The succession of rodent faunas from the Mio/Pliocene lacustrine deposits of the Florina-Ptolemais-Servia Basin (Greece)*

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ABSTRACT: A series of successive rodent assemblages from lacustrine deposits in the intramontane Florina-Ptolemais-Servia Basin have been collected from various sections exposed in the lignite mines south of Ptolemais (Greece). The main interest of the assemblages studied is the extension of the currently known fossil rodent record in the region and integration of this record into the existing high-resolution age model based on magneto- and cyclostratigraphy, pollen data and radio-isotopic dating of intercalated volcanic ashes.

Except for new species of the otherwise African genus *Arvicanthis* and the genus *Microtodon*, all rodent species identified are known from Central- and Western European localities of similar age. Three assemblage types have been recognized. The composition of these faunas, in combination with pollen data, indicates different biotopes surrounding a lake. The stratigraphically oldest type is interpreted as representing a relatively dry environment. The second assemblage type indicates a swamp environment without extensive forests nearby. The youngest assemblage type suggests an open forest biotope.

The co-occurrence of endemic species of widespread genera and exotic immigrants, such as *Arvicanthis*, confirms the characteristic combination commonly known from Late Turolian rodent assemblages in the East Mediterranean.

It is shown that the Turolian/Ruscinian boundary is dated to the interval between 5.23-5.40 Ma, but is likely to be younger than the Messinian/Zanclian boundary (5.33 Ma). It is demonstrated that the entry of key taxa used for biostratigraphical correlation, *Promimomys* and *Mimomys*, is highly diachronous in different regions across Europe.

Key-words: *Miocene, Pliocene, rodents, integrated stratigraphy, Mediterranean.*

ΠΕΡΙΛΗΨΗ: Μια σειρά διαδοχικών τρωκτικών συναθροίσεων από τις λιμναίες αποθέσεις της ενδοορεινής λεκάνης Φλώρινα-Πτολεμαΐδα-Σερβία συλλέχθησαν από πλήθος τομών που εκτίθενται στα ορυχεία λιγνίτη στο νότο τμήμα της Πτολεμαΐδας (Ελλάδα). Το κύριο ενδιαφέρον των μελετώμενων συναθροίσεων έγκειται στην διεύρυνση των απολιθωμένων δεδομένων για τα τρωκτικά αυτής της περιόδου στην περιοχή και τη συμπλήρωση των στοιχείων με υψηλής ανάλυσης χρονολόγηση που βασίζεται στη μαγνητο- και κυκλοστρωματογραφία, παλυνολογική ανάλυση και ράδιο- ισοτοπική χρονολόγηση ηφαιστειακής τέφρας.

Εκτός από τα νέα είδη που ανήκουν στα αφρικανικά γένη *Arvicanthis* και *Microtodon*, όλα τα είδη των τρωκτικών που προσδιορίστηκαν είναι γνωστά από περιοχές παρόμοιας ηλικίας στην Κεντρική και Δυτική Ευρώπη. Αναγνωρίστηκαν τρεις τύποι συναθροίσεων. Η σύνθεση αυτών των πανίδων, σε συνδυασμό με τα παλυνολογικά δεδομένα, αποδεικνύουν διαφορετικούς βιότοπους που περιβάλλουν μια λίμνη. Ο παλαιότερος στρωματογραφικά τύπος συνάθροισης, αντιπροσωπεύει ένα σχετικά ξηρό περιβάλλον. Ο δεύτερος τύπος συνάθροισης υποδηλώνει ένα ελώδη περιβάλλον χωρίς κοντινά εκτενή δάση. Ο νεώτερος τύπος συνάθροισης υπαινίσσεται έναν ανοικτό δασικό βιότοπο.

Η ταυτόχρονη παρουσία των ενδημικών ειδών ευρέως διαδεδομένων γενών και μακρινών μεταναστών, όπως το γένος *Arvicanthis*, επιβεβαιώνει τη χαρακτηριστικό σύνθεση που παρατηρείται συχνά στις συναθροίσεις των τρωκτικών από το Ανώτερο Τουρώλιο στις περιοχές της Ανατολικής Μεσογείου.

Σύμφωνα με τα δεδομένα, το όριο Τουρώλιο/Ρουσίνιο χρονολογείται στα διάστημα μεταξύ 5.23-5.40 Ma, αλλά πιθανόν να είναι νεότερο από το όριο Μεσσήνιο/Ζάγκλιο (5.33 Ma). Καταδεικνύεται ότι η χρήση βασικών ταξινομικών μονάδων στις βιοστρωματογραφικές συσχετίσεις, *Promimomys* και *Mimomys*, παρουσιάζει διαχρονικότητα στις διάφορες περιοχές της Ευρώπης.

Λέξεις-κλειδιά: *Μειόκαινο, Πλειόκαινο, τρωκτικά, ολοκληρωμένη στρωματογραφία, Μεσόγειος.*

INTRODUCTION

Rodent faunas and pollen floras from the lignite mines in the Early Pliocene Ptolemais Formation exploited by the Public Power Corporation have been published by Van De Weerd (1979, 1983). Recent studies focusing on the cyclicity of these lacustrine sediments, the magnetostratigraphy, the radio-isotopic dating of the intercalated volcanic ashes and the relationship of the sedimentary cycles and the pollen floras provide an exceptionally precise chronological framework for the levels containing rodent fossils (Kloosterboer-Van Hoeve, 2000; Van Vugt, 2000; Steenbrink, 2001).

The main interests of the study are the extension of the fossil rodent record published by Van De Weerd (1979) and integration of the rodent record into the existing

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* Η διαδοχή των τρωκτικών πανίδων από τις Μειο/Πλειοκαινικές λιμναίες αποθέσεις της λεκάνης Φλώρινα-Πτολεμαΐδα-Σερβία (Ελλάδα)

high-resolution time framework. The extension covers older levels from the underlying Late Miocene Komnina Formation and younger levels from the top of the Ptolemais Fm (Fig. 1).

Through comparison with similarly well studied sections in other basins we will discuss the synchronicity of entries, exits and similar stages-of-evolution in rodent lineages.

The rodent assemblages studied have been collected either from palaeosols that often occur at the bottom of the lithological cycles defined by VAN VUGT *et al*. (1998) and STEENBRINK *et al*. (1999), from emersion levels containing a high percentage of mollusks within lignite beds and one from a clay rich layer. The mammal assemblages from these deposits contain a limited number of rodent species and are all dominated by Muroidea. Other taxa that are present in the succession, but are not discussed, are *Tamias*, a castorid, lagomorphs, insectivores, a primate, rhino remains, fish, small amphibians and reptiles.

We shall focus most attention on the taxonomy and paleoecological interpretation of the first record from Europe of a representative of the otherwise African murine genus *Arvicanthis*, the records of the genera *Occitanomys*, *Castillomys*, *Apodemus*, *Rhagapodemus*, *Micromys*, the primitive arvicolines and microtoid cricetids.

GEOLOGICAL SETTING AND LITHOSTRATIGRAPHY

The Ptolemais and Servia Basins are parts of the intramontane Florina-Ptolemais-Servia Basin, which is situated in a 120 km long NNW-SSE trending graben system that extends from Kozani (Greece) to the border of the Former Yugoslav Republic of Macedonia (Fig. 1). The sedimentary

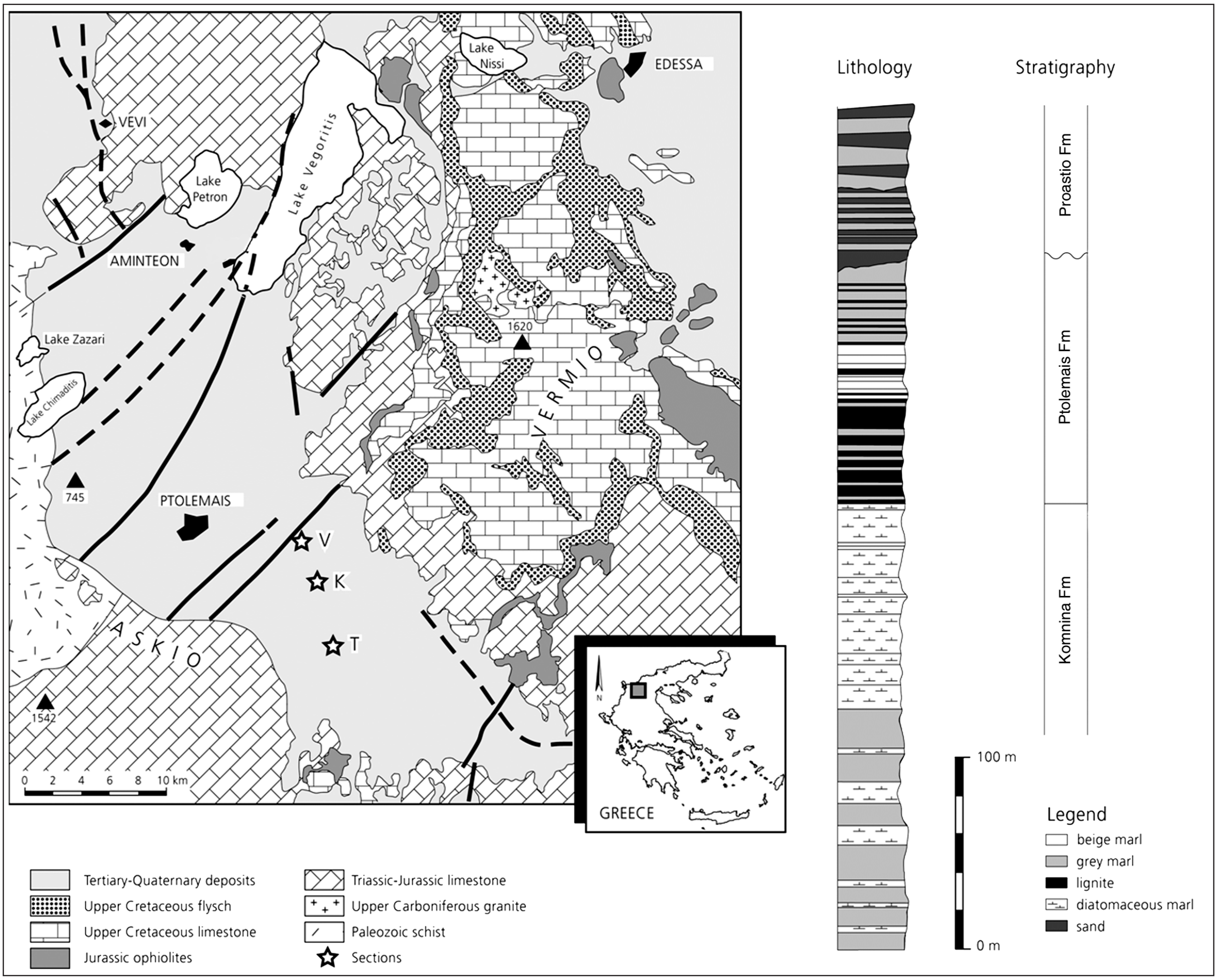


Fig. 1. A simplified geological map of the Ptolemais Basin showing the locations of the three subsections of the Ptolemais composite section: Tomea Eksi (T), Komanos (K) and Vorio (V) (STEENBRINK *et al*., 1999; modified after PAPAKONSTANTINOU, 1979). The column on the right shows the generalized stratigraphy of Neogene sediments in the Ptolemais Basin (STEENBRINK *et al*., 1999, and references therein).

succession in the Ptolemais Basin consists mainly of rhythmically bedded lacustrine marls of Late Miocene to Early Pleistocene age, with intercalations of fluvial deposits and lignite layers. The depositional history of the Florina-Ptolemais-Servia Basin is outlined by STEENBRINK (2001) and STEENBRINK *et al*. (2006).

Basin-wide, STEENBRINK (2001) recognises four lithostratigraphical units: the Komnina Fm, the Ptolemais Fm, the Proastio Fm and the Perdika Fm (Fig. 1). The Komnina Fm is also known as the Lower Formation (VAN DE WEERD, 1983; VAN VUGT *et al*., 1998; STEENBRINK *et al*., 1999) and the Proastio Fm is also known as the Upper Formation (STEENBRINK *et al*., 1999; VAN VUGT *et al*., 1998). The Komnina Fm has a Late Miocene to possibly earliest Pliocene age, the Ptolemais Fm has an Early Pliocene age and the Proastio and Perdika formations have been deposited during the Pleistocene (STEENBRINK, 2001).

STEENBRINK (2001) distinguished four members in the Komnina Fm: the Servia mb, the Lava mb, the Prosilio mb and Tomea Eksi mb. The Tomea Eksi mb, the youngest member, is composed of rhythmic alternations of lacustrine (diatomaceous) marls and thin lignite seams or palaeosols. An abrupt change in the lithology marks the boundary between the Komnina Fm. and the more lignite-rich Ptolemais Fm.

Three members have been distinguished in the Ptolemais Fm: the Kyrio, the Theodoxus and the Notio mb (VAN VUGT *et al*., 1998; STEENBRINK *et al*., 1999). The Kyrio and Notio members consist of rythmically bedded alternations of lignite and grey marl. The Theodoxus member mainly consists of beige marl with intercalated lignite layers.

The Ptolemais composite column (Fig. 2) has been reconstructed by VAN VUGT *et al*. (1998) and STEENBRINK *et al*. (1999, 2006) by correlating the characteristic intervals of the Vorio, Komanos and Tomea Eksi sections, which have been named after the lignite-pits in which they were recorded.

The fossil material studied has been collected from the Tomea Eksi mb, Kyrio mb and Notio mb in the Ptolemais Basin, and from the Tomea Eksi mb in the Servia Basin. No mammalian material has been recovered from the Theodoxus mb, but fish remains are common.

TIME CONTROL

The cyclic sedimentary sequence with intercalated ash-beds in the Ptolemais Basin provides excellent time control in a terrestrial setting. VAN VUGT *et al*. (1998) found five reversed and four normal intervals in the magnetostratigraphic record of the Ptolemais composite section (Fig. 2). The normal intervals were correlated to the Thvera, Sidufjall, Nunivak and Cochiti sub-chrons of the Gilbert chron. The paleomagnetic data indicate that precession-controlled orbital forcing has resulted in the cyclic lithological pattern observed. The calculated average duration of the cycles, 21.6 ± 0.5 kyr, is in excellent agreement with the 21.7 kyr average periodicity of astronomical precession (VAN VUGT *et al*., 1998).

STEENBRINK *et al*. (1999) have obtained $^{40}Ar/^{39}Ar$ ages from nine volcanic ash beds in the Ptolemais Fm. The ages of the ash layers independently confirm the precession-controlled orbital forcing of the lithological cycles, which show an average duration of 21.7 ± 0.8 kyr (STEENBRINK *et al*., 1999). The radio-isotopic ages corroborate the magnetostratigraphical correlation of the Ptolemais composite section to the Gilbert chron.

VAN VUGT *et al*. (1998) and STEENBRINK *et al*. (1999) derived a cyclostratigraphic framework by tuning the sedimentary succession to the $La90_{(1,1)}$ 65ºN summer insolation curve, in which the lignite-marl alternations of the Ptolemais composite section reflect the regional (basin-wide) climatic response to orbital precession. KLOOSTERBOER-VAN HOEVE (2000) and STEENBRINK (2001) have indicated that the lithological cycles in the Tomea Eksi mb are most likely related to precession as well. The pollen record shows that the palaeosol and lignite intervals have been deposited during drier periods and relatively low lake levels, while the marl intervals have been deposited during more humid periods in which the lake level was higher (KLOOSTERBOER-VAN HOEVE, 2000).

Despite the overall agreement between the magnetostratigraphical record and the radio-isotopic ages, there are discrepancies between the radio-isotopic ages and the ages obtained through astronomical tuning of individual cycles. Three solutions have been published for the tuning of the Ptolemais composite column: the "hiatus" option (VAN VUGT *et al*., 1998), the "continuous" option (STEENBRINK *et al*., 1999; KUIPER *et al*., 2004) and the "intercalibrated" option (KUIPER, 2003). At present, it is impossible to decide which of these options is to be preferred. The three age model options are summarised in Fig. 2.

VAN VUGT *et al*. (1998) attempted to establish a bed-to-bed correlation of the continental Ptolemais composite section and the marine Rossello composite section (HILGEN, 1991; LOURENS *et al*., 1996), which includes the unit-stratotype for the Zanclean Stage (VAN COUVERING *et al*., 2000). They assume a hiatus of short duration at the top of the Sidufjall sub-chron between cycle K18 and K19. This hiatus option is based on the short duration of the normal polarity interval relative to the number of lithological cycles in the Ptolemais composite column and on the presence of a shallow scouring surface with an overlying palaeosol between cycles K18 and K19.

STEENBRINK *et al*. (1999) published the continuous tuning option, which is without a significant hiatus between K18 and K19. These authors have compared the astronomical ages to the radio-isotopic ages of nine intercalated ash layers. The $^{40}Ar/^{39}Ar$ ages of the ashes are

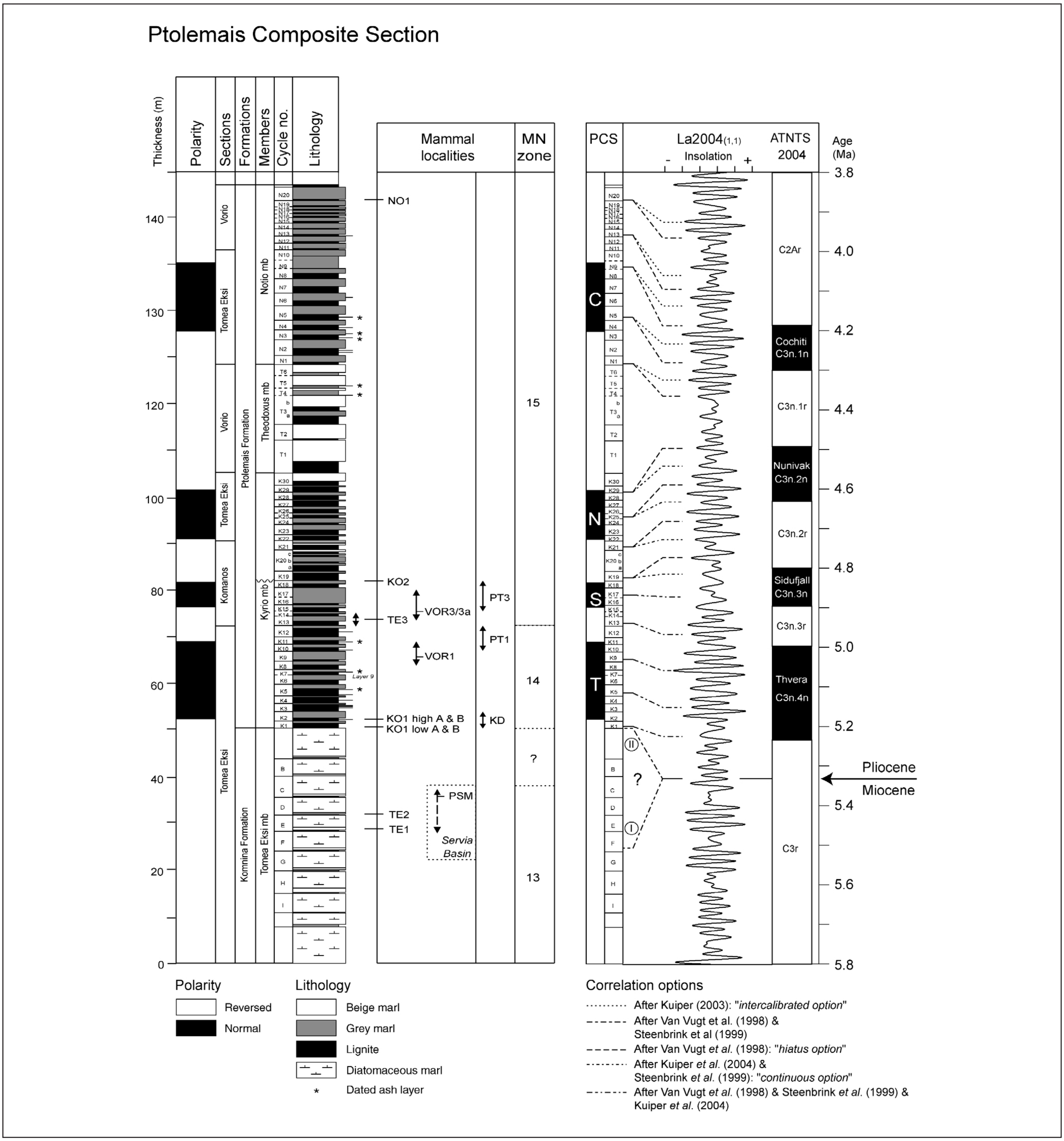


Fig. 2. The Ptolemais composite section (PCS) and coding of lithological cycles is after VAN VUGT *et al.* (1998) and STEENBRINK *et al.* (1999, 2006). The magnetic polarity and the lithostratigraphy summarized in 4 end-member sediment types is shown on the left-hand side along with the names of sub-sections, formations, members and cycle numbers. Horizontal lines adjacent to the right of the lithological column indicate ash layers and asterisks indicate radio-isotopically dated ash layers. L9 denotes the ash layer known as "layer 9" (VAN DE WEERD, 1979). The center part shows the inferred stratigraphic position of mammal localities sampled in the Tomea Eksi (TE), Komanos (KO), Vorio (VOR) and Notio (NO) mines. The locality Prosilion-Mercurion (PSM) was sampled in the Servia Basin southeast of the Ptolemais Basin. The estimated stratigraphic position of the assemblages studied by VAN DE WEERD (1979), Kardia (KD) and Ptolemais (PT1 & PT3) is indicated alongside our localities. The right part of the figure shows the correlation of the polarity and the lithological cycles in the PCS to the La2004$_{(1,1)}$ 65°N summer insolation curve (LASKAR *et al.*, 2004) and ATNTS2004 (LOURENS *et al.*, 2005). The letters T, S, N and C indicate the Thvera, Sidufjall, Nunivak and Cochiti subchrons, respectively. A summarized overview of the three tuning options for the PCS is given by the differently dashed lines. The correlation options I and II bracket the uncertainty interval in correlating the position of the Miocene/Pliocene boundary. Option I assumes a continuous record and option II assumes a discontinuous or condensed record.

systematically ~200 kyr younger than the astronomical ages. A satisfactory explanation for this discrepancy was not available at that time (STEENBRINK *et al*., 1999).

Recently, KUIPER (2003) and KUIPER *et al*. (2004) focused on the intercalibration of astronomical and radio-isotopic ages and on the refinement of the procedure for obtaining radio-isotopic ages. These authors remeasured the ashes previously analysed by STEENBRINK *et al*. (1999) and improved error propagation calculations, which reduced the discrepancy between astronomical and radio-isotopic ages significantly. KUIPER *et al*. (2004) have refined and retuned the continuous tuning option of STEENBRINK *et al*. (1999).

A third solution for the astronomical tuning of the younger part of the Ptolemais composite section, the intercalibrated option, was explored by KUIPER (2003). The age discrepancy between astronomical ages and radio-isotopic ages is larger in the Notio mb than in the Kyrio mb. On the basis of a proposed intercalibration between ^{40}Ar/^{39}Ar ages and astronomical time in the Melilla Basin (Morocco), KUIPER (2003) retuned the lithological cycles of the Notio mb two precession cycles younger and indicated that the paleomagnetic data allow for reinterpretation of the position of the Cochiti polarity reversals. With this intercalibration, the age discrepancy of the younger ashes with astronomical time is comparable to that of the older ashes in the Kyrio mb.

Regardless which tuning option is followed, the correlation of the Ptolemais composite section to the Gilbert chron is unambiguous. Similarly, the relation between the lithological cycles and orbital forcing (precession) has been firmly established. Despite these certainties, the tuning of individual cycles remains slightly equivocal. When considering all three options, there appears to be an error margin in the astronomical tuning of two or three precession cycles.

The lithological cycles in the Tomea Eksi mb of the Komnina Fm have not been astronomically tuned. The formation boundary at the top of this member is marked by a sharp and distinct facies shift and by a shift in the pollen floras (KLOOSTERBOER-VAN HOEVE, 2000). The general cycle pattern forced by precession is visible in both formations. There is no indication for erosion or a hiatus at the formation boundary in the field, which suggests that the sedimentary record is continuous at the boundary. However, it cannot be ruled out that, given the distinct change in facies, flora and fauna at the formation boundary, that the record is condensed or discontinuous in this interval.

Figure 2 shows two extremes for the correlation of the Miocene-Pliocene boundary to the Ptolemais composite column. Option one, which is preferred, assumes a continuous record, in which the shift in the facies and flora postdates the Miocene-Pliocene boundary by about five precession cycles (~100 kyr). Option two assumes a condensed or discontinuous record in which the formation boundary is approximately coeval with the Miocene-Pliocene boundary.

STRATIGRAPHICAL POSITION OF MAMMAL LOCALITIES

The stratigraphical position of the localities in the Ptolemais Basin is indicated in Figure 2. At some of the localities sampled, the rhythmic bedding was less pronounced or absent due to (local) periods of erosion or non-deposition. Nevertheless, the stratigraphical position of these mammal sites could be determined in the field. Except for the level of Vorio 3 and 3a (VOR3 & VOR3a), the accuracy of the correlation is within one to two lithological cycles.

The associations Tomea Eksi 1 and 2 (TE1 & TE2) have been recovered from palaeosols from successive cycles in the Tomea Eksi member of the Komnina Fm in the Tomea Eksi pit.

The Komanos 1 localities are situated in a thick lignite bed at the base of the Ptolemais Fm, which represents two lithological cycles. This thick lignite layer contains an erosional surface that disappears laterally. Four sites have been sampled from this lignite: Komanos 1 low A and Komanos 1 low B (KO1lowA & KO1lowB) from the lower emersion horizon, and Komanos 1 high A and Komanos 1 high B (KO1highA & KO1highB) from the upper emersion horizon. The letters A and B indicate a lateral distance in the order of 50 metres between two sites in the same layer. The lateral samples have been collected in order to get some idea of the lateral variation in the fauna composition of samples from the same bed.

The stratigraphical positions of the localities in the Vorio section are less accurately known, due to the loss of cyclicity near the edge of the basin. Vorio 1 (VOR1) and Vorio 3/3a (VOR3&3a) have been correlated to the Ptolemais composite column by using the ash layer that is locally known as Layer 9 (VAN DE WEERD, 1979). Layer 9 is situated in lithological cycle K7 and is referred to as ash layer SL7L by STEENBRINK *et al*. (1999) and KUIPER *et al*. (2004). VOR1 has been collected 4 m above layer 9 and VOR3 and VOR3a have been collected 14 m above layer 9. The lateral distance between VOR3 and VOR3a is about 50 m.

The sample Komanos 2 (KO2) has been collected at the boundary between cycle K18 and K19, which is characterized by a shallow scouring surface and a palaeosol (VAN VUGT *et al*., 1998).

The fauna from the Notio 1 locality (NO1), which has been recovered from the Notio pit, has been correlated to cycle N20 in the Ptolemais composite column. The fossiliferous bed is, in contrast to the other levels, a rather thick (40 cm) grey clay lens containing mollusc fragments. This bed is of supposedly fluviatile origin and also contains some fragmentary remains of larger mammals (i.e. *Dolichopithecus*).

TABLE 1

The astronomically calibrated age estimates of the studied localities are listed. Calibration is after VAN VUGT *et al*. (1998), STEENBRINK *et al*. (1999), KUIPER (2003) and KUIPER *et al*. (2004). The age estimates for localities correspond to the ages of appropriate summer insolation minima. Coding of lithological cycles is adopted from VAN VUGT *et al*. (1998), STEENBRINK *et al*. (1999) and STEENBRINK (2006). The uncertainty in the tuning of individual layers is shown in Fig. 2. The indices I and II for the ages of TE1 & TE2 correspond to alternative correlation options with respect to the Miocene/Pliocene boundary. The localities KD, PT1 and PT3 (VAN DE WEERD, 1979) are correlated to the Ptolemais composite section on the basis of their lithostratigraphic position relative to the base of the Ptolemais Formation or to Layer 9. * The astronomical age corresponds to the "continuous" tuning option. The ^{40}Ar/^{39}Ar age of "Layer 9" (ash layer SL7L) is determined at 5.028 ±0.072 by KUIPER *et al*. (2004). ** Cycles D and E in STEENBRINK (2006) correspond to L4 and L5 of KLOOSTERBOER-VAN HOEVE (2000).

Locality/Level	Locality code	Lithological Cycle	Lithostratigraphic distance to Layer 9 (m)	Astronomical age estimate (Ma)
Notio 1	NO1	N20		3.92 - 3.97
Komanos 2	KO2	Base K19		4.77 - 4.81
Ptolemais 3	PT3		+18.5	
Vorio 3 & 3a	VOR3/VOR3a		+14	±4.9
Tomea Eksi 3	TE3	K13-K14		4.93 - 4.97
Ptolemais 1	PT1		+8	
Vorio 1	VOR1		+4	±5.04
Layer 9	ash SL7L	K7	0	5.099 ±0.025*
Komanos 1 high (A and B)	KO1highA&B	K2	-8	5.22
Kardia	KD	K1-K2	-10	
Komanos 1 low (A and B)	KO1lowA&B	K1	-10	5.23
Prosilion-Mercurion	PSM			
Tomea Eksi 2	TE2	D**		5.30^{I} - 5.40^{II}
Tomea Eksi 1	TE1	E**		5.32^{I} - 5.43^{II}

The locality Prosilion-Mercurion (PSM) is situated in the Servia Basin that lies southeast of the Ptolemais Basin. Its lithostratigraphical position is in the lower part of the Tomea Eksi mb (STEENBRINK, 2001; STEENBRINK *et al*., 2006).

The astronomically calibrated age estimates of the studied localities are shown in Table 1. The three localities described by VAN DE WEERD (1979) have been correlated to the Ptolemais composite section as follows. Kardia (KD) was situated 1.5 m above the base of the Main Field beds and approximately 10 m below Layer 9. This level corresponds to cycle K1 or K2 of the Ptolemais Fm which yielded our KO1 low and KO1 high associations. The stratigraphic position of Ptolemais 1 (PT1) and Ptolemais 3 (PT3) is estimated on the basis of their position with respect to Layer 9.

METHODS

Collecting

The rodent material has been collected from eleven localities in the lignite mines south of the town of Ptolemais that are exploited by The Public Power Corporation of Greece (DEI) and one from the locality PSM situated in a natural section of the upper part of the Komnina Fm. All fossiliferous levels have been lithostratigraphically correlated and entered into the Ptolemais composite section (Fig. 2) (STEENBRINK *et al*., 1999, 2006).

The mammal fossil localities from the Komnina Fm are from palaeosols. The mammal fossil localities in the Ptolemais Fm are from emersion levels within or at the top of lignite beds, which contain a high percentage of mollusc debris.

All samples have been wet-screened. The finest of the screens used has a 0.5 mm precision mesh. All lignite containing samples have been treated in a solution of caustic soda and peroxide prior to screening in order to break up and eliminate the plant remains. Sample size could not be standardized, because the fossiliferous beds are often thin, discontinuous, and exposed in vertical cliffs. As a result sample size ranges between 500 to 2000 kg per site.

The material studied is stored in the collections of the Institute of Earth Sciences (IVAU), Utrecht University, the Netherlands.

Measuring

The measurements have either been taken with a Leitz Ortholux measuring microscope or with a Reflex measuring microscope. The length (L) and the width (W) of isolated murine teeth have been measured as suggested by VAN DE WEERD (1976). The method of VAN DE WEERD (1979) and FEJFAR *et al.* (1990) is followed for measuring the cheek teeth of arvicolines and microtoid cricetines (Fig. 3B). The nomenclature proposed by VAN DER MEULEN (1973) is used for these groups (Fig. 3A). We prefer the use of occlusal length (L) and occlusal width (W) in combination with crown height (h) for arvicoline teeth instead of length and width of the crown base.

The height of the undulations of the enamel border at the crown base is a diagnostic feature of arvicoline cheek teeth. However, in the primitive species, these undulations or enamel free areas are low or absent. The height of three undulations has been measured: the anterior undulation (e_a) on the anterior cap and the posterior undulation (e_p) on the BSA1 of the m1 (Fig. 3B). The undulation on the LSA2 (e_m) has been measured of the M1. The undulation height is measured as the distance between the base of the enamel below the BRA1 (m1) or the LRA2 (M1) and the apex of the enamel free area (FEJFAR *et al*., 1990).

The evolutionary change of the dental pattern of arvicolines is generally most apparent in the m1 and the M3. Therefore, additional measurements have been taken from these elements (Fig. 3B). The length of the anteroconid complex of the m1 (A) is defined as the distance between the apex of the BRA2 and the anterior limit of the anterior cap measured parallel to the longitudinal axis of the occlusal surface (VAN DE WEERD, 1979). The width of the anteroconid complex (AW) is its maximum width measured at right angles to the length axis of the

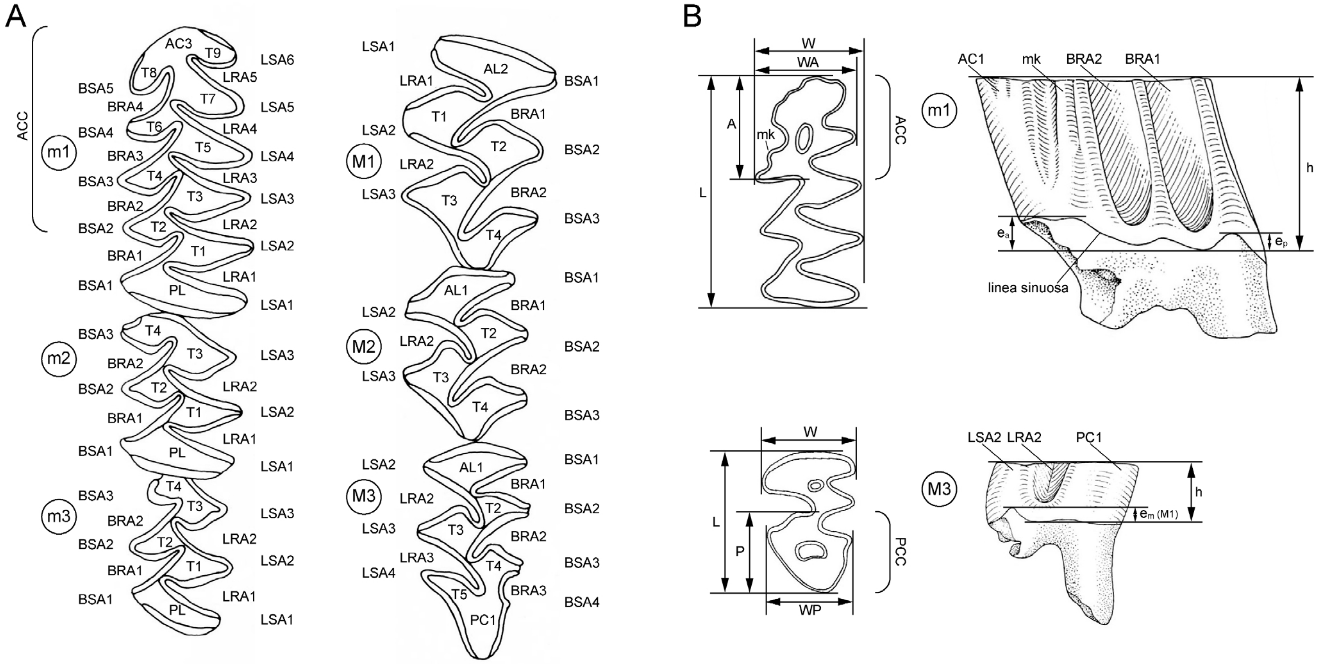


Fig. 3. A: Nomenclature of arvicoline tooth morphology (modified after VAN DER MEULEN, 1973). T: triangle; AC: anterior cap; PL: posterior lobe; AL: anterior lobe; PC: posterior cap; LSA: lingual salient angle; LRA: lingual re-entrant angle; BSA: buccal salient angle; BRA: buccal re-entrant angle; ACC: anterior cap complex. B: Measurements on primitive arvicoline teeth follow the methods of VAN DE WEERD (1979) and FEJFAR *et al*. (1990) with some additions. PCC denotes the posterior cap complex, mk indicates the “mimomys kante”. Length (L) and width (W) are at right angles, as are the crown height (h) and the height of enamel free areas (e) with respect to the occlusal surface. Note that e_a and e_p are measured on the m1 and e_m on the M1. A & WA are the length and width of the ACC, and P & WP of the PCC, respectively. Drawings of the m1 and M3 are modified after VAN DE WEERD (1979).

occlusal surface. The length of the posterior complex of the M3 (P) is, in analogy with A, defined as the distance between the apex of the LRA2 and the posterior limit of the occlusal surface. The width of the posterior complex of the M3 (WP) is its maximum width measured at right angles to the length axis of the occlusal surface.

In order to show differences in the relative dimensions of parts of the cheek teeth in different species, ratios of the measurements defined may be illustrative. A/L is used to show the relative length of the anterior complex (VAN DER MEULEN, 1973), A/WA is a measure that gives the length of the anterior cap relative to its width. Similar ratios calculated to show differences in the relative dimensions in the M3 are: P/L and P/WP.

The relative hypsodonty (h/L) allows the comparison of the crown height in species of different size (MAUL, 1996). However, the relative hypsodonty may be biased by changes between the relative length of the anterior and posterior parts through evolution of the dental pattern of the m1 and M3. We consider the relative hypsodonty of the m2 and M2 as most useful for interspecific comparisons, because these molars are less susceptible to changes of the proportions of their occlusal surface.

TAXONOMY

Introduction

The existing classifications of the order Rodentia above the genus level are, in particular if fossils are included, highly inconsistent. Although this lack of unanimity among specialists is of minor concern for this study, a short discussion seems appropriate because stability of the categories above the genus level is crucial for the creation and vitality of databases. Since parallel and convergent evolution is common within the order the cladistic approach for distinguishing major groups is inappropriate. However, other, more subjective, methods to reconstruct evolutionary lineages and their phylogenetic context have, in spite of the now impressive fossil record, not led to a comprehensive generally accepted classification of the Rodentia. Problems seem to be most imminent in the very diverse and successful infraorder Myodonta SCHAUB 1958, which includes the super families Dipodoidea FISCHER VON WALDHEIM 1817 and Muroidea ILLIGER 1811.

The Muroidea have traditionally been divided into the families Muridae (true mice) and Cricetidae (hamsters, gerbils, voles etc. as well as a variety of extinct groups with hamster-like dentitions). After it became clear that the Cricetidae in this concept do not form a clade, this subdivision has been abandoned, so in modern classifications Muroidea contain either one family only (the Muridae) (MCKENNA & BELL, 1997) or a very large number of families (Muridae, Gerbillidae, Dendromuridae, Spalacidae, Rhizomyidae, Anomalomyidae, Melissiodontidae etc.). In either case there remain a large number of genera that cannot be confidently allocated to any supra-generic group below the rank of the (super)-family because their phylogenetic context is not known.

We do not follow WILSON & REEDER (2005) who recognise six families within the Muroidea, because the content of some of these (ie. the Spalacidae) is conflicting with the fossil evidence. We divide the family Muridae (= Muroidea) into groups of subfamily rank, in our case these are the Murinae, Cricetinae, Gerbillinae and Arvicolinae. The Gliridae MUIRHEAD 1819, the Pteromyidae BRANDT 1858 and the Sciuridae FISCHER VON WALDHEIM 1817 will not be referred to groups hierarchically between the genus and family level.

Family Muridae ILLIGER 1811
Subfamily Murinae ILLIGER 1811

The *Arvicanthis* material from the Ptolemais composite section

The presence of a species of non-striped grass mouse in the assemblages from the upper part of the Komnina Fm of the Florina-Ptolemais-Servia Basin is of particular interest, because this genus is, with the exception of its occurrence in some Late Pleistocene cave deposits of Israel, restricted to Africa and the Arabian Peninsula. We tested whether or not the cheek teeth of extant *Arvicanthis* can be distinguished from those of the rather similar single striped mouse *Lemniscomys* TROUESSART 1881, the striped mouse *Rhabdomys* THOMAS 1916 and *Dasymys* PETERS 1875 and reached the conclusion that this is the case. The differences between the six species of *Arvicanthis* discussed below are diffuse because all these have retained some primitive dental characteristics such as the presence of the t3 in the M2, the four-leaved clover configuration of the anterior cusps in the m1 or the presence of the terminal heel in the m1 and m2. However, the fossil and extant species of *Arvicanthis* share a, for murines, exceptionally high number of roots in the upper cheek teeth and a similar dental pattern.

Opinions on the number of different extant species vary widely. MISONNE (1969) recognizes *niloticus* only, while ELLERMAN (1941) lists *niloticus*, *lacernatus*, *abyssinicus* and *somalicus* and WILSON & REEDER (2005) distinguish *niloticus*, *abyssinicus*, *blicki*, *neumanni*, *ansorgei*, *rufinus* and *nairobae*. Of these *abessinicus* and *blicki* are endemic species living at high altitudes in Ethiopia. Non-striped grass mice have been reported from a variety of dry biotopes at different altitudes. They seem to do particularly well along the fringes of desertic areas provided that there is some permanent water.

Genus *Arvicanthis* LESSON 1842
Type species: *Arvicanthis niloticus* (DESMAREST, 1822),
Recent Africa

(Pl. 4, Figs 1-4)

Fossil (sub)-species recognised:
- *A. niloticus irhoudae* JAEGER 1975
- *A. arambourgi* JAEGER 1975 (Pl. 3, Figs 3-7)
- *A. primaevus* JAEGER 1976
- *A. musisii* MEIN 1994 (Pl. 3, Figs 1-2)
- *A. broekhuisi* n. sp. (Pl. 1, Figs 1-6, Pl. 2, Figs 1-6)

Remarks
Arvicanthis ectos BATE 1942 from the Late Pleistocene of Israel is considered to be a junior synonym of *A. niloticus* on the basis of observations made by JAEGER (1975) and a cast of the upper dentition of *A. ectos* from Qafzeh cave layer xvii (A 13) kindly sent to us by Dr. Rivka Rabinovich (Hebrew University of Jerusalem). The width/length ratio of the M1 of 0.65, given by BATE (1942) as one of the characteristics of *A. ectos*, is apparently the result of inaccurate measuring, because that value as measured on the cast is between 0.73 and 0.74, just as in all other species of the genus whether fossil or recent.

The second author (HdB) takes this opportunity to correct his mistake in DE BRUIJN *et al*. (1970) where the M1 and M2 of some rat from Israel were erroneously identified and figured as *A. ectos*. I thank Pierre Mein (pers. comm. 1973) and Jean-Jacques Jaeger (JAEGER, 1976) for detecting this mistake.

Arvicanthis broekhuisi n. sp.
(Pl. 1, Figs 1-6; Pl. 2, Figs 1-6)

Derivatio nominis: This species is named in honour of Mr. Eli Broekhuis MD, gratefully acknowledging his actions that led to the recovery from Legionnairs Disease of the second author (HdB).

Type locality: Tomea Eksi 2 (TE2), from sedimentary cycle D of the Komnina Fm (STEENBRINK, 2006; Fig. 2)

Holotype: M1 dex, no: TE2-271, Pl. 2, Fig. 1
Other localities with *A. broekhuisi:* Tomea Eksi 1 (TE1) and Prosilion-Mercurion (PSM)
Type level and age: latest Miocene or earliest Pliocene

Diagnosis
Arvicanthis broekhuisi is a large species of *Arvicanthis* with

a five or six-rooted M1 and five-rooted M2. The t3 is rather well developed in the M2, vestigial in the M3. The antero-labial accessory cusp is absent in the m1, of variable size in the m2 and weak in the m3. The postero-labial accessory cusp (c1) is well developed in the m1, but shows much variation in size in the m2. The m1 is rather short and wide. The terminal heel is small and oval in the m1, but developed as a long transverse ridge in the m2.

Differential diagnosis

Arvicanthis broekhuisi is larger than all other species of the genus whether fossil or recent (Fig. 4). It further differs from the extant species in having a five or six-rooted M1, more robust m1 and larger terminal heels in the m1 and m2. *Arvicanthis broekhuisi* differs from *A. niloticus irhoudae* and *A. musisii* in having the t3 in the M2 well developed and the large postero-labial extra cusp and posterior heel in the m1 and m2. Furthermore the m1 of our species is more robust (less elongate) than in geologically younger representatives of the genus. The difference in robustness between the dentitions of *A. broekhuisi* and *A. arambourgi* is even more pronounced than in the species discussed above, although the development of the t3 in the M2 is similar in these two species. Furthermore the postero-labial cusp is lacking in *A. arambourgi*. Among fossil arvicantines the dental morphology of *A. broekhuisi* seems to be closest to that of *A. primaevus*, a species of which we have seen neither specimens nor casts, but the size difference between these two is much too pronounced to include these specimens into the same species (Fig. 4).

Material and measurements of Arvicanthis broekhuisi: Table 2

Description

M1. The cusps are arranged in three laminae that are separated by transverse valleys. The t1 or the t4 may occur as isolated round cusps (one out of four). The t8 and the t9 form the third ridge. The t12 is absent. The M1 has five or six roots. The lingual root of some specimens is split into two roots (two out of three) and there is a pair of thin extra roots between the two labial main roots.

M2. The drop-shaped t1 is much larger than the round t3. The second and third laminae are strong and developed in a similar way as in the M1, but there is a narrow ridge connecting t4 and t8. The M2 is five-rooted. The lingual root is halfway split into two roots and there is one extra root between the two labial roots.

M3. The t1 is large and the t3 vestigial. The t5 has a more labial position than in the M2, but has not shifted so far labially as in other species of *Arvicanthis*. An indentation on the anterior face of the posterior lamina marks the limit between the t8 and the t9. The M3 has three roots.

m1. The three lamina of the robust m1 are basically separated by two postero-labially to antero-lingually inclined valleys. The lingual cusp of the anteroconid may

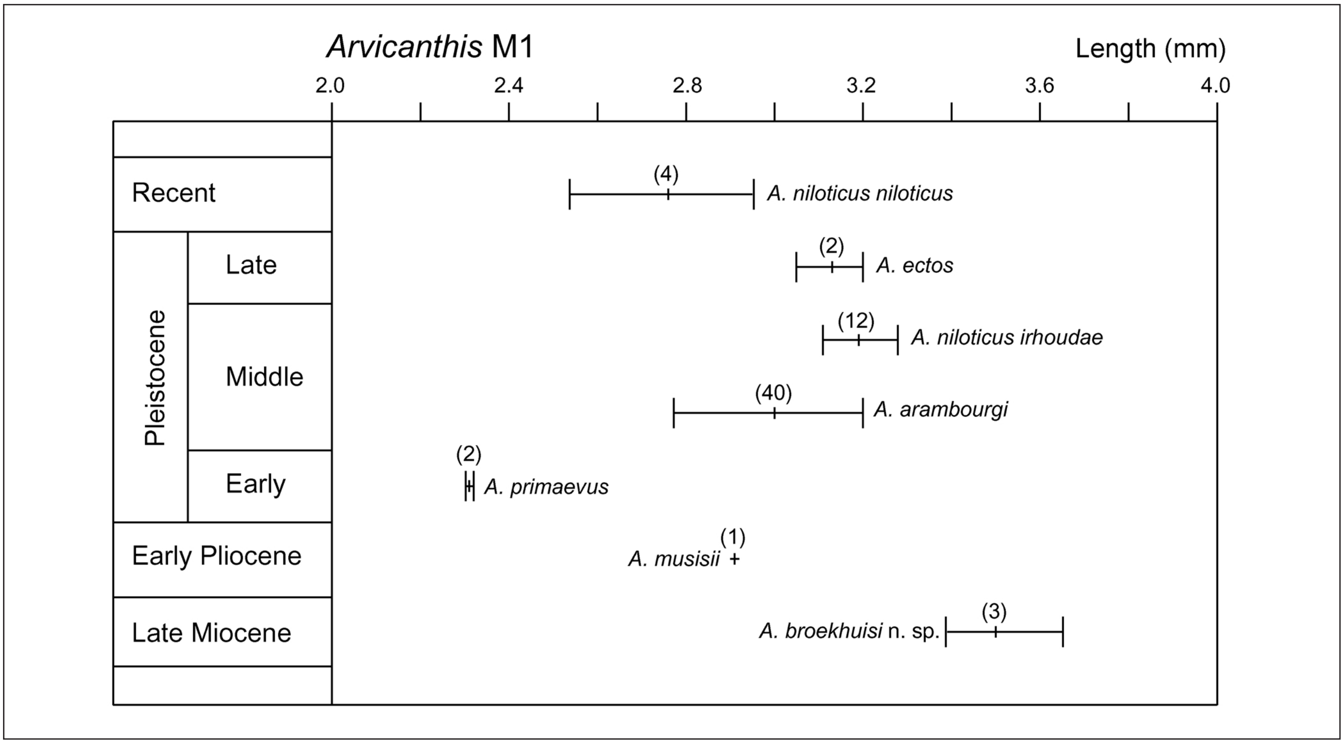


Fig. 4. The range and mean of the length of the M1 of *Arvicanthis*. The number of measured specimens is indicated between brackets.

TABLE 2

Material and measurements of *Arvicanthis broekhuisi*.

Locality		Length (mm)				Width (mm)			
		N	min.	mean	max.	N	min.	mean	max.
Prosilion-Mercurion	M2	1		2.33		1		2.45	
Prosilion-Mercurion	m2	2	2.48		2.48	2	2.52		2.53
Tomea Eksi 2	M1	3	3.39	3.50	3.65	3	2.56	2.58	2.60
Tomea Eksi 2	M2	3	2.39	2.50	2.62	3	2.67	2.77	2.83
Tomea Eksi 2	M3	1		1.90		2	2.04	2.15	2.25
Tomea Eksi 2	m1	6	2.90	2.99	3.08	6	2.16	2.21	2.25
Tomea Eksi 2	m2	8	2.33	2.49	2.71	8	2.42	2.52	2.59
Tomea Eksi 2	m3	9	2.22	2.38	2.48	9	2.16	2.26	2.40
Tomea Eksi 1	M1					1		2.57	

TABLE 3

Material and measurements of *Occitanomys debruijni*.

Locality		Length (mm)				Width (mm)			
		N	min.	mean	max.	N	min.	mean	max.
Tomea Eksi 2	M1	4	1.85	1.92	1.99	7	1.20	1.34	1.53
Tomea Eksi 2	M2	7	1.26	1.32	1.37	7	1.27	1.33	1.43
Tomea Eksi 2	M3	6	0.76	0.85	0.98	6	0.81	0.89	0.96
Tomea Eksi 2	m1	9	1.67	1.76	1.92	8	1.03	1.10	1.23
Tomea Eksi 2	m2	5	1.10	1.22	1.35	5	1.11	1.15	1.26
Tomea Eksi 2	m3	4	0.83	0.92	1.00	4	0.75	0.87	0.92
Tomea Eksi 1	M1	2	1.75		1.80	3	1.28	1.30	1.32
Tomea Eksi 1	M2	1		1.26		2	1.23	1.25	1.26
Tomea Eksi 1	M3	1		0.91		1		0.98	
Tomea Eksi 1	m1	1		1.71		1		1.12	
Tomea Eksi 1	m2	1		1.30		2	1.15		1.21
Tomea Eksi 1	m3	2	0.88		0.94	2	0.89		0.99

touch the metaconid. The anterior face of the two-cusped anteroconid shows hardly any indentation, but the valley separating the two cusps of the anteroconid posteriorly is rather deep. In this respect the anteroconid complex of the m1 of *Arvicanthis broekhuisi* is different from that in all other species of the genus. The only labial extra cusp present is the rather well-developed posterior one. This makes the wide posterior lamina even wider. The small, but distinct, oval posterior heel is situated lingually relative to the longitudinal axis of the occlusal surface. In some specimens this cusp sits on a narrow ridge, but in others it is isolated. The anterior and posterior root is very strong and there is a variable number (1-3) of extra roots below the central part of the crown.

m2. The dental pattern of the m2 consists of three ridges that are separated by almost transverse valleys. The third ridge is formed by an exceptionally strong transversally elongate posterior heel. The antero-labial extra cusp is small. In some specimens it is developed as a cusp, but in others it has the shape of a cingulum that is reminiscent of the configuration seen in cricetines. The posterior extra cusp is small and round and becomes gradually incorporated into the second lamina through wear. The posterior heel is exceptionally strong for any murine and for *Arvicanthis* in particular. The two roots are exceptionally strong and wide supporting the complete width of the crown. In some specimens the anterior root is split into two more or less separate roots.

m3. The occlusal pattern consists of two strong laminae separated by a transverse valley. The antero-labial extra cusp is developed as a cingulum. The anterior face of the second lamina is almost straight. There is an extra cusp in the antero-labial part of the central valley in one out of the nine specimens. Another extra cusp in the lingual part of the central valley is indicated in four out of nine and developed in two other specimens. The roots are exceptionally strong and the anterior one is split halfway into a number (usually three) of smaller roots that stand out as a fan.

Discussion on the Arvicanthis material

The slightly damaged *Arvicanthis* M1 and M2 from TE1 resemble the type material of *A. broekhuisi* in detail. The only complete *Arvicanthis* cheek teeth from PSM are two m2. These teeth, representing two individuals, are both somewhat smaller and more square in occlusal view than the type material of *broekhuisi*. Moreover, the postero-labial accessory cusp is absent in one and vestigial in the other. In the type material of *broekhuisi* this cusp shows considerable individual variation, but is always present. The material from PSM is therefore referred to as *A.* cf. *broekhuisi*.

Arvicanthis broekhuisi, the oldest record of the Kusu rats other than *Arvicanthis* sp. from the Lukeino Formation of Kenia (Winkler, 2002), already has a highly specialised dentition. Its robust cheek teeth with thick enamel and, for a murine, unusually strong and numerous roots suggest that it was feeding on tough vegetable matter (grass, reed?). The reconstruction of the vegetation on the basis of pollen during sedimentary cycle four and five of the Komnina Fm by Kloosterboer-Van Hoeve (2000) shows that the climate was cool and dry during the time of deposition of the sediments yielding *Arvicanthis* (absence of Taxodiacaea in wetland vegetation, presence of Asteracaea, Chenopodiacaea, *Ephedra* and *Artemisia*). This reconstruction suggests that *Arvicanthis broekhuisi* was adapted to a dry biotope similar to, but probably cooler than, that preferred by its extant relatives that inhabit the savannas south of the Sahara all the way from the Sahel of Senegal to the high plateaux of Ethiopia and along the Nile valley to its delta (Misonne, 1969; Jaeger, 1975). This up to the present day extremely successful genus has apparently managed to enlarge its geographical range northwards into Greece during the “Lago Mare” phase of the Messinian, surviving there until the local climate became too humid.

The position of *A. broekhuisi* in the evolutionary history of the Kusu rats is not clear, because this oldest, yet largest, species of the genus, has more specialised and stronger roots of the cheek teeth and a more specialised elongate terminal heel in the m2 than any later representative. These peculiarities suggest that the European *Arvicanthis* record represents a side branch of the African main stream and is not in the ancestry of the later African arvicanthines. This conclusion implies that the group probably originated in East Africa during Late Vallesian or Early Turolian times, which is in line with genetic evidence (Ducroz *et al*., 1998; Castiglia *et al*., 2006).

The question whether *Arvicanthis* has reached the Magreb by a south-north route or by an east-west route parallel to the coast was raised by JAEGER (1975). Now that there is evidence that northeast Africa was a centre of dispersal as early as the Late Miocene, the latter option seems the more likely.

The brachyodont, stephanodont Murinae of the *Occitanomys/Castillomys* group

MICHAUX (1969) has been the first to recognise that the Mio/Pliocene murines of Southwestern Europe without t7 in the M1, M2, contain a number of groups of generic rank. In his associations from Mio/Pliocene fissure fillings in France and Spain he distinguished among others two genera of brachyodont, stephanodont murines differing in size and stage of evolution, but sharing a number of dental characteristics: t1 of M1 retracted, tending to develop a t1bis and reduce the t12 in the M1 and M2, tma absent in the m1, tending to develop a longitudinal spur between the second and third chevron of the m1 and m2. MICHAUX (1969) considered the type species of his *Occitanomys* and *Castillomys* to be related, but sufficiently different in dental pattern and size to characterise two genera. Michaux's decision to create a taxonomy that reflects phylogeny was followed with enthusiasm by other specialists of fossil murines (i.e. AGUILAR *et al*., 1986; MARTÍN SUÁREZ & MEIN, 1991; FREUDENTHAL & MARTÍN SUÁREZ, 1999) who created new (sub) generic names for species that did not fit the supposed evolutionary lineages of *Castillomys* and *Occitanomys*, but that themselves do not have sufficiently characteristic dental features to make them readily identifiable (see below). These (sub) genera are: *Centralomys* DE GIULI 1989 based on the species *benericettii* from Brisighella, Italy, MN13 and *Rhodomys* MARTÍN SUÁREZ & MEIN 1991 based on the species *debruijni* from Maritsa, island of Rhodes, Greece, MN13/14.

As early as 1976, VAN DE WEERD (p. 75) warned: "It appears now that the difference between *Occitanomys* and *Castillomys* is one of degree, because assemblages have been found which are intermediate in dental pattern". More recently SEN (1998, p. 362) criticised the allocation by MARTÍN SUÁREZ & MEIN (1991) of his *Castillomys magnus* from Çalta to *Centralomys*, and of *Castillomys debruijni* from Maritsa to *Occitanomys* (*Rhodomys*). We fully agree with the remarks made by VAN DE WEERD (1976) and SEN (1998) and like to add that some of the (sub)-generic allocations suggested by MARTÍN SUÁREZ & MEIN (1991) and FREUDENTHAL & MARTÍN SUÁREZ (1999, p. 406) who assign *Occitanomys sondaari* from the Early Turolian and *O. adroveri* from the Middle Turolian of the Teruel basin, Spain, to the subgenus *Rhodomys*, imply migrations that are otherwise not substantiated. We think that the analyses of cheek tooth morphology has, in this case, been carried beyond the limit of its possibilities. However, we agree with MARTÍN SUÁREZ & MEIN (1991) that *Castillomys* proper is confined to southwestern Europe and contains the species *crusafonti* MICHAUX 1969, gracilis VAN DE WEERD 1976, *rivas* MARTÍN SUÁREZ & MEIN 1991 and possibly *margaritae* ANTUNES & MEIN 1989. The identity of the latter species remains uncertain for the time being because it is based on one isolated M1 only.

We consider *Centralomys* DE GIULI 1989, *Rhodomys* MARTÍN SUÁREZ & MEIN 1991 as junior synonyms of *Occitanomys* MICHAUX 1969. Consequently *Occitanomys* contains the species *brailloni* MICHAUX 1969, *adroveri* (THALER, 1966), *magnus* (SEN, 1977), *debruijni* (SEN *et al*., 1989), *benericettii* (DE GIULI, 1989), *alcalai* ADROVER *et al*. 1988, *sondaari* VAN DE WEERD 1976 and *montheleni* AGUILAR 1986. Judging on the basis of the plates of the type material it seems to us that the species *O. clauzoni* AGUILAR *et al*. 1986 and *O. faillati* AGUILAR *et al*. 1986 are synonyms and do not belong in the genus *Occitanomys* (FREUDENTHAL & MARTÍN SUÁREZ, 1999).

Two other (sub)-genera of murines with brachyodont, moderately stephanodont cheek teeth that should be briefly discussed because of the similarity of their cheek teeth to those of the *Occitanomys/Castillomys* group are: *Hansdebruijnia* STORCH & DAHLMANN 1995 and *Senia* SARICA-FILOREAU 2002. The type species of these (sub)-genera, *O.*? *neutrum* DE BRUIJN 1976 and *S. amasyaensis* SARICA-FILOREAU 2002 differ essentially in the size and the relative width of their cheek teeth only, characteristics we think do not warrant generic separation. *Senia* is therefore considered to be a junior synonym of *Hansdebruijnia*. The latter, with its well developed tma in the m1 and t12 in the M1 and weakly developed stephanodonty seems to be sufficiently different from *Occitanomys* and *Castillomys* to be maintained. The genus *Hansdebruijnia* contains the species *neutrum* (DE BRUIJN, 1976), *pusillus* (SCHAUB, 1938), *perpusillus* STORCH & NI 2002 and *amasyaensis* SARICA-FILOREAU 2002.

Within the context of this discussion it is of interest that MCKENNA & BELL (1997) simplify the classification of the brachyodont, stephanodont murines from the Eurasian Mio/Pliocene even more than has been suggested above by including them all in a single genus. Since *Castillomys* has page priority over *Occitanomys* they maintain *Castillomys* only. We do not follow MCKENNA & BELL (1997) because the type species of *Occitanomys*, *Castillomys* and *Hansdebruijnia* are different.

The *Occitanomys* material from the Ptolemais composite section

The *Occitanomys* assemblages from Ptolemais are of particular interest because they were collected from seven different levels with roughly the same lithology covering a time-span of about 1.4 My. Since the composition of the assemblages collected is similar also (limited diversity, abundance of *Micromys*), we expected the *Occitanomys* samples to show in situ evolution, but this appeared not to be the case. The succession contains four known species that seem to have replaced each other rather than that they have an ancestor-descendant relationship. This replacement of one species by another (Fig. 5) with roughly similar cheek tooth morphology in subsequent beds with the same lithology suggests that the phylogenetical history of the group is much more complex than has been hitherto supposed.

Genus *Occitanomys* MICHAUX 1969
Type species: *Occitanomys brailloni* MICHAUX 1969

Occitanomys debruijni (SEN *et al*., 1989)
(Pl. 5, Figs 1-9; Pl. 6, Figs 9-17)

Selected references:

Castillomys crusafonti MICHAUX, 1969 in: DE BRUIJN *et al*. (1970)

Castillomys debruijni SEN *et al*., 1989 in: SEN *et al*. (1989)

Occitanomys (Rhodomys) debruijni (SEN *et al*., 1989) in: MARTÍN SUÁREZ & MEIN (1991)

Type locality and level: Maritsa, island of Rhodes, Greece, MN13
Localities: Tomea Eksi 1 and 2 (TE1 & TE2)

Age: latest Miocene or earliest Pliocene

Material and measurements of Occitanomys debruijni: Table 3

Description and discussion:
The cheek teeth of *Occitanomys debruijni* from TE1 & TE2 are on average slightly larger than the material from the type locality Maritsa, but the overlap is large. Morphologically the resemblance of the two samples is striking. The posterior spur of the t3 is weaker in the M1 from Tomea Eksi and the t1bis in the M2 from this locality is on average less separate from the t1 than in the specimens from Marisa, but some are virtually identical in these respects also. The two M2 from TE1 and two out of the five M2 from TE2 that have the roots preserved have four roots because the lingual root is fully split. The main diagnostic characteristic of *Centralomys* is, according to DE GIULI (1989), a four-rooted configuration. But apparently this originated several times independently within the *Occitanomys* group and should therefore not be used for separating (sub)-genera (see MARTÍN SUÁREZ & MEIN, 1991, this paper). In this context it is of interest to note that none of the M2 of *O. debruijni* from the type locality shows even an incipiently split lingual root. The difference between the lower cheek teeth of *O. debruijni* from TE1 & TE2 on the one hand and those from Maritsa on the other hand is limited to the degree of development of the longitudinal spur between the second and third chevron in the m1 and m2. In the specimens from Ptolemais this spur is weak or absent, while it varies between strong and absent in the specimens from the island of Rhodes.

Occitanomys debruijni was chosen by MARTÍN SUÁREZ & MEIN (1991) as the type species of their subgenus *Rhodomys*. Since the material described above shows that

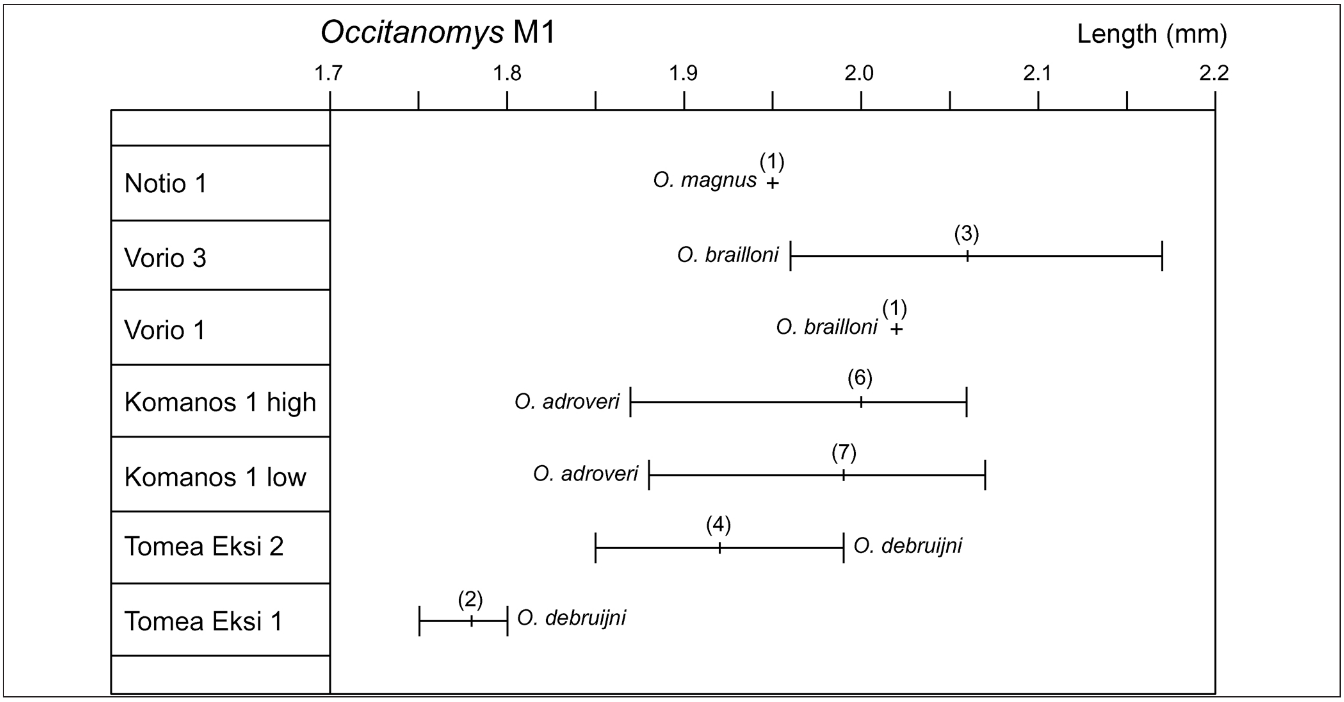


Fig. 5. The range and mean of the length of the M1 of *Occitanomys*. The number of measured specimens is indicated between brackets.

the main diagnostic characters of the subgenera *Rhodomys* and *Centralomys*, may occur as intraspecific variation we consider these subgenera insufficiently defined and junior synonyms of *Occitanomys*.

Occitanomys adroveri (Thaler, 1966)
(Pl. 6, Figs 1-9; Pl. 7, Figs 1-12)

Selected references:

Occitanomys adroveri (Thaler, 1966) in: Michaux (1969)

Occitanomys adroveri (Thaler, 1966) in: Van De Weerd (1976)

Occitanomys adroveri (Thaler, 1966) in: Freudenthal & Martín Suárez (1999)

Type locality and level: Los Mansuetos, Teruel basin, Spain, MN 12

Localities: Komanos 1 low (KO1lowA&B), Komanos 1 high (KO1highA&B)

Age: Early Pliocene

Material and measurements of Occitanomys adroveri: Table 4

Description and discussion

The *Occitanomys* cheek teeth from Komanos 1 are of about the same size and have a very similar morphology as those of *O. adroveri* from its type locality Los Mansuetos. Considering the geographical and stratigraphical distance between these associations this similarity is surprising. Minor differences are that the t4-t5 connection in the M1 and M2 from Komanos is somewhat stronger, and the t12 is on average weaker. These differences suggest that the population from Komanos is slightly more evolved than the one from Los Mansuetos, but this could be the effect of sampling since the individual morphological variation in *Occitanomys* assemblages is known to be wide. In the m1 and m2 from Komanos the anteriorly directed central spur of the last chevron is slightly better developed than in the modal specimen from Los Mansuetos, which again suggests a somewhat more advanced degree of evolution of the Greek population. This conclusion is contradicted by the better developed terminal heel in these specimens. In three of the M2 from Komanos the roots are preserved. One of these has two fully developed lingual roots, a configuration that is not known to occur in any specimen of *O. adroveri* from the type locality. In spite of the minor differences between the Greek specimens from the Early Ruscinian and the Spanish specimens from the Middle Turolian the overall similarity is striking. These two assemblages are therefore allocated to the same species.

TABLE 4

Material and measurements of *Occitanomys adroveri*.

Locality		Length (mm)				Width (mm)			
		N	min.	mean	max.	N	min.	mean	max.
Komanos 1 high	M1	6	1.87	2.00	2.06	6	1.34	1.36	1.40
Komanos 1 high	M2	6	1.37	1.43	1.47	6	1.35	1.39	1.44
Komanos 1 high	M3	6	0.87	0.94	1.01	6	0.91	0.95	0.98
Komanos 1 high	m1	8	1.74	1.82	1.90	8	1.08	1.16	1.26
Komanos 1 high	m2	4	1.38	1.45	1.51	4	1.22	1.29	1.32
Komanos 1 high	m3	5	0.98	1.07	1.22	5	0.96	1.03	1.07
Komanos 1 low	M1	7	1.88	1.99	2.07	7	1.33	1.38	1.45
Komanos 1 low	M2	3	1.30	1.37	1.46	3	1.39	1.42	1.46
Komanos 1 low	M3	4	0.91	0.95	0.97	4	0.93	1.03	1.09
Komanos 1 low	m1	10	1.72	1.83	1.91	9	1.02	1.13	1.29
Komanos 1 low	m2	9	1.20	1.36	1.43	9	1.02	1.20	1.29
Komanos 1 low	m3	5	1.00	1.04	1.09	5	0.90	0.98	1.05

TABLE 5

Material and measurements of *Occitanomys brailloni*.

Locality		Length (mm)				Width (mm)			
		N	min.	mean	max.	N	min.	mean	max.
Vorio 3	M1	3	1.96	2.06	2.17	3	1.47	1.50	1.54
Vorio 3	M2	2	1.49		1.50	2	1.51		1.58
Vorio 3	M3	1		1.04		1		1.12	
Vorio 3	m1	2	1.95		1.99	2	1.27		1.40
Vorio 3	m2	2	1.41		1.51	2	1.32		1.38
Vorio 3	m3	2	1.11		1.13	2	1.06		1.13
Vorio 1	M1	1		2.02		1		1.53	

Occitanomys brailloni Michaux 1969
(Pl. 8, Figs 1-7; Pl. 9, Figs 1-7)

Selected references:

O. brailloni Michaux, 1969 in: Michaux (1969)

O. brailloni Michaux, 1969 in: Van De Weerd (1979)

Type locality and level: Layna, Spain, MN 15

Localities: Vorio 1 and Vorio 3 (VOR 1 & VOR 3)

Age: Early Pliocene

Material and measurements of Occitanomys brailloni: Table 5

Description and discussion

The cheek teeth from VOR1 and VOR3 allocated to *Occitanomys brailloni* are in morphology and size strikingly similar to the specimens from the type locality (Pl. 8, Figs 1-7. Pl. 9, Figs 1-7) of this species and to the ones described by Van De Weerd (1979) from KD and PT1 & PT3. This author noted that his M1 from the Ptolemais basin have a better developed spur on the t3 and that the m1 and m2 have a weaker longitudinal ridge than the ones from the type locality figured by Michaux (1969). Judging by the specimens from Layna available to us for comparison these slight differences are well inside the range of morphological variation of the type assemblage.

The locality Kardia of Van De Weerd (1979) was situated in the first lignite bed of the Ptolemais Fm that directly overlies the Komnina Fm and thus correlates lithostratigraphically with our Komanos 1 levels that yielded *O. adroveri*. This means that *O. brailloni* and *O.*

adroveri either were coeval in the Ptolemais Basin or that there was an age difference of the formation boundary between the Komnina and Ptolemais Formations in the Kardia and Komanos pit. Unfortunately this former section does not exist anymore due to mining activities, so this option could not be verified in the field.

Occitanomys magnus (SEN, 1977)
(Pl. 9, Figs 8-11)

Selected references:

Castillomys magnus SEN, 1977 in: SEN (1977)
Centralomys magnus (SEN, 1977) in: MARTÍN SUÁREZ & MEIN (1991)
Centralomys magnus (SEN, 1977) in: FREUDENTHAL & MARTÍN SUÁREZ (1999)
Centralomys magnus (SEN, 1977) in: SEN (1998)

Synonymy:

Occitanomys sp. from Çalta in: SEN (1998)

Type locality and level: Çalta, Turkey, MN 15

Locality: Notio 1 (NO1)

Age: Early Pliocene

Material and measurements of Occitanomys magnus: Table 6

Discussion

The two and a half *Occitanomys* cheek teeth from NO1 show the same size and high degree of stephanodonty as the type material of *O. magnus* from Çalta (Pl. 9, figs 8-11). The very long posterior spur of the t3 in the M1 that is connected to the garland formed by the t4, t5, t6, t9 and t8 is characteristic and very similar to the configuration seen in *Castillomys*. The homologue of this spur in the M2 connects the t3 to the t5. The original allocation of the species *magnus* to *Castillomys* by SEN (1977) is therefore better than its transfer to *Centralomys* suggested by MARTÍN SUÁREZ & MEIN (1991). The more so because SEN (1977 and 1998) assigned a couple of less stephanodont murine teeth from Çalta, which we think that are within the range of variation of *O. magnus*, to *Occitanomys* sp. Reasons to include these specimens into the species *magnus* are: 1) These teeth are about the same size as those of *magnus*, 2) The individual morphological variation within homogeneous associations of *Occitanomys* cheek teeth is large, 3) It seems unlikely, from a biological point of view, to have two species of low-crowned stephanodont murines of the same size in one association.

TABLE 6
Material and measurements of *Occitanomys magnus*.

Locality		Length (mm)				Width (mm)			
		N	min.	mean	max.	N	min.	mean	max.
Notio 1	M1	1		1.55		2	1.35		1.54
Notio 1	M2	1		1.37		1		1.40	

The allocation of *Occitanomys magnus* to *Centralomys* by MARTÍN SUÁREZ & MEIN (1991) seems primarily based on the presence of four roots in the M2 of *magnus*. Now that we know that the M2 of a number of different *Occitanomys* species from the eastern Mediterranean area may have a four-rooted M2, and that three as well as four-rooted specimens may occur in an assemblage of the same species (i.e. *C. beniricettii*) from one locality, it has become clear that this characteristic is not relevant for distinguishing (sub)-genera within the *Occitanomys* group.

Conclusions on the Occitanomys material

The *Occitanomys* finds from the Ptolemais composite section originate from seven levels embracing about 1.4 My. The four species recognised (Fig. 5) seem to belong to at least three different lineages. The same species occurs in subsequent levels only. All four species are known from elsewhere and have their type localities outside of the Ptolemais basin. With the exception of *O. adroveri*, the age of the occurrences of the different species in the Ptolemais basin is roughly the same as that of their type levels. Since the various species do not constitute a cline, they are all considered to be immigrants into the area. The mechanism of this peculiar replacement of one species by another with roughly the same dental structure in sediments indicating the same sedimentary environment is not understood.

The phylogenetical relationships of the various species of *Occitanomys*, *Castillomys* and *Hansdebruijnia* remains so far obscure, so grouping these species in higher categories on anything but dental similarity is discouraged. At this stage it seems that true *Castillomys* remained restricted to southwestern Europe and, during a short period, northern Africa. *Hansdebruijnia* remained restricted to Asia and the eastern Mediterranean area, while *Occitanomys* had an Eurasiatic range. It is therefore suggested that this rather poorly defined clade is the stem-group of all the old world Mio/Pliocene stephanodont Murinae.

The *Apodemus-Rhagapodemus* group

The definition of *Apodemus* differs among specialists and still is a matter of dispute (MUSSER *et al.*, 1996; MARTÍN SUÁREZ & MEIN, 1998; DE BRUIJN *et al.*, 1999 and literature therein). Although this discussion is outside the scope of this paper, which aims at documenting the sequence of assemblages from the Ptolemais composite section, we feel the necessity to define our usage of the genus name *Apodemus*.

We follow SCHAUB (1938) and DE BRUIJN *et al.* (1999) who include a species into *Apodemus* if the majority of the specimens in an otherwise homogeneous sample of at least ten M1 has a distinct t7, but exclude *Micromys* (t1bis in M1, M2, weak labial cingulum in m1, m2) and *Rhagapodemus* (robust semi-hypsodont cheek teeth with "vertical" cusps, t1 in M1 isolated). Thus defined, *Apodemus* is known to be polyphyletic (DE BRUIJN *et al*., 1999). Unfortunately this cannot be avoided, because the *Apodemus* dental pattern originated several times in different places and time-slices. The oldest fully developed *Apodemus* morphotypes known to us are from the Late Vallesian locality of Hayranlı, Sivas Basin, Central Anatolia (DE BRUIJN, unpublished data). These specimens that occur associated with i.e. *Parapodemus*, *Byzantinia*, *Spermophilinus* and *Pliopetaurista bressana* seem to be considerably older than the assemblages containing *Apodemus* as well as *Parapodemus* morphotypes from Spain (VAN DE WEERD, 1976), Greece and Turkey (DE BRUIJN *et al*., 1999). Since such intermediate assemblages from the eastern Mediterranean area may show this transition in two size-groups, our working hypothesis is that the *Apodemus* dental pattern originated independently several times.

We agree with MARTÍN SUÁREZ & MEIN (1998) that the monophyly of the *Rhagapodemus* group of species cannot be demonstrated either. The reallocation of *Apodemus debruijni* KOTLIA 1992 from Kashmir (KOTLIA *et al*., 1998) and of *Apodemus maximus* THALER 1972 from Monte Pellegrino, Sicily to *Rhagapodemus* (PETRUSO & DE BRUIJN, unpublished data) have enlarged the geographical as well as the morphological range within this group.

Apodemus occurs throughout the Ptolemais composite section, and is, except for the locality VOR3, not abundant (Fig. 6). The assemblages from the lower part of the section (TE1, TE2, KO1 low, KO1 high) show limited individual variation and are therefore considered to contain one species each. The variation in the assemblages from TE3 and VOR3a overlaps the size ranges of *A. atavus* as well as of *A. dominans*, which suggests that these assemblages may contain a mixture of these species (Fig. 6). Since bimodality in size and/or morphology in these assemblages cannot be demonstrated they will be listed below, under one heading: *A. atavus*. The *Apodemus* assemblage from the youngest fossiliferous level can be divided into two species on the basis of the length of the M1 alone (Fig. 6).

The sequence of *Apodemus* assemblages from our section shows similarity to that of *Occitanomys* described above in that the three species recognised do not seem to have an ancestor-descendant relationship. Moreover, the species from the Komnina Fm (TE1 & TE2) differs sharply from the species collected from the first sedimentary cycle of the Ptolemais Fm (KO1 low, KO1 high) (Fig. 6).

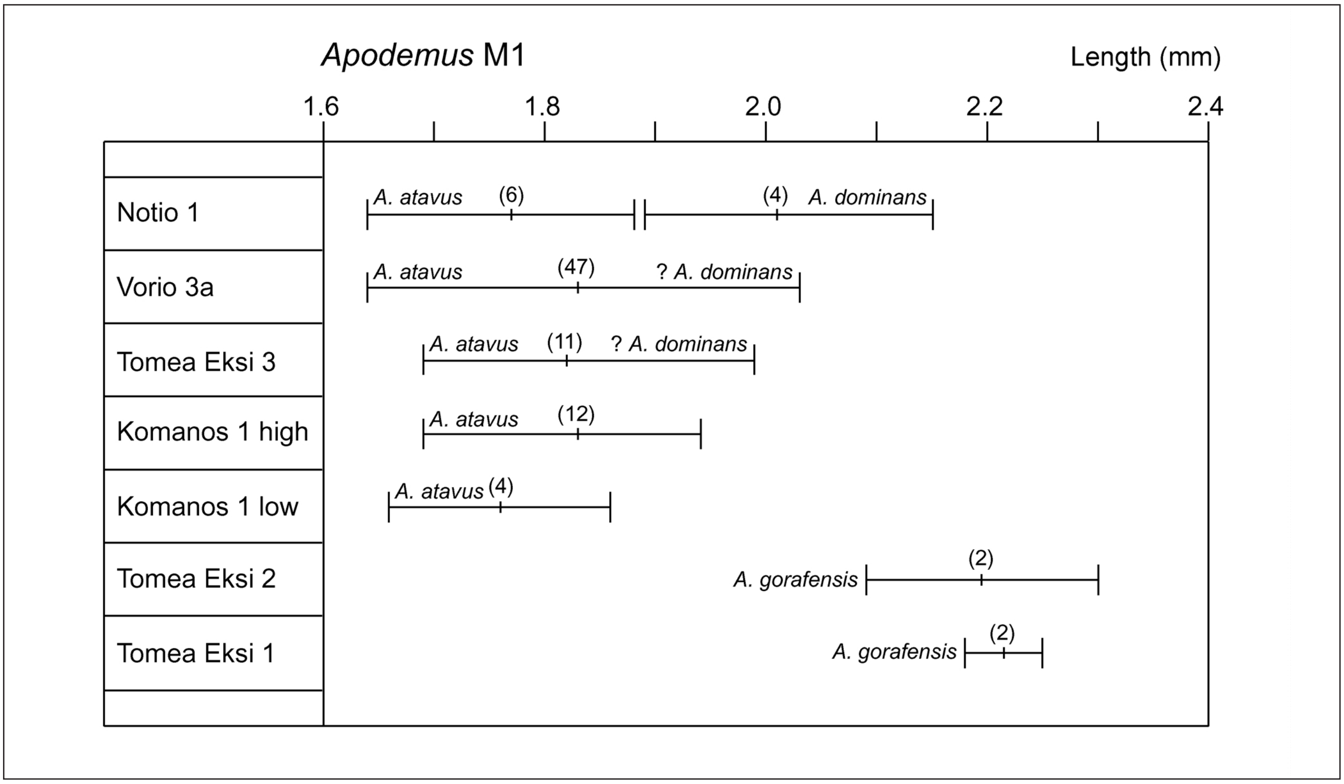


Fig. 6. The range and mean of the length of the M1 of *Apodemus*. The number of measured specimens is indicated between brackets.

Genus *Apodemus* Kaup 1829
Type species: *Apodemus agrarius* (Pallas, 1771)

Apodemus gorafensis Ruiz Bustos *et al*. 1984
(Pl. 10, Figs 13-16)

Selected references:

Apodemus gorafensis Ruiz Bustos *et al*., 1984 in: Storch & Dahlmann (1995)

Apodemus gorafensis Ruiz Bustos *et al*. 1984 in: Martín Suárez & Mein (1998)

Type locality and level: Gorafe A, MN 14

Localities: Tomea Eksi 1 and 2 (TE1 & TE2)

Age: latest Miocene or earliest Pliocene

Material and measurements of Apodemus gorafensis: Table 7

Description and discussion

The *Apodemus* cheek teeth from TE1 & TE2 are on average somewhat smaller than the comparative material of *A. gorafensis* from Gorafe 4 and Caravaca (Spain), but somewhat larger than *A. gudrunae* Van De Weerd 1976 from its type locality Valdecebro 3 (Spain). Since the size of the specimens from TE1 & TE2 shows an overlap with either species, and there is no marked difference in dental morphology between these two species, the identification of our specimens is more or less arbitrary. The choice of *gorafensis* is based on the slightly better size match and the greater similarity in the development of the posterior spur of the t3 in the M1 in that species.

Apodemus atavus Heller 1936
(Pl. 10, Figs 5-12)

Selected references:

Apodemus dominans Kretzoi, 1959 in: Van De Weerd (1979)

Apodemus atavus Heller, 1936 in: Fejfar & Storch (1990)

Type locality and level: Gundersheim MN 16

Localities: Komanos 1 low (KO1lowA&B), Komanos 1 high (KO1highA&B), Tomea Eksi 3 (TE3), Vorio 3a (VOR3a) and Notio1 (NO1)

Age: Pliocene

Material and measurements of Apodemus atavus: Table 8

TABLE 7

Material and measurements of *Apodemus gorafensis*.

Locality		Length (mm)				Width (mm)			
		N	min.	mean	max.	N	min.	mean	max.
Tomea Eksi 2	M1	2	2.09		2.30	8	1.36	1.42	1.49
Tomea Eksi 2	M2	2	1.46		1.56	2	1.23		1.40
Tomea Eksi 2	M3	3	0.92	0.97	1.02	3	1.00	1.03	1.05
Tomea Eksi 2	m1	3	1.93	1.99	2.03	3	1.22	1.23	1.23
Tomea Eksi 2	m2	2	1.19		1.37	2	1.07		1.23
Tomea Eksi 2	m3	1		1.14		1		1.14	
Tomea Eksi 1	M1	2	2.18		2.25	3	1.41	1.45	1.49
Tomea Eksi 1	M2	1		1.53		1		1.41	
Tomea Eksi 1	m1	2	1.99		2.15	2	1.23		1.27
Tomea Eksi 1	m2	1		1.43		1		1.36	

TABLE 8

Material and measurements of *Apodemus atavus*.

Locality		Length (mm)				Width (mm)			
		N	min.	mean	max.	N	min.	mean	max.
Notio 1	M1	6	1.64	1.77	1.88	7	1.03	1.07	1.19
Notio 1	M2	3	1.24	1.27	1.29	3	1.08	1.11	1.16
Notio 1	m1	4	1.63	1.72	1.92	4	0.93	0.99	1.03
Notio 1	m2	2	1.16	1.17	1.17	2	1.04	1.06	1.08
Vorio 3a	M1	47	1.64	1.83	2.03	47	1.01	1.11	1.27
Vorio 3a	M2	33	1.11	1.25	1.42	33	1.01	1.09	1.24
Vorio 3a	m1	27	1.51	1.63	1.88	27	0.84	0.94	1.08
Vorio 3a	m2	30	1.14	1.24	1.77	30	0.97	1.08	1.14
Tomea Eksi 3	M1	11	1.69	1.82	1.99	11	1.03	1.16	1.22
Tomea Eksi 3	M2	11	1.10	1.28	1.38	11	1.07	1.14	1.23
Tomea Eksi 3	M3	1		0.96		1		0.95	
Tomea Eksi 3	m1	9	1.66	1.73	1.82	9	0.95	1.02	1.10
Tomea Eksi 3	m2	9	1.15	1.22	1.29	9	1.03	10.7	1.14
Komanos 1 high	M1	12	1.69	1.83	1.94	11	1.02	1.10	1.18
Komanos 1 high	M2	13	1.20	1.25	1.31	13	1.02	1.19	1.18
Komanos 1 high	M3	4	0.72	0.79	0.84	4	0.77	0.80	0.83
Komanos 1 high	m1	13	1.49	1.67	1.80	13	0.90	0.99	1.13
Komanos 1 high	m2	7	1.09	1.21	1.28	7	0.99	1.02	1.06
Komanos 1 high	m3	2	0.83	0.88	0.93	2	1.00	1.05	1.09
Komanos 1 low	M1	4	1.66	1.76	1.86	4	1.08	1.12	1.15
Komanos 1 low	M2	4	1.17	1.26	1.31	4	1.10	1.12	1.17
Komanos 1 low	m1	9	1.63	1.70	1.76	9	0.96	1.02	1.07
Komanos 1 low	m2	7	1.13	1.21	1.26	7	0.94	1.03	1.13

TABLE 9

Material and measurements of *Apodemus dominans*.

Locality		Length (mm)				Width (mm)			
		N	min.	mean	max.	N	min.	mean	max.
Notio 1	M1	4	1.89	2.01	2.15	5	1.18	1.30	1.36
Notio 1	M2	5	1.17	1.33	1.40	5	1.13	1.21	1.27
Notio 1	m1	4	1.83	1.86	1.87	4	1.08	1.12	1.15
Notio 1	m2	4	1.17	1.26	1.36	5	1.11	1.17	1.24

Description and discussion

The size of the cheek teeth from TE3 and VOR3 assigned to *A. atavus* is on average somewhat larger than the type material and the material from the other levels (Fig. 6). Although the size distribution in these assemblages is normal, it can not be excluded that these assemblages are not homogeneous and contain some specimens of *A. dominans*.

The specific identity of assemblages of small to medium sized *Apodemus* of Ruscinian and Villanyian age presents a problem, because they all share primitive characteristics such as a three-rooted M1 and M2, a relatively well-developed t12 in the M1 and M2 and the presence of the c1 in the m1 and m2. The dental pattern in what are assumed to be homogeneous samples is quite variable, but samples of different age and geographical provenance often show great similarity. Although there are size differences between samples, these do not allow the recognition of discrete groups, so the identification of species within the small to medium-sized *Apodemus* remains unsatisfactory.

The assemblages from the Ptolemais composite section assigned above to *A. atavus* show the following dental characteristics:

M1: t7 and t12 is always well developed, t3 with short posteriorly directed spur, t4 and t7 not connected until a very advanced stage of wear is reached. M1 is slender and has three roots.

M2: t7 and t12 always well developed, t4 and t7 not connected until a very advanced stage of wear is reached. M2 has, except for one specimen out of 32 from VOR3a, three roots.

m1: The anterior central cusp and the posterior heel are always well developed, the medial spur of the protoconid/metaconid chevron is connected to the lingual cusp of the anteroconid complex. The medial spur of the hypoconid/entoconid chevron is either short or absent. Other than the c1, which is always well developed, the cusps on the labial cingulum show much variation: In some specimens there are two isolated cusps in front of the c1, in others there are a variable number of small semi-fused cusps. A few m1 have a small isolated cusp behind the c1.

m2: The medial spur of the hypoconid/entoconid chevron is weak or absent, the antero-labial cusp is always well developed, the size of the c1 shows great variation: in most specimens it is very small, but it may sometimes be either well developed or absent

Comparison of the older assemblage assigned to *A. atavus* (KO1lowA&B) with the younger one from our section (NO1) shows that there are minor differences (i.e. the m1 from NO1 are more slender). In the absence of a clear trend these differences are interpreted as intraspecific variation.

Apodemus dominans KRETZOI 1959
(Pl. 10, Figs 1-4)

Selected references:

Apodemus dominans KRETZOI, 1959 in: DE BRUIJN & VAN DER MEULEN (1975)

Apodemus dominans KRETZOI, 1959 in: STORCH & DAHLMANN (1995)

Type locality and level: Csarnóta 2, Hungary, MN 15

Locality: Notio 1 (NO1)

Age: Pliocene

Material and measurements of Apodemus dominans: Table 9

Description and discussion

The cheek teeth of *A. dominans* from NO1 are very similar to the teeth from Csarnóta 2. In three out of the five M1 from NO1 the posterior outline of the t1 is rounded, in the two others the t1 has a spur that reaches the base of the t5. The two M1 from the type locality show the same variation.

The t3 of three of the M1 from NO1 has a short posterior spur, but the two others do not. Both M1 from Csarnóta have a well-developed posterior spur on the t3. Other than such minor differences our material is identical to the material from the type locality. The M2 from NO1 show a wide variation in the relative size of the t1 and t3 and in the degree of development of the t12. In one M2 the t1 and t3 are about the same size, in three others the t1 is clearly larger than the t3 and in one the t1 is much larger than the t3. The t12 is very strong in two M2, small in two others and absent in one specimen.

The antero-central cusp is well developed in three out of the four m1, in the fifth it is weak and situated somewhat labially. The anterior spur of the protoconid-metaconid chevron is connected to the lingual cusp of the anteroconid complex. The hypoconid – entoconid chevron has a short anterior spur in one specimen, but in the others this spur is absent. The c1 is always strong. The number of cusps on the labial cingulum varies between two and four. The five m2 from NO1 differ from the single specimen from Csarnóta available for comparison in being wider. The c1 is rather small (four) or absent (one), but the cusps on the labial cingulum are better developed in the m2 from NO1 than in our specimen from Csarnóta.

Genus *Rhagapodemus* KRETZOI 1959
Type species: *Rhagapodemus frequens* KRETZOI 1959

The first record of the genus *Rhagapodemus* in the Ptolemais composite section is from the base of the Ptolemais Fm (KO1 low). This genus seems to occur as a rare fauna element throughout the formation and its absense from some assemblages is considered to be due to sampling bias. The genus is represented by two species: *R. primaevus* (HUGUENEY & MEIN, 1965) occurring in the lower part of the formation is replaced by *R. frequens* KRETZOI 1959 in younger fossiliferous level (NO1). The number of specimens collected from each level is limited and does therefore not allow detecting evolutionary change. Unfortunately, there is a gap of about 0.9 My between the last record of *R. primaevus* and the first record of *R. frequens* so it is not clear whether or not the one evolves into the other.

Rhagapodemus primaevus (HUGUENEY & MEIN, 1965)
(Pl. 11, Figs 5-8)

Selected references:

Apodemus primaevus Hugueney & Mein, 1965

Rhagapodemus hautimagnensis Mein & Michaux, 1970 in: Van De Weerd (1979)

Rhagapodemus primaevus (Hugueney & Mein, 1965) in: Storch & Dahlmann (1995)

Rhagapodemus primaevus (Hugueney & Mein, 1965) in: Martín Suárez & Mein (1998)

Type locality and level: Lissieu, MN13

Localities: Komanos 1 low (KO1lowA&B), Komanos 1 high (KO1highA&B), Vorio 1 (VOR1) and Vorio 3(VOR3)

Age: Early Pliocene

Material and measurements of Rhagapodemus primaevus: Table 10

Description and discussion

The size and morphology of the cheek teeth from the Ptolemais section assigned to *Rhagapodemus primaevus* is within the range of variation of the material of that species from the type locality (Martín Suárez & Mein, 1998). Judging by the figures, the two first lower molars of the presumably smaller, *R. ballesioi* Mein & Michaux 1970 from Hautimagne and *R. debruijni* (Kotlia *et al*., 1998) from Kashmir share the near absence of extra cusps with *primaevus*.

The *Rhagapodemus* material from the Ptolemais Basin identified by Van De Weerd (1979) as *R. hautimagnensis* obviously represents the same species as the specimens allocated above to *R. primaevus*, a species that was still included into the genus *Apodemus* in 1979. All the levels of the Ptolemais section containing *R. primaevus* have an Early Ruscinian (MN 14) age and are thus younger than the type locality of that species. This means that the stratigraphic range of *R. primaevus* in central Greece overlaps the range of *R. hautimagnensis* in France.

TABLE 10

Material and measurements of *Rhagapodemus primaevus*.

Locality		Length (mm)				Width (mm)			
		N	min.	mean	max.	N	min.	mean	max.
Vorio 3	M1	1		1.90		1		1.27	
Vorio 3	M2	3	1.26	1.28	1.30	3	1.17	1.27	1.30
Vorio 3	M3	1		1.00		1		0.93	
Vorio 3	m3	2	1.11	1.21	1.30	2	0.99		1.10
Tomea Eksi 3	m1	2	1.85		2.02	2	1.17		1.28
Tomea Eksi 3	m2	1		1.38		1		1.28	
Vorio 1	M1	1		2.05		1		1.26	
Komanos 1 high	M1	6	2.00	2.11	2.24	6	1.21	1.26	1.29
Komanos 1 high	M2	9	1.29	1.39	1.52	8	1.21	1.28	1.34
Komanos 1 high	M3	5	0.94	1.05	1.12	4	0.92	0.97	1.01
Komanos 1 high	m1	1		1.79		2	1.09		1.10
Komanos 1 high	m2	6	1.21	1.34	1.53	6	1.06	1.16	1.34
Komanos 1 high	m3	6	1.04	1.15	1.26	6	0.98	1.02	1.25
Komanos 1 low	M1	4	1.99	2.04	2.08	4	1.18	1.26	1.36
Komanos 1 low	M2	4	1.17	1.37	1.48	4	1.20	1.24	1.29
Komanos 1 low	M3	2	1.00		1.04	2	0.91		0.92
Komanos 1 low	m2	1		1.32		1		1.09	
Komanos 1 low	m3	2	1.30		1.34	2	1.07		1.10

TABLE 11

Material and measurements of *Rhagapodemus frequens*.

Locality		Length (mm)				Width (mm)			
		N	min.	mean	max.	N	min.	mean	max.
Notio 1	M1	1		2.23		1		1.48	
Notio 1	M2	3	1.43	1.47	1.53	3	1.27	1.37	1.44
Notio 1	M3	2	1.18		1.27	1		1.07	
Notio 1	m1	3	1.94	2.16	2.28	3	1.20	1.28	1.33
Notio 1	m2	3	1.53	1.58	1.67	3	1.31	1.38	1.48
Notio 1	m3	2	1.40		1.44	3	1.15	1.23	1.28

Rhagapodemus frequens Kretzoi 1959
(Pl. 11, Figs 1-4)

Selected references:

Rhagapodemus frequens Kretzoi, 1959 in: Fejfar & Storch (1990)

Type locality and level: Csarnóta 2 (MN 15)

Locality: Notio 1 (NO1)

Age: Pliocene

Material and measurements of Rhagapodemus frequens Table 11

Description and discussion

The specimens from NO1 assigned to *Rhagapodemus frequens* are in every respect similar to the few cheek teeth of that species from the type locality available for comparison. The round t1 of the M1 is isolated from the fused t2 and t3. The size of the t3 of the M2 is variable and this cusp is antero-posteriorly compressed. The antero-central cusp of the m1 shows considerable variation in size, and the anteroconid complex is connected to the protoconid-metaconid chevron in one out of the four m1 only. The c1 of the m1 fuses completely with the hypoconid at an early stage of wear. The extra cusps on the labial cingulum of the m2 are very weak or absent, and there is not even a trace of the c1.

The composition of the assemblage from NO1 (Fig. 7) suggests that this level has about the same age as the type locality of *Rhagapodemus frequens* Csarnóta 2.

Conclusions on the Apodemus-Rhagapodemus group

The sequence of the *Apodemus* assemblages and the record of *Occitanomys* from the Ptolemais composite section show surprising analogy in that the species do not seem to have any ancestor descendant relationship. *Apodemus gorafensis* occurs in the Miocene part of the section only. *Apodemus atavus* is present throughout the Pliocene part of the section, while *Apodemus dominans* can be distinguished with certainty in the younger fossiliferous level only. These three *Apodemus* species seem to represent different lineages.

Rodent species	*Pseudomeriones* sp.	*Occitanomys debruijni*	*Arvicanthis broekhuisi* n. sp.	*Apodemus gorafensis*	*Micromys bendai*	*Micromys steffensi*	*Occitanomys adroveri*	*Microtodon komanensis* n. sp.	*Microtodon* sp.	*Promimomys cor*	*Rhagapodemus primaevus*	*Allocricetus ehiki*	*Apodemus atavus*	*Tamias* sp.	*Glis minor*	*Pliopetaurista dehneli*	Castoridae indet.	*Occitanomys brailloni*	*Mimomys davakosi*	*Apodemus dominans*	*Rhagapodemus frequens*	*Occitanomys magnus*	*Prospalax priscus*	*Dolomys nehringi*	*Propliomys hungaricus*	*Sciurus anomalus*	*Myomimus maritsensis*	PCS		MN zone
Localities																												Formations	Members	
Notio 1													■		■		■			■	■	■	■	■ cf.	■	■	■ aff.	Ptolemais	Notio	15
Vorio 3/3a					■			■ aff.			■		■			■	■	■	■	■ ?									Kyrio	
Tomea Eksi 3					■						■		■						■ aff.	■ ?										
Vorio 1					■					■	■		■					■												14
Komanos 1 high						■	■	■		■	■	■	■			■ cf.	■													
Komanos 1 low						■	■	■	■	■	■	■	■	■	■															
Tomea Eksi 2	■	■	■	■																								Komnina	Tomea Eksi	13
Tomea Eksi 1	■	■	■	■																										

Fig.7. Overview of the occurrence of rodent species in the Ptolemais composite section (PCS). The localities are ranked in stratigraphic order. Localities representing the same stratigraphic level that have been sampled at a lateral distance from each other have been combined (i.e. KO1lowA&B, KO1highA&B and VOR3&3a). KO2 and PSM have been omitted because of its poor faunal contents and its position outside the Ptolemais Basin, respectively. The corresponding formations and members from the PCS are indicated on the right hand side, along with the correlation to the MN zonation.

The five subsequent assemblages of *A. atavus* cover about 1.25 My, but show no evolutionary change. The three species recognised all have their type localities outside of Greece and the ages allocated to these type localities are roughly the same as their occurrences in the Ptolemais composite section.

The oldest record of the genus *Rhagapodemus* in the Ptolemais composite section is *R. primaevus* from the base of the Ptolemais Fm (Pliocene, MN14). This relatively late local appearance of this genus suggests that its absence from the Komnina Fm is due to ecological factors. *R. primaevus* is present throughout the lower part of the Ptolemais Fm and seems to have had a longer stratigraphic range in Greece than in southwestern Europe. The nature of the succession of *R. primaevus* by *R. frequens* in the local top of the Ptolemais Fm cannot be verified because there is a gap of about 0.9 My between the last occurrence of *primaevus* and the first record of *frequens*.

The *Micromys* material from the Ptolemais composite section

Micromys DEHNE 1841
Type species: *Mus minutus* PALLAS 1771

The genus *Micromys* comprises seven species of which only *Micromys minutus* (PALLAS, 1771), the harvest mouse, is extant. The oldest *Micromys* known is *M. chalceus* STORCH 1987 from the Late Miocene of Inner Mongolia (STORCH, 1987), suggesting an Asian origin of this genus. The fossil record indicates that *Micromys* attained its greatest diversity during the Early Pliocene. VAN DE WEERD (1979) and STORCH & DAHLMANN (1995) have noted that the genus *Micromys* does not represent one single lineage, but that its phylogenetic history is complex. Fossil representatives are known from localities throughout Europe and Asia. However, most fossil species are known from small geographical areas only. These limited geographical ranges may be caused by incompleteness of the fossil record.

Extant *Micromys minutus* is widespread in Eurasia. Its biotope includes grasslands, reed lands and wheat fields. *M. minutus* is well adapted to living in tall vegetation. It uses its tail as a fifth limb and nests are built above the ground.

Fossil species recognized:

- *M. praeminutus* KRETZOI 1959
- *M. bendai* VAN DE WEERD 1979
- *M. steffensi* VAN DE WEERD 1979
- *M. paricioi* MEIN, MOISSENET & ADROVER 1983
- *M. chalceus* STORCH 1987
- *M. cingulatus* STORCH & DAHLMANN 1995

Remarks

We consider the species *Micromys kozaniensis* VAN DE WEERD 1979 and *Micromys tedfordi* WU & FLYNN 1992 to be junior synonyms of *Micromys bendai*. QIU & STORCH (2000) described *M. kozaniensis* from Bilike, China. The size of their material compares very well with that of the type material from PT3. Direct comparison of the *Micromys* material from Bilike and Greece showed that the assemblage from Bilike contains M1 morphotypes of both *M. bendai* and *M. kozaniensis*. We therefore consider *M. kozaniensis* a junior synonym of *M. bendai*. We choose the latter name, because of page priority.

WU & FLYNN (1992) have described the species *Micromys tedfordi* from YS50 in the Yushe Basin, China. Its morphology is very similar to *M. bendai*. Both species have a 5-rooted M1, a posterior spur on t3 of M1, a t7 in M1 and M2, a smaller t9 compared to t6 in M1 and M2, and a t1bis on M2. The m1 of both species have a weak labial cingulum and a small, but distinct, anterocentral cusp. The size of *M. tedfordi* molars is very similar to the size of *M. bendai* molars from PT1 and from the new localities. WU & FLYNN (1992) did not provide a differential diagnosis for the distinction between *M. tedfordi* and *M. bendai*. QIU & STORCH (2000) have indicated that the M2 of *M. tedfordi* has five or six roots, while the M2 of the type material of *M. kozaniensis* has only four. In our material, some M2 have 5 roots, indicating that there is some variation. Given this variation, we consider the difference in the number of roots insufficient for the distinction between *M. tedfordi* and *M. bendai*. We therefore consider *M. tedfordi* to be a junior synonym of *M. bendai*. CAI & QIU (1993) have used the name *Micromys* aff. *tedfordi* for material from Daodi, China. A consequence of our rejection of the name *M. tedfordi* is that the name *Micromys* aff. *tedfordi* is no longer appropriate.

STORCH & DAHLMANN (1995) have assigned the species *Parapodemus coronensis* (SCHAUB, 1938) to *Micromys*, but do not give clear arguments for this reassignment. The type material of this species, one fragment of a maxilla with a heavily worn M1 and M2, is inconclusive. We therefore consider *Parapodemus coronensis* a *nomen dubium*.

VAN DE WEERD (1979) has shown that the genus *Micromys* is quite abundant in the Early Pliocene deposits of the Ptolemais Basin. We have examined the metric homogeneity of twelve new *Micromys* assemblages from the Florina-Ptolemais-Servia Basin by applying the method proposed by FREUDENTHAL & CUENCA BESCOS (1984), in which variability coefficients are calculated for the length and width of the M1.

The variability coefficient V' = (100·R)/M, in this equation M is the midpoint between the maximum and minimum value of the measured parameter and R the range (maximum - minimum). Variability coefficients were calculated for assemblages that contain at least five measurable specimens in order to obtain a statistically significant value, as recommended by FREUDENTHAL & CUENCA BESCOS (1984). The range and the sample size show a logarithmic relationship. To minimize the effect of sample size, the variability is expressed relative to √(logN) in which N is the sample size (FREUDENTHAL & MARTÍN SUÁREZ, 1990). The calculated variability values for the M1 are shown in Table 12. The variability of the M1 in Murinae as calculated by FREUDENTHAL & MARTÍN SUÁREZ (1990) is given for comparison. The variability values in Table 12 show that the size variation in M1 in the studied *Micromys* assemblages falls within the maximum range for monospecific murine assemblages.

Micromys bendai VAN DE WEERD 1979

(Pl. 12, Figs 1-14)

Type locality and level: Ptolemais 1 (PT1), Ptolemais Basin, Greece, MN14

Synonymy:

Micromys kozaniensis VAN DE WEERD, 1979 in: VAN DE WEERD (1979)

Micromys bendai VAN DE WEERD, 1979 in: AGUILAR *et al*. (1989)

Micromys tedfordi WU & FLYNN, 1992 in: WU & FLYNN (1992)

Micromys kozaniensis VAN DE WEERD, 1979 in: QIU & STORCH (2000)

Localities: Prosilion-Mercurion (PSM), Tomea Eksi 1, 2 and 3 (TE1, TE2 & TE3), Vorio 1 (VOR1), Vorio 3 & 3a (VOR3 & VOR3a) and Komanos 2 (KO2)

Age: latest Miocene and Early Pliocene

Material and measurements of Micromys bendai: Table 13

Description

M1: The t1 is connected to the t2. Some specimens have a faint t1bis. Small additional cuspids are common near the molar outline between the t2 and t3 (= prestyle of STORCH, 1987) and sometimes between t1 and t2 (= t0, of STORCH, 1987). The two specimens from VOR1 show a relatively deep inflexion in the molar outline between t1 and t2. The t3 has a posterior spur in sixtytwo specimens. The t3, t6 and t9 are usually narrow, but inflated in some M1. The t9 is smaller than the t6. Fifteen specimens have a narrow shallow valley between the t6 and t9. The t7 is well developed. The t4 and t7 are usually well separated, but may show a low connection at the base. In some specimens t4 and t7 are connected. The t12 is always present, either as a small cusp or as a ridge. The M1 has five roots, but one specimen has a small sixth rootlet under the t5.

TABLE 12

Variability coefficients for the M1 in all studied *Micromys* assemblages. Coefficients have been calculated for assemblages containing 5< specimens and are normalised w.r.t. sample size. The standard deviation of the variability of the M1 in Murinae (FREUDENTHAL & MARTÍN SUÁREZ, 1990) indicates the maximum variability observed in monospecific murine samples.

Locality	Length			Width		
	N	V'/√(log(N))	SD	N	V'/√(log(N))	SD
Murinae	180	13.94	4.01	183	13.02	3.95
Komanos 2	2	-		4	-	
Vorio 3a	38	14.02		38	13.21	
Vorio 3	10	10.58		9	15.10	
Tomea Eksi 3	11	11.65		12	14.17	
Vorio 1	2	-		2	-	
Komanos 1 high A	33	9.95		37	8.46	
Komanos 1 high B	30	10.52		30	7.50	
Komanos 1 low A	30	13.74		36	13.64	
Komanos 1 low B	4	-		5	15.16	
Tomea Eksi 2	23	15.33		29	9.81	
Tomea Eksi 1	7	9.20		9	15.48	
Prosilion	3	-		5	7.58	

TABLE 13

Material and measurements of *Micromys bendai*.

Locality		Length (mm)				Width (mm)			
		N	min.	mean	max.	N	min.	mean	max.
Komanos 2	M1	2	1.79	1.81	1.83	4	1.10	1.16	1.21
Vorio 3a	M1	38	1.76	1.94	2.10	38	1.16	1.27	1.37
Vorio 3	M1	10	1.79	1.94	1.99	9	1.13	1.23	1.31
Tomea Eksi 3	M1	11	1.74	1.85	1.96	12	1.07	1.17	1.24
Vorio 1	M1	2	1.79	1.80	1.82	2	1.14	1.14	1.15
Tomea Eksi 2	M1	23	1.68	1.84	2.01	29	1.11	1.18	1.25
Tomea Eksi 1	M1	7	1.81	1.87	1.97	9	1.10	1.19	1.28
Prosilion-Merc.	M1	3	1.74	1.82	1.90	5	1.07	1.12	1.14
Vorio 3a	M2	57	1.14	1.27	1.37	58	1.06	1.16	1.23
Vorio 3	M2	15	1.19	1.26	1.30	15	1.06	1.14	1.18
Tomea Eksi 3	M2	14	1.12	1.22	1.30	14	1.05	1.11	1.15
Vorio 1	M2	2	1.15	1.21	1.26	2	1.03	1.04	1.04
Tomea Eksi 2	M2	25	1.16	1.24	1.34	28	1.01	1.12	1.21
Tomea Eksi 1	M2	6	1.23	1.27	1.31	7	1.07	1.13	1.17
Prosilion-Merc.	M2	2	1.11	1.13	1.14	2	1.00	1.01	1.01
Komanos 2	M3	1	-	0.73	-	1	-	0.83	-
Tomea Eksi 3	M3	4	0.78	0.84	0.90	4	0.78	0.82	0.87
Tomea Eksi 2	M3	4	0.72	0.78	0.83	5	0.72	0.77	0.83
Tomea Eksi 1	M3	3	0.71	0.77	0.82	3	0.76	0.76	0.76
Komanos 2	m1	2	1.63	1.63	1.63	2	1.05	1.05	1.05
Vorio 3a	m1	31	1.64	1.75	1.89	31	0.92	1.03	1.14
Vorio 3	m1	7	1.68	1.78	1.87	7	0.96	1.02	1.10
Tomea Eksi 3	m1	6	1.59	1.63	1.65	6	0.96	1.00	1.04
Vorio 1	m1	1	-	1.52	-	1	-	0.85	-
Tomea Eksi 2	m1	13	1.56	1.67	1.77	17	0.92	1.01	1.06
Tomea Eksi 1	m1	7	1.56	1.64	1.72	9	0.96	1.03	1.13
Prosilion-Merc.	m1	10	1.51	1.63	1.70	10	0.87	0.93	1.00
Komanos 2	m2	1	-	1.23	-	1	-	1.09	-
Vorio 3a	m2	50	1.12	1.23	1.31	50	0.98	1.05	1.12
Vorio 3	m2	8	1.10	1.20	1.23	8	0.97	1.01	1.06
Tomea Eksi 3	m2	9	1.12	1.16	1.27	9	0.95	1.01	1.13
Vorio 1	m2	2	1.05	1.08	1.11	2	0.95	0.96	0.96
Tomea Eksi 2	m2	25	1.11	1.19	1.29	27	0.98	1.05	1.14
Tomea Eksi 1	m2	9	1.09	1.17	1.23	9	0.99	1.05	1.12
Prosilion	m2	7	1.05	1.09	1.17	6	0.93	0.97	1.05
Komanos 2	m3	1	-	0.98	-	1	-	0.80	-
Vorio 3	m3	1	-	0.84	-	1	-	0.76	-
Tomea Eksi 3	m3	18	0.80	0.93	1.04	18	0.75	0.84	0.95
Tomea Eksi 2	m3	14	0.79	0.88	0.99	14	0.77	0.83	0.92
Tomea Eksi 1	m3	4	0.83	0.84	0.85	4	0.82	0.83	0.84

M2: A distinct t1bis is present on all but three specimens. In fourty one specimens the t6 and t9 are well separated. In the remaining specimens the t6 and t9 are either connected or positioned very closely. The t9 is usually narrow and elongate. However, some specimens have a rather round t9, while the t9 is reduced to a narrow ridge in others. A t12 is present, but sometimes indistinct. The M2 has four roots, but six specimens have

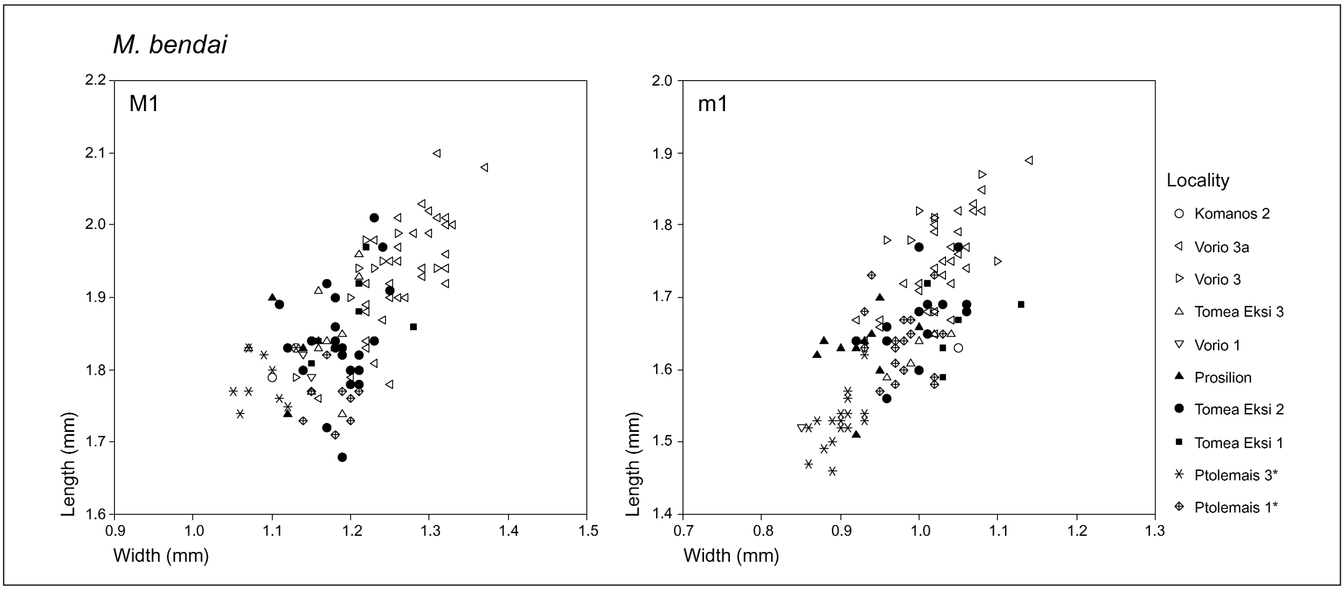


Fig. 8. Scatter diagrams showing the length and width of the M1 and m1 specimens of *Micromys bendai* from the Ptolemais Basin and the Servia Basin. The asterisks indicate the measurements from VAN DE WEERD (1979).

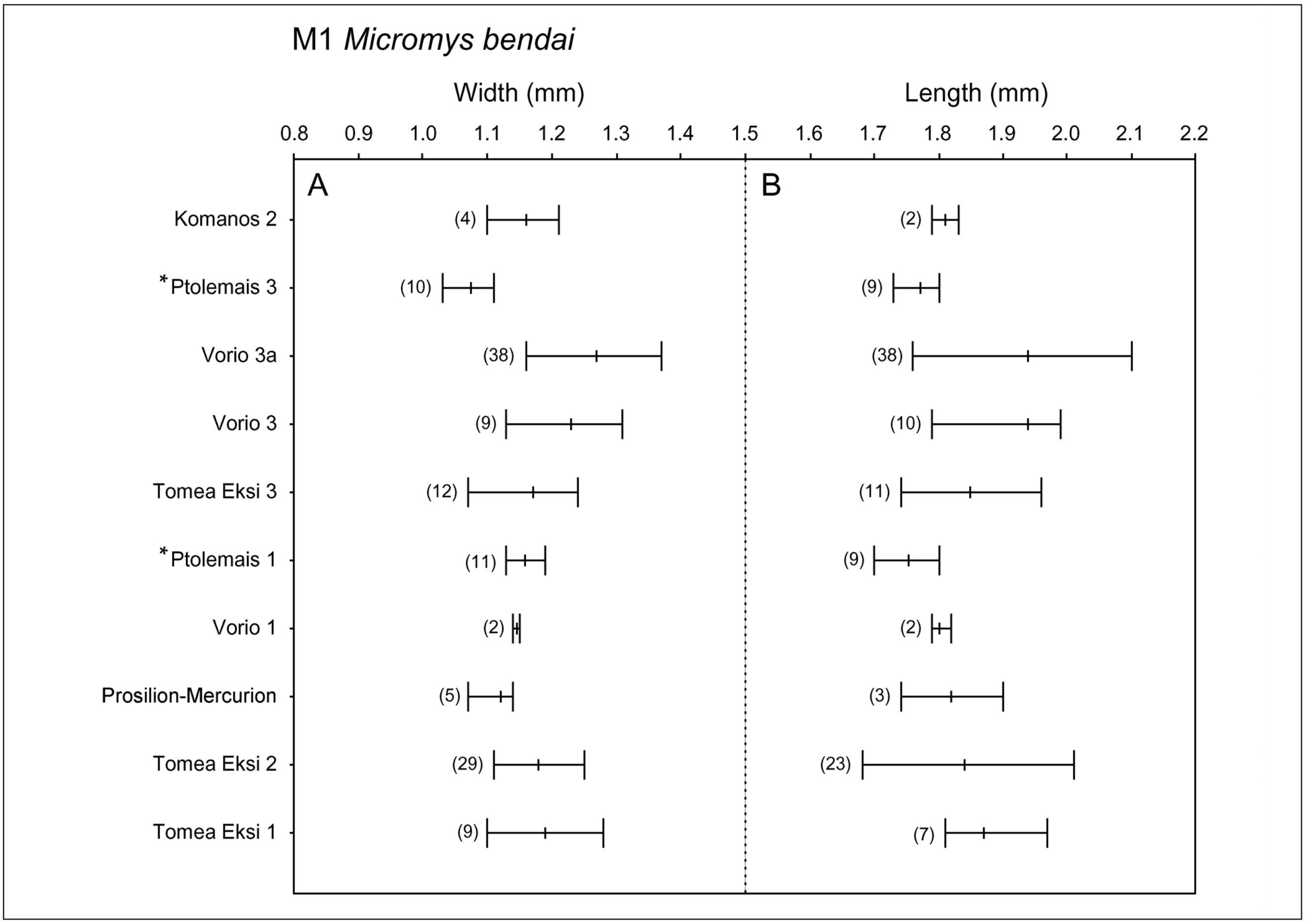


Fig. 9. The range and mean of the width (A) and length (B) of the M1 of *Micromys bendai* from the Ptolemais Basin and the Servia Basin. The number of measured specimens is indicated between brackets. The asterisks indicate the measurements from VAN DE WEERD (1979).

a small additional fifth rootlet under the t5.

M3: The t3 is absent or indistinct. The t4 is rather large. The t8 is connected to the t4 in seven specimens. The t6 and t8 are connected in 11 specimens. A small t9 is present in four specimens. The M3 has two main roots. In some specimens the lower part of the root under the t5 is divided into two rootlets.

m1: A small, but distinct, antero-central cusp is present in all specimens. The labial cingulum is low and narrow. Next to the protoconid, the cingulum is somewhat higher in several specimens, but there is no accessory cusp. A posterior accessory cusp of variable size is always present. In 16 specimens the posterior accessory cusp is connected to the hypoconid. The m1 has two main roots and a smaller third rootlet. One specimen has an additional fourth rootlet between the main roots.

m2: The labial cingulum is narrow and low. The cingulum next to the protoconid is often somewhat irregular. In 12 specimens a weak accessory cusp (c2) is visible. Most specimens have a posterior accessory cusp, but this cusp is sometimes indistinct or absent. The posterior accessory cusp is connected to the hypoconid in 20 specimens. The m2 has two roots.

m3: The antero-labial cusp is small. The hypoconid has a groove on its postero-labial side in most specimens, indicating a small incipient posterior accessory cusp on the labial side of the hypoconid. The m3 has two roots. In some specimens the root under the protoconid and metaconid is bifurcated near the tip.

Discussion

The morphology of the cheek teeth in the eight *Micromys bendai* assemblages described above is very similar to that of the type material, although a short posterior spur on the t3 of M1 is more common in our material. There seems to be no morphological change in these molars through time. In the stratigraphically youngest assemblages (TE3 and KO2), however, the cusps of some M1 are slightly more inflated, which is most apparent in the t3. The *M. bendai* M1 with inflated cusps in the TE3 assemblage are similar to *Apodemus*. In case the roots are not preserved, identification is difficult and errors can therefore not be excluded.

The size-ranges of the M1 and m1 in the *Micromys bendai* assemblages are shown in Fig. 8. The size-range of the *M. bendai* type material (VAN DE WEERD, 1979) is given for comparison. Both diagrams show a wide variation in the size of M1 and m1. The average size of M1 and m1 in the type assemblage is somewhat smaller than in the *M. bendai* assemblages described in this study. However, the size-ranges of *M. bendai* from the new localities overlap with the type material. The size of the *M. bendai* material described by AGUILAR *et al*. (1989) from Péage de Roussillon (France) is also slightly larger than the type material from PT1.

The size of M1 through time is shown in Fig. 9. The figure shows no trend, but rather a randomly changing size through time. Figure 8 shows that the difference in molar size between *M. bendai* assemblages can be quite large and exceeds the size variation of the type material from PT1.

Micromys steffensi VAN DE WEERD 1979
(Pl. 13, Figs 1-10)

Type locality and level: Kardia (KD), Ptolemais Basin, Greece, MN14

Localities: Komanos 1 low A and B (KO1lowA&B) and Komanos 1 high A and B (KO1highA&B)

Age: Early Pliocene

Material and measurements of Micromys steffensi: Table 14

Description

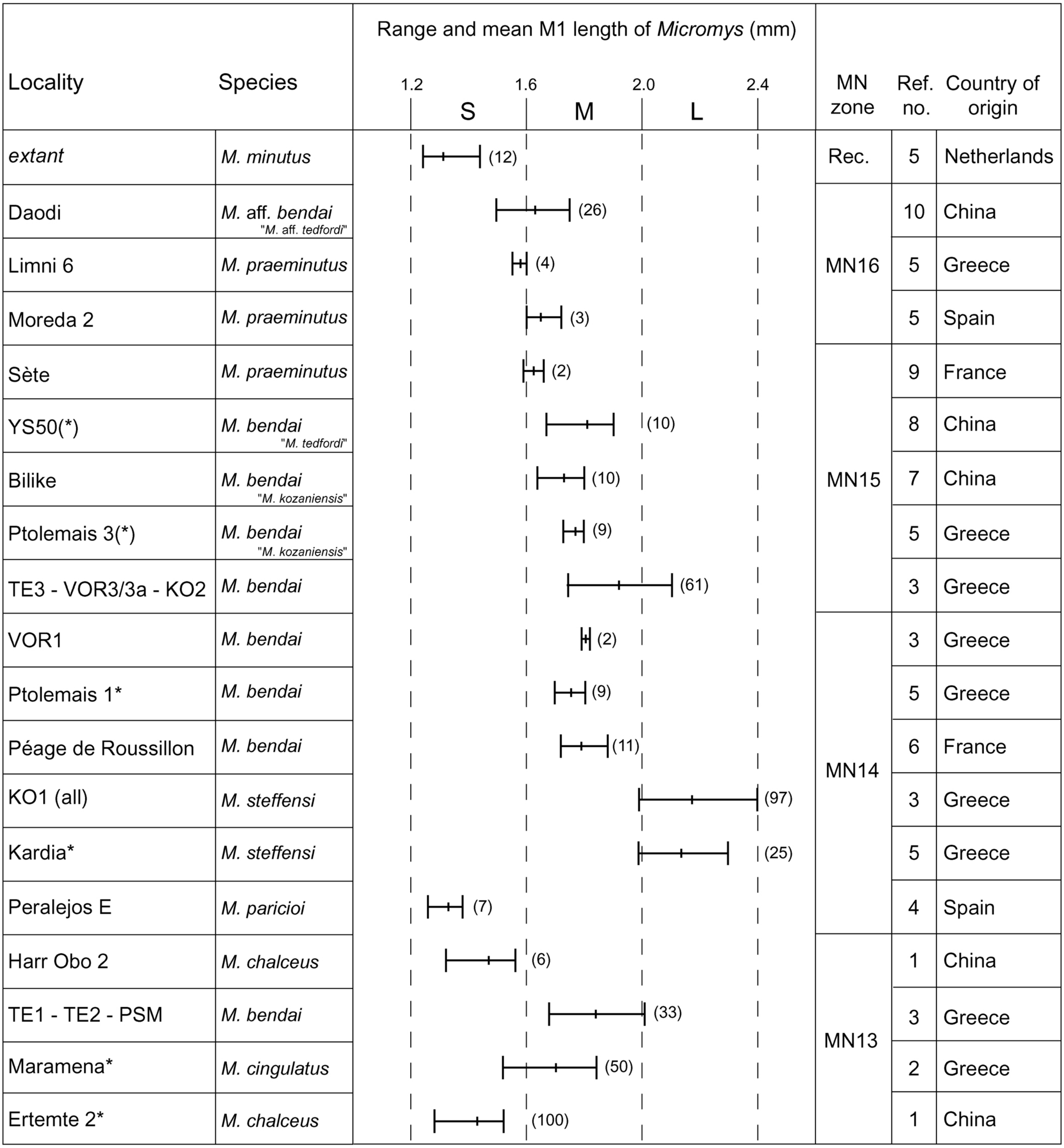
M1: The t1 has a weak posterior spur in most specimens. In 13 specimens this spur forms a low connection between the t1 and t5. A t1bis of variable size is present in 73 specimens. A distinct posterior spur is present on the t3. This spur is connected to the t6 in some specimens. The t7 and t12 are well developed. The M1 has five roots.

M2: A t1bis is present in all specimens. The posterior spur on the t1 is weak in most specimens, but it can be distinct or absent. Six specimens exhibit a low connection between the t1 and t5. The t6 and t9 are usually connected. The t9 is elongate and smaller than the t6. In some specimens the t9 is reduced to a ridge. The t12 is small and sometimes indistinct. The M2 has four roots.

M3: The t3 is either absent or indistinct. A small t9 is

TABLE 14
Material and measurements of *Micromys steffensi*.

Locality		Length (mm)				Width (mm)			
		N	min.	mean	max.	N	min.	mean	max.
Komanos 1 high B	M1	30	2.05	2.20	2.33	30	1.36	1.42	1.49
Komanos 1 high A	M1	33	1.99	2.15	2.25	37	1.34	1.41	1.49
Komanos 1 low B	M1	4	2.06	2.18	2.37	5	1.33	1.43	1.51
Komanos 1 low A	M1	30	2.03	2.17	2.40	36	1.29	1.41	1.53
Komanos 1 high B	M2	24	1.34	1.49	1.62	25	1.18	1.32	1.41
Komanos 1 high A	M2	53	1.28	1.48	1.59	53	1.15	1.31	1.43
Komanos 1 low B	M2	11	1.37	1.48	1.56	9	1.25	1.35	1.43
Komanos 1 low A	M2	42	1.40	1.49	1.67	41	1.20	1.31	1.41
Komanos 1 high B	M3	27	0.84	0.93	1.03	28	0.84	0.89	0.96
Komanos 1 high A	M3	25	0.78	0.91	1.00	25	0.75	0.88	0.95
Komanos 1 low B	M3	8	0.88	0.93	1.00	8	0.85	0.89	0.96
Komanos 1 low A	M3	28	0.82	0.90	1.03	28	0.79	0.87	0.95
Komanos 1 high B	m1	24	1.88	2.01	2.10	25	1.12	1.22	1.30
Komanos 1 high A	m1	33	1.81	1.94	2.09	31	1.09	1.20	1.29
Komanos 1 low B	m1	13	1.78	1.95	2.08	14	1.02	1.18	1.29
Komanos 1 low A	m1	47	1.76	1.96	2.09	47	1.06	1.20	1.30
Komanos 1 high B	m2	47	1.33	1.43	1.55	47	1.09	1.22	1.30
Komanos 1 high A	m2	50	1.29	1.42	1.57	50	1.08	1.22	1.38
Komanos 1 low B	m2	16	1.32	1.45	1.54	16	1.15	1.23	1.31
Komanos 1 low A	m2	47	1.27	1.41	1.53	48	1.09	1.21	1.30
Komanos 1 high B	m3	38	0.95	1.04	1.20	38	0.86	0.96	1.05
Komanos 1 high A	m3	44	0.81	1.04	1.13	44	0.86	0.96	1.05
Komanos 1 low B	m3	13	0.92	1.04	1.14	13	0.87	0.98	1.09
Komanos 1 low A	m3	52	0.91	1.05	1.16	51	0.84	0.97	1.04



Locality	Species	Range and mean M1 length of *Micromys* (mm)	MN zone	Ref. no.	Country of origin
extant	*M. minutus*	(12)	Rec.	5	Netherlands
Daodi	*M.* aff. *bendai* "*M.* aff. *tedfordi*"	(26)	MN16	10	China
Limni 6	*M. praeminutus*	(4)		5	Greece
Moreda 2	*M. praeminutus*	(3)		5	Spain
Sète	*M. praeminutus*	(2)	MN15	9	France
YS50(*)	*M. bendai* "*M. tedfordi*"	(10)		8	China
Bilike	*M. bendai* "*M. kozaniensis*"	(10)		7	China
Ptolemais 3(*)	*M. bendai* "*M. kozaniensis*"	(9)		5	Greece
TE3 - VOR3/3a - KO2	*M. bendai*	(61)		3	Greece
VOR1	*M. bendai*	(2)	MN14	3	Greece
Ptolemais 1*	*M. bendai*	(9)		5	Greece
Péage de Roussillon	*M. bendai*	(11)		6	France
KO1 (all)	*M. steffensi*	(97)		3	Greece
Kardia*	*M. steffensi*	(25)		5	Greece
Peralejos E	*M. paricioi*	(7)		4	Spain
Harr Obo 2	*M. chalceus*	(6)	MN13	1	China
TE1 - TE2 - PSM	*M. bendai*	(33)		3	Greece
Maramena*	*M. cingulatus*	(50)		2	Greece
Ertemte 2*	*M. chalceus*	(100)		1	China

Fig. 10. A generalized overview of *Micromys* M1 lengths in the Late Miocene and Early Pliocene. Asterisks denote type localities, asterisks between brackets denote type localities of species that we propose to include in *M. bendai*. Numbers between brackets indicate the number of specimens. Some of the localities in this study have been combined in one size distribution for convenience. S, M and L denote small, middle and large size-classes, respectively. The stratigraphical arrangement shown is our interpretation of the available information. References: 1. STORCH (1987), 2. STORCH & DAHLMANN (1995), 3. this study, 4. ADROVER *et al.* (1988), 5. VAN DE WEERD (1979), 6. AGUILAR *et al.* (1989), 7. QIU & STORCH (2000), 8. WU & FLYNN (1992), 9. MICHAUX (1971), 10. CAI & QIU (1993).

present in most specimens. The t8 and t9 are connected. The t4 is large and usually connected to the t9 or to the t8-9 by a thin ridge. The connection between t4 and t5 is variable in thickness. A low connection is present between the t6 and t9. The M3 has two roots.

m1: The slightly elongate posterior accessory cusp (c1) is connected to the hypoconid. The labial cingulum is narrow. The cingulum ridge next to the protoconid is slightly elevated in many specimens, but only few specimens have a distinct accessory cuspid. The antero-labial cusp is small. A small third root is present between the two main roots on the labial side of the m1. Four specimens have a small additional fourth rootlet adjacent to the rootlet under the protoconid.

m2: Two small accessory cusps are present. The c1 is connected to the hypoconid. A small accessory cuspid adjacent to the protoconid varies in size may be absent. The m2 has two roots. In four specimens a third rootlet is present between the main roots.

m3: The antero-labial cusp is distinct. In many specimens a small second posterior cusp, which is separated from the main posterior cusp by a shallow posterior furrow, is present.

Discussion

The size of the molars measured in all four Komanos 1 assemblages compare very well with the size of the type specimens from KD (Van De Weerd, 1979). The morphology of the specimens collected at the four Komanos 1 sites is identical to the morphology of the type material from KD (Van De Weerd, 1979). *Micromys steffensi* is not known from localities outside the Ptolemais Basin. Morphologically, *M. steffensi* is very similar to *M. bendai*.

Concluding remarks on Micromys in the Late Miocene/ Early Pliocene

Since the publication by Van De Weerd (1979) on Early Pliocene *Micromys*, more data have become available on this genus (e.g. Mein *et al*., 1983; Storch, 1987; Aguilar *et al*., 1989; Wu & Flynn, 1992; Cai & Qiu, 1993; Storch & Dahlmann, 1995; Qiu & Storch, 2000). Figure 10 shows the M1 lengths of several *Micromys* assemblages. The absolute age of the localities in the Ptolemais Basin is well established. However, the stratigraphical position relative to some of the other localities shown in Fig. 10 is rather uncertain in some cases. The localities occur scattered over Eurasia and radiometrical ages are often not available. The stratigraphical arrangement of the available information (Fig. 10) is our interpretation. Since this figure is intended to give a general overview, some of the localities from the Ptolemais Basin have been grouped.

The genus *Micromys* incorporates species of roughly three size-classes (Fig. 10). The small-size class (length M1 ≅ 1.20 – 1.60) includes *M. chalceus*, *M. paricioi* and *M. minutus*. The species *M. bendai*, *M. cingulatus* and *M. praeminutus* represent the middle size class (length M1 ≅ 1.60 – 2.00), which partly overlaps with the small-sized group. *M. steffensi* is the only species in the large-size class (length M1 ≅ 2.00 – 2.40). The approximate range of these size classes is chosen for convenience.

TABLE 15

Morphological characteristics of latest Miocene and earliest Pliocene *Micromys* species (Van De Weerd, 1979; Mein *et al*., 1983; Storch, 1987; Storch & Dahlmann, 1995). Over 50 % of the *M. chalceus* M2 have a t1bis and some M1 have a fifth rootlet, a t7 on M1 is distinct in 50 % of *M. paricioi* and incipient in the remainder, and in 66 % of *M. chalceus* the t4 and t8 are connected by a ridge (Storch, 1987). The S, M and L refer to the small, middle and large size classes in Fig. 10.

	t_2 and t_3 closely placed (M1)	t_3 - t_6 widely separated (M1)	Labial cingulum weak (m1)	roots + rootlets >3 (M1)	presence t_{1bis} (M2)	roots + rootlets 5 (M1)	$t_6 > t_9$ (M1)	t_7 (M1)	Size class
M. cingulatus	+	+	-	-	-	-	-	-	M
M. chalceus	+	+	+	+	+ / -	-	-	-	S
M. paricioi	+	+	+	+	+	+	+	+ / -	S
M. bendai	+	+	+	+	+	+	+	+	M
M. steffensi	+	+	+	+	+	+	+	+	L

Table 15 lists several morphological characteristics that we regard to be distinctive for species of the genus *Micromys* during the latest Miocene and earliest Pliocene (see Van De Weerd, 1979; Mein *et al*., 1983; Storch, 1987; Storch & Dahlmann, 1995). These characteristics suggest that *M. cingulatus* is slightly more primitive than *M. chalceus*, which contradicts the opinion of Storch & Dahlmann (1995). The developed cingulum may be a derived feature. However, the assignment of this species to *Micromys* is somewhat doubtfull, since its strong cingulum more like that of *Apodemus*.

The presence of a t1bis in M2 and the weak development of the labial cingulum in m1 indicate that *M. paricioi*, *M. bendai* and *M. steffensi* are more similar to *M. chalceus* than to *M. cingulatus*. The development of the t7 in M1 and its small size indicate that *M. paricioi* is slightly more primitive than *M. bendai*. *Micromys steffensi* is morphologically very similar to *M. bendai*, but is considered slightly more evolved because of its larger size and its more common and more distinct t1bis on the M1.

Van De Weerd (1979) and Storch & Dahlmann (1995) have already indicated that the phylogenetic history of *Micromys* is complex, and not a single evolutionary lineage leading to the extant species. This observation is confirmed by the data in Fig. 10 and Table 15. These show that speciation in *Micromys* occurred during the latest Miocene and earliest Pliocene. The evolutionary trend of decreasing size and narrowing molars supposed by Van De Weerd (1979) is not substantiated. Given the new data all three size-classes were present in the earliest Pliocene. The data in Table 15 suggest an evolutionary gradient in the development of the t1bis in M2, the t7 in M1 and in (body) size, going from *M. chalceus* - *M. paricioi* - *M. bendai* - *M. steffensi*. This gradient is not restricted to one single anagenetic lineage. Several species appear to have been contemporaneous during the latest Miocene and earliest Pliocene.

The ages of several localities in Fig. 10 are uncertain, but some conclusions can be drawn. The Maramena fauna, containing *Micromys cingulatus*, is considered to be transitional between the Turolian and Ruscinian (SCHMIDT-KITTLER *et al*., 1995). The regional stratigraphical context suggests a latest Miocene age (DE BRUIJN, 1995). The Spanish localities containing *M. paricioi* are correlated to the Early Pliocene on the basis of the arvicoline *Promimomys* (MEIN *et al*., 1983). Ertemte 2, containing *M. chalceus*, is correlated to the late Miocene reversed chron C3r (QIU & QIU, 1995; FLYNN *et al*., 1995; FLYNN *et al*., 1997; QIU *et al*., 1999). The range chart shown by FLYNN *et al*. (1997) indicates that the range of *M. chalceus* continues up to chron C3n.2r, which is well into the Early Pliocene.

These ages imply that *Micromys chalceus* is contemporaneous with *M. cingulatus*, *M. paricioi*, *M. bendai* and *M. steffensi*. The new localities from the Ptolemais Basin indicate that the ranges of *M. bendai* and *M. paricioi* probably overlap and that *M. bendai* and *M. steffensi* are contemporaneous as well.

The microtoid cricetids from the Ptolemais composite section

The microtoid cricetids form a polyphyletic group of murids that develop prismatic cheek teeth (FEJFAR, 1999; FAHLBUSCH & MOSER, 2004) during the latest Miocene and Early Pliocene. The term "microtoid cricetid" is a non-systematic term that came into use after SCHAUB (1934) and STEHLIN & SCHAUB (1951) described "Microtoide Molarstrukturen bei Cricetidae von unsicherer systematischer Stellung".

KRETZOI (1955b) introduced the subfamily Baranomyinae, which initially included the genera *Microtodon* MILLER 1927, *Baranomys* KORMOS 1933 and *Anatolomys* SCHAUB 1934. More recently, the genera *Celadensia* MEIN, MOISSENET & ADROVER 1983 and *Bjornkurtenia* KOWALSKI 1992 have been added to this subfamily (MEIN *et al*., 1983; FEJFAR & STORCH, 1990; ROOK & TORRE, 1995). FAHLBUSCH & MOSER (2004) indicate that the status of this subfamily name is doubtful. We consider the affinities of *Microtodon*, *Celadensia* and *Anatolomys* to be unresolved.

Microtoid cricetids occur throughout Eurasia during the Early Pliocene and are often associated with (generally) larger and "true" arvicolines.

Microtodon MILLER 1927
Type species: *Microtodon atavus* (SCHLOSSER, 1924)

Synonymy: Bjornkurtenia KOWALSKI, 1992

Type locality: Ertemte, Inner Mongolia (China)

Other species recognized:
M. loczyi (KORMOS, 1933)
M. longidens KOWALSKI 1960
M. canterranensis (MICHAUX, 1976)

Remarks

MILLER (1927) defined the genus *Microtodon* on the basis of the type material of the species *atavus* (SCHLOSSER, 1924), which had originally been assigned to the genus *Sigmodon* SAY & ORD 1825 from America. FAHLBUSH & MOSER (2004) evaluated this material while describing a new large collection of *M. atavus* and *Anatolomys teilhardi* SCHAUB 1934 from Ertemte 2 and Harr Obo 2, Inner Mongolia, that had been collected in 1980 (FAHLBUSCH *et al*., 1983). Their study provides an extensive overview of the morphological variation in *M. atavus* and an improved basis for the genus *Microtodon*, which is important in the debate on the status of *Baranomys* (KOWALSKI, 1956; SULIMSKI, 1964; FEJFAR & STORCH 1990; FAHLBUSCH, 1996).

FAHLBUSH & MOSER (2004) concluded that the type material of *M. loczyi*, which is the type species of the genus *Baranomys*, is within the morphological variation of *M. atavus*. These authors therefore consider *Baranomys* to be a junior synonym of *Microtodon*, a conclusion we follow.

KRETZOI (1969) established the genus *Wartamys* for the species *kowalskii* (KRETZOI, 1962), a species that was usually placed in *Baranomys*. We follow FAHLBUSCH & MOSER (2004) who suggest assignment of the species *kowalskii* to the genus *Anatolomys*, but indicate that this remains to be verified.

FAHLBUSH & MOSER (2004) suggest that the genera *Celadensia* and *Bjornkurtenia* may be junior synonyms of *Microtodon*, but they have not explored this option. In our opinion the morphology of *Microtodon atavus* from Ertemte 2 and of *Bjornkurtenia canterranensis* from Podlesice show striking similarities, in particular with regard to the structure of the M3. Therefore, we consider the genus *Bjornkurtenia* to be a junior synonym of *Microtodon*.

In the original description the species *canterranensis* MICHAUX 1976 was assigned to the genus *Trilophomys* DEPÉRET 1892. The type material from La Jasse (close to Terrats) did not include M3 and m3. AGADJANIAN & KOWALSKI (1978) revised the microtoid cricetids from Podlesice and assigned specimens that had previously been included in other species, to "*Trilophomys*" *canterranensis*, a species that they consider generically different from *Trilophomys*. FEJFAR & STORCH (1990) removed the species *canterranensis* from *Trilophomys* also in their analysis of the material from Gundersheim 4 (Findling) (Germany) and Ivanovce (Czech Republic). KOWALSKI (1992) later based his genus *Bjornkurtenia* on the "*Trilophomys*" *canterranensis* material from Podlesice.

We refrain from synonymizing *Celadensia* with *Microtodon*, although there are morphological similarities. *Celadensia nicolae* MEIN, MOISSENET & ADROVER 1983, the type of *Celadensia*, has a primitive appearance with respect to features such as the size of the anterior cap in m1 and the presence and depth of re-entrant folds.

ROOK & TORRE (1995) assigned a second species, *Celadensia grossetana* from the Messinian/Turolian of the Baccinello-Cinigiano Basin (Italy) to *Celadensia*. After inspection of a cast of the type, a mandible fragment containing an m1 and m2, we came to the conclusion that this species should not be included in *Celadensia* and can better be assigned to the subfamily Gerbilinae GRAY 1825.

Microtodon atavus from the Late Miocene of Inner Mongolia is currently the oldest known and most primitive representative of *Microtodon*. European representatives of this genus first appeared in the earliest Pliocene, where they occur associated with the first arvicoline: *Promimomys* KRETZOI 1955a.

Microtodon komanensis n. sp.
(Pl. 14, Figs 1-8; Pl. 15, Figs 1-8)

Derivatio nominis: This species is named after the lignite pit, Komanos, where it was found.

Type locality: Komanos 1 low A (KO1lowA)

Type level: Lowermost lignite-bed of the Ptolemais Fm, cycle K1 (Fig. 2)

Holotype: isolated m1, no: KO1lowA-147, Pl. 14, Fig. 1

Localities: Komanos 1 low A and B (KO1lowA&B) and Komanos 1 high A (KO1highA)

Age: Early Pliocene

Diagnosis

Large member of the genus *Microtodon* with mesodont molars and clearly alternating re-entrant folds. The enamel is generally undifferentiated, but may show slight differences in thickness. The enamel border at the crown base is almost straight. The anterior cap in m1 is small, but relatively well developed. A small round enamel islet is present in the anterior cap of slightly worn m1. The LRA2 in some m1 is curved forward. The dentine fields are confluent. The m3 is primitive. Its LRA2 is deep and wide, its BRA2 is shallow and the LRA1 and posterior lobe are poorly or undeveloped. The anterior lobe of M3 is usually isolated from the posterior dentine fields in juvenile specimens, the anterior lobe and T2 are connected in moderately worn specimens and an anterior enamel islet is present on deeply worn specimens due to the closure of the BRA1. The M3 has a short and wide posterior cap with a deep oval posterior enamel islet. The BRA2 in M3 is generally closed, enclosing a small deep round postero-labial enamel islet.

Differential diagnosis

Microtodon komanensis differs from *M. atavus*, *M. loczyi*, *M. longidens* and *M. canterranensis* by its larger size. *M. atavus*, *M. loczyi* and *M. longidens* show no, or only a weak, alternation of the apices of the LRA2 and BRA2 in the m2. In the m2 of M. *komanensis* these apices alternate clearly.

Microtodon atavus differs from *M. komanensis* in having a smaller anterior cap in m1, and more variation in the morphology of M3 with respect to dentine field connections. The prisms in *M. atavus* are less pronounced.

Microtodon longidens differs from *M. komanensis* in the structure of M3, lacking the small labial enamel islet in the BRA2. The T3-T4 lobe in the m3 of *M. longidens* tends to be isolated in slightly worn specimens, (see figures in SULIMSKI, 1964; FEJFAR & REPENNING, 1998), which is not the case in *M. komanensis*.

The anterior cap of the m1 of *M. komanensis* is slightly better developed compared to that of *M. canterranensis*. The LRA2 in m1 is not curved in *M. canterranensis*. The two enamel islets in the posterior cap of M3 of *M. canterranensis* show more variation compared to those of M. *komanensis*. In some M3 of *M. canterranensis* (Podlesice), the LRA3 is open in slightly worn specimens, which is not the case in *M. komanensis*. The closure of BRA2 appears to be weaker and more variable in *M. canterranensis*. The molars of *M. komanensis* seem to be slightly more hypsodont, although this has not been verified.

Compared to *Celadensia nicolae, M. komanensis* has better developed prisms. The anterior cap in m1 is relatively larger and more advanced in *M. komanensis*. The posterior cap of M3 in *C. nicolae* is more reduced and the BRA2 and LRA1 in the m3 are more reduced compared to *M. komanensis*.

Material and measurements of Microtodon komanensis: Table 16-18

Description

M1: The T1, T2, T3 and T4 are widely connected. The connection between the anterior lobe and the T1 is slightly narrower. The enamel is generally undifferentiated, but some specimens show slightly varying enamel thicknesses on either leading or trailing edges. One slightly worn specimen clearly shows thicker leading

TABLE 16

Material and measurements of *Microtodon* sp., *Microtodon komanensis*, *Microtodon* aff. *komanensis*.

M. aff. *komanensis*		N	Length (mm) min	Length (mm) mean	Length (mm) max	N	Width (mm) min	Width (mm) mean	Width (mm) max	h_{max} (mm)	$(h/L)_{max}$ (mm)
Vorio 3a	M1	3	1.99	2.13	2.21	2	1.15	1.21	1.27	0.92	0.46
Vorio 3a	M2	2	1.47		1.51	1		0.78		1.19	0.81
Vorio 3a	M3	1		1.36		1		1.01		0.83	0.61
Vorio 3a	m1	1		2.48		1		1.23		0.47	0.19
Vorio 3a	m2	2	1.74		1.74	1		1.20		0.78	0.45
Vorio 3a	m3	2	1.01	1.19		2	0.96		1.01	0.80	0.79
M. komanensis		N	Length (mm) min	Length (mm) mean	Length (mm) max	N	Width (mm) min	Width (mm) mean	Width (mm) max	h_{max} (mm)	$(h/L)_{max}$ (mm)
KO1 high A	M1	3	2.02	2.11	2.22	3	1.08	1.16	1.23	1.10	0.54
KO1 high A	M2	2	1.76		1.81	2	1.18		1.50	1.23	0.56
KO1 high A	M3	2	1.39		1.51	1		1.14		0.70	0.50
KO1 high A	m1	2	2.29		2.33	2	1.25		1.26	0.65	0.28
KO1 high A	m2	1		1.74		1		1.04		1.12	0.54
KO1 high A	m3									0.69	
KO1 low B	M3	1		1.64		1		1.12		0.36	0.22
KO1 low A	M1	2	2.05		2.26	2	1.16		1.37	0.95	0.46
KO1 low A	M2	5	1.69	1.71	1.73	4	1.04	1.19	1.36	1.09	0.63
KO1 low A	M3	6	1.42	1.55	1.63	6	1.09	1.19	1.26	0.59	0.41
KO1 low A	m1	5	2.18	2.31	2.43	6	1.12	1.21	1.31	0.86	0.39
KO1 low A	m2	2	1.87		1.93	2	1.24		1.41	0.55	0.29
KO1 low A	m3	6	1.18	1.31	1.44	6	0.92	1.05	1.17	0.72	0.61
Microtodon sp.		N	Length (mm) min	Length (mm) mean	Length (mm) max	N	Width (mm) min	Width (mm) mean	Width (mm) max	h_{max} (mm)	$(h/L)_{max}$ (mm)
KO1 low A	M1	1		1.70		1		0.99		1.05	0.62

TABLE 17

Cap size measurements of m1 and M3 of *Microtodon komanensis* and *Microtodon* aff. *komanensis*.

M. aff. *komanensis*		N	P and A (mm) min	P and A (mm) mean	P and A (mm) max	N	WP and WA (mm) min	WP and WA (mm) mean	WP and WA (mm) max
Vorio 3a	M3	1		0.62		1		0.84	
Vorio 3a	m1	1		0.75		1		0.94	
		N	P/WP and A/WA min	P/WP and A/WA mean	P/WP and A/WA max	N	P/L and A/L min	P/L and A/L mean	P/L and A/L max
Vorio 3a	M3	1		0.74		1		0.45	
Vorio 3a	m1	1		0.80		1		0.30	
M. komanensis		N	P and A (mm) min	P and A (mm) mean	P and A (mm) max	N	WP and WA (mm) min	WP and WA (mm) mean	WP and WA (mm) max
KO1 high A	M3	2	0.65		0.78	1		0.81	
KO1 high A	m1	2	0.69		0.71	2	0.99		1.03
KO1 low B	M3	1		0.82		1		1.04	
KO1 low A	M3	6	0.69	0.76	0.85	6	0.92	0.97	1.05
KO1 low A	m1	7	0.61	0.67	0.72	7	0.83	0.95	1.02
		N	P/WP and A/WA min	P/WP and A/WA mean	P/WP and A/WA max	N	P/L and A/L min	P/L and A/L mean	P/L and A/L max
KO1 high A	M3	1		0.79		2	0.46		0.51
KO1 high A	m1	2	0.67		0.72	2	0.30		0.31
KO1 low B	M3	1		0.79		1		0.50	
KO1 low A	M3	6	0.74	0.78	0.88	6	0.45	0.49	0.53
KO1 low A	m1	7	0.64	0.71	0.79	5	0.28	0.29	0.30

TABLE 18

Undulation height (mm) of enamel free areas of microtoid cricetids and arvicolines.

		Undulation height (mm) of enamel free areas											
		N	min.	mean	max.	N	min.	mean	max.	N	min.	mean	max.
		M. komanensis.				*P. cor*				*D.* cf. *nehringi*			
m1	e_a	7	0.05	0.10	0.20	7	0.07	0.19	0.40				
m1	e_p	7	0.03	0.07	0.12	10	0.08	0.20	0.27				
M1	e_m	5	0.03	0.07	0.10	8	0.09	0.19	0.28	1		0.53	
		M. aff. *komanensis*				*M.* aff. *davakosi*				*P. hungaricus*			
m1	e_a					3	0.23	0.28	0.32	1		0.78	
m1	e_p	1		0.19		4	0.10	0.20	0.25	2	0.20		0.29
M1	e_m	3	0.04	0.06	0.08	4	0.12	0.14	0.15	2	0.39		0.49
		Microtodon sp.				*M. davakosi*							
m1	e_a					2	0.53		0.85				
m1	e_p					3	0.15	0.27	0.49				
M1	e_m	1		0.06		3	0.17	0.26	0.34				

edges (Pl. 15, Fig. 1). The anterior lobe is short and flattened on the anterior side. The re-entrant folds are wide. The LRA2, BRA1 and BRA2 are deep. The latter is slightly deeper than the other two. The apex of the BRA2 is slightly curved backwards in five out of six specimens. Four specimens show a shallow inflexion on the postero-labial side of the T4 that disappears with wear. The enamel border at the crown base shows a slight undulation.

M2: The prisms are confluent. In all moderately to well worn specimens the connection between the anterior lobe and the T2 is narrower than the connections between the other triangles. The enamel is generally undifferentiated. However, in three out of seven specimens the leading edge of T4 is thicker. Two of these also have a slightly thickened trailing edge of T2. The LRA2 is wide. Its apex does not curve backward, except in one worn specimen. The BRA1 and BRA2 are narrow near their apex and become narrower with wear. The apex of the deepest re-entrant fold, BRA2, is curved backward in all specimens, although only weakly so in one slightly worn specimen. The degree of curving increases with wear. The AL1 is flattened on its antero-lingual side. One out of seven specimens shows a shallow inflexion on the postero-labial side of the T4 that disappears with wear. The apex of BRA1 is closed off at the base of the crown in four out of five specimens from KO1lowA. In these molars a small and shortly persisting enamel islet would be formed if they would be deeply worn. In KO1highA the BRA1 will become shallow with wear in two out of three specimens.

M3: The M3 is relatively short and wide. The enamel is generally undifferentiated, although the leading edge of the AL1 can be slightly thicker, while the enamel on the postero-labial side of the molar can be slightly thinner. The AL1 is thick and the LRA2 is wide. The posterior cap is short (Fig. 11), and always bears a large oval or laterally elongate enamel islet. The length axis of this islet is roughly placed at right angles to the length axis of the occlusal surface in four out of nine specimens and slightly turned in an antero-labial to postero-lingual direction in the others. The T2-T3 connection, separating the LRA2 and BRA2, is present in all specimens. The BRA2 is closed in eight out of nine specimens, resulting in a small, but deep, circular postero-labial enamel islet. In two of these, a juvenile and a worn specimen, the postero-labial islet is still open at the occlusal surface, but closes just below it. In this worn specimen the large posterior enamel islet is connected to the postero-labial islet. The morphotypes that can be recognized in the occlusal surface are correlated with the crown height (Fig. 12). In slightly worn specimens the deep, narrow BRA1 is connected to the LRA2, isolating the AL1 from the T2 (Pl. 15, Figs 3a, 6a). In moderately worn specimens the AL1 and T2 are connected. The BRA1 is deep and remains open (Pl. 15, Fig. 4). In worn specimens a large, and laterally elongate, anterior enamel islet is formed by closing the BRA1 (Pl. 15, Figs 5, 7). All 3 enamel islets remain present until a late stage of wear. All specimens with the roots preserved (three out of nine) show three roots. The lower enamel border of the crown is straight.

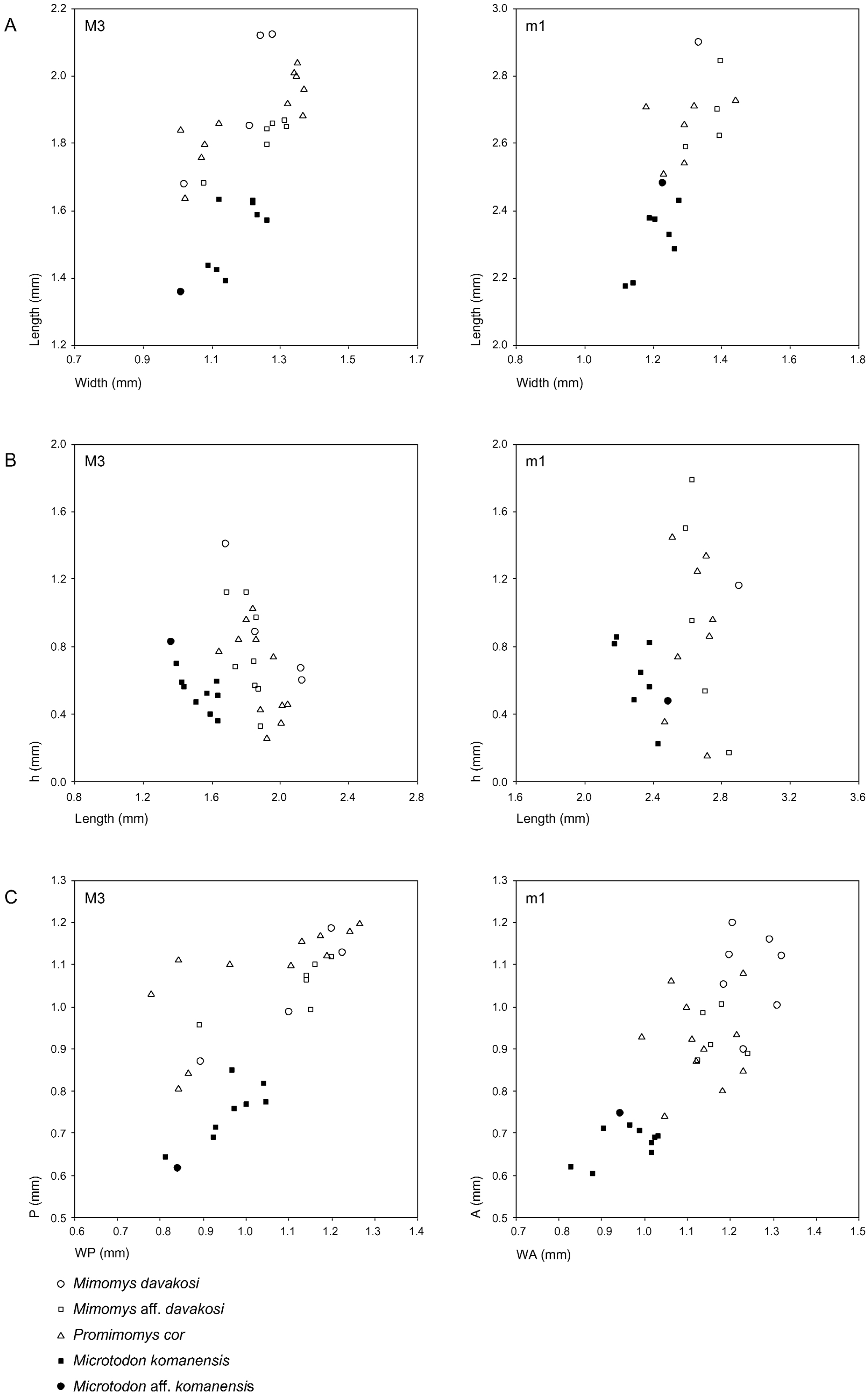


Fig. 11. Scatter diagrams showing sizes of the M3 and the m1 of *Mimomys davakosi*, *Mimomys* aff. *davakosi*, *Promimomys cor*, *Microtodon komanensis* and *Microtodon* aff. *komanensis* from the new assemblages from the Ptolemais composite section. A: the length (L) versus width (W). B: the crown height (h) versus length. C: the posterior complex length (P) versus posterior complex width (WP) in M3, and the anterior complex length (A) versus anterior complex width in m1. Filled symbols represent the microtoid cricetids, open symbols indicate the arvicoline species.

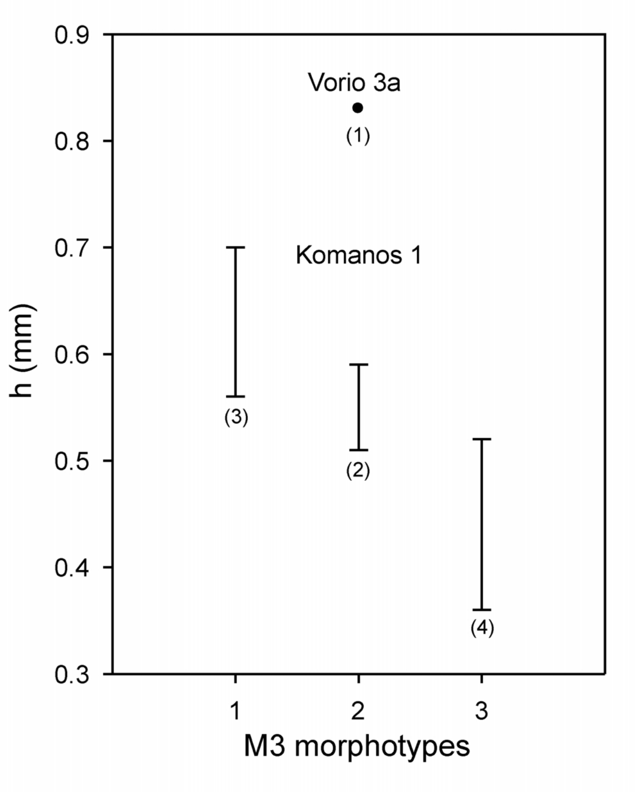


Fig. 12. The correlation between crown height and three morphotypes recognized in the occlusal surface of the M3 of *M. komanensis* from KO1lowA&B and KO1highA is shown. Type 1: the BRA1 is open, the AL1 and T2 are separated. Type 2: the BRA1 is open, the AL1 and T2 are connected. Type 3: the BRA1 is closed off, forming an enamel islet, the AL1 and T2 are connected. The occlusal surface of the M3 specimen from VOR3a shows the features of type 2. Its BRA1 closes just below the occlusal surface, which is type 3-like (Pl. 16, Figs 7a-b).

m2: The prisms are generally confluent. The posterior lobe and T1 have the narrowest dentine connection. This connection becomes narrower with wear and is therefore very narrow in one worn specimen. The dentine connections between the prisms widen toward the anterior part of the molar. The T3 is compressed on its mesial side by a shallow inflexion, while the T4 protrudes anteriorly. This inflexion becomes less distinct with wear, which increases the dentine connection between T3 and T4. The BRA2 and LRA2 alternate (Pl. 14, Figs 5, 7a). The BRA2 is shallow. The apices of the re-entrants do not show curving. The enamel is undifferentiated in the two slightly worn specimens from KO1highA. The posterior enamel wall of the posterior lobe of the two worn specimens from KO1lowA is slightly thicker, while the enamel wall on the mesial side of T3-T4 in these specimens is slightly thinner. The enamel border at the crown base is straight.

m3: The dentine connections are wide. The T1-T2 connection is least confluent. The laterally elongate T3 and the small T4 form an anterior lobe. The posterior lobe is small and poorly developed. The LRA1 is very shallow and weak. The distinctness of LRA1 varies and depends on the stage of wear. It is absent in one specimen. The LRA2 is deep and the BRA2 is shallow. In two out of seven specimens the BRA2 and LRA2 alternate poorly. The posterior enamel wall of the posterior lobe is slightly thicker than the enamel in the rest of the crown in five out of seven specimens. The enamel border at the crown base is straight.

Discussion

We have compared *Microtodon komanensis* with a large collection of casts of *M. atavus* that was made available to us by Prof. V. Fahlbusch, and concluded that the general morphology of the dentition is strikingly similar, in particular with regard to the structure of M3 and m3. The M3 of *M. canterranensis* shown by KOWALSKI (1992) have this morphology as well.

The presence of a small labial enamel islet in M3 at the position of BRA2 is observed in *M. atavus*, *M. canterranensis* and *M. komanensis*. The material of *M. komanensis* from the Komanos 1 localities shows that the LRA2 and BRA2 are separated in all stages of wear and that the postero-labial enamel islet is formed by the closure of the BRA2. This is exemplified by one specimen in which the BRA2 has remained open (Pl. 15, Fig. 7) and by two specimens in which the BRA2 is closed at a later stage of wear. KOWALSKI (1992) relates the formation of this islet in *M. canterranensis* to the closure of the LRA2. In our opinion, the formation of the islet in *M. atavus* and *M. canterranensis* is the result of the closure of the BRA2 as well, despite that the LRA2 may be connected to it. The morphology with respect to the T2-T3 connection and the closure of BRA2 is more variable in these two species.

The three patterns of the occlusal surface that are correlated to crown height (Fig. 12) are not immediately apparent in other species. These crown-height related pattern changes may not exist in other species, but may also be unknown due to the absence of crown height measurements.

Within the genus *Microtodon*, *M. komanensis* resembles *M. canterranensis* and *M. atavus* most. Its size, the development of the prisms relative to the crown height and features such as the curvature of the LRA2 in m1 indicate that *M. komanensis* is more evolved than *M. atavus* and *M. canterranensis*. Given the morphological differences between species of *Microtodon* and the observation that some of its species seem to be contemporaneous; this genus appears not to represent one single lineage, but rather several branches of the same group.

Microtodon komanensis has been found associated with arvicoline species in KO1 low B and high A. As is shown in Fig. 11, the sizes of the M3 and m1 of *M. komanensis* clearly differ from the arvicoline species. The M3 and m1 of *M. komanensis* are relatively shorter. The

M3 have a relatively shorter posterior complex with respect to molar length and the m1 have a smaller anterior complex. These are primitive characteristics.

Microtodon aff. *komanensis*
(Pl. 16, Figs 1-7)

Locality: Vorio 3a (VOR3a)

Age: Early Pliocene

Material and measurements of Microtodon aff. komanensis: Table 16-18

Description

M1: The dentine fields are confluent. The T1-AL2 connection is the narrowest connection in all three specimens. The T2-T3 connection is weak in one out of three M1. The T1-T2 and T3-T4 connections are wide. The posterior enamel wall of T3-T4 is convex. The AL2 is short and becomes wider with wear. The leading edges of labial prisms are slightly thicker than the trailing edges. The re-entrant folds are wide. The apex of the BRA2 is curved backwards in two worn specimens and shows that tendency in one slightly worn specimen. The labial re-entrants are deep and have similar depths. The LRA1 is shallow. There is no development of enamel free areas. The enamel border is slightly undulating at the crown base.

M2: The prisms are confluent, but the T3-T4 connection is relatively narrow. The T2-T3 is weaker in a worn specimen also. The two specimens, a juvenile (Pl. 16, Figs 6a-b) and a worn damaged specimen in which the T3 is missing, show that the depth of the BRA1 decreases with wear. The BRA2 of the juvenile specimen tends to curve backward at the occlusal surface, but distinctly curves backward in the lower part of the crown as in the worn specimen. The LRA2 does not curve backward. The T4 is large. The enamel border at the crown base is straight.

M3: The specimen is slightly worn. The short and laterally elongate AL1 is well connected to the T2. The BRA1 is deep, but closes in the early stage of wear, forming a broad enamel islet. The very deep LRA2 separates the T2 and T3 and reaches the enamel wall between T2 and T4 that would close the BRA2 just below the occlusal surface (Pl. 16, Figs 7a-b). The isolated posterior cap is short and wide, and contains a large oval enamel islet, of which the labial apex has a slightly more anterior position. The enamel is undifferentiated, although the antero-lingual side of the AL1 is somewhat thicker. This M3 has three roots.

m1: The specimen is deeply worn. The prisms are confluent. The anterior cap is small and simple. The PL-T1 and T1-T2 connection are narrow. The BRA2 is narrow and points in an anterior direction. The re-entrant folds curve forward at their apices. The anterior cap and the T3 are less wide on their lingual side than the posterior lobe and the T1. The enamel is thick. The trailing edge of the T3 and the posterior enamel wall of the posterior lobe are slightly thicker. The anterior enamel of the anterior cap is slightly thinner. The molar has two thick roots.

m2: The two specimens, one slightly worn damaged and one moderately worn, show a very narrow dentine connection between the posterior lobe and the T1. The BRA2 and LRA2 alternate well. The BRA2 is shallow compared to the other re-entrants. The enamel is undifferentiated apart from a slightly thicker posterior enamel wall of the posterior lobe. The enamel border at the crown base is nearly straight.

m3: The dentine fields are widely connected in both specimens. The laterally elongate T3 and the T4 form an anterior lobe. The T4 is very small. The posterior lobe is small and undeveloped. The BRA2 and LRA2 alternate slightly. The LRA2 is very deep and is not curved forwards at its apex. The BRA2 is very shallow and reduces through wear. The LRA1 is weakly developed in the upper part of the crown in one specimen. In the other specimen it is absent.

Discussion

The *Microtodon* aff. *komanensis* specimens from VOR3a are very similar to *M. komanensis* from KO1lowA and KO1highA. However, there are slight differences of which the most important involve the M3. The limited number of specimens from VOR3a, the single m1 and M3 in particular, do not give insight in the morphological and metrical variation of these elements. The size of the M3 and m1 of M. aff. *komanensis* are distinct from that of the associated arvicoline *Mimomys davakosi* (Fig. 11).

The worn m1 of *Microtodon* aff. *komanensis* is slightly larger than the m1 of *M. komanensis*. This slightly larger size may be caused by the stage of wear of the molar and is considered to be of minor importance. Its morphology cannot be distinguished from the m1 of *M. komanensis*. The LRA2 is not curved anteriorly at its apex, but this is within the morphological variation of *M. komanensis*. The T4, BRA2 and LRA1 in the m3 are slightly more reduced in the specimens from VOR3a than in those from KO1lowA and KO1highA. The M2 from VOR3a differ slightly in the morphology of the BRA1, which becomes shallower through wear. This is not observed in the specimens from KO1lowA, although there is a tendency to close the BRA1 at the crown base. Specimens from KO1highA show this shallowing slightly less distinctly.

The M3 from VOR3a differs from the M3's from KO1lowA, KO1lowB and KO1highA in several characteristics. It is slightly higher crowned, its BRA1 closes earlier during ontogeny (Fig. 12) and the LRA2 separates the T2 and T3. The morphological variation of the M3 of *Microtodon atavus* from Ertemte 2 and of *M. canterranensis* from Podlesice suggests that this kind of variation in the morphology of the BRA1 and LRA2 occurs in a sample from one population. A similar deviation from the common morphology (i.e. the separation of the T2 and T3) is known in *Promimomys mimus* (Repenning, 1968). The slightly higher crown of the VOR3a specimen is possibly a more significant difference, but this can not be verified.

The material from VOR3a appears to be slightly more evolved compared to *Microtodon komanensis*. The available material does not warrant naming a new species due to the similarity to *M. komanensis* and the lack of information on morphological and metrical variability. The specimens from VOR3a are therefore assigned to *M* aff. *komanensis*.

Microtodon sp.
(Pl. 15, Fig. 9)

Locality: Komanos 1 low A (KO1lowA)

Age: Early Pliocene

Material and measurements of Microtodon sp.: Table 16 & 18

Description
M1: This slightly worn specimen has thick enamel. At the apices of re-entrant and salient angles, the enamel is slightly thinner, while the trailing edge of T2 and the leading edge of T4 appear to be slightly thicker. The apices of the prisms are round. The dentine fields are highly confluent between the alternating re-entrant folds. Cement in the re-entrant folds is absent. The BRA2 is only slightly deeper than the BRA1 and the LRA2, which have approximately equal depths. The LRA1 is shallow. The re-entrant folds do not curve backward at their apices. The anterior lobe is narrow and short. The enamel border at the crown base shows a very shallow undulation.

Discussion
This specimen is too small to be included in *M. komanensis*. In size this specimen from KO1lowA is within the size range of M1 of *M. atavus* from Ertemte 2 (L = 1.77 mm (1.55 – 2.00), W = 0.88 mm (0.70 – 1.06); Fahlbusch & Moser, 2004), but its prisms are slightly better developed.

The size of our M1 is also within the size range of the M1 of *M. canterranensis* from Podlesice (L = 1.75 mm (1.65 – 1.81), W = 1.06 mm (0.93 – 1.28); Kowalski, 1992) and is very close to the size of the three specimens from Terrats (L = 1.83 mm (1.72 – 1.95), W = 1.10 mm (1.03 – 1.15); Michaux, 1976) and the two specimens from Gundersheim-4 (Findling) (L = 1.65 mm, W = 1.15 mm (1.13 – 1.17); Fejfar & Storch, 1990). The size of our specimen also fits the size range of M1 of *M. longidens* from Weze 1 (L = 1.6 mm (1.4 – 1.8), W = 1.0 mm (0.8 - 1.2); Sulimski, 1964).

This single M1 cannot be identified at species level, because the M1 of several species of *Microtodon* are morphologically and metrically very similar.

Subfamily Arvicolinae Gray 1821
Genus *Promimomys* Kretzoi 1955a
Type species: *Promimomys* cor Kretzoi 1955

Synonymy:
Prosomys Shotwell 1956
Polonomys Kretzoi 1959

Other species recognized:
P. mimus (Shotwell, 1956)
P. insuliferus Kowalski 1958

Remarks
The genus *Promimomys* Kretzoi 1955a is one of the most primitive and oldest genera assigned to the “true” voles. It is defined on the basis of the species *Promimomys cor* Kretzoi 1955. The type material of *P. cor* consists of a mandible fragment with a worn m1, which is a surface find in the vicinity of Csarnóta 2 (Hungary). The poor type material, the uncertainty of its stratigraphic position, and the lack of accompanying fauna have resulted in debates concerning the status of *Promimomys*. The recognizability of *P. cor* and the validity of the genus have been evaluated by Agadjanian & Kowalski (1978), Radulescu & Samson (1989) and Fejfar *et al.* (1990).

The original diagnosis of *Promimomys* is as follows: “Mittelgrosse Arvicolide mit brachyodonten, massigen Molaren, ohne Zementausfüllung der einbuchten, mit niedrig-helmförmiger, einfacher Paralophid-Schlinge, konfluent ausgebildetem Proto- und Endolophid-Prisma, massiger Hypolophid-Schlinge.” Modified translation: Medium-sized arvicoline with brachyodont, massive molars, without cement in the re-entrant folds, with a short helm-shaped, simple anterior cap, confluent T1-T2 prisms, and a well developed posterior lobe.

Kretzoi (1955a) includes two species in *Promimomys*: the type species *P. cor* and *Promimomys moldavicus* (Kormos, 1932). The latter was originally described from Mălușteni (Romania) as *Mimomys moldavicus*.

Kowalski (1958) assigned a third species to *Promimomys*, *P. insuliferus* Kowalski 1958, from the karst fillings of Podlesice (Poland). Shortly thereafter Kretzoi (1959) created the genus *Polonomys* to which the latter species was transferred. Kretzoi (1959) separated *Polonomys insuliferus* from the slightly more advanced *Promimomys cor*: “In letzter Zeit wurde von

Podlesice ein kleinerer wurzelzähniger Arvicolide mit einfacher Vorderkappe und ohne Zementeinlagerung in den Einbuchtungen unter die Namen *Promimomys insuliferus* eingeführt, der aber auf Grund des Kauflächenbildes von m1 und m3 des Typusexemplares besser als Vertreter einer zwischen primitiven echten Arvicoliden und *Baranomys* vermittelnden besonderen Gattung angesehen werden könte, für die hier die Bezeichnung *Polonomys* n.g. vorgeschlagen wird."

REPENNING (1968) did not follow KRETZOI (1959) and included four species in *Promimomys*: *P. cor*, *P. moldavicus*, *P. insuliferus* and the North American *P. mimus*. The latter was originally described as *Prosomys mimus* from the McKay local fauna, Oregon USA, and is slightly more primitive than *P. insuliferus* (REPENNING, 1968). Based on *P. insuliferus* material from Podlesice and on new *P. mimus* material from the Christmas Valley local fauna (Oregon, USA), REPENNING (1968) revised the diagnosis of the genus *Promimomys*: "Anterior cingulum or cap of m1 large but uncomplicated, cricetine enamel islet present and persists through much of the tooth wear; lingual valleys of lower teeth rounded to slightly angular with no tendency to curve forward at their apices; anterior labial valleys of upper teeth rounded to slightly angular with no tendency to curve backward at their apices; hypoconal complex of M3 simple and in some individuals separated from the anterior part of the tooth until tooth is very worn; all upper teeth three-rooted; teeth without cement; hypsodonty minimum."

KRETZOI (1969) disagreed with REPENNING (1968) and separated the four known species in three genera: the primitive North American arvicolid *Prosomys mimus*; the primitive European arvicolid *Polonomys insuliferus* and the slightly more evolved European arvicolids *Promimomys cor* and *Promimomys moldavicus*.

Because of the strong resemblance of the genera *Promimomys*, *Prosomys* and *Polonomys*, it is in our opinion better to incorporate these species into one genus: *Promimomys* (following REPENNING, 1968).

AGADJANIAN & KOWALSKI (1978) have discussed the validity of the genus *Promimomys* in their redescription of *P. insuliferus* from Podlesice (Poland), Antipovka and Chugunovka (former Soviet Union). In their opinion the name *Promimomys cor* should be put among the forms *incertae sedis*. Partly based on REPENNING (1968) and partly based on their own comparisons AGADJANIAN & KOWALSKI (1978) have assigned the primitive European *P. insuliferus* from Podlesice (Poland; KOWALSKI, 1958), Vendargues (France; MICHAUX, 1971), Terrats (France; MICHAUX, 1976), Antipovka and Chugunovka (Russia) to the genus *Prosomys*. However, AGADJANIAN & KOWALSKI (1978) explicitly state that they disagree on this generic assignment. According to Agadjanian the North American species *Prosomys mimus* differs from the European *Polonomys insuliferus* on the generic level, which is in agreement with the opinion of KRETZOI (1969).

As a result of the uncertain status of the typus generis of *Promimomys*, the generic assignment of the species *moldavicus* is not clear. AGADJANIAN & KOWALSKI (1978) have neither reassigned it to an alternative existing genus nor created a new generic name for this species. This lack of action is due to the poor condition of the type material from Măluşteni, which consists of few, worn specimens.

One of the main arguments of AGADJANIAN & KOWALSKI (1978) for considering *Promimomys cor* a *nomen nudum* is that the worn type specimen of *P. cor* may possibly be a senile individual of *Cseria gracilis* KRETZOI 1959. KOWALSKI (1960) and others in more recent literature, (e.g. FEJFAR *et al.*, 1998), consider *Cseria* KRETZOI, 1959 a junior synonym of *Mimomys* FORSYTH MAJOR 1902, an opinion that we follow). AGADJANIAN & KOWALSKI (1978) base their suggestion on the low crown of the type m1 and on the similarity of its size and morphology with an m1 of *M. gracilis* from Weze 1. If this conclusion is correct, *M. gracilis* is a junior synonym of *P. cor*. However, AGADJANIAN & KOWALSKI (1978) suggest that in case the holotype of *P. cor* truly is a senile specimen, it is better to abandon the name *P. cor*. They argue that the specific determination of senile specimens of rooted Arvicolinae is uncertain and that the possibility that the holotype of *P. cor* belongs to another species of *Mimomys* cannot be excluded.

The determination of deeply worn molars of primitive voles is indeed uncertain. The crown of the holotype of *Promimomys cor* is worn to beyond the deepest level of the enamel islet in the anterior cap, judging from the pictures in KRETZOI (1955a, p. 92), but it does not appear to be extremely senile. Its initial crown height was probably never very high to begin with, although this can not be verified. Nonetheless, the argumentation of AGADJANIAN & KOWALSKI (1978) is justified.

The supposed synonymy of *Promimomys cor* and *Mimomys gracilis* is doubted based on both size and morphology. The size of *M. gracilis* from Csarnóta 2 (type locality) is distincly smaller (m1 = 2.4 - 2.5 mm; KRETZOI, 1962) than the holotype of *P. cor* (m1 = 2.9 mm). Similarly, the size of the m1 of *P. cor* lies outside the size-range of *M. gracilis* (N = 282) from Weze 1 (m1 = 2.0 - 2.8 mm; SULIMKSKI, 1964). In the *P. cor* holotype, the linea sinuosa on the labial side of the anterior cap is very low and remains below the deepest point of the BRA2. The enamel free area on the anterior cap of *M. gracilis* on the other hand clearly rises to above the deepest point of the BRA2 (SULIMSKI, 1964, p.215; VAN DE WEERD, 1976, p.99). The enamel on the mesial side of the worn *M. gracilis* specimen shown by AGADJANIAN & KOWALSKI (1978, p.45) is distinctly reduced, which is not the case in the *P. cor* holotype. We therefore agree with FEJFAR *et al.* (1990) who concluded that the holotype of *P. cor* is not a worn specimen of *M. gracilis*.

VAN DE WEERD (1979) did not follow AGADJANIAN

& KOWALSKI (1978) when he described *Promimomys insuliferus* from KD and PT1 (Greece). *Promimomys* is treated as a valid genus and *Polonomys* KRETZOI, 1959 is regarded as its junior synonym. The material from his localities differs slightly from *P. insuliferus* from Podlesice with respect to the apex curvature of the re-entrant folds. Based on this difference and on similar observations on *Promimomys* material from Vendargues and Terrats in southern France (MICHAUX, 1971, 1976), VAN DE WEERD (1979) modified Repenning's diagnosis of *Promimomys*: "The diagnosis of *Promimomys* by REPENNING (1968) must be altered in such a way that specimens with re-entrant folds with curved apices can be included in *Promimomys*". By assigning the Greek material to *insuliferus*, Van de Weerd emended the diagnosis of this species to allow for variation.

RADULESCU & SAMSON (1989) re-described the type material of *Promimomys moldavicus* from Măluşteni, which is a right mandible with the incisor and three deeply worn molars, a left lower mandible fragment containing a damaged m1 and m2 and an isolated M1. On the basis of the presence of a prism fold and an LRA4 they concluded that the material from Măluşteni should be reassigned to the genus *Mimomys*, which is in agreement with the original assignment by KORMOS (1932).

FEJFAR *et al*. (1990) studied the holotype of *P. cor* and compared it with new material from the Teruel Basin (Spain). They concluded that *Promimomys* is a valid genus. However, FEJFAR *et al*. (1990) state that *M. moldavicus* is similar to *P. cor* and regard the latter species to be a junior synonym of *moldavicus*.

FEJFAR *et al*. (1990) note that *P. moldavicus* (i.e. *P. cor*) should not be included in the Csarnóta 2 fauna, because the specimen was found on the surface outside the Csarnóta 2 fissure filling and has never been found again at that locality. FEJFAR *et al*. (1990) prefer the assignment of *M. moldavicus* to the genus *Promimomys* on the basis of the shape of the molars seen in lateral view and the low degree of alternation of enamel synclines.

FEJFAR *et al*. (1990) regard the genera *Promimomys*, *Prosomys* and *Polonomys* as subgenera of the genus *Promimomys*, recognizing: *Promimomys* (*Promimomys*) *moldavicus*, *Promimomys* (*Prosomys*) *mimus* and *Promimomys* (*Polonomys*) *insuliferus*. Since these species are very similar and each subgenus contains a single species only, we see no basis for maintaining these subgenera.

FEJFAR *et al*. (1997, 1998) changed their view concerning the status of *M. moldavicus* with regard to *Promimomys* and follow RADULESCU & SAMSON (1989). The names *P. cor* and *M. moldavicus* are restored.

As is discussed above, the status of *Promimomys* has been challenged because of the poor type material, uncertain type locality and the lack of associated fauna. Since FEJFAR *et al*. (1990) have concluded that *Promimomys* is a valid genus after comparing the *Promimomys* holotype with Spanish material, it appears that there are enough arguments for maintaining *P. cor* as the type of *Promimomys*, an opinion which we will follow here. More complete material showing the characteristics of *P. cor* from Hungary from other localities has been described in the decades following the publication of KRETZOI (1955a), providing the basis for an improved diagnosis of *Promimomys*.

FEJFAR *et al*. (1990, 1998) noted that the *Promimomys* from Southern European assemblages is more evolved than that from Podlesice, following similar observations made by MICHAUX (1976) concerning the material from Terrats and Podlesice. FEJFAR *et al*. (1998) have assigned the more primitive assemblages from Podlesice, Antipovka and Chugunovka (AGADJANIAN & KOWALSKI, 1978) to *P. insuliferus* and the more evolved assemblages from Vendargues (MICHAUX, 1971), Terrats (MICHAUX, 1976), KD and PT1 (VAN DE WEERD, 1979), and La Gloria 4 and Celadas 9 (FEJFAR *et al*., 1990) to *P. cor*, a point of view that we follow, although we consider this matter unresolved.

P. mimus from North America is generally regarded as the most primitive species in *Promimomys* and also appears to be stratigraphically oldest (latest Miocene). However, given the large geographical distance between the American and European *Promimomys*, the inclusion of *P. mimus* in *Promimomys* should be treated with caution.

Promimomys cor KRETZOI 1955
(Pl. 17, Figs 1-7; Pl. 18, Figs 1-5; Pl. 19, Figs 1-8)

Selected references of included assemblages:

P. insuliferus KOWALSKI, 1958 from Vendargues in: MICHAUX (1971)

P. insuliferus KOWALSKI, 1958 from Terrats in: MICHAUX (1976)

P. insuliferus KOWALSKI, 1958 from Kardia and Ptolemais 1 in: VAN DE WEERD (1979)

P. insuliferus Kowalski, 1958 from La Gloria 4 and Celadas 9 in: FEJFAR *et al*. (1990)

Type locality and level: surface find in the vicinity of Csarnóta 2, Hungary

Localities: Komanos 1 low B (KO1lowB), Komanos 1 high A (KO1highA) and Vorio 1 (VOR1)

Age: Early Pliocene

Material & measurements of Promimomys cor: Table 18-20

Description

The molars of *P. cor* are mesodont (sub-hypsodont) and have well developed, slightly alternating prisms without cement in the re-entrant folds. The lower molars are asymmetrical with respect to re-entrant depth, having slightly wider lingual prisms compared to labial prisms. Of the upper molars only the M1 is somewhat asymmetrical with its slightly larger labial prisms and re-entrants. The enamel is undifferentiated, although the posterior enamel on the posterior lobe in lower molars and the anterior enamel of the anterior lobe in upper molars is usually slightly thicker, particularly in more worn specimens. The linea sinuosa is very simple, but small undulations in the enamel border are present. Lower molars have two roots and the M1 and M2 have three roots. The number of roots of the M3 varies between two roots, three roots with fused anterior roots or three well separated roots.

M1: The prisms in slightly worn specimens are confluent. The alternation of re-entrants and prisms decreases during wear, widening the connections between T1-T2 and between T3-T4, while narrowing those between AL2-T1 and between T2-T3 (Pl. 18, Figs 4, 5). The anterior lobe is short and slightly compressed on its antero-labial side in slightly worn specimens. A shallow concave inflexion is present on the postero-lingual and postero-labial side of the T4, making the T4 extend posteriorly from the molar outline (Pl. 18, Figs 4), which gradually disappears with wear. The LRA1 is the shallowest re-entrant fold in all specimens, the BRA2 is the deepest labial re-entrant fold in five, and the BRA1 is the deepest labial re-entrant three specimens. In four out of ten specimens the apex of BRA1 bends slightly posteriorly. The apex of the BRA2 bends backwards in all M1. The linea sinuosa is very simple. A small but distinct undulation may be visible on the LSA2 (Pl. 18, Fig. 5).

M2: The anterior lobe is short and narrow, its labial side (BSA1) in particular is not developed (Pl. 19, Figs 1-3). The AL1-T2 and T2-T3 connection are relatively narrow in the specimens from Komanos 1. The T2-T3 connection is generally the narrowest connection in the material from VOR1, in which the BRA1 becomes shallow with wear, broadening the AL1-T2 connection. The BRA2 is deep and curved posteriorly in all specimens. The apex of LRA2 is slightly curved in ten out of sixteen M2. The T4 is well developed, but lacking a distinct convex inflexion between T3 and T4 as is seen in M1. In three out of six specimens from VOR1 a small cingulum-like ridge at the antero-lingual side of the anterior lobe is present at the crown base (Pl. 19, Fig. 3).

M3: All M3 have a posterior enamel islet. In most this islet shows a small concavity on the postero-labial side (Pl. 19, Fig. 4). In the two specimens from KO1highA the islet is oval shaped, touching the enamel of the BRA2 in one (Pl. 19, Fig. 5), and the enamel wall on the LRA3 position in the other. An LRA3 is present in two out of the three M3 from VOR1 (Pl. 19, Fig. 7). The LRA3 is absent in the specimens from both Komanos 1 localities. The apex of the LRA2 shows a tendency to curve posteriorly. The connection between the AL1 and T2 becomes wider during wear, due to the reduction of the BRA1, while the connection between the T2 and T3 remains relatively narrow (Pl. 19, Figs 4-6). In one specimen a shallow enamel islet is present in the BRA1 in the late stages of wear. A shallow BRA3 is present in six out of eleven specimens. A very small undulation may be visible in the enamel border on the LSA2. The Komanos 1 specimens have two or three roots. The anterior roots may be reduced to a single root or fused. All specimens from VOR1 have three well separated roots.

m1: The T1 and T2 are broadly confluent. The PL-T1 connection is weaker and the T2-T3 and the T3-AC1 connections show some variation. The anterior cap is simple. Its lingual side is relatively well developed. Weak crenulations are present in the enamel of slightly worn specimens. Three slightly worn specimens show an incipient LRA4 (Pl. 17, Figs 4, 5). Two specimens have a small vertical ridge that forms a weak *Mimomys*-kante (Pl. 17, Fig. 6). Four specimens show a shallow inflexion close to this position. A round or oval enamel islet is present, which persists approximately through the upper half of the molar. The apex of the LRA1 shows a tendency for curving anteriorly in two specimens. The apex of the LRA2 is curved anteriorly in all but 2 strongly worn specimens. The apex of LRA3 is very slightly curved forwards in four specimens. The linea sinuosa is very simple. The most distinct and consistent enamel reduction is seen on the BSA1 (posterior lobe). The specimens from VOR1 show slightly more enamel reduction than those from Komanos 1.

m2: The T3 and T4 are broadly connected, while the PL-T1 and the T2-T3 connections are relatively narrow. The mesial side of the T3 is compressed in slightly worn specimens, and the T4 shows a short-lasting anterior extension of the molar outline (Pl. 18, Figs 1, 3) that disappears with wear (Pl. 18, Fig. 2). In three slightly worn specimens from VOR1, the T4 extends lingually as well, forming a primitive short-lasting small apex in the position of the LRA3. The apex of LRA2 is curved anteriorly in five specimens from Komanos 1. The linea sinuosa is almost absent, but may show a very weak undulation, which is most pronounced in the specimens from VOR1.

m3: The T3 and T4 are well connected as in the m2. In slightly worn specimens, the T3 is compressed on the mesial side and the T4 extends from the molar outline. An extension that disappears with wear (Pl. 17, Figs 1-3). The lingual re-entrant folds are deeper than the labial ones in all slightly to moderately worn specimens. In two well-worn specimens from VOR1, the BRA2 and LRA1 are reduced, widening the T2-T3 and the PL-T1 connection. There is a minor tendency for the apex of the LRA2 to curve anteriorly. The linea sinuosa is straight.

Discussion

The *Promimomys cor* material from KO1lowB, KO1highA and VOR1 compares very well with the material from

TABLE 19

Material and measurements of *Promimomys cor*.

			Length (mm)				Width (mm)			h_{max} (mm)	$(h/L)_{max}$ (mm)
		N	min	mean	max	N	min	mean	max		
Vorio 1	M1	2	2.34		2.51	1		1.60		1.35	0.58
Vorio 1	M2	5	1.90	1.96	2.03	6	1.30	1.43	1.53	1.19	0.61
Vorio 1	M3	3		1.99	2.04	3	1.32	1.34	1.35	0.46	0.23
Vorio 1	m1	6	2.47	2.61	2.74	4	1.18	1.25	1.29	1.45	0.58
Vorio 1	m2	9	1.87	1.94	2.03	8	1.17	1.24	1.37	1.33	0.68
Vorio 1	m3	3	1.55	1.71	1.81	2	0.91	1.10	1.29	1.05	0.68
KO1 high A	M1	2	2.34		2.50					1.48	0.63
KO1 high A	M2	4	1.90	1.93	1.96	3	1.36	1.49	1.58	1.41	0.73
KO1 high A	M3	2	1.64		1.84	2	1.01		1.02	1.03	0.56
KO1 high A	m1	1		2.71		1		1.32		1.37	0.06
KO1 high A	m2	4	1.88	1.96	2.06	4	1.24	1.30	1.44	1.33	0.65
KO1 high A	m3	3	1.57	1.64	1.73	4	0.97	1.09	1.22	1.02	0.59
KO1 low B	M1	3	2.33	2.43	2.51	3	1.24	1.35	1.57	1.63	0.70
KO1 low B	M2	6	1.82	1.92	2.03	5	1.24	1.36	1.46	1.44	0.75
KO1 low B	M3	6	1.76	1.88	2.00	6	1.07	1.23	1.37	0.96	0.54
KO1 low B	m1	1		2.73		3	1.16	1.37	1.52	1.58	0.32
KO1 low B	m2	4	1.76	1.98	2.14	3	1.25	1.33	1.50	1.20	0.61
KO1 low B	m3	3	1.51	1.62	1.72	3	1.01	1.06	1.12	0.93	0.58

TABLE 20

Cap size measurements of m1 and M3 of *Promimomys cor*.

P. cor			P and A (mm)				WP and WA (mm)		
		N	min	mean	max	N	min	mean	max
Vorio 1	M3	3	1.12	1.17	1.20	3	1.19	1.23	1.26
Vorio 1	m1	7	0.71	0.94	1.08	6	0.99	1.10	1.23
KO1 high A	M3	2	0.81		0.84	2	0.84		0.87
KO1 high A	m1	3	0.74	0.81	0.90	3	1.05	1.12	1.18
KO1 low B	M3	6	1.03	1.11	1.17	6	0.78	1.00	1.17
KO1 low B	m1	3	0.85	0.90	0.93	2	1.22		1.23
			P/WP and A/WA				P/L and A/L		
		N	min	mean	max	N	min	mean	max
Vorio 1	M3	3	0.94	0.95	0.95	3	0.58	0.59	0.59
Vorio 1	m1	6	0.78	0.89	1.00	6	0.29	0.36	0.39
KO1 high A	M3	2	0.96		0.97	2	0.46		0.49
KO1 high A	m1	3	0.68	0.72	0.79	1		0.27	
KO1 low B	M3	6	0.99	1.13	1.32	6	0.56	0.59	0.62
KO1 low B	m1	2	0.69		0.77	1		0.34	

KD and PT1. The material from the two Komanos 1 localities lacks certain morphotypes that are found in the younger VOR1 assemblage, i.e. the M2 from Komanos 1 do not have the antero-lingual cingulum at the crown base that is present in some specimens in the VOR1 assemblage. VAN DE WEERD (1979) indicated similar differences between the assemblages from KD and PT1.

An LRA3 is present in the M3 from VOR1, which may be connected to the posterior islet. This feature is not observed in the material from KO1lowB and KO1highA. Similarly, the posterior islet is closed and the LRA3 is absent in the M3's in the KD assemblage, while the PT1 material contains a few specimens that have this feature. The open connection of the islet in the posterior cap to the BRA2 in the early stages of wear in M3, seen in more than 20 % of the PT1 assemblage, does not occur in our material.

The roots of the M3 differ distinctly between the Komanos 1 localities and the slightly younger VOR1 level. The three specimens from VOR1 all have three thin, well-separated roots. The anterior roots of specimens from Komanos 1 are either fused or reduced to a single root. Direct comparison with the KD and PT1 material has shown that the M3 from KD do not have 3 separate roots either, but rather fused anterior roots or a single anterior root. The molars from PT1 on the other hand, predominantly have three well-separated roots, although a few two-rooted M3 are present.

According to the emended diagnosis of REPENNING (1968), which is primarily based on the primitive species *Prosomys mimus* and *Promimomys insuliferus*, all upper teeth of *Promimomys* have three roots. This is not the case in the *P. cor* assemblages from Komanos 1, KD and PT1. The diagnosis of *Promimomys* therefore needs to be emended to allow for more variation in the roots of M3, i.e. the anterior roots may be fused or the M3 may have two roots.

In the evolution of arvicolines the number of roots in the upper molars becomes generally reduced. Contrary to this large-scale evolutionary trend, the assemblages from the Ptolemais Basin show the reversed trend in a smaller-scaled stratigraphic context. This indicates that conclusions regarding the detailed relative stratigraphic position of primitive arvicolines cannot simply be drawn on the basis of the stage of evolution of the roots of the M3. It appears that during the initial stages of root reduction, the morphology is quite variable. Abundances of certain morphotypes may be differently distributed in populations, spatially as well as temporally resulting in a mosaic pattern of characters. In the case of the sequence in M3 root morphology in the Ptolemais Basin such variation may apparently have the reversed stratigraphic order.

The lithostratigraphic position of KD and Komanos 1 levels is approximately the same (Table 1), but there are faunistic differences (see *Occitanomys*). VOR1 and PT1 are, based on their position relative to layer 9, thought to have approximately the same stratigraphical position. These lithostratigraphical correlations are supported by observations on the tooth morphology of the arvicolids.

KRETZOI (1969) states that Arvicolinae have evolved more rapidly towards efficient grass eaters than the microtoid cricetids. This conclusion is confirmed by our material. *Microtodon komanensis* approaches the general morphology of *Promimomys*, but has some primitive features. Figure 11 shows the difference in the size of the anterior (m1) and posterior caps (M3) between primitive arvicolines and microtoid cricetids from the Ptolemais Basin. The structure of m3 in *Promimomys cor* is arvicoline, while that of *Microtodon* is more cricetine. The teeth of *P. cor* show incipient enamel free areas, but this is not the case in *M. komanensis*.

The shallow concavity seen between T3 and T4 in slightly worn M1 of *Promimomys cor* mimics the shape of a curved re-entrant fold, suggesting a higher degree of specialization of *P. cor* compared to *M. komanensis*. This inflexion is slightly more pronounced and persistent with wear in the M1 from PT1 than in those from KD. This difference is not observed between the M1's from Komanos 1 and VOR1 in which this feature is quite weak. Some of the slightly worn M2 from PT1 show this concave T3-T4 as well. However, both *Promimomys cor* and *Microtodon komanensis* show the relatively advanced feature of having a curved LRA2 in m1. In this respect, the stage of evolution of *M. komanensis* approaches that of *P. cor* and is more advanced than *P. insuliferus*.

cf. *Promimomys* sp.

Locality: Prosilion-Mercurion (PSM)

Age: latest Miocene or earliest Pliocene

Material: heavily damaged M1

Description and discussion

This M1 fragment consists almost entirely of enamel. Only the lingual and mesial sides and part of the anterior root of this deeply worn specimen have been preserved. The mesial enamel of the anterior lobe is slightly thicker than the lingual enamel.

The extremely poor state of this specimen excludes specific determination. However, this fragment closely resembles the M1 of *Promimomys cor* from Komanos 1 and therefore it has been provisionally assigned to cf. *Promimomys* sp.

Genus *Mimomys* FORSYTH MAJOR, 1902

Type species: *Mimomys pliocaenicus* FORSYTH MAJOR, 1902

Type locality: Upper Val d'Arno (Italy) & Norwich Crag (Thorpe, U.K.)

Selected primitive species:

M. moldavicus KORMOS 1932
M. davakosi VAN DE WEERD 1979
M. antiquus (ZAZHIGIN, 1980)

Remarks

FORSYTH MAJOR (1902) defined the genus *Mimomys* on the basis of *M. pliocaenicus*. More primitive forms that lack certain features that are present in *M. pliocaenicus* have been assigned to *Mimomys* later (KORMOS, 1932; VAN DE WEERD, 1979; FEJFAR *et al*., 1990). MARTIN (2003) discussed the status of *Mimomys* in North America and lists the following characteristics for *M. pliocaenicus*: "(1) relatively high-crowned cheek teeth with roots, (2) relatively high dentine tracts, (3) m1 with three triangles plus a simple anterior cap, (4) m1 with a *Mimomys*-kante and enamel atoll in lightly worn dentitions, (5) provergent lingual re-entrant angles on lower molars that are deeper than labial ones, but not excessively so, (6) M3 with posterior enamel atoll, (7) negatively differentiated enamel, (8) cement in the re-entrant angles, and (9) a schmelzmuster composed of L-R on leading and R-T on trailing edges of triangles" (L is lamellar, R is radial and T is tangential enamel; the combination is listed from the dentine outward).

Within the mosaic of characters in the evolution of voles, MARTIN (2003) proposes a set of three criteria to define *Mimomys*: (1) highly developed negative enamel differentiation, (2) a *Mimomys* schmelzmuster and (3) presence of rooted molars. Other features, such as the height of dentine tracts or the presence of enamel islets or cement in re-entrant folds, may vary between species, which allows these characters to be added or lost within the evolution of *Mimomys* (MARTIN, 2003).

The core criteria of this relatively broad systematic concept of *Mimomys* pose a problem for the assignment of primitive species like *Mimomys davakosi* to *Mimomys*. MARTIN (2003) proposes to include this group of species in *Promimomys*.

We will retain the current assignment of primitive species like *M. davakosi* to *Mimomys*, although we take notion of the important issue raised by MARTIN (2003). Taxonomic problems at the species level still need to be resolved within this group of primitive *Mimomys* species. The schmelzmuster of the various primitive vole species, such as *M. davakosi*, needs to be analysed, but is beyond the scope of this paper.

We assign species to *Mimomys* on the basis of the following criteria: A weak or relatively well-developed and persistent LRA4 on m1, a *Mimomys*-kante on m1 and development of dentine tract ea on m1. It is evident from the overview given by MARTIN (2003) that the characteristics used for assigning species to *Mimomys* are debatable, but for our purpose this set is useful.

Mimomys davakosi VAN DE WEERD 1979

(Pl. 22, Figs 1-5; Pl. 23, Figs 1-5)

Type level: Ptolemais 3 (PT3), Early Pliocene, Greece

Localities: Vorio 3 & 3a (VOR3 & 3a) and Komanos 2 (KO2)

Age: Early Pliocene

Selected references of included assemblages:

M. occitanus THALER, 1955 from Villalba Alta and Arquillo 3 in: CHALINE *et al*. (1981)

M. davakosi VAN DE WEERD, 1979 from Villalba Alta and Arquillo 3 in: FEJFAR *et al*. (1990)

M. vandermeuleni FEJFAR, MEIN & MOISSENET, 1990 from a.o. Villalba Alta Rio, La Gloria 2, Villalba Alta Sabot, in: FEJFAR *et al*. (1990)

Material & measurements of Mimomys davakosi: Table 18, 21-22

Remarks

Van De Weerd (1979) suggests that *M. davakosi* may be a descendent of *Promimomys*, because of the strong resemblance of *M. davakosi* and *Promimomys insuliferus* (= *P. cor*) from PT1. However, he also notes that the enamel islet in the anterior cap of m1 of *P. cor* is already more reduced than that of *M. davakosi* and argues that the origin of *M. davakosi* has to be looked for in a *Promimomys* group having an enamel islet that is less reduced. Both *P. cor* and *M. davakosi* are considered to be immigrants in the Ptolemais Basin.

Radulescu & Samson (1989) evaluated primitive *Mimomys* species in their redescription of *Mimomys moldavicus* from Măluşteni. They include *Mimomys davakosi* from PT3, which they regard to be slightly more primitive than the specimens from Măluşteni, in *M. moldavicus*. Contrary to Radulescu & Samson (1989), Fejfar *et al*. (1997) maintain *M. davakosi* and *M. moldavicus* as separate species, because of the paucity of the type material from Măluşteni.

We follow Radulescu & Samson (1989) and Fejfar *et al*. (1997, 1998) in assigning *M. moldavicus* to *Mimomys*. We were unable to verify whether *M. davakosi* and *M. moldavicus* represent the same species, because we have not studied the *M. moldavicus* material. Hence, we refrain from including *M. davakosi* in *M. moldavicus* at this moment, which is in agreement with Fejfar *et al*. (1997, 1998).

TABLE 21
Material and measurements of *Mimomys davakosi* and *Mimomys* aff. *davakosi*.

M. davakosi			Length (mm)				Width (mm)			h_{max} (mm)	$(h/L)_{max}$ (mm)
		N	min	mean	max	N	min	mean	max		
Komanos 2	M1	2	2.41		2.48	2	1.45		1.58	1.69	0.68
Komanos 2	M3	4	1.68	1.94	2.13	4	1.02	1.19	1.28	1.41	0.84
Komanos 2	m1					1		1.39		1.58	
Komanos 2	m2	3	1.94	1.99	2.04	1		1.31		1.37	0.69
Komanos 2	m3	6	1.61	1.76	1.85	6	1.11	1.20	1.32	1.12	0.61
Vorio 3a	m1					1		1.37		1.16	
Vorio 3	M1	2	2.28		2.53	1		1.50		1.24	0.55
Vorio 3	M2	2	1.95		2.19	2	1.29		1.45	2.07	0.91
Vorio 3	m1	1		2.90		1		1.33		1.92	0.40
Vorio 3	m2	1		1.92		1		1.25		1.67	0.87
M. aff. *davakosi*			Length				Width			h_{max} (mm)	$(h/L)_{max}$ (mm)
		N	min	mean	max	N	min	mean	max		
Tomea Eksi 3	M1	4	2.35	2.42	2.58	4	1.36	1.52	1.62	1.33	0.57
Tomea Eksi 3	M2	3	1.79	1.88	1.96	2	1.48	1.52	1.56	0.98	0.37
Tomea Eksi 3	M3	8	1.69	1.82	1.88	6	1.08	1.25	1.32	1.12	0.67
Tomea Eksi 3	m1	5	2.59	2.68	2.85	4	1.29	1.37	1.40	1.79	0.68
Tomea Eksi 3	m2	8	1.87	1.99	2.18	8	1.13	1.28	1.44	1.35	0.71
Tomea Eksi 3	m3	13	1.44	1.59	1.86	13	1.04	1.17	1.27	1.04	0.72

TABLE 22
Cap size measurements of m1 and M3 of *Mimomys davakosi* and *Mimomys* aff. *davakosi*.

M. davakosi			P and A (mm)				WP and WA (mm)		
		N	min	mean	max	N	min	mean	max
Komanos 2	M3	5	0.87	1.08	1.21	4	0.89	1.10	1.23
Komanos 2	m1	7	0.90	1.06	1.16	6	1.18	1.26	1.32
Vorio 3	m1	2	1.13		1.20	2	1.20		1.20
			P/WP and A/WA				P/L and A/L		
		N	min	mean	max	N	min	mean	max
Komanos 2	M3	4	0.90	0.95	0.99	4	0.52	0.54	0.56
Komanos 2	m1	5	0.73	0.83	0.90				
Vorio 3	m1	2	0.94		1.00	1		0.41	
M. aff. *davakosi*			P and A (mm)				WP and WA (mm)		
		N	min	mean	max	N	min	mean	max
Tomea Eksi 3	M3	8	0.96	1.05	1.12	6	0.89	1.11	1.20
Tomea Eksi 3	m1	8	0.87	0.96	1.10	5	1.12	1.17	1.24
			P/WP and A/WA				P/L and A/L		
		N	min	mean	max	N	min	mean	max
Tomea Eksi 3	M3	6	0.87	0.95	1.08	8	0.55	0.58	0.60
Tomea Eksi 3	m1	5	0.72	0.80	0.87	5	0.31	0.35	0.42

Description

M1: The dentine fields are confluent, of which the T1-T2 and the T3-T4 connection are relatively wide. Shallow inflexions are present on the postero-lingual and postero–labial side of the T4 in slightly worn specimens, forming an extension of the occlusal outline (Pl. 23, Figs 2, 5). The apices of BRA1 and the BRA2 are curved posteriorly in all M1. The apex of the LRA2 is curved in three out of four and the apex of the LRA1 is tending to curve in two out of five specimens. The linea sinuosa is simple. Small undulations in the basis of the enamel are present on the LSA2 (T1) and, to a lesser degree, on the LSA3. The M1 has three roots. However, the two specimens from VOR3 have the basal part of a very small extra rootlet preserved below the center of the molar on the labial side of the root under T1.

M2: The prisms are confluent. The narrowest dentine connection is between the T2 and T3. The antero-labial side of the AL1 is slightly compressed. Similar to the M1, a shallow inflexion is present between T4 and T3 in slightly worn specimens (Pl. 23, Fig. 1). The apices of the LRA2 and BRA2 are curved posteriorly in three specimens. The apex of the BRA1 is curved posteriorly in two out of five specimens (including three fragments). The linea sinuosa is simple in the two VOR3 specimens, showing shallow, but distinct, undulations on the LSA2 and the LSA3. The M2 has three roots.

M3: The four specimens and two fragments are from KO2. An elongate enamel islet is present in the posterior cap, the apices of which may be curved posteriorly. The islet may be connected to the outer enamel on the labial and lingual side in the earliest stages of wear (Pl. 23, Fig. 3). The apex of the LRA2 is curved posteriorly in four out of five specimens. The apex of the BRA1 is curved in two out of five and the apex of BRA2 is curved posteriorly in one out of five specimens. A shallow BRA3 is present in all M3. In two specimens, a very slight undulation is also visible on the lingual side at the position of the LRA3. The BRA1 is reduced in the lower part of the crown. In two out of five specimens a short-lived islet is present at the crown base due to the closure of the BRA1. The linea sinuosa is nearly straight. Two specimens have two roots.

m1: The enamel is undifferentiated. The dentine fields are confluent. The T1 and T2 are widely connected, while the PL-T1 and T2-T3 connections are relatively narrow and may be almost closed (Pl. 22, Fig. 4a). A variable number of small folds or grooves are present on the anterior cap of slightly worn specimens. These grooves disappear in the early stages of wear. The anterior cap encloses an oval enamel islet in slightly and moderately worn specimens. A *Mimomys*-kante is present in six out of ten specimens. This *Mimomys*-kante can either be weak or distinct and can have a short persistence with wear or can still be visible at lower levels of the crown. The LRA4 is present in all specimens. It is usually distinct and persistent with wear, but is only weakly developed in some. The apex of the LRA2 is curved anteriorly to a variable degree in all specimens. The apex of the LRA1 is curved forwards in three out of five specimens. The apex of LRA3 is curved in ten out of twelve specimens. The curvature is strongest in moderately worn specimens. The linea sinuosa is simple, but shows distinct undulations of variable height. The reduction of enamel is most prominent at the base of the anterior cap, where the top of the enamel free area may reach up to above the base of the BRA2, and the BSA1 (Pl. 22, Figs 1-2 & 4-5).

m2: The dentine fields are connected. The T1-T2 and the T3-T4 connection are wide. The PL-T1 and the T2-T3 connection are relatively narrow and become slightly narrower with wear. The mesial side of the T3 is concave, similar to the posterior wall of the lingual re-entrant folds, in lesser worn specimens. The lingual re-entrant folds are deep and the labial folds are relatively shallow. The apex of the LRA2 is curved anteriorly in all specimens. The apex of the LRA1 shows a very weak tendency to curve forwards in the three specimens from KO2. The linea sinuosa is nearly straight.

m3: All specimens available are from KO2. The connection of the dentine fields is similar to that of the m2. The mesial side of the T3 of slightly worn specimens is somewhat concave. The LRA2 is the deepest re-entrant fold. Its apex is slightly curved forwards in five out of seven moderately to well worn specimens (Pl. 22, Fig. 3), and shows only a tendency to do so in one. The other re-entrants do not show curving. The BRA2 is the shallowest fold and is reduced in an extremely senile specimen. The linea sinuosa is straight.

Discussion

The molars described above resemble the specimens from PT3. The material from KO2 seems to be slightly more evolved than the specimens from VOR3, but this may be due to the small sample size.

In comparison to *Promimomys cor*, the shape of the anterior cap, the curvature of the apices of re-entrant folds and the development of the small undulations at the crown base are more evolved in *Mimomys davakosi*. The morphological variation of these species overlaps and determination of a single specimen may be difficult. The size of the anterior cap in m1 of *M. davakosi* and *Promimomys cor* shows overlap, but on average appears to be larger in *M. davakosi* (Fig. 11).

As was shown by VAN DE WEERD (1979), the enamel islet of m1 is on average deeper in *Promimomys cor* from PT1 than in *Mimomys davakosi* from PT3. This led to the conclusion, that *M. davakosi* did not evolve from *P. cor*, but from another *Promimomys* population that retained more primitive characteristics.

FEJFAR *et al*. (1990) have suggested that the species *Mimomys vandermeuleni* from the Villalba Alta – Villalba Alta Rio composite section (Teruel Basin, Spain) is a likely ancestor of *M. davakosi*. *M. vandermeuleni* is indeed a very primitive member of *Mimomys*. We propose to include *M. vandermeuleni* in *M. davakosi* on the basis of the absence of distinctive characteristics to separate these two species.

Hypsodonty measurements indicate that the crown-height of *M. vandermeuleni* is not lower than that of *M. davakosi*. The maximum hypsodonty (h_{max}) of m1 of *M. vandermeuleni* from Villalba Alta Rio 2b1 (h = 2.24 mm) is, in fact, slightly above that of *M. davakosi* from PT3 (h = 2.02 mm; VAN DE WEERD (1979). (Note: The maximum hypsodonty value of 1.395 mm. given by FEJFAR *et al*. (1990) for *M. davakosi* from PT3 appears to be incorrect). The h_{max} of m1 of *M. davakosi* from Villalba Alta 1 and Arquillo 3, [1.77 and 1.65 mm respectively (FEJFAR *et al*., 1990)], and of the m1 described here are smaller as well.

In the description of *M. vandermeuleni* the slender appearance of the mesial side of the m1 is seen as an important diagnostic feature. The measurements of FEJFAR *et al*. (1990), VAN DE WEERD (1979), and this study show that the length and width of the m1 of *M. vandermeuleni* and *M. davakosi* are very similar. The pictures shown by FEJFAR *et al*. (1990) along with the listed hypsodonty values suggest that the *M. vandermeuleni* assemblages contain more juvenile specimens than the *M. davakosi* assemblages, which could cause the more slender appearance of *M. vandermeuleni* m1 compared to those of *M. davakosi*.

The presence and persistence of a variable number of crenulations on the mesial side of the anterior cap of m1 is considered to be an important diagnostic feature for *M. vandermeuleni* (FEJFAR *et al*., 1990). These crenulations are present in *M. davakosi* also, but establishing their presence depends strongly on the availability of suitable specimens. During the first stages of wear most of the small grooves and folds will disappear in both species, as can be observed in the *M. vandermeuleni* and *M. davakosi* molars shown by FEJFAR *et al*. (1990).

FEJFAR *et al*. (1990) consider the undulations of the lower enamel border of the m1 to be more primitive in *M. vandermeuleni* than in *M. davakosi*. However, the e_a measurements given for the two species are very similar. The range of e_a values for *M. davakosi* given by VAN DE WEERD (1979) shows the variability of this feature. In our opinion, the height of this undulation can therefore not be used to separate *M. vandermeuleni* and *M. davakosi*.

The most prominent diagnostic features of *M. vandermeuleni* relate to the morphology of M3. The diagnosis of *M. vandermeuleni* indicates that two roots and two enamel islets in the M3 are characteristic for this species. However, the molars pictured by FEJFAR *et al.* (1990, p. 161, Figs 7, 8, 14) indicate that the M3 of *M. vandermeuleni* may have three roots, although the two-rooted predominate. The M3 of *M. davakosi* from PT3 (VAN DE WEERD, 1979; FEJFAR *et al.*, 1990; this study) can have either two or three roots. Therefore the number of roots of the M3 is not distinctive.

Similar to the variation and stratigraphic sequence seen in *Promimomys cor* from the Ptolemais Basin, the reduction of roots on M3 shows a reversed order in the succession of *M. vandermeuleni* to *M. davakosi* relative to the general evolutionary trend of root reduction in arvicolines.

The BRA1 in the M3 of *M. vandermeuleni* is closed during the early stages of wear, which results in a second enamel islet in the occlusal surface. *M. davakosi* does not show an anterior enamel islet during the early stages of wear. However, during the later stages of wear a short-lived enamel islet may be present in the BRA1 (VAN DE WEERD, 1979; FEJFAR *et al.*, 1990; this study). This feature seems to distinguish *M. vandermeuleni* from *M. davakosi*. However, bearing in mind the considerable morphological variability of M3 in assemblages of primitive arvicolines, this characteristic may ultimately not be sufficient to distinguish these species.

The magnetostratigraphy of the Villalba Alta – Villalba Alta Rio composite section has been correlated to the Gauss chron (OPDYKE *et al.*, 1997), which implies that the *M. vandermeuleni* material is distinctly younger (~600 kyr) than the *M. davakosi* type material from PT3. This rules out that *M. vandermeuleni* is ancestral to *M. davakosi*, because, judging from the literature (OPDYKE *et al.*, 1997; AGUSTÍ *et al.*, 2001), alternative correlation options for this composite section appear to be unlikely.

Mimomys aff. *davakosi* VAN DE WEERD 1979
(Pl. 20, Figs 1-6; Pl. 21, Figs 1-7)

Locality: Tomea Eksi 3 (TE3)

Age: Early Pliocene

Material and measurements of Mimomys aff. davakosi: Table 18, 21-22

Description

M1: The prisms are bulging somewhat anteriorly. The T1-T2 and the T3-T4 connections are broad, and the AL2-T1 and the T2-T3 connection are relatively narrow. The T4 extends posteriorly from the molar outline, but a weak concave inflexion on the postero-lingual side of T4 is visible in one specimen. The labial re-entrant folds have approximately equal depth. The apex of the BRA1 is curved posteriorly in seven out of eight specimens. The apex of the BRA2 is curved backwards in all M1. The LRA2 is slightly curved backwards in two out of five specimens. The linea sinuosa is very simple, showing a very weak undulation on the LSA2. The M1 has three roots.

M2: The dentine connections of AL1-T2 and T2-T3 are narrow in slightly worn specimens. In well-worn specimens the AL1-T2 connection is broadly confluent due to the reduction of BRA1. The T4 is large. A concave inflexion on the postero-lingual side is absent. The BRA2 and LRA2 are deep. Their apices are curved posteriorly. The BRA1 is relatively shallow and reduces with wear. The linea sinuosa is very simple, showing minor undulations.

M3: The dentine fields are confluent. The T2-T3 connection becomes narrower with wear. The BRA1 is deep in slightly worn specimens. In four M3 a short-lived islet is present in the BRA1 (Pl. 21, Fig. 4). The BRA1 is very shallow in deeply worn specimens. A deep elongate enamel islet is present in the posterior cap. In one unworn specimen this islet is open toward the BRA2 (Pl. 21, Fig. 7). The apex of the LRA2 is slightly curved posteriorly in five out of ten specimens. A distinct BRA3 is absent, but the T4 forms a small ridge on the labial side of six out of ten specimens. The linea sinuosa is nearly straight. Seven specimens have three roots, two of these have an additional fourth rootlet below the T3. Two roots are present in one specimen, in this M3 the two anterior roots and the additional rootlet are fused.

m1: The enamel is undifferentiated (Pl. 20, Fig. 1). The dentine fields are connected. The T1-T2 connection is wide. The PL-T1 and the T2-T3 connections are narrower. The anterior cap of slightly worn specimens shows a variable number of small narrow folds or grooves that disappear in the early stages of wear. A large oval enamel islet is present in the upper half of the crown. In the two slightly worn specimens a shallow LRA4 is present. This fold disappears below the upper 30 % of the crown. A small shortly persisting *Mimomys*-kante is present. The apex of the LRA2 is curved anteriorly to a variable degree in all but two worn specimens. The linea sinuosa is simple and shows small undulations anterior and posterior to the base of the BRA1. Enamel reduction is most distinct on the anterior cap where the enamel border reaches the base of BRA2.

m2: The posterior enamel of the posterior lobe is slightly thicker than elsewhere. The dentine fields are confluent. The connections of the T1-T2 and the T3-T4 become slightly wider with wear, while those of the PL-T1 and T2-T3 become narrower. The T3 has a concave mesial inflexion in slightly worn specimens. The T4 forms a distinct anterior extension on the occlusal outline that disappears with wear (Pl. 20, Figs 2, 4). The lingual re-entrant folds are deeper than the labial ones. The LRA2 is the deepest syncline. The apices of the LRA2 and BRA2 show a slight tendency to curve forward in one worn specimen only. The linea sinuosa is very simple, but may show shallow undulations, particularly on the BSA1.

m3: The prisms are confluent, in particular the T3-T4 connection. The PL-T1 and the T2-T3 connection become wider with increasing wear, because of the reduction of the BRA2 and the LRA1 (Pl. 20, Figs 3, 5, 6). The T1-T2 connection remains relatively narrow. The LRA2 is the deepest and the BRA2 is the shallowest re-entrant fold. The T3 has a mesial inflexion in slightly worn specimens. The linea sinuosa is straight.

Dicussion

The material from TE3 represents an intermediate evolutionary stage between *Promimomys cor* and *Mimomys davakosi*. Assignment of this material to either *Mimomys* or *Promimomys* is conceivable. The TE3 material has been assigned to *Mimomys* on the basis of the presence of a primitive LRA4, a *Mimomys*-kante, and the reduction of the enamel at the crown base, which reaches up to the base of the BRA2 in the m1.

Despite that the TE3 material has features intermediate between *Promimomys cor* and *Mimomys davakosi*, it seems that the transition between *Promimomys* and *Mimomys* took place outside the Ptolemais Basin. *M. davakosi* is found in levels slightly above TE3, but the change in morphology appears to be abrupt, indicating the local immigration of *M. davakosi*.

The TE3 material resembles *Mimomys antiquus* from West Siberia also (REPENNING, 2003). We have not been able to verify whether the material from TE3 should be assigned to that species.

Genus *Dolomys* NEHRING 1898
Type species: *Dolomys milleri* NEHRING, 1898

Type locality and level: Beremend, Pliocene of Hungary

Other species recognised:
D. nehringi KRETZOI 1959
D. adroveri FEJFAR, MEIN & MOISSENET 1990

Dolomys cf. *nehringi* KRETZOI 1959
(Pl. 24, Fig. 2; Pl. 25, Figs 1 & 5)

Locality: Notio 1 (NO1)

Age: Pliocene

Material and measurements of Dolomys cf. nehringi: Table 18, 23-24

The *Dolomys* material from NO1 is very limited, consisting of two m1 fragments, four m3 (two damaged), one M1 fragment and one damaged M3.

TABLE 23
Material and measurements of *Dolomys* cf. *nehringi*
and *Propliomys hungaricus*.

D. cf. *nehringi*			Length (mm)				Width (mm)			h_{max}	$(h/L)_{max}$
		N	min	mean	max	N	min	mean	max	(mm)	(mm)
Notio 1	M1					1		1.62		1.56	
Notio 1	M3					1		1.39			
Notio 1	m3	3	1.91	2.01	2.13	4	1.11	1.18	1.27	1.64	.74
P. hungaricus			Length (mm)				Width (mm)			h_{max}	$(h/L)_{max}$
		N	min	mean	max	N	min	mean	max	(mm)	(mm)
Notio 1	M1	2	2.12	2.19	2.25	2	1.19	1.21	1.23	2.46	1.10
Notio 1	M2	6	1.88	1.98	2.06	5	1.23	1.32	1.42	2.04	1.08
Notio 1	M3	10	1.41	1.49	1.67	12	0.79	0.92	1.05	2.06	1.45
Notio 1	m1	1		2.70		3	1.09	1.17	1.33	1.63	0.61
Notio 1	m2	5	1.63	1.71	1.78	4	1.09	1.17	1.26	1.74	1.03
Notio 1	m3	6	1.20	1.33	1.54	5	0.84	0.90	0.98	1.74	1.42

TABLE 24
Cap size measurements of m1 and M3 of *Dolomys* cf. *nehringi*
and *Propliomys hungaricus*.

D. cf. *nehringi*			P and A (mm)				WP and WA (mm)		
		N	min	mean	max	N	min	mean	max
Notio 1	M3					1		1.27	
Notio 1	m1					1		1.38	
P. hungaricus			P and A (mm)				WP and WA (mm)		
		N	min	mean	max	N	min	mean	max
Notio 1	M3	11	0.77	0.86	1.00	12	0.71	0.82	0.97
Notio 1	m1	4	1.09	1.22	1.38	4	1.04	1.07	1.12
			P/WP and A/WA				P/L and A/L		
		N	min	mean	max	N	min	mean	Max
Notio 1	M3	11	0.86	1.05	1.34	10	0.53	0.58	0.67
Notio 1	m1	4	1.03	1.14	1.32	1		0.51	

Description

M1: The enamel of the fragment is negatively differentiated (Pl. 25, Fig. 5), having thick enamel on the anterior and thinner enamel on the posterior side of triangles The dentine fields of the well-preserved T1 and T2 are confluent, while the connections between the AL2 and T1 and the T2 and T3 are narrow. The apices of the LRA1, LRA2 and BRA1 are curved posteriorly. The enamel border on the LSA2 shows a distinct undulation.

M3: The specimen has a damaged posterior cap. Its enamel of all prisms is negatively differentiated. The T3-T4 connection is confluent, the T1-T2 connection is somewhat weaker and the T2-T3 connection is narrow. The AL1 forms the widest part of the molar. Enamel islets are absent. The two lingual re-entrant folds are deep, the LRA3 being deeper than the LRA2, but both reaching past the central longitudinal axis of the molar. The LRA3 and BRA1 have similar depths. The three labial re-entrant folds become shallower towards the posterior, the BRA3 being very shallow. The apices of the BRA1, BRA2, LRA2 and LRA3 are curved posteriorly. A slight undulation is visible in the enamel border of the LSA2. This specimen has three roots.

m1: In one fragment the T1 and T3-T5 are preserved (Pl. 24, Fig. 2), in the other only the T1, T3 and T5 are present. Both fragments show negatively differentiated enamel, having thin enamel on the anterior side and slightly thicker enamel on the posterior side of the triangles. Dentine fields are connected. One specimen shows an oval enamel islet in the anterior cap (Pl. 24, Fig. 2). A distinct *Mimomys*-kante is present, which persists to the base of the crown. The LRA4 is well developed in one specimen, but shallow in the other, worn specimen. Except for the LRA4 of the latter, the apices of the preserved re-entrant folds are curved anteriorly. Part of a distinct enamel free area on the labial side of the anterior cap is present. Cement is lacking in the re-entrant folds.

m3: The lingual prisms of two out of four specimens show slightly negatively differentiated enamel. The T1-T2 and T3-T4 connections are confluent (Pl. 25, Fig. 1). The anterior enamel wall (T3-T4) is somewhat rounded. The apices of BRA2 and LRA2 curve anteriorly. The curvature in the BRA1 and LRA1 is weak or absent. Shallow undulations are present on the enamel border.

Discussion

Identification of this limited material at the species level is tentative. However, the size and morphology of these fragments appears to be very similar to that of *Dolomys nehringi* from Csarnóta 2 (KRETZOI, 1959, 1962). The fragments resemble the "*Mimomys*" *rhabonensis*/*Dolomys nehringi* material from the Dacic Basin (Romania) shown by RADULESCU *et al*. (1997) as well. Given the paucity of our material, we provisionally assign this material to *Dolomys* cf. *nehringi*.

Genus *Propliomys* KRETZOI, 1959
Type species: *Dolomys hungaricus* KORMOS, 1934

Propliomys hungaricus (KORMOS, 1934)
(Pl. 24, Figs 1, 3-7; Pl. 25, Figs 2-4, 6; Pl. 26, Figs 1-6)

Type level: Csarnóta 2, Upper Ruscinian of Hungary

Selected references:

Propliomys hungaricus (KORMOS, 1934), in: KRETZOI (1962)

Propliomys hungaricus (KORMOS, 1934), in: FEJFAR & STORCH (1990)

Propliomys hungaricus (KORMOS, 1934), in: RADULESCU & SAMSON (1996)

Propliomys hungaricus (KORMOS, 1934), in: FEJFAR *et al*. (1998)

Locality: Notio 1 (NO1)

Age: Pliocene

Material and measurements of Propliomys hungaricus: Table 18, 23-24

The material is limited, comprising one complete m1 and five fragments (three ACC's), five m2, six m3, three M1 (one damaged), six M2 (three damaged) and two fragments, and twelve M3 (four damaged) and a fragment.

Description:

M1: The enamel is undifferentiated. The T1-T2 and the T3-T4 connections are confluent, while the T2-T3 connection is narrow. The apices of the prisms are relatively angular in the two complete specimens. Except for the LRA1, the apices of the re-entrant folds curve posteriorly. The molar outline on the postero-lingual side (T3-T4) and the postero-labial side (T4) is concave in the two slightly worn complete specimens, giving the T4 a posteriorly protruding appearence. The M1's have three roots.

M2: The enamel is generally undifferentiated. Dentine fields are poorly connected, except for the confluent T3-T4 connection. The apices of all re-entrant folds curve posteriorly. The AL1 is slightly bulging on the anterior side in the molar outline. The postero-lingual side (T3-T4) and the postero-labial side (T4) are somewhat concave in slightly to moderately worn specimens. The M2 has three roots.

M3: The enamel shows some variation in thickness, but is not clearly differentiated. The M3 are relatively narrow. An enamel islet is present in the posterior cap (Pl. 26, Figs 1-6). In six out of twelve M3 this islet is closed, in five out of twelve it is open on the lingual side (LRA3) and in one it is open on the labial side (BRA3) in the early stages of wear. In five out of thirteen specimens an enamel islet is present in the BRA1. This islet is absent in three out of thirteen specimens. The latter are one slightly worn and two worn specimens with a very shallow BRA1. Most specimens have a distinct, but shallow, BRA3 and LRA3. The enamel at the crown base is slightly reduced, showing low undulations. Roots are preserved in four specimens, two of these have two roots and two have three roots.

m1: The complete specimen is rather slender. Apart from the thinner enamel on the mesial side of the anterior cap, the enamel is undifferentiated. The BRA3 is relatively deep and narrow, and an enamel islet is lacking. A shallow LRA5 is present in the anterior cap that disappears slightly lower in the crown (Pl. 24, Fig. 1). The other three preserved anterior complexes lack this fold. In three out of four m1 the *Mimomys*-kante persists down to the lower part of the crown. A shallow enamel islet is present in two out of four specimens. The apices of LRA1-3 show a tendency to curve anteriorly. Distinct enamel reduction is visible at the lower enamel border, particularly on the anterior cap (Pl. 24, Figs 1, 5). The only complete specimen has two roots.

m2: The enamel is undifferentiated, although the posterior enamel of the posterior lobe is somewhat thicker. The T1-T2 and the T3-T4 connections are confluent while the PL-T1 and the T2-T3 connections are very narrow. The mesial side of the T3 is slightly concave. The apices of the lingual re-entrant folds curve anteriorly in four out of five specimens. In one only the LRA2 is curved. The apices of the labial re-entrants curve anteriorly in two worn specimens, while this is not the case in slightly worn specimens. The m2 has two roots.

m3: The enamel is undifferentiated. Except for the LRA2 in one specimen, the re-entrant folds do not curve forward. The lingual re-entrants are distinctly deeper than the labial ones. The dentine field connections are very similar to those of the m2. In slightly worn specimens the mesial side of the T3 is slightly concave. In lateral view the m3 is somewhat oblique.

Discussion

The m1 and fragments from NO1 have been compared to drawings of Csarnóta 2 material made by Dr. Albert van der Meulen (unpublished). The morphology corresponds very well. The presence or absence of an enamel islet and the variation in the shape of the anterior cap seen in the NO1 material appears to fall within the range of variation of the material from Csarnóta 2. The complete *P. hungaricus* m1 from NO1 also compares very well with a morphotype from Csarnóta 2 that is shown by FEJFAR *et al*. (1998, pl. 3 Fig. 10). The size of our specimen falls within the size range of m1 from Csarnóta 2 as given by FEJFAR & STORCH (1990).

The size of the M3 of *P. hungaricus* from Gundersheim 4 (Findling) listed by FEJFAR & STORCH (1990) falls within the size range of the M3's from NO1. The morphology of M3 from NO1 shows variation, but is similar to the specimen figured by KRETZOI (1962). This material from NO1 is therefore assigned to *Propliomys hungaricus*.

Subfamily Anomalomyinae SCHAUB 1925

Genus *Prospalax* MEHELY 1908
Type species: *Spalax priscus* NEHRING 1897

Other species recognised:

Prospalax petteri BACHMAYER & WILSON 1970

Remarks

Judging on the basis of figures of the cheek teeth of *Anomalospalax viretschaubi* (KRETZOI, 1971) and of *Anomalospalax tardosi* KORDOS 1985 we consider *Anomalospalax* KORDOS 1985 a junior synonym of *Prospalax*. *Anomalomys gernoti* DAXNER-HÖCK 1980 is considered to be a junior synonym of *Prospalax petteri*. The status of the names *Prospalax rumanus* (SIMIONESCU, 1930) and *Prospalax kretzoii* JÁNOSSY 1972 is uncertain and needs to be verified.

Prospalax priscus (NEHRING, 1897)
(Pl. 27, Figs 7, 8)

Selected references:

Prospalax priscus (NEHRING, 1897) in: KRETZOI (1959)

Prospalax priscus (NEHRING, 1897) in: TOPACHEVSKI (1969)

Prospalax priscus (NEHRING, 1897) in: KORDOS (1987)

Type locality and level: Beremend, Hungary, (MN16)

Locality: Notio1 (NO1)

Age: Pliocene

Material and measurements of Prospalax priscus: Table 25

Discussion

The three *Prospalax* teeth from NO1 are very similar in dental pattern and crown height to the material from Csarnóta 2 and 4 available for comparison. A peculiar derived feature of the cheek teeth of *P. priscus* that has, as far as we know, not attracted attention so far, is the very pronounced differentiation of the thickness of the enamel. The enamel of the anterior face of the M1 and M2 and of the posterior face of the m1 and m2 is much thicker than that of the reciprocal sides.

TABLE 25

Material and measurements of *Prospalax priscus*.

Locality		Length (mm)				Width (mm)			
		N	min.	mean	max.	N	min.	mean	max.
Notio 1	M1	1		2.06		1		1.69	
Notio 1	m2	2	2.06		2.07	2	1.61		1.90

Subfamily Cricetinae FISCHER VON WALDHEIM 1817

Genus *Allocricetus* SCHAUB 1930
Type species: *Allocricetus bursae* SCHAUB 1930

Other species recognised:

Allocricetus ehiki SCHAUB 1930

Remarks

There are a number of other species of small cricetines that possibly belong in *Allocricetus*. However, the group seems to have been over-split on the generic level and needs to be revised. Moreover, a larger part of the fossil material of the small "modern" cricetines available in collections has not been studied. It is therefore impossible at this stage to give a comprehensive list of the species of *Allocricetus*. The revision needed would be far beyond the aim of this paper.

Allocricetus ehiki SCHAUB 1930
(Pl. 8, Figs 8, 9)

Type locality and level: Villany (? 5), Kalkberg, MN16

Selected references:
Allocricetus ehiki SCHAUB, 1930 in: DAXNER-HÖCK (1992)

Locality: Komanos 1 high (KO1highA&B) and Komanos 1 low (KO1lowA&B)

Age: Early Pliocene

Material and measurements of Allocricetus ehiki: Table 26

Description and discussion

The three teeth from both Komanos 1 levels show the basic dental pattern of a "modern" cricetine. The four-rooted M1 has a wide anterocone with two cusps that are anteriorly as well as posteriorly connected. The anterior face of the anterocone is flat. The cusp pairs formed by the protocone and paracone and by the hypocone and metacone are showing asymmetrical double connections. The posterior connection is stronger than the anterior one. The two lingual and the two labial sinuses are about equal in depth. The two cusps of the anteroconid of the m1 are connected and the anterior face of the anteroconid is smoothly rounded as in *Kowalskia* FAHLBUSCH 1969. The anterolophulid is weak. The metalophid and hypolophid are directed forwards and the mesolophid is absent.

The dental morphology of the three teeth described above matches the few specimens of *Allocricetus ehiki* from Villany in the comparative collection of the IVAU and seem to be well inside of the range of variation of that species.

TABLE 26
Material and measurements of *Allocricetus ehiki*.

Locality		Length (mm)				Width (mm)			
		N	min.	mean	max.	N	min.	mean	max.
Komanos 1 high	M1	1		2.39		1		1.49	
Komanos 1 low	M1	1		2.36		1		1.61	
Komanos 1 low	m1	1		2.23		1		1.36	

Subfamily Gerbillinae GRAY 1825

Genus *Pseudomeriones* SCHAUB 1934

Type species: *Lophocricetus abbreviatus* TEILHARD DE CHARDIN 1926

Other species recognised:
P. tchaltaensis SEN 1977
P. rhodius SEN 1977
P. pythagorasi BLACK, KRISHTALKA & SOLOUNIAS 1980
P. latidens SEN 1998
P. megistos SYLVESTROU & KOSTOPOULOS 2007

Pseudomeriones sp.
(Pl. 11, Figs 9, 10)

Localities: Tomea Eksi 1 and 2 (TE 1 & 2)

Age: latest Miocene of earliest Pliocene

Material and measurements of Pseudomeriones sp.: Table 27

The assemblage from TE1 contains one M3, two fragments of m1 and one damaged m2. From TE2, one m1 and one damaged m2 are present. The fossiliferous levels TE1 & TE2 are palaeosols present in two successive sedimentary cycles. Since the fauna content of these levels is identical we assume that the few *Pseudomeriones* teeth listed above represent the same species.

TABLE 27
Material and measurements of *Pseudomeriones* sp.

Locality		Length (mm)				Width (mm)			
		N	min.	mean	max.	N	min.	mean	max.
Tomea Eksi 2	m1	1		2.47		1		1.50	
Tomea Eksi 2	m2	1		1.40		1		1.58	
Tomea Eksi 1	M3	1		0.77		1		1.03	

Description

M3: The dental pattern of this rather high-crowned, one rooted M3 is very simple and consists of the connected protocone and paracone only. A shallow antero-labially directed sinus divides the occlusal surface into a smaller lingual part and a larger labial part.

m1: The two-rooted high-crowned m1 is robust. The lingual sinuses are longer and wider than the labial ones. A vestigial posterolophid is indicated by a notch. The large anteroconid is very asymmetrical. Its straight labial border is in line with the protoconid and the hypoconid.

m2: The occlusal surface of the two-rooted high-crowned fragment of m2 is wider than long. The protosinusid is long, just as the forwards directed sinusid. The postero-lingual side of this tooth is damaged.

Discussion

The three *Pseudomeriones* teeth described above are robust and high-crowned. Among the named species they resemble those of *Pseudomeriones latidens* in their relative width, deep protosinusid of the m2 and very simple M3. The teeth from TE1 & TE2, are, however, larger and have much higher crowns than in that species. In this respect they are more similar to those of the geologically younger species *tchaltaensis*. The shape of the anteroconid of the m1 and the extremely reduced pattern of the M3 make these specimens from TE1 & TE2 unique. There seems therefore no doubt that our specimens represent a new species, but we refrain from naming it because the available material is considered insufficient. The status of a new species is confirmed in the phylogenetic analysis of

Pseudomeriones SYLVESTROU & KOSTOPOULOS (2007) who included these TE1 & TE2 specimens. They suggest this species represents an isolated offshoot descending from *P. abbreviatus*.

Family Pteromyidae BRANDT 1855

Genus *Pliopetaurista* KRETZOI 1959

Type species: *Sciuropterus pliocaenicus* DEPÉRET 1897

Type locality and level: Perpignan, MN14

Other species recognised:

P. dehneli (SULIMSKI, 1964)
P. bressana MEIN 1970
P. meini BLACK & KOWALSKI 1974
P. rugosa QIU 1991

Pliopetaurista dehneli (SULIMSKI, 1964)

(Pl. 5, Fig.10)

Selected references:

Pliopetaurista dehneli (SULIMSKI, 1964) in: BLACK & KOWALSKI (1974)

Pliopetaurista dehneli (SULIMSKI, 1964) in: DE BRUIJN (1995)

Localities: Komanos 1 high (KO1highA&B) and Vorio 3 (VOR3)

Age: Early Pliocene

Material and measurements of Pliopetaurista dehneli: Table 28:
One m3 fragment is present in the assemblages from KO1highA&B. From VOR3, one fragment of M1-2 and one m3 have been found.

Description and discussion
The presence of *Pliopetaurista* in two levels (KO1high A&B, VOR3) of the Ptolemais Fm is of interest, because it shows that there must have been forests with tall trees around the lake during the deposition of that formation. The rare specimens of *Pliopetaurista* were presumably transported by birds of prey to the place of deposition. This kind of "post mortem" transport by birds of prey that perch in a (dead) tree in the middle of extensive wetlands, is quite possible (observations by the second author (HdB) in the wetlands of the Pantanal, Brazil). The few remains of *Pliopetaurista* from the Ptolemais Fm fit perfectly within the range of variation of the *P. dehneli* assemblage from Maramena (DE BRUIJN, 1995).

TABLE 28
Material and measurements of *Pliopetaurista dehneli*.

Locality		Length (mm)				Width (mm)			
		N	min.	mean	max.	N	min.	mean	max.
Vorio 3	m3	1		3.30		1		2.38	

Family Sciuridae FISCHER VON WALDHEIM 1817

Genus *Sciurus* LINNAEUS 1758

Type species: *Sciurus vulgaris* LINNAEUS 1758

Fossil species recognised:

Sciurus warthae SULIMSKI 1964
Sciurus anomalus GUELDENSTAEDT 1785

Sciurus anomalus GUELDENSTAEDT 1785

(Pl. 27, Fig. 10)

Selected reference:

Sciurus anomalus GUELDENSTAEDT, 1785 in: TCHERNOV (1968)

Locality: Notio 1 (NO1)

Age: Pliocene

Material and measurements of Sciurus anomalus: Table 29

Description and discussion
This *Sciurus* m1 has robust cusps and the strong entoconid and angular postero-lingual outline of the occlusal surface that characterise the m1 and m2 of tree squirrels. The metalophid reaches about half way the occlusal surface. The mesoconid is very small, and there is a notch between the mesostylid and the entoconid. Comparison of the specimen from NO1 with material of *Sciurus anomalus* from some Late Pleistocene cave deposits in Israel that was kindly donated to the IVAU by the late Professor Tchernov, shows a perfect match.

TABLE 29
Material and measurements of *Sciurus anomalus*.

Locality		Length (mm)				Width (mm)			
		N	min.	mean	max.	N	min.	mean	max.
Notio 1	m1	1		2.30		1		2.65	

Family Gliridae MUIRHEAD 1819

Genus *Glis* BRISSON 1762

Type species: *Myoxus glis* LINNAEUS 1758

Other species recognised:

Glis sussenbornensis SOERGEL 1919

Glis sackdillingensis (Heller, 1930)
Glis minor Kowalski 1956
Glis major De Bruijn & Rümke 1974
Glis truyolsi Daams 1976
Glis apertus Mayr 1979
Glis vallesiensis Agustí 1981
Glis galitopouli Van der Meulen & De Bruijn 1982
Glis guerbuzi Ünay 1989
Glis transversus Ünay 1994

Glis minor Kowalski 1956

(Pl. 27, Fig. 9)

Type locality and level: Podlesice, Poland, MN14

Selected references:
Glis minor Kowalski, 1956 in: Kowalski (1963)
Glis minor Kowalski, 1956 in: Fejfar & Storch (1990)

Locality: Komanos 1 low (KO1lowA&B) and Notio 1 (NO1)

Age: Pliocene

Material and measurements of Glis minor: Table 30

Description and discussion

The m1 from NO1 shows the characteristic features of *Glis*: One extra ridge in the anterior and one extra ridge in the posterior valley that are about as wide as the main ridges. The long centrolophid is isolated from the metaconid and connected to the entoconid as well as to the mesoconid. The posterior extra ridge is connected to the entoconid. The m2 from KO1 low has basically the same dental pattern as the one from NO1, but the anterior extra ridge is thin and the centrolophid reaches neither the lingual nor the labial edge of the occlusal surface. In these respects this specimen is very similar to the m1 from Gundersheim figured in Fejfar & Storch (1990). As far as can be judged from the figures in Kowalski (1963) our specimens fit in every respect within the assemblage from the type locality, which has approximately the same age as the material from Ptolemais.

TABLE 30

Material and measurements of *Glis minor*.

Locality		Length (mm)				Width (mm)			
		N	min.	mean	max.	N	min.	mean	max.
Notio 1	m1	1		1.55					
Komanos 1 low	m2	1		1.67		1		1.64	

TABLE 31

Material and measurements of *Myomimus* aff. *maritsensis*.

Locality		Length (mm)				Width (mm)			
		N	min.	mean	max.	N	min.	mean	max.
Notio 1	P4	1		0.96		1		1.12	
Notio 1	M1-2	2	1.21		1.22	2	1.52		1.59
Notio 1	M3	2	1.06		1.10	2	1.35		1.37
Notio 1	m1	1		1.40		1		1.34	
Notio 1	m2	1		1.31		1		1.22	
Notio 1	m3	1		1.20		1		1.16	

Genus *Myomimus* Ognev 1924

Type species: Myo*mimus* personatus Ognev 1924

Other species recognised:
Myomimus roachi (Bate, 1937)
Myomimus dehmi (De Bruijn, 1966)
Myomimus maritsensis De Bruijn, Dawson & Mein 1970
Myomimus compositus (Bachmayer & Wilson 1970)
Myomimus qafsensis (Haas, 1973)
Myomimus sumbalenwalicus Munthe 1980
Myomimus sinensis Wu 1985

Myomimus aff. *maritsensis* De Bruijn, Dawson & Mein 1970

(Pl. 27, Figs 1-6)

Type locality and level: Maritsa, Greece, MN 13

Locality: Notio 1 (NO1)

Age: Pliocene

Material and measurements of Myomimus aff. maritsensis: Table 31

Description and discussion

These cheek teeth from NO1 are larger than those of any other known species of *Myomimus*. Their dental pattern, however, is very similar to that in *M. maritsensis*. The P4 has no centrolophs and its anteroloph is developed as a cusp. In this respect it resembles the specimens of *M. maritsensis* from Monastiri (Daxner-Höck, 1995). One of the two M1-2 from NO1 has the posteroloph isolated from the protocone and two centrolophs, the other has the posteroloph connected to the protocone and the anterior centroloph only. The two M3 have a long anterior centroloph and a shorter and weaker posterior one. Both these ridges are isolated from the para- and metacone, a configuration that is common in the M3 from the type assemblage. The three-rooted m1 has a rather long centrolophid and no extra ridge, but the m2 has a rather strong posterior extra ridge. The m3 is simple and has the basic pattern of a glirid lower molar. Other than that these teeth from NO1 are much larger, they fit within the range of morphological variation of *M. maritsensis*. The material from Monastiri (N. Greece) that was allocated by Daxner-Höck to *M. maritsensis* has been shown to be significantly larger than the type material also, but it is smaller than the specimens from NO1.

The material described above is listed as *Myomimus* aff. *maritsensis* because it differs from that species in size only and is represented by a few isolated teeth.

Ecological interpretation of the rodent succession

The potential of fossil rodent assemblages for reconstructing palaeoecology is limited by the extraordinary ability of many members of the order to adapt to almost any climate and biotope on the condition that there is food. Their almost global extant dispersal and diversity demonstrates their ability to adapt to a wide range of biotopes. About 35 % of all mammal genera and about 50 % of all mammal species are rodents. In spite of this overwhelming potential, specific adaptations are often difficult to recognise in the dental morphology of fossil species while the postcranial skeleton is most of the time not known. The dentitions of rodent species with very different ecological preferences are often remarkably similar. This makes it difficult to recognise the ecological groups required for reconstructing the past.

In reconstructing palaeoecology on the basis of the rodent succession from the Ptolemais composite section it is essential to realise that these assemblages were collected from cyclical sediments. It has been demonstrated that these cycles are due to precession and that the mammal yielding levels represent precession maxima (= insolation minima and lake level low-stands). We are thus dealing with a discontinuous series of samples that were primarily accumulated during lake-level low stand. The compositions of the faunas reflect local species as well as species from the nearby areas surrounding the lake.

The assemblages

The range chart (Fig. 7) listing the rodent species from eight successive levels from the Ptolemais Basin shows that, with the exception of the youngest one, all assemblages contain five to eleven species only. This limited diversity is considered to be due to the biotope sampled. The five species present in the two samples from the Komnina Fm seem are considered to represent the local habitat. The rare occurrences of *Allocricetus*, *Tamias*, *Glis* and *Pliopetaurista* in the Kyrio mb of the Ptolemais Fm are considered to reflect biotopes from a wider area around the lake. These specimens have probably been transported, “post-mortem”, by birds of prey or other processes to their place of deposition.

The range chart shows clearly two discontinuities in composition, defining three types of assemblages. The ones of the first interval that comprises the localities TE1 & TE2 contain five species. Only one of these (*Micromys bendai*) occurs in younger levels also. Among the other four there is *Arvicanthis broekhuisi* and a *Pseudomeriones*, both representatives of extant groups that live in savanna biotopes. The two others are *Occitanomys debruijni* and *Apodemus gorafensis*, species that occur in their type localities associated with a gerbil also and seem therefore to have preferred an arid climate. Arboreal and aquatic rodent species are missing in this interval. We therefore think that the association suggests a savanna or steppe biotope and an arid climate, a conclusion that is strongly supported by the botanical data presented by Klooster-boer-Van Hoeve (2000) who shows that the levels sampled contain high percentages of herbaceous and minima for arboreal pollen.

The second interval comprises the assemblages KO1lowA&B, KO1highA&B, VOR1, TE3 and VOR3/3a. The local species present in this interval are: *Micromys bendai/steffensi*, *Apodemus atavus/dominans*, *Rhagapodemus primaevus*, *Microtodon komanensis*, *Promimomys cor*, *Mimomys davakosi* and a castorid. The dominance of *Micromys*, a genus of which the extant representatives live and build their nests in tall grasses and cereals, the presence of *Promimomys* and *Mimomys*, of which some species are associated with semi-aquatic habitats, and the occurrence of true beaver, is in agreement with the sedimentary environment sampled indicating a swamp environment. The absence of arboreal and fossorial species suggests that there were no extensive forests. This is in line with the abundant macroscopical botanical remains of reed and the absence of wood Kloosterboer-Van Hoeve (2000). The pollen diagram of the cycles K14-K19 of the Kyrio mb of the Ptolemais Fm presented by Kloosterboer-Van Hoeve (2000) shows no correlation between pollen content and lithology through these cycles, so the local signal seems to be suppressed. This means that the pollen data enables a reconstruction of the regional vegetation only.

The third interval is represented by the locality NO1 only. The fossiliferous bed is in contrast to the other levels a rather thick (40 cm) grey clay lens containing mollusc fragments. This bed of supposedly fluviatile origin has yielded a rather poor rodent collection and some fragmentary remains of larger mammals (i.e. *Dolichopithecus*). Although the number of rodent specimens from NO1 is limited the assemblage is more diverse (eleven species). All these are considered to be of local origin. The presence of the arboreal species *Sciurus anomalus* and the fossorial species *Prospalax priscus* suggests an open forest biotope. Unfortunately, the pollen content of cycle N20 (= NO1) has not been analysed.

CORRELATION OF RODENT ASSEMBLAGES

Biostratigraphy

Correlation of the mammal assemblages to the MN zonation is shown in Fig. 7. The levels from the Komnina Fm (TE1 & TE2, PSM), are correlated to MN13 on the basis of the presence of the large rat *Arvicanthis broekhuisi*. *Micromys bendai* represents an MN14 element in an otherwise Late Turolian assemblage.

A peculiar trait of the Late Turolian (Messinian) rodent assemblages of the Eastern Mediterranean is their patchiness, in the sense that genera are often represented by different species in different basins. This suggests (local) endemic evolution during a time-slice that is also well known for the occurrence of exotic elements, which is in this case *Arvicanthis*. The gerbil genus *Pseudomeriones* is known throughout Eurasia during the Late Miocene, but its species seem to have limited geographical ranges. The occurrences in our assemblages confirm this characteric combination of endemic evolution of rodent species and the presence of exotic immigrants.

The assemblages from the Komnina Fm are considered to have roughly the same age as the assemblages of Maramena and Maritsa. VAN DER MEULEN & VAN KOLFSCHOTEN (1986) previously assigned the fauna from Maritsa to MN14, but considered a correlation to MN13 to be an option. This correlation is preferred here.

In contrast to Late Turolian assemblages, Early Ruscinian faunas have a more uniform composition over large geographical distances, due to the immigration of the Arvicolinae and the extinction of the Late Turolian exotic species. The change from MN13 to MN14 is characterized in the Ptolemais Basin by a faunal shift that is marked by the immigration of *Promimomys cor*, *Microtodon komanensis* and *Rhagapodemus primaevus*, and by the disappearance of *Arvicanthis broekhuisi* and *Pseudomeriones* sp.

The appearance of *Mimomys* and absence of *Promimomys* are commonly used to distinguish MN14 from MN15 (OPDYKE *et al*., 1997; FEJFAR *et al*., 1998; AGUSTÍ *et al*., 2001). Also in our sequence the presence of *Mimomys* and the absence of *Promimomys* are used as markers for the onset of MN15. The onset of MN15 is not marked in the Ptolemais composite section by a significant faunal shift.

The arvicolines in the NO1 assemblage, *Dolomys* cf. *nehringi* and *Propliomys hungaricus*, lack cement in the reentrant folds and are associated with *Prospalax priscus*, *Rhagapodemus frequens* and *Occitanomys magnus*. The species assemblage is very similar to that of Csarnóta 2, suggesting a late MN15 age.

In contrast to the MN14/MN15 transition, the difference between early and late MN15 is characterized by a distinct shift in the rodent composition. Unfortunately, data from that interval are lacking in the Ptolemais composite section. According to the current usage, the immigration of a single genus marks the difference between MN zones 14 and 15, while a distinct shift in the species composition occurs within MN15.

Calibration and correlation

The assemblages from the Ptolemais Basin have been dated means of an integrated stratigraphical approach (VAN VUGT, 2000; STEENBRINK, 2001; KUIPER, 2003) (Fig. 2). This framework provides a firm basis and allows establishing syn- or diachronicities of genera and species between remote areas.

Magnetostratigraphy is currently the most useful and widely available tool for providing independent age estimates of mammal faunas. Unfortunately, long (continuous) stratigraphic sections yielding both mammal faunas and reliable paleomagnetic data are relatively scarce. In case of short paleomagnetic sections that contain one polarity or a single polarity reversal, magnetostratigraphic correlations are generally inconclusive.

The MN-system is relatively flexible since it is based on a sequence of selected reference faunas. Boundaries between zones are on purpose not defined. With the increasing availability of magnetostratigraphically calibrated mammal faunas, this system appears to be changing into a more rigid regionally true zonation system in which zone boundaries are defined by entries and exits of key taxa (e.g. AGUSTÍ *et al*., 2001). However, we think it is impossible to apply such a rigid biozonation system on a continental scale, due to the diachronic arrival and/or disappearance of key species, their limited geographical range. For a discussion regarding the use and history of the European Neogene mammal chronology we refer to DE BRUIJN *et al*. (1992), VAN DAM *et al*. (2001) and VAN DAM (2003).

In an effort to extend the calibrated mammal record in the Florina-Ptolemais-Servia Basin from late MN13 to early MN13, the magnetostratigraphically calibrated assemblage from Lava 2 (Servia Basin; DE BRUIJN *et al*., 1999; STEENBRINK *et al*., 2000). This section consists of a precession controlled alternation of dark- and light-colored lacustrine sediments. Lava 2 predates the lower boundary of chron C3An.2n (Fig. 13) by about four lithological cycles and its astronomical age is estimated at approximately 6.81 Ma (STEENBRINK *et al*., 2000).

Figure 13 shows a selection of mammal successions that cover the Gilbert chron and part of chron C3A. These successions show some similarities, but also marked differences in the correlation of MN units to the polarity time scale. The age difference between the assemblages containing *Promimomys cor* and *Mimomys davakosi* in Greece and Spain has already been noted by STEENBRINK (2001) and POPESCU (2001).

The three composite sections shown in Fig. 13 are insufficient to give a well constrained age estimate for the MN12-MN13 transition, which is mostly due to lack of mammal assemblages. However, the minimum age estimate of about 6.8 Ma for early MN13, below chron C3An.2n, is in general agreement.

The age estimates for the shift from MN13 to MN14 in the different composite sections show important differences. OPDYKE *et al*. (1997) have correlated this transition to the base of chron C3n.3n (Sidufjall) on the basis of the Fuente del Viso fauna from the Cabriel section (Teruel Basin), which they correlated to latest MN13 and to chron C3n.3r. The MN13-MN14 transition occurs distinctly earlier in the Ptolemais composite section, in which MN14 assemblages have been found just below the base of chron C3n.4n (Thvera). The transition is therefore correlated to the upper part of chron C3r. Its age can be bracketed between 5.40 Ma and 5.23 Ma, and is probably slightly younger than the Miocene/Pliocene boundary (5.33 Ma). The minimum numerical age difference between the correlation of OPDYKE *et al.* (1997) and that of this study is in the order of about 350 kyr.

In contrast to the correlation of OPDYKE *et al.* (1997), the correlation of the MN13-MN14 transition in the Fortuna Basin (GARCÉS *et al.*, 2001) is approximately coincident with the correlation in the Ptolemais Basin. Although the age constraints for the MN13-MN14 transition correspond very well in these sections, this is not necessarily the case for individual species or genera. The associated rodent assemblages listed by AGUSTÍ *et al.* (2006) from Sifón 413 & 430 just below and above the base of the Thvera chron, respectively, do not include any arvicolines, microtoid cricetids or *Micromys*.

The calibrated age given by OPDYKE *et al.* (1997) differs considerably from that of GARCÉS *et al.* (2001) even though both sections are in Spain. OPDYKE *et al.* (1997) correlate the Fuente del Viso fauna to chron C3n.3r on the basis of a single paleomagnetic sampling site slightly above this locality in the Cabriel (south) section, which yielded a normal polarity. This normal polarity has been correlated to the Sidufjall chron. MARTÍN SUÁREZ *et al.* (2000) and AGUSTÍ *et al.* (2001) prefer to correlate the Fuente del Viso fauna to early MN14 instead of late MN13.

We have confidence in the calibration of the MN13-MN14 transition on the basis the Sifón de Librilla section in the Fortuna Basin (GARCÉS *et al.*, 2001), because the magnetostratigraphy appears to be unambiguous, and both MN13 and MN14 faunas have been found. This age calibration is in agreement with the conclusions of HERNÁNDEZ-FERNÁNDEZ *et al.* (2004) and with the magnetostratigraphically inferred ages of the late MN13 Purcal-4 and Zorreras 3A faunas from sections in the Granada Basin and Sorbas Basin (Spain), respectively (MARTÍN SUÁREZ *et al.*, 1998, 2000).

OPDYKE *et al.* (1997) have correlated the MN14-MN15 transition to the top of chron C3n.1n (Cochiti) in the Orrios and Villalba Alta Rio sections (Teruel Basin), which corresponds to an age of approximately 4.19 Ma. The onset of MN15 is characterized by the entry of *Mimomys* in these sections. GARCÉS *et al.* (2001) have not recorded the MN14-MN15 transition. The top of the Sifón de Librilla section includes the lower part of chron C3n.2n (Nunivak), and MN14 assemblages have been found at the base of this chron, which is in agreement with the correlation of OPDYKE *et al.* (1997).

The calibrated age of the MN14-MN15 transition in the Ptolemais Basin differs distinctly from the ages obtained from the Spanish record. Similar to the Teruel Basin, the onset of MN15 is characterized by the immigration of *Mimomys*. In the Ptolemais composite section this entry is correlated to the upper part of chron C3n.3r, at approximately 4.95 Ma. This correlation suggests that there is a time gap in the order of approximately 750 kyr between the arrival of *Mimomys* (and disappearance of *Promimomys*) in Spain and Greece. This gap may have several causes. First, the magneto-

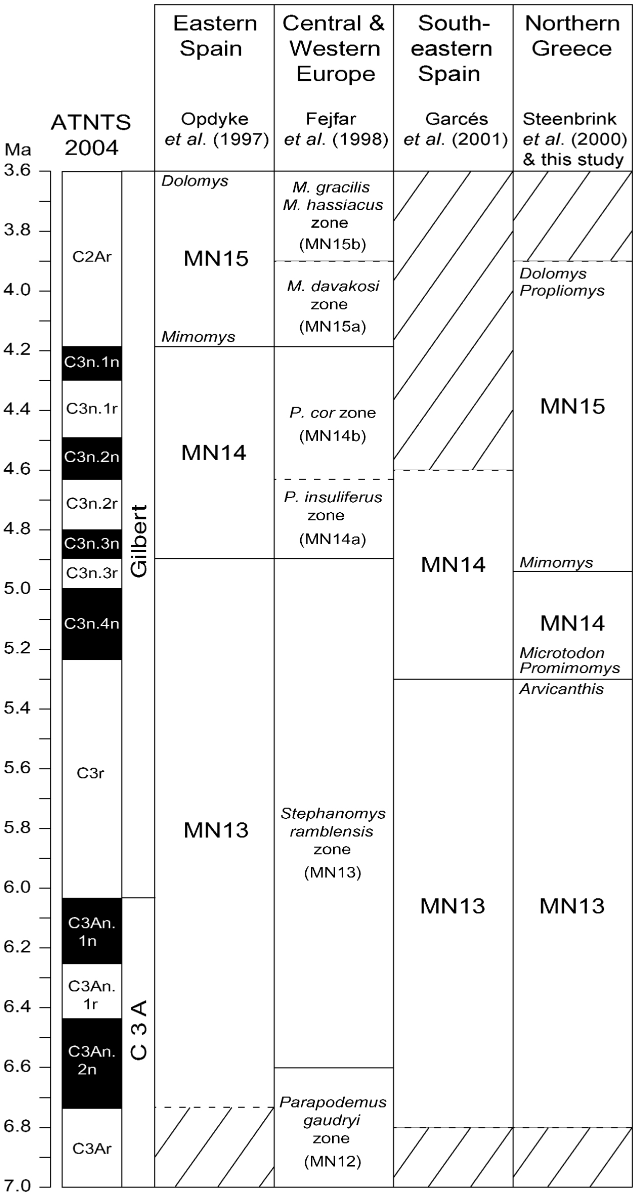


Fig. 13. An overview of the integrated bio- and magnetostratigraphical correlations in the Late Miocene and Early Pliocene of Europe is shown. Polarity reversals in the ATNTS2004 (LOURENS *et al.*, 2005) are correlated to magnetostratigraphically calibrated sections containing mammal faunas in different regions. The numbers denote correlations of local faunas to the MN system. Data of OPDYKE *et al.* (1997) and GARCÉS *et al.* (2001) are from multiple sections in Spain. Data of VAN VUGT *et al.* (1998), STEENBRINK *et al.* (1999, 2000) and this study are based on sections in Greece. The names of several genera are added to the zonations to indicate stage of evolution. The European biochronological overview of muroid rodents of FEJFAR *et al.* (1998) is shown to indicate relevant marker species and their inferred age.

stratigraphic calibration of mammal assemblages may be incorrect. Since the magnetostratigraphic correlation in the Ptolemais composite section is unambiguous, given the availability of radio-isotopically dated ashes and cyclostratigraphic control, and the magnetostratigraphic correlation in the Teruel Basin appears to be sound, this seems unlikely. A second possible cause for the observed age discrepancy is in the criteria used for separating MN14 from MN15. In particular, the use of the entry of *Mimomys* and the absence of *Promimomys* as the only criteria for assigning an assemblage to MN15 should be discouraged. Assuming the current age calibrations are correct, the distinctly diachronic arrival of *Mimomys* in southeastern Europe and Southwestern Europe implies that the value of the entry of this genus and species as an MN15 indicator is limited for biostratigraphy.

Although there is room for discussion regarding the criteria for the onset of MN15, certain stages of evolution of the Arvicolinae appear to occur earlier in Southeastern Europe than in Southwestern Europe. The MN15 assemblage from NO1 in the Ptolemais Basin is correlated to chron C2Ar, at a level that is slightly younger than 4 Ma. This is approximately coeval with assemblages containing distinctly more primitive arvicolines in the Villalba Alta Rio section. The stage of evolution of assemblages from the Teruel Basin that are correlated to the upper part of chron C2Ar is more similar to that of NO1 in having *Dolomys adroveri*.

The difference in the stage of evolution between Southeastern Europe and Spain is also seen in the small mammals from the Dacic Basin (Romania), which is situated relatively close to the Florina-Ptolemais-Servia Basin. RADULESCU *et al*. (1989) have described the subspecies *Mimomys occitanus rhabonensis* RADULESCU, SAMSON & STIUCA 1989 from the base of lignite VIII in the Lupoaia section. This species has later been referred to as "*Mimomys*" *rhabonensis* by RADULESCU *et al*. (1997) and is thought to be the ancestor of *Dolomys nehringi* (RADULESCU & SAMSON, 1996). The magnetostratigraphy of the Lupoaia section shown by RĂDAN & RĂDAN (1998) indicates that the Lupoaia VIII assemblage correlates to the upper part of chron C3n.1n (Cochiti). *Mimomys rhabonensis* is more evolved than *Mimomys davakosi*, which is in agreement with the correlation to the Ptolemais composite section. The entry of *Mimomys* in Spain, which is characterized by *M. davakosi* is correlated to the top of the Cochiti chron (Fig. 13).

POPESCU (2001) acknowledges the correlation of KD and PT1 (*Promimomys cor*) and PT3 (*Mimomys davakosi*) to the Thvera and Sidufjall chron respectively. She disagrees with the correlation of the Lupoaia section as suggested by RĂDAN & RĂDAN (1998) and VAN VUGT *et al*. (2001) and provides an alternative correlation on the basis of the pollen record. POPESCU (2001) correlates the Lupoaia VIII level to the upper part of chron C2n.2n (Nunivak), which is in agreement with the correlation of the mammal record in the Ptolemais composite section, but which implies a larger difference in the stage of evolution of arvicolines with respect to Spain.

We have confidence in the correlation of RĂDAN & RĂDAN (1998) and VAN VUGT *et al*. (2001). The Lupoaia section continues to younger levels beyond the interval studied by POPESCU *et al*. (2001) as is shown by RĂDAN & RĂDAN (1998) and VAN VUGT *et al*. (2001). A relatively long interval with reversed polarity is present in the upper part of the section, which is correlated to chron C2Ar. The magnetostratigraphy and mammal assemblages from the Dranic section appear to support this correlation (RĂDAN & RĂDAN, 1998; RADULESCU *et al*., 1997).

The MN15-MN16 transition could not be established in the Ptolemais Basin. The maximum age of early MN16 in this region is younger than 3.97 Ma, which is in agreement with the calibrations in Spain (OPDYKE *et al*., 1997; GARCÉS *et al*., 1997; OMS *et al*., 1999) and Romania (RADULESCU *et al*., 1997).

It is clear from Fig. 13 that the entry of marker species that are used for biostratigraphical correlation, i.e. *Promimomys cor* and *Mimomys davakosi*, is highly diachronous in different areas.

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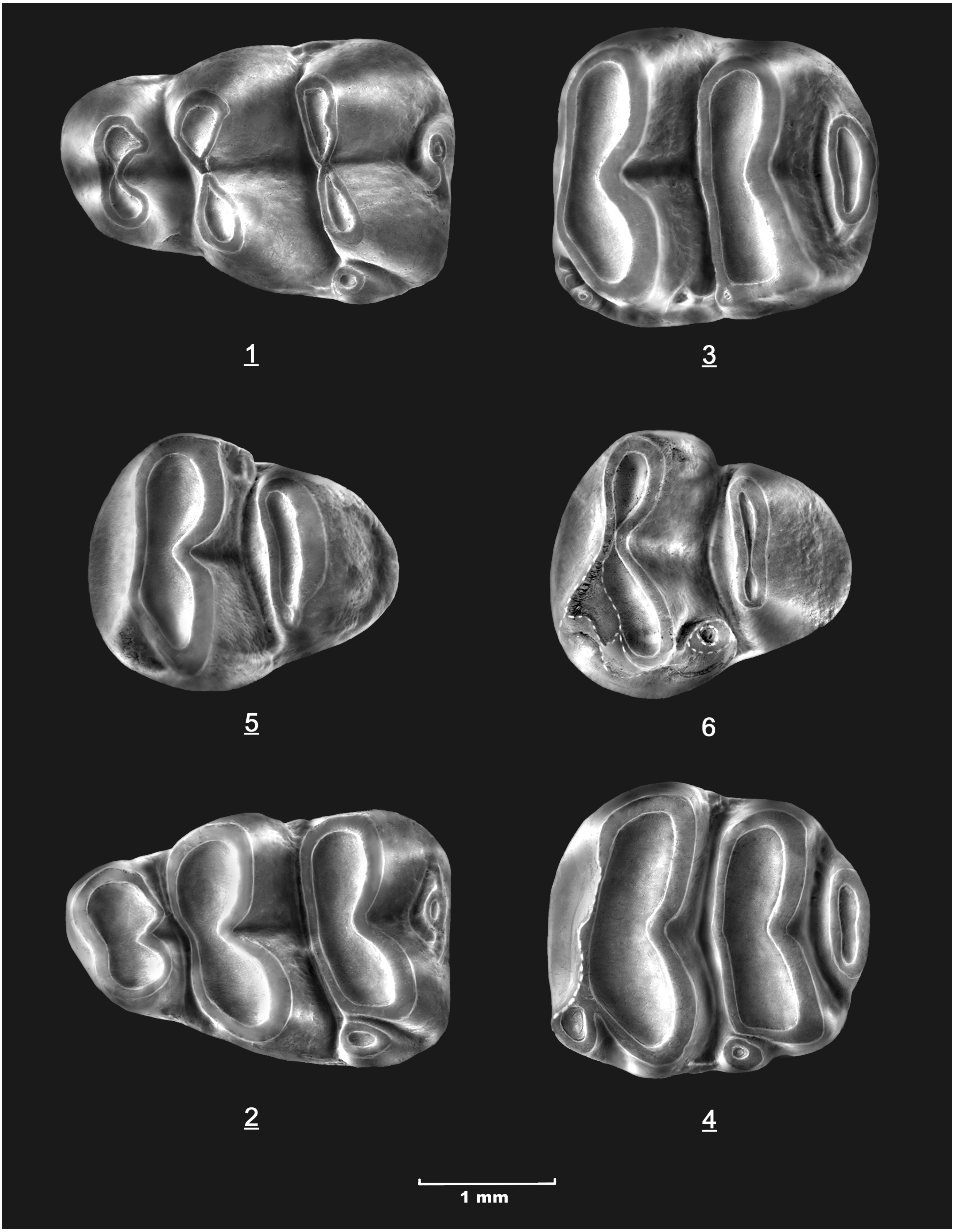

PLATE 1

Arvicanthis broekhuisi n. sp. from TE2. Figs 1, 2: m1, no. 291, 293; Figs 3, 4: m2, no 304, 302; Figs 5, 6: m3, no. 314, 317.

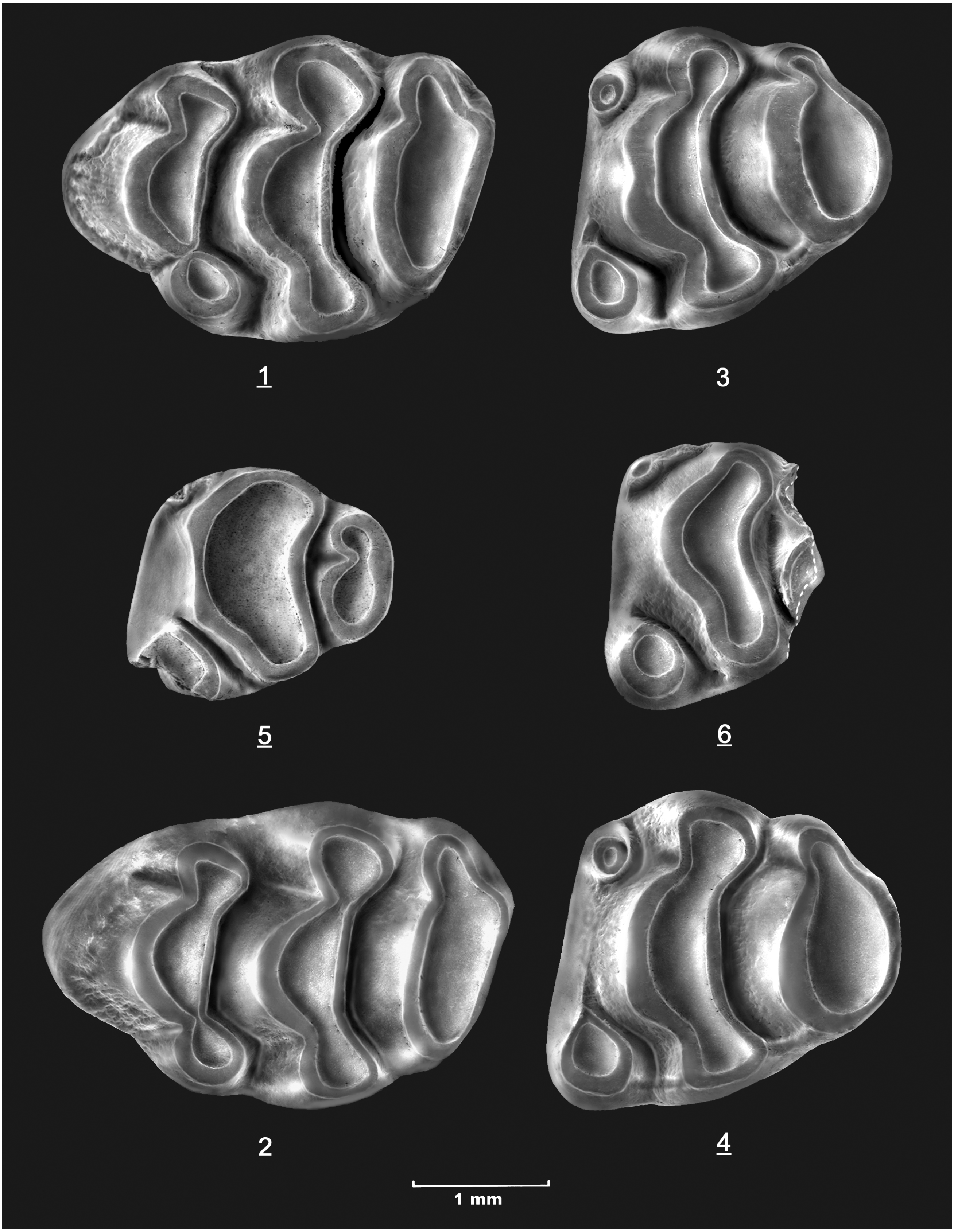

PLATE 2

Arvicanthis broekhuisi n. sp. from TE2. Figs 1, 2: M1, no. 271 (holotype), 274; Figs 3, 4: M2 no. 285, 281; Figs 5, 6: M3, no. 287, 288.

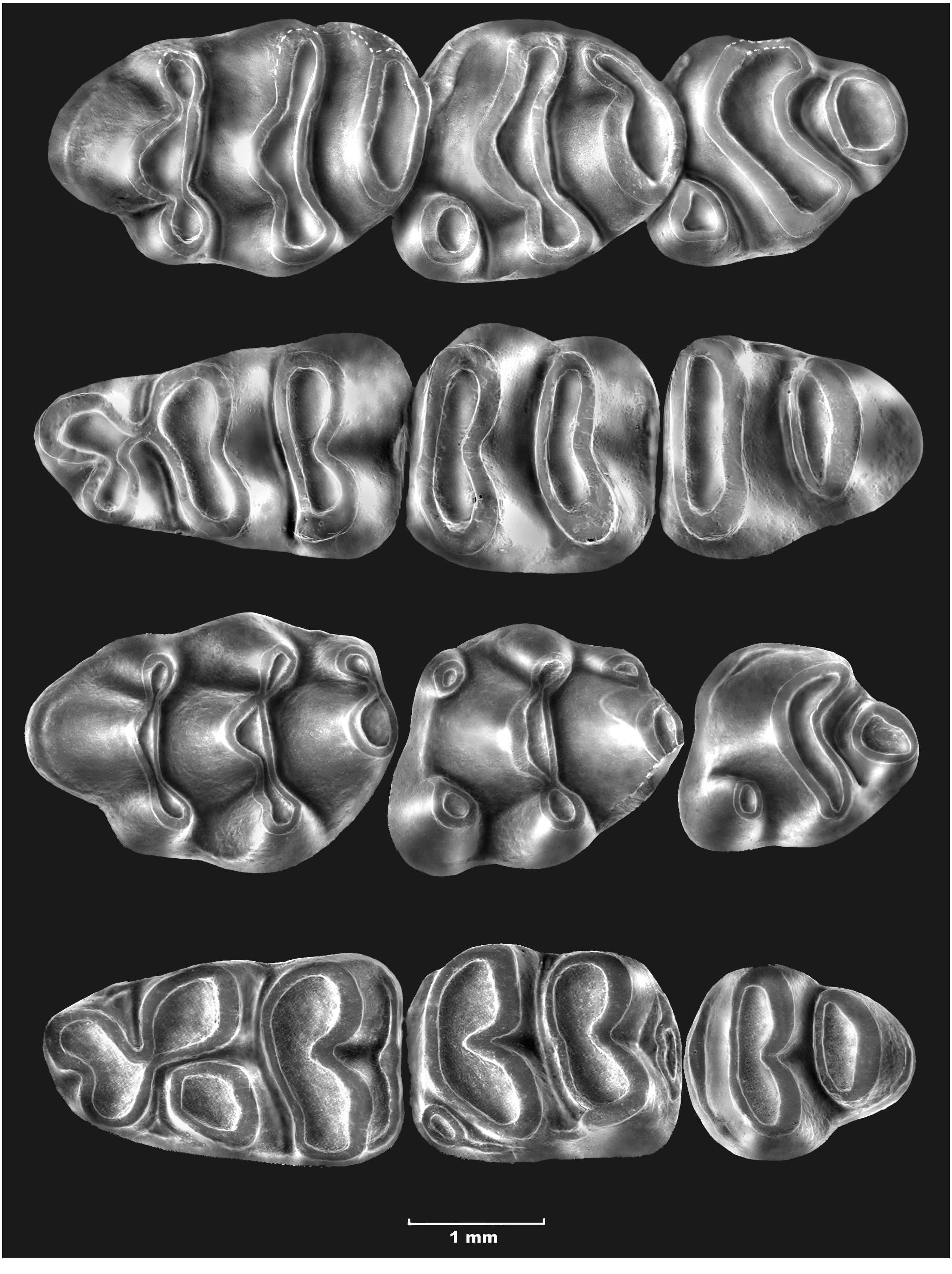

PLATE 3

Arvicanthis musisii MEIN 1994, in MEIN (1994). Fig. 1: M1-M3; Fig. 2: m1-m3.

Arvicanthis arambourgi JAEGER 1975, in JAEGER (1975). Fig. 3: M1; Fig. 4: M2; Fig. 5: M3; Fig. 6: m1-m2; Fig. 7: m3.

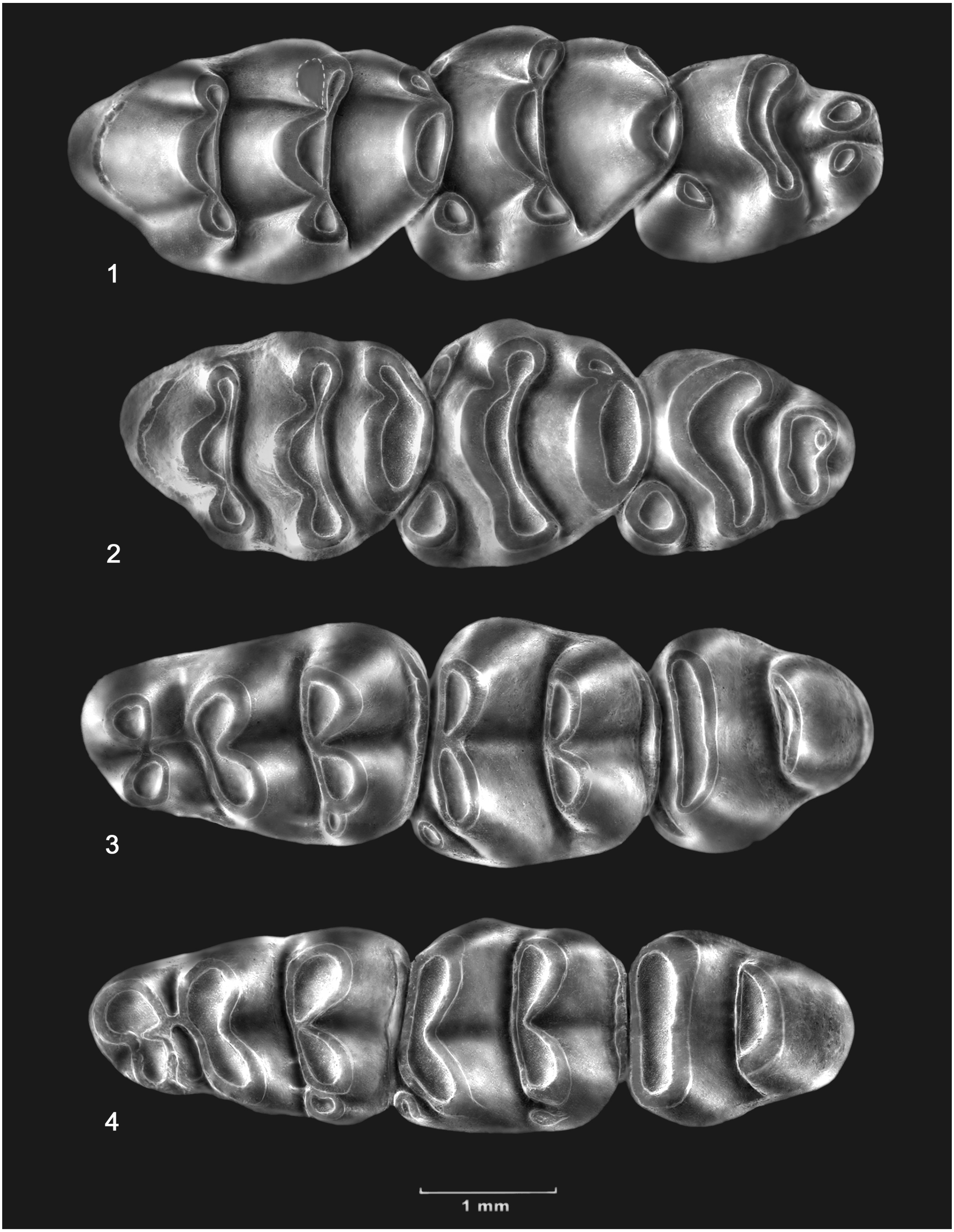

PLATE 4

Arvicanthis niloticus (DESMAREST, 1822). Recent, Kenia. Figs 1, 2: M1-M3; Figs 3, 4: m1-m3.

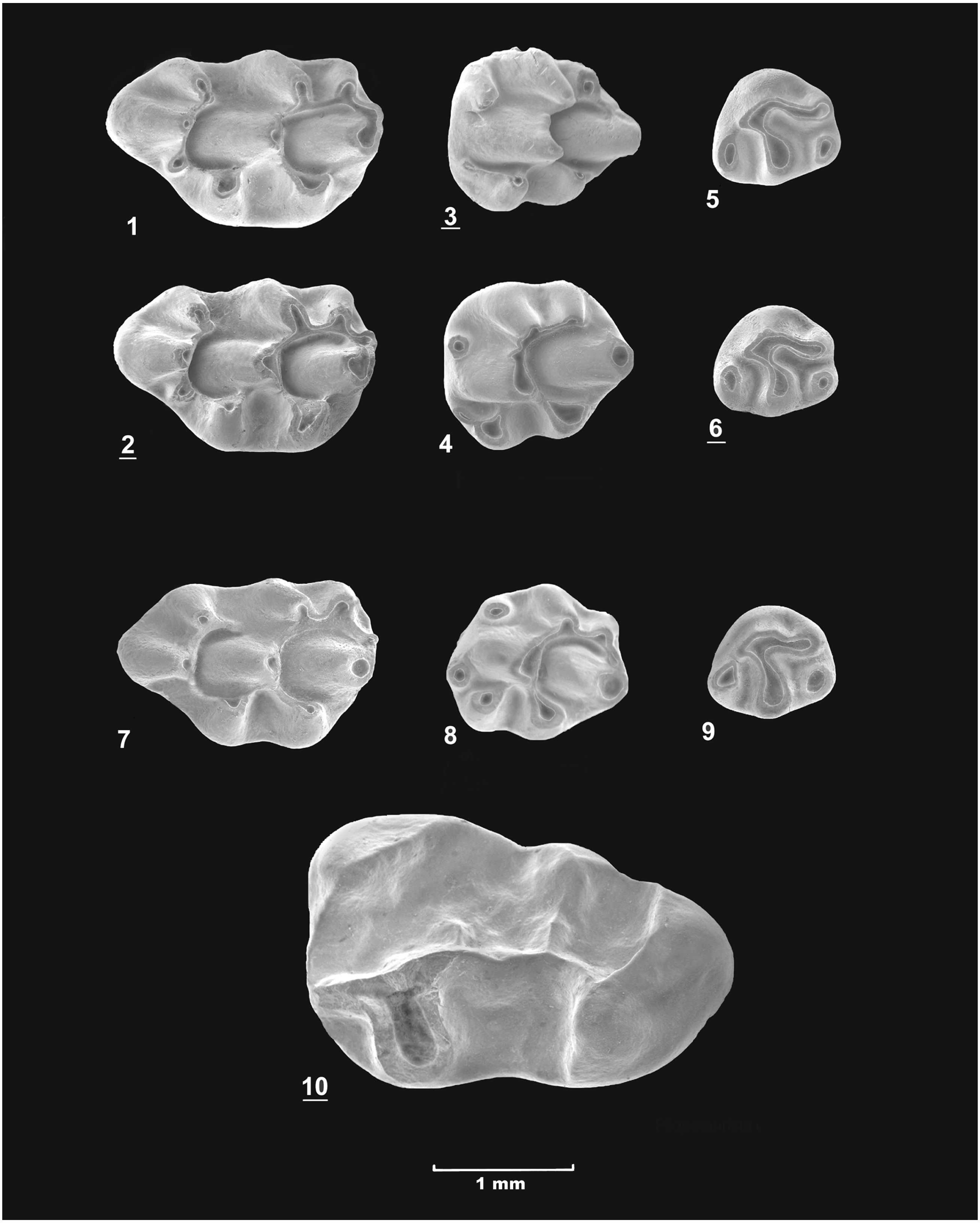

PLATE 5

Occitanomys debruijni (Sen *et al*., 1989) from TE2. Figs 1, 2: M1, no. 321, 326; Figs 3, 4: M2, no. 338, 331; Figs 5, 6: M3, no. 346, 341
Occitanomys debruijni (Sen *et al*., 1989) from Maritsa (type locality) in the comparative collection at IVAU. Fig. 7: M1; Fig. 8: M2; Fig. 9: M3.
Pliopetaurista dehneli (Sulimsky, 1964) from VOR 3. Fig. 10: m3, no. 811.

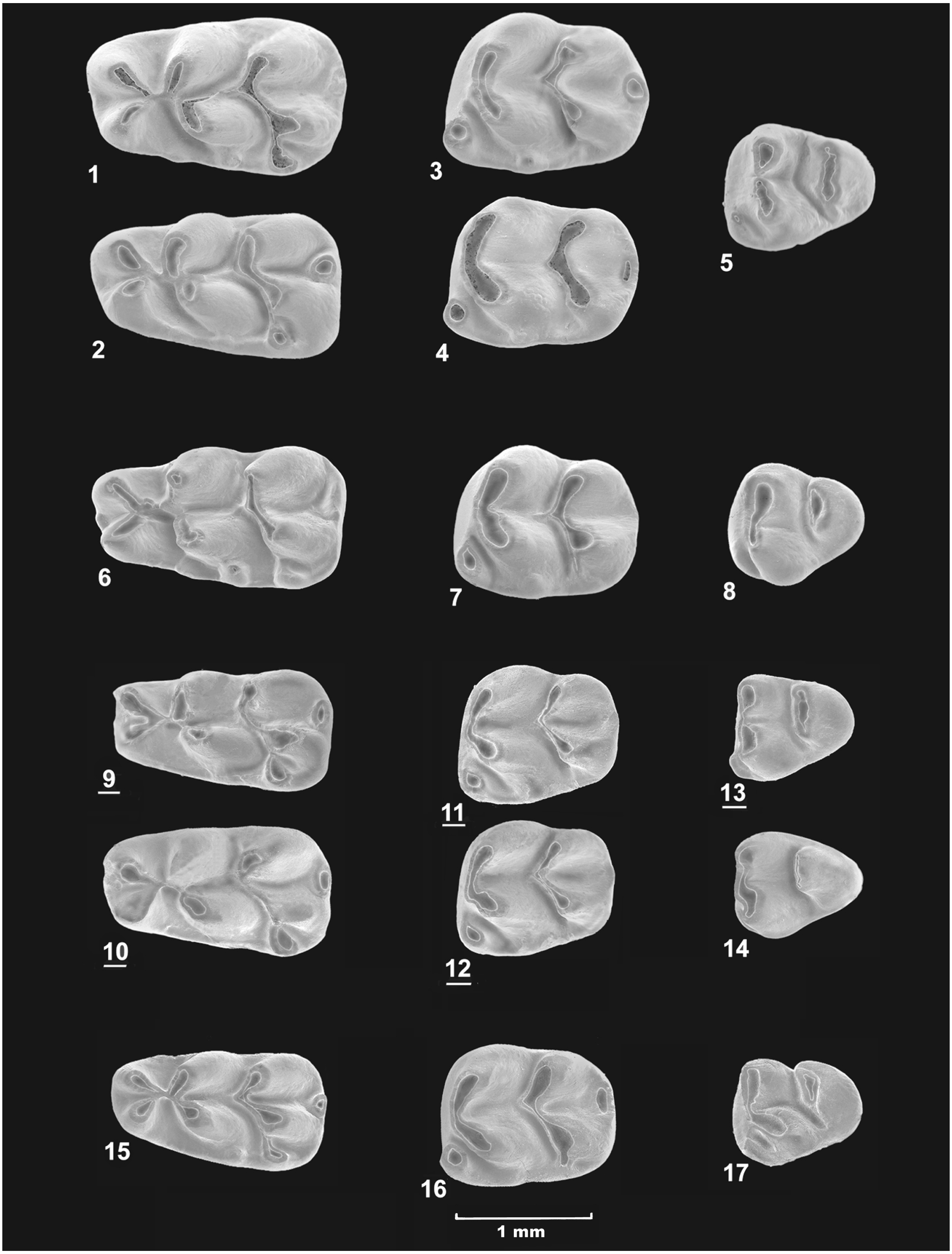

PLATE 6

Occitanomys adroveri (THALER, 1966) from KO1highA. Figs 1, 2: m1, no. 1041, 1044; Figs 3, 4: m2, no. 1051, 1054; Fig. 5: m3, no. 1056.
Occitanomys adroveri (THALER, 1966) from Los Mansuetos (type locality) in the comparative collection of IVAU. Fig. 6: m1; Fig. 7: m2; Fig. 8: m3.
Occitanomys debruijni (SEN *et al*., 1989) from TE2. Figs 9, 10: m1, no. 351, 358; Figs 11, 12: m2, no. 362, 366; Figs 13, 14: m3, no. 371, 374.
Occitanomys debruijni (SEN *et al*., 1989) from Maritsa (type locality) in the comparative collection of IVAU. Fig. 15: m1; Fig. 16: m2; Fig. 17: m3.

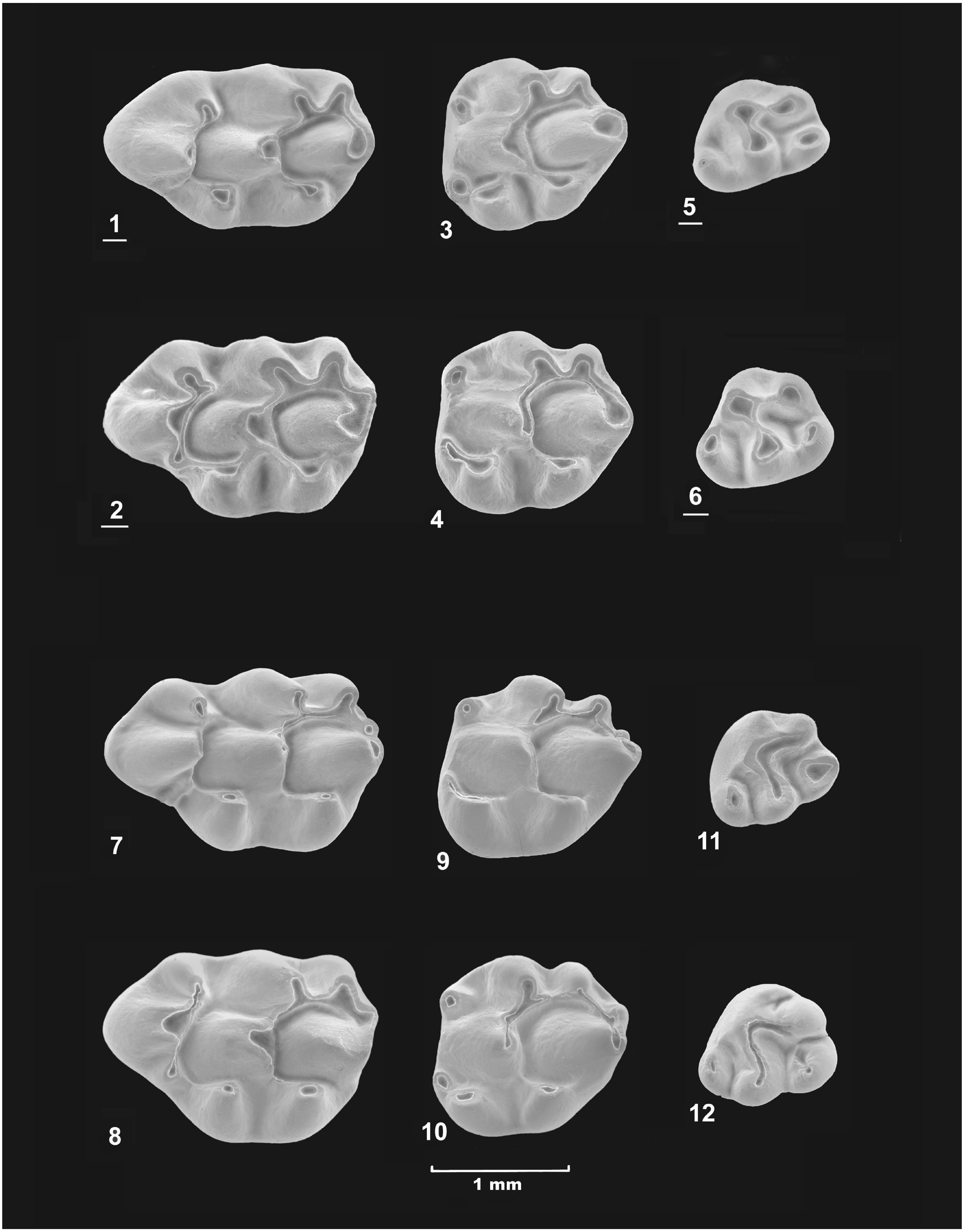

PLATE 7
Occitanomys adroveri (THALER, 1966) from KO1highA. Figs 1, 2: M1, no. 1031, 1033; Figs 3, 4: M2, no. 1035, 1037; Figs 5, 6: M3, no. 1038, 1039. *Occitanomys adroveri* (THALER, 1966) from Los Mansuetos (type locality) in the comparative collection of IVAU. Figs 7, 8: M1; Figs 9, 10: M2; Figs 11, 12: M3.

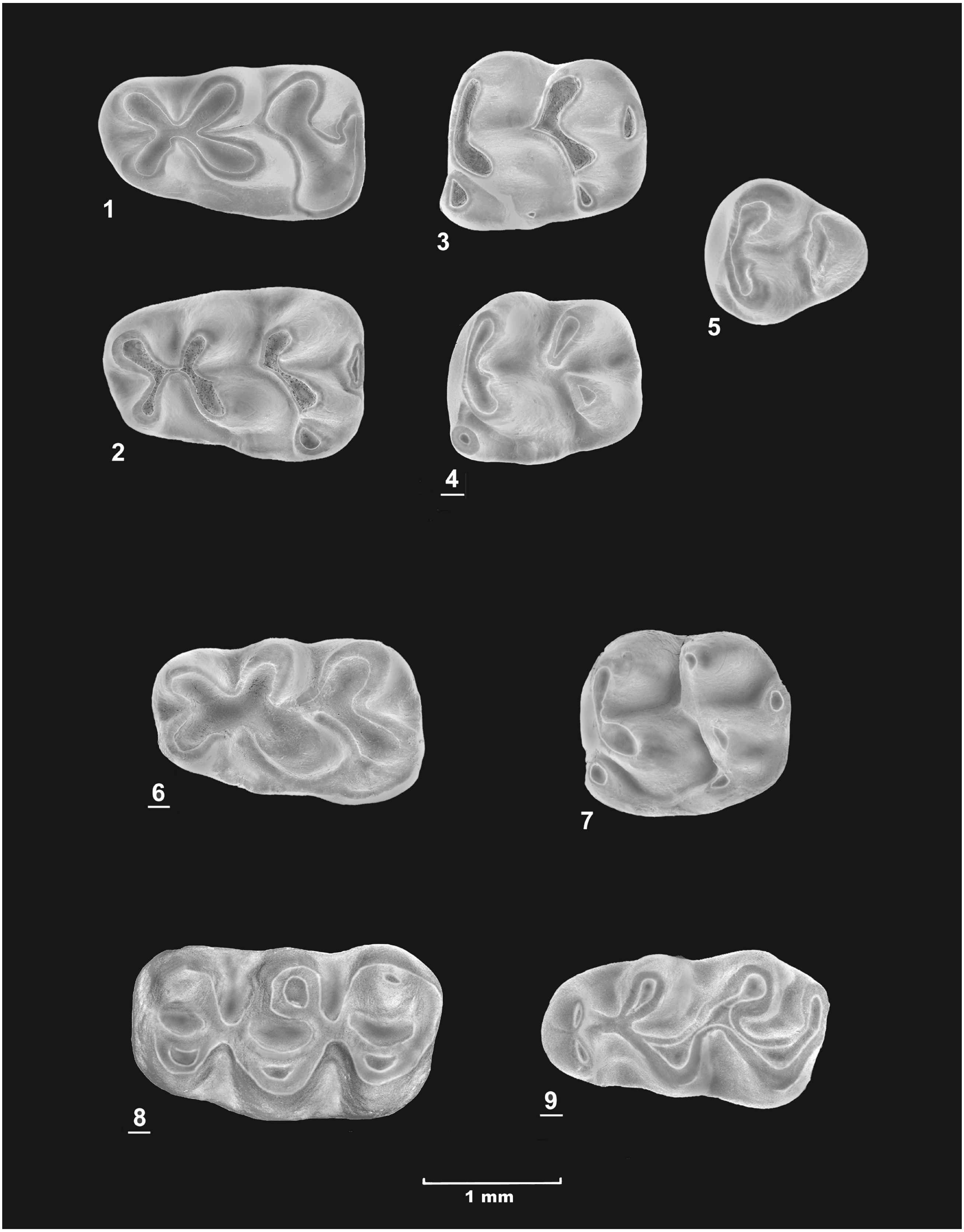

PLATE 8
Occitanomys brailloni MICHAUX 1969 from VOR3a. Figs 1, 2: m1, no. 791, 792; Figs 3, 4: m2, no. 794, 796; Fig. 5: m3, no. 798.
Occitanomys brailloni MICHAUX 1969 from Layna (type locality) in the comparative collection of IVAU. Fig. 6: m1; Fig. 7: m2.
Allocricetus ehiki SCHAUB 1930 from KO1 lowA. Fig. 8: M1, no. 901; Fig. 9: m1, no. 905.

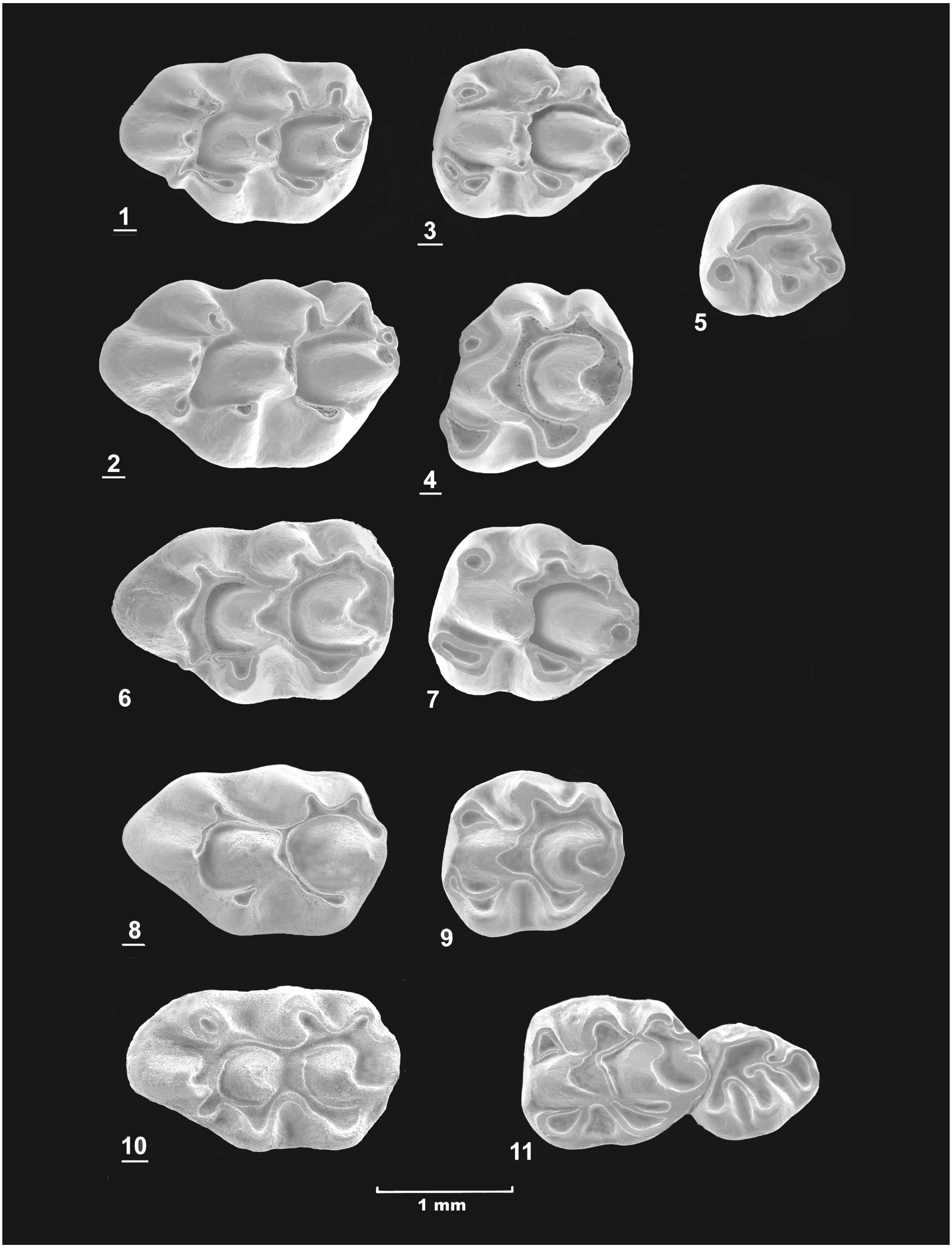

PLATE 9
Occitanomys brailloni MICHAUX 1969 from VOR3. Fig. 2: M1, no. 551 and from VOR3a.
Fig. 1: M1, no. 782; Figs 3, 4: M2, no. 785, 784; Fig. 5: M3, no. 787.
Occitanomys brailloni MICHAUX 1969 from Layna (type locality) in the comparative collection at IVAU. Fig. 6: M1; Fig. 7: M2.
Occitanomys magnus (SEN, 1977) from NO1. Fig. 8: M1, no.101; Fig. 9: M2, no. 105.
Occitanomys magnus (SEN, 1977) from Çalta (type locality) in the comparative collection at IVAU. Fig. 10: M1; Fig. 11: M2-M3.

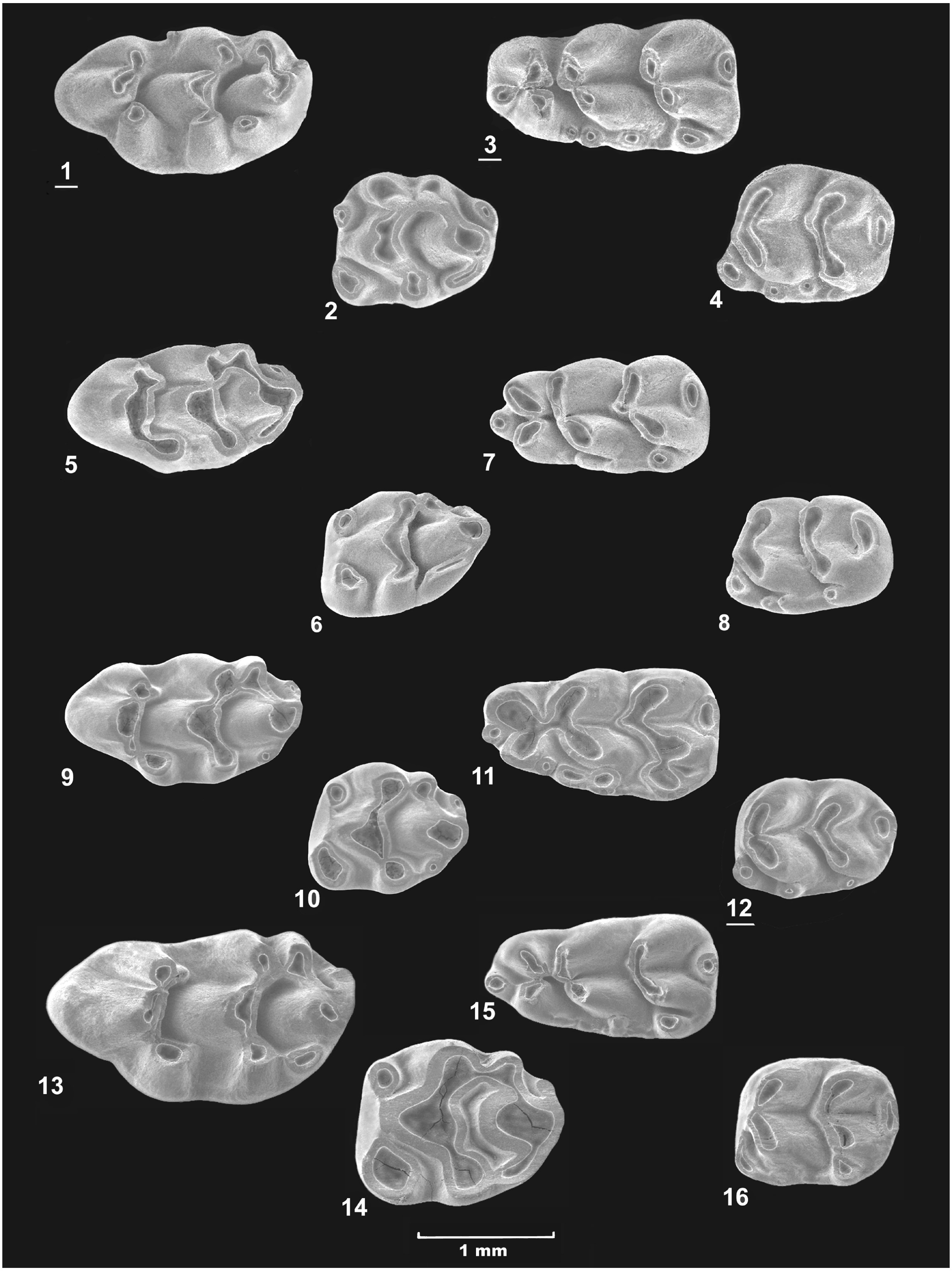

PLATE 10
Apodemus dominans KRETZOI 1959 from NO1. Fig. 1: M1, no. 167; Fig. 2: M2, no. 173; Fig. 3: m1, no. 176; Fig. 4: m2, no. 165.
Apodemus atavus HELLER 1936 from NO1. Fig. 5: M1, no. 131; Fig. 6: M2, no. 141; Fig. 7: m1, no. 152; Fig. 8: m2, no. 158.
Apodemus atavus HELLER 1936 from KO1highB. Fig. 9: M1, no. 502; Fig. 10: M2, no. 512; Fig. 11: m1, no. 532; Fig. 12: m2, no. 546.
Apodemus gorafensis RUIZ BUSTOS *et al*. 1984 from TE2. Fig. 13: M1, no.503; Fig. 14: M2, no. 521; Fig. 15: m1, no. 542; Fig. 16: m2, no. 551.

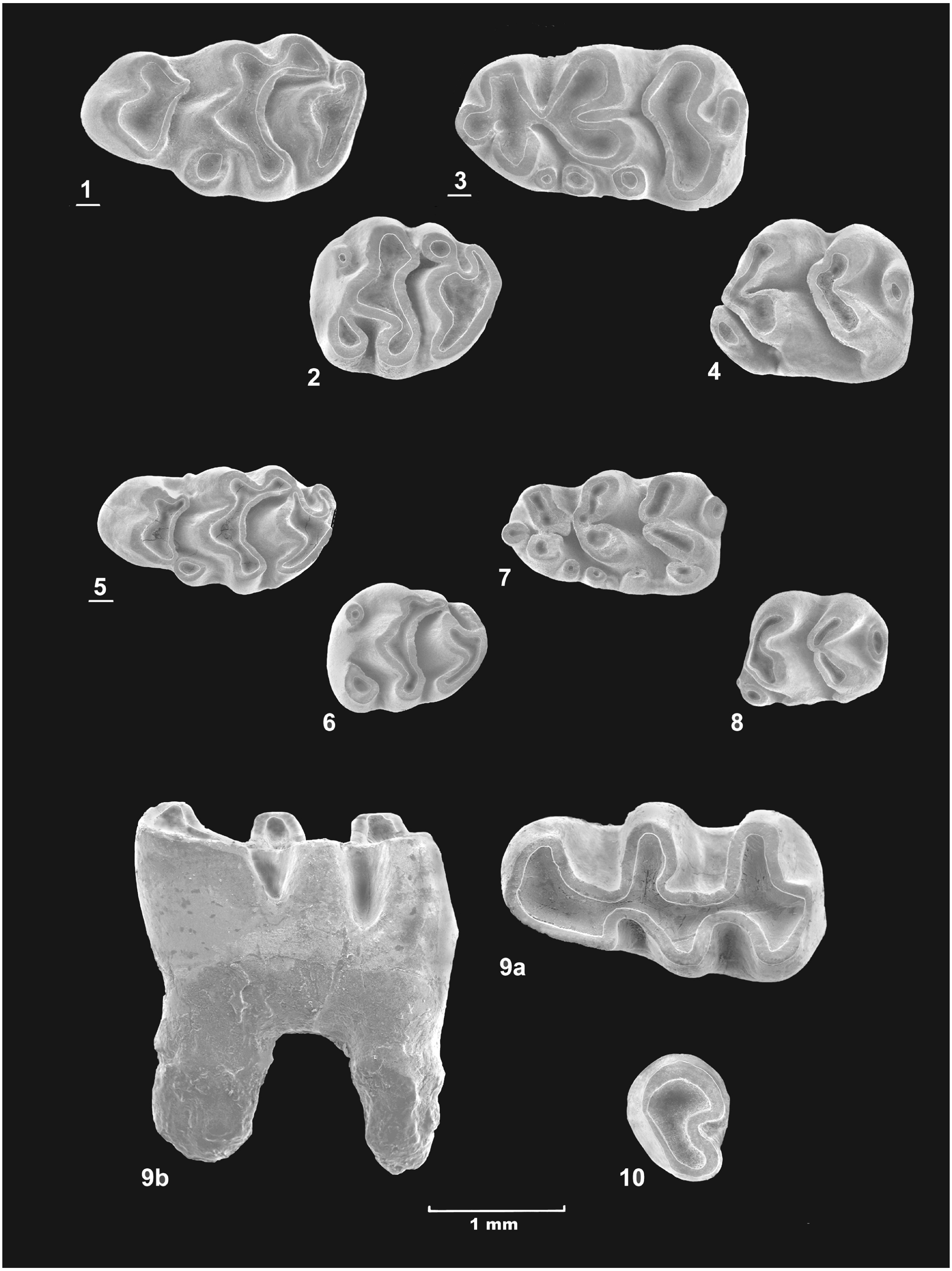

PLATE 11

Rhagapodemus frequens KRETZOI 1959 from NO1. Fig. 1: M1, no. 111; Fig. 2: M2, no. 114; Fig. 3: m1, no. 121; Fig. 4: m2, no. 125.
Rhagapodemus primaevus (HUEGUENEY & MEIN, 1965) from KO1highB. Fig. 5: M1, no. 611; Fig. 6: M2, no. 621; Fig. 7: m1, no. 635; Fig. 8: m2, no. 641.
Pseudomeriones sp. from TE1. Fig. 9: m1 (labial view), no. 571; Fig. 9a: same m1 as Fig. 9 (occlusal view).
Psuedomeriones sp. from TE2. Fig. 10: M3, no. 381.

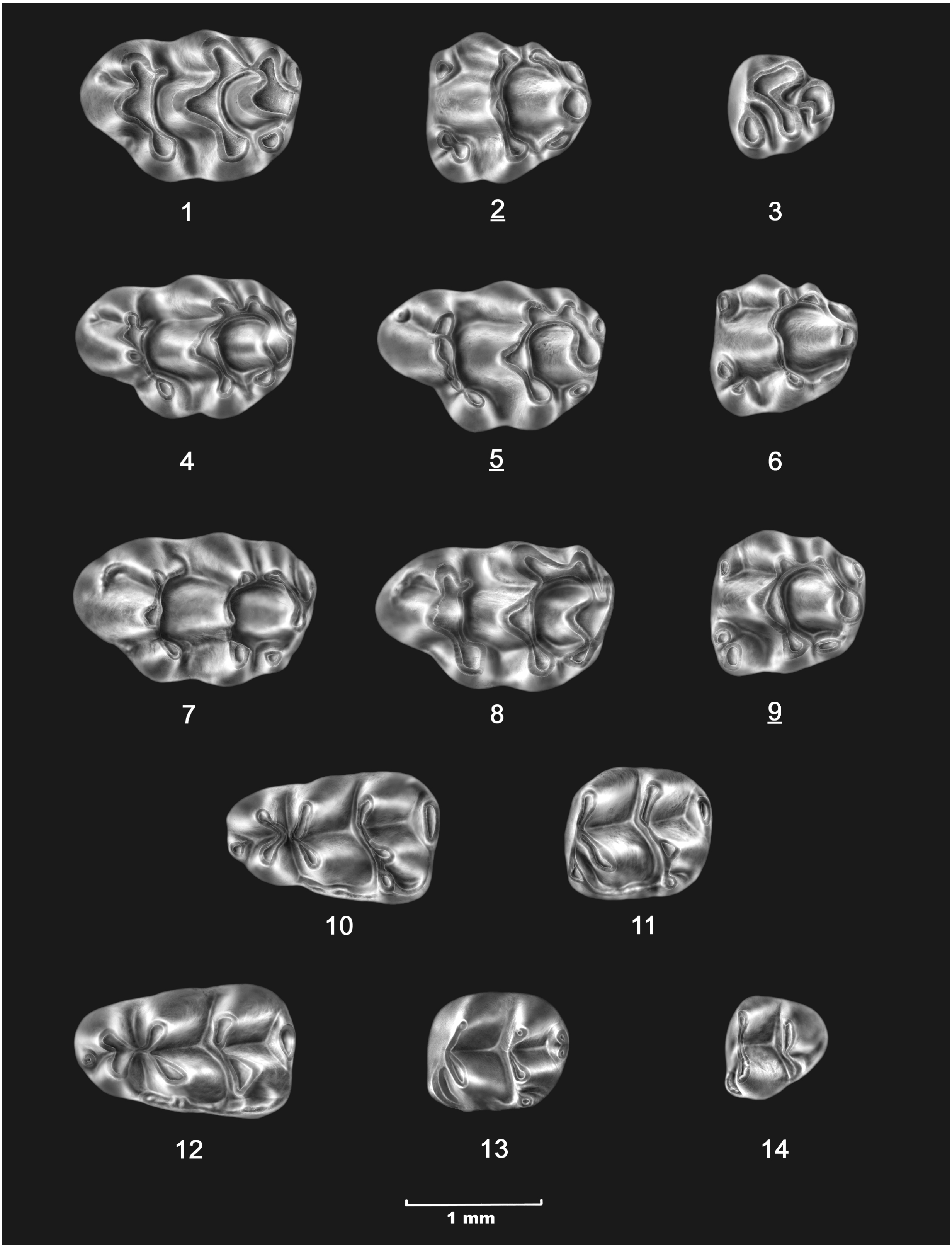

PLATE 12

Micromys bendai Van De Weerd 1979 from TE3. Fig. 1: M1, no.107; Fig. 3: M3, no. 151; Fig. 10: m1, no. 173 ; Fig. 11: m2, no. 193.
Micromys bendai Van De Weerd 1979 from VOR3a. Fig. 2: M2, no.187.
Micromys bendai Van De Weerd 1979 from VOR1. Figs 4, 5: M1, no. 101, 102.
Micromys bendai Van De Weerd 1979 from TE2. Fig. 6: M2, no. 142; Figs 7, 8: M1, no. 103, 104; Fig. 12: m1, no. 191.
Micromys bendai Van De Weerd 1979 from TE1. Fig. 9: M2, no. 289; Fig. 13: m2, no. 318; Fig. 14: m3, no.330.

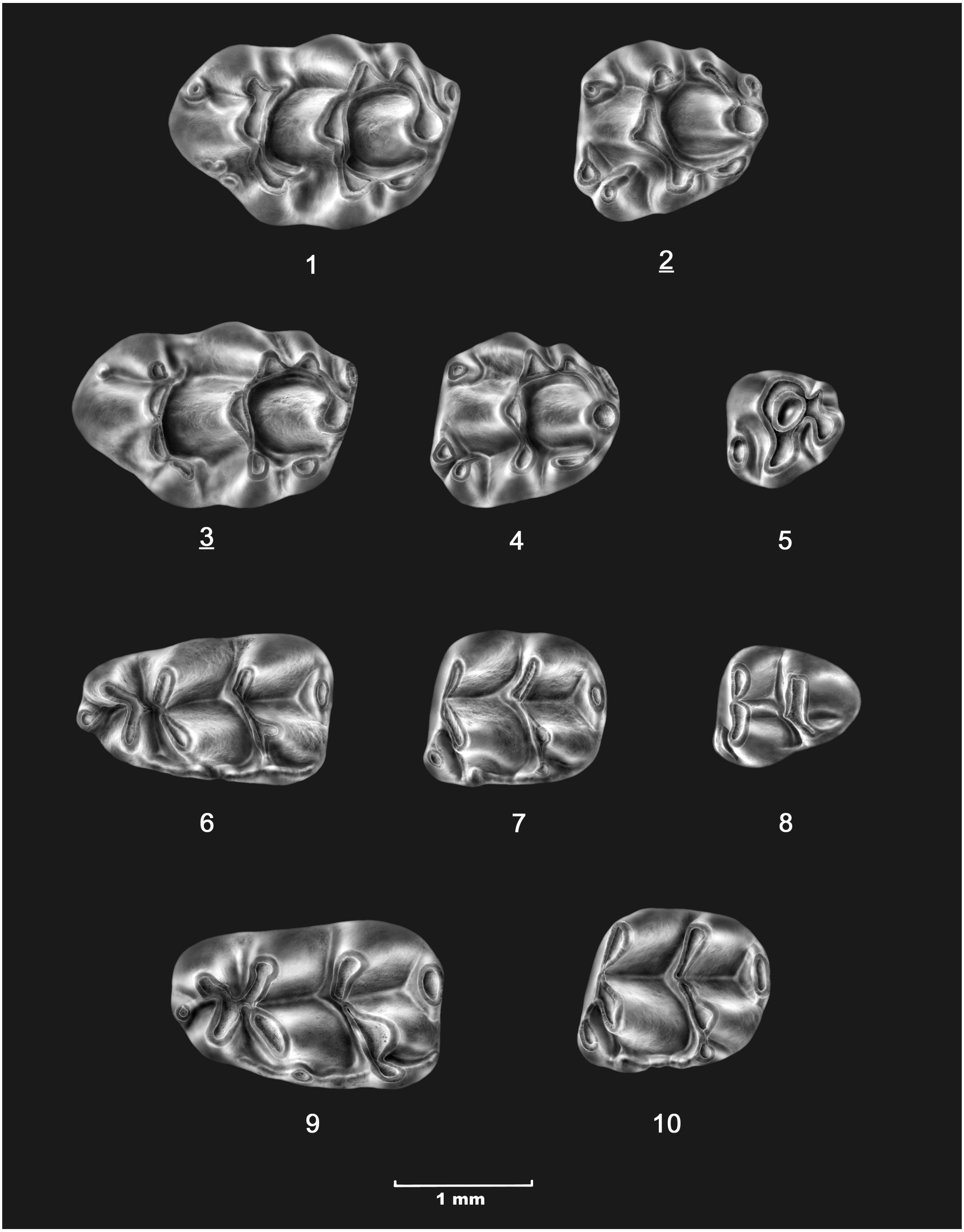

PLATE 13
Micromys steffensi Van De Weerd 1979 from KO1highB. Figs 1, 3: M1, no. 111, 128.
Micromys steffensi Van De Weerd 1979 from KO1lowA. Figs 2, 4: M2, no. 400, 393; Fig. 5: M3, no. 444; Figs 6, 9: m1, no. 484, 488; Figs 7, 10: m2, no. 530, 526; Fig. 8: m3, no. 598.

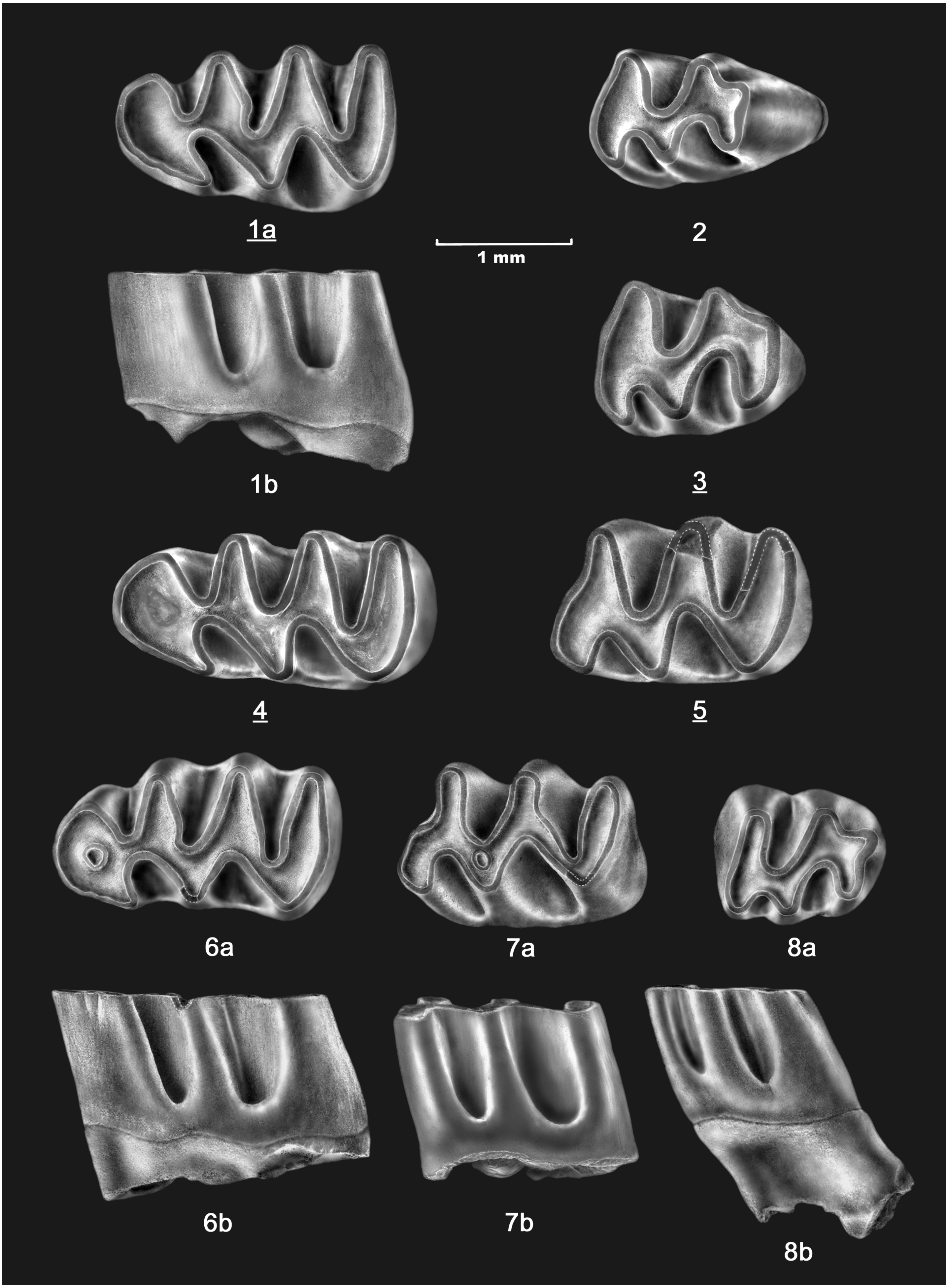

PLATE 14

Microtodon komanensis n. sp. from KO1lowA. Figs 1a-b: m1 (holotype), no. 147, 6a-b: m1, no. 141; Figs 2, 3, 8a-b: m3, no. 162, 168, 161; Fig. 5: m2, no. 156.
Microtodon komanensis n. sp. from KO1highA. Fig. 4: m1, no. 136; Figs 7a-b: m2, no.141.

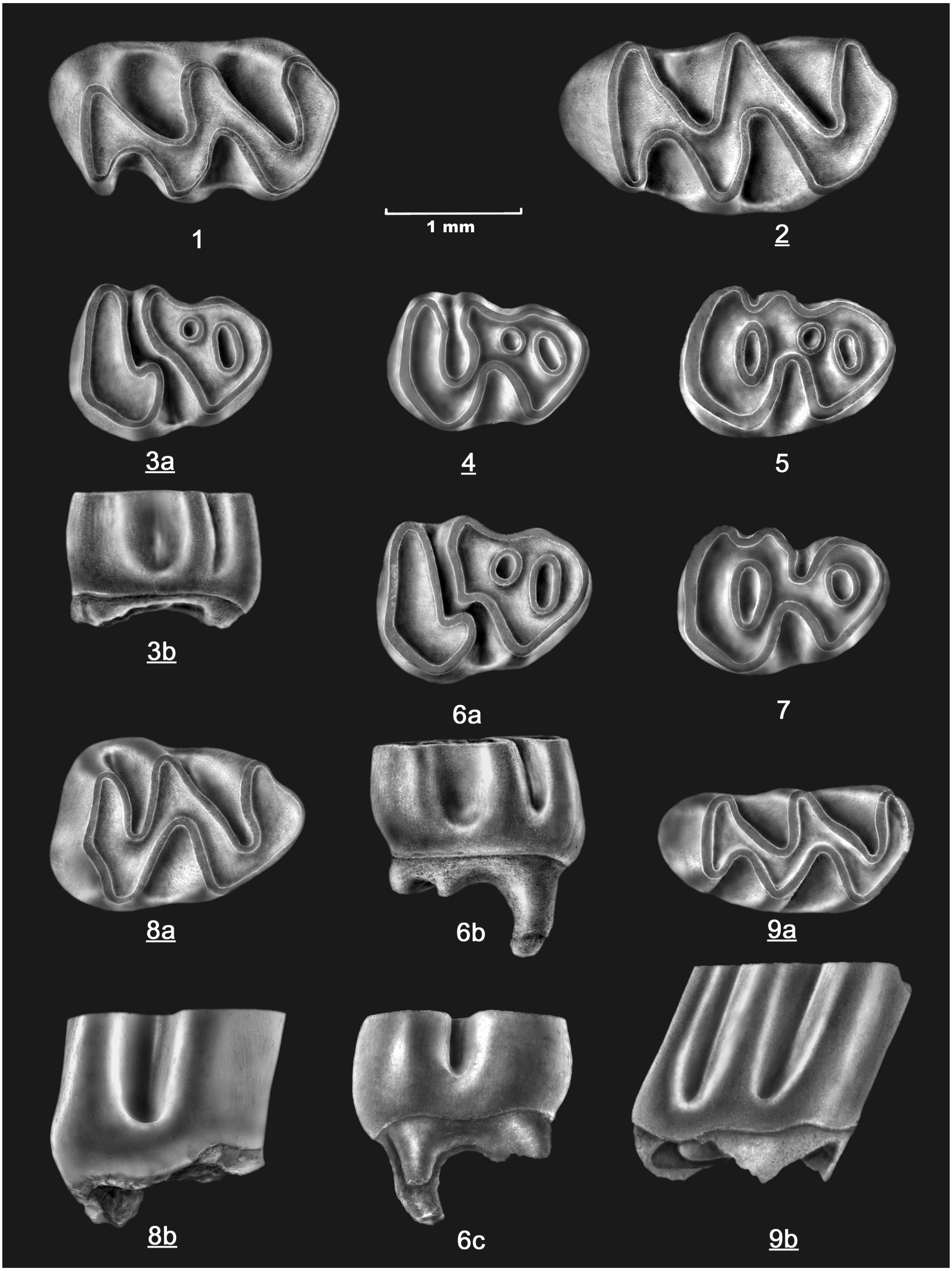

PLATE 15

Microtodon komanensis n. sp. from KO1highA. Fig. 1: M1, no. 101; Figs 8a-b: M2, no. 116.

Microtodon komanensis n. sp. from KO1lowA. Fig. 2: M1, no. 106; Figs 3a-b: M3 (occlusal and labial view), no. 138: Figs 4, 5: M3, no. 137, 134; Figs 6a-c: M3 (occlusal, labial & lingual view), no. 132; Fig. 7: M3, no. 133.

Microtodon sp. from KO1lowA. Figs 9a, b: M1 (occlusal & labial view), no. 116.

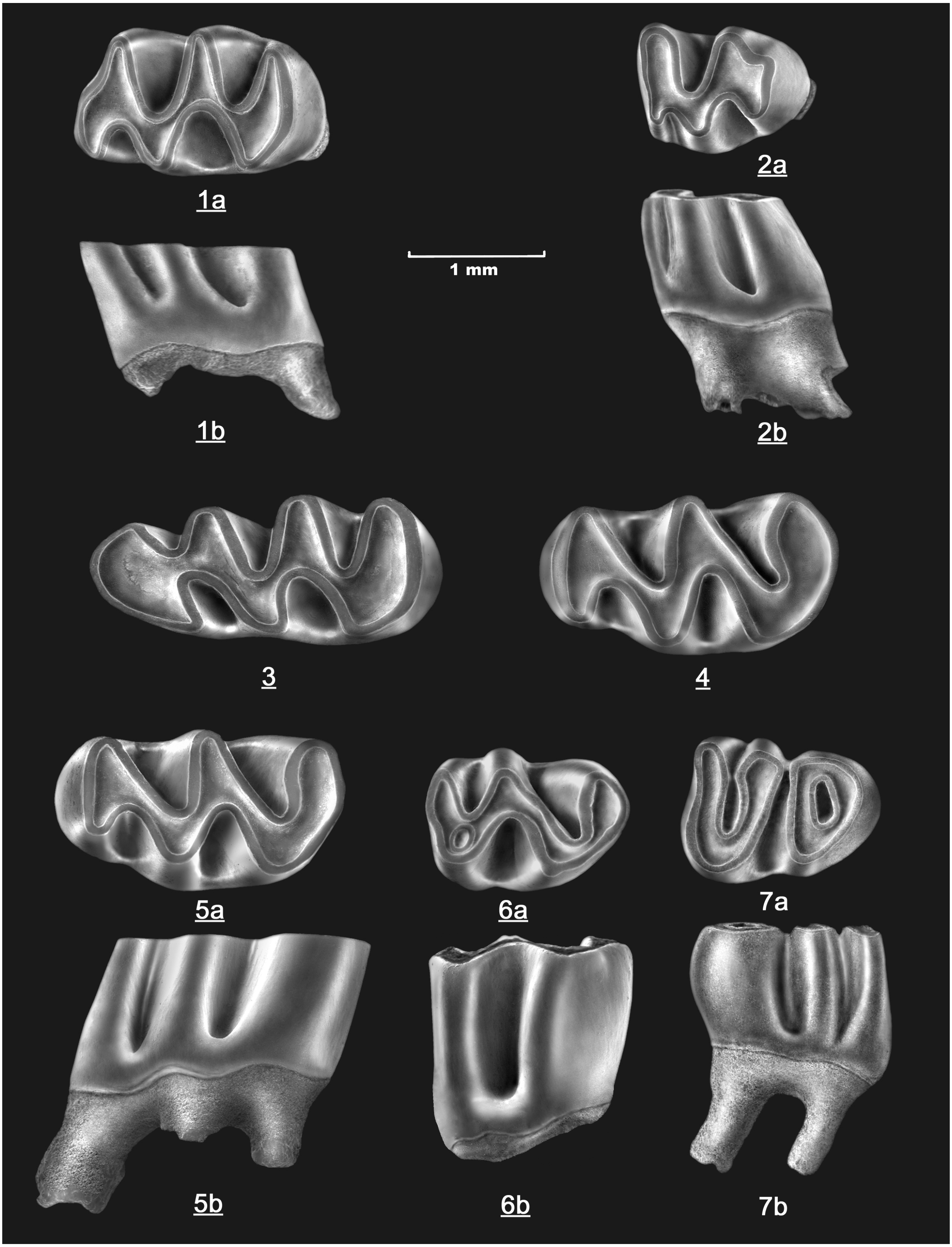

PLATE 16

Microtodon aff. *komanensis* n. sp. from VOR3a. Figs 1a-b: m2 (occlusal & labial view), no. 546; Figs 2a-b: m3 (occlusal & lingual view), no. 556; Fig. 3: m1, no. 536; Fig. 4: M1, no. 506; Figs 5a-b: M1 (occlusal & lingual view), no. 507; Figs 6a-b: M2 (occlusal & lingual view), no. 516; Figs 7a-b: M3 (occlusal & labial view), no.521.

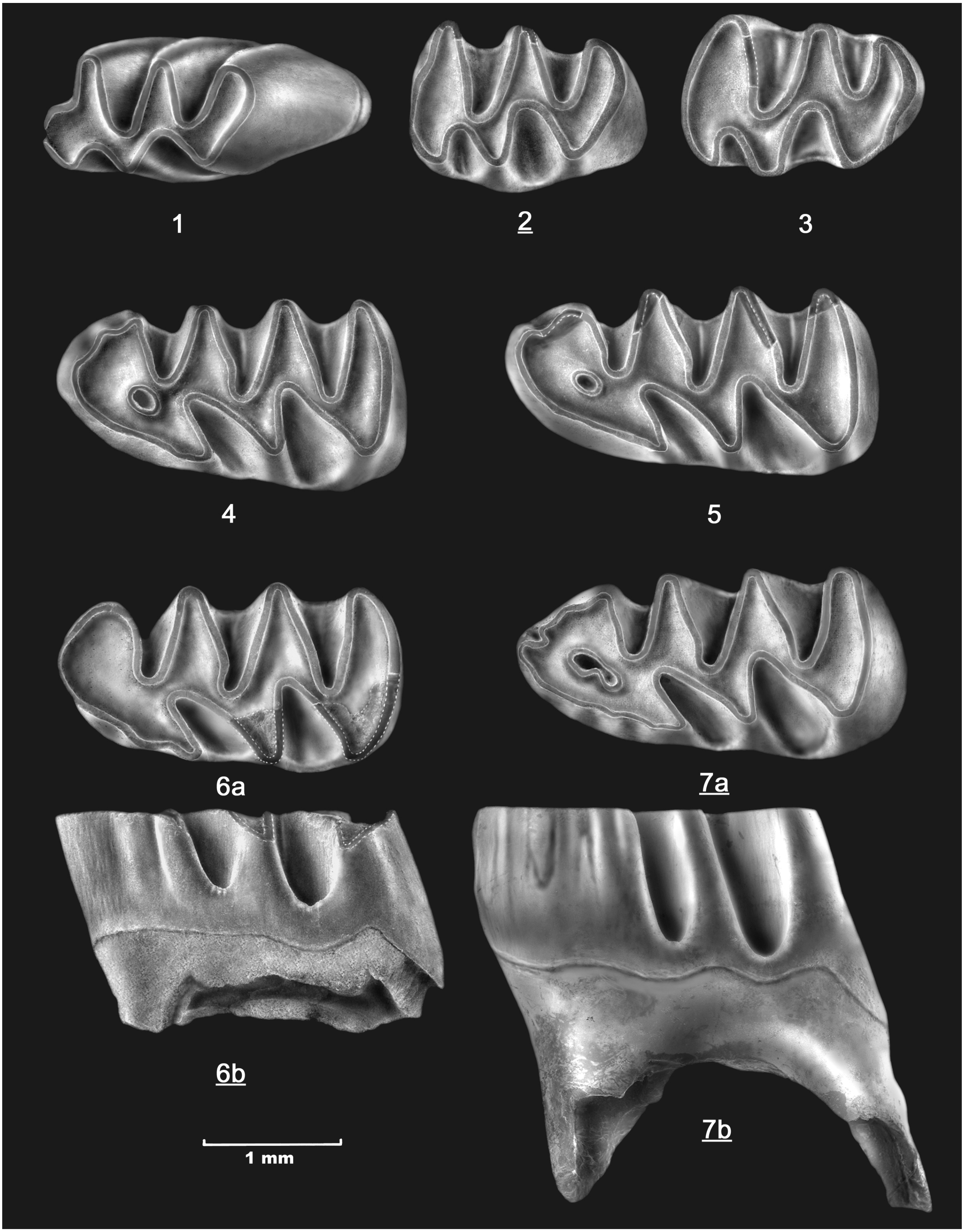

PLATE 17

Promimomys cor KRETZOI 1955 from KO1highA. Figs 1, 2: m3, no. 211, 217.

Promimomys cor KRETZOI 1955 from VOR1. Fig. 3: m3, no. 361; Figs 4, 5: m1, no. 336, 331; Figs 7a-b: m1 (occlusal & labial view), no. 331.

Promimomys cor KRETZOI 1955 from KO1low B. Figs 6a-b: m1 (occlusal & labial view), no. 131.

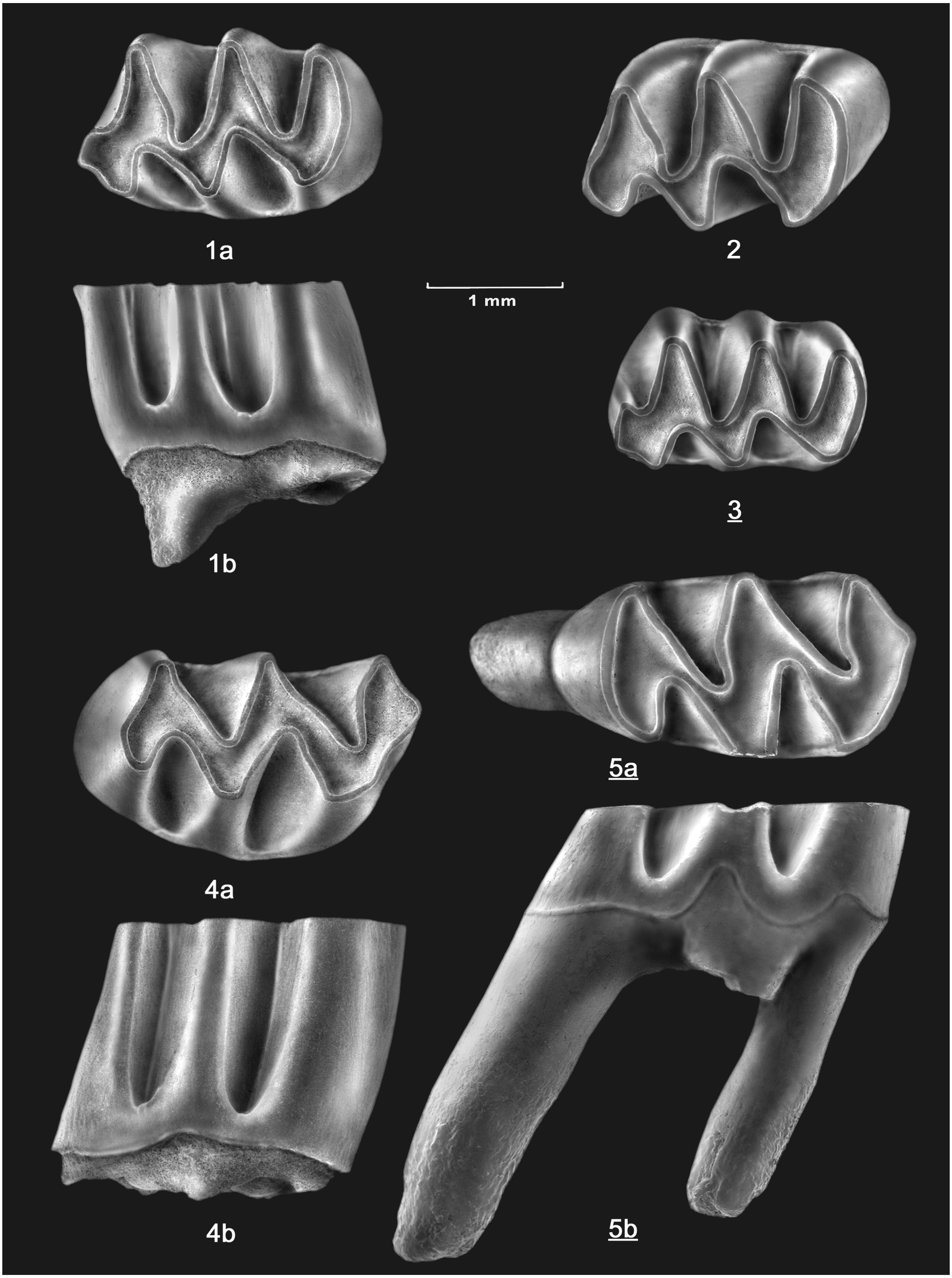

PLATE 18

Promimomys cor Kretzoi 1955 from KO1lowB. Figs 1a-b: m2 (occlusal & labial view), no. 141; Figs 4a-b: M1 (occlusal & lingual view), no. 101.
Promimomys cor Kretzoi 1955 from KO1highA. Fig. 2: m2, no. 202.
Promimomys cor Kretzoi 1955 from VOR1. Fig. 3: m2, no. 352; Figs 5a-b: M1 (occlusal & lingual view), no. 306.

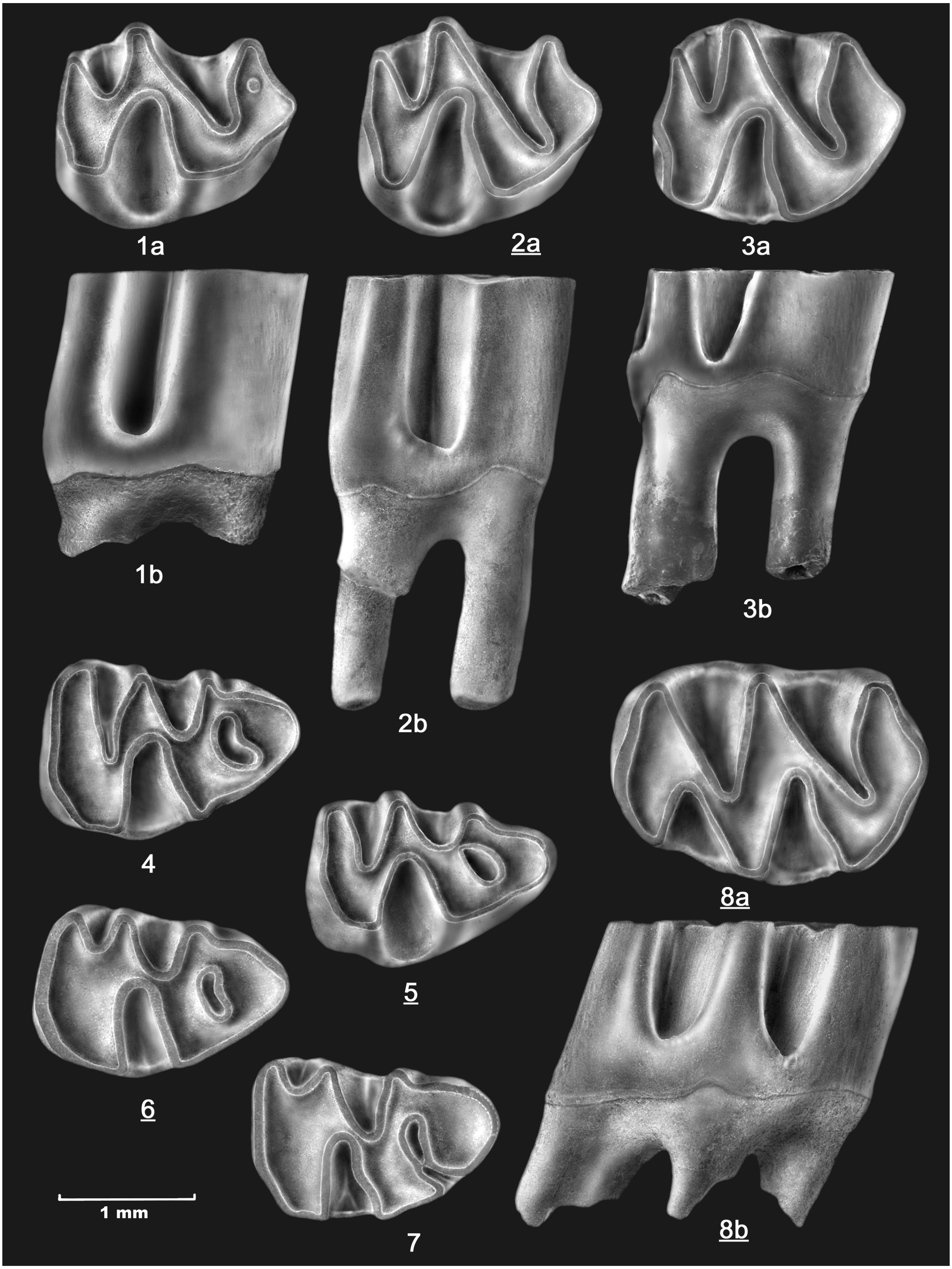

PLATE 19

Promimomys cor KRETZOI 1955 from KO1lowB. Figs 1a-b, 2a-b: M2 (occlusal & lingual view), no. 114, 117; Figs 4, 6: M3, no. 121, 128; Figs 8a-b: M1 (occlusal & lingual view), no. 106.
Promimomys cor KRETZOI 1955 from VOR1. Figs 3a-b: M2 (occlusal & lingual view), no. 313; Fig. 7: M3, no.322.
Promimomys cor KRETZOI 1955 from KO1highA. Fig. 5: M3, no. 187.

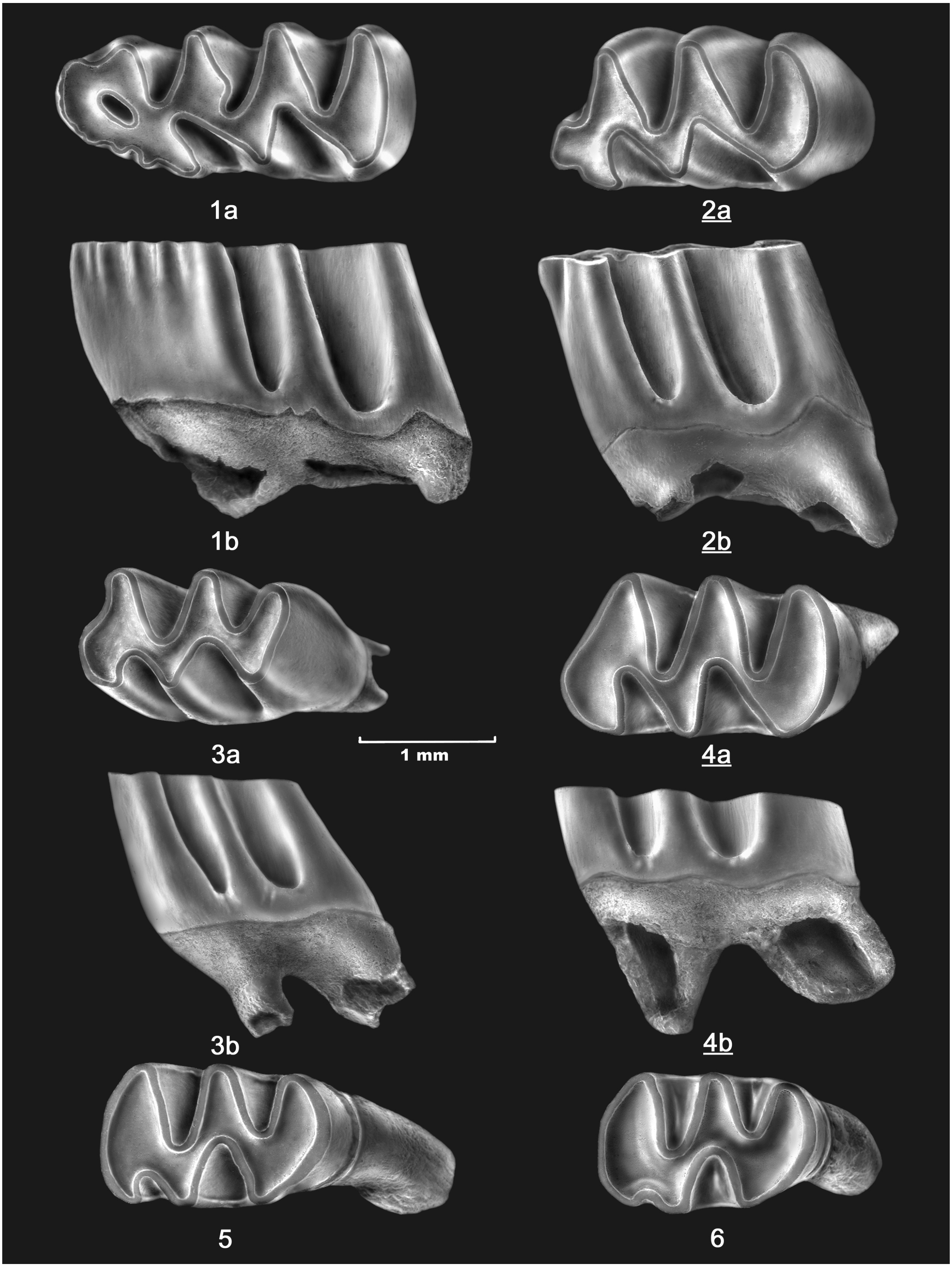

PLATE 20

Mimomys aff. *davakosi* Van De Weerd 1979 from TE3. Figs 1a-b: m1 (occlusal & labial view), no. 341; Figs 2a-b, 4a-b: m2 (occlusal & labial view), no. 366, 367; Figs 3a-b: m3 (lingual & labial view), no. 374; Figs 5, 6: m3, no. 371, 373.

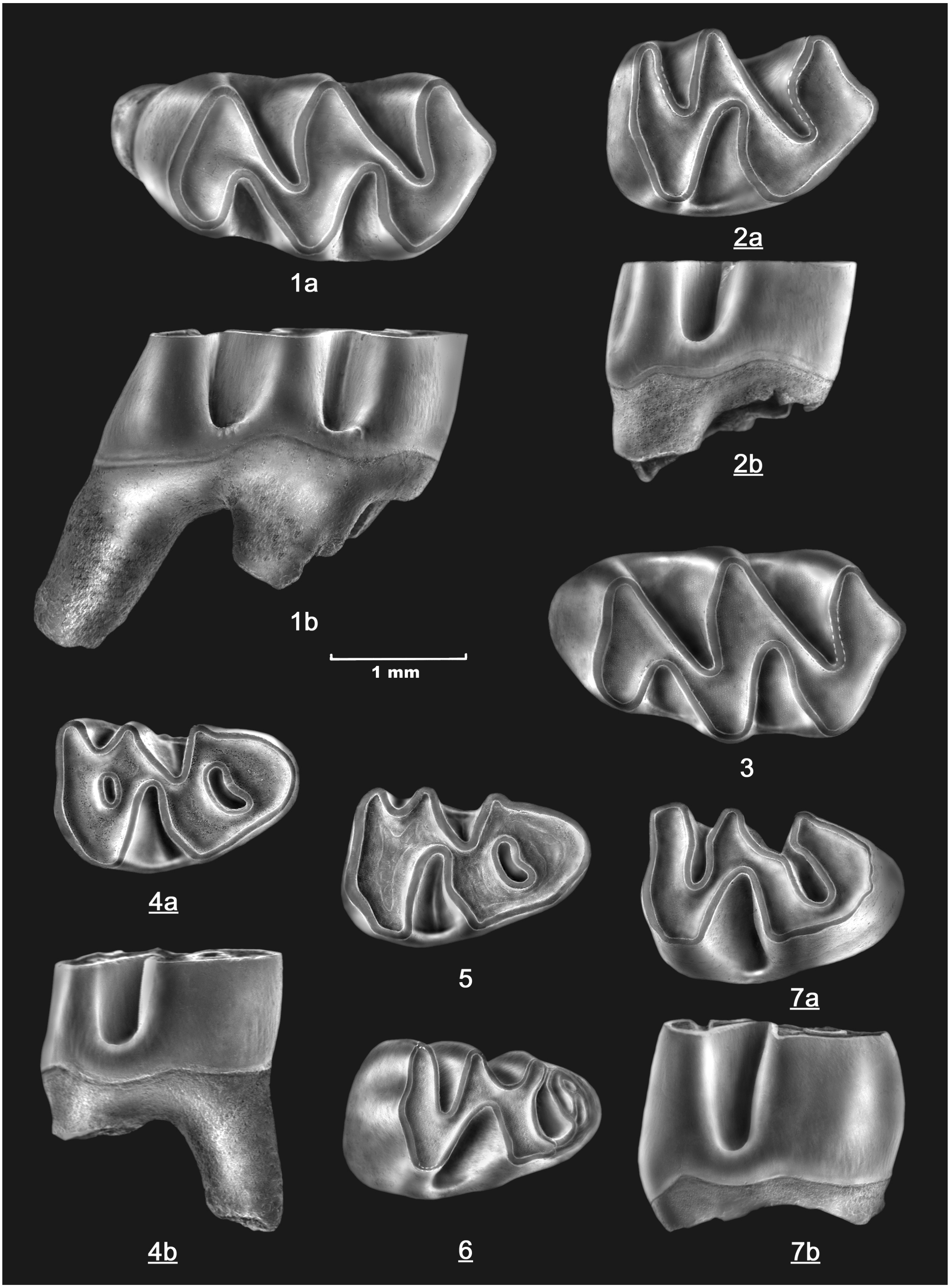

PLATE 21

Mimomys aff. *davakosi* VAN DE WEERD 1979 from TE3. Figs 1a-b, 3: M1 (occlusal & lingual view), no. 301; Fig. 3: M1, no. 303; Figs 2a-b: M2 (occlusal & lingual view), no. 317; Figs 4a-b M3 (occlusal & lingual view), no. 337; Figs 5, 6: M3, no. 321, 332; Figs 7a-b: M3 (occlusal & lingual view), no.331.

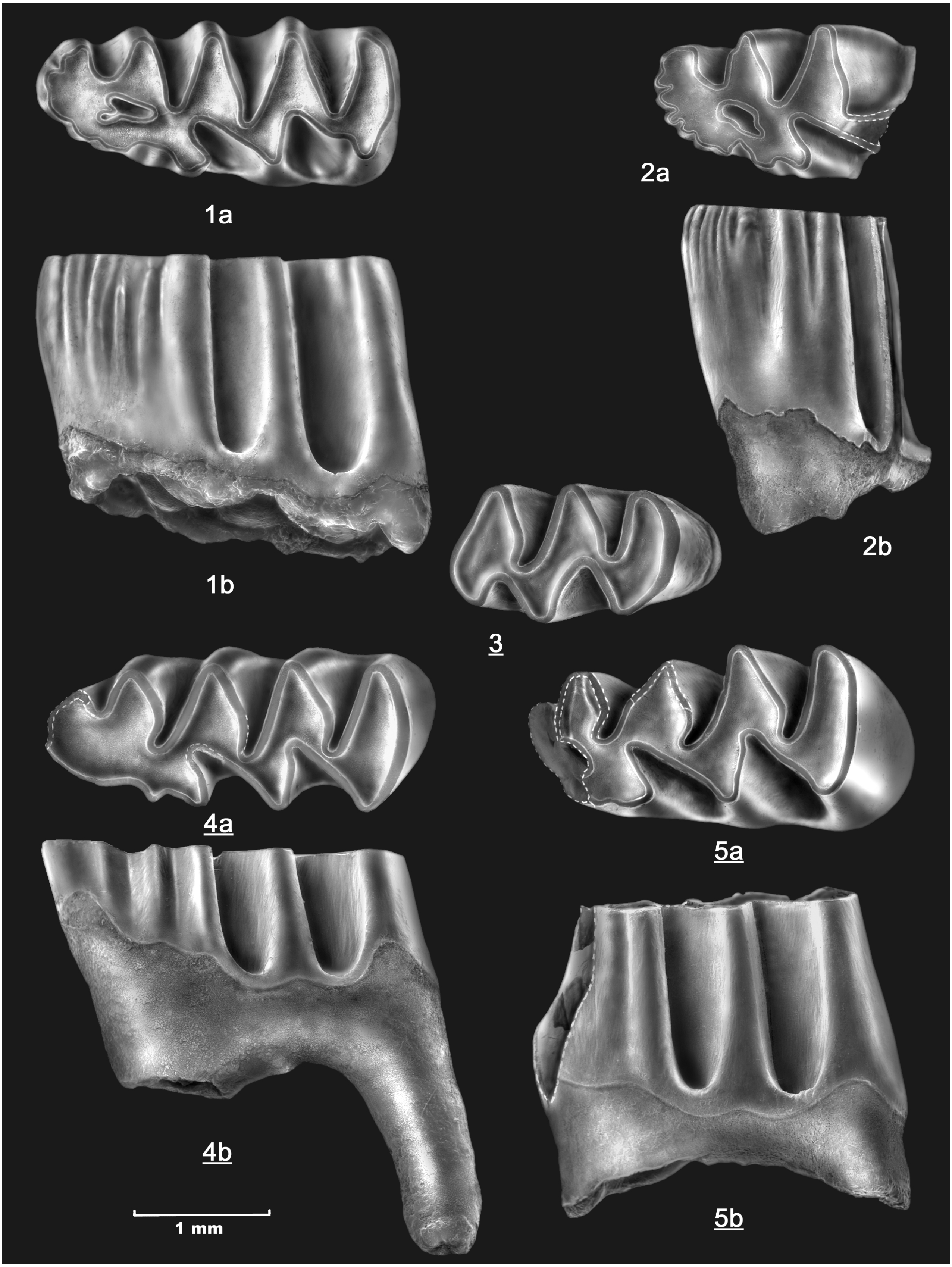

PLATE 22
Mimomys davakosi Van De Weerd 1979 from VOR3. Figs 1a-b, 4a-b: m1 (occlusal & labial view), no. 321, 326.
Mimomys davakosi Van De Weerd 1979 from KO2. Figs 2a-b, 5a-b: m1 (occlusal & labial view), no. 336, 341; Fig. 3: m3, no. 367.

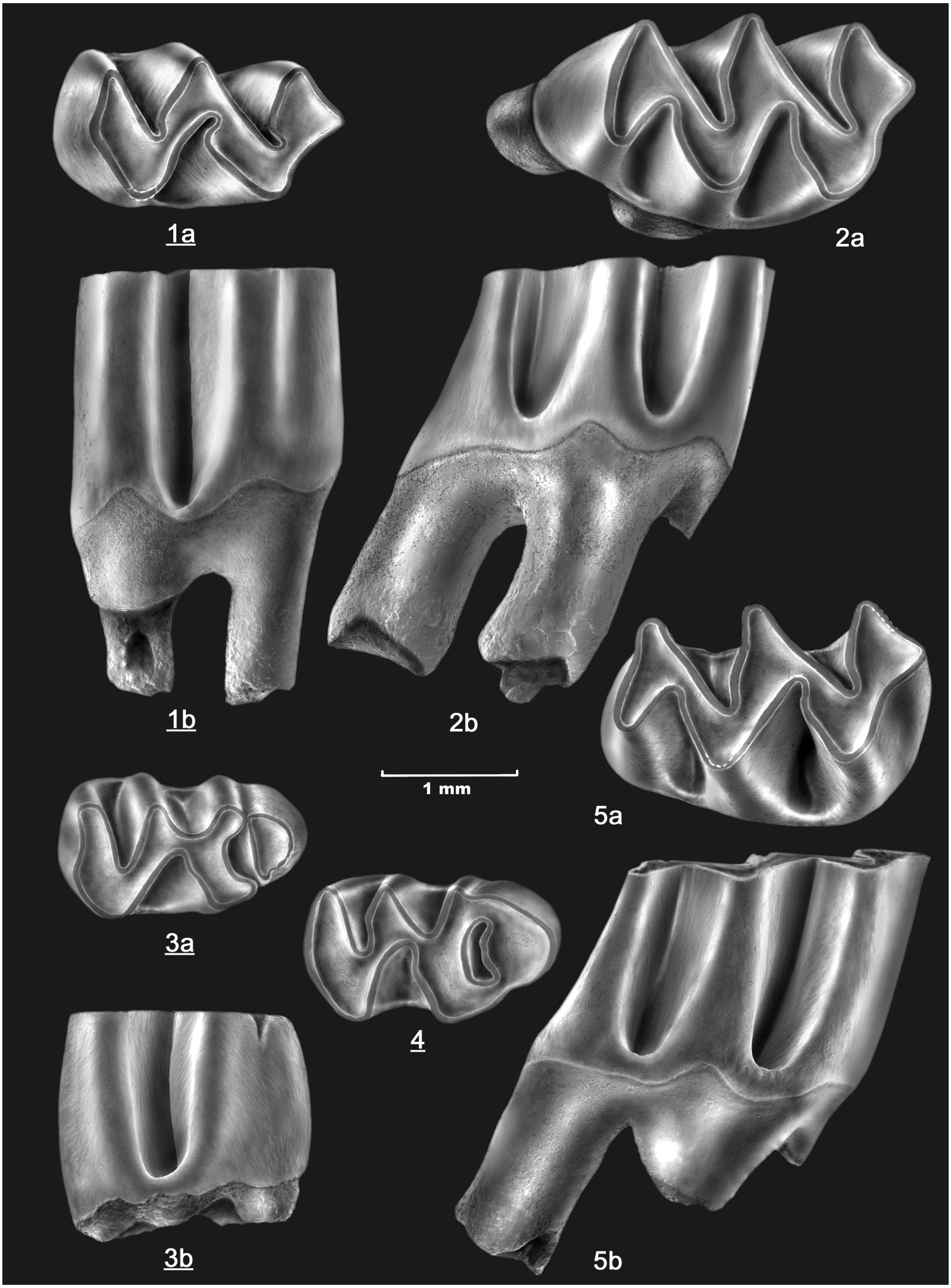

PLATE 23

Mimomys davakosi VAN DE WEERD 1979 from VOR3. Figs 1a-b: M2 (occlusal & lingual view), no. 316;
Figs 2a-b: M1 (occlusal & lingual view), no. 301.
Mimomys davakosi VAN DE WEERD 1979 from KO2. Figs 3a-b: M3 (occlusal & lingual view), no. 328;
Fig. 4: M3, no. 326; Figs 5a-b: M1 (occlusal & lingual view), no. 302.

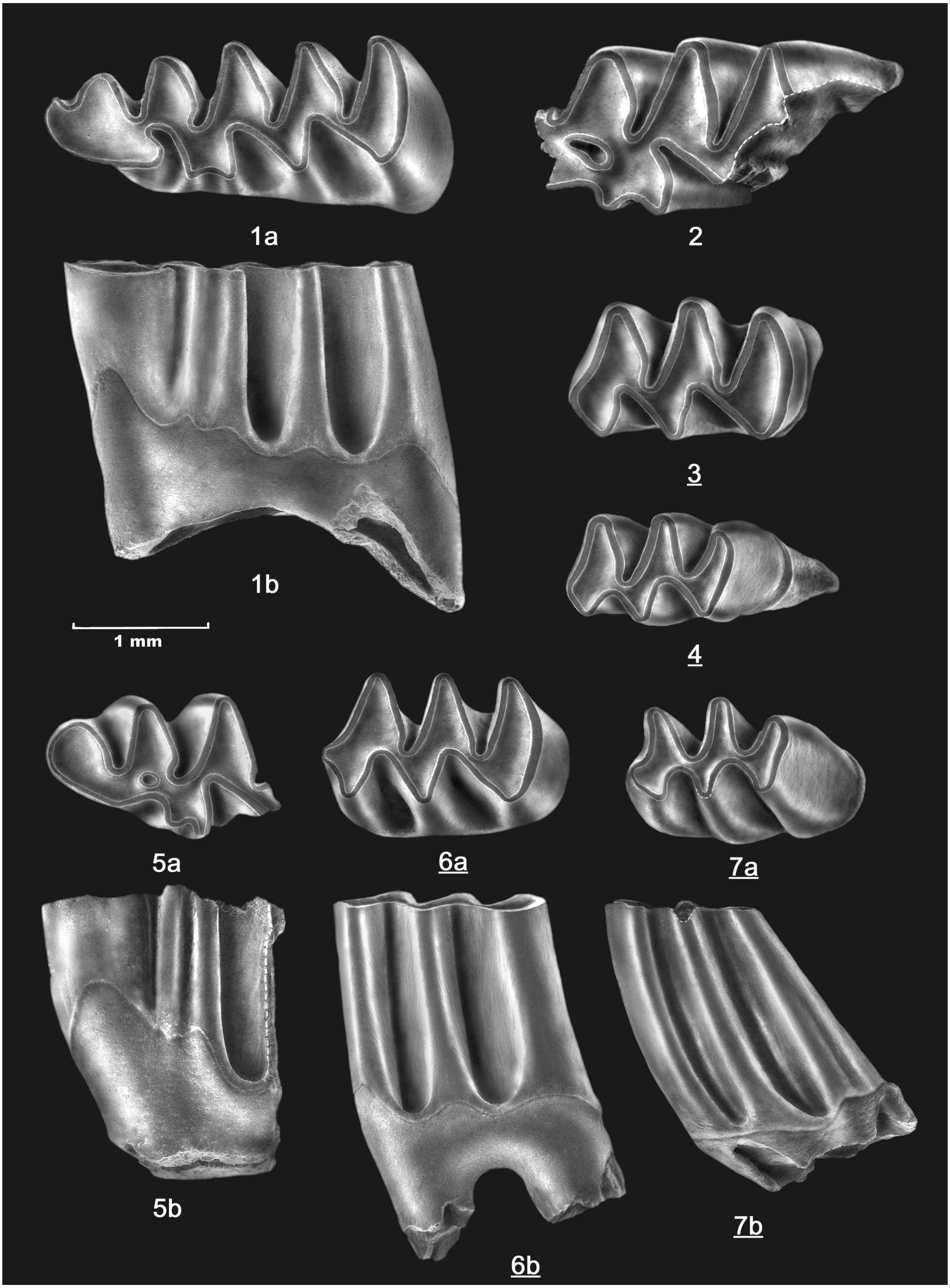

PLATE 24
Propliomys hungaricus (Kormos, 1934) from NO1. Figs 1a-b, 5a-b: m1 (occlusal & labial view), no. 501, 505; Fig. 3: m2, no. 523; Figs 6a-b: m2 (occlusal & labial view), no. 524; Fig. 4: m3, no. 532; Figs 7a-b: m3 (occlusal & labial view), no. 531.
Dolomys cf. *nehringi* Kretzoi 1959 from NO1. Fig. 2: fragment of m1, no. 511.

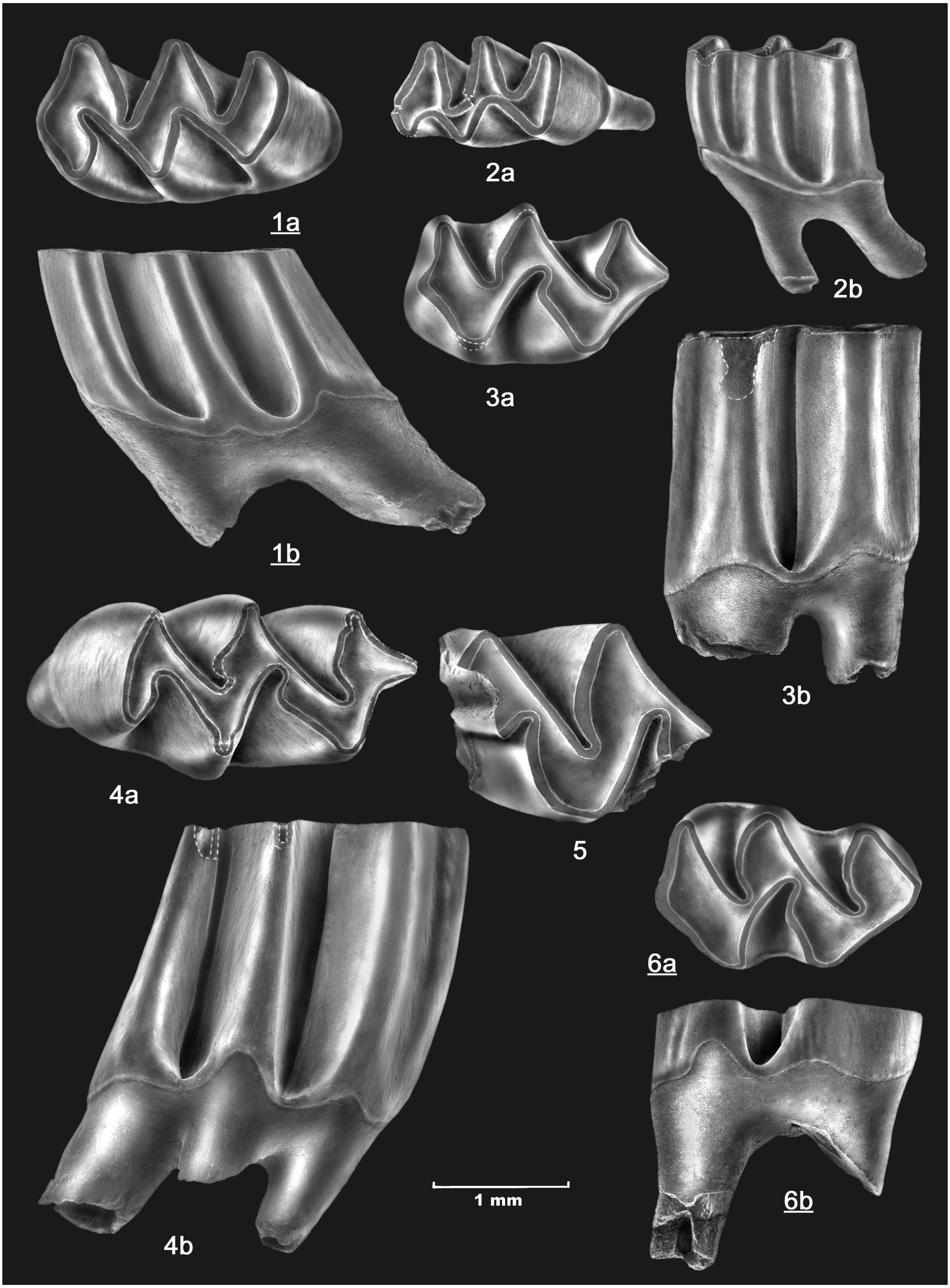

PLATE 25

Dolomys cf. *nehringi* KRETZOI 1959 from NO1. Fig. 1a-b: m3 (occlusal & labial view), no. 543; Fig. 5: fragment of M1, no. 556.
Propliomys hungaricus (KORMOS, 1934) from NO1. Figs 2a-b: m3 (occlusal & labial view), no. 538; Figs 4a & b: M1 (occlusal & lingual view), no. 551; Figs 3a-b, 6a-b: M2 (occlusal & lingual view), no. 561, 566.

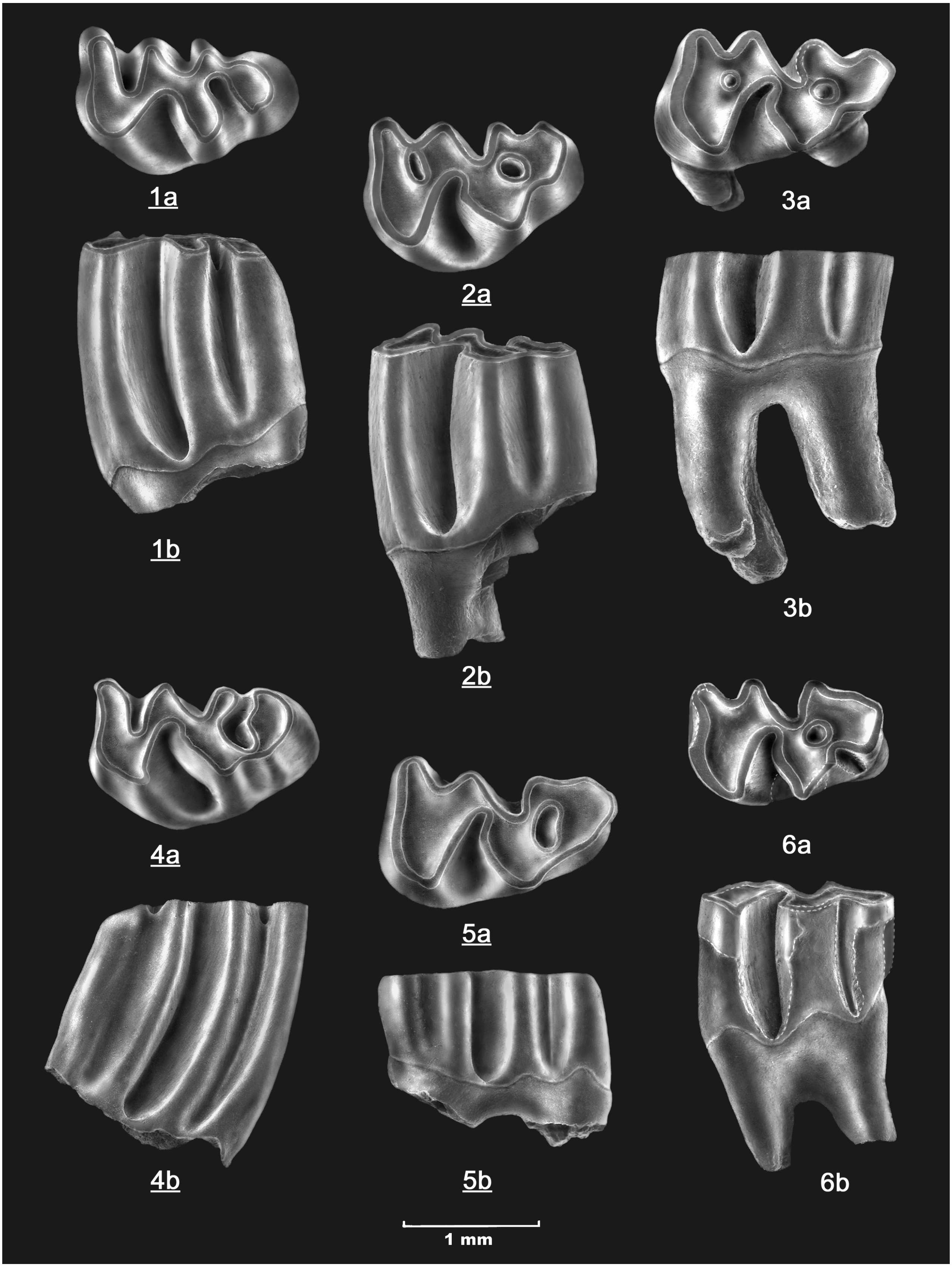

PLATE 26
Propliomys hungaricus (KORMOS, 1934) from NO1. Figs 1a-b, 2a-b, 3a-b, 4a-b, 5a-b, 6a-b:
M3 (occlusal & lingual view), no. 579, 578, 572, 577, 584, 587.

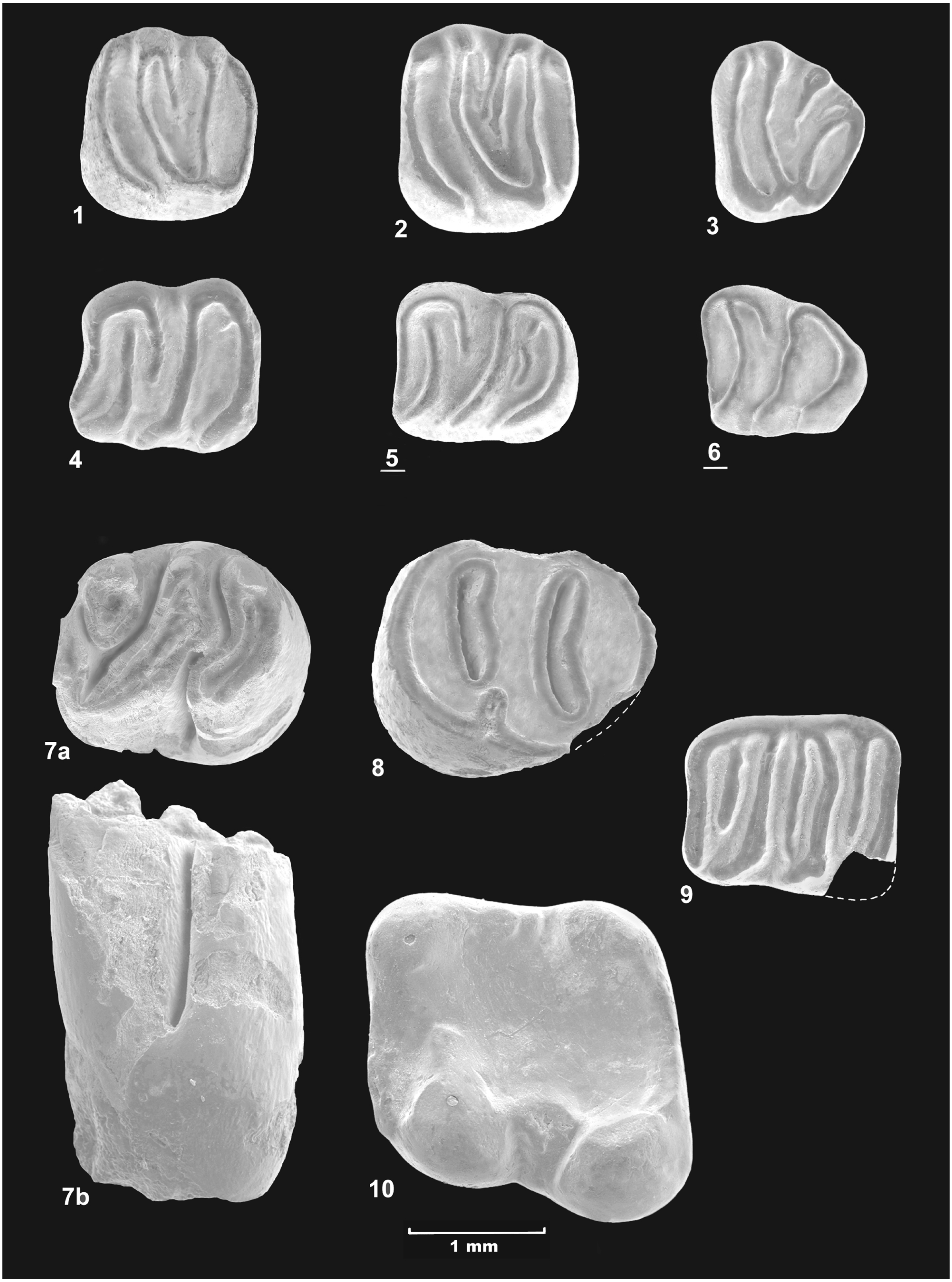

PLATE 27

Myomimus aff. *maritsensis* De Bruijn, Dawson & Mein 1970 from NO1. Fig. 1: M1, no. 181; Fig. 2: M2, no. 182; Fig. 3: M3, no. 183; Fig. 4: m1, no. 188; Fig. 5: m2, no. 189; Fig. 6: m3, no. 190.
Prospalax priscus (Nehring, 1897) from NO1. Figs 7a-b: m2 (occlusal & labial view), no. 203; Fig 8: M1, no. 201.
Glis minor Kowalski, 1956 from NO1. Fig. 9: m1, no. 191.
Sciurus anomalus Gueldenstaedt 1785 from NO1. Fig. 10: m1, no. 211.