



AN EXCEPTIONAL LARGE SAMPLE OF THE EARLY MIOCENE CTENODACTYLIN RODENT *SAYIMYS GIGANTEUS*, SPECIFIC VARIATION AND TAXONOMIC IMPLICATIONS

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Abstract: An assemblage of the early Miocene *Sayimys giganteus* (Ctenodactylinae, Rodentia) from its type locality Keseköy, and smaller assemblages of Yapıntı and Horlak (Anatolia, Turkey) are described. Almost all *Sayimys* species are known from small collections of isolated cheek teeth. The very large assemblage from Keseköy is of special interest, because it allows the study of the intra-specific variation of dental morphology: size, the morphological changes through wear and the criteria for recognition of the tooth position of molars. The results have been used to review the formally named *Sayimys* species and to evaluate the dental features used to define the species. The review of the early and middle Miocene succession of *Sayimys* in the Siwaliks (Pakistan) resulted in the resurrection of *S. minor*; *S. baskini* is considered to be a junior synonym of *S. minor*. *S. sivalensis* and *S. obliquidens* are nomina dubia, and restricted to their holotypes, *S. hintoni* n. sp. is established for medium-sized *Sayimys* from the Kamlial, lower Chinji and Manchar Formations and *S. chinjiensis* is resurrected for *Sayimys* from the upper Chinji and Nagri Formations. It is suggested that the middle Miocene species *Sayimys intermedius* and *S. assarrarensis* from Saudi Arabia are synonymous.

Key words: Anatolia, Pakistan, Siwaliks, fossil rodents, Ctenodactylidae, revision *Sayimys*, synonymy, new species

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Introduction

The first time one of the authors (H. de B.) heard about Gerhard Storch was in 1968 through Prof. G. H. R. von Koenigswald who, after deciding to exchange his position at the university of Utrecht for one with Senckenberg, told us about this charming, promising biologist who had just been appointed there. Those were the days of international focus on the palaeontology of small mammals. Sharing the passions for palaeontology and hunting, Gerhard and I became closer over the years. We miss his charm, knowledge and mild judgment, and we are happy to dedicate this study to him.

Jens Munthe (1980) noticed the large variability in *Sayimys* WOOD, 1937, and wrote “New names for Miocene ctenodactylids should probably be proposed only if based on large samples or very distinctive morphological characters” (p. 22). Since 1980, seven new species of *Sayimys* have been described, six of them are these based on very small samples, while the distinctiveness of the features used is limited or debatable. The message of Munthe went

unheeded, suggesting the need for a description of the large variability within *Sayimys* populations. In the following, we describe a large sample of *S. giganteus* LÓPEZ-ANTOÑANZAS, SEN et SARAC, 2004 from Keseköy (Turkey), from the same level and locality as the type of the species. Our sample was collected in 1988 – 1989 by the team of Gerek Saraç, Engin Ünay (both Maden Tektik ve Arama, Ankara) and H. de B. (Utrecht University). The *Sayimys* specimens from two other sites in Turkey, Horlak and Yapıntı, were collected by the same team. While the *Sayimys* specimens from Keseköy collected in 1988 – 1989 were under study, López-Antoñanzas et al. (2004) defined *Sayimys giganteus*, based on a small sample from the same site. This small sample consists of 10 cheek teeth only, possibly representing two individuals. The collection described here consists of over 336 measurable specimens, representing a minimum number of 30 individuals, Yapıntı has delivered 65 specimens derived from a minimum of six individuals and Horlak yielded five specimens only. This material enlarges our knowledge of the

genus, underscores the intra-specific variability and allows for a better understanding of small *Sayimys* assemblages.

In general, large collections of fossil and extant Ctenodactylinae species are relatively rare; most fossil species and genera are based on small numbers of specimens, in some cases on a single specimen. The large collection of *Sayimys giganteus* from Keseköy is thus an excellent, but rare, opportunity to study the variation within a single population, and to test the significance of the morphological and size differences within and between small assemblages.

Localities

A short description of the geological setting of the Keseköy locality (Text-fig. 1) is provided in Sümengen et al. (1990) and Krijgsman et al. (1996). Additional information is in Wessels et al. (2001), and a list of the rodent assemblage is given in Theodoropoulos (2000). The locality is correlated to the Mammal Neogene (MN) zone 3. The type of *Sayimys giganteus* LÓPEZ-ANTOÑANZAS, SEN et SARAÇ, 2004 comes from the same locality as the material studied here. In the description of the species, it is mentioned that the type material is from two localities: Keseköy 1 and 2. However, all Keseköy material is from a thin (about 5 cm) greenish clay bed intercalated in thick lacustrine diatomitic sediments. Normal faulting has dislocated the single thin fossiliferous bed, which is now at several locations in the hillside. A volcanic tuff below the fossiliferous bed has been dated as approximately 20.1 ± 2.2 Ma (Krijgsman et al. 1996). Illustrations of upper and lower dentitions of *Sayimys* sp. (now *S. giganteus*) from Keseköy were published by de Bruijn (1999).

The Yapıntı locality with a summary of the faunal assemblage has been described in Ünay et al. (2001). Based on the ages given in Ünay et al. (op. cit.), Yapıntı is slightly younger than the Keseköy locality. A lower and an upper premolar of *Sayimys* have been illustrated in Ünay et al.

(2001: fig. 4g, h); the material described here has been collected after 2001.

A description of the Horlak 2 locality is provided in Sümengen et al. (1990), along with a summary of the faunal assemblage. De Bruijn (1999) assigned the Horlak site to MN 4. Text-fig. 1 shows the location of the three sites in Turkey.

Material and methods

Measurements, photographs, nomenclature

A Leitz Ortholux microscope with a mechanical stage and measuring clocks was used for measuring dental elements. Measurements are given in millimetres. The measuring methods are shown in Text-fig. 2. Electron microscope photographs have been taken of a selection of the specimens. The specimens are depicted on the plates from the right side. If the original is from the left side, the specimen number has been underlined. The nomenclature used for parts of the cheek teeth is shown in Text-fig. 3, the terminology of the valleys (flexi and flexids) is after Baskin (1996), the anterolophulid is after de Bruijn et al. (1989). A sill is a slight elevation in the bottom of flexids or flexa near the tooth margin. Upper cheek teeth are indicated by upper case, lower cheek teeth by lower case.

Abbreviations

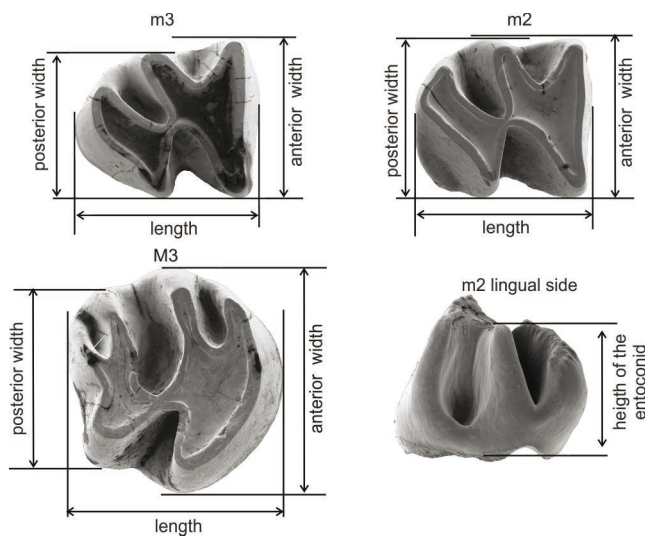
KES	Keseköy
YAP	Yapıntı
H.-GSP	the Howard University-Geological Survey of Pakistan localities

Recognizing tooth positions

The distinction between isolated first and second molars in the Ctenodactylinae can be difficult, due to overlap in



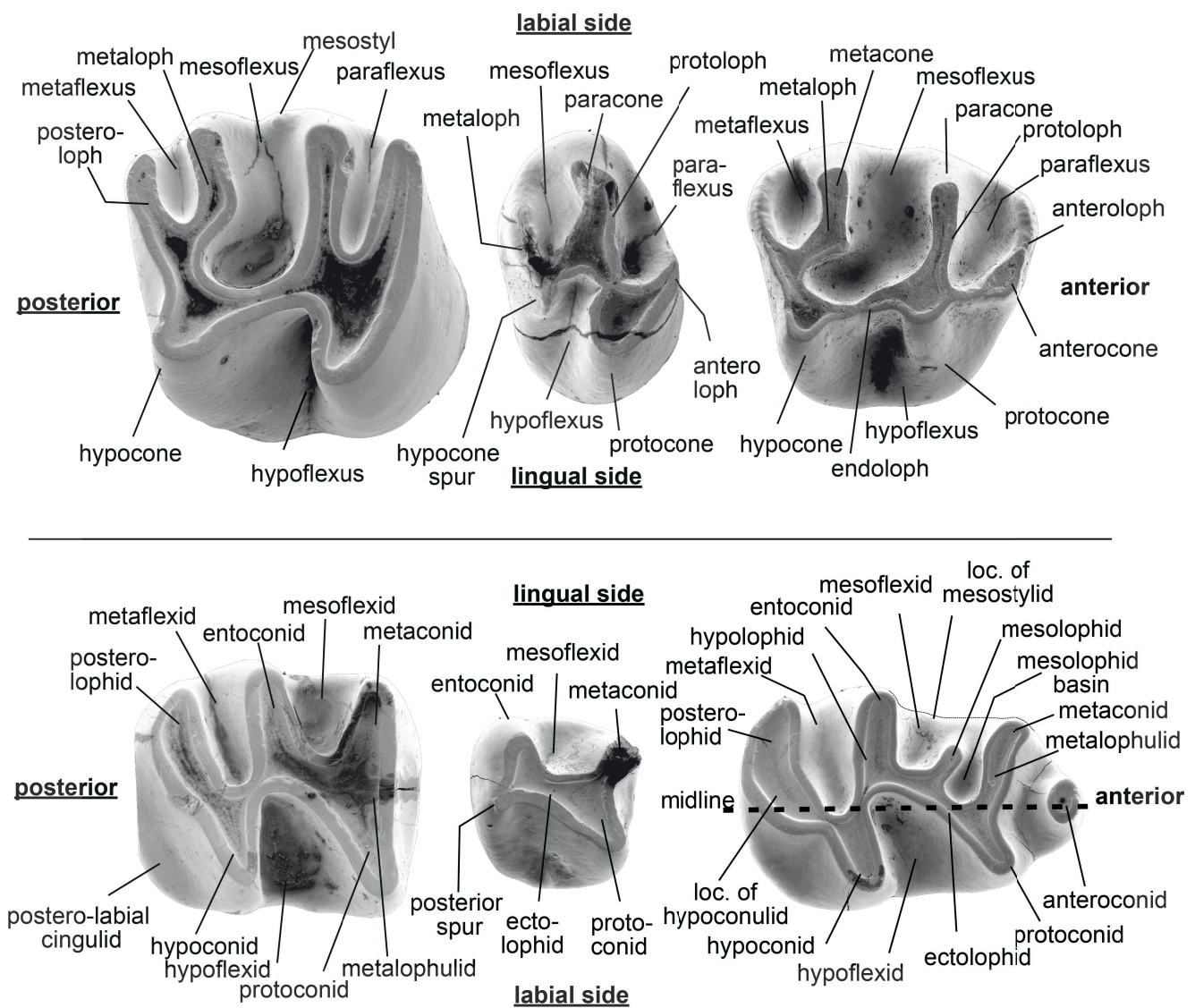
Text-fig. 1. Map of Turkey showing the localities Keseköy, Yapıntı and Horlak.



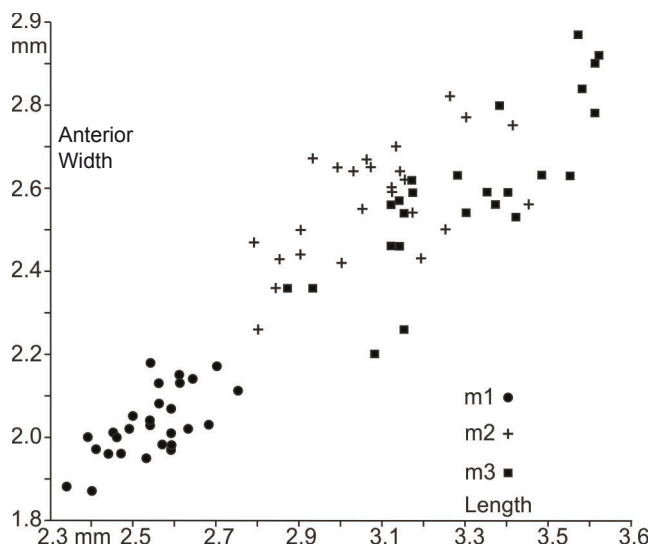
Text-fig. 2. Methods of taking measurements.

size and morphology. However, the large number of teeth available from Keseköy allowed a clear distinction. This

distinction is based on size difference, the morphology of the posterior margin and the metaloph-posteroloph configuration. Text-fig. 4 shows that the m1 is smaller than the m2; the m2 and m3 have a similar size, but the m3 is on average larger. The m1 can be distinguished from the m2 by its anterior width; all m1 have an anterior width smaller than 2.20 mm, while all second molars have an anterior width larger than 2.26 mm. The distinction between the m2 and m3 is based on the shape of the posterior margin, strongly convex in m3, and absence of the interdental facet. In addition, most m3 lack a postero-labial cingulid. Text-fig. 5 shows the size differences in upper molars; a bimodal distribution can be observed in the distribution of tooth lengths of the m1–2 and M1–2 (Text-fig. 6), and this is also observed in other larger samples of *Sayimys*. The M1 is not longer than 2.41 mm, and the M2 not shorter than 2.43 mm. The metaloph and posteroloph configuration of the M1 tend to form a μ -shape, because the metaloph connects at right angles to the posteroloph. The metaloph-posteroloph tends to be μ - to y-shaped in M2, whereas in the M3 it is more y-shaped. The posterior part of the M3 is less wide than its anterior side; this is reflected in the ratio anterior width/



Text-fig. 3. Nomenclature of tooth parts. Upper row left to right: M1, P4, DP4; lower row left to right m1, p4, dp4. Loc. = location. The anterolophulid is not on this picture, it is the mid-line connection between anteroconid and the metalophulid.

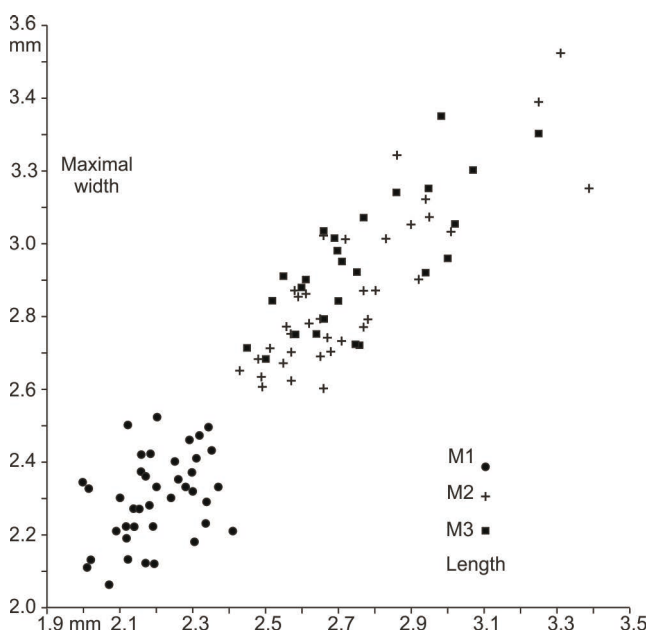


Text-fig. 4. Length-width scatter diagrams of lower molars of *Sayimys giganteus* from Kesköy.

posterior width: the ratio is relatively large in the M3 and small in the M2 (Text-fig. 7), it shows that there is a small area of overlap between the M2 and M3 near the ratio 1.15. In addition, the morphology of the posterior part of the M2 and M3 shows differences. In the M3 the posterior margin is concave, the metaloph-posteroloph aspect is y-shaped and the metaloph extends as a straight loph to about halfway the posteroloph.

Crown height

Teeth of *Sayimys* species are high-crowned and may show evolutionary trends toward higher crowns, as is suggested by Baskin (1996) for middle and late Miocene species in Pakistan. For that reason, the crown height has been measured in the manner shown in Text-fig. 2. The enamel-dentine border at the base of the crown thins gradually; its lower limit



Text-fig. 5. Length-width scatter diagrams of upper molars of *Sayimys giganteus* from Kesköy.

is fragile and variable and can be difficult to see. In addition, older individuals may show rather irregular occlusal surfaces. This results in large variation of measured crown heights of teeth showing the same degree of wear. In Text-fig. 8, five wear stages in cheek teeth, illustrated with line-drawings, have been defined; the corresponding measured maximum and minimum heights (h) for each wear stage are presented. For lower molars the height of the entoconid and for upper molars the height of the paracone has been measured.

Systematic palaeontology

Family Ctenodactylidae Gervais, 1854

Subfamily Ctenodactylinae Hinton, 1933

Genus *Sayimys* Wood, 1937

Type species. *Sayimys perplexus* Wood, 1937.

Sayimys giganteus López-Antoñanzas,

Sen et Sarac, 2004

Text-figs 9–11

Holotype. KSK1–100, a fragmentary left maxilla with P4–M1 (López-Antoñanzas et al. 2004: fig. 5C, D).

Type locality. Kesköy 1 (Kizilcahamam, Ankara, Turkey).

Type horizon. Güvem Formation.

Age. Early Miocene, MN 3 (López-Antoñanzas et al. 2004), 20.2 ± 2.2 Ma (Krijgsman et al. 1996, Wessels et al. 2001).

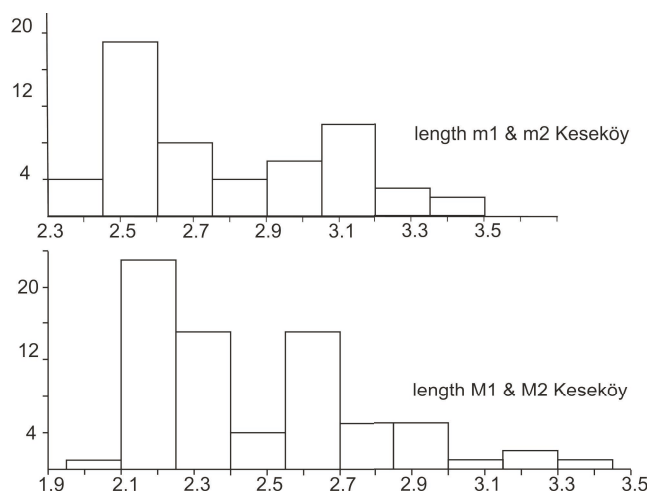
Material. 335 cheek teeth, 261 isolated and 74 in partial jaws.

Measurements. Length-width measurements in Tab. 1, Text-figs 4 and 5, crown-height measurements in Text-fig. 8.

Original diagnosis. “*Sayimys* species of large size with the m3 lacking a constriction in the posterolophid; dp4 with a metalophulid II [= the mesolophid of Text-fig. 3] connecting with the metaconid or nearly reaching it. DP4 without 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” (in López-Antoñanzas et al. 2004).

Emended diagnosis. Large-sized species of *Sayimys*. On the dp4 the mesolophid can be: 1) absent, 2) present and half the length of the metalophulid or, 3) long and connected to a mesostylid. The rounded anteroconid is isolated; protoconid is extending less far labially than the hypoconid, mesolophid connecting at right angles to the ectolophid. The hypolophid connected to ectolophid at obtuse or about right angle.

Some p4 have a posterior spur at the junction of the hypolophid and the ectolophid, a stylid can be present on the postero-labial cingulid (lower arrow on Text-fig. 9, no 4058), as well as a vestigial mesolophid (upper arrow on Text-fig. 9, no 4058). The metalophulid of lower molars is wide near

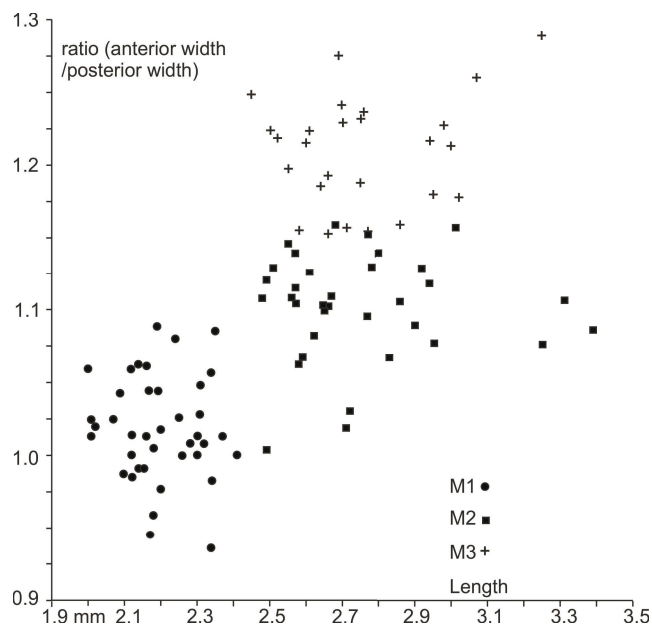


Text-fig. 6. Histograms of the length of *Sayimys giganteus* m1–m2 and M1–M2 from Keseköy showing bimodality.

the protoconid, the mesoflexid is short and v-shaped. The m2 and m3 are lacking a constriction in the posterolophid; a vestigial mesolophid is present in some lower molars (upper arrows on Text-fig. 9, no 4064 and 4084); m1 and m2 with a distinct postero-labial cingulid.

DP4 with paraflexus reaching the protocone, paraflexus longer than metaflexus; metaloph connecting at right angles to the posteroloph. P4 with metaloph of variable length and connected to the protoloph; a small hypocone or a hypocone spur is present, protocone is large.

Upper molars with a well-developed paraflexus and metaflexus, paraflexus longer than metaflexus reaching the protocone; M1 with a metaloph connecting at right angles to the posteroloph, M2 and M3 with a metaloph connecting not at right angles to the posteroloph.



Text-fig. 7. Scatter diagram of molar length against the ratio anterior width/posterior width of upper molars of *S. giganteus* from Keseköy.

Description. dp4. The dp4 has a low crown, its anteroconid is isolated, circular to slightly ovoid and positioned on the mid-line of the tooth. The metaconid is located slightly anterior to the protoconid. The metalophulid of some slightly worn specimens appears to be vaguely S-shaped (4023 in Text-fig. 9) or can have a convex anterior side (4013 in Text-fig. 9). A mesolophid is present in 43 out of 48 specimens, but vestigial in 12 of these (4006 in Text-fig. 9). In the other 31 it is long, that is, extending halfway or more toward the lingual tooth margin. In six

wear stages	dp4	h	m1	h	m2	h	DP4	h	M1	h	M2	h
unworn to little worn		1.20		1.60		2.20		0.90		0.95		1.25
		0.95		1.00		1.70		0.60		0.85		1.10
little to moderately worn		1.10		1.20		1.70		0.90		1.00		1.10
		0.80		0.90		1.10		0.70		0.65		0.90
moderately worn		0.90		1.00		1.30		0.80		0.90		1.00
		0.60		0.60		0.85		0.45		0.65		0.75
moderately to heavy worn		0.80		0.95				0.50		0.75		1.00
		0.40		0.50				0.40		0.60		0.70
heavy worn		0.60						0.50		0.85		
		0.40						0.30		0.57		

Text-fig. 8. Wear stages and height (h) of cheek teeth of *Sayimys giganteus* from Keseköy. Height in mm of the entoconid (arrow) in lower cheek teeth and paracone (arrow) in upper cheek teeth. Shown are the high value and a low value for each wear stage. Note that h of the different wear stages may show large overlaps, in particular in those of worn teeth. This is due to the often-irregular occlusal surfaces of older individuals.

Table 1. Measurements in mm of *Sayimys giganteus* from Kesköy.

	Length				Anterior width				Posterior width			
	range	average	SD	N	range	average	SD	N	range	average	SD	N
DP3	0.69–0.87	0.759	0.068	5	–	–	–	–	0.68–0.93	0.754	0.092	7
DP4	1.78–2.32	2.066	0.126	52	1.45–1.99	1.823	0.109	53	1.40–2.06	1.841	0.125	52
P4	1.09–1.46	1.272	0.116	18	–	–	–	–	1.59–2.07	1.884	0.143	18
M1	2.00–2.41	2.201	0.109	40	2.06–2.50	2.286	0.112	40	2.01–2.52	2.248	0.134	40
M2	2.62–3.30	2.736	0.231	36	2.61–3.52	2.875	0.220	35	2.33–3.18	2.624	0.221	36
M3	2.45–3.25	2.748	0.200	27	2.38–3.35	2.922	0.209	27	1.89–2.73	2.414	0.186	27
dp4	2.49–3.08	2.727	0.137	45	1.04–1.30	1.180	0.072	47	1.43–1.78	1.561	0.080	47
p4	1.29–1.77	1.496	0.113	18	–	–	–	–	1.27–1.71	1.484	0.140	18
m1	2.34–2.75	2.543	0.098	32	1.65–2.15	1.915	0.105	31	1.87–2.18	2.031	0.077	31
m2	2.79–3.45	3.076	0.179	25	2.26–2.82	2.569	0.135	25	2.09–2.95	2.486	0.184	25
m3	2.87–3.62	3.302	0.218	25	2.20–2.97	2.596	0.191	26	2.07–2.79	2.439	0.159	29

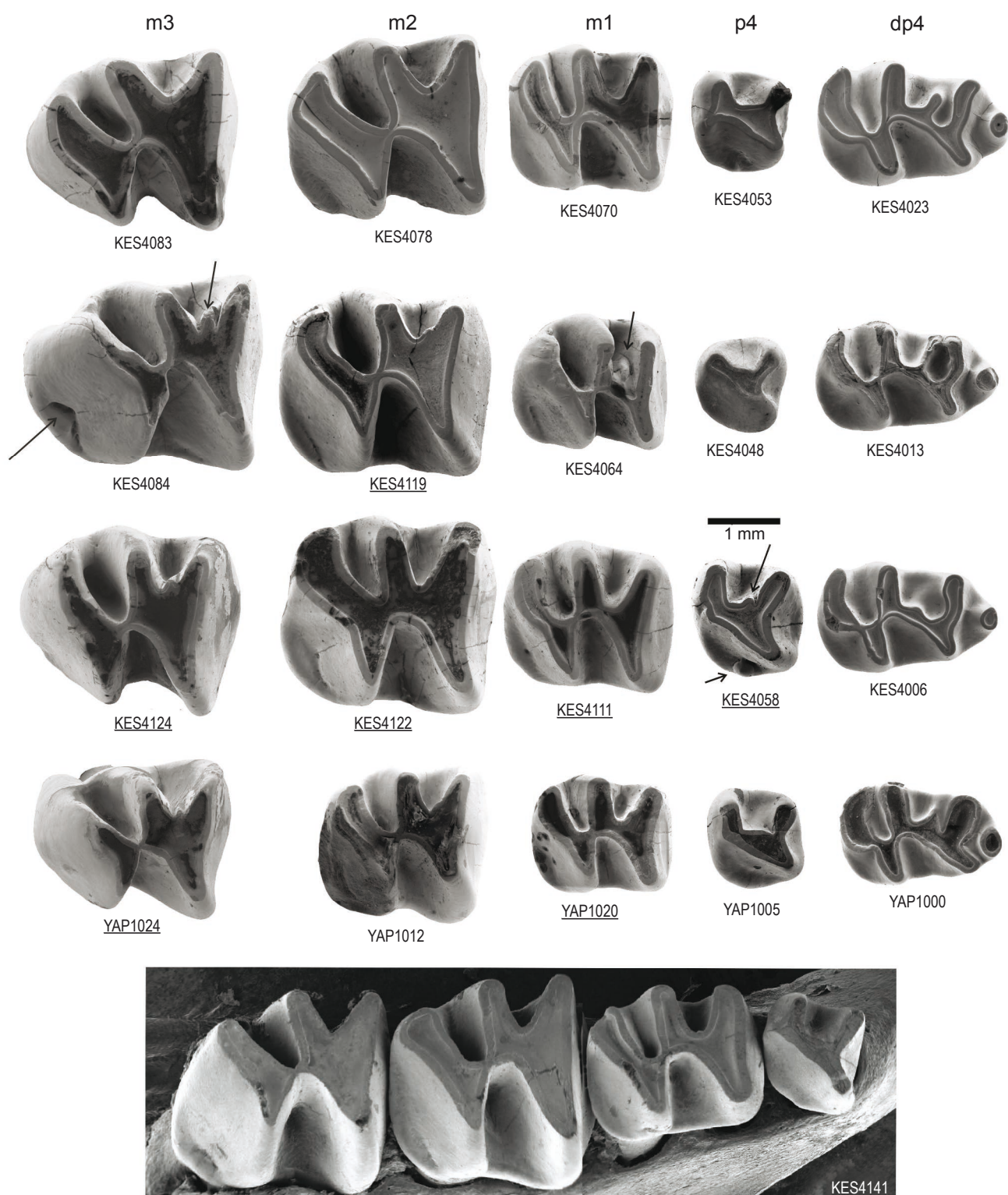
of the specimens, a small mesostylid is present; in three of these specimens a (vestigial) mesolophid is also present. In slightly worn specimens, the lingual end of the mesolophid is wide, suggesting a mesostylid. With increasing wear, the mesolophid eventually connects to the metalophulid to form an enamel lake (see the line drawings in Text-fig. 8). The mesolophid basin extends to the mid-line of the tooth or slightly beyond, but withdraws toward the lingual border with increasing wear. The mesoflexid has no sill at its entrance; it is deeper and wider than the metaflexid (Text-fig. 11), whereas the mesolophid basin is shallower than the mesoflexid. The hypolophid connects at approximately a right angle to the ectolophid. In unworn condition, the connection of the hypolophid to the ectolophid is narrow, but it widens with increasing wear. The constriction at the connection of the hypolophid to the anterior arm of the hypoconid is more persistent. The hypoflexid is deep; it has no sill at the tooth margin. The posterolophid is curved. It is narrow at its connection with the hypoconid. An elevation in the posterolophid of unworn dp4 marks a hypoconulid. In some specimens, a low sill at the lingual border is present in the metaflexid, and an enamel lake appears with increasing wear. The metaflexid is deepest close to the hypoconid. The development of the postero-labial cingulid varies from weak to distinct.

p4. In little worn specimens, protoconid, metaconid and entoconid form a V-shape. The metalophid connects at right angles to the posterior side of the protoconid. In some premolars, the metalophid is constricted where it meets the protoconid. In five out of 18 specimens, a vestigial mesolophid is present (Text-fig. 9, 4058, arrowed). The ectolophid plus a short and a transversely oriented hypolophid connect to the entoconid; a posterior spur may be present. The postero-labial cingulum is distinct in most teeth; in eight a prominent cingulid-stylid is present (4058 on Text-fig. 9, lower arrow).

m1. The m1 has a high crown. The anterior margin of the occlusal surface is slightly concave, and becomes straighter and a bit convex with increasing wear. The metalophulid is broad at the protoconid-side and tapers lingually. In general, the metalophid extends less far lingually than the hypolophid.

In some slightly worn specimens a small short mesolophid is present (Text-fig. 9, 4064, arrowed), it is separated from the metalophulid by a narrow, very shallow valley, and fuses with the metalophulid at an early stage of wear. The mesoflexid does not reach the mid-line of the tooth; in occlusal view it is V-shaped when slightly worn, changing into U-shape with wear. The mesoflexid is shorter but deeper than the metaflexid (Text-fig. 11). The metaflexid may have a low sill at the tooth border. The connection between hypolophid and ectolophid becomes more confluent with wear, but the posterior margin of the hypolophid remains offset with respect to the ectolophid. The connection of the hypolophid to the anterior arm of the hypoconid is narrow. The hypoflexid is deeper than the mesoflexid and metaflexid. In two specimens, a low sill is present in the hypoflexid. In little-worn specimens, the posterolophid is slightly curved; in unworn specimens, a hypoconulid can be recognized as an elevation of the posterolophid. The metaflexid extends to the mid-line of the tooth, or slightly beyond it. In about half of the specimens, a prominent sill is present and connects to the posterolophid and hypolophid with wear, to form an enamel lake. The postero-labial cingulid is distinct in most specimens, weak in some specimens.

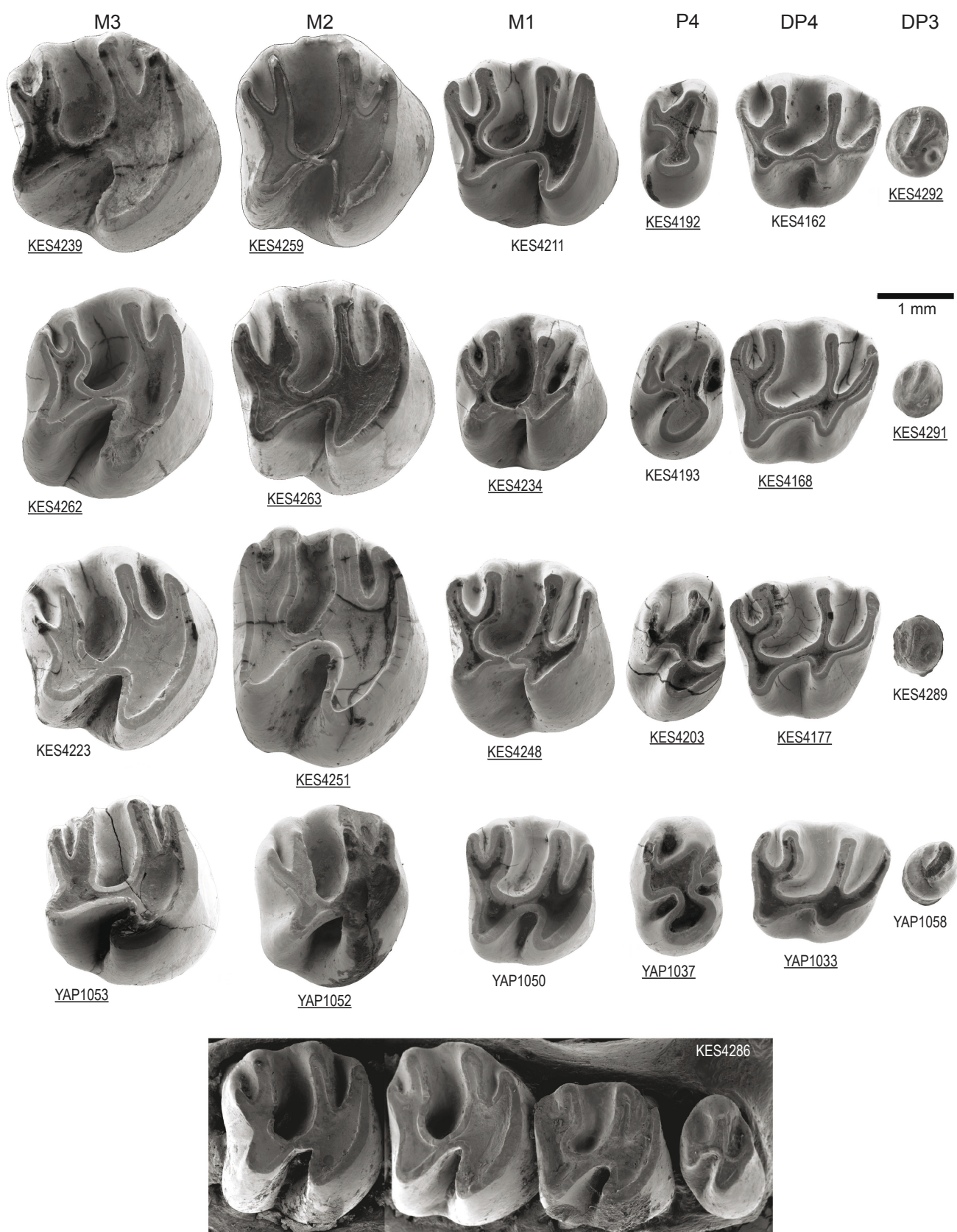
m2. The m2 and m1 are similar in morphology, but differ in length and width (Text-fig. 4), moreover, in unworn condition the crown of the m2 is higher (Text-fig. 11). Also, there are some minor morphological differences. On m2, the connection between ectolophid and hypolophid is wider, and these lophids are oriented more in line than on m1. As on m1, a short mesolophid branch may be present in unworn specimens, but it fuses with the metalophulid in an early stage of wear. The mesoflexid is similar to that in the m1, but a weak sill is present in more specimens. In m2, the hypoflexid is more in line with the metaflexid compared to the m1. The connection between hypolophid and anterior arm of the hypoconid is narrow. The posterolophid is less curved than in the m1 in early stages of wear, and when moderately worn, it is straight and obliquely oriented. The posterolophid-hypoconid connection is wide. The sill at the lingual tooth border in the metaflexid is similar to m1; with increasing wear, the metaflexid becomes narrower at its lingual margin.



Text-fig. 9. Lower molars and premolars of *Sayimys giganteus* from Keseköy and Yapıntı (= YAP numbers) shown as right specimens. Left side specimens are shown in mirror image, these have underlined specimen numbers.

m3. The m3 is somewhat larger (Text-fig. 4) and higher than m2. It can be distinguished by its narrow convex posterior margin; its posterior width is smaller than its anterior width. The metaconid lies anterior to the labial part of the protoconid. The apex of the unworn protoconid lies slightly more toward the mid-line of the molar relative to that of the hypoconid. The protoconid is oblique and the hypoconid is transverse. In little-worn m3, a short

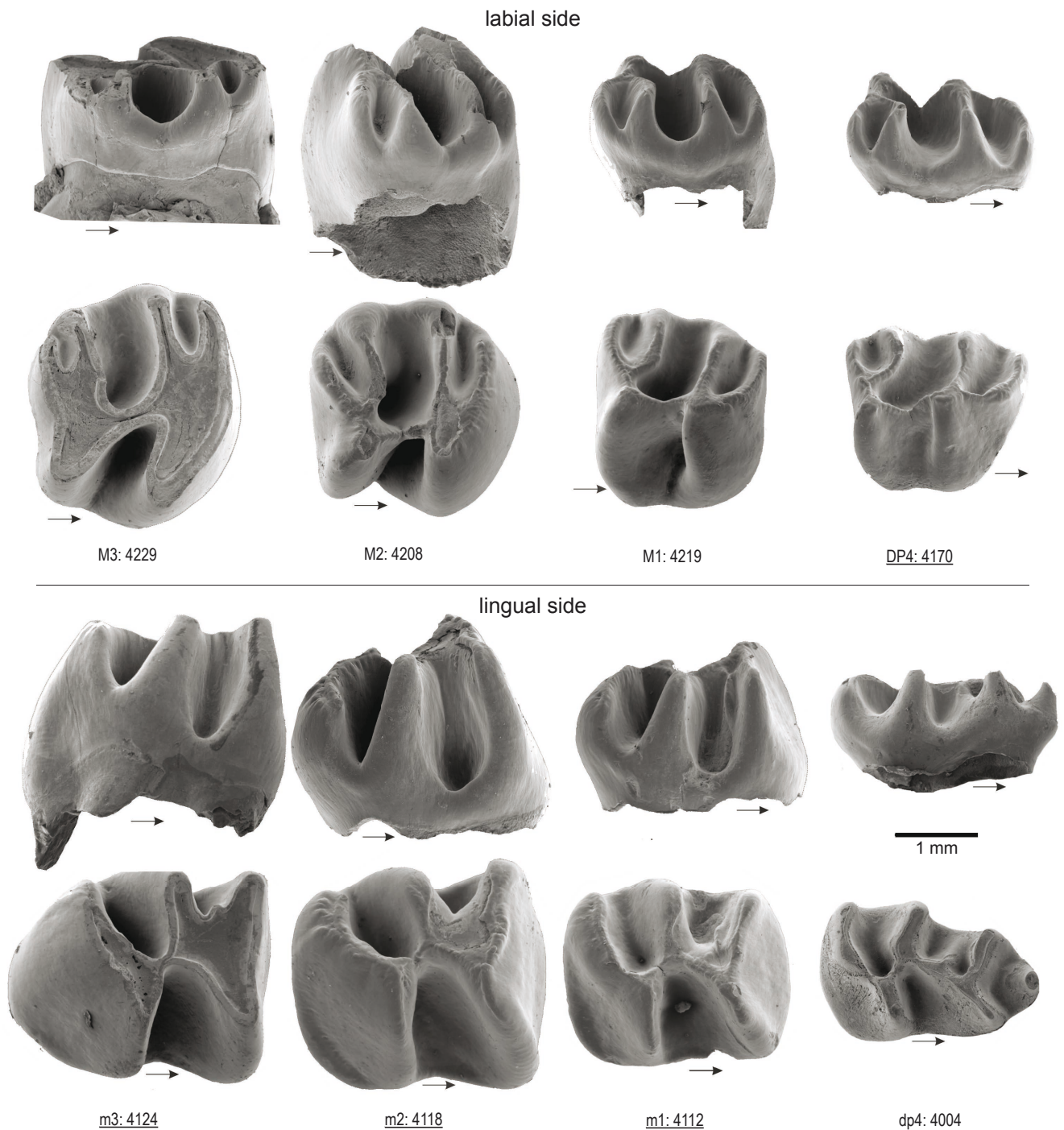
mesolophid is present, but it merges with the metalophulid at an early wear stage. The mesoflexid has a V-shape, which does not reach the mid-line of the tooth. In lingual view, the mesoflexid is deeper than the metaflexid (Text-fig. 11); a minor sill may be present. The metaflexid is long and has a prominent sill. The straight hypolophid is confluent, in line with the ectolophid. The connection of the hypoconid to the ectolophid is narrow. The hypoflexid is deeper than



Text-fig. 10. Upper cheek teeth of *Sayimys giganteus* from Keseköy and Yapıntı (= YAP numbers) shown as right specimens. Left side specimens are shown in mirror image, these have underlined specimen numbers.

the meso- and metaflexid. The posterolophid is more or less straight and directed obliquely. The postero-labial cingulid can be absent, weak or distinct, with a stylid positioned on it in some specimens (Text-fig. 9, 4084, arrowed).

DP3. This small low-crowned element has a variable morphology. A complex specimen is in Text-fig. 10 (no 4292); it shows an obliquely oriented loph, which is wider and highest at its labial end. An anterocone is present.



Text-fig. 11. Cheek teeth of *Sayimys giganteus* from Kesköy. Anterior sides are indicated by arrows. Top row: labial sides of M3, M2, M1 and DP4, images horizontally-mirrored. Second row: occlusal surfaces of M3, M2, M1 and DP4 of the same specimens. Third row: lingual sides of m3, m2, m1 and dp4, images horizontally-mirrored. Lower row: occlusal surfaces of m3, m2, m1 and dp4 of the same specimens.

Posteriorly, a low cingulum is separated from the oblique loph by a valley. Other specimens show a single sharp cusp with traces of a subsidiary cusp and cingulum.

DP4. The DP4 has a low crown, with morphology showing minor variation (Text-fig. 10). Some DP4 have a thickening in the anteroloph at the anterocone position, in others, this is absent. The labial end of the anteroloph shows a thickening in some specimens, in others it tapers. In some unworn specimens, the paracone seems isolated, due to a low protoloph. Unworn specimens show that the apex of

the protocone is located more labially than the hypocone; protocone and hypocone are higher than paracone and metacone. With increasing wear, the labial end of the posteroloph connects to the metacone, due to the presence of a sill in the metaflexus. In late stages of wear, the metaloph merges with the posteroloph, and the protoloph with the anteroloph. In such specimens, the anterior fused loph is wider than the posterior fused loph.

P4. We are not certain about the homology of the elements of the P4; we follow here Text-fig. 3, where a

relatively unreduced specimen is shown. Text-fig. 10 shows the morphological variety from strongly reduced (no 4192) to relatively weakly reduced (no 4203). The strongly-reduced specimens show two cusps, the protocone and the paracone, connected by a transversely oriented loph and a small posterior spur. Its hypoflexus is at the posterior side, while the paraflexus is absent. In the weakly-reduced specimen, the mesoflexus and paraflexus are both present, the hypoflexus is located lingually. Protoloph and posteroloph (= metaloph) are both well-developed.

M1. The M1 is high-crowned. Its protoloph is straight or slightly curved; the posterior rim is convex and confluent with the labial margin of the endoloph. The apex of the protocone of unworn specimens is located more internally than that of the hypocone; protocone and hypocone are higher than metacone and paracone. The posteroloph is straight and obliquely oriented; its tip at the labial end is often slightly curved. The metaloph is connected about halfway to the posteroloph. The straight paraflexus extends to the protocone, decreasing in length with wear. In labial view (Text-fig. 11), the paraflexus is as low and wide as the metaflexus. In heavily worn specimens, protoloph and anteroloph are fused (Text-fig. 8). The mesoflexus extends beyond the mid-line of the tooth, is deepest internally, and a low sill is present near the tooth margin. The sill in the short metaflexus is not prominent; an enamel lake does not form in all worn specimens. The metaloph and posteroloph are completely fused in worn specimens (Text-fig. 8). The fused anterior loph is wider than the fused posterior loph.

M2. The M2 is distinctly wider and longer, and in unworn condition, higher than the M1 (Text-figs 5, 6, 11), and it is widest anteriorly. The lophs and cusps are confluent fused into ridges that are arc-shaped. Anteroloph and protocone form the smoothly bow-shaped anterior side of the molar. The protoloph is transverse or slightly oblique. The posterior side of the protoloph curves smoothly and confluent into the labial margin of the endoloph. There is some variation in the configuration of the posteroloph and metaloph, related to stages of wear. The posteroloph seems an offshoot from the curved loph formed by metacone, metaloph and

hypocone. In other specimens, the posteroloph seems to split smoothly from the metaloph. Unlike in M1, the metaloph and posteroloph do not meet at a right angle. The paraflexus extends to the protocone in lightly worn specimens, but decreases in length with wear (Text-fig. 8). Usually a low sill is present, and the paraflexus can form an enamel lake in later wear stages. The paraflexus and metaflexus are about equally deep and wide (Text-fig. 11); both are shallower than the mesoflexus and hypoflexus. The mesoflexus extends beyond the mid-line. A sill is present in the mesoflexus; the deepest part of the mesoflexus lies internally. The hypoflexus is deeper than the mesoflexus, but it is shorter, not reaching the mid-line of the tooth. A sill is present in the metaflexus of most specimens; in advanced stages of wear, the metaflexus forms an enamel lake, in later stages of wear the metaloph and posteroloph are completely fused.

M3. The isolated M3 is similar in length and width to the M2 (Text-fig. 5), but higher in an unworn condition. The posterior side of the M3 is relatively narrow, resulting in an anterior/posterior width ratio that is larger in the M3 than in the M2 (Text-fig. 7). The M3 has a smooth convex anterior margin, and a concave posterior margin. Similar to the M2, the ridges formed by the confluent fused lophs and cusps are more or less arc-shaped, but in the M3 arcs are stronger bowed, the labial tips more posteriorly located. The metaloph meets halfway to the posteroloph, the posteroloph seems a posterior offshoot from the curved ridge formed by the metacone, metaloph and hypocone. In some specimens and stages of wear, the metaloph seems an anterior offshoot of a confluent arc formed by posteroloph and hypocone. The morphology of the occlusal surface and depth of flexi are like those in the M2.

Variation in size. Most samples of *Sayimys* are small. The two large samples of *Sayimys* previously known are Daud Khel and H.-GSP82.24 in Pakistan (Munthe 1980, de Bruijn et al. 1989). Together with the Keseköy assemblage, these allow a reliable estimate of the variation in length and width. Length-width variation (size) of rodent teeth is discussed in Freudenthal and Cuenca Bescos (1984). These authors introduced a simple coefficient of variation,

Table 2. Coefficient of variation V' in three large samples of *Sayimys*, Keseköy, Daud Khel and H.-GSP82.24. N = number of specimens.

	Upper premolars and molars							Lower premolars and molars					
	Keseköy		Daud Khel		H.-GSP82.24			Keseköy		Daud Khel		H.-GSP82.24	
	V'	N	V'	N	V'	N		V'	N	V'	N	V'	N
DP4 length	29	50	8	14	22	26	dp4 length	21	46	12	12	21	24
DP4 width	26	53	25	14	33	26	dp4 width	22	48	14	12	38	24
P4 length	31	18	22	14	30	5	p4 length	31	18	13	25	24	12
P4 width	30	18	28	14	25	5	p4 width	30	18	18	25	34	12
M1 length	19	40	20	29	13	21	m1 length	16	32	26	33	13	21
M1 width	19	40	34	29	25	21	m1 width	15	32	29	33	24	21
M2 length	33	37	28	31	17	16	m2 length	21	24	19	28	24	18
M2 width	35	36	28	31	22	16	m2 width	22	24	16	28	19	16
M1–2 length	52	77	34	60	33	37	M1–2 length	38	56	33	61	28	38
M1–2 width	52	76	50	60	44	37	M1–2 width	41	56	51	61	47	36
M3 length	31	26	30	21	21	10	m3 length	25	27	16	18	25	18
M3 width	33	26	18	21	22	10	m3 width	30	27	20	18	21	17

Table 3. An estimate for the range of the length (in mm) of the dp4 and m1–2 in small samples (n = 1 to n = 5). The range has been estimated using values for the coefficient of variation V' calculated from large assemblages of related species. See text for further explanation.

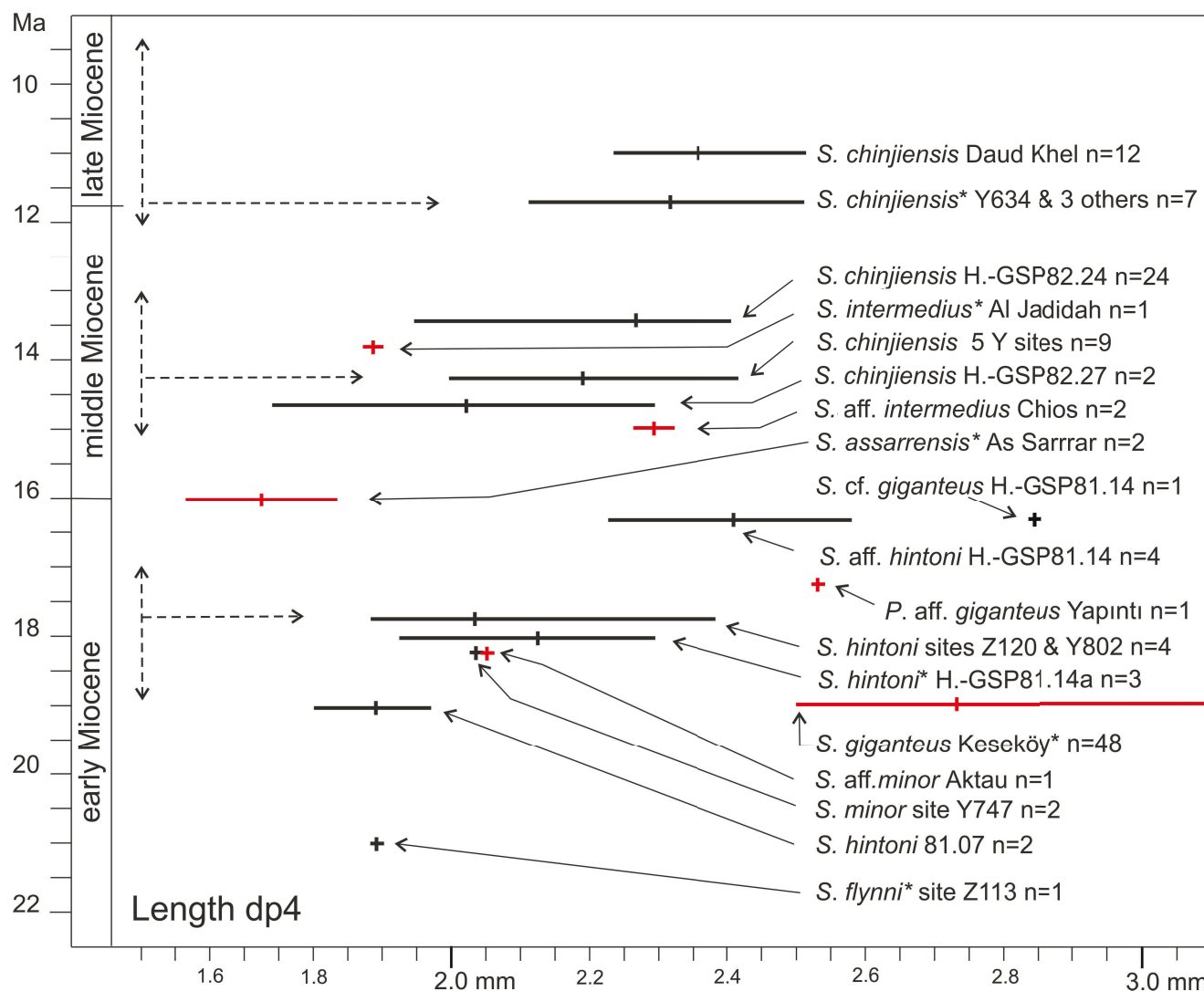
	midpoint	V'	range	min	max
dp4 As Sarrar	1.73 (n = 2)	20	0.35	1.56	1.90
dp4 Al Jadidah	1.90 (n = 1)	20	0.38	1.71	2.09
dp4 Chios	2.30 (n = 2)	20	0.46	2.07	2.53
m1–2 As Sarrar	2.46 (n = 3)	40	0.98	1.97	2.95
m1–2 Al Jadidah	2.44 (n = 2)	40	0.98	1.95	2.93
m1–2 Chios	2.24 (n = 5)	40	0.90	1.79	2.69

$V' = 100r/m$ in which r is the range (the difference between the maximum and minimum) and m is the midpoint between maximum and minimum. Tab. 2 shows values for V' for the three large samples of *Sayimys*; note that the value of V' for undivided assemblages of first and second molars is large.

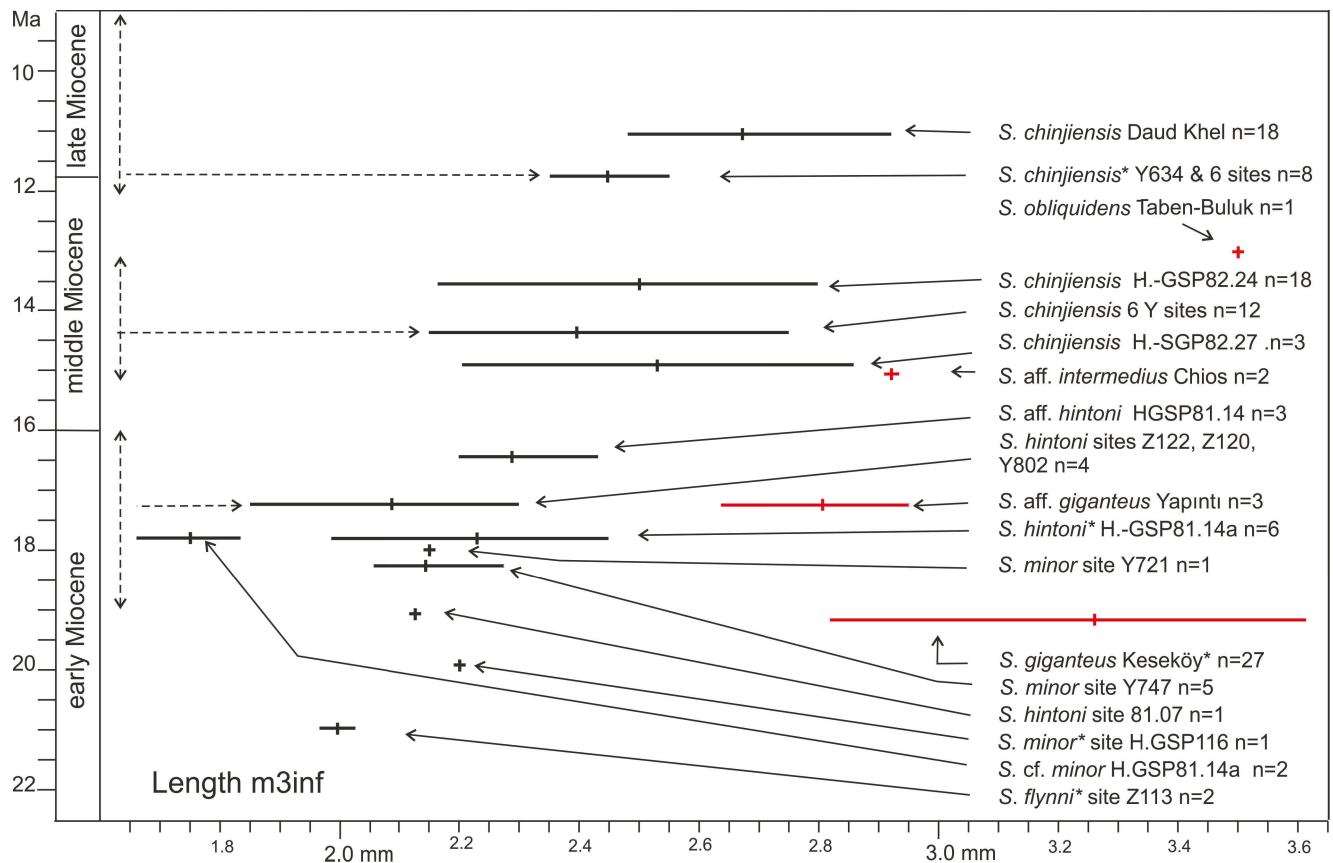
The values for V' calculated from the three large *Sayimys* populations may be used to estimate a size range if only a small sample is available. To show this, we have estimated a size range for the dp4 and m1–2 of three small samples: *Sayimys intermedius* from its type locality Al Jadidah, *S. assarrarensis* from As Sarrar and *Sayimys* aff. *intermedius* from Chios (data in López-Antoñanzas and Sen 2004, López-Antoñanzas et al. 2005). Tab. 3 shows that the estimated ranges for the m1–2 and dp4 of Al Jadidah and As Sarrar are largely overlapping. The Chios m1–2 is similar in size to that from Al Jadidah and As Sarrar, but its dp4 is much larger and outside the range of the other two sites.

The calculated ranges are indicative; in this exercise the available measurements are assumed to be close to the midpoint of the constructed range, a presumption not necessarily true.

Text-figs 12 and 13 show the ranges and averages of the length of dp4 and m3 of most species of *Sayimys* compiled from the literature; length ranges of DP4 and M3 show a similar picture, but are not shown here. Diagrams of first and second molars are not helpful, because these molars are



Text-fig. 12. Ranges of the length of the dp4 based on data from the literature. Vertical scale in Ma, the samples are from the Siwaliks (black) and Turkey, Greece and Arabia (red). Type localities of species are indicated with an asterisk. The Y and Z sites are from Baskin (1996), its size ranges are composed of data from several localities and the vertical arrowed broken line indicates the age range of these sites.



Text-fig. 13. Ranges of the length of the m3 based on data from the literature, see Text-fig. 12 for explanation.

rarely separated in the literature, though different in size: large assemblages have therefore very large ranges, whereas those of small assemblages are erratic.

The height of the crown has been measured in the Keseköy assemblage; for this measure, the height of the entoconid in the lower teeth and of the paracone in the upper teeth has been selected. Results are shown in Text-

fig. 8 for different wear classes. Even in the large Keseköy assemblage, the number of un- or lightly worn cheek teeth is low.

Variation in morphology. Presence and length of the mesolophid in the dp4 is considered an important species-specific character. This feature varies strongly

Table 4. Measurements in mm of *Sayimys* aff. *giganteus* from Yapıntı and Horlak.

	Length				Anterior width				Posterior width			
	range	average	SD	N	range	average	SD	N	range	average	SD	N
Yapıntı												
DP3	0.72–0.77	0.745	–	2	–	1.100	–	–	0.75–0.80	0.775	–	2
DP4	1.86–1.97	1.915	–	2	1.50–1.72	1.633	0.117	3	1.63–1.64	1.635	–	2
P4	1.20–1.34	1.298	0.066	4	–	–	–	–	1.78–2.03	1.928	0.108	4
M1	1.85–2.10	1.997	0.086	6	1.94–2.17	2.062	0.079	6	2.04–2.20	2.095	0.057	6
M2	2.47–2.56	2.510	0.046	3	2.50–2.52	2.515	0.010	4	2.30–2.78	2.408	0.208	5
M3	2.21–2.42	2.330	0.108	3	2.33–2.43	2.385	0.440	4	1.86–2.03	1.948	0.059	6
dp4	–	2.540	–	1	–	1.100	–	1	1.35–1.46	1.413	0.570	3
p4	1.38–1.61	1.465	0.083	6	–	–	–	–	1.43–1.66	1.508	0.085	6
m1	2.16–2.47	2.291	0.113	9	1.51–1.83	1.690	0.118	8	1.63–1.93	1.799	0.109	8
m2	–	2.990	–	1	2.33–2.47	2.400	0.099	2	2.26–2.48	2.387	0.114	3
m3	2.64–2.95	2.807	0.156	3	2.08–2.56	2.333	0.155	7	2.02–2.30	2.165	0.115	4
Horlak												
M3	–	–	–	–	–	–	–	–	–	1.91	–	1
m1	2.23–2.32	2.270	–	2	1.57–1.65	1.615	0.034	4	1.67–1.83	1.753	0.068	4

among the 47 specimens of *Sayimys* from Keseköy; it can be complete, extending to the lingual tooth margin, relatively short, or absent. Absence of a mesolophid in a single or a few dp4 is thus not a species-specific character. A mesostylid is present in some dp4 from Keseköy either as a separate tubercle or recognizable as a thickening of the lingual end of the mesolophid.

The development of the anteroloph in P4, considered species-specific by some authors, occurs in the Keseköy assemblage with four character stages: a) well-developed, extending from the protocone to halfway the anterior tooth margin, paraflexus well-developed (Text-fig. 10, no 4203); b) short, extending to about a quarter of the anterior tooth margin, paraflexus short; c) anteroloph and paraflexus absent (Text-fig. 10, nos 4192 and 4193) and d) anteroloph absent, but with a small isolated cusp in front of the anteroloph (similar to YAP 1037 in Text-fig. 10). This suggests that this character has little value if only a few premolars are available. In general, the morphology of the P4 is rather variable (Text-fig. 10), and better not used as a species diagnostic element.

A variable character is the postero-labial cingulid of lower molars (Text-fig. 3). In the Keseköy material it is present in most m1 and m2, but variable in size. In general, it is better developed in m1 than in m2, and weak or absent in m3. A stylid on the postero-labial cingulid is present in 11 of the 18 p4 from Keseköy, and three specimens of *Sayimys baskini* (= *S. minor*) from Pakistan (Baskin 1996); it seems present in the single specimen of *S. obliquidens* from Taben-Buluk and in '*S. perplexus*' (= *S. sivalensis*) from Hari Talyangar, India (Wood 1937), but it has not been described in other species.

***Sayimys* aff. *giganteus* LÓPEZ-ANTOÑANZAS,
SEN et SARAC, 2004**
Text-figs 9, 10

Localities and formations. Yapıntı (Derinçay Formation) and Horlak 2 (Yeniçubuk Formation).

Age range. MN 4, possibly also late MN 3 (Ünay et al. 2001, Sümengen et al. 1990).

Material and measurements. See Tab. 4.

Discussion. The Yapıntı and Horlak material has been compared with early and middle Miocene species *Sayimys flynni* BASKIN, 1996, *S. minor* DE BRUIJN, HUSSAIN et LEINDERS, 1981, *S. giganteus*, *S. obliquidens* BOHLIN, 1946, *S. assarrarensis* LÓPEZ-ANTOÑANZAS et SEN, 2004 and *S. intermedius* (SEN et THOMAS, 1979). The Yapıntı and Horlak material is smaller than *S. giganteus* or overlaps with the smaller specimens of Keseköy (Text-figs 12, 13). *Sayimys flynni*, *S. minor*, *S. assarrarensis* and *S. intermedius* are considerably smaller, but *S. obliquidens* is about of the same size. The dental morphology of the specimens from Yapıntı and Horlak is very similar to the material from Keseköy, and therefore not described in detail. There are morphological differences in the dp4 and lower molars, in the mesolophid, with *S. flynni*, *S. obliquidens* and *S. minor*. Considering the size differences and agreement in dental morphology, the assemblages from Yapıntı and Horlak material are classified as *S. aff. giganteus*.

López-Antoñanzas et al. (2005) described *Sayimys intermedius* from the early Miocene of Chios (Greece). The Yapıntı dp4 resembles one of the three figured specimens from Chios in having a rounded, isolated anteroconid; the other two Chios specimens have an elongate transverse anteroconid. The Chios dp4 do not show a clear mesolophid, but the area of the mesolophid basin is less deep than the mesoflexid. Text-figs 12 and 13 suggest that the Chios material is too large to be included in *S. intermedius*; noteworthy is the long m3 from Chios. In dental morphology and size, the Chios material is close to that of Yapıntı, and should be classified as *Sayimys* aff. *giganteus*.

Other formally named species of *Sayimys*

Remarks. The oldest *Sayimys* species are known from the early part of the early Miocene, the youngest from the Pliocene. The ranges of the length of the dp4 and m3 relevant for the discussion of *Sayimys* assemblages are shown in chronological order (Text-figs 12, 13). The length of the DP4 and M3 show a very similar picture and are therefore not included. We follow Kordikova and de Bruijn (2001) in synonymizing *Prosayimys* BASKIN, 1996 and *Sayimys* WOOD, 1937. The geographical range of the genus is from Jebel Zelten, Libya in the west (Wessels et al. 2003) to Jianghu province in eastern China (Qui 2017). The genus is best known from the Siwaliks of Pakistan and India. Hereafter we discuss the formally named species of *Sayimys*, starting with the oldest known species with a typical *Sayimys* morphology.

***Sayimys flynni* (BASKIN, 1996)**

Original combination. *Prosayimys flynni* BASKIN, 1996.

Holotype. A left m3 no 295.

Type locality. Z113 Zinda Pir dome, Pakistan; age of the site: late Oligocene, 23–26 Ma. See Lindsay and Flynn (2016) for correlation of this site to the GPTS scale.

Paratypes. 43 cheek teeth representing all tooth positions, unfortunately the dp4 is represented by two damaged and worn specimens only.

Discussion. These small teeth represent the oldest *Sayimys* species. The size ranges of dp4 and m3 are in Text-figs 12, 13. The badly worn and damaged dp4 figured in Baskin (1996) does not show a clear mesolophid, but it has been described as having one. All fifteen known lower molars have a well-developed mesolophid. The m1–2 shown by Baskin (1996: pl. 1, fig. D) has a cusp-shaped metaconid with a narrow connection to the protoconid, a feature seen as well in *Sayimys hintoni* n. sp. and *S. chinjiensis* (see below).

***Sayimys minor* DE BRUIJN, HUSSAIN et LEINDERS, 1981**

Holotype. A left m1–2 no 313.

Type locality. H.-GSP116, Murree Formation near Banda Daud Shah, Pakistan; age of the site: 18.5–19.5 Ma (Baskin 1996).

Paratypes. One damaged dp4, one m3 and one M1–2.

Discussion. A well-developed mesolophid is present in the dp4, but absent in the m1–2 and m3. The sizes of the specimens are like those of *Sayimys flynni*, or slightly larger.

This small collection of only four molars has been the subject of some discussion. Baskin (1996) suggested that the rather worn M1–2 is too large to fit in the same species as the other three teeth, without testing the homogeneity of the sample. The m1–2 and M1–2 of all large *Sayimys* populations have a large size variability if first and second molars are not separated (Tab. 2). This M1–2 may very well be a large second molar belonging to the same species as the other three teeth. Wang (1997) suggested that *Sayimys minor* could be a junior synonym of *S. intermedius* (Sen and Thomas 1979), because these species are similar in size, the only difference being the presence of a mesolophid in the single dp4 of *S. minor* and absence of this lophid in the single known dp4 of *S. intermedius*. But, as Baskin (1996: 41) mentioned: “persistence of a rodent species over 5 million years and 3,500 km distance would be highly unusual”, and we therefore hesitate to follow Wang. López-Antoñanzas and Sen (2003, 2004) subdivided the sample of *S. minor* from the type locality (only four teeth) into two or three species. The holotype (the m1–2, no 313) was included in *S. intermedius* (Sen and Thomas 1979) because “this molar cannot be differentiated from the equivalent tooth of *S. intermedius*”. The dp4 and m3 were separated from the m1–2 for unknown reasons, and included into *S. baskini* LÓPEZ-ANTOÑANZAS et SEN, 2003, see below. It is not clear in this publication how to classify the fourth tooth in the sample from the type locality (the large M1–2). The clear remark by Munthe (1980) on the large variability in *Sayimys* was here completely forgotten or ignored. In our opinion, the assemblage from H.-GSP116 (Murree Formation) is homogenous, and there is no valid reason to split up the small collection of *S. minor* and include the holotype in *S. intermedius*, and thus to synonymize *S. minor* and *S. intermedius*.

***Sayimys baskini* LÓPEZ-ANTOÑANZAS et SEN, 2003**

Holotype. An isolated right P4.

Type locality. Y747, Potwar Plateau, Pakistan; age of the site: 18.3 Ma.

Additional material from the type locality. 52 cheek teeth, representing all tooth positions except DP3.

Other localities with *Sayimys baskini*. According to López-Antoñanzas and Sen (2003): site Y721 Potwar Plateau, Pakistan and site H.-GSP116 (Banda Daud Shah, the type locality of *S. minor*).

Discussion. The collections from the type locality Y747 and from Y721 were studied by Baskin (1996). He concluded that the specimens from these two sites may represent a new species, but refrained from naming it because awaiting additional material of *Sayimys minor* from its type locality in the Murree Formation at Banda Daud Shah. However, López-Antoñanzas and Sen (2003) did not have this restraint, and described the species *S. baskini* with type locality Y747, and included specimens from Y721. Not having studied the collection from Pakistan themselves,

López-Antoñanzas and Sen (2003) refer to Baskin (1996) for figures, description and measurements. The selection of the P4 as holotype is unfortunate, as it is morphologically the most variable element in large *Sayimys* populations. Regrettably, the published figures in Baskin (1996) are simplified line drawings, inadequate for a good evaluation of dental morphology. Baskin writes that the single unworn dp4 has a short mesolophid, its hypolophid is transversely directed, lower molars lack a mesolophid, the “M1–2 lack an anteroloph”, thus the paraflexus is absent and proto- and anteroloph are fused. Unfortunately, the only M1–2 of *S. minor* is rather worn, so the anteroloph is completely fused with the protoloph. We conclude that without more material from the type locality of *S. minor* that can ascertain the specific difference, *S. baskini* is a junior synonym of *S. minor*.

***Sayimys obliquidens* BOHLIN, 1946**

Holotype. A part of a mandible with damaged and worn cheek teeth, no 268.

Type locality. The bad-lands near Taben-Buluk, Gansu Province, China; age of the site: middle (13 Ma?) Miocene. Taben-Buluk is now known as the Danghe area. The fossils described are surface finds from several locations in a tectonized area. Bohlin himself was unsure if all his material belonged to the same species, for a discussion, see Wang (1997), who concluded that all material can be included in the same species.

Paratypes. If all material described by Bohlin is included: Tb 254 right upper tooth row, Tb 261 right upper tooth row, Tb 279a partial skull, Tb 279b lower tooth row, TB 268 a left mandible with damaged molars.

Discussion. The geology of the Taben-Buluk (Danghe) area was studied by Wang et al. (2003), who were unable to fit Bohlin’s *Sayimys* locations precisely into their sections, which span an age from 24 to 10 Ma. They state that three of the Bohlin localities are close to their fossil site Dh199913, correlated to the geomagnetic polarity timescale at 13 Ma, making the Taben-Buluk *Sayimys obliquidens* some 5 Ma younger than previously assumed. The material described and measured by Bohlin is of large size, in the lower-end of the range of *S. giganteus*, however, the m3 is in the high-end part of the range (Text-fig. 13). Considering the doubts about the homogeneity of the collection, and the exact location(s) and age of the type locality *S. obliquidens* is a nomen dubium, we therefore ring-fence the species name, that is, restrict it to its holotype.

The early Miocene material from Aktau (Kazakhstan) described by Kordikova and de Bruijn (2001) as *Sayimys* aff. *obliquidens* is much smaller. It shows a long mesolophid in the m2, but not in the m1, like in the holotype from Taben-Buluk. A more appropriate classification for the material from Aktau is *S. aff. minor*.

***Sayimys intermedius* (SEN et THOMAS, 1979)**

Original combination. *Metasayimys intermedius* SEN et THOMAS, 1979.

Holotype. A part of a left mandible with dp4–m1–m2.

Type locality. Al Jadidah (Saudi Arabia); age of the site: middle Miocene, 14? Ma.

Discussion. This adequately described and figured species by López-Antoñanzas and Sen (2004) is known by its holotype only. *Sayimys intermedius* is small (Text-fig. 12), Baskin (1996) noted that the length of m1 is not 2.9 mm as described, but 2.09 mm. A mesolophid is neither present on the dp4 nor on the two molars.

***Sayimys assarrarensis* LÓPEZ-ANTOÑANZAS et SEN, 2004**

Holotype. A fragmentary left maxilla with P4–M2.

Paratypes. Some 18 isolated cheek teeth.

Type locality. As-Sarrar, Dam Formation, Saudi Arabia; assigned age of the site: later part of the early Miocene, 15–17 Ma.

Discussion. This small species is similar in size to *Sayimys intermedius*. The As Sarrar locality is slightly older than the type locality of *S. intermedius*. The single reasonably preserved dp4 of *S. assarrarensis* shows a well-developed mesolophid and a slightly elongated anteroconid. Considering the large variation in dental morphology and size of large *Sayimys* assemblages, we consider *S. assarrarensis* a junior synonym of *S. intermedius*. More material is needed from the type localities to ascertain specific differences, if any.

***Sayimys sivalensis* (HINTON, 1933)**

Original combination. *Pectinator sivalensis* HINTON, 1933.

Holotype. A left partial mandible with m2 and m3, see Black (1972) for a good illustration.

Type locality. Surface find near Chinji village (Pakistan), Chinji Formation; the age of the formation near Chinji village ranges from 14.3 to 10.8 Ma (Johnson et al. 1985).

Discussion. Munthe (1980) allocated a fine collection of isolated *Sayimys* teeth from the upper part of the Chinji Formation near Daud Khel (age approximately 11–10 Ma; Jacobs et al. 1989) to *S. sivalensis*. He provided an emended diagnosis of *S. sivalensis* based on the Daud Khel assemblage.

Baskin (1996) recognized two species of *Sayimys* from the area near Chinji. He allocated the older relatively low-crowned to *S. sivalensis* and described the younger relatively high-crowned as *S. chinjiensis*. This *S. sivalensis* material comes from thirteen small assemblages in the Kamlial and the lower Chinji Formations (age range 15.1–13 Ma), while eight small collections from the upper Chinji and Nagri Formations (age range 12.1–9.1 Ma) were included in *S. chinjiensis*. The Daud Khel assemblage described by Munthe was allocated to *S. chinjiensis*. Baskin (1996) considered the holotype of *S. sivalensis* primitive because of the position of its masseteric crest. He therefore assumed that it came from the lower Chinji beds. We consider *Sayimys sivalensis* a nomen dubium; its holotype is of unknown location and lacks diagnostic criteria, whereas the intraspecific variability

of masseteric crest is not known. We therefore restrict the name *S. sivalensis* to the holotype, and create a new species to house the assemblages with relatively low-crowned molars.

***Sayimys hintoni* n. sp.**

Text-figs 14, 15

Holotype. An isolated dp4 no H.-GSP82.14a no 3001, Text-fig. 14; shown by de Bruijn et al. (1989) on pl. II, fig.10. Temporarily housed in Faculty of Earth Sciences, University Utrecht, the Netherlands.

Derivatio nominis. Named after M. A. C. Hinton who described *Pectinator sivalensis*.

Type locality. H.-GSP81.14a, lower Manchar Formation, Sind, Pakistan; early Miocene, age approximately 18 Ma (Wessels 2009).

Occurrences. H.-GSP82.06, H.-GSP82.07 and H.-GSP82.14. Lower Manchar Formation, Sind, Pakistan; early Miocene (approximate range 19.5–16.3 Ma; Wessels 2009). Assemblages from Z120 and Z122 (Baskin 1996).

Material and measurements. See Tab. 5 for type locality H.-GSP81.14a, Tab. 6 for locality H.-GSP81.07, Tab. 7 for locality H.-GSP81.06. See the table in de Bruijn et al. (1989: 196). Text-fig. 16 shows length-width scatter diagrams of the molars of *Sayimys hintoni* and *S. cf. minor*.

Diagnosis. *Sayimys hintoni* is relatively small. The anteroconid of the dp4 is elongate, ovoid in shape, and tends to form low ridges to metaconid and protoconid, anterolophid absent. A long confluent diagonal ridge is formed by the protoconid, ectolophid, hypolophid and entoconid. The metalophid of most m1–3 has a narrow-constricted connection to the protoconid (arrow in Text-fig. 14). In upper molars the para- and metaflexus are short and poorly developed.

Differential diagnosis. *Sayimys hintoni* is larger than *S. flynni* and *S. intermedius*, roughly similar *S. minor* and *S. baskini*, but smaller than *S. obliquidens* and *S. giganteus*; it is slightly smaller and partially overlapping in size with *S. chinjiensis*. It differs from *S. flynni*, *S. minor*, *S. obliquidens* and *S. intermedius* in the absence of a mesolophid. Its dp4 is different from *S. flynni*, *S. minor*, *S. obliquidens* and *S. intermedius* in the long, smooth and confluent diagonal lophid formed by protoconid, ectolophid, hypolophid and entoconid, and in the narrow connection between protoconid and metaconid. It differs from *S. intermedius* and *S. chinjiensis* in the shape of the anteroconid. Assemblages of *S. chinjiensis* tend to have dp4 and lower molars with more oblique lophids, whereas para- and metaflexus in the upper molars are more reduced, or absent. In contrast to *S. hintoni*, almost all dp4 of *S. chinjiensis* have a well-developed anterolophid.

Discussion. In the *Sayimys* assemblage of H.-GSP81.14a, type locality of *S. hintoni*, the two smallest lower molars are subject to discussion. The outline of the teeth suggests that they could be m1 or m3. The lack of a posterior interdental facet indicates m3; if so, these m3 are too small to fit the assemblage of *S. hintoni* n. sp. Text-fig. 16

Table 5. Measurements in mm of *Sayimys hintoni* n. sp. from the type locality H.-GSP81.14a (lower Manchar Formation, Sind, Pakistan) and of *S. cf. minor* from the same site.

	Length				Anterior width			
	range	average	SD	N	range	average	SD	N
<i>S. hintoni</i>								
D4	1.62–1.88	1.763	0.101	7	1.50–1.80	1.667	0.104	7
P4	1.20–1.42	1.290	0.080	6	1.80–2.07	1.920	0.110	6
M1–2	1.79–2.17	2.024	0.142	8	2.02–2.36	2.188	0.110	8
M3	1.89–2.21	2.018	0.136	4	2.13–2.40	2.298	0.116	4
d4	1.93–2.30	2.133	0.188	3	1.18–1.37	1.305	0.090	3
p4	1.51–1.58	1.545	–	2	1.51–1.54	1.525	–	2
m1–2	1.85–2.50	2.174	0.217	7	1.59–2.22	1.844	0.229	7
m3	1.98–2.45	2.235	0.197	6	1.92–2.29	2.092	0.159	5
<i>S. cf. minor</i>								
M3	–	1.700	–	1	1.92	–	–	1
m3	1.66–1.85	1.755	–	2	1.67	1.42–1.92	–	2

Table 6. Measurements in mm of *Sayimys hintoni* n. sp. from H.-GSP81.07 (lower Manchar Formation, Sind, Pakistan).

	Length			Width		
	range	mean	N	range	mean	N
d4	1.80–1.97	1.89	2	1.06–1.11	1.09	2
m1–2	2.05–2.38	2.22	2	1.79–2.01	1.90	2
m3	–	2.13	1	1.68–1.85	1.77	2

compares the *Sayimys* molars of locality H.-SGP14a with the outline of the size clouds of m1 and m2–3 from the large sample of *S. chinjiensis* from H.-SGP82.24. The two size-cloud outlines are indicative of the size and variation of m1 and m2–3, and demonstrate that the two m3 identified as *Sayimys cf. minor* are much smaller than those of *S. hintoni* n. sp. The molars are the smallest m3 of *Sayimys* known (Text-fig. 13); these differ in morphology from *S. hintoni* in their short V-shaped mesoflexid and a triangular metalophid (Text-fig. 14). We have also identified a small unworn M3 that could be included in *S. cf. minor* (Text-figs 15, 16). The M3 of *Sayimys* species have the same length and width as the M2 (Text-figs 5, 17), therefore this small M3 does not fit in with the group of probable M3 of *S. hintoni* in Text-fig. 16.

Baskin (1996) compared 34 isolated cheek teeth from five sites, two in the Zinda Pir area (Z120 and Z122) and three on the Potwar Plateau (Y591, Y592 and Y802), to *Sayimys intermedius*. The measurements of these are not presented for each location separately, but have been lumped into one table (Baskin 1996: tab. 4). The anteroconid of the four dp4 in this collection is ovoid in shape (Baskin 1996: fig. 5h); the entoconid is cusate with a narrow connection to the protoconid (Baskin 1996: fig. 5i, j, k) and the mesoflexid is long and forward directed, the paraflexus and metaflexus of M1–2 are short, with wear the paraflexus persists longer than the metaflexus. These teeth are morphologically and in size like *Sayimys hintoni*, and are labelled *S. hintoni* in Text-figs 12, 13.

Sayimys chinjiensis BASKIN, 1996

H o l o t y p e . Left mandible fragment with p4–m1.

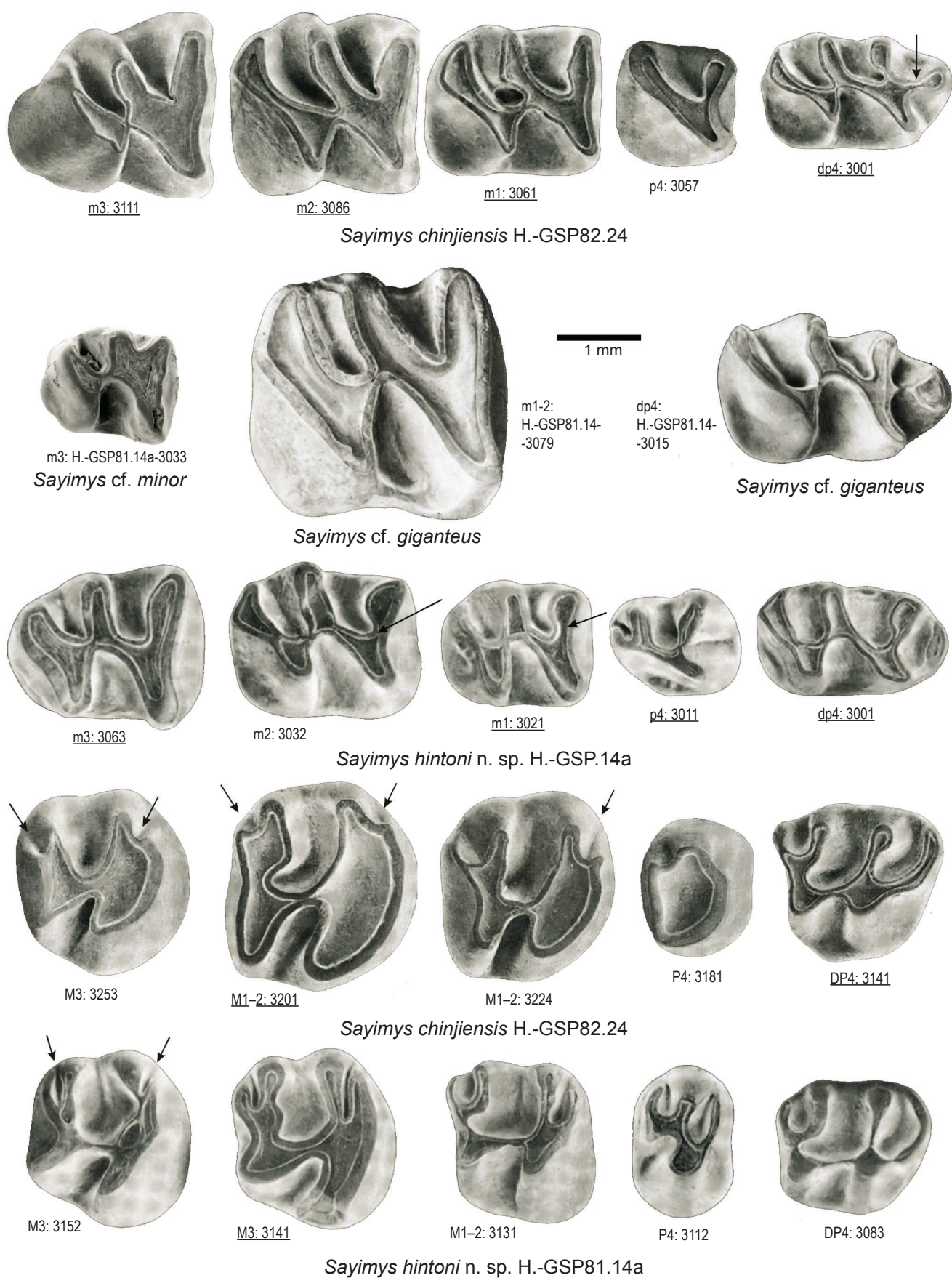
P a r a t y p e s . Two P4, one M1–2, one p4, one m3.

T y p e l o c a l i t y . Site Y634, upper Chinji Formation, Potwar Plateau, Pakistan; age of the site: 11.9 Ma.

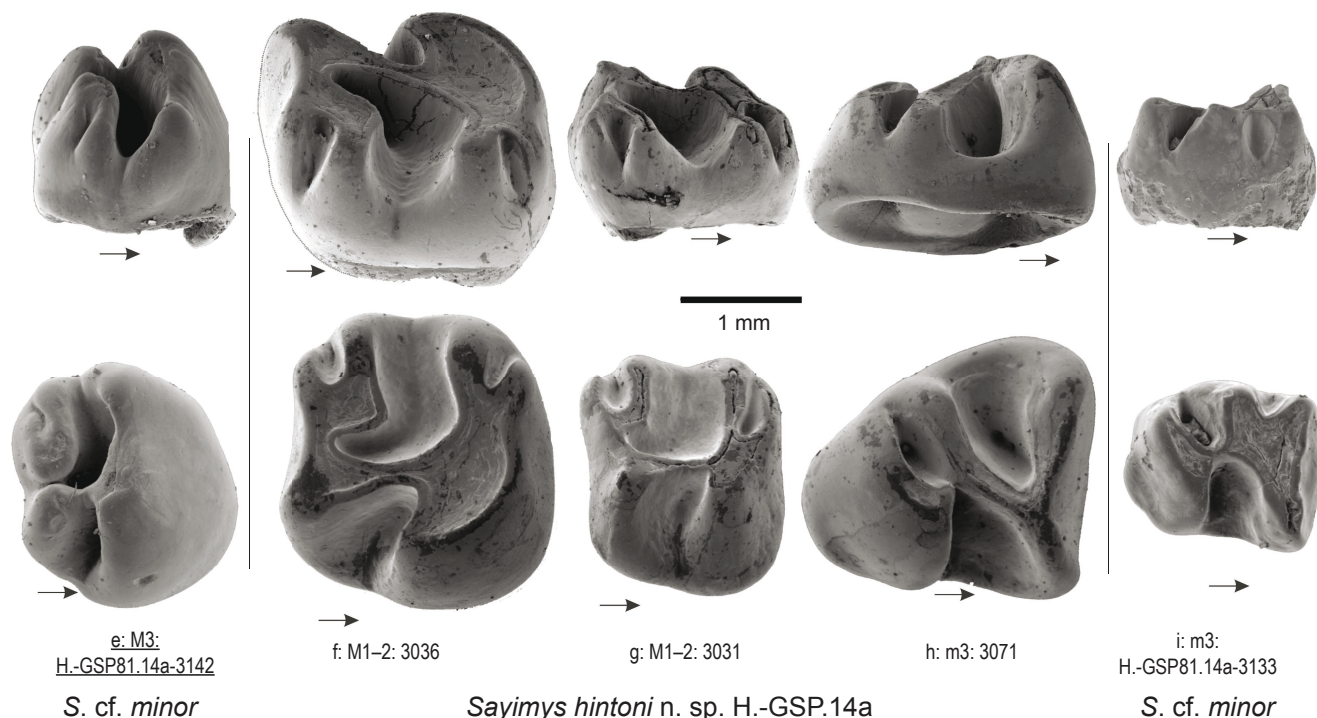
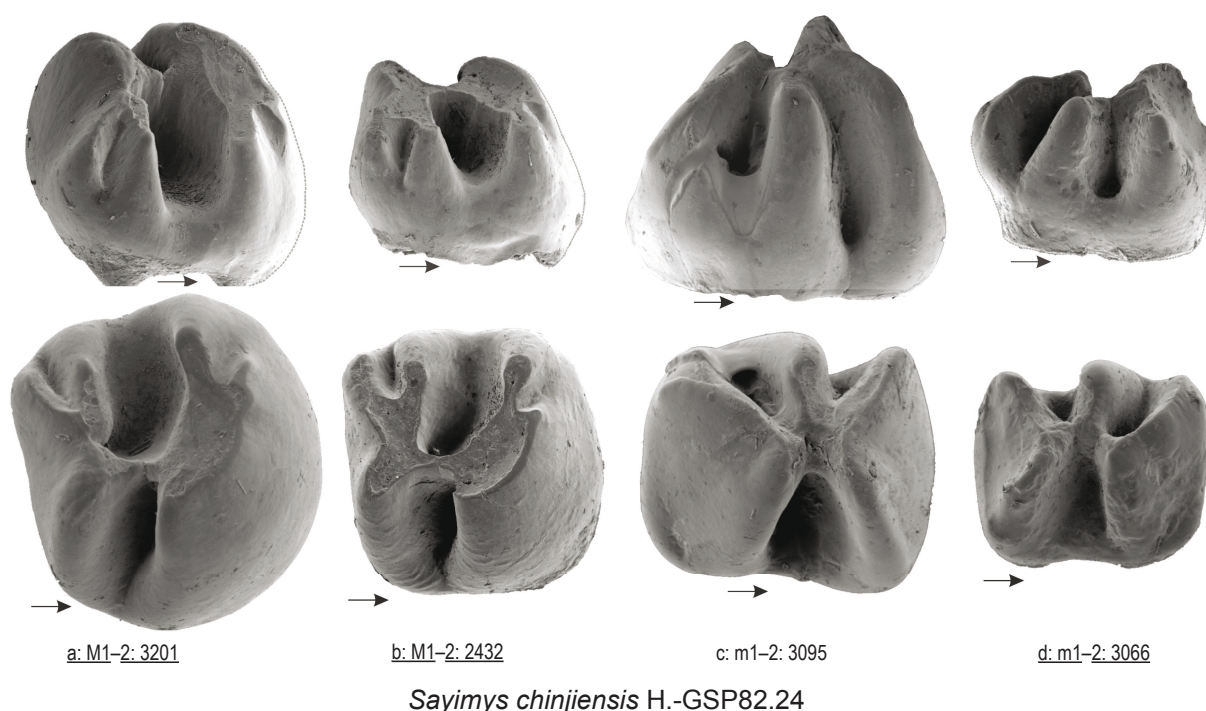
O t h e r s i t e s . Eight sites in the upper Chinji and Nagri Formations (age range 12.1–9.1 Ma; see Baskin 1996), Daud Khel, upper Chinji Formation, age according to Jacobs et al. (1989) is 11–10 Ma (see Munthe 1980).

Table 7. Measurements in mm of *Sayimys hintoni* n. sp. from H.-GSP81.06 (lower Manchar Formation, Sind, Pakistan).

	Length				Width			
	range	mean	SD	N	mean	range	SD	N
DP4	1.63–1.70	1.663	0.036	3	1.563	1.52–1.60	0.040	3
M1–2	1.78–2.19	1.993	0.186	4	2.270	2.10–2.45	0.171	4
M3	1.77–1.96	1.843	0.102	3	2.087	1.94–2.25	0.156	3
p4	1.31–1.32	1.315	–	2	1.265	1.22–1.31	–	2
m1–2	2.00–2.23	2.078	0.104	4	1.770	1.64–20.2	0.174	4
m3	1.90–1.95	1.925	–	2	1.675	1.64–1.71	–	2



Text-fig. 14. Cheek teeth of *Sayimys hintoni* n. sp. and *S. cf. minor* from H.-GSP81.14a, *S. cf. giganteus* from H.-GSP81.14 and *S. chinjiensis* from H.-GSP82.24.



Text-fig. 15. Lightly worn molars of *Sayimys hintoni* n. sp. (f, g, h) and *S. cf. minor* (e and i) from locality H.-GSP81.14a and *S. chinjiensis* from H.-GSP82.24 (a, b, c, d). Upper molars: occlusal surfaces and labial sides, lower molars occlusal surfaces and lingual sides. Side views horizontally-mirrored, anterior indicated by arrows.

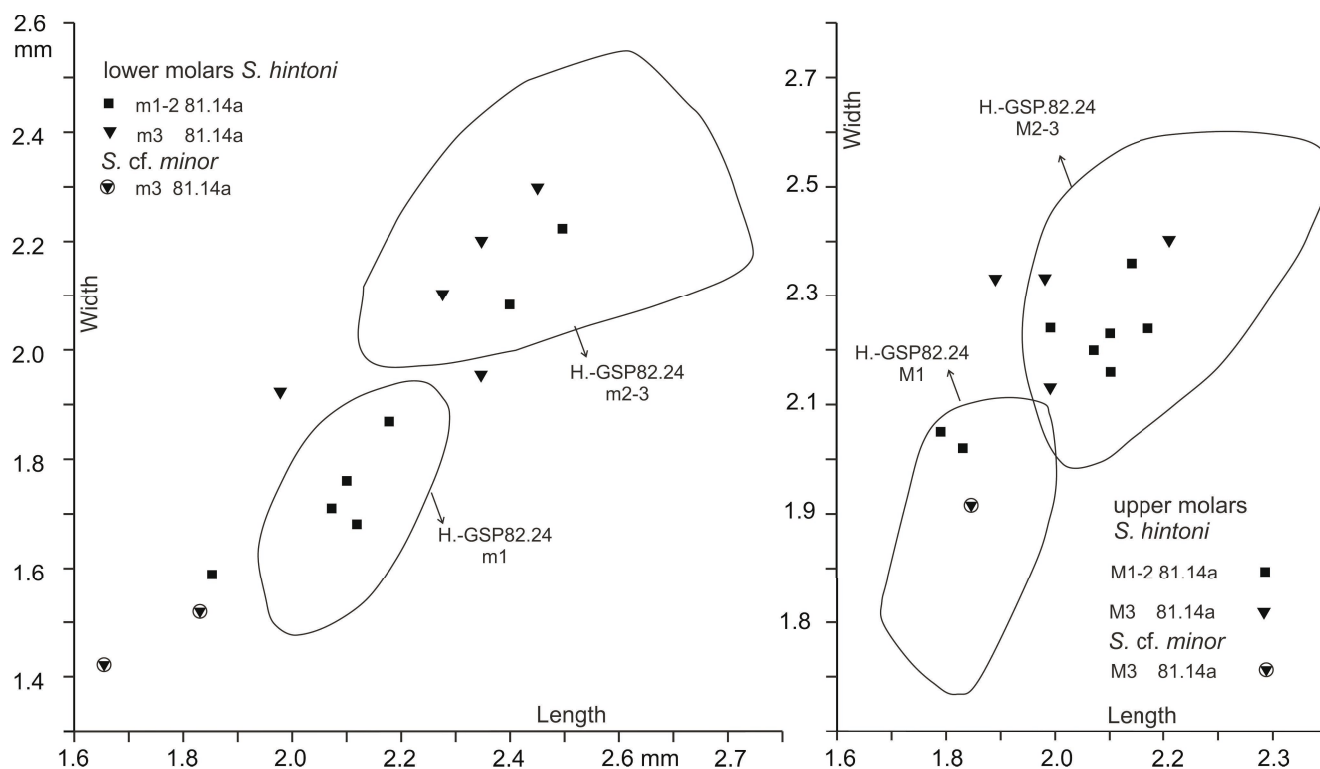
H.-GSP107, Chinji Formation near Banda Daud Shah (Wessels et al. 1982), age ~14 Ma (Jacobs et al. 1989, Wessels 2009).

H.-GSP82.24, lower Manchar Formation, age 13.5 Ma (Wessels 2009).

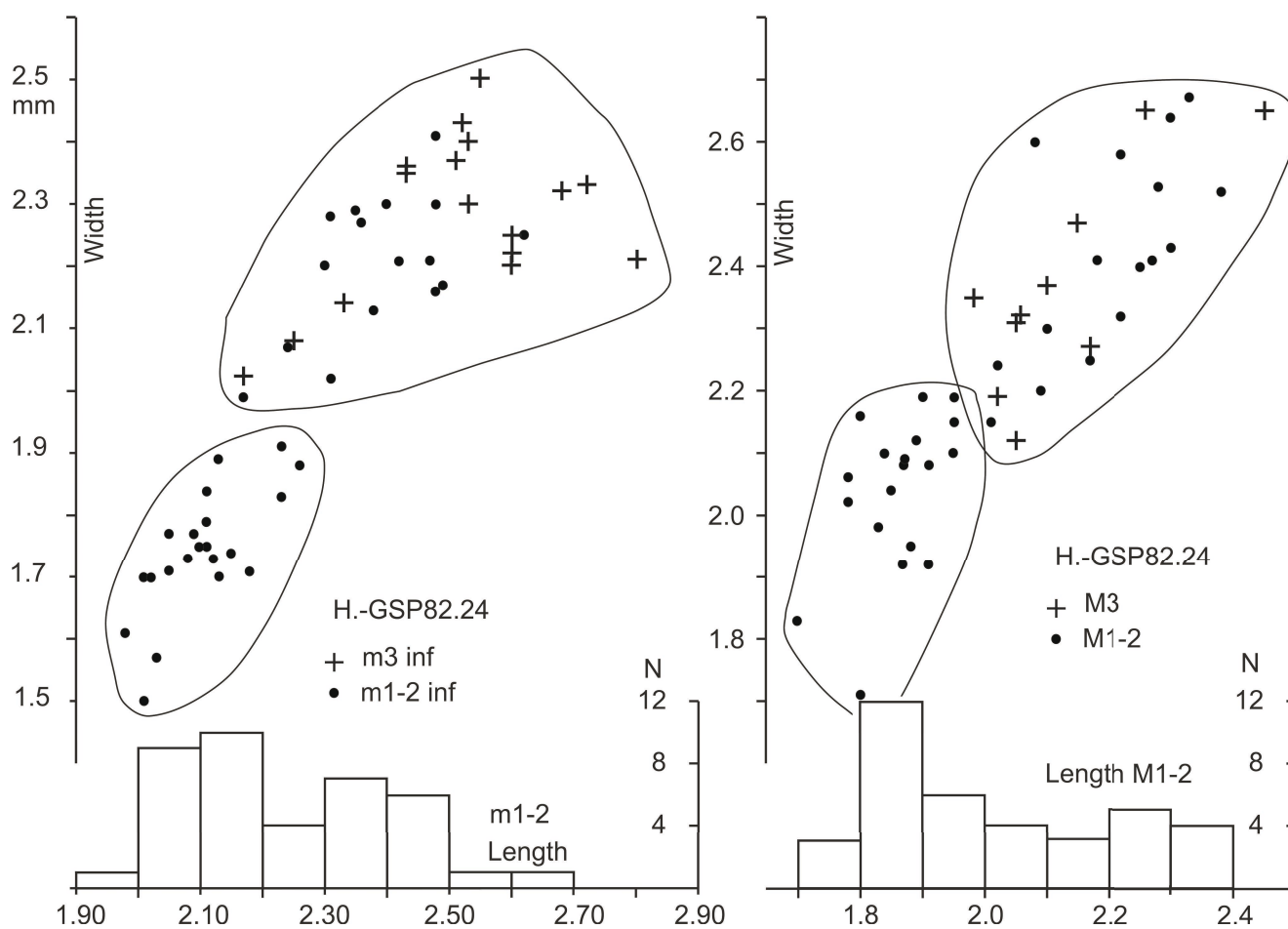
Original diagnosis. “Moderately high crowned cheek teeth with relatively thick enamel base. The paraflexus is absent on the upper molars. A short metaflexus is present on the M1 and M2, it is usually absent on M3. On m3 the

metastrid [= metaflexid in lingual view] extends relatively deeply on the internal face” (Baskin 1996).

Emended diagnosis. dp4 with rounded anteroconid and well-developed anterolophulid in medial position. In dp4 and molars, the mesolophid is absent, hypolophid is oblique, and the metalophulid-protoconid connection is narrow. A confluent, long diagonal lophid is formed by protoconid, ectolophid, hypolophid and entoconid in the dp4. Lophids of the lower molars are



Text-fig. 16. Length-width scatter diagram of isolated molars of *Sayimys hintoni* n. sp. and *S. cf. minor* from sites H.-SGP 81.14a (lower Manchar Formation, Sind, Pakistan) with the size-cloud outlines of molars of the large sample of *S. chinjiensis* from H.-GSP.24 shown in Text-fig. 17.



Text-fig. 17. Length-width scatter diagram and histograms of isolated molars of *Sayimys chinjiensis* from locality H.-SGP82.24 in the lower Manchar Formation (Sind, Pakistan).

Table 8. Measurements in mm of *Sayimys chinjiensis* from H.-GSP82.24 (lower Manchar Formation, Sind, Pakistan). The width is the maximum width.

	Length				Posterior width			
	range	average	SD	N	range	average	SD	N
DP4 sup	1.65–2.05	1.855	0.089	26	1.45–2.02	1.704	0.108	26
P4 sup	1.02–1.38	1.196	0.142	5	1.53–1.96	1.762	0.174	5
M1 sup	1.70–1.95	1.861	0.062	21	1.71–2.19	2.028	0.122	21
M2 sup	2.01–2.38	2.200	0.113	16	2.15–2.67	2.416	0.163	16
M3 sup	1.98–2.45	2.129	0.139	10	2.12–2.65	2.370	0.196	10
dp4 inf	1.95–2.50	2.274	0.132	24	1.06–1.56	1.375	0.124	24
p4 inf	1.26–1.69	1.493	0.130	12	1.24–1.75	1.521	0.126	12
m1 inf	1.98–2.26	2.104	0.077	21	1.50–1.91	1.742	0.101	21
m2 inf	2.05–2.62	2.370	0.133	18	1.99–2.41	2.204	0.112	16
m3 inf	2.17–2.80	2.498	0.164	18	2.02–2.50	2.272	0.130	17

strongly diagonal. Upper molars have poorly developed paraflexus and metaflexus, disappearing early with wear; these flexids may be totally absent in molars of assemblages from the younger Nagri Formation.

Discussion. Unfortunately, the illustrations in Baskin (1996) are inadequate. Moreover, not all tooth positions are known from the type locality. In addition to the type locality, Baskin allocated 75 specimens from eight localities to this species. The eight assemblages are thus small; the largest has 17 teeth, the smallest two. The eight sites are in the upper Chinji Formation and overlying Nagri Formation, and range in age from 12.1 to 9.1 Ma. Baskin (1996) defined this species as having no paraflexus (and thus no anteroloph) in the upper molars, and in being more hypsodont than those of *Sayimys sivalensis*. It appears from the description that the paraflexus is absent in molars from the Nagri Formation. Baskin assigned the large collection from Daud Khel (described by Munthe 1980 as *S. sivalensis*) to *S. chinjiensis*.

Using measurements obtained from Baskin, López-Antoñanzas and Sen (2003) plotted the height of M1–2 and m3, and observed that the highest M1–2 are those classified in *Sayimys chinjiensis*, but the overlap with *S. sivalensis* is large; the m3 do not show a difference in height. The differences between the assemblages allocated to the two species are relatively small, and considering the large variability in *Sayimys* species, small samples are difficult to allocate. López-Antoñanzas and Sen (2003) therefore synonymized *Sayimys chinjiensis* with *S. sivalensis*. This decision is unfortunate, because *S. chinjiensis* has a clear type locality and *S. sivalensis* does not. Moreover, the holotype of *S. sivalensis* is not considered diagnostic. We therefore do not follow López-Antoñanzas and Sen, and maintain *S. chinjiensis* and restrict the name *S. sivalensis* to its holotype (see above). With the inclusion of the Daud Khel assemblage in *Sayimys chinjiensis*, this species is morphologically well defined. We also include the large assemblage from H.-GSP82.24 from the lower Manchar Formation (described by de Bruijn et al. 1989, illustrated here in Text-figs 14, 15), and from site H.-GSP107 Banda Daud Shah (Wessels et al. 1982) in *Sayimys chinjiensis*. Text-fig. 17 shows length-

width scatter diagrams of *S. chinjiensis* from H.-GSP82.24, and Tab. 8 the measurements.

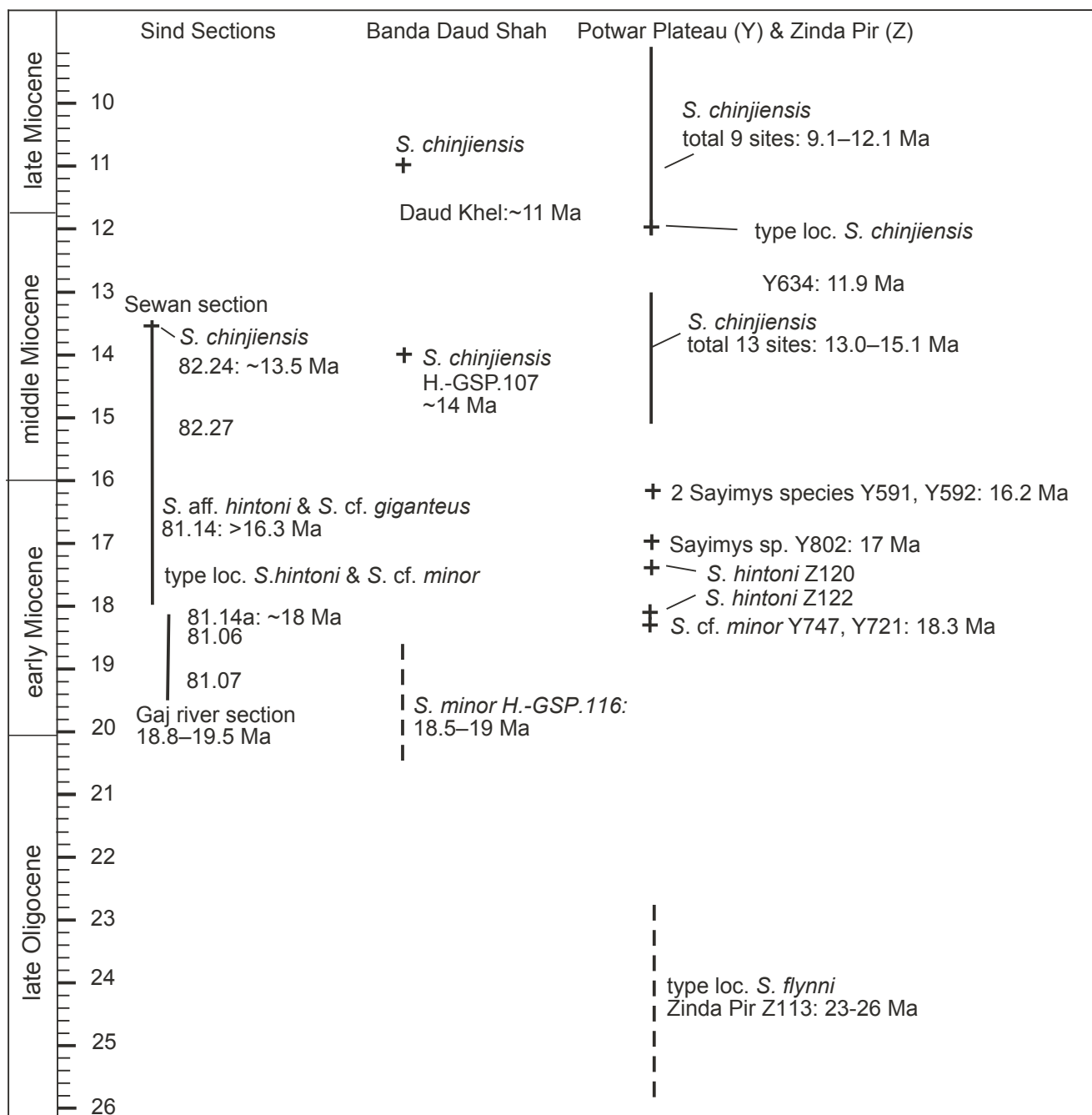
Our designation H.-GSP14a in the lower Manchar Formation as the type locality of *S. hintoni* n. sp. is pragmatic. The material from this site is well described and figured (de Bruijn et al. 1989), and the morphotypes are sufficiently different from the younger *S. chinjiensis* and the older *S. baskini*, *S. minor* to allow classification of all but the smallest assemblages.

***Sayimys perplexus* WOOD, 1937, *S. badauni* VASISHAT, 1985 and *S. sihingensis* QIU, 2017**

Comments. Baskin (1996) remarked that *Sayimys* is rare in Siwalik deposits younger than 9 Ma. *Sayimys perplexus* WOOD, 1937 with type locality near Haritalyangar (India) in the Nagri Formation (age approx. 7 Ma; Baskin 1996), has been considered a junior synonym of *S. sivalensis* by some specialists (e.g. Munthe 1980). *Sayimys badauni* was described by Vasishat (1985) from the Pliocene Tatrot Formation, near Badauni (India). See López-Antoñanzas and Sen (2003) and López-Antoñanzas and Knoll (2011) for some remarks on these two poorly known species. These two occurrences extend the stratigraphic range of *Sayimys* in the Siwaliks into the Pliocene. The recently described *Sayimys sihingensis* (Qiu 2017) from the later part of the early Miocene, Jiangsu Province (China) is based on very limited material. This record extends the geographical range of the genus to eastern China. Judging from the figures, *S. sihingensis* seems more hypsodont than the time-equivalent material from Pakistan.

Evolutionary trends and biogeography

The best succession of *Sayimys* is known from the early and middle Miocene of Pakistan. After a discussion of the chronology of the faunas in Pakistan with ctenodactylids (Text-fig. 18), the evolutionary trends observed in this succession are briefly discussed. The localities with fossil rodents from the Potwar Plateau and the Zinda Pir Dome have been correlated to the magnetostratigraphic time scale, and their ages can be expressed in Ma (Text-fig.



Text-fig. 18. Chronostratigraphic table showing the positions of the *Sayimys*-bearing localities in three areas in Pakistan. In the Sind Province (lower Manchar Formation) are the localities in the Sehwan section H.-GSP82.14, -82.27, -82.14, and -82.14a; in the Gaj River section are H.-GSP81.06 and -81.07. In the Banda Daud Shah area are the localities of Daud Khel, H.-GSP107 and the site at the base of the Murree Formation H.-GSP116. On the Potwar Plateau and in Zinda Pir are the Y and Z localities.

18). Magnetostratigraphic work has not been carried out in the Sind and Banda Daud Shah areas, but biostratigraphic correlations with the Zinda Pir and Potwar Plateau allowed us to fit these sites into the chronology of the Potwar Plateau and Zinda Pir Dome. For the construction of Text-fig. 18, Lindsay et al. 2005, Lindsay and Flynn (2016), Métais et al. (2009), Wessels and de Bruijn (2001), Baskin (1996) and Jacobs et al. (1989) were consulted.

A size increase can be observed from the oldest known species *Sayimys flynni* (age approx. 23–26 Ma) to *S. chinjiensis* (age approx. 12 Ma) as is shown in Text-figs 12 and 13, however, the increase does not seem regular.

Crown height correlates strongly with the length of the molars, but a relative increase in crown height from *S. flynni* to *S. chinjiensis* is difficult to demonstrate, due to lack of measurements of unworn teeth. However, when comparing M1–2 with the same stage of wear from an assemblage of *S. hintoni* with those from an assemblage of *S. chinjiensis*, those of the younger assemblage are higher crowned (de Bruijn et al. 1989).

The oldest assemblage *Sayimys flynni* has a mesolophid on dp4, m1–2 and a well-developed long paraflexus on upper molars; younger assemblages of *Sayimys* have lost the mesolophid.

Sayimys minor (= *S. baskini*) is small. The single available P4 has no anteroloph, however, this feature is variable in *Sayimys* assemblages. Further, Baskin (1996) states that most M1–2 have no anteroloph, that is to say, the paraflexus is poorly developed or absent, suggesting that the simplification of the upper molars started with *S. minor*. This simplification (reduction of the paraflexus and metaflexus) continued in *Sayimys hintoni* and *S. chinjiensis*. In the upper molars, in particular the M3, the paraflexus is absent or not much more than a groove on the antero-labial side of the tooth, and thus the anteroloph has disappeared. The metaflexus is poorly developed as well, even in lightly worn specimens, leaving the posteroloph as a small spur.

Another morphological trend is in the development of the anteroconid on the dp4. That of *Sayimys hintoni* is elongate, or crescent shaped with no, or relatively rare presence of an anterolophulid; that of *S. chinjiensis* is rounded, with mostly a well-developed anterolophulid. Further in the dp4, the hypolophid, ectolophid, protoconid and anterolophulid developed into a prominent confluent-curved oblique ridge. A similar development is seen in the molars, for which de Bruijn et al. (1989) showed that the lophids of m1–2 of *S. chinjiensis* in site H.-GSP82.24 are more oblique than those of the older *S. hintoni* in sites H.-GSP81.14 and -81.14a.

Baskin (1996) suggested the presence of two species of *Sayimys* in the Potwar plateau and Zinda Pir sites during the latest part of the early Miocene (shown in Text-fig. 18 as *S. cf. minor* and *Sayimys* sp.); the sites Y991 and Y592 have two species that have a small size difference, and are supposed to differ in morphology. All these *Sayimys* assemblages consist of a few isolated cheek teeth only. The intraspecific variation is thus unknown; this, combined with poor illustrations and the merged size tables in Baskin hampers a thorough evaluation.

De Bruijn et al. (1989) described from site H.-GSP14 (Text-fig. 18) dp4 and m1–2 that are far too large to fit the assemblage of *Sayimys* aff. *hintoni* from that location. These teeth are indicated on Text-fig. 12 and illustrated in Text-fig. 14 as *Sayimys* cf. *giganteus*, because they are similar in size to *S. giganteus*, but the morphology of the anteroconid in the dp4 differs from that of *S. giganteus* in showing a tendency to form an anterolophulid. The small *S. cf. minor* occurs together with *S. hintoni* n. sp. in H.-GSP81.14a (Text-fig. 14). The two assemblages H.-GSP81.14a and H.-GSP81.14 thus clearly show the presence of at least three roughly contemporaneous *Sayimys* species in the early Miocene of Pakistan.

The assemblages *Sayimys hintoni* and *S. chinjiensis* from the Siwaliks differ from contemporaneous *Sayimys* assemblages from Turkey, Greece, Saudi Arabia and Northern Africa in some subtle, but clearly stable, morphological features. The dp4 of western assemblages do not have an anterolophulid; the dp4 and lower molars lack the constriction of the metalophulid where it connects to the ectolophid. In the dp4 of the Siwaliks species, the hypolophid tends to be diagonally oriented, and together with the ectolophid and the protoconid, form a confluent curved ridge; the m1 and m2 shows this character as well, but less clearly. This is not seen in the western species, where in particular in the dp4, the hypolophid tends to be transversely oriented. Siwalik species show a trend to reduce paraflexus and metaflexus in the upper molars, in particular in the M3. This reduction is not seen in

western assemblages. Caution is needed, because apart from Keseköy and Yapıntı, the western assemblages are small, and not all tooth positions are known.

Conclusions

The large collection of the high-crowned ctenodactylid *Sayimys giganteus* from the early Miocene site of Keseköy consists of at least 30 individuals; that of *S. aff. giganteus* from Yapıntı suggests of a minimum number of five individuals. The size of the collections of isolated cheek teeth permitted the differentiation of all molar positions. The overall dental morphology appears to be stable, but some characters, such as the mesolophid in dp4, used for species identification appear to show large intra-specific variation. The fourth premolars also show a rather variable morphology. The size of the cheek teeth (length, width and height) shows large ranges. The large number of cheek teeth allowed the calculation of reliable coefficients of variation. These can be used to estimate size ranges of small assemblages. Dental pattern and height of *Sayimys* cheek teeth change with wear; the large collection of *Sayimys giganteus* allowed definition of wear classes, and the changing dental pattern can be illustrated. The Yapıntı fauna is slightly younger than that of Keseköy, but its *Sayimys* is distinctly smaller. However, in dental morphology, these two assemblages are very similar.

Using the knowledge of the large *Sayimys* collections from Keseköy and Yapıntı, the *Sayimys* succession from the Himalayan foreland basin have been reviewed. The succession spans an age ranging from late Oligocene (about 26 Ma) till in the Pliocene. Formerly named species are discussed in the light of intra-specific variation. Depending on more material from the type localities to ascertain specific identity, *Sayimys baskini* is considered a junior synonym of *S. minor*, and *S. assarrarensis* is considered a junior synonym of *S. intermedius*. Since the type localities of *Sayimys obliquidens* and *S. sivalensis* are not known, and their type series are small, these names are considered nomina dubia and restricted to their holotypes. The early Miocene *Sayimys hintoni* n. sp. evolved into the middle and late Miocene *S. chinjiensis*. The middle Miocene *Sayimys* species from the Indian subcontinent are different from those of more western regions: Turkey, Greece and Saudi Arabia. *Sayimys* from the Indian subcontinent shows a trend toward larger size: increase in crown-height, simplification of the upper molars by reduction of the para- and metaflexus, to oblique lophids in lower molars and the development of an anterolophulid on the dp4. Most faunas seem to contain one ctenodactylid species, but two early Miocene faunas from the Manchar Formation in the Sind Province of Pakistan record three species: a very small species, *Sayimys* cf. *minor*, a medium-sized one, *S. hintoni* and the large *S. cf. giganteus*.

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Conflicts of interest: The authors declare that they have no conflicts of interests.

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