn et al., 1989; Baskin, 1996). The m3 of *Sayimys sivalensis* figured by Wessels et al. (1982:pl.4, fig. 1) has mesoflexid and metaflexid that extend equally far labially. The hypolophid, in KSK2-103 and HJ-108, is less oblique than that usually observed in the m3s of *Sayimys sivalensis*. KSK2-103 and HJ-108, like the m3s of *Sayimys sivalensis*, have the anterior arm of the hypoconid constricted at its connection with the posterior arm of the protoconid.

The dental pattern of the DP4 from Keseköy and Hisarcik displays a few differences from that of *Sayimys sivalensis* (Munthe, 1980; Wessels et al., 1982; Bruijn et al., 1989; Baskin, 1996). The main difference is the presence of an obliterated metaflexus in all Turkish specimens, which suggests that the metaflexus shortened more quickly with wear than the paraflexus. No DP4 of *Sayimys sivalensis* presents this pattern of wear.

The asymmetrical dental pattern of the P4s from Keseköy (KSK1-100 and KSK2-101) is very different from the symmetrical pattern of the P4s of *Sayimys sivalensis*. The Turkish specimens show a well developed posteroloph and an anteroloph of variable length. In *Sayimys sivalensis* both structures are only vaguely recognizable. The protocone of KSK1-100 and KSK2-101 is not fused to the paracone, whereas in *Sayimys sivalensis* the large protocone is fused to the smaller paracone. In addition, the P4s of *Sayimys sivalensis* lack the lingual re-entrant fold observed in *Sayimys giganteus*.

The M1s from Keseköy and Hisarcik have the paraflexus longer than the metaflexus. In contrast, in the M1s of *Sayimys sivalensis* the paraflexus is usually shorter than the metaflexus; it is absent in some specimens (Bruijn et al., 1989:pl. 3, fig. 3; Munthe, 1980:fig. 6E). Moderately worn teeth of *Sayimys sivalensis* show a pattern of three lophs because the anteroloph and the protoloph are fused at an early stage of wear. Even at a moderate wear stage, the M1s of *Sayimys giganteus* have four lophs.

The wear pattern with deep flexi in the M2s and M3s from Keseköy and Hisarcik is also different from that of *Sayimys sivalensis*, in which the paraflexus and metaflexus are short or absent. In *Sayimys giganteus* both folds are well developed.

#### **Comparison with Sayimys obliquidens Bohlin, 1946**

T.b. 268b, the holotype of this species (Bohlin, 1946:figs. 30b, 30b', 30b'') is a left lower jaw with p4-m3 (the lingual halves of p4 and m1 are missing). It is from Taben-buluk (Gansu, China), a locality that is probably Early Miocene (Wang et al., 2003). Recently

similar material was recorded (as *Sayimys* aff. *obliquidens*) from the middle members of the Chul'adyr Formation (Early Miocene) of the Aktau Mountains (Kazakhstan) on the basis of an isolated dp4, m1, m2, DP4, M2, and M3 (Kordikova and Bruijn, 2001), and from the Akzhar Formation of Batpaksunde (Kazakhstan), on the basis of one left dp4 that Lopatin and Zazhigin (2000) considered to be a left m1 of a new zapodid taxon: *Asiazapus ingens*.

The dp4s from Hisarcik and Keseköy (HJ-107 and KSK2-104) and the dp4 of *Sayimys obliquidens* are primitive in possessing a metalophulid II. In the dp4 of *Sayimys obliquidens* and in the Turkish specimens, it can extend to the metaconid to help form an enamel lake. In HJ-107 and KSK2-104, the anteroconid is larger than in the dp4 of *Sayimys obliquidens*, but it is isolated in both taxa. In both species the mesoflexid is shorter than the metaflexid, and the labial re-entrant folds are transverse. However, in the dp4 from Kazakhstan, the metaflexid appears to be narrower than that of the dp4s from Turkey, especially KSK2-104. As in *Sayimys obliquidens*, neither of the dp4s from Turkey show a constriction of the posterolophid before it reaches the triangular wear surface of the hypoconid. The dp4 of *Sayimys obliquidens* has a well-developed posterolabial cingulum.

The only known m3 of *Sayimys obliquidens* (Bohlin, 1946:fig. 30b") is heavily worn. It lacks metalophulid II, but this is probably a result of wear because it is present on the other molars. Unlike the m3s of *Sayimys giganteus*, in the m3 of *Sayimys obliquidens* the lingual end of the posterolophid bends toward the lingual end of the entoconid. In both *Sayimys obliquidens* and *Sayimys giganteus*, the mesoflexid is shorter than the metaflexid. On the m3s from Keseköy and Hisarcik the hypolophid is roughly transverse, whereas it is oblique in *Sayimys obliquidens*. As in the m3 of *Sayimys obliquidens*, HJ-108 does not show a constriction of the posterolophid close to the hypoconid.

The main difference between the DP4s of *Sayimys obliquidens* and *Sayimys giganteus*, is that in *Sayimys giganteus* the metaflexus is obliterated, whereas in the only DP4 referred to

*Sayimys* cf. *Sayimys obliquidens* it is well developed (Kordikova and Bruijn, 2001). Another difference is that the Turkish specimens are significantly larger.

The P4s from Keseköy (KSK1-100 and KSK2-101) are different from that of *Sayimys obliquidens*. The Keseköy specimens have a long posteroloph, which connects labially to the protoloph, and an anteroloph of variable length that joins the protocone lingually. In the P4 of *Sayimys obliquidens*, the posteroloph and anteroloph are short and both join the protoloph. In *Sayimys giganteus*, the anterior re-entrant is larger than in the P4 of *Sayimys obliquidens*, in which it is nearly nonexistent (Bohlin, 1946:fig. 30d).

Comparison between the M1s from Turkey (KSK1-100, KSK2-101, HJ-100, HJ-101, and HJ-102) and that of *Sayimys obliquidens* is based on a single upper tooth row attributed to this species by Bohlin (1946:fig. 30a"). Interestingly enough, all the *Sayimys* specimens from Taben-buluk described by Bohlin (1946) may belong to *Sayimys obliquidens* as proposed implicitly by Stehlin and Schaub (1951:fig. 182) and Schaub (1958:fig. 212) and explicitly by Wang (1997:63). On the M1s of *Sayimys giganteus*, the paraflexus is longer than the metaflexus and both re-entrants are well developed. In the M1 of specimen UU 279a of *Sayimys obliquidens* (Bohlin, 1946:fig. 30a"), the metaflexus is nearly obliterated because of occlusal wear, and the paraflexus is very short. The M1 described by Bohlin (1946) has the mesoflexus much shorter and narrower than in the specimens from Turkey. In both taxa, the M2 is larger than the M1. The hypoflexus of *Sayimys giganteus* is wider than that of *Sayimys obliquidens*.

The M2s and M3s from Hisarcik and Keseköy (HJ-103, HJ-104, KSK1-101, KSK1-102, and KSK2-100) have the paraflexus longer than the metaflexus. In the M2 of *Sayimys* cf. *Sayimys obliquidens* (Kordikova and Bruijn, 2001) both re-entrants are equal in length and extend farther lingually than in the specimens from Turkey. The metaflexus seems to be wider than in the Turkish specimens. The M2 of *Sayimys obliquidens* (Bohlin, 1946:fig. 30a") has

heavy occlusal wear and the paraflexus and the metaflexus are nearly obliterated. In that specimen, the mesoflexus is much narrower and shorter than in the Turkish specimens, the protocone extends farther lingually and the hypoflexus is narrower and more anteriorly directed. The M3 of *Sayimys* cf. *Sayimys obliquidens* (Kordikova and Bruijn, 2001) has the mesoflexus much narrower and extending farther lingually than in the Turkish taxon. In the M3 of *Sayimys obliquidens* (Bohlin, 1946:fig. 30a"), the mesoflexus is much narrower and more anteriorly directed.

### **Comparison with *Sayimys badauni* Vasishat, 1985**

PUA 74-70, the holotype of this species is a left lower jaw with i1 and p4-m2 (Vasishat, 1985:pl. 24). It comes from the Pliocene of the Tatrot Formation (Upper Siwaliks, India). The illustrations presented by Vasishat (1985) are not fully satisfactory, but the morphology of *Sayimys badauni* 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. Like in *Sayimys sivalensis*, the dental pattern of the P4 of *Sayimys badauni* is 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 wear pattern consisting of two lophs. Therefore, even if *Sayimys badauni* is larger than *Sayimys sivalensis*, the validity of the former taxon name should not be assumed.

Only a single m3 of *Sayimys badauni* (PUA-74-74) is known (Vasishat, 1985:114-116). It is not figured or described.

The P4s from Keseköy (KSK1-100 and KSK2-101) are very different from the P4 of *Sayimys badauni* (Vasishat, 1985:pl. 25). According to Vasishat (1985), the details of the crown of the P4 of this specimen (PUA 74-73) are not discernable due to the high degree of wear. However, Vasishat's illustration (1985:pl. 25) shows a more-or-less symmetrical pattern

for the occlusal surface. This pattern is different from the asymmetrical one of the Turkish taxon. The protocone is not fused to the paracone in KSK1-100 and KSK2-101; the well developed posteroloph joins the protoloph, and the well developed anteroloph joins the protocone.

The upper molars from Keseköy and Hisarcik show a wear pattern different from that of *Sayimys badauni*. All Turkish specimens have the paraflexus and the metaflexus well developed, whereas *Sayimys badauni* shows a pattern of two lophs, with the anterior loph larger than the posterior loph.

## SYSTEMATICS AND PHYLOGENY

Wood (1977) presented a comprehensive study of the evolution of the ctenodactylids from Eocene forms to extant species. He considered *Sayimys sivalensis* to be closer to *Metasayimys* than to *Sayimys obliquidens* and placed *Sayimys sivalensis* in the genus *Africanomys*. However, Munthe (1980) proposed a phylogenetic sequence proceeding from *Sayimys obliquidens* through *Sayimys sivalensis* to *Metasayimys*. In contrast, Bruijn et al. (1989) and Baskin (1996) advocated that *Metasayimys* is derived from *Sayimys minor* (*S. baskini*). Baskin (1996) also considered *Prosayimys* to be derived from a form similar to *Yindertemys* or *Tataromys*, and, moreover, he judged it almost certainly ancestral to *Sayimys*. Wang (1997:fig. 38) provided a cladogram of the relationships of the Ctenodactylinae (including *Sayimys*) with other ctenodactylids, but did not investigate species relationships within the genus *Sayimys*, or between this genus and other closely related genera such as *Prosayimys* and *Metasayimys*. Recently, Kumar and Kad (2002:739) suggested that *Sayimys minor* (*S. baskini*) is a plesiomorphic taxon of the lineage leading to *Sayimys sivalensis*.

To help elucidate relationships between known species of *Sayimys*, *Prosayimys*, and *Metasayimys* we conducted a cladistic analysis. The taxa included are *Prosayimys flynni*, *Sayimys obliquidens*, *Sayimys* sp. nov. from As-Sarrar (Saudi Arabia; often erroneously cited as ‘Al-Sarrar’), *Sayimys intermedius*, *Sayimys sivalensis*, *Sayimys baskini*, *Sayimys giganteus*, and *Metasayimys curvidens* (*Sayimys badauni* is not included because of uncertainty about its validity). The monophyly of the ingroup is not questioned and *Tataromys* is selected as the outgroup. The data matrix (19 characters, see Appendices I and II) was processed with PAUP version 3.1.1 (Swofford, 1993), using the exhaustive search option. Five equally most-parsimonious trees were generated (tree length 35, consistency index 0.514, homoplasy index 0.486, rescaled consistency index 0.249). The majority consensus solution from these trees is shown in Figure 7.

As suggested by Baskin (1996), *Prosayimys flynni* appears basal to the remaining species of the ingroup. *Sayimys intermedius* and *Sayimys sivalensis* are most derived. *Sayimys giganteus* emerges as the sister-species of *Sayimys obliquidens*. *Metasayimys curvidens* is placed between *Sayimys* sp. nov. from As-Sarrar and *Sayimys baskini*. The transfer of *Metasayimys curvidens* to the genus *Sayimys* as the new combination *Sayimys curvidens* (Lavocat, 1961) would seem reasonable. However, a formal reallocation must be delayed until a comprehensive cladogram of the Ctenodactylinae (including notably the species of *Sardomys*, *Pireddamys*, *Akzharomys*, *Africanomys*, and of the four extant genera), in which the present ingroup is monophyletic, is available. In contrast, if the most recent common ancestor of *Prosayimys flynni* and *Sayimys sivalensis* is also ancestral to any of the above mentioned ctenodactylina species, then the genus *Metasayimys* will have to be conserved and other species of the present ingroup will have to be reallocated to another genus. This would thus be the case of *Sayimys obliquidens*, an option already suggested by Munthe (1980:25-27).

According to Baskin (1996), the main diagnostic character of the genus *Prosayimys* is the presence of a metalophulid II in the lower molars and the lower deciduous premolars. However, the presence of the metalophulid II in the dp4s is a plesiomorphic character of the ingroup considered in the present analysis. Its absence is a synapomorphy of the most derived clade: (*Sayimys intermedius* + *Sayimys sivalensis*). Likewise, the metalophulid II is present in lower molars of *Sayimys obliquidens* (but we cannot establish that this is a symplesiomorphy rather than a reversion). Consequently, this character is unsuitable for generic distinction. In other respects the teeth of *Prosayimys flynni* are very similar to those of other species of *Sayimys*. The suggestion by Kordikova and Bruijn (2001:398) that *Prosayimys* is a junior synonym of *Sayimys* thus remains as a worthy consideration. Nevertheless, the results of the present partial analysis of ctenodactyline relationships does not require synonymy because *Prosayimys flynni* nests basal to all other species of the ingroup.

## DISCUSSION AND CONCLUSION

In a short article on European Miocene Ctenodactyloidea Bruijn (1999:264) briefly mentioned a number of Early to Middle Miocene localities situated across Anatolia that have yielded *Sayimys* remains. These are Horlak, Çatalarkaç, Paşalar, and Kesökoy. He wrote that all the *Sayimys* cheek teeth from Turkey are similar in size and morphology and that they have about the same stage of evolution as *Sayimys minor* (*S. baskini*) from the Murree Formation of Pakistan. Unfortunately, he did not provide any description and limited himself to figure (without scale), as *Sayimys* sp., an upper and a lower tooth row (exclusive of the dp4 and DP4) from Kesökoy (Bruijn, 1999:figs. 25.2A, 25.3A). These teeth seem to resemble those from Kesökoy and Hisarcik described in the present paper. Based on Bruijn's (1999:fig. 25.2A) drawing, it appears that the p4 from Kesökoy differs from *Prosayimys flynni* in having

a posterolophid, from *Sayimys baskini* in having a posterolophid and in the absence of a prominent stylid (which is observed in the posteroexternal cingulum in most of the specimens of the Kamliyal Formation), from *Sayimys sivalensis* in having a posterolophid, and from *Sayimys obliquidens* in the absence of an accessory lophulid on the posterior side of the metaconid and in having a posterolophid. Further, there is no doubt that the mesoflexid is shorter than the metaflexid in the m3 from Keseköy (Bruijn, 1999:fig. 25.2A). Despite intensive sampling, no other *Sayimys* species are recorded in Keseköy besides *Sayimys giganteus*, so it appears more reasonable that the material figured by Bruijn (1999:figs. 25.2A, 25.3A) belongs to this latter species. Interestingly enough, completing accordingly our matrix with p4 data does not change the length, indices, and topology of our tree.

With respect to the *Sayimys* material from Paşalar, Flynn and Jacobs (1990:fig. 1C) figured one m1 or m2 from this locality that they identified as *Sayimys* cf. *Sayimys intermedius*. This determination was accepted by Peláez-Campomanes and Daams (2002) and we believe it to be correct as well. The comment by Bruijn (1999:264) about the similarity of the *Sayimys* material from Paşalar and Keseköy, therefore, appears troubling. In addition, regarding Hórlak, Sümengen et al. (1990:71) mentioned a few *Sayimys* specimens morphologically like *Sayimys minor* (*S. baskini*), but “somewhat larger than the type material.” Unfortunately, as for the *Sayimys* material mentioned by Bruijn (1999:264) from the coeval site of Çatalarkaç, no description nor illustration of specimens from Hórlak has been made available to date. To complete the Turkish *Sayimys* record, the Yapinti locality, in the lower Miocene Derinçay Formation (Mut Basin, southern Anatolia), must be mentioned. It yielded dental material that, unfortunately, cannot be determined at the species level (Ünay et al., 2001).

In conclusion, only a few Miocene localities have yielded ctenodactylid remains in Turkey so far. Two taxa are recognized: *Sayimys* cf. *Sayimys intermedius* at Paşalar, Middle

Miocene (Flynn and Jacobs, 1990; Peláez-Campomanes and Daams, 2002), and *Sayimys giganteus* sp. nov. at Hisarcik and Kesökoy, Lower Miocene. *Sayimys giganteus* appears to be endemic to Turkey, but *Sayimys intermedius* (or *Sayimys* cf. *Sayimys intermedius*) is also known from outside of this country. This species was originally recognized in the Middle Miocene part of the Hofuf Formation of Saudi Arabia at Al Jadidah (Sen and Thomas, 1979). It also occurs at Tayma, north-western Saudi Arabia (López-Antoñanzas and Sen, in press), but preliminary results suggesting the presence of *Sayimys* cf. *Sayimys intermedius* in the Dam Formation (Early Miocene) of Saudi Arabia (Thomas et al., 1982) are inaccurate (López-Antoñanzas and Sen, in press). *Sayimys intermedius* was recorded subsequently in the Lower Manchar (Early Miocene), Vihowa (Middle Miocene), and Kamlial (Middle Miocene) formations of Pakistan (Bruijn et al., 1989; Baskin, 1996). Finally, this species is recorded in the Keramaria Formation (Middle Miocene) of Chios Island, Greece (López-Antoñanzas et al., in press). *Sayimys intermedius* documents an Early-Middle Miocene dispersal from Pakistan westwards into Saudi Arabia, Turkey, and Chios (the latter at that time not yet isolated from the Asiatic continent).

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TABLE 1. Occlusal measurements (mm) of the teeth of *Sayimys giganteus* sp. nov. from Turkey. All measurements were obtained with Mitutoyo measuring equipment, and represent greatest length and greatest width.

	Specimen	Length	Width
P4	KSK1-100	1.19	1.97
M1	KSK1-100	2.13	2.04
M2 or M3	KSK1-101	2.73	3.10
M2 or M3	KSK1-102	2.84	3.13
dp4	KSK2-104	2.83	1.61
m3	KSK2-103	–	2.90
DP4	KSK2-102	2.14	2.12
P4	KSK2-101	1.43	1.85
M1	KSK2-101	2.18	2.41
M2	KSK2-100	2.61	2.89
M3	KSK2-100	2.77	2.86
dp4	HJ-107	2.60	1.53
m3	HJ-108	3.63	2.67
DP4	HJ-105	~1.92	2.06
DP4	HJ-106	~1.91	1.94
M1	HJ-100	2.10	2.16
M1	HJ-101	2.29	2.29
M1	HJ-102	2.34	2.31
M2 or M3	HJ-103	2.94	2.95
M2 or M3	HJ-104	2.74	2.69

## APPENDIX I

Characters used in phylogenetic analysis. All characters are binary (0, 1), polarity of character determined by outgroup comparison with Tataromys spp.

### **dp4**

1. Metalophulid II: (0) present, (1) absent.
2. Mesoflexid: (0) shorter, (1) equal or longer than the metaflexid.
3. Mesoflexid: (0) not anteriorly directed, (1) anteriorly directed.
4. Posterolabial cingulum: (0) absent or weak, (1) strong.
5. Hypolophid: (0) oblique, (1) transverse.

### **p4**

6. Posteroloph: (0) absent or weak, (1) well developed.
7. Shape in occlusal view: (0) U-shaped pattern, (1) Y-shaped pattern.
8. Postero-labial ledge: (0) weak or absent, (1) strong.

### **m1-m3**

9. Metalophulid II: (0) present, (1) absent.
- 10 Mesoflexid: (0) not anteriorly directed, (1) anteriorly directed.
11. Mesoflexid: (0) shorter, (1) equal or longer than the metaflexid.
12. Postero-labial ledge: (0) absent or weak, (1) moderate to strong.
13. Hypolophid: (0) oblique, (1) transverse or slightly oblique.

### **DP4**

14. Metaflexus: (0) as long as the paraflexus, (1) shorter than the paraflexus.

**P4**

15. Anteroloph: (0) absent or weak, (1) well developed.

16. Posteroloph: (0) longer than anteroloph, (1) shorter than anteroloph.

**M1-M2**

17. Paraflexus: (0) present, (1) absent.

18. Metaflexus: (0) large, (1) small or absent.

**APPENDIX 2**

Matrix of character codings used in the analysis of relationships of Sayimys species, Prosayimys flynni, and Metasayimys curvidens. Characters are listed in Appendix I. Tataromys spp is used as outgroup. Character codings: 0, postulated plesiomorphic condition of character; 1, postulated derived conditions of character; -, uncodable character; ?, character state uncertain.

Taxa	Characters																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<u>Tataromys</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>P. flynni</u>	0	0	0	0	0	0	0	?	0	0	0	1	1	0	1	1	0	0
<u>'S. baskini'</u>	0	1	0	0	1	0	1	1	1	0	0	0	1	1	0	-	1	0
<u>S. intermedius</u>	1	1	1	0	1	1	1	1	1	1	1	0	1	1	1	1	0	0
<u>S. sp. nov (As-Sarrar)</u>	0	0	0	0	1	1	1	1	1	0	0	0	1	0	1	0	0	1
<u>S. sivalensis</u>	1	1	1	1	0	0	1	0	1	1	1	1	0	1	0	-	1	1
<u>S. obliquidens</u>	0	0	0	1	1	0	1	1	0	0	0	1	0	0	1	0	0	1
<u>S. giganteus</u>	0	0	0	1	1	?	?	?	1	0	0	1	1	1	1	0	0	0
<u>M. curvidens</u>	0	1	0	0	1	0	1	?	1	0	0	0	1	0	0	-	1	1

FIGURE 1. Paleogeographic map of Turkey and surrounding areas at the Burdigalian-Langhian boundary (modified from Rögl, 1998:pl. 5) and localities yielding Early-Middle Miocene Sayimys and Prosayimys. Saudi Arabia: **1**, As-Sarrar; **2**, Al Jadidah; **3**, Tayma. Turkey: **4**, Paşalar; **5**, Hórlak; **6**, Keseköy; **7**, Hijarcik; **8**, Mut; **9**, Çatalarkaç; **10**, Bozalan. Greece: **11**, Thimiana (Chios). India and Pakistan: **12**, Sind; **13**, Siwaliks; **14**, Dera Ghazi Khan area. Kazakhstan: **15**, Aktau Mountains; **16**, Batpaksunde. Black areas represent evaporite basins, grey areas are exposed land surfaces, and white areas represent seas.

FIGURE 2. Scatter diagram showing the variation in length and width of the M1 and M2 of all species of Sayimys. All measurements in mm.

FIGURE 3. Scatter diagram showing the variation in length and width of the m3 of all species of Sayimys. All measurements in mm.

FIGURE 4. Sayimys giganteus sp. nov. **A**, right dp4 (HJ-107, occlusal view). **B**, left dp4 (KSK2-104, occlusal view). **C**, left dp4 (KSK2-104, lingual view). **D**, right m3 (HJ-108, occlusal view) **E**, right m3 (HJ-108, lingual view). **F**, left m3 (KSK2-103, occlusal view). **G**, right DP4 (HJ-105, occlusal view). **H**, left DP4 (HJ-106, lingual view). **I**, right DP4 (KSK2-102, occlusal view). **J**, right DP4 (KSK2-102, lingual view). Scale bar equals 1 mm.

FIGURE 5. Sayimys giganteus sp. nov. **A**, fragmentary left maxilla with P4-M1 (KSK2-101, occlusal view). **B**, fragmentary left maxilla with P4-M1 (KSK2-101, labial view). **C**, fragmentary left maxilla with P4-M1 (KSK1-100, holotype, occlusal view). **D**, fragmentary left maxilla with P4-M1 (KSK1-100, holotype, labial view). **E**, left M1 (HJ-100, occlusal

view). **F**, left M1 (HJ-100, labial view). **G**, right M1 (HJ-101, occlusal view). **H**, right M1 (HJ-102, occlusal view). **I**, right M1 (HJ-102, labial view). Scale bar equals 1 mm.

FIGURE 6. Sayimys giganteus sp. nov. **A**, right M2 or M3 (HJ-103, occlusal view). **B**, right M2 or M3 (HJ-103, labial view). **C**, right M2 or M3 (HJ-104, occlusal view). **D**, right M2 or M3 (HJ-104, labial view) **E**, left M2 or M3 (KSK1-101, paratype, occlusal view). **F**, left M2 or M3 (KSK1-101, paratype, labial view). **G**, fragmentary left maxilla with M2 and M3 (KSK2-100, occlusal view). **H**, fragmentary left maxilla with M2 and M3 (KSK2-100, labial view). **I**, left M2 or M3 (KSK1-102, paratype, occlusal view). **J**, left M2 or M3 (KSK1-102, paratype, labial view). Scale bar equals 1 mm.

FIGURE 7. Cladogram illustrating the relationships among Prosayimys, Sayimys, and Metasayimys species and the phylogenetic position of Sayimys giganteus sp. nov.

Tree length 35, consistency index 0.514, homoplasy index 0.486, rescaled consistency index 0.249.

Figure 1

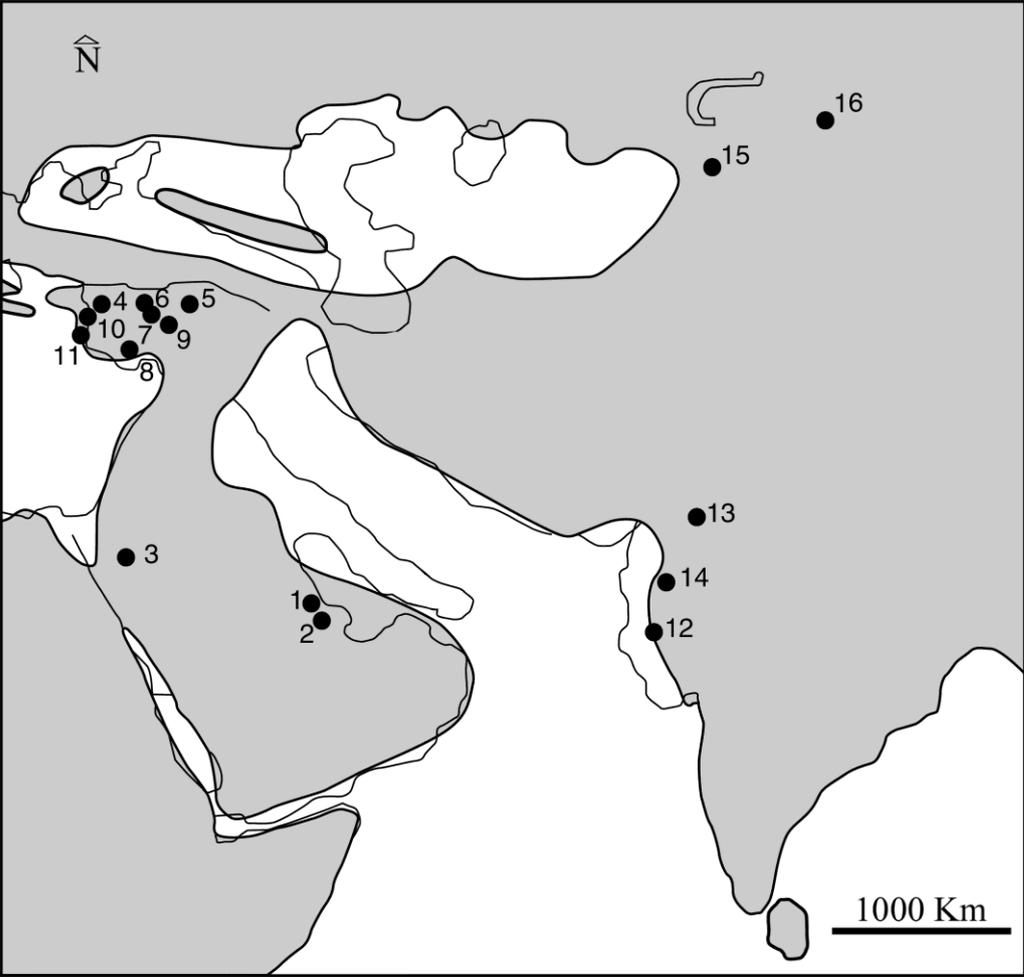


Figure 2

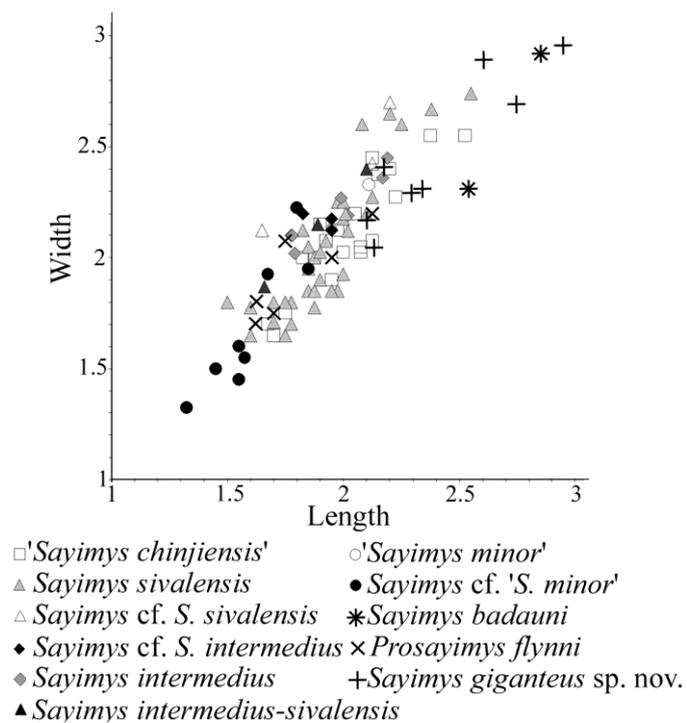


Figure 3

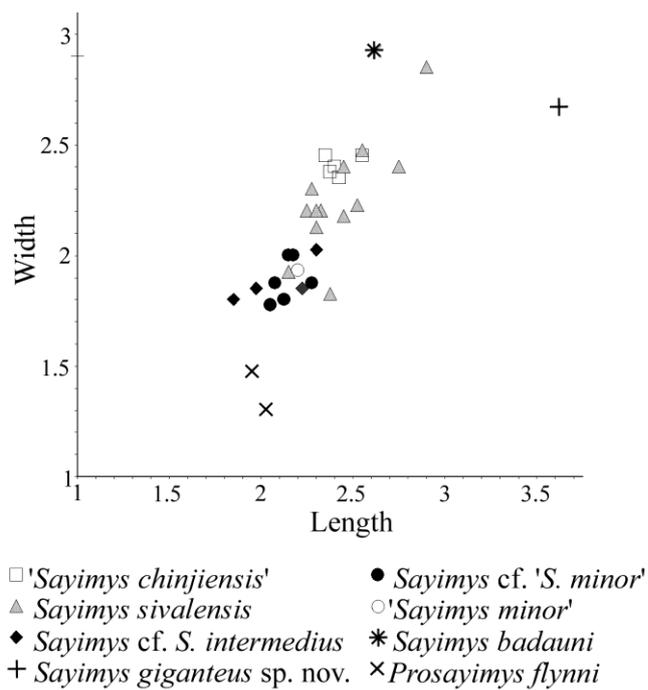


Figure 4

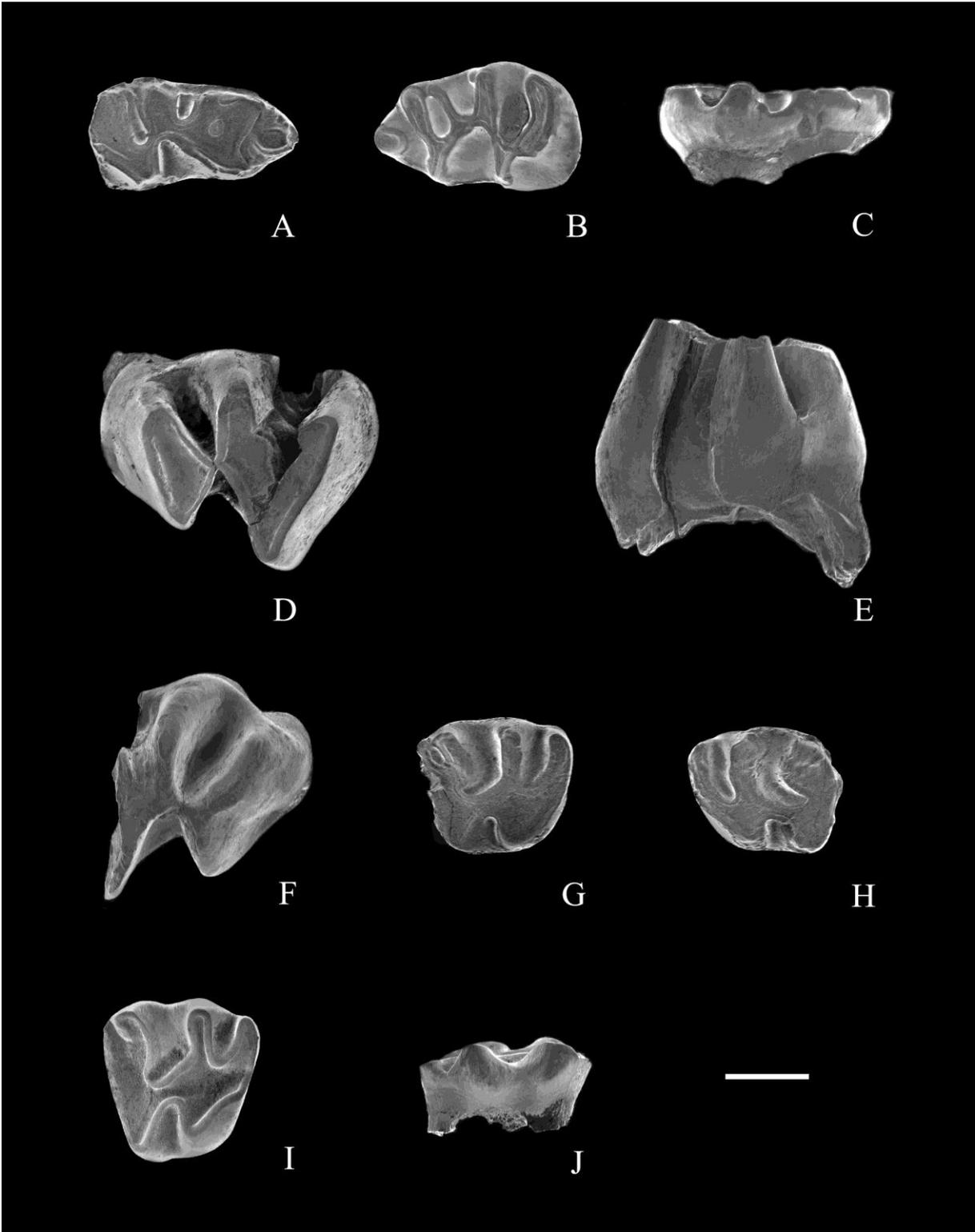


Figure 5

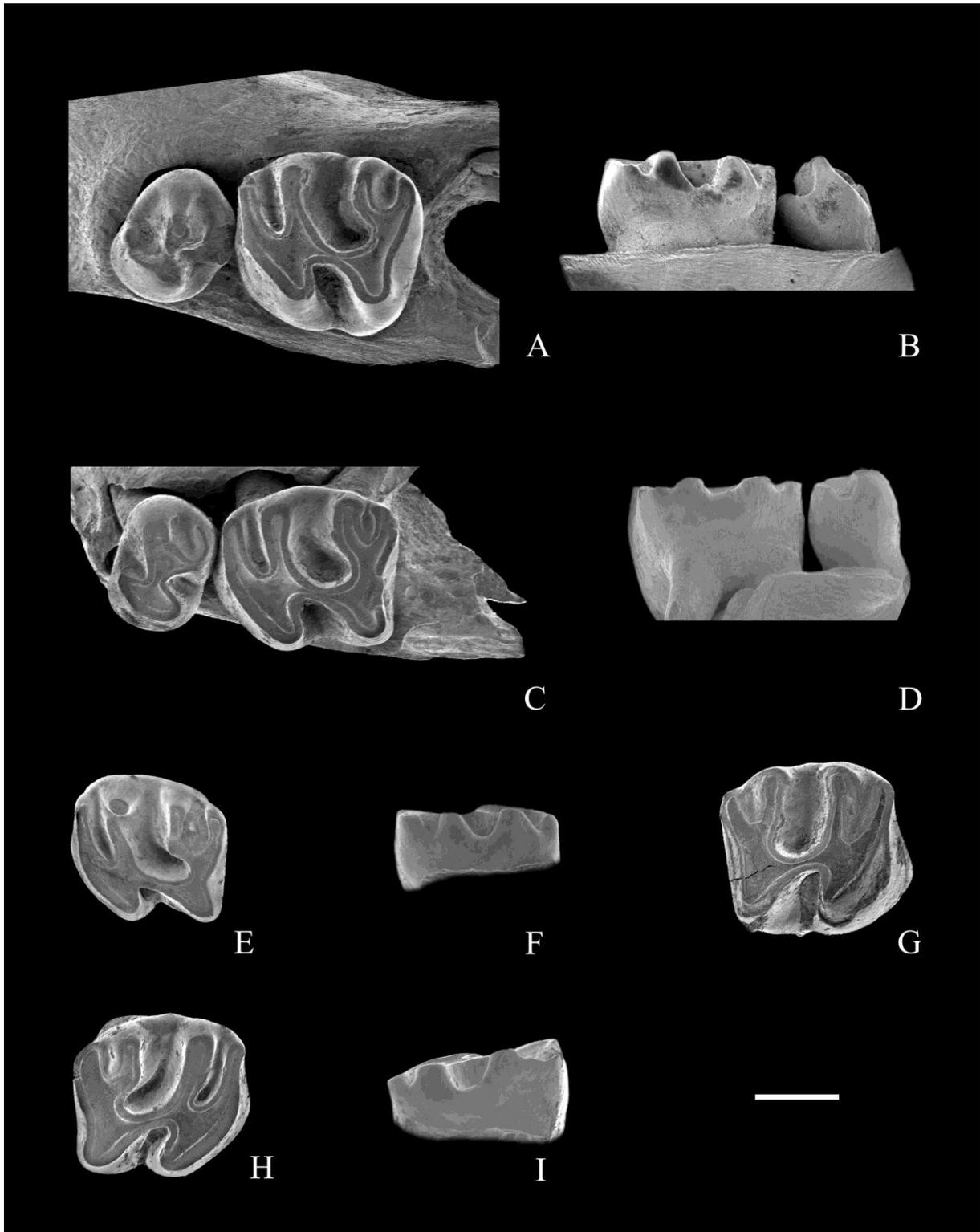


Figure 6

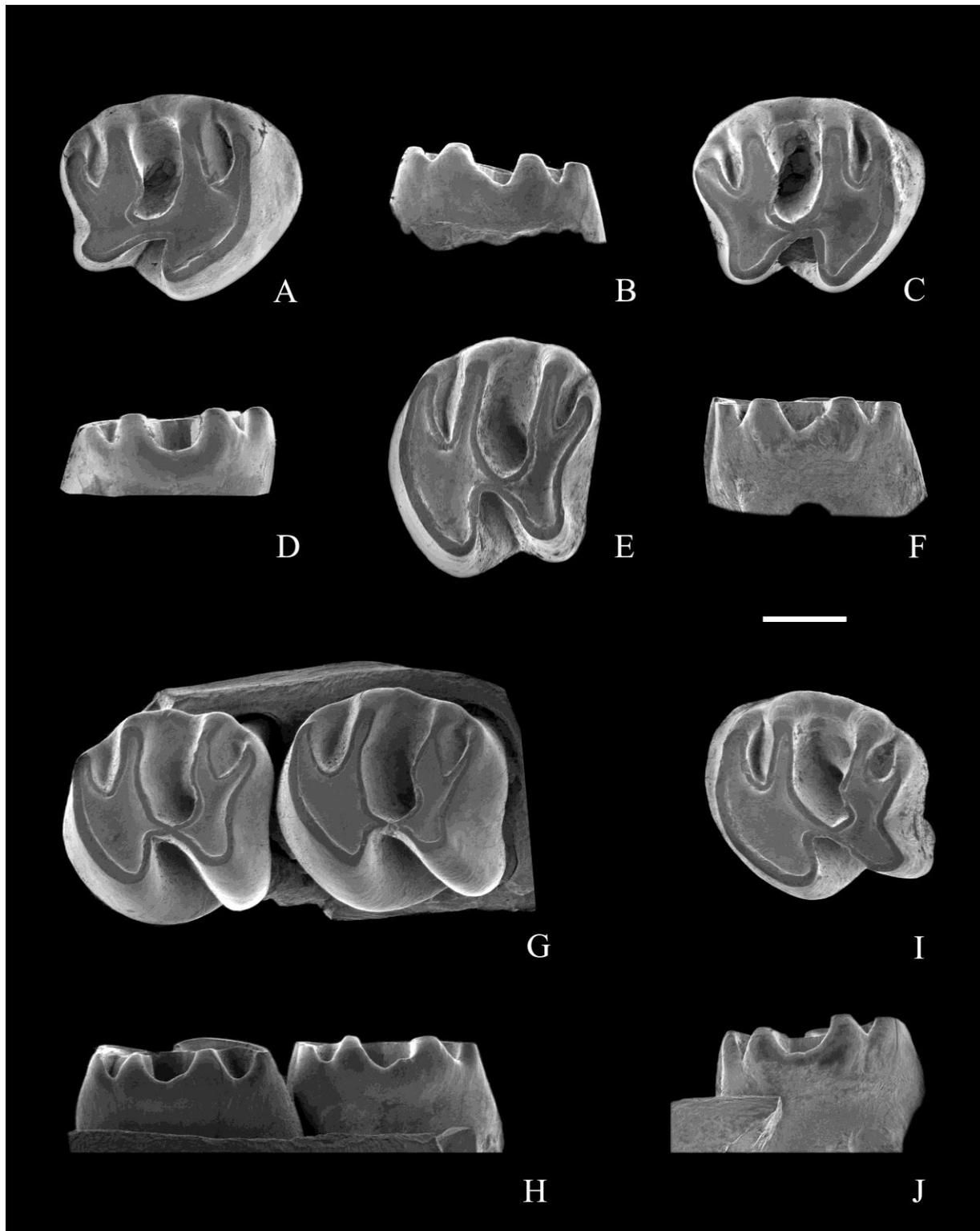


Figure 7

