UTRECHT MICROPALEONTOLOGICAL BULLETINS

SPECIAL PUBLICATION

C. G. RÜMKE

A REVIEW OF FOSSIL AND RECENT DESMANINAE
(TALPIDAE, INSECTIVORA)

4

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A REVIEW OF FOSSIL AND RECENT DESMANINAE (TALPIDAE, INSECTIVORA)

C.G. RÜMKE

CONTENTS

ABSTRACT

Numerous new finds have been described since Schreuder published "A revision of the fossil water-moles (Desmaninae)" in 1940. In addition to these described assemblages there are many undescribed collections in various institutions and museums. Most of the finds are from isolated localities scattered over Europe.

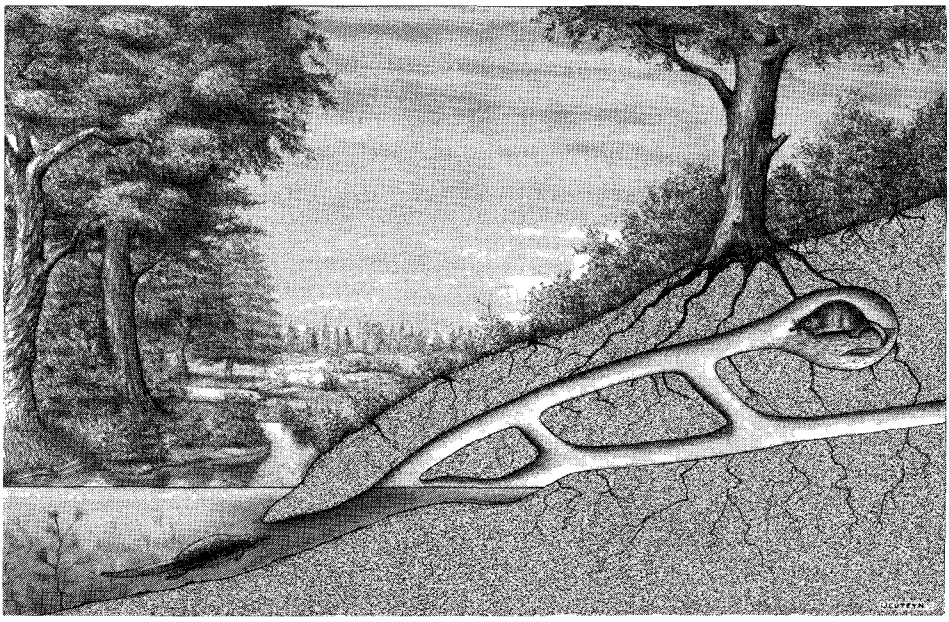
This new revision of the subfamily Desmaninae is based primarily on the collection of the Institute of Earth Sciences of the Rijksuniversiteit Utrecht, which includes many assemblages of desmanine moles. As well as our own collections, however, we have been able to study many assemblages put at our disposal by colleagues from other institutions. We have also made use of published data from various countries.

Nearly all the material studied is allocated to one of the following three genera, i.e. the newly erected genus *Dibolia,* characterized by its small size and a bifid straight first upper incisor, *Galemys,* characterized by its small size and a pointed curved first upper incisor and *Desmana,* characterized by its medium to large size and a pointed curved first upper incisor. A fourth genus belonging to the Desmaninae, the genus *Mygalinia,* characterized by its very small size and aberrant mandibular ramus, is not represented in the material studied. The material from Hammerschmiede, described by Mayr and Fahlbusch (1975), although apparently belonging to a desmanine mole, could not be assigned to any of the known genera.

A new classification of the subfamily is proposed. In this classification the genera are distinguished on the basis of the morphology of the i1 and the I1 and the overall size, whereas the species are distinguished by the absolute length and more in particular the relative length of six selected teeth, viz. p2, p3 and p4 and C, P2 and P3. In the genus *Dibolia* nine species are distinguished, in the genus *Galemys* four species and in the genus *Desmana* six species. In order to facilitate the determination of water-moles a general description of all desman teeth is given.

A short discussion of the various types of lower jaw and their possible function, as well as a description of the chevrons (tail bones), which are indicative of an aquatic life, are added.

The results of the measurements, a detailed description of the teeth used in the classification for each locality and some comments on the age of the assemblages are included.



Desmana moschata, free after Barabasch-Nikoforow

Chapter 1

INTRODUCTION

General remarks

Clusius (1605) was the first author to refer to the water-mole. He gives a description of the animal, which he names *Mus aquaticus exotica*, as he regards it as a kind of mouse.

Daubenton (1663) mentions the name desman for the first time. According to him the word desman is a popular name given to *Mus aquaticus* by Lapp furriers who deal in the animals' fur and tails (the tails were used as mothrepellants because of their strong musk scent).

Charleston (1673) seems to have been the first to recognize that the water-mole should be placed in the Insectivora, as he proposes the name *Sorex moscovites.* However, not everyone agreed with this view. Linnaeus (1758) for instance still regarded it as a rodent, closely related to *Castor.* It was Gueldenstaedt who in 1777, in an extensive description of the animal, proposed *Desmana* as a genus name. As his publication escaped general notice, the name *Mygale* – proposed by Cuvier in 1800 – became better known. A second water-mole, *Mygale pyrenaica,* was described by Geoffroy in 1811. Although Kaup (1829) placed this much smaller new species in a separate genus, *Galemys,* throughout the 19th century names like *Mygale, Myogale* and *Myogalea* were in use for both the living genera. Miller (1912) put an end to the confusion by calling the Russian water-mole *Desmana moschata* and the Pyrenean species *Galemys pyrenaicus,* giving a short diagnosis for each genus. Although *Mygale* has priority over *Galemys,* the name *Galemys* has been in common use for so long now that it is considered to be a nomen conservandum.

Schreuder published "A revision of the fossil water-moles (Desmaninae)" in 1940. In this review she gives measurements, descriptions and figures of most of the material known at the time. To this descriptive part she added a historical review, the taxonomy, phylogeny, range and habits of the subfamily and a survey of the genera and species of fossil and living water-moles.

Schreuder's "Revision" was followed for many years. It is only since

*) The collection of the Museum of Natural History, Leyden, includes one specimen labelled '*Galemys pyrenaicus* found near Grenoble'. It is not possible to check the reliability of this entry.

larger collections of fossil remains have become available that her species concept has begun to give problems. Some of the species described in the "Revision" are based on limited material from a locality that does not exist any more; in other instances material from more than one locality was used. Small collections do not show the variation in the dental morphology. Now that much larger collections from single localities – sometimes comprising hundreds of teeth – can be studied, the morphological criteria used by Schreuder to define the species have proved to be so variable that they have become almost useless. Our study of recent and fossil material shows that features such as the number of roots of the premolars, the way p1, P1, p3 and P3 are set in the jaw, the metaconid in p4, the extension of the cingula and the number of foramina mentale, may vary within a single assemblage. Moreover, the size of the dental elements may differ considerably within what is considered to be one species.

Since the collections of the Institute of Earth Sciences of the Rijksuniversiteit of Utrecht contain a large number of *Desmana* remains and clearly include more than one genus, it was felt that a more up-to-date classification of the Desmaninae was needed. This survey of the subfamily is based on this material, on the material used by Schreuder, on a number of collections – partly published, but mostly unpublished – made available by colleagues in eastern and western Europe, and on data from the literature. Only dental elements are studied. Material of Middle and Late Pleistocene age is scattered over many small collections, and as a study of this material was considered to be too time-consuming, it is not included here. This does not mean that a critical appraisal is considered superfluous.

Since not every reader may agree with the interpretations presented below, data and conclusions have been kept strictly separate.

Some information on the living representatives of the Desmaninae

Most of the information given in this section is taken from Barabasch-Nikiforow's book "Die Desmane" (1973), from Trutat's thesis "Essay sur l'histoire naturelle du Desman des Pyrenées" (1891) and from Niethammer's publication "Beobachtungen am Pyrenäen-Desman" (1970).

The Desmaninae are represented by two living species, allocated to different genera. The smallest form – *Galemys pyrenaicus* – is found in the Pyrenees and the Cantabrian Mountains*). The much larger *Desmana moschata* is restricted to the south-west U.S.S.R., namely the basins of the Don, the Volga and the Ural rivers. The animal is known to have lived in the basin of the Dnieper until a century ago. Both *Desmana* and *Galemys* are regarded

as relict forms, the distribution area of which is shrinking rapidly. This is not only due to human activities, but also a result of climatic changes.

Galemys and *Desmana* are well adapted to an amphibian way of life. The body is strongly streamlined, the eyes are small, the auricles small or absent. The tail is long and more or less flattened laterally. The hind legs are much longer than the front legs and the feet are webbed or partly so. The long snout is used as a snorkel.

The dental formula is complete. The large I1 is inserted at right angles to the jaw, which makes it very suitable for opening shells and holding wriggling prey. The relatively low upper canine is not used for these purposes. Functional milk teeth are not present.

Sexual dimorphism with regard to size and weight is inconspicuous – if present at all. The statement by Barabasch-Nikiforow that the skull is asymmetrical relative to the sagittal plane, which is said to be typical for amphibian mammals in general, is not corroborated by the material at hand and does not show in the measurements of the teeth.

Barabasch-Nikiforow mentions that the size of *Desmana moschata* may be an adaptation to its aquatic or burrowing way of life. According to this theory burrowing and aquatic forms need an optimum surface-to-volume ratio to improve the heat regulation and the musculature and lung functions. It is true that *Desmana moschata,* the larger of the extant species, is better adapted to sub-aquatic conditions than is *Galemys pyrenaicus* and it is – contrary to *Galemys* – a burrowing animal.

The Desmaninae are "typical" insectivores in so far as they have a very intensive metabolism. This means that they have to feed most of the time. *Galemys* is primarily a nocturnal animal, feeding all night and often during the day as well. *Desmana* is active around the clock, with activity-peaks at sunrise and sundown.

Galemys pyrenaicus

Galemys seems to be slightly better adapted to a life on land than *Desmana.* Although its front legs are short, they are long enough to enable the animal to walk on land without letting its belly touch the ground. The larger part of the tail is round, with only the tip flattened. The hind feet are webbed at the base of the digits only.

The length of the body of an adult specimen may vary between 10.0 and 15.6 cm., the length of the tail varies between 12.6 and 15.6 cm. The teeth are long and narrow and feature sharp cusps and ridges. In both the premolars and the molars these ridges run more or less parallel, at an angle of about 60 degrees to the length axis of the jaw.

Galemys feeds mostly on small, sub-aquatic invertebrates, sometimes it catches small fish, more rarely terrestrial prey. The animal eats exclusively on land. The biotope of *Galemys* is by preference fast-running streamlets, i.e. typical trout streams, more rarely wider streams, mountain lakes and mountain marshes. The animal hides between stones and vegetation along the river banks, it seldom burrows. On the rare occasions when it does burrow, it uses the first incisors and the snout for digging, not the front legs. *Galemys* is strictly territory-bound throughout the year.

Desmana moschata

Desmana is well adapted to an underwater way of life. The nostrils can be closed, the tail is strongly flattened and both front and hind feet are webbed. The front legs are so short that the animal drags its belly over the ground when walking on land. In the water only the hind legs and the tail are used for locomotion.

For an insectivore *Desmana moschata* is very large: the length of an adult specimen may vary between 20 and 23 cm, the length of the tail between 18.5 and 21 cm. The crowns of the teeth are rather low, both premolars and molars are sturdy and wide with well rounded cusps.

Desmana lives on larvae of (water)insects, worms and molluscs; sometimes small fish and frogs are caught. When nothing better is available, water-plants are eaten too. The biotope of *Desmana* is quite different from that of *Galemys*. *Desmana moschata* lives preferably in lakes and river-forelands with a depth of 2–5 m. with rather steep, sandy-clayey banks, and in small, slow-running streams. A vegetation of trees and shrubs along the banks as well as water-plants – enough to provide a suitable biotope for a teeming invertebrate life without taking away too much light – are needed. The water-level must remain more or less constant all the year round: areas that are flooded during the winter months or dry up in summer are not suitable. Water-masses that freeze as a body are also unsuitable habitats. The animal avoids larger rivers with strong currents, large lakes and storage lakes.

Desmana is a burrower. The animal burrows in steep riverbanks, where the roots of the land vegetation prevent that the hole caves in (frontispiece). A (long) passage leads to a nesting room. The entrance to the passage lies just below the usual lower limit of the ice.

Although *Desmana* is territory-bound, migration does take place. Most treks have been observed during and after spring floods, fewer occur during summer and autumn droughts. The treks usually occur along small, dry stream-beds; *Desmana* specimens have been found up to 50 km. from the nearest water.

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Chapter 2

THE CURRENT VIEW ON THE TAXONOMY OF THE DESMANINAE

Characteristics of the subfamily

The following diagnostic features, common to all members of the Desmaninae, have been extracted from various textbooks and papers (Miller, 1912; Schreuder, 1940; Saban, 1958; Gromova, 1968; Hugueney, 1972) and our own observations.

The dental formula is invariably $\frac{3.1.4.3}{3.1.4.3}$. The mandible is thickened under the i3–p1. The p2 and P2 are longer or at least as long as the p3 and the P3.

The i2 has a high crown; it is the largest of the lower incisors. The lower canine is small and incisiform. The p4 often features a small metaconid or a metaconal rib. The oblique cristid of the lower molars ends either against the tip of the metaconid or against the protoconid-metaconid crest. The m3 is slightly reduced.

The I1 is greatly enlarged and may be straight and bilobate or curved with a pointed tip. The upper canine is small and premolariform. The upper molars have a divided mesostyle and a strongly developed lingual part featuring a protoconule, a protocone, a metaconule and often a small tubercle on the posterocrista of the protocone.

Genera and species

A number of genera have been allocated to the Desmaninae:

genus	stratigraphic range according to this paper
Asthenoscapter Hutchison, 1974	Astaracian
Desmagale Kretzoi, 1953	Villanyian
Desmana Gueldenstaedt, 1777	Ruscinian – Recent
Desmanella Engesser, 1972	Astaracian – Ruscinian ?
Galemys Kaup, 1829	Ruscinian – Recent
Mygalea Schreuder, 1940	Astaracian
Mygalinia Schreuder, 1940	Turolian
Mygatalpa Schreuder, 1940	Arvernian – Agenian

When the diagnoses of these genera are compared with that of the subfamily, it becomes apparent that the genera *Asthenoscapter, Desmanella, Mygalea* and *Mygatalpa* do not fit into the subfamily.

Asthenoscapter from La Grive L7 and *Desmanella* from numerous localities in Europe and Turkey are closely related genera. They both have a reduced dentition. They have been assigned in turn to the Desmaninae (Engesser, 1972; Hutchison, 1974), to the Uropsilinae (Rümke, 1974, 1976; Engesser, 1980) and to the Talpinae (Storch, 1978). The extensive discussion in Engesser (1980) seems to have settled the argument in favour of their inclusion in the Uropsilinae.

N.B. *"Desmanella" quinquecuspidata.* Mayr and Fahlbusch (1975) described a desman-like species of Vallesian age from Hammerschmiede 1 in Bavaria, West Germany. The species was originally allocated to the genus *Desmanella,* but clearly belongs to the Desmaninae (Engesser, 1980). As the relative size of the teeth differs greatly from that of *Dibolia* n.gen. (see p. 10) and of *Mygalinia,* it seems probably that ? *quinquecuspidata* is a representative of a primitive, hitherto undescribed genus. The material has not been studied in sufficient detail and discussion of it falls outside the scope of our study.

The genus *Desmagale* – described by Kretzoi (1953) from Kisláng (Hungary) – is based on a misinterpretation of the material and the name should be discarded (see p. 97).

Mygalea (Schreuder, 1940; Baudelot, 1972) – known from Sansan only – is of the same size as *Galemys pyrenaicus* but is more robust. The conical premolars increase in size from the front backwards. The lower canine is not incisiform, but conical. It may be that *Mygalea* is ancestral to the Desmaninae, but allocation to the subfamily is not justified, unless its intermediate position can be demonstrated.

Mygatalpa (Schreuder, 1940; Hugueney, 1972) has been described from several localities in France. Although Hugueney and Hutchison (1974) found reasons for placing *Mygatalpa* in the Desmaninae, the dentition shows several features that are atypical for this subfamily. The alveoles of the three lower incisors are of about the same size in *Mygatalpa*, while in the Desmaninae the i2 is characteristically enlarged. In *Mygatalpa* the p1 is a large tooth – nearly as large as the p4 – while the p2 is very small and often set obliquely in the mandible. In my opinion these features indicate that *Mygatalpa* should be placed outside the Desmaninae.

The remaining genera – *Desmana, Galemys* and *Mygalinia* – are regarded as true water-moles. *Mygalinia* (Kormos 1913, 1938; Schreuder, 1940) is known from Polgárdi only. The species unquestionably belongs to – or is

closely related to – the Desmaninae. It is the smallest water-mole known, the length of the m1 varies between 1.8 and 2.1 mm. The mandible has an ascending ramus with a rather strong backward inclination. Since only five dental elements are known and no jaws of the type described above – with a backwards inclined ramus – have been encountered in our material, the genus is not included in the following discussions.

N.B. Apart from the three mandibular fragments with p4–m3 which are stored in the Museum of Natural History in Budapest, a mandibular fragment with p2, p4–m3 is present in the collection of the Université Claude Bernard, Lyon 1. This specimen is not mentioned by Kormos.

To the three genera belonging to the water-moles, i.e. *Desmana, Galemys* and *Mygalinia,* a fourth – *Dibolia* – is added. This genus includes among others two of the species originally allocated to *Desmana,* i.e. *"Desmana" pontica vinea* and *Desmana bifida.*

Storch (1978) described *"Desmana" pontica vinea* from Dorn-Dürkheim in Rheinhessen, West Germany. The assemblage is of Early Turolian age. Since the I1 of this species differs from that of all Desmaninae described so far, Storch allocated the species provisionally to the genus *Desmana.*

Engesser (1980) described the first water-mole from Turkey, i.e. *Desmana bifida* from Dinar Akçaköy (Early Ruscinian). The shape of the I1 of this species is similar to that of *"Desmana" pontica vinea* from Dorn-Dürkheim. Engesser states that forms with a bifid I1 – such as are present in *Desmana bifida* and *"Desmana" pontica vinea* – should be allocated to a separate genus, but in his opinion not enough was known of the fossil Desmaninae to do this.

Formal and extensive diagnoses of the three genera treated in this paper will be given in Chapter 6. The most characteristic features of each genus are briefly listed below.

Dibolia Small sized water-moles. The crown of the i1 is of medium size in relation to its root; the enamel of the crown extends just as far down anteriorly as posteriorly. The I1 is straight with a bilobate tip. The p2 and P2 are longer than the p3 and P3.

Galemys Small sized water-moles. The crown of the i1 is small in relation to its long root; the enamel of the crown extends further down anteriorly than posteriorly. The I1 is curved with a pointed tip. The p2 and P2 are of the same length as the p3 and P3.

Desmana Medium to large sized water-moles. The crown of the i1 is small in relation to its very long root; the enamel of the crown extends further down anteriorly than posteriorly. The I1 is curved with a pointed tip. The p2 and P2 are longer than the p3 and P3.

More than twenty species and subspecies of *Desmana,* and two of *Galemys* have been described. Species have been distinguished on the basis of morphological features and overall differences in size. In this paper a classification based on the relative length of teeth is proposed. For a critical evaluation of previously described species the reader is referred to Chapter 6.

Chapter 3

MATERIAL AND METHODS

Localities and material (table 1 and fig. 1)

Table 1 gives in stratigraphic order all the localities from which material has been studied. The justification for the allocation of the localities to a specific zone is given in the appendix. In those instances where several assemblages are found in superposition their order is indisputable, but in all other cases the order of the localities within a zone is arbitrary.

Material derived from Middle and Late Pleistocene localities is usually very limited. For this reason and because no material is available in Utrecht, assemblages of this age are disregarded. However, material of the two living species has been studied. The variability observed in the extant species is used to evaluate the variability of comparable measurements observed in fossil assemblages.

The localities are grouped according to their geographical position, i.e. (1) south-west Europe, comprising Spain and the south of France; (2) central Europe, including the Netherlands, The Federal Republic of Germany, the Democratic Republic of Germany, Poland, Austria and Hungary and (3) south-east Europe and west Asia, with Roumania, the Union of Soviet Socialist Republics, Greece and Turkey.

An (F) or (C) placed after the name of the locality means that the faunal assemblage is collected from a fissure filling or a cave filling respectively.

The number of specimens – incisors excluded – are listed per locality.

A column is added, giving the name(s) of the person(s) who measured the specimens. This is done because small differences between measurements may be due to the use of different techniques. In those instances where it is clear that the orientation of certain specimens differs fundamentally from the one used by us, the measurements have not been used. The abbreviations of names of authors used are:

En = Engesser	Ko = Kormos	St = Storch
Fe = Fejfar	Ru = Rümke	Te = Terzea
Ja = Jánossy	Sch = Schreuder	To = Topachevski

The city names in the last column of table 1 indicate where the collections are housed:

Basle = Museum of Natural History

Beauvais = Dr. J. Braillon, private collection

EPOCHS	STAGES	NEOGENE MAMMAL ZONES	LOCALITIES (Type localities of genera/species described in literature underlined)			
			CODE	SOUTH-WEST EUROPE	CENTRAL EUROPE	SOUTH-EAST EUROPE AND WEST-ASIA
HOLOCENE			Rd			div. loc. U.S.S.R
			Rg	div. loc. Spain, France		
EARLY PLEISTOCENE	EARLY BIHARIAN		Vo		Voigtstedt	
			Be			Betfia 2
	VILLANYIAN	MN17	Vi 5		Villány 5 (F)	
			V4	Valdeganga 4		
			V3	Valdeganga 3		
			Ki		Kislang	
			V2a	Valdeganga 2a		
			V2b	Valdeganga 2b		
			V2e	Valdeganga 2e		
			Vi 3		Villány 3 (F)	
			V1	Valdeganga 1		
			Te		Tegelen	
		MN16b	RK2		Rebielice Krol. 2 (F)	
			RK1		Rebielice Krol. 1 (C)	
			Ba	Baza		
			Hj		Hajnácka	
			Br '36		Beremend 1936 (F)	
			Br 5		Beremend 5	
			Br 4		Beremend 4	
			Br 1-3		Beremend 1-3	
			Li			Limni 6
PLIOCENE	RUSCINIAN	MN16a	Mo	Moreda (F)		
			Es	Escorihuela		
		MN15b	We1		Weze 1 (C)	
			Se	Sète (F)		
			Sp3			Spilia 3/4
			Go2	Gorafe 2		
		MN15a	DA			Dinar-Akçaköy
			Pt3			Ptolemais 3
		MN14	Ks			Kosyakin
			Ci			Ciuperceni
			Pt1			Ptolemais 1
			Ka			Kardia
			Sp1			Spilia
			Or	Orrios		
			Go1	Gorafe 1		
LATE MIOCENE	TUROLIAN	MN13	Me			Maramena 1
			Po		Polgárdi (C)	
			VB	Villalba Baja 1		
			LF	La Fontana 1a		
			Ma7	Masada del Valle 7		
			Va	Valdecebro 3		
			Ma6	Masada del Valle 6		
		MN12	Ma5	Masada del Valle 5		
			LM	Los Mansuetos		
			Cu	Cubla		
			LA	Aljezar B		
			Ma2	Masada del Valle 2		
		MN11	DD		Dorn-Dürkheim	
			Ko		Kohfidisch (F)	
	VALLESIAN	MN10				
		MN 9	Ha		Hammerschmiede	

Table 1 For explanation see pp. 19, 23–24.

GENERA / SPECIES DESCRIBED IN LITERATURE	NUMBER OF MEASURED SPECIMENS	MEASURED BY	STORAGE
Desmana moschata	217	Ru	Leyden(1), London(1)
Galemys pyrenaicus	509	Ru	Leyden(1), London(1)
	20	Ja	Weimar
Desmana thermalis	24	Ru,Sch	Budapest(1), Basel, London(2)
Galemys semseyi	4	Sch	Budapest(1)
	10	Ru	Budapest(2)
	11	Ru	Villeurbanne
	45	Ru	Villeurbanne
Desmana crassidens	5	Ru	Budapest(1)
Desmagale pannonica			
	257	Ru	Lyons-Villeurbanne
	22	Ru	Lyons-Villeurbanne
	292	Ru	Lyons-Villeurbanne
	41	Ru,Sch	Budapest(2), Kiel
	15	Ru	Lyons-Villeurbanne
Desmana tegelensis	315	Ru	Leyden(2), Utrecht
	12	Ru	Kraków
	165	Ru	Kraków
	15	Ru	Utrecht
	5	Fe	Prague
	6	Ru	Budapest(2)
	6	Ru	Budapest(2)
Desmana kormosi	4	Ru	Budapest(2)
Desmana nehringi	2	Ko	Vienna?
	24	Ru	Utrecht
	4	Ru	Utrecht
	37	Ru	Utrecht
	112	Ru	Krákow, Warsaw
	157	Ru	Beauvais Utrecht
	7	Ru	Utrecht
	7	Ru	Utrecht
Desmana bifida	68	En	Basel
	135	Ru	Utrecht
Desmana verestchagini	6	To	U.S.S.R
Desmana getica	5	Te	Bucharest
	192	Ru	Utrecht
	505	Ru	Utrecht
	98	Ru	Utrecht
	29	Ru	Utrecht
	24	Ru	Utrecht
	105	Ru	Utrecht
Desmana pontica	21	Sch,Ru	Budapest(2)
Mygalinia hungarica			
	17	Ru	Utrecht
	3	Ru	Utrecht
	57	Ru	Utrecht
	54	Ru	Utrecht
	10	Ru	Utrecht
	46	Ru	Utrecht
	6	Ru	Utrecht
	115	Ru	Utrecht
	525	Ru	Lyons-Villeurbanne
	120	Ru	Utrecht
D.pontica vinea	63	St	Frankfurt a/M
	37	Ru	Vienna
Desmanella quinque-cuspidata	16	Ru	Munich

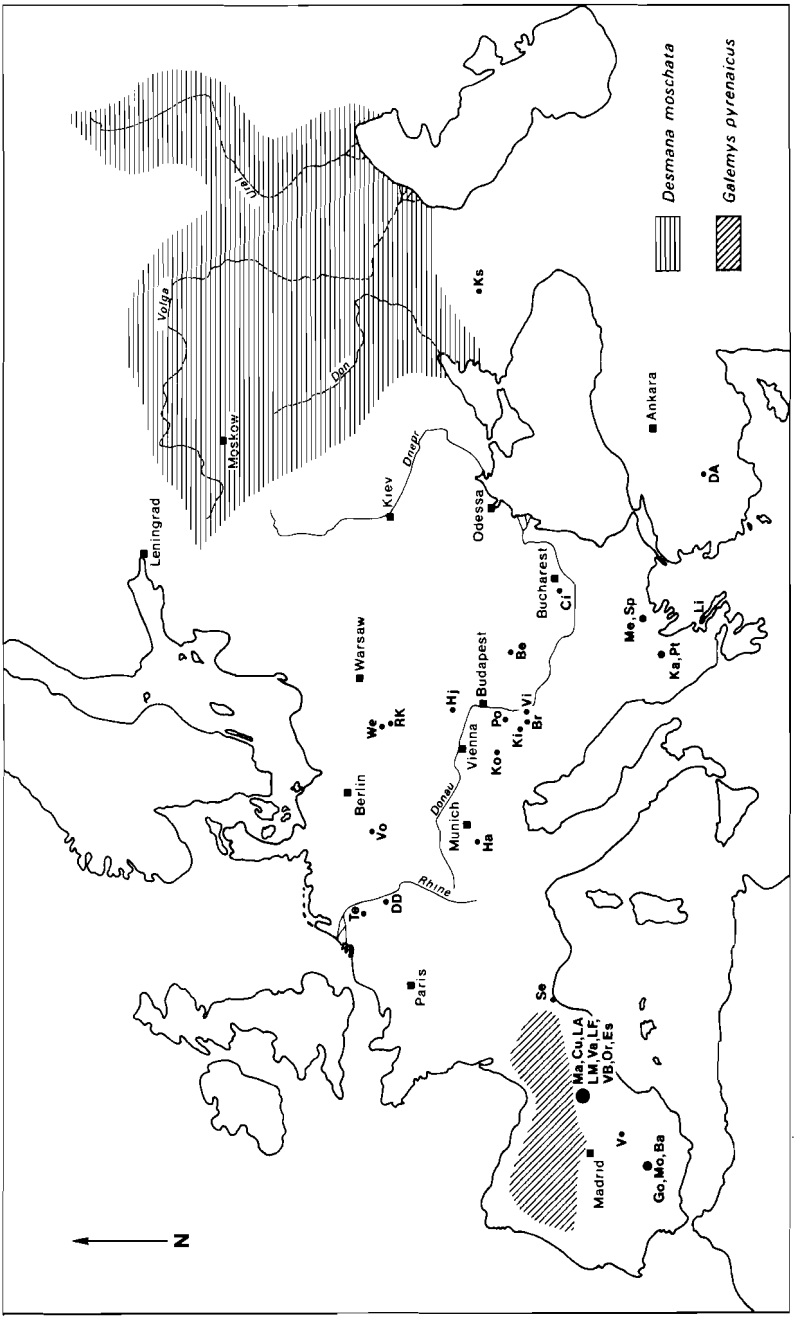


Fig. 1 Map showing the location of the sites from which fossil Desmaninae are studied. For an explanation of the abbreviations used for the localities see table 1. The approximate areas of distribution of *Desmana moschata* and *Galemys pyrenaicus* are hatched.

Bucharest = Speleological Institute Emile Racovitza
Budapest (1) = Geological Survey of Hungary
Budapest (2) = Museum of Natural History, Geological-Paleontological Department
Frankfurt a/M = Research Institute Senckenberg
Kiel = University of Kiel, Geological-Paleontological Institute
Kraków = Polish Academy of Sciences, Institute of Systematic and Experimental Zoology
Leyden (1) = National Museum of Natural History
Leyden (2) = The Netherlands National Museum of Geology and Mineralogy
London (1) = British Museum, Department of Zoology, Mammals Section
London (2) = British Museum, Department of Paleontology, Mammals Section
Munich = University of Munich, Institute for Paleontology and Historical Geology
Prague = Geological Survey of Czechoslovakia
Sabadell = Provincial Institute for Paleontology
Utrecht = State University Utrecht, Institute of Earth Sciences
Vienna = Museum of Natural History, Geology and Paleontology Division
Villeurbanne (Lyon 1) = University Claude Bernard, Department of Earth Sciences

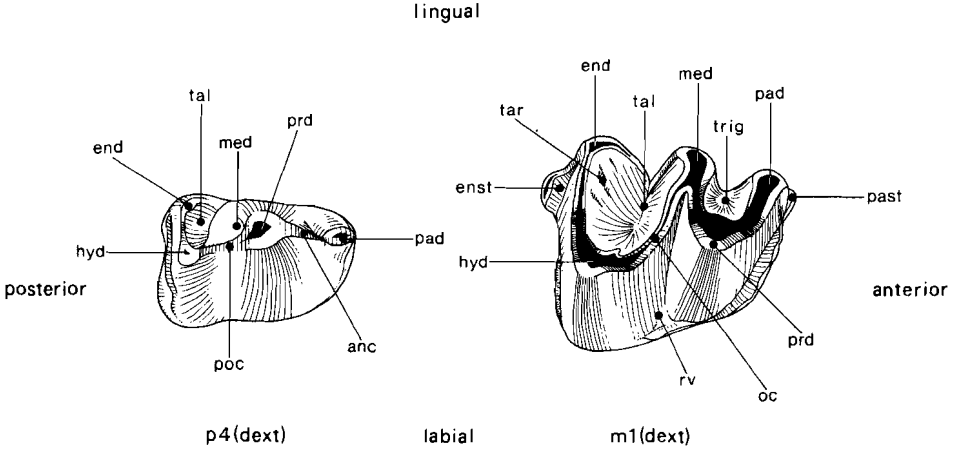


Fig. 2 The abbreviations used for parts of the lower teeth:

anc	=	anterocristid	oc	=	oblique cristid	rv	=	re-entrant valley
end	=	entoconid	pad	=	paraconid	tal	=	talonid basin
enst	=	entostylid	past	=	parastylid	tar	=	talonid ribs
hyd	=	hypoconid	poc	=	posterocristid	trig	=	trigonid
med	=	metaconid	prd	=	protoconid			

Warsaw = Polish Academy of Sciences, Paleozoological Laboratory
Weimar = Institute for Quaternary Paleontology

Nomenclature (figs. 2 and 3)

The nomenclature for parts of the lower and upper premolars and molars is given in figs. 2 and 3 respectively.

The abbreviations used for teeth is according to Jepsen's system, i.e. lower teeth in lower case letters and upper teeth in upper case letters, with the number on the line.

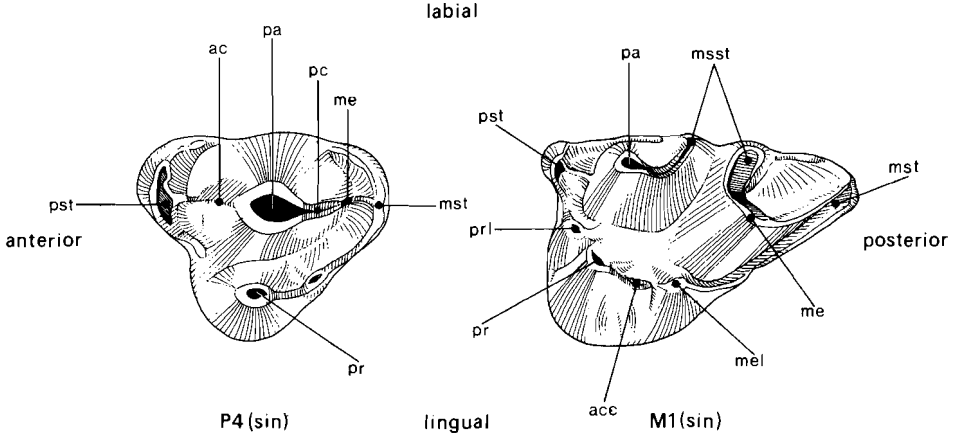


Fig. 3 The abbreviations used for parts of the upper teeth:

ac	=	anterocrista	msst	=	mesostyle	pr	=	protocone
acc	=	accessory cusp	mst	=	metastyle	prl	=	protoconule
me	=	metacone	pa	=	paracone	pst	=	parastyle
mel	=	metaconule	pc	=	posterocrista			

Measurements (fig. 4)

Several measurements of each of the upper and lower molars were taken at the beginning of this study. However, in due course it became apparent that some of these measurements varied so much, even within one assemblage, that they could not be considered characteristic for that assemblage. For the molars only the measurements shown in fig. 4 have been taken throughout; the measurements include cingula and styli. Of the canines and premolars the maximum length (L) and the maximum width (W) at right angles to the length have been taken. The incisors have not been measured.

All measurements have been taken with a Leitz Orthoplan microscope

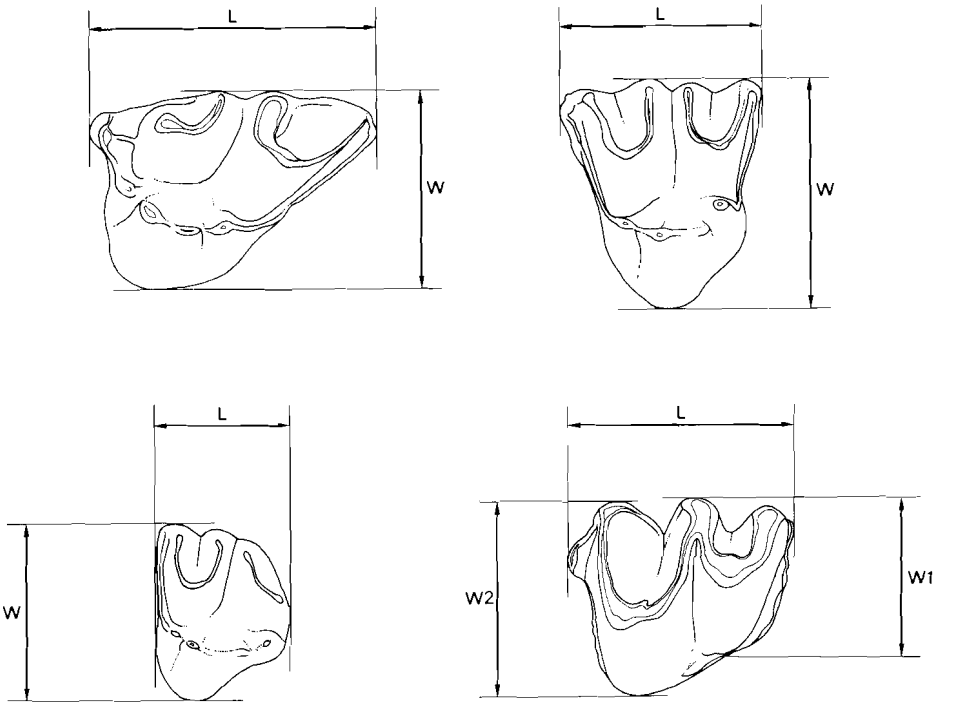


Fig. 4 Method of measuring the upper and lower molars.

with a mechanical stage and measuring clocks. A pair of ocular lenses with a magnification of X8 and a X4 objective have been used. All measurements are given in mm.

Figures

All figures are X 12.5 unless stated otherwise.

Chapter 4

MORPHOLOGY OF THE TEETH

Introduction

In this part the morphological features of the teeth and their variations will be discussed. Homologous teeth are surprisingly similar in all three genera, but they differ in size. In the following descriptions teeth of all three genera are included.

The lower jaw will be discussed in Chapter 8. Detailed information about the number of foramina mentale and their position is included in the species descriptions in Chapter 9.

The lower teeth

There are two types of i1. In morphotype a the crown is large in relation to the root; the enamel of the crown extends just as far down – or slightly further down – anteriorly as posteriorly. In morphotype b the crown is small in relation to the very long root, while the enamel of the crown extends further down anteriorly than posteriorly. Morphotype a is characteristic for the genus *Dibolia,* morphotype b for *Galemys* and *Desmana.*

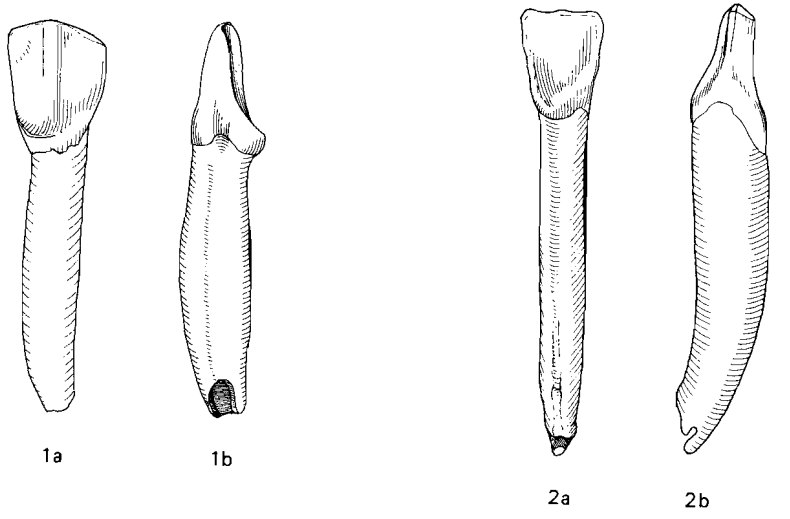


Fig. 5 1. i1 (dext) – morphotype a – of *Dibolia dekkersi,* Ka-513
a) posterior view b) medial view.
2. i1 (dext) – morphotype b – of *Galemys kormosi,* Te-443
a) posterior view b) labial view.

i1 Morphotype a (fig. 5.1) *The crown* The large, high crown is chisel-shaped and has a wide base with a sub-triangular cross-section and a sharp upper edge. Its anterior face is flat or slightly convex, its posterior face flat but for a more or less pronounced central rib of varying height. Near its base the posterior face becomes concave, forming a pronounced postero-lingual projection. This projection is partly bordered by a narrow cingulum. The triangular medial face of the crown is high and flat, at its base the enamel curves upwards.

The root The strong root has a triangular cross-section. Often the labial and/or medial sides are grooved.

The position in the jaw The i1 has an oblique position relative to the length axis of the jaw, which causes the sharp upper edge to run diagonally, from antero-medial to postero-labial. The i1 is partly overlapped by the i2 and the two teeth are pressed firmly against each other. The labial side of the i1 – that part of the crown that is overlain by the i2 – is narrow, while the medial part is much wider. The central rib marks the end of the overlapping area.

i1 Morphotype b (fig. 5.2) *The crown* The small, low crown is at its upper edge hardly wider than at its base. Its anterior face is flat or slightly convex, its posterior face is concave or flat. The medial part of the crown-base is somewhat enlarged posteriorly, without forming the well defined postero-medial extension found in morphotype a. A central rib and a posterior cingulum are rarely present. The medial face of the crown is flat and of irregular shape, as the enamel extends far downwards anteriorly.

The root The very long, thin root is curved.

The position in the jaw The tooth has a straight position relative to the length axis of the jaw, and the upper edge runs from medial to labial.

i2 (fig. 6) *The crown* The i2 is the strongest and the highest of the lower incisors. It has a somewhat triangular cross-section, tapering to a sharp cutting edge. The anterior face is in line with the root, but the top slants more steeply than the basal part.

The triangular antero-medial face is flat. At its base the enamel-dentine boundary is curved upwards: the enamel-free area thus formed is higher in geological younger forms. The labial face is convex. The slightly undulating postero-medial face is bordered labially by a sharp edge, comparable to the posterocristid of the premolars. In some assemblages a faint short rib runs diagonally from the posterior tip of the cutting edge in the direction of the antero-medial corner of the base. In other specimens this rib is indicated only by a thickening of the posterior tip of the crown.

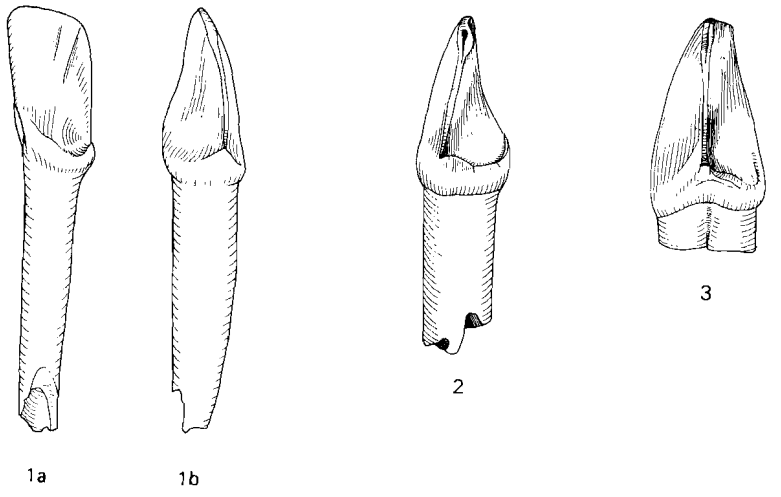


Fig. 6 1. i2 (dext) of *Dibolia dekkersi*, Ka-541
a) postero-medial view b) posterior view.
2. i2 (sin) of *Dibolia turolense*, Cu-22
posterior view.
3. i2 (sin) of *Desmana inflata*, V2a-17
posterior view.

A postero-medial cingulum is present in geologically older assemblages, forming a small distinct bulge at the base of the posterocristid. In younger assemblages, where the cingulum is often absent, this cingular bulge is replaced by a small cusplet. There may be a narrow depression in front of the cingulum. This feature is quite variable, even within one assemblage.

The root The strong root is flattened antero-posteriorly and has an elliptical cross-section.

The position in the jaw The tooth slants strongly forwards. In geologically older assemblages the cutting edge is straight and parallel to that of the i1 – antero-medially to postero-labially – while in younger species it is often curved as the labial face becomes more convex and the postero-medial face concave.

The posterocristid of i2 is parallel to – but lying somewhat labially of – those of the i3, the c and the premolars. The i3 is pressed against the medial part of the base of the i2, checked labially by the small basal bulge. The function of the diagonal rib is not clear.

i3 (fig. 7) *The crown* The i3 is the smallest of the lower incisors. It is low compared to the i2 and has a triangular cross-section with one of the apexes situated in the middle of the lingual side. The anterior margin of the crown slopes upwards. Although the tooth is incisiform, a short anterocristid is present.

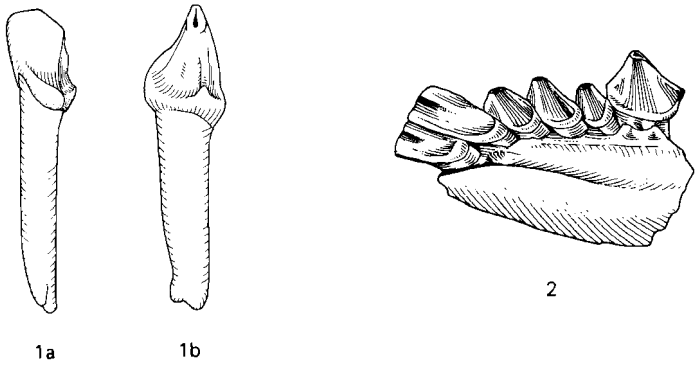


Fig. 7 1. i3 (dext) of *Dibolia dekkersi*, Ka-551
a) lingual view b) posterior view.
2. mandibular fragment with i1—p2 (sin) or *Dibolia adroveri*, LA-1
lingual view.

The anterior face is wide and flat. The narrow flat or gently curved labial face, combined with the wide concave lingual portion, makes the crown strongly asymmetrical. The posterocristid and the anterocristid are blunt. In some assemblages a faint diagonal rib, similar to that found in i2, is present, but usually only the tip of the crown is inflated.

A postero-lingual cingulum, varying in strength and length, may be present; in some assemblages the tooth has a vague and short labial cingulum as well. The cingulum forms an – often hook-like – bulge at the base of the posterocristid.

The root The root has an elliptical or a triangular cross-section.

The position in the jaw The tip of the crown of the i3 is pressed against the base of the i2, fitting into the slight postero-medial depression. The tooth slants strongly forwards.

c (fig. 8) *The crown* The lower canine is incisiform. It is of roughly the same size and height as the i3. It has an elliptical outline with a more or less pronounced flattening of the antero-labial corner. The anterior part of the crown slopes upwards at an angle with the length axis of the root.

The lingual side is flat or concave and is only slightly wider than the convex labial side, which gives the tooth a more symmetrical appearance than the i3; infrequently the crown is biconvex. Its top is usually inflated; a rib is never present.

A cingulum runs around the posterior part of the crown, ending further anteriorly lingually than labially. The cingulum may be replaced by an ill-defined inflated zone. At the base of the posterocristid the cingulum is

higher and thicker than elsewhere, but a real bulge is seldom present. A vague depression may be present postero-lingually.

The root The root is usually triangular in cross-section with a broad posterior face and the apex of the triangle situated anteriorly. More rarely the cross-section is round.

The position in the jaw The canine stands more upright than the i3. Its flattened antero-labial corner fits either against the posterocristid and the small hook-like bulge or into the flat or concave lingual part of the i3.

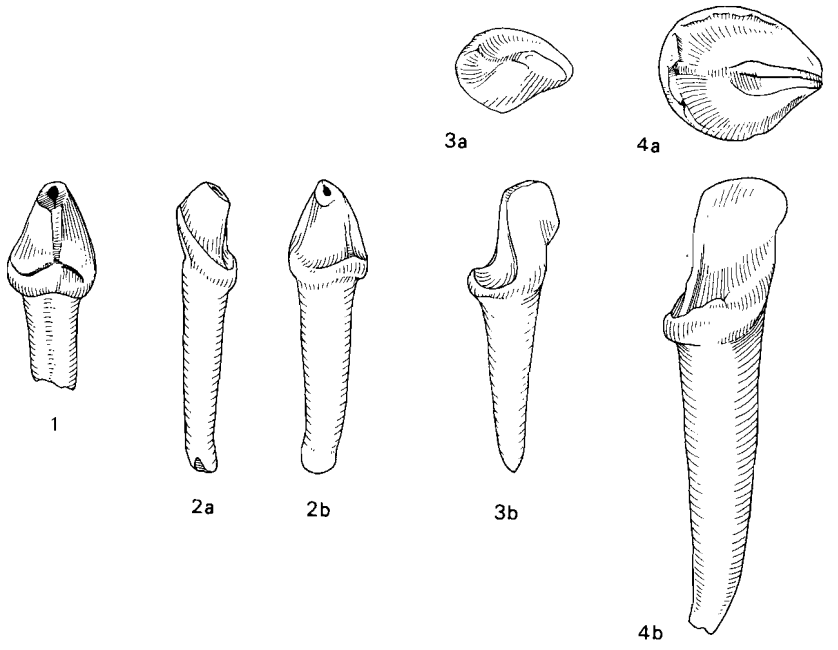


Fig. 8
1. c (dext) of *Dibolia major*, Ma7-511 posterior view.
2. c (dext) of *Dibolia dekkersi*, Ka-561 a) lingual view b) postero-lingual view.
3. c (dext) of *Galemys kormosi*, Te-501 a) occlusal-labial view b) labial view.
4. c (dext) of *Desmana thermalis*, Te-64 a) occlusal-labial view b) labial view.

p1 (fig. 9) *The crown* The variation in the morphology of the p1 is greater than in the incisors or in the canine. It has a rounded, elongated or more or less rhombic cross-section and a $\overline{W}/\overline{L}$ ratio ranging from 0.77 to 1.03. The enamel-dentine boundary rises steeply towards the anterior end of the crown.

The lingual side of the crown may be either convex or convex at the top and concave at the base. A flat postero-lingual face is sometimes present in geologically younger assemblages. The antero-lingual side is often flat and this feature, together with a strong postero-lingual cingulum gives the tooth a somewhat rhombic outline. The labial face is always convex. The anterior end of the crown may be rounded or straight, the posterior end rounded or pointed. The p1 of some assemblages features a small, usually inconspicuous, paraconid.

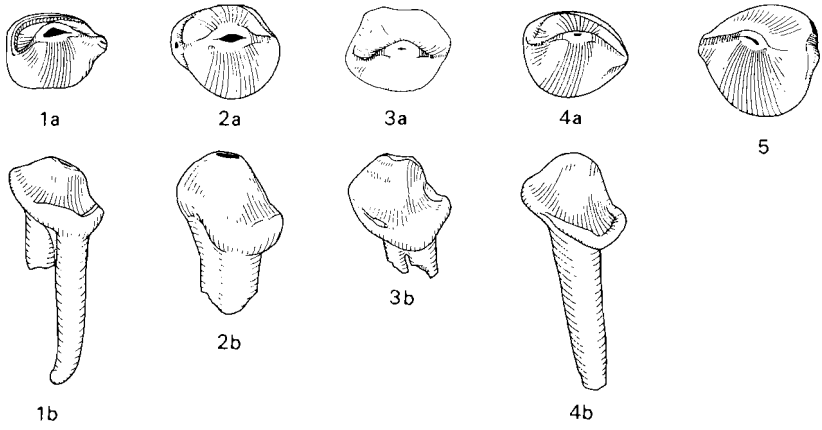


Fig. 9
1. p1 (dext) of *Dibolia turolense,* Cu-61
a) occlusal-labial view b) lingual view.
2. p1 (dext) of *Dibolia major,* Ma7-516
a) occlusal-labial view b) lingual view.
3. p1 (dext) of *Galemys kormosi,* Te-521
a) occlusal-labial view b) lingual view.
4. p1 (dext) of *Desmana verestchagini,* Pt1-641
a) occlusal-labial view b) lingual view.
5. p1 (sin) of *Desmana inflata,* V2a-41
occlusal-labial view.

A cingulum or an inflated zone runs partly round the posterior end, petering out somewhere along the lingual side or against the anterocristid. A short labial cingulum is sometimes present. In some instances the cingulum may form a small bulge at the base of the posterocristid, but when the cingulum is a continuation of the posterocristid no such bulge is present.

The roots The tooth may have one root with a rounded or an elliptical outline, a vertically grooved root, two fused or two separate roots. Some assemblages show all these variations, in others one type may prevail.

The position in the jaw When one root is present, the tooth may slant slightly forwards. In double-rooted specimens the two roots may stand side

by side or the one in front of the other. In some assemblages the p1 has an oblique position relative to the axis of the mandible, with the anterior (part of the) root placed labially.

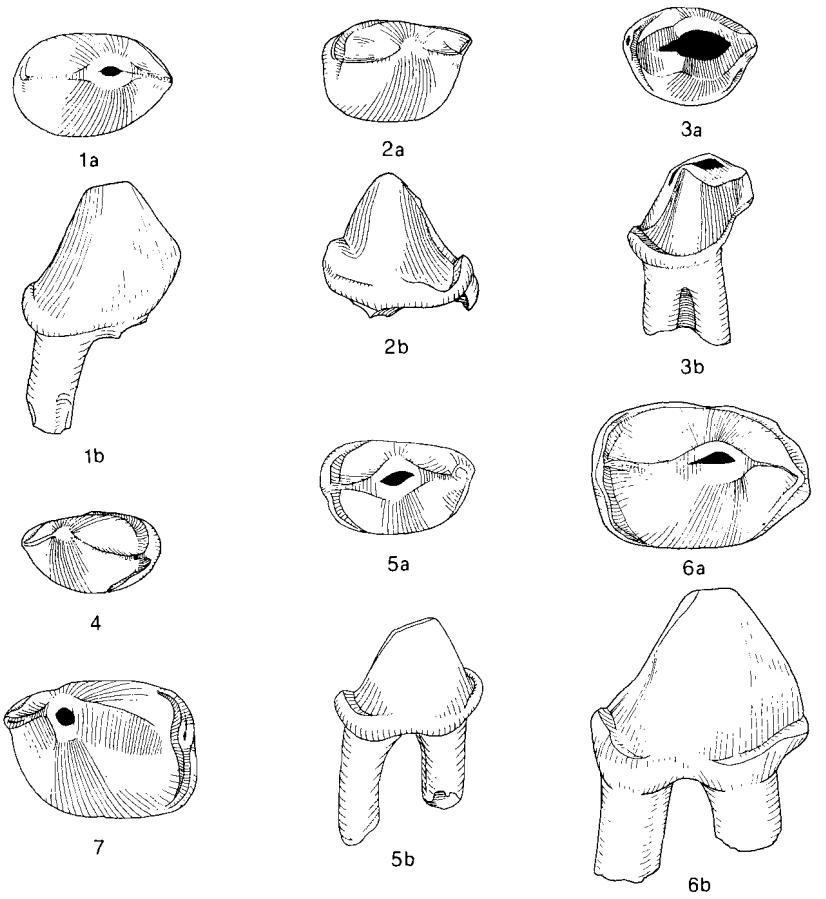


Fig. 10
1. p2 (dext) of *Dibolia major*, Va3-1012
a) occlusal-labial view b) labial view.
2. p2 (dext) of *Dibolia brailloni*, Or-1011
a) occlusal-labial view b) lingual view.
3. p2 (dext) of *Dibolia bifida*, Li-1006
a) occlusal-labial view b) labial view.
4. p2 (sin) of *Dibolia dekkersi*, Pt3-656
occlusal-labial view.
5. p2 (dext) of *Galemys kormosi*, Te-542 (rev.)
a) occlusal-labial view b) labial view.
6. p2 (dext) of *Desmana thermalis*, Te/St-102/797
a) occlusal-labial view b) labial view.
7. p2 (sin) of *Desmana inflata*, V2a-53
occlusal-labial view.

p2 (fig. 10) *The crown* The crown is high and stout. It has an elliptical or more rarely a rectangular cross-section, with a $\overline{W}/\overline{L}$ ratio ranging from 0.58 to 0.79. The enamel-dentine boundary slopes upwards towards the anterior end of the crown, in particular in geologically older assemblages.

Except for the occasional concave or flat postero-lingual face, both lingual and labial sides are convex. The antero-labial corner of the crown may be somewhat flattened, but this feature is never as pronounced as it is sometimes in p1 or p3. The posterior end of the crown is either rounded or straight, the anterior end may be pointed or obtuse. In most assemblages the medial crest is sharp.

In general the p2 is molarized to a certain extent: a weak paraconid is often present and a talonid may occur in the form of a valley or a narrow basin.

A heavy postero-lingual cingulum is nearly always present. It may form a bulge at the base of the posterocristid and/or at the postero-lingual corner of the tooth. When the cingulum is a continuation of the posterocristid these bulges are absent. The posterior cingulum continues for some distance along the lingual and labial sides. Short and weak anterior cingula may occur.

The roots The tooth has two heavy roots which are strongly divergent in geologically older assemblages. In the specimens from Limni 6 the roots are fused on the lingual side.

The position in the jaw With only a few exceptions the p2 has a straight position relative to the length axis of the jaw.

p3 (fig. 11) *The crown* The crown is very variable in size and morphology: marked differences occur within single assemblages as well as between assemblages. It is low compared with the p2, otherwise the two teeth resemble each other in many respects. The enamel-dentine boundary rises steeply towards the anterior end of the crown, less so towards its posterior end. The outline varies from rounded or elliptical to rhombic; the $\overline{W}/\overline{L}$ ratio ranges from 0.59 to 1.04.

The postero-lingual face, the lingual and labial sides and the posterior and anterior ends vary in much the same way as in the p2, but – contrary to the situation in the p2 – the lingual side may be wider than the labial one. In general the antero-labial corner is flattened, less often the postero-lingual one is flat as well.

A paraconid is usually present in varying degrees of development, but may be absent. There is a general tendency for the paraconid to become larger through time. The talonid valley – if present at all – is narrow.

The posterior cingulum may be a continuation of the posterocristid or

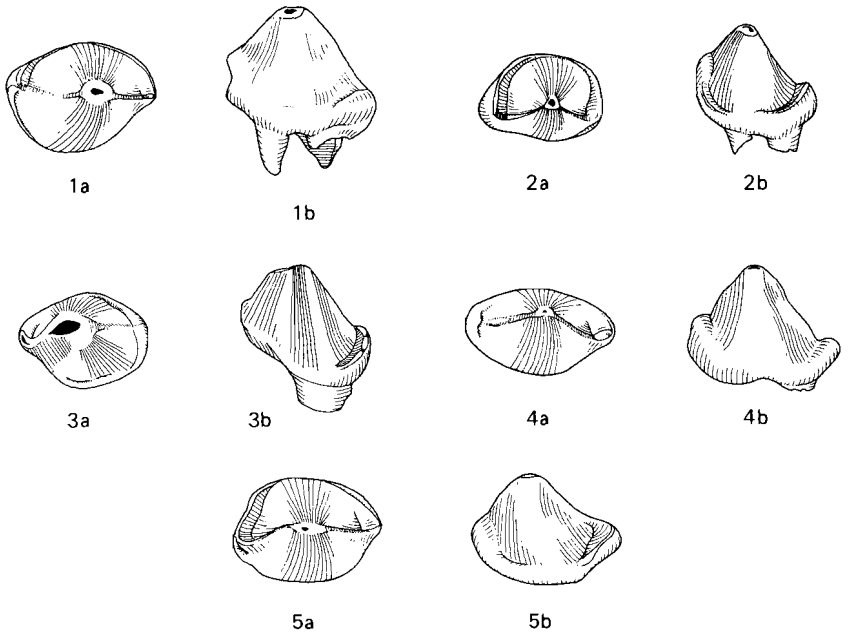


Fig. 11
1. p3 (dext) of *Dibolia major*, Ma7-537
a) occlusal-labial view b) lingual view.
2. p3 (dext) of *Dibolia dekkersi*, Ka-646
a) occlusal-labial view b) lingual view.
3. p3 (sin) of *Dibolia bifida*, Li-1008
a) occlusal-labial view b) labial view.
4. p3 (dext) of *Galemys kormosi*, Te-564
a) occlusal-labial view b) lingual view.
5. p3 (dext) of *Desmana verestchagini*, Pt1-680
a) occlusal-labial view b) lingual view.

may be a separate feature. In geologically younger assemblages it is usually strong and long, petering out either along the lingual side or at the base of the anterocristid. Younger species have a short posterior cingulum or none at all. Short labial cingula are sometimes present. The bulge at the base of the posterocristid varies as in the p2.

The roots The round or antero-posteriorly compressed roots stand close together, the one situated in front of the other. The p3 found in Limni 6 and the p3 of *Galemys pyrenaicus* are single-rooted.

The position in the jaw The tooth often has an oblique position relative to the length axis of the mandible, with the anterior root situated lingually. However, this feature – unless it is very pronounced – is variable. The degree of antero-labial and postero-lingual flattening is not correlated with the way the tooth is set in the jaw.

p4 (fig. 12) *The crown* The p4 is the most variable element of the lower teeth as far as the morphology is concerned. The cross-section is elliptical or somewhat rectangular. The $\overline{W/L}$ ratio varies between 0.52 and 0.81.

The lingual side is slightly convex with concave or flat posterior and anterior faces. The lingual margin is straight; the labial side is strongly convex with a more or less curved border. The straight posterior end is wider than the obtuse or pointed anterior one, which in most forms is asymmetrical as the anterocristid ends near the antero-lingual corner of the tooth. In general the medial crest is sharp.

The tooth is molarized to a certain extent. The paraconid is stronger than in the preceding premolars and is hardly ever absent. The posterolingual face may be bordered anteriorly by an inflated rib or crest. In most assemblages

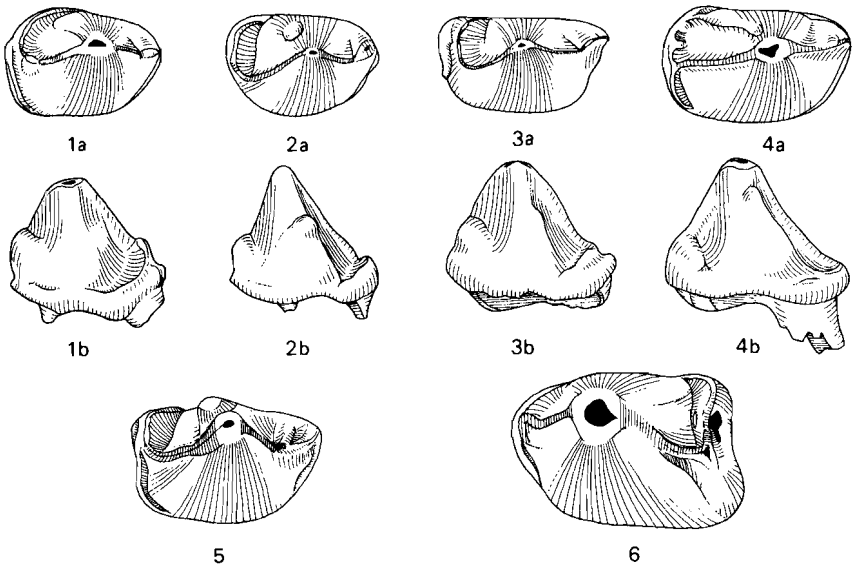


Fig. 12
1. p4 (dext) of *Dibolia turolense*, Ma2-2089
a) occlusal-labial view b) lingual view.
2. p4 (dext) of *Dibolia dekkersi*, Ka-660
a) occlusal-labial view b) lingual view.
3. p4 (dext) of *Galemys kormosi*, Te-583
a) occlusal-labial view b) lingual view.
4. p4 (dext) of *Desmana verestchagini*, Pt1-693
a) occlusal-labial view b) lingual view.
5. p4 (dext) of *Galemys kormosi*, Ba-17
occlusal-labial view.
6. p4 (sin) of *Desmana inflata*, V2a-83
occlusal-labial view.

the rib peters out against or just below the tip of the protoconid, but in some assemblages it forms a small individualized cuspule – the metaconid.

A conspicuous talonid basin is present at the base of the postero-lingual face. It is closed posteriorly and usually lingually as well, by a continuation of the posterocristid. A small cuspule – the hypoconid – is present at the base of the posterocristid and highly molarized p4's may possess a second accessory cuspule – the entoconid – at their postero-lingual corner.

Narrow cingula run around the posterior end and along the antero-lingual and -labial corners of the crown.

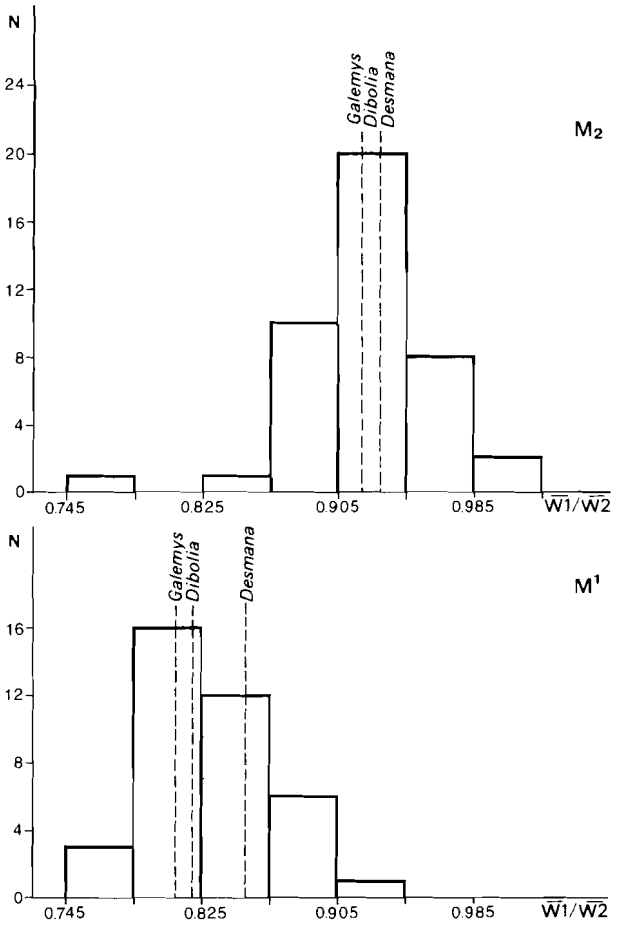


Fig. 13 Histograms showing the $\overline{W}1/\overline{W}2$ distribution of the m1's and the m2's of all the assemblages of *Dibolia, Desmana* and *Galemys* taken together.

The roots The tooth has two heavy roots, which have a round cross-section.

The position in the jaw The p4 stands straight in the mandible in all species except *Galemys pyrenaicus,* all the premolars of which have an oblique position relative to the length axis of the mandible.

m1–m3 (figs. 13–16) *The crown* The lower molars have the morphology which is typical for talpids in general. The outline does not vary much from assemblage to assemblage. Although one gets the impression – looking at the material – that the ratio between the width of the trigonid and that of the talonid ($\overline{W}1/\overline{W}2$) varies considerably, the histograms which include all three genera show a normal distribution for both the m1 and the m2 (fig. 13). The $\overline{W}2/\overline{L}$ ratio ranges from 0.69 to 0.92 for the m1, from 0.65 to 0.86 for the m2 and from 0.59 to 0.79 for the m3. It became apparent in the course of our study that the parameters L1 (length of the trigonid) and L2

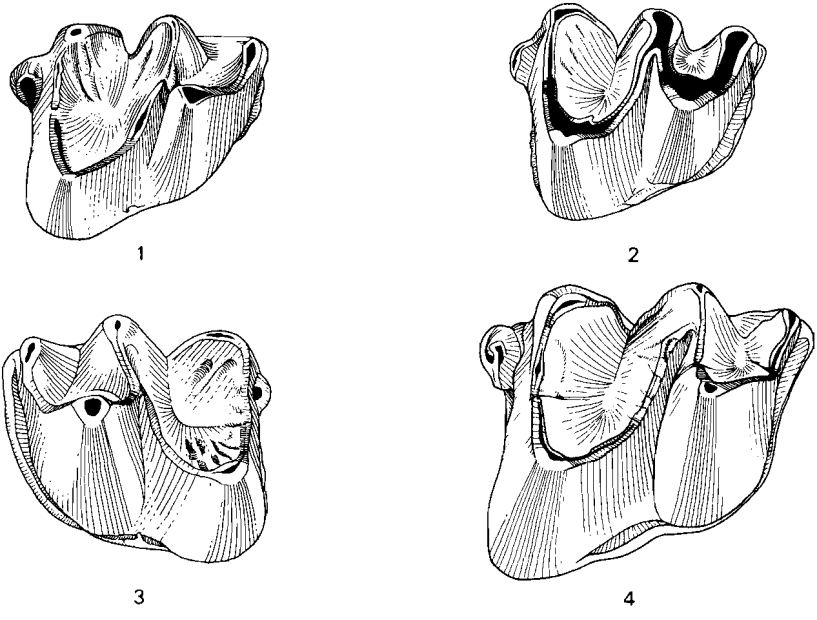


Fig. 14
1. m1 (dext) of *Dibolia major,* Va3-1031 occlusal-labial view.
2. m1 (dext) of *Galemys kormosi,* Te-606 occlusal-labial view.
3. m1 (sin) of *Desmana inflata,* V2a-103 occlusal-labial view.
4. m1 (dext) of *Desmana thermalis,* Te-161 occlusal-labial view.

(length of the talonid) cannot be measured with great accuracy as the measurements are influenced to a large extend by the degree of wear.

Although the shape of the molars does not vary much, the general appearance may differ greatly. In some assemblages the teeth are heavy with sturdy obtuse cusps and high connecting ridges, in others they are more slender with sharp cusps and low crests. The oblique cristid may be short or long, ending either against the protoconid-metaconid crest or near the tip of the metaconid. In the m3 the oblique cristid may be shorter, meaning that it ends further labially than in the m1 and the m2 of the same assemblage. Often faint ribs, radiating from the tips of the cusps, are visible on the cusps ajoining the talonid basin.

A strong entostylid is always present in m1 and m2; in some assemblages a relatively high percentage of the m3's possess one too. It can be either a bulge formed by the posterior cingulum or a rounded or elliptical tubercle situated near the enamel-dentine boundary.

A strong anterior cingulum is common in all three molars. In the m1 it

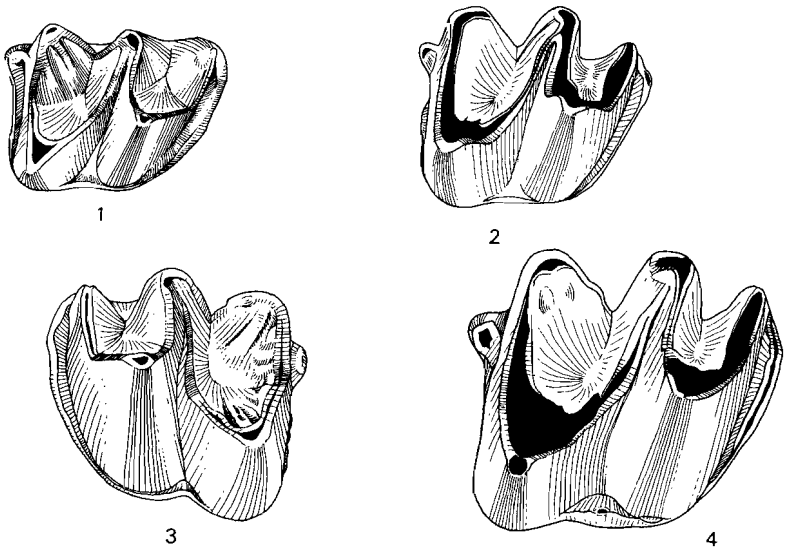


Fig. 15
1. m2 (dext) of *Dibolia dekkersi*, Me-389 occlusal-labial view.
2. m2 (dext) of *Galemys kormosi*, Te-622 occlusal-labial view.
3. m2 (sin) of *Desmana inflata*, V2a-136 occlusal-labial view.
4. m2 (dext) of *Desmana thermalis*, Te-185 occlusal-labial view.

sometimes shows a narrow stretch or an interruption at some distance from the antero-lingual corner. In the m2 and the m3 it widens before it ends rather abruptly just before reaching the lingual border, forming a kind of parastylid. Posterior and labial cingula vary greatly in width and length.

The roots The molars have two heavy roots: one is situated below the trigonid, the other one below the talonid. They support the entire crown-base, but for a narrow transverse trench; at their tip they are laterally flattened.

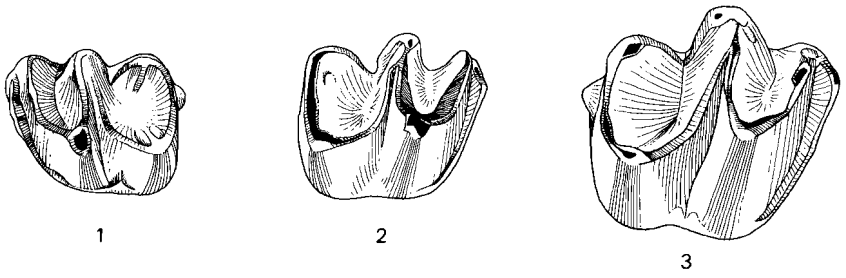


Fig. 16 1. m3 (sin) of *Dibolia major*, Va3-1046 occlusal-labial view.
2. m3 (dext) of *Galemys kormosi*, Te-646 occlusal-labial view.
3. m3 (dext) of *Desmana thermalis*, Te-204 occlusal-labial view.

The upper teeth

Within the subfamily two types of first upper incisors can be distinguished. Type A is a short straight tooth with a bifid tip that occurs in the new genus *Dibolia* and type B – a long curved tooth ending in a pointed tip – is characteristic for the genera *Galemys* and *Desmana.*

I1 Type A (figs. 17 and 18) *The crown* The crown is low and triangular, with a short medial face, a convex anterior face and a flat or slightly convex labial face. The ventral edge of the anterior face, which forms the top of the crown, is indentated. This indentation is of varying depth and may be situated in the middle of the edge or – more frequently – further medially. The medial lobe may be low and thick, high and relatively thin or of intermediate height and thickness. The thin labial lobe forms a long straigth cutting blade.

On the external side of the tooth the anterior and labial faces merge at an obtuse angle. A cingulum or an ill-defined inflated zone may be present along the external – labial margin. The inner side of the crown may be either

relatively flat and wide or concave and narrow with a conspicuous bend between the medial and the labial sides. The medial edge may feature a blunt or a sharp crest or – more rarely – a true cutting blade. An inner cingulum is usually present. Its width and length may vary considerably; it may be a separate feature or the continuation of the medial crest or cutting blade.

The enamel of the crown is characteristically thick on the external side and thin on the inner side. In geologically younger assemblages there is a triangular enamel-free zone on the medial face.

On the basis of these features two morphotypes can be distinguished in the I1 of type A. The crown of morphotype AW is characterized by a wide

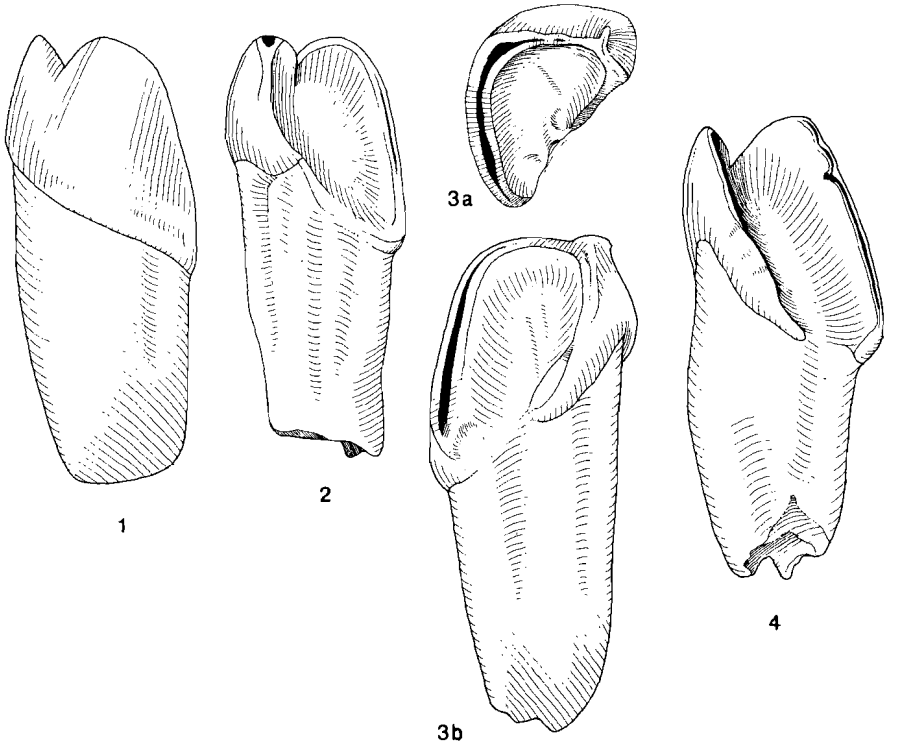


Fig. 17 1. I1 (dext) – morphotype AW – of *Dibolia turolense*, Cu-140 external view.
2. I1 (sin) – morphotype AW – of *Dibolia dekkersi*, Me-10 internal view.
3. I1 (dext) – morphotype AW – of *Dibolia major*, Ma7-262 a) occlusal view b) inner view.
4. I1 (sin) – morphotype AN – of *Dibolia* sp, Mo-4511 inner view.

and relatively flat inner side, a low and thick medial lobe with a low enamel-free area, a blunt medial edge or a low crest and an inner cingulum that is short and weak in Early and Middle Turolian assemblages and longer and/or stronger in Late Turolian occurrences. The crown of morphotype AN is characterized by a narrow and strongly concave inner side, a high and rather thin medial lobe with a high enamel-free area, a strong medial crest or a cutting blade and (usually) a long and strong inner cingulum. In this morphotype the medial lobe is often higher than the labial one.

Morphotype AW occurs in Dorn-Dürkheim, Masada del Valle 2, Aljezar B, Cubla, Masada del Valle 5, Masada del Valle 6, Valdecebro 3, Masada del Valle 7, La Fontana 1a, Villalba Baja 1, Maramena 1, Gorafe 1, Orrios and Sète. Morphotype AN is found in Kardia, Dinar-Akçaköy, Ptolemais 3, Moreda, Limni 6 and according to Fejfar (pers. comm.) in Ivanovce.

The root In both morphotypes the root is strongly compressed laterally. It has an irregular surface with longitudinal, rope-like ribs. It it straight or very slightly curved.

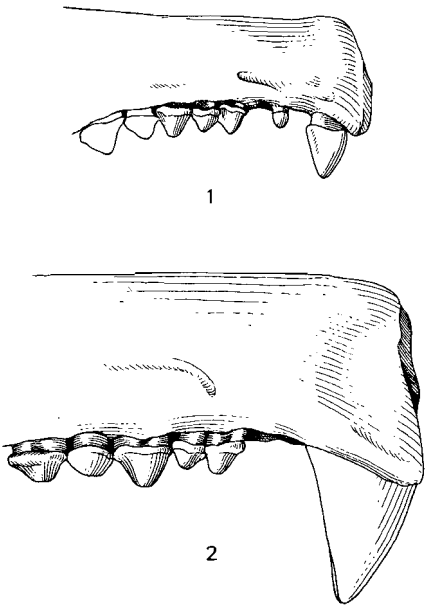


Fig. 18 1. Fragment of a maxillary with I1–I2, C–P4 of *Dibolia brailloni*, Sète. The I1 is allocated to morphotype AW.
2. Fragment of a maxillary with I1–P2 of *Desmana moschata*. The I1 is allocated to type B.
X 3.2.

Fig. 19 1. I1 (dext) – type B – of *Desmana inflata,* V2e-255
external view.
2. I1 (sin) – type B – of *Desmana verestchagini,* Sp1-311
external view.
3. I1 (dext) – type B – of *Desmana thermalis,* Te-228
a) external view b) inner view.

The position in the jaw The I1 stands nearly vertically (see fig. 18). At the tip of the rostrum the premaxillary forms a low ridge between the sockets of the left and right tooth. The enamel-free area on the medial face of the teeth is the part of the crown that is covered by this ridge. The labial wear-facet of the I1 reaches from the tip of the crown to the level of the occlusal surfaces of the very small and low I2 and I3. A short diastema is always present between the I1 and the I2.

I1 Type B (figs. 18 and 19) *The crown* The crown is long and strongly compressed laterally. It is usually curved in the medial plane, which means that it has a slightly concave medial and a somewhat convex labial side. The strongly curved anterior border and the straight or slightly concave posterior one are characteristic.

The anterior face is shallow V-shaped in geologically older assemblages, flat in younger ones. It may either merge gradually – at an obtuse angle – into the flat labial face, or at an acute angle. If the angle is obtuse the tip of the crown lies medially, if it is acute the tip is situated labially. The latter situation is found more often in geologically older occurrences. The thin labial border forms a sharp cutting edge. The wide and flat medial face shows a high enamel-free area.

The inner side of the crown is either concave with a strong medial crest, or flat with or without an inconspicuous crest. The enamel on the inner side of the crown is very thin – it may even be absent in some assemblages – and the boundary between the enamel and the dentine of the root is vague. In the extant species *Desmana moschata* the internal enamel surface is coarsely striated longitudinally.

Cingula and inflated zones are absent.

The root The root is more compressed than the crown. It is strongly convex anteriorly and concave posteriorly.

The position in the jaw (based on the skull of *Desmana moschata*) The rostrum is broad. At the front the premaxillary comes down sharply, medially more so than labially, filling the medial gap between the left and right I1. The bone forms a ridge, which causes the high enamel-free area on the medial face of the tooth. A diastema is present between the I1 and the I2.

I2 and I3 (figs. 18 and 20) *The crown* It is difficult, often even impossible, to distinguish the I2 from the I3. Both teeth are small and roughly of the same size: the I2 may be smaller, of the same size or larger than the I3. The morphological variation in the I2 and the I3 is similar. As a rule the cross-section of the I2 is elliptical, that of the I3 rounded, but the reverse is also found. As is the case in the premolars, the labial side is convex, the lingual side varying from concave to convex. The medial crest is often sharp.

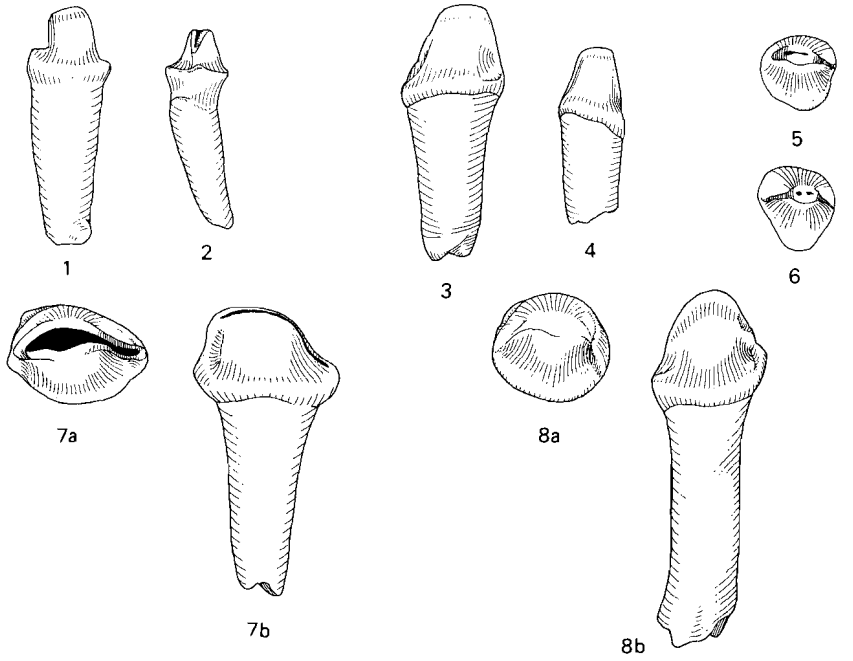


Fig. 20
1. I2 (dext ?) of *Dibolia turolense*, Cu-143 side view.
2. I3 (?) of *Dibolia turolense*, Cu-152 anterior or posterior view.
3. I2 (dext) of *Desmana verestchagini*, Pt1-761 lingual view.
4. I3 (sin ?) of *Desmana verestchagini*, Pt1-772 side view.
5. I2 (sin) of *Desmana inflata*, V2e-265 occlusal-lingual view.
6. I3 (sin ?) of *Desmana inflata*, V2e-268 occlusal-lingual? view.
7. I2 (sin) of *Desmana thermalis*, Te-242 a) occlusal-lingual view b) lingual view.
8. I3 (dext) of *Desmana thermalis*, Te-262 a) occlusal-lingual view b) lingual view.

In both teeth the crown is surrounded by an inflated zone or a cingulum. The inflated zone may form a wide rim around the cusp, but in most assemblages the I2 and the I3 look like "normal" unicuspids.

The root The straight root of the I2 is heavy, that of the I3 is thinner and sometimes hooked or curved.

The position in the jaw The teeth stand either upright or inclined backwards in the jaw. A diastema may be present between the I2 and the I3 and between the I3 and the C.

N.B. At the least in *Desmana moschata* both the I2 and the I3 are set in the maxillary, not in the premaxillary as is normally the case.

C (fig. 21) *The crown* In contrast to the lower canine, which is incisiform, the upper canine is premolariform. The relative size of the canine varies considerably: in some assemblages the C is about as large as the P2, while in others it is a small tooth. As a rule the crown is high relative to its length. Characteristically the gradient of the anterocrista is steeper than that of the posterocrista. The outline of the crown is elliptical – either wide or narrow – or egg-shaped with a wide posterior part. The $\overline{W}/\overline{L}$ ratio ranges from 0.60 to 0.92. In many assemblages, especially in geologically older ones, the enamel-dentine boundary curves upwards in the middle of the lingual and the labial sides.

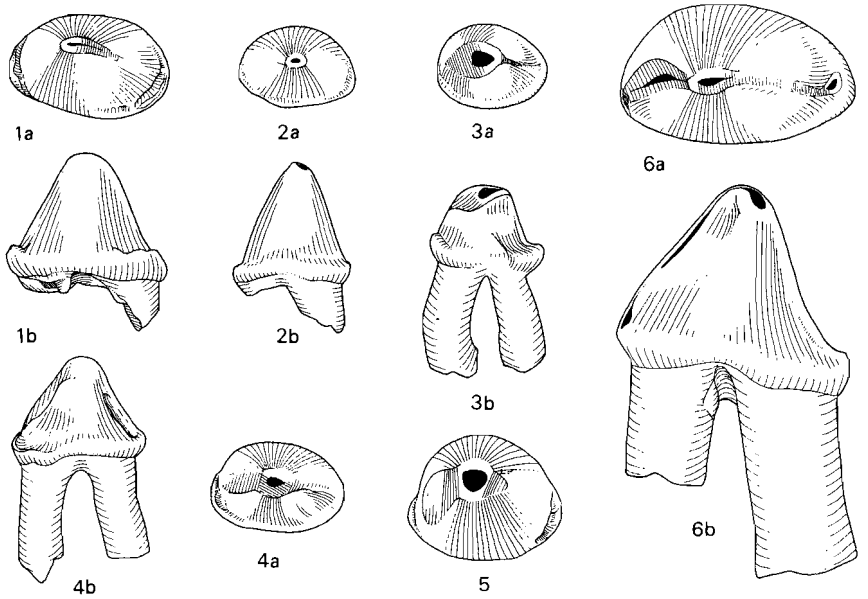


Fig. 21
1. C (sin) of *Dibolia turolense*, Ma5-1062
   a) occlusal-lingual view b) lingual view.
2. C (sin) of *Dibolia dekkersi*, Go1-861
   a) occlusal-lingual view b) lingual view.
3. C (sin) of *Dibolia dekkersi*, Ka-964
   a) occlusal-lingual view b) lingual view.
4. C (sin) of *Galemys kormosi*, Te-722
   a) occlusal-lingual view b) lingual view.
5. C (sin) of *Desmana inflata*, V2e-305
   occlusal-lingual view.
6. C (sin) of *Desmana thermalis*, Te-287
   a) occlusal-lingual view b) lingual view.

The lingual side may be flat or convex, the labial side is always convex. The posterocrista is sharp – causing a pointed posterior end – or obtuse, in which case the end of the crown is rounded. The anterocrista is nearly always obtuse and consequently the anterior end will normally be rounded.

In geologically older assemblages the anterior and posterior cingula are heavy and long and often connected by a lingual cingulum. In younger occurrences the cingula are replaced by inflated zones. Small cingular bulges are sometimes present.

The roots The two roots may be divergent or parallel. In rare instances they are fused, either at their base or along the lingual side.

The position in the jaw The canine has always a straight position relative to the length axis of the jaw.

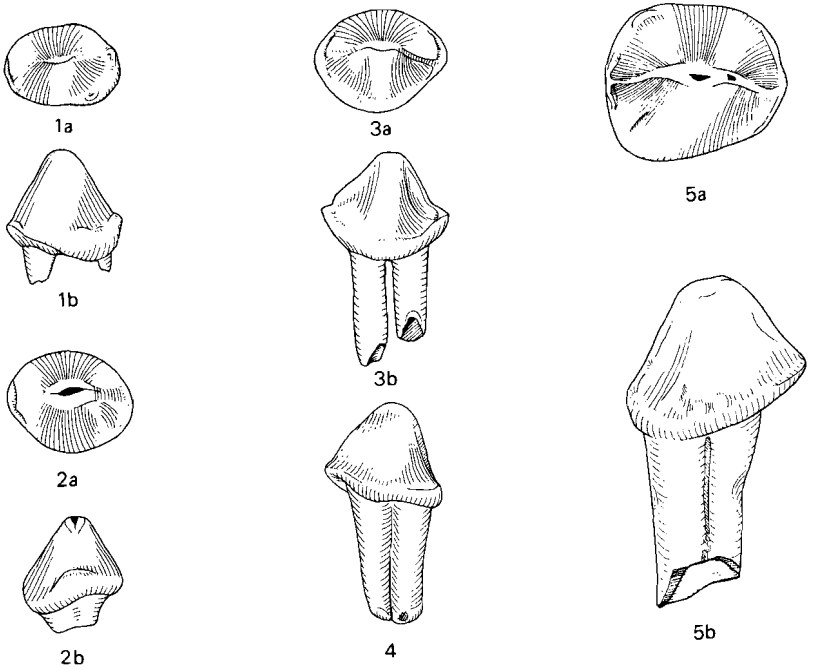


Fig. 22
1. P1 (sin) of *Dibolia turolense*, Cu-173
a) occlusal-lingual view b) lingual view.
2. P1 (sin) of *Dibolia major*, Ma7-578
a) occlusal-lingual view b) posterior view.
3. P1 (sin) of *Galemys kormosi*, Te-742 (rev.)
a) occlusal-lingual view b) lingual view.
4. P1 (sin) of *Desmana verestchagini*, Pt1-804
lingual view.
5. P1 (dext) of *Desmana thermalis*, Te-303
a) occlusal-lingual view b) lingual view.

P1 (fig. 22) *The crown* The P1 is the smallest of the upper premolars. The low crown has usually a rounded or an elliptical cross-section, but more irregular shapes may occur. The $\overline{W}/\overline{L}$ ratio ranges from 0.65 to 0.98. The enamel-dentine boundary may curve upwards in the middle of the labial side.

The lingual side is slightly concave, flat or slightly convex; the labial side is always convex. In many specimens the crown partly overhangs the root, but this feature falls within the variation of a single assemblage. Both ends of the crown are rounded or somewhat pointed and may show a slight flattening. An antero-lingual flattening combined with a postero-labial one is most common, but other combinations as well as symmetrical forms occur.

Posterior and anterior cingula are rarely very pronounced; lingual and especially labial cingula are rare. Cingula are often indicated by inflated zones. Small cingular bulges – though rare – may be present.

The roots The P1 may have one or two roots. If the tooth is single-rooted, the root is extremely wide and compressed anterior-posteriorly; if it is double-rooted, the roots may be fused either at their base or all the way down or they may be separate. They have a rounded or an anterior-posteriorly compressed cross-section.

The position in the jaw The P1 is sometimes situated obliquely in the jaw relative to the length of the jaw. When this does happen, the anterior end of the crown may be placed either lingually or labially.

P2 (fig. 23) *The crown* The tooth has a sturdy crown. Usually it has sharp cristae and a sharp tip, more rarely it is rounded or inflated with blunt cristae. With only a few exceptions it has an egg-shaped outline, i.e. it is wider posteriorly than anteriorly. The $\overline{W}/\overline{L}$ ratio ranges from 0.58 to 0.82.

The labial side of the crown is strongly convex, the lingual side less so. Concave or flat posterior faces may be present lingually as well as labially. The anterior and posterior ends are rounded. The crown sometimes overhangs the root labially.

In many assemblages a high and heavy cingulum runs around the posterior and postero-lingual parts of the crown, ending about half-way along the lingual side where it causes a widening of the crown-base. The cingulum may end either at the level of the crown-base or against the slope of the paracone. In this last case it often forms a flat spur or a small bulge. This lingual extension is comparable with the lingual lobe of the P4. In some assemblages the lingual extension is not formed by the cingulum, but by the paracone. In rare instances an extension is present not only on the lingual side, but on the labial side as well. Finally there are assemblages which lack a lingual extension. A labial cingulum is usually missing; an anterior cingulum – however

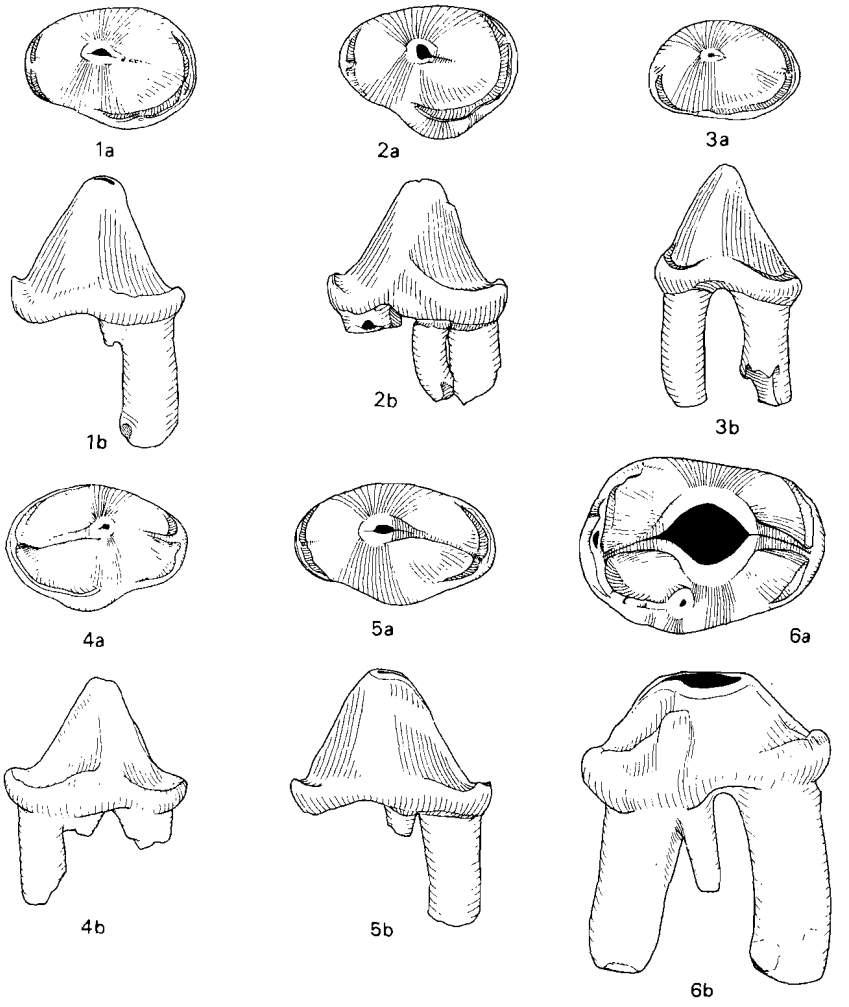


Fig. 23
1. P2 (sin) of *Dibolia turolense*, Ma2-3171
a) occlusal-lingual view b) lingual view.
2. P2 (sin) of *Dibolia turolense*, Cu-183
a) occlusal-lingual view b) lingual view.
3. P2 (sin) of *Dibolia dekkersi*, Pt3-778
a) occlusal-lingual view b) lingual view.
4. P2 (dext) of *Galemys kormosi*, Te-764
a) occlusal-lingual view b) lingual view.
5. P2 (sin) of *Desmana verestchagini*, Pt1-823
a) occlusal-lingual view b) lingual view.
6. P2 (dext) of *Desmana thermalis*, Te-328
a) occlusal-lingual view b) lingual view.

short – is always present and may form a small bulge at the base of the anterocrista.

The roots The tooth may have two or three roots. The lingual extension is supported by a wide posterior root or by a third rootlet. Intermediates are common and in most assemblages more than one type occurs. When the P2 is very heavily built, as is the case in the Valdeganga assemblages, it may happen that two accessory rootlets – a lingual and a labial one – are present or that a third root is situated labially instead of lingually. When the crown has an elliptical outline and no lingual widening is present, the posterior root is not enlarged and it has a rounded cross-section.

The position in the jaw The P2 is always set straight in the mandible, except in the living species *Galemys pyrenaicus.*

P3 (fig. 24) *The crown* The third upper premolar is – with only a few exceptions – smaller than the P2. The crown is low and relatively wide: the $\overline{W}/\overline{L}$ ratio varies from 0.60 to 1.02. The cross-section is rounded, sub-triangular or elliptical. The P3 may be heavy and obtuse or slender and sharp.

Both the lingual and labial sides of the crown are convex, often strongly so; the well developed postero-lingual and postero-labial faces are flat or concave. The posterior and anterior ends are usually rounded, but may be pointed in the more elliptical specimens.

The lingual widening of the tooth is similar in the P2 and the P3. In P3 – as in the P2 – the lingual extension may be formed by the cingulum, by the paracone or by both. As the P3 is as a rule more molarized than the P2, the lingual extension is often more conspicuous and a pronounced bulge, sometimes even a small basin which is closed by the postero-lingual cingulum, is present. The postero-lingual cingulum, which may end level with the crown-base in the P2, always ends against the slope of the paracone in the P3. A labial extension is found in some heavily built forms, resulting in either a very symmetrical shape or a rather irregular one. The labial, posterior and anterior cingula are slightly stronger in the P3 than in the P2, but otherwise the morphological variation in these teeth is similar.

The roots The P3 may have two or three roots; the variations are largely similar to those found in the P2. A labial accessory rootlet has not been observed: in specimens where a labial extension is present the posterior root is elongated and occupies a diagonal position.

The position in the jaw The position of the P3 in the mandible may vary from straight to strongly oblique relative to the length of the jaw. In many assemblages the position is somewhat variable, but in those where the P3 stands very obliquely this is the position encountered in all mandibles found

in that particular locality. It is apparent that the general shape of the P3 is not directly linked with its position in the jaw.

P4 (fig. 25) *The crown* The P4 is strongly molarized and has – apart from the main cusp (the paracone) and a pronounced lingual cusp (the protocone)

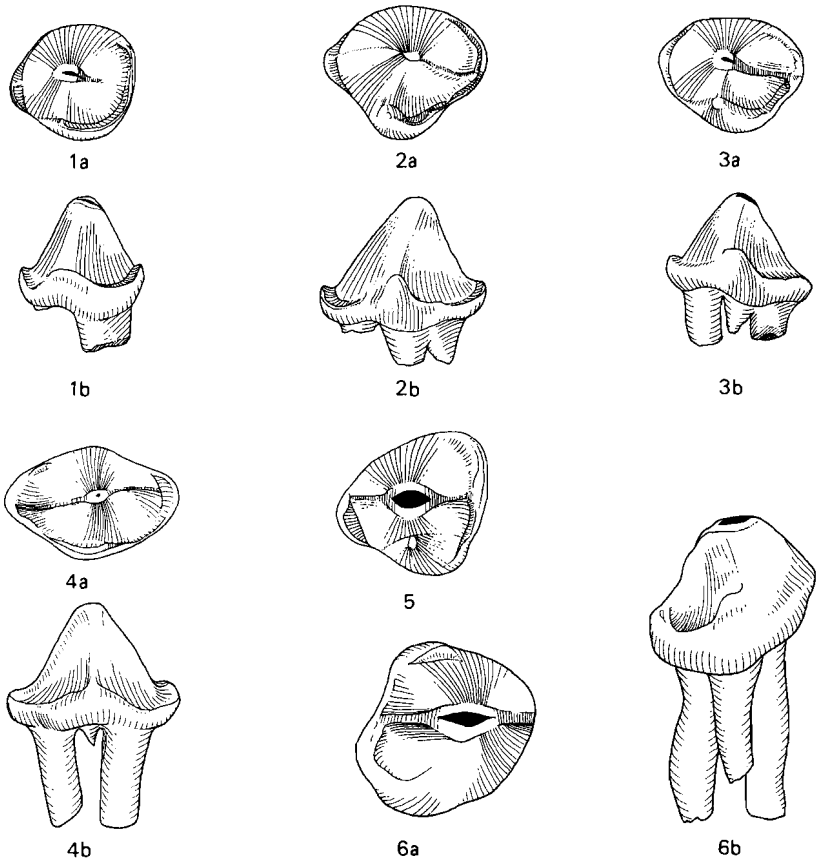


Fig. 24
1. P3 (sin) of *Dibolia turolense*, Ma2-3184
   a) occlusal-lingual view b) lingual view.
2. P3 (sin) of *Dibolia brailloni* Or-1066
   a) occlusal-lingual view b) lingual view.
3. P3 (sin) of *Dibolia dekkersi*, Ka-1056
   a) occlusal-lingual view b) lingual view.
4. P3 (dext) of *Galemys kormosi*, Te-783
   a) occlusal-lingual view b) lingual view.
5. P3 (sin) of *Desmana verestchagini*, Ka-1651
   occlusal-lingual view.
6. P3 (dext) of *Desmana thermalis*, Te-344
   a) occlusal-lingual view b) lingual view.

– a varying number of accessory cusplets. These have been homologized with the cusps of the molars. The P4 has characterically a sub-triangular outline with a curved labial border and straight or gently concave postero-lingual and antero-lingual borders. The $\overline{W}/\overline{L}$ ratio ranges from 0.73 to 0.95.

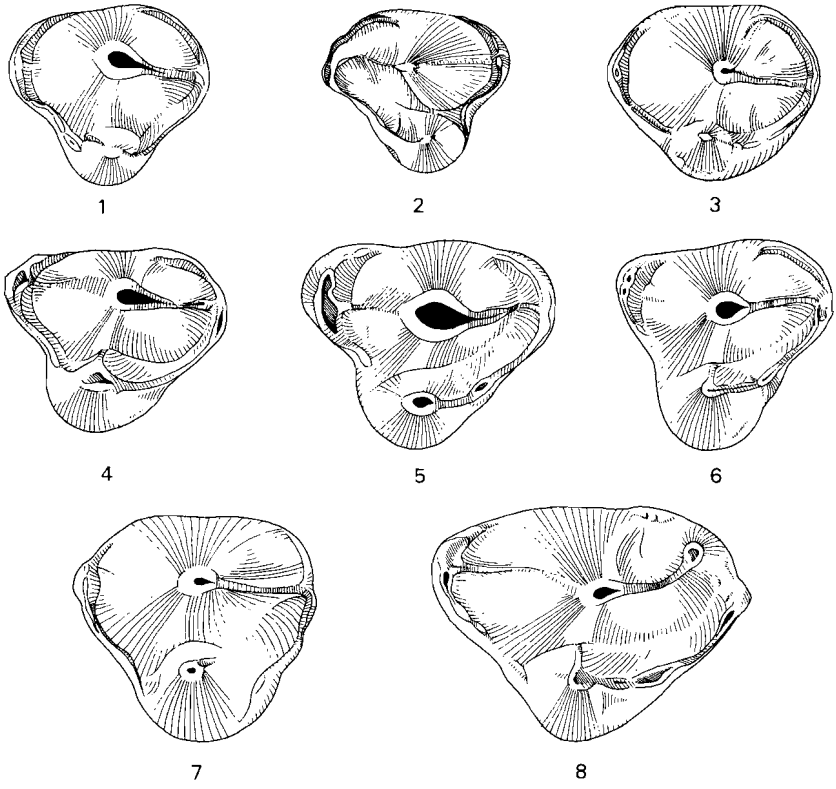


Fig. 25
1. P4 (sin) of *Dibolia turolense*, Ma2-3211 occlusal-lingual view.
2. P4 (dext) of *Dibolia dekkersi*, Me-121 occlusal-lingual view.
3. P4 (sin) of *Dibolia brailloni*, Go2-517 occlusal-lingual view.
4. P4 (sin) of *Galemys kormosi*, Te-810 occlusal-lingual view.
5. P4 (sin) of *Desmana verestchagini*, Ka-1661 occlusal-lingual view.
6. P4 (sin) of *Desmana verestchagini*, Pt1-862 occlusal-lingual view.
7. P4 (sin) of *Desmana inflata*, V2a-317 occlusal-lingual view.
8. P4 (sin) of *Desmana thermalis*, Te-361 occlusal-lingual view.

Both the lingual and the labial sides are convex apart from a flat or concave posterior face. The posterior end of the crown is rounded. The postero-crista which is always pronounced and sharp, either ends medially or bends to the labial side where it forms a small cusp – the metacone. The anterior end is more or less rounded. The anterocrista is usually obtuse but may be missing. Posteriorly and anteriorly the cingulum may form an extension of the crown; these extensions often bear cusplets: the metastyle and the parastyle.

The lingual lobe is very pronounced. In most assemblages the protocone is well individualized and separated from the paracone by a valley that continues far posteriorly.

The postero-lingual cingulum often bears a small cuspule – the hypocone. It is a wide and long cingulum that either ends at the foot of the protocone or at its tip. The postero-labial cingulum is strong and short. It may enclose a small basin at the foot of the concave postero-lingual face. The wide and long antero-lingual cingulum ends at the foot of the protocone; the strong antero-labial cingulum is short.

The roots The tooth has three roots – two main roots and an accessory rootlet that supports the lingual lobe – which are round in cross-section. Variations in the root pattern have not been observed.

M1 (fig. 26) *The crown* As in all talpids, the crown of the M1 has a lop-sided triangular outline due to the great difference in the morphology of the labial cusps. The single – posterior – arm of the paracone ends in the anterior cusp of the divided mesostyle. The anterior arm of the metacone ends in the posterior cusp of the mesostyle; the strongly extended posterior arm forms a long cutting blade. The labial border of the tooth may be straight or slightly convex. The $\overline{W}/\overline{L}$ ratio ranges from 0.70 to 0.94.

In addition to the paracone and the metacone the labial part of the crown bears three styles, i.e. the parastyle, the divided mesostyle and the metastyle. Of these the mesostyle is the largest. It consists of two conical or elongated cusps – the anterior one of which is the strongest – separated by a deep valley. The stoutness of the cusps and the depth and width of the valley between them vary from one assemblage to the other. The second largest style is the parastyle. It may be rounded or elongated, attached to the paracone by means of a high ridge or separated from it by a deep valley. The parastyle is always firmly connected to the protoconule by a short crest. The metastyle is a mere widening of the posterior cingulum and is sometimes missing.

The lingual part of the crown is made up of three cusps, to which a fourth accessory cusplet may be added. The main cusps are (from the front back-

wards): the protoconule, the protocone and the metaconule. The protoconule and the metaconule are of about the same size; they may vary from being weakly to strongly individualized. The protoconule is connected to the parastyle and may lie close to the protocone or be well separated from it. The metaconule is connected to the posterior cingulum, but separated from the posterocrista of the protocone by a wide valley. The degree of de-

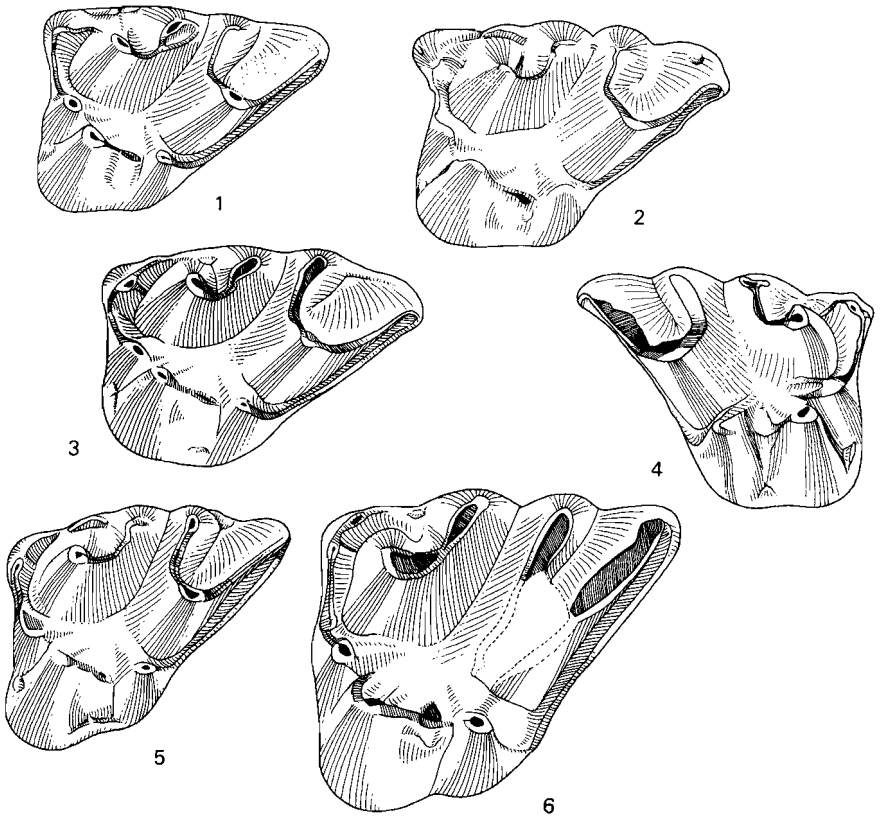


Fig. 26
1. M1 (sin) of *Dibolia dekkersi*, Ka-1141 occlusal-lingual view.
2. M1 (sin) of *Dibolia brailloni*, Or-1076 occlusal-lingual view.
3. M1 (sin) of *Dibolia brailloni*, Go2-518 occlusal-lingual view.
4. M1 (dext) of *Galemys kormosi*, Te-825 occlusal-lingual view.
5. M1 (sin) of *Desmana verestchagini*, Pt1-889 occlusal-lingual view.
6. M1 (sin) of *Desmana thermalis*, Te-381 occlusal-lingual view.

velopment of the protoconule and the metaconule influence the lingual outline of the crown: a strong development causes the anterior and/or the postero-lingual side to bulge outwards. Strong individualization results in deep trenches in the lingual face of the tooth. On the posterocrista of the protocone lies a small, hardly individualized cusplet in some assemblages.

The cingula of the M1 are made up of a long posterior cingulum, short stretches or beads at the base of the lingual trenches and short, weak antero-labial and postero-labial cingula.

The roots The tooth has three heavy roots: a long one below the lingual part of the crown, another running from the postero-labial corner to the centre of the crown-base and a wide antero-labial root. A low accessory root is situated in the centre of the crown. It is connected to the lingual root – and sometimes to the labial roots as well – by low crests.

M2 (fig. 27) *The crown* The labial part of the crown is symmetrical; the labial border shows three emarginations: between the two arms of the paracone and of the metacone respectively and between the two cusps of the divided mesostyle. In many specimens the posterior arm of the metacone ends further labially than the anterior arm of the paracone. The $\overline{W}/\overline{L}$ ratio varies between 1.07 and 1.34.

The mesostyle and the metastyle of the M2 are similar to the ones found in the M1; the small parastyle may be either an isolated cusp or a widening of the cingulum around (part of) the antero-labial corner of the crown.

The main lingual cusps are of the same shape and size as those of the M1. The lingual portion may be either symmetrical or asymmetrical, depending on the position of the protocone. The anterior and posterior borders are straight or somewhat concave. The accessory cuspule on the posterocrista of the protocone is usually weaker in the M2 than in the M1 of the same assemblage.

The cingula found in the M2 are of the same kind and have the same extension as those of the M1.

The roots The roots are similar to those in the M1, the only difference being that in the M2 the postero-labial root has the same shape as the antero-labial one, and that the connecting ridges are distinctly stronger.

M3 (fig. 28) *The crown* The crown has a sub-triangular outline with a long and straight anterior border and a strongly convex postero-labial side. The paracone is symmetrical; the metacone is asymmetrical because only its proximal arm is present. The labial side is indentated between the arms of the paracone and sometimes between the two cusps of the mesostyle as well. The $\overline{W}/\overline{L}$ ratio ranges from 1.26 to 1.48.

The parastyle – if present – is a small cingular cuspule or a slight widening of the cingulum. The mesostyle cusps are low and ill-defined.

The protoconule is low and usually weakly developed. A small cusplet may be found on the posterocrista of the protocone. The low metaconule is usually strong and sturdy. It is separated from both the lingual crest and the metacone and is situated either lingually or posteriorly of the latter. If the metaconule is well developed, the outline of the tooth shows a posterior bulge.

The wide and strong anterior cingulum is connected to the tip of the protoconule. A narrow cingulum is often present along the postero-labial

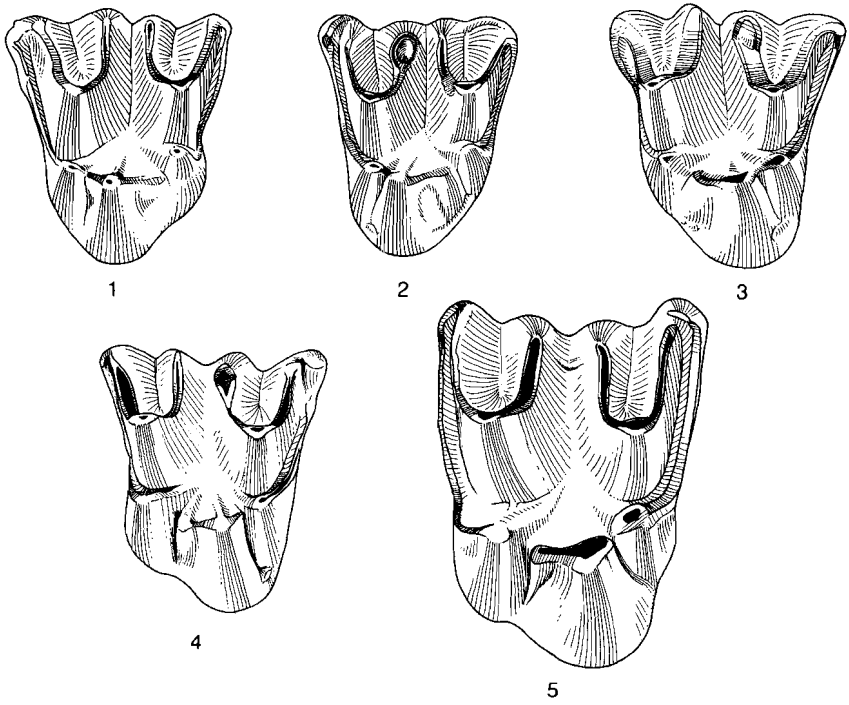


Fig. 27
1. M2 (sin) of *Dibolia major*, Va3-1092 occlusal-lingual view.
2. M2 (sin) of *Dibolia dekkersi*, Ka-1179 occlusal-lingual view.
3. M2 (dext) of *Dibolia brailloni*, Es-7091 occlusal-lingual view.
4. M2 (dext) of *Galemys kormosi*, Te-844 occlusal-lingual view.
5. M2 (dext) of *Desmana thermalis*, Te-404 occlusal-lingual view.

side and small beads or short stretches of interrupted cingulum may be found along the lingual border.

The roots The three roots are heavy. The one supporting the metacone and the metaconule is much enlarged. In some specimens the labial roots are connected by a low crest to a minuscule, centrally situated rootlet.

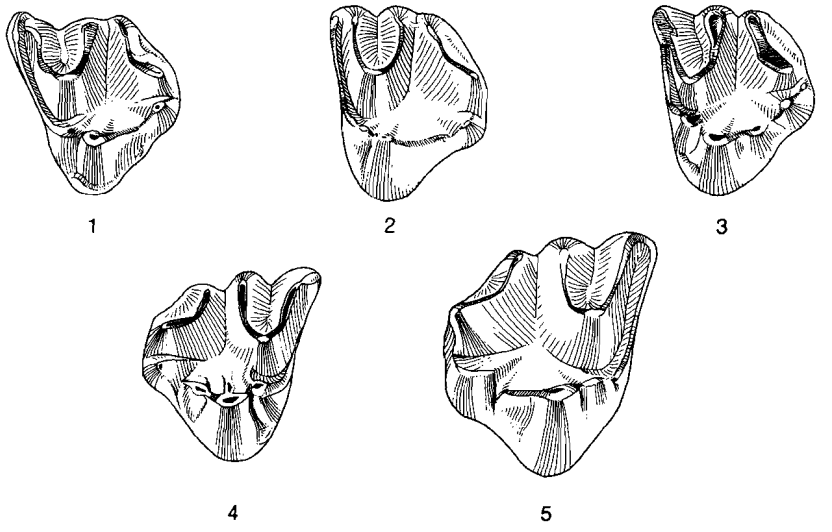


Fig. 28
1. M3 (sin) of *Dibolia turolense*, Cu-232 occlusal-lingual view.
2. M3 (sin) of *Dibolia major*, Va3-1096 (rev.) occlusal-lingual view.
3. M3 (sin) of *Dibolia dekkersi*, Pt3-852 occlusal-lingual view.
4. M3 (dext) of *Galemys kormosi*, Te-864 occlusal-lingual view.
5. M3 (dext) of *Desmana thermalis*, Te-421 occlusal-lingual view.

Remarks

Two clearly distinct types of first upper incisors can be distinguished, i.e. type A (a stout, straight tooth with a bifid tip) and type B (a slender, curved tooth with a pointed tip). A fragmentary I1 with a weakly indentated upper edge but without a medial lobe is found in Spilia 4 (Late Ruscinian). It is the only specimen that does not fit our morphotypes and it probably represents a type of I1 that is intermediate between type A and type B.

The I1 found in the oldest known water-moles show morphotype AW (figs. 29.1 and 29.2). This morphotype has been found in Dorn-Dürkheim

and in Turolian to Early Ruscinian assemblages from Spain. Incisors showing morphotype AN occur during the Early Ruscinian in eastern Europe and Turkey and during the Late Ruscinian in Spain (fig. 29.3). The incisor found in Limni 6 (earliest Villanyian, Greece) is also of this type. Incisors of type B occur from the Early Ruscinian onwards; the oldest known I1 of this type is found in Spilia 1 (fig. 29.6).

The fragmentary I1 from Spilia 4 is shown in combination with a fragment found in Spilia 1 (figs. 29.4 and 29.5 respectively). Together the two fragments give a picture of an incisor that could be regarded as intermediate between type A and type B. Unfortunately the I1's found in Spilia 1 are all very worn, but it is striking that the top of the crown is spatulate (fig. 29.6), while in younger forms it is pointed (fig. 29.7, a specimen from Tegelen, Late Villanyian).

From the preceding sections it becomes obvious that – with exception of the i1 and the I1 – the morphological variations found in the teeth of the Desmaninae seem to occur at random, that means that no distinct morphotypes are apparent on which species can be based. Moreover, a change in one element is not necessarily accompanied by a change in the adjacent or occluding teeth. The two types of I1 differ so much in their morphology and size that one must assume that their function differed completely, but the differences are not expressed in the morphology of the rest of the dentition with the exception of the i1.

Features such as the presence or absence of cingular bulges and small cuspules, and inconspicuous variations in the shape of the crown of incisors, canines and premolars fall within the range of variation of an assemblage. When the two jaws of a single individual or a skull are studied, one can see the difference between the left and right teeth. Apparently these differences have no diagnostic value whatsoever.

Another group of variations concern features like the presence or absence of a metaconid or a metaconal rib in the p4, the number of roots in the P2 and P3 and pronounced changes in the shape and outline of the crown of the teeth. These – too – may vary within a single assemblage, but most assemblages are uniform. These phenomena appear time and time again in desmanine teeth and although they may be useful for distinguishing assemblages, their appearance often seems to be random and they are considered to have no diagnostic value. This does not alter the fact that some of these features, such as the reduction of the number of roots in p1 and P1, the increase in the size of the paraconid in p1–p3 and the decrease in strength and extension of the cingula show more or less pronounced trends that are found in all genera of the Desmaninae.

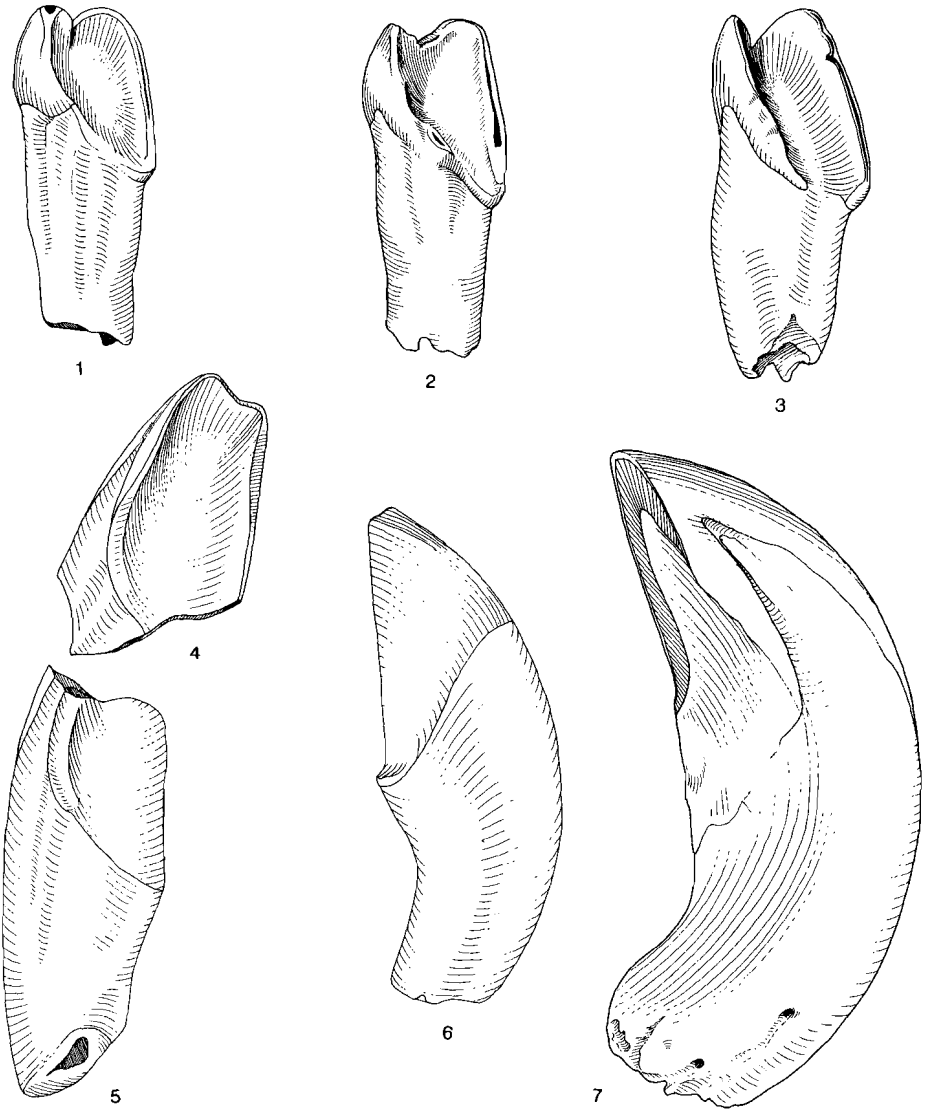


Fig. 29
1. I1 (sin), morphotype AW, Me-10 Late Turolian inner view.
2. I1 (sin), morphotype AW, VB-211 Late Turolian inner view.
3. I1 (sin), morphotype AN, Mo-4511 Late Ruscinian inner view.
4. I1 (sin), intermediate type, Sp4-1 Late Ruscinian inner view.
5. I1 (sin), type B, Sp1-314 Early Ruscinian inner view.
6. I1 (sin), type B, Sp1-311 Early Ruscinian outer view.
7. I1 (dext), type B, Te-228 Late Villanyian inner view.

X 7.3

A third group of peculiarities that appear to vary greatly are for instance the way p1/P1 and p3/P3 are set in the jaw and the general appearance of the dentition: the teeth may be gracile with high slender cusps and sharp ridges, or bulky with low obtuse cusps. Slight discrepancies from modality are insigificant, but when the differences are great and consistent throughout the assemblage, they may be an expression of a different diet and a different mode of life. These differences are regarded as characteristic and diagnostic on the species level because they are considered to express genetic changes.

Conclusions

The dentition of the Desmaninae is uniform and stable throughout time. The only features which in our opinion should be regarded as diagnostic on the generic level are the morphological characteristics of the i1 and the I1. The genus *Dibolia* n.g. is characterized by the fact than the individuals possess an i1 of type a and an I1 of type A, while *Desmana* and *Galemys* have an i1 of type b and an I1 of type B. Less pronounced morphological changes – even when showing a trend – are considered to have no taxonomic value except the few which show an adaptation to a different diet. This adaptation is revealed in the general appearance of the teeth and in a deviation from the way the teeth are normally set in the jaw.

Chapter 5

MEASUREMENTS

Introduction

Of the canines, premolars and upper molars the maximum length (L) and the maximum width taken at right angles to the length (W) have been measured; of the lower molars the maximum length (L), the width of the trigonid (W1) and that of the talonid (W2) were taken (see fig. 4). The data have been plotted in three kinds of diagrams, namely length – width diagrams, minimum – maximum diagrams and tooth length diagrams.

Length–width diagrams (figs. 30–35)

Diagrams were made for each of the sixteen different elements that have been measured. Of each assemblage the mean value of the length ($\overline{L}$) was plotted against the mean width ($\overline{W}$), in case of the lower molars the width of the talonid ($\overline{W}2$) was taken. For each element all available data – irrespective of to which genus or species the associations belong – were plotted in one diagram. Different symbols were used for the three genera recognized.

The pictures obtained from the diagrams prove to be basically the same for all teeth; however, some teeth appear to be more variable than others. Those six that show the most pronounced trends, namely p2–p4 and P2–P4 are included here.

Although the values of the *Dibolia* teeth cluster, length and width are but moderately correlated. The differences in size between the various assemblages are small.

In some of the $\overline{L}/\overline{W}$ diagrams a certain grouping of values is apparent, but the groups are not the same in all diagrams. For instance, on the $\overline{L}/\overline{W}$ diagrams of the p3 and the P3 (figs. 31 and 34) the values of Valdecebro 3 (Va3), Masada del Valle 7 (Ma7) and Escorihuela (Es) lie close together, but on the diagrams of the p2 and the P2 (figs. 30 and 33) the values of these assemblages lie far apart. Still more pronounced differences are found in the case of Aljezar B (LA), Ptolemais 3 (Pt3), Dinar-Akçaköy (DA) and Sète (Se), which show a close similarity in the size of the p3 (fig. 31), while the points representing the p2 and the p4 are dispersed over the entire range (figs. 30 and 32).

Two groups – based on size differences – can be distinguished in the

material not belonging to the genus *Dibolia,* i.e. the assemblages with a curved, pointed I1. The teeth of the small sized group, which includes *Galemys pyrenaicus,* are of the same length as those of the *Dibolia* assemblages. A striking difference exists between the values of the teeth from Weze 1 (We) and those of the younger assemblages belonging to this group (Rebielice Królewskie 1 and 2 [RK1, RK2], Tegelen [Te], *Galemys pyrenaicus* [Rg]). The teeth from Weze 1 fall invariably in the *Dibolia* cluster, while the teeth of the younger assemblages are relatively narrower. They cluster on a straight line, showing a stronger $\overline{L}/\overline{W}$ correlation than the teeth of *Dibolia.* The few teeth from Beremend (Br) seem to occupy an intermediate position. This small sized group, to which belong also the small desmanine mole from Venta Micena (Gibert in Moyà-Solà et al, 1981) and the four

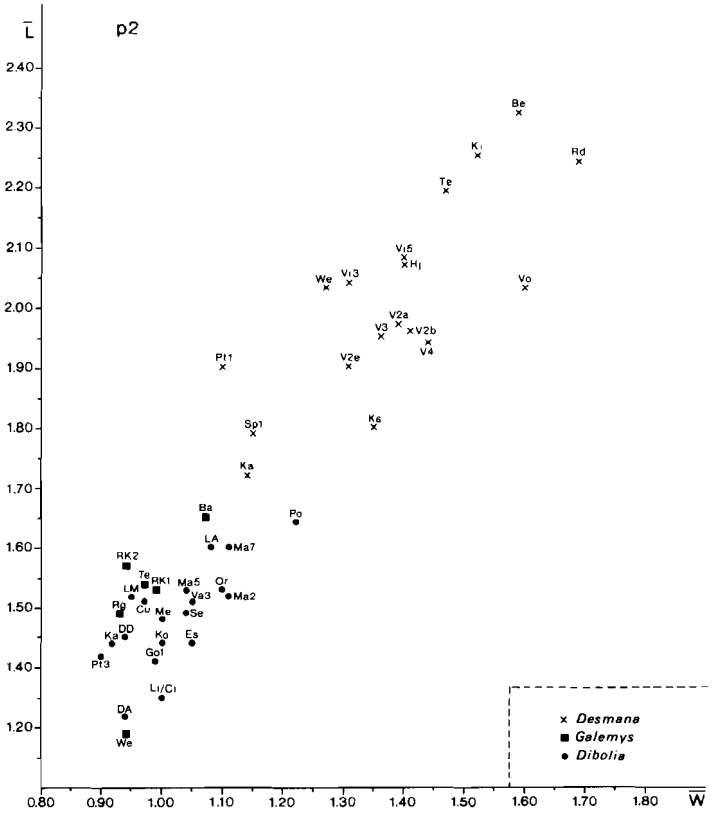


Fig. 30 Diagram showing the $\overline{L}/\overline{W}$ ratio of the p2. For the explanation of the abbreviations used for the localities see table 1.

teeth described as *Galemys semseyi* (Kormos, 1913) from Betfia 2 (Be), has been allocated to the genus *Galemys*.

The teeth of the second non-*Dibolia* group are medium to large sized, showing a small overlap with the *Dibolia/Galemys* clusters. This overlap includes the oldest assemblages with a "modern" type of I1, viz. Spilia 1 (Sp1), Kardia (Ka) and Ptolemais 1 (Pt1). The group as a whole occupies a broad, straight zone with the same direction as – and forming a continuation of – the *Dibolia/Galemys* clusters. The group includes *Desmana moschata* (Rd) and the assemblages are therefore allocated to the genus *Desmana*.

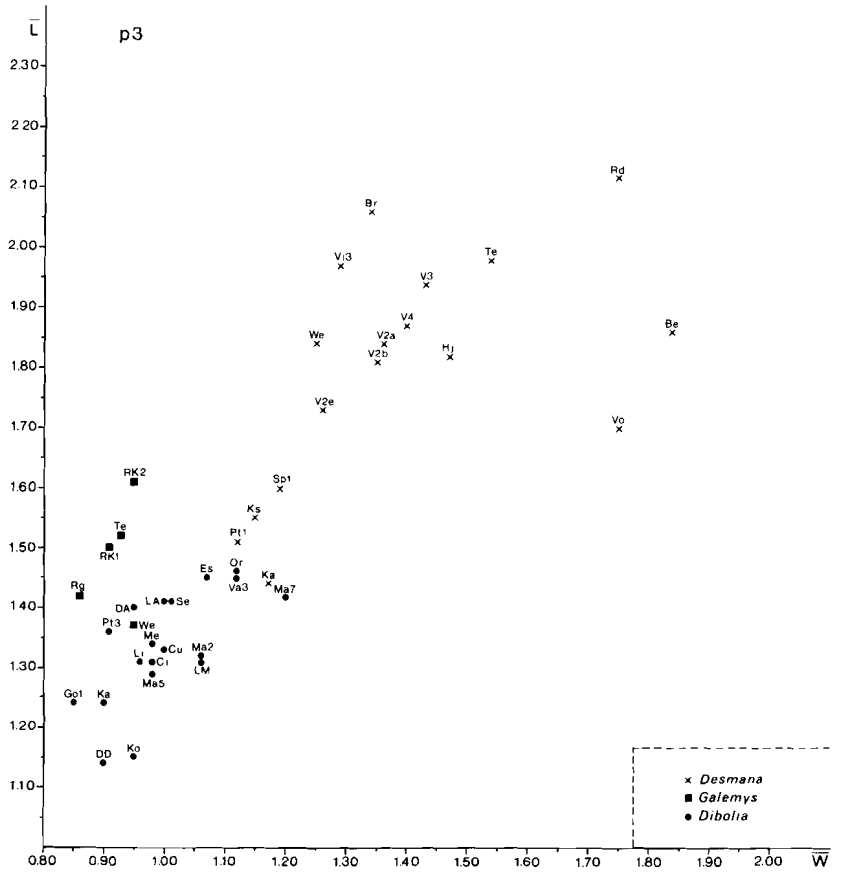


Fig. 31 Diagram showing the $\overline{L}/\overline{W}$ ratio of the p3. For the explanation of the abbreviations used for the localities see table 1.

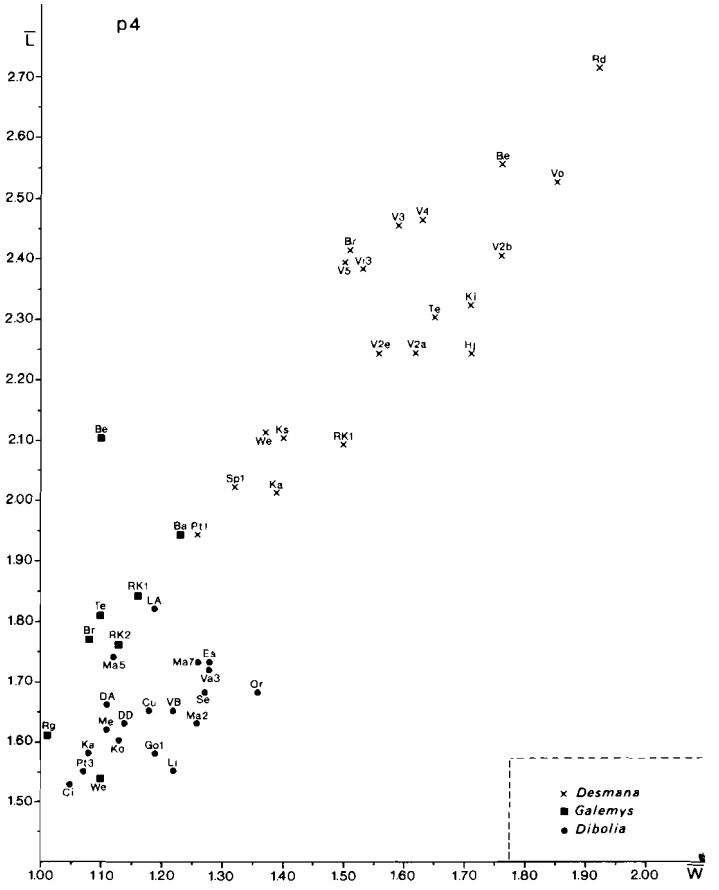


Fig. 32 Diagram showing the $\overline{L}/\overline{W}$ ratio of the p4. For the explanation of the abbreviations used for the localities see table 1.

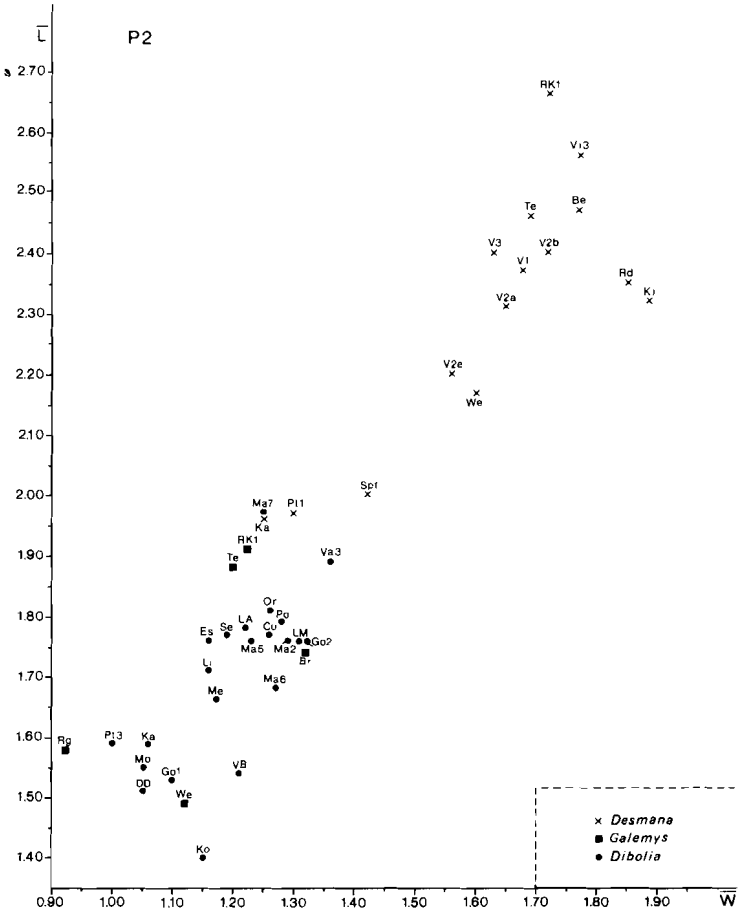


Fig. 33 Diagram showing the $\overline{L}/\overline{W}$ ratio of the P2. For the explanation of the abbreviations used for the localities see table 1.

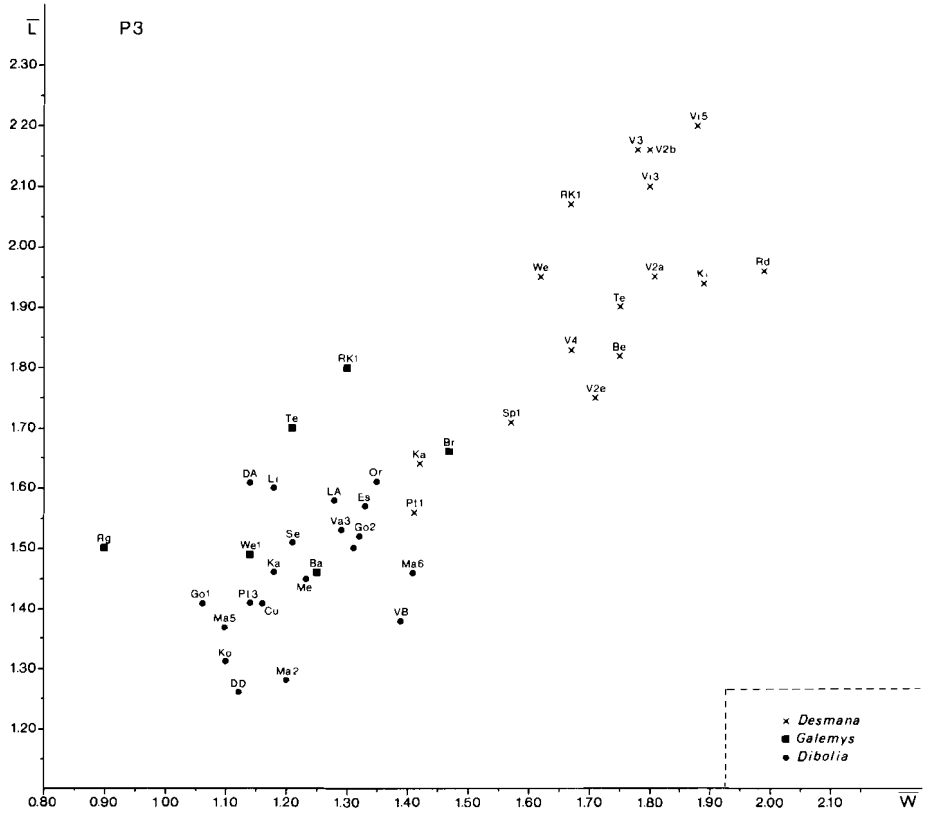


Fig. 34 Diagram showing the $\overline{L}/\overline{W}$ ratio of the P3. For the explanation of the abbreviations used for the localities see table 1.

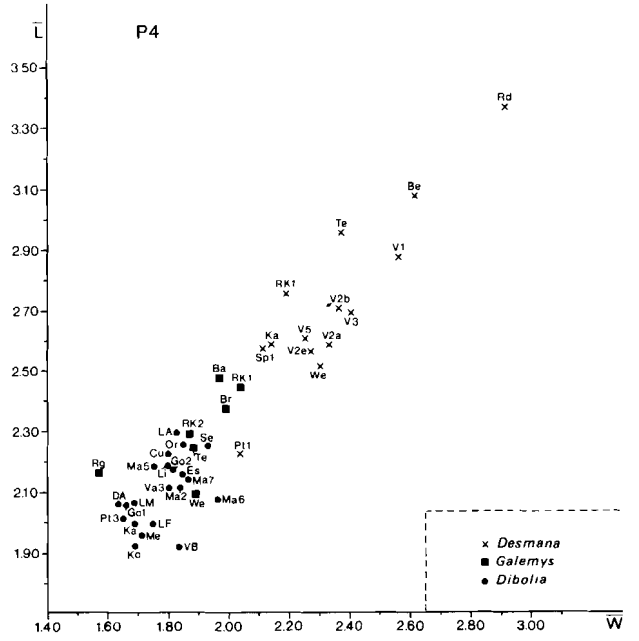


Fig. 35 Diagram showing the $\overline{L}/\overline{W}$ ratio of the P4. For an explanation of the abbreviations used for the localities see table 1.

Minimum–maximum diagrams (figs. 36–45)

These diagrams have been made for the length of the p2, p3, p4, m1, m2 and the C, P2, P3, P4, M2. Of the other teeth some are found in small quantities (p1 and P1), others do vary little (c, m3 and M3) or in an irregular way (M1). Each entry gives – in addition to the measured length range – the mean length and the number of specimens measured per assemblage. Figs. 36 to 40 are diagrams of the *Dibolia* teeth, figs. 41 to 45 of the elements of *Galemys* and *Desmana*. The width of the teeth are not given; they will be brought into the picture when needed.

Tooth length diagrams (figs. 46–48)

These diagrams give the absolute as well as the relative length of the teeth within each assemblage, allowing for comparison of assemblages. The mean length of each element has been plotted; the solid line connects the dots giving the values of the lower teeth, the dashed line those of the upper teeth. The number next to the dot gives the number of specimens measured.

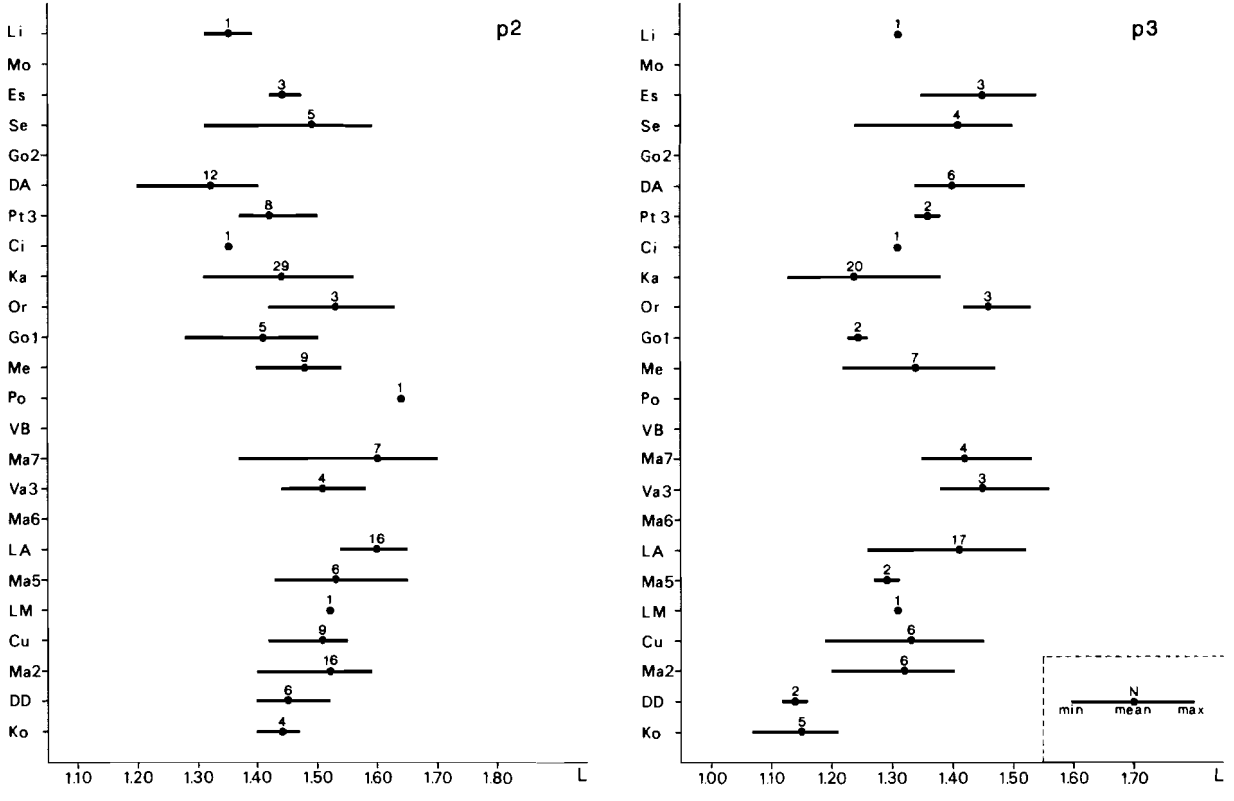


Fig. 36 Minimum-maximum diagrams of the length of the p2 and the p3 of *Dibolia* assemblages. For the explanation of the abbreviations used for the localities see table 1.

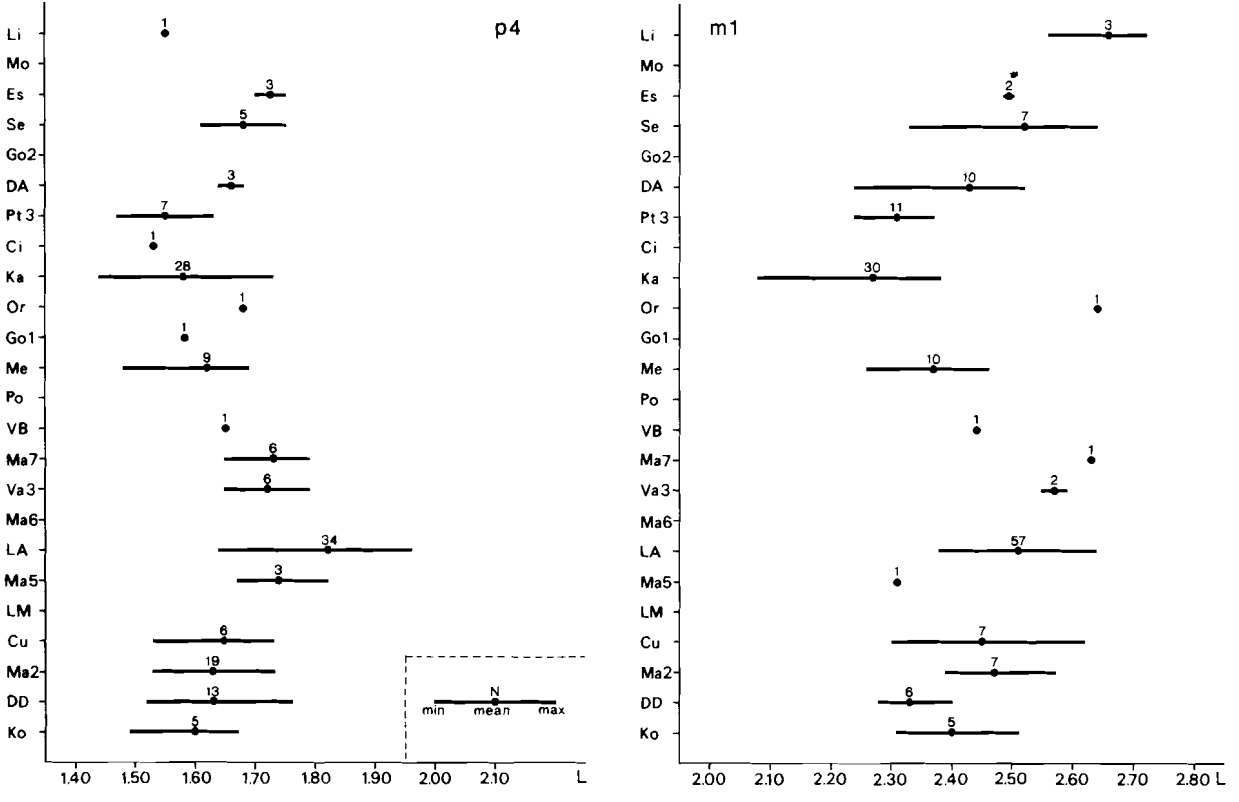


Fig. 37 Minimum-maximum diagrams of the length of the p4 and the m1 of *Dibolia* assemblages. For the explanation of the abbreviations used for the localities see table 1.

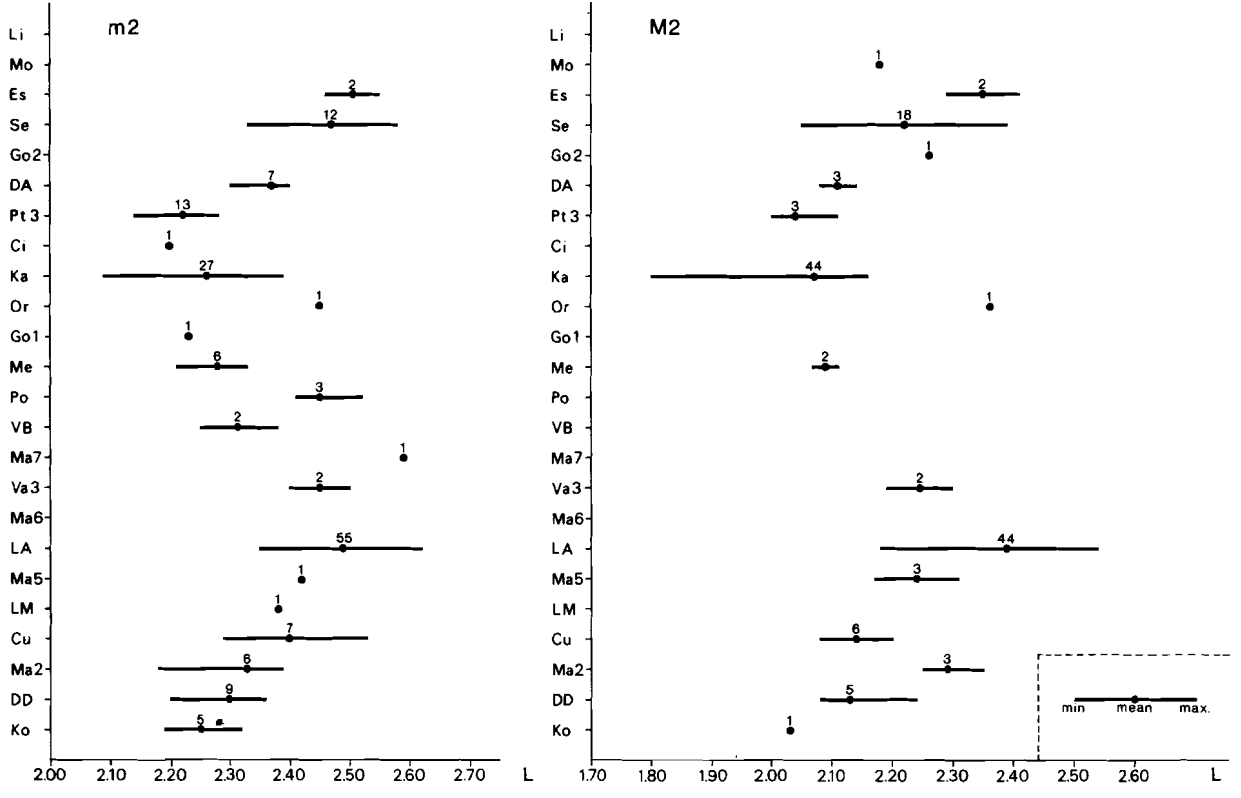


Fig. 38 Minimum-maximum diagrams of the length of the m2 and the M2 of *Dibolia* assemblages. For the explanation of the abbreviations used for the localities see table 1.

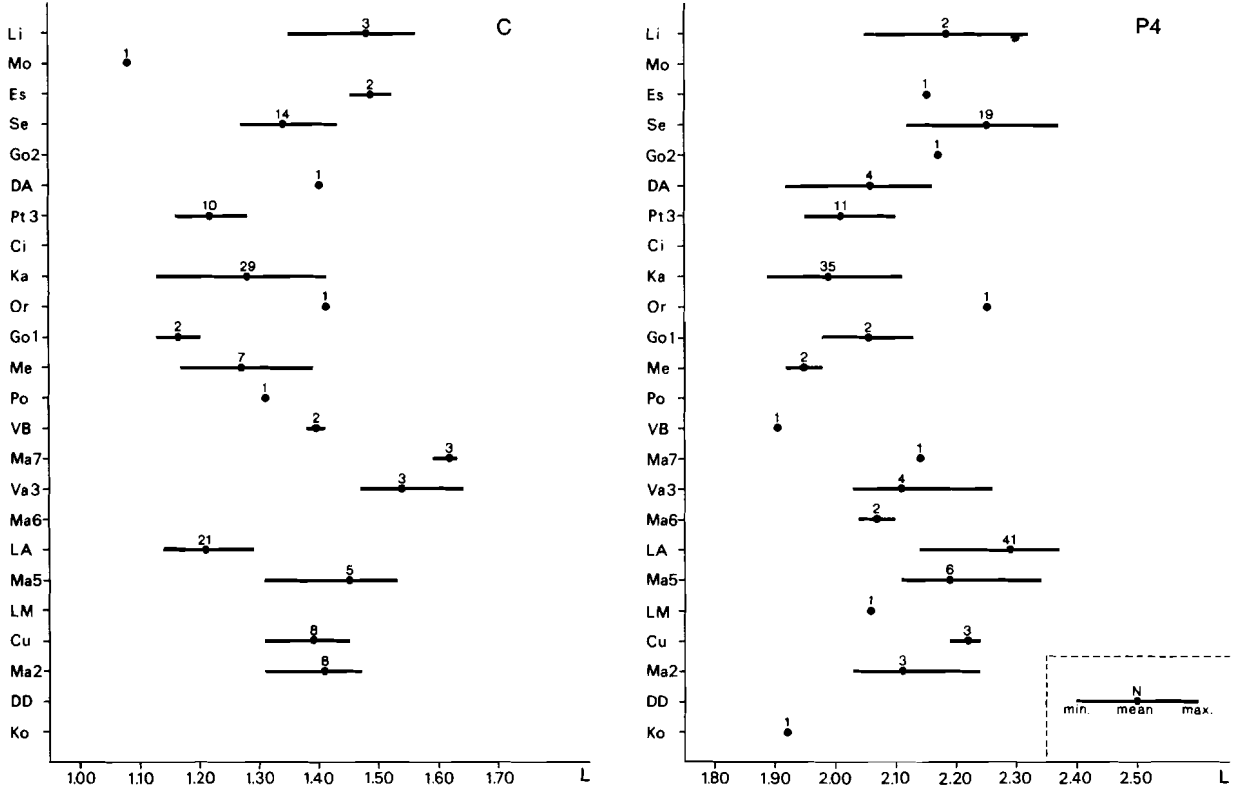


Fig. 39 Minimum-maximum diagrams of the length of the C and the P4 of *Dibolia* assemblages. For the explanation of the abbreviations used for the localities see table 1.

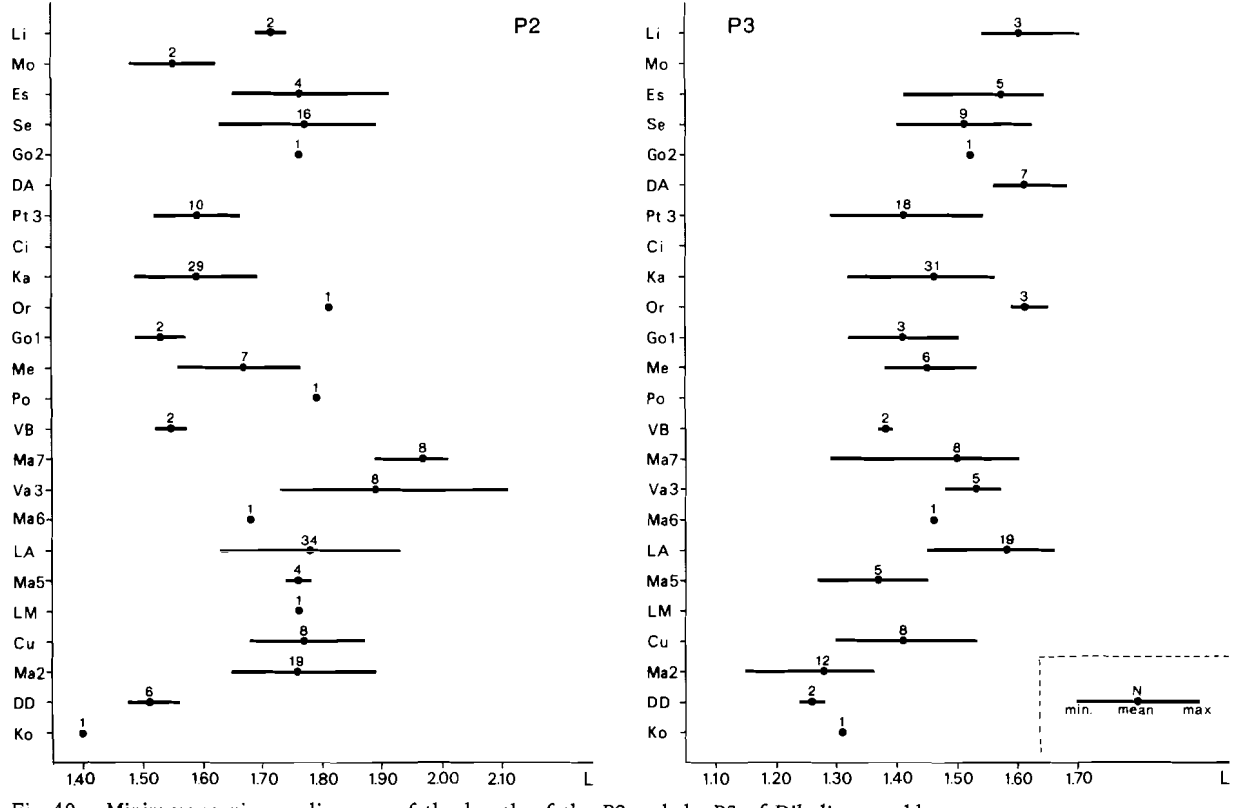


Fig. 40 Minimum-maximum diagrams of the length of the P2 and the P3 of *Dibolia* assemblages. For the explanation of the abbreviations used for the localities see table 1.

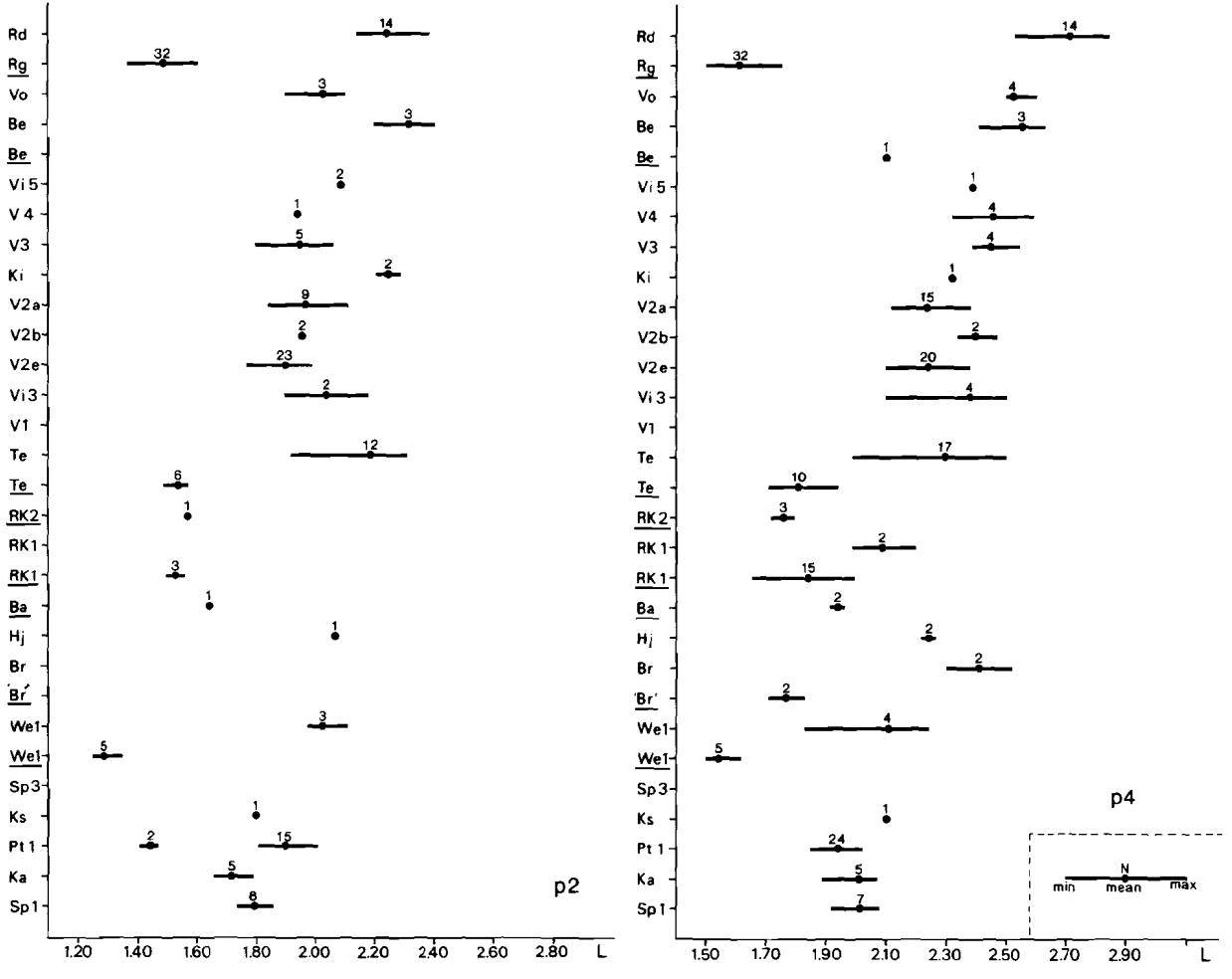


Fig. 41 Minimum-maximum diagrams of the length of the p2 and the p4 of *Galemys* and *Desmana* assemblages. *Galemys* assemblages are underlined. For the explanation of the abbreviations used for the localities see table 1.

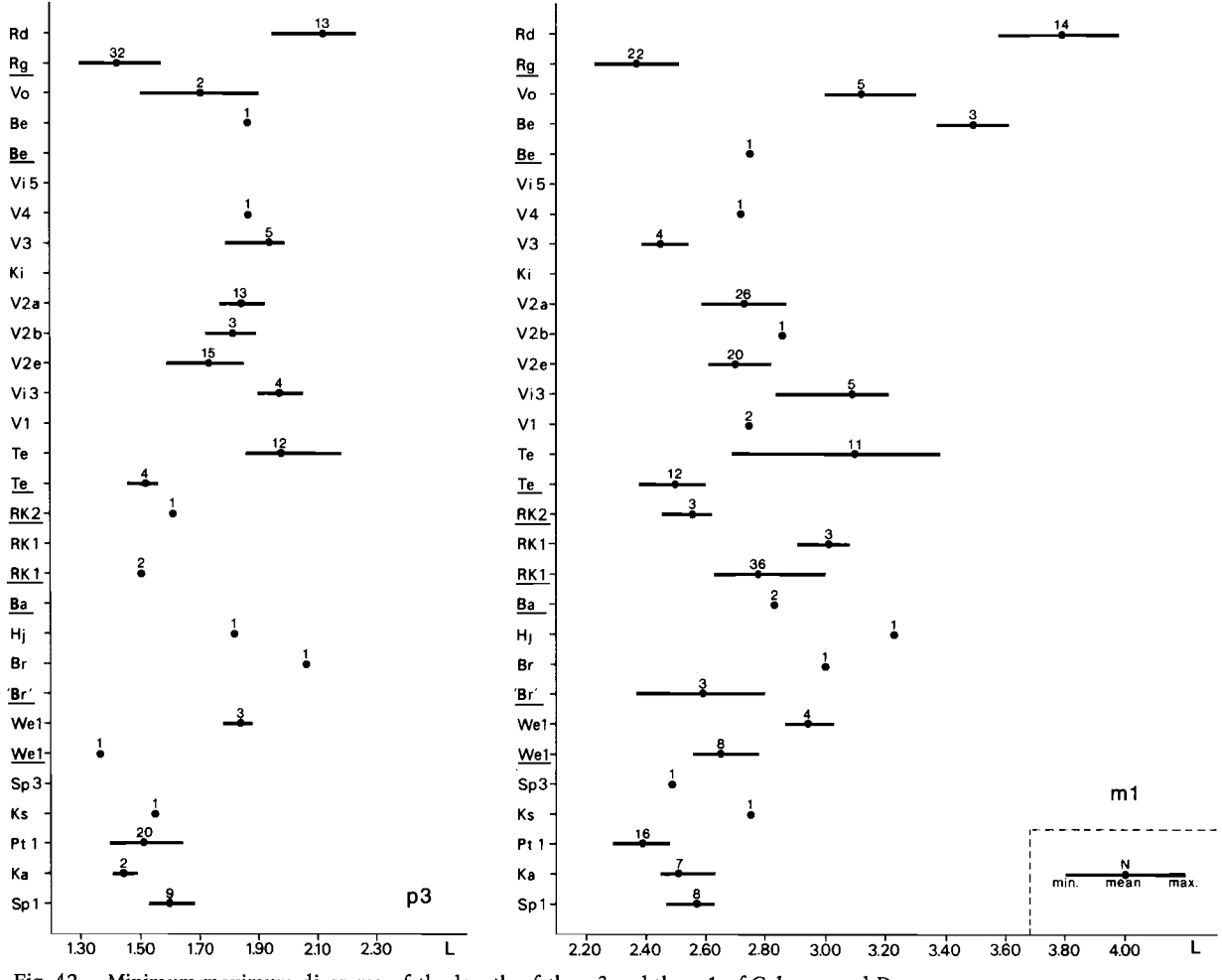


Fig. 42 Minimum-maximum diagrams of the length of the p3 and the m1 of *Galemys* and *Desmana* assemblages. *Galemys* assemblages are underlined. For the explanation of the abbreviations

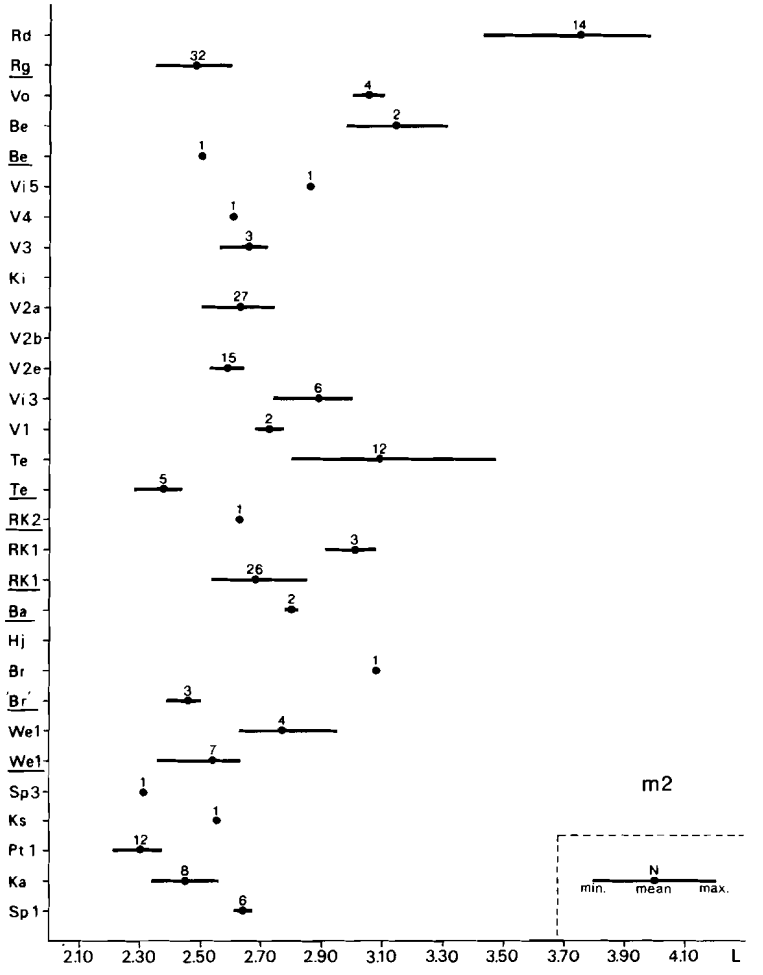


Fig. 43 (a) Minimum-maximum diagram of the length of the m2 of *Galemys* and *Desmana* assemblages. *Galemys* assemblages are underlines. For the explanation of the abbreviations used for the localities see table 1.

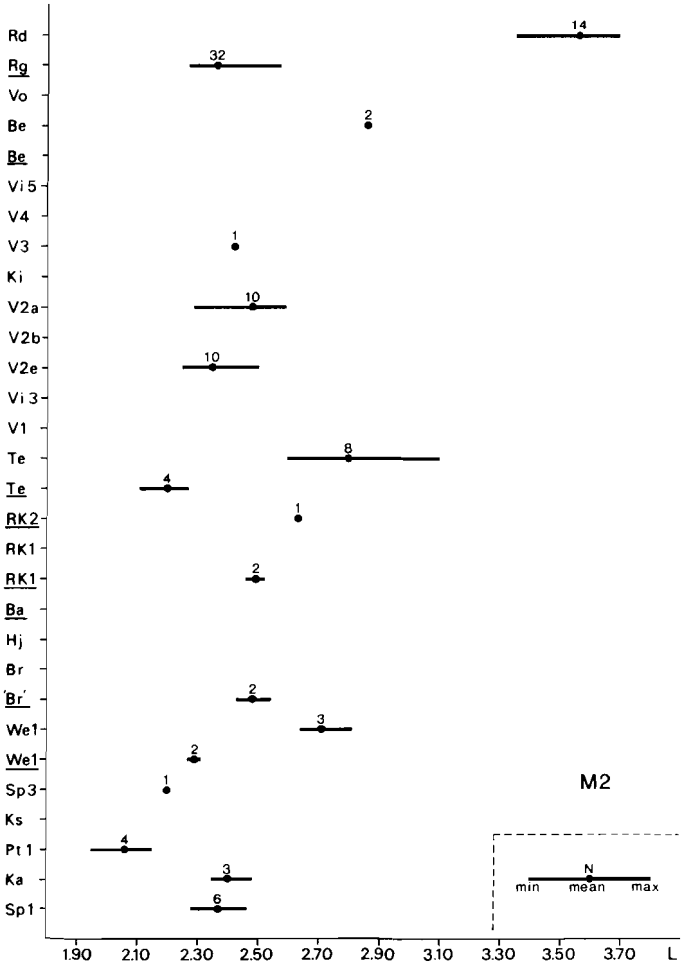


Fig. 43 (b) Minimum-maximum diagram of the length of the M2 of *Galemys* and *Desmana* assemblages. *Galemys* assemblages are underlined. For the explanation of the abbreviations used for the localities see table 1.

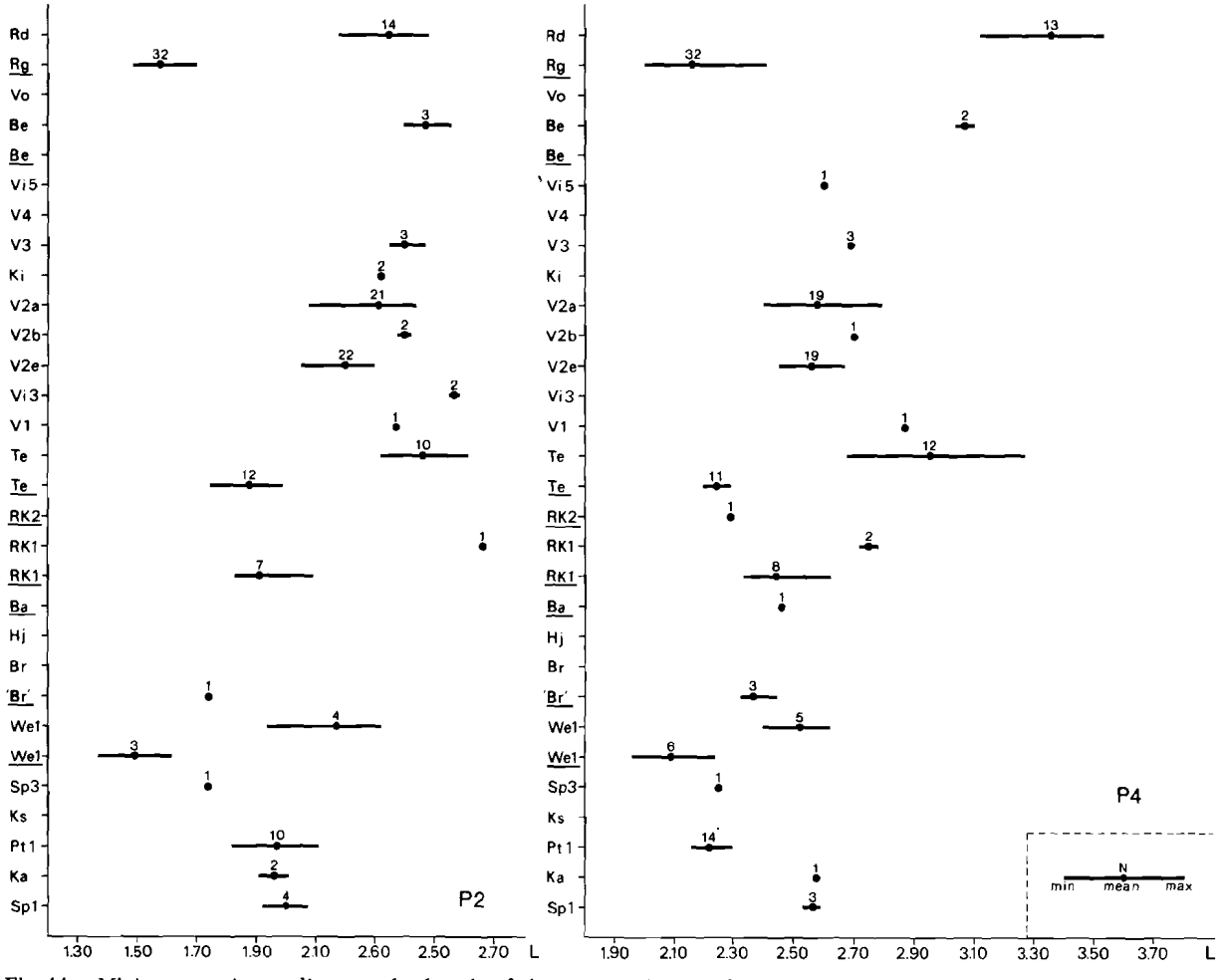


Fig. 44 Minimum-maximum diagrams the length of the P2 and the P4 of *Galemys* and *Desmana* assemblages. *Galemys* assemblages are underlined. For the explanation of the abbreviations used for the localities see table 1.

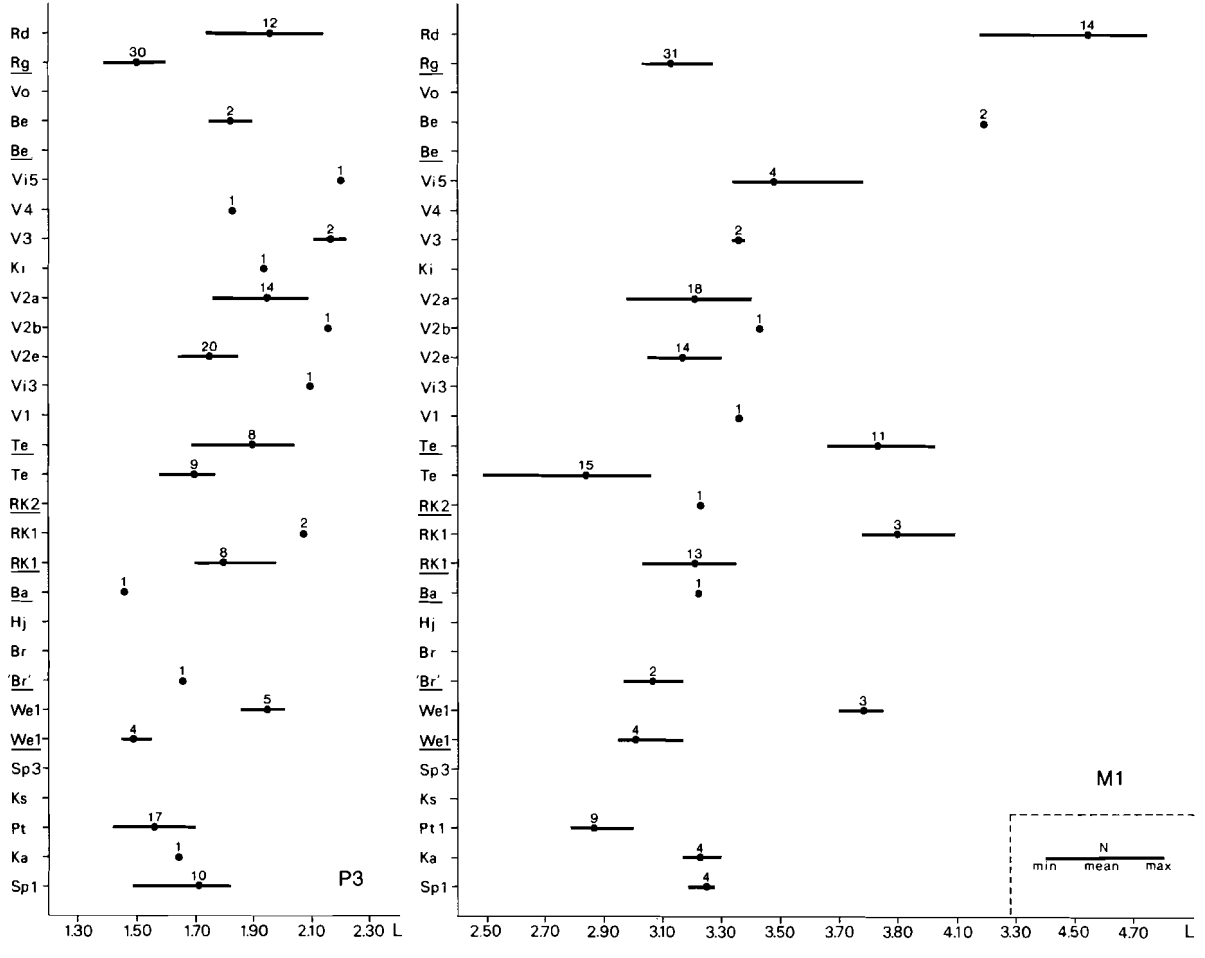


Fig. 45 Minimum-maximum diagrams of the length of the P3 and the M1 of *Galemys* and *Desmana* assemblages. *Galemys* assemblages are underlined. For the explanation of the abbreviations used for the localities see table 1.

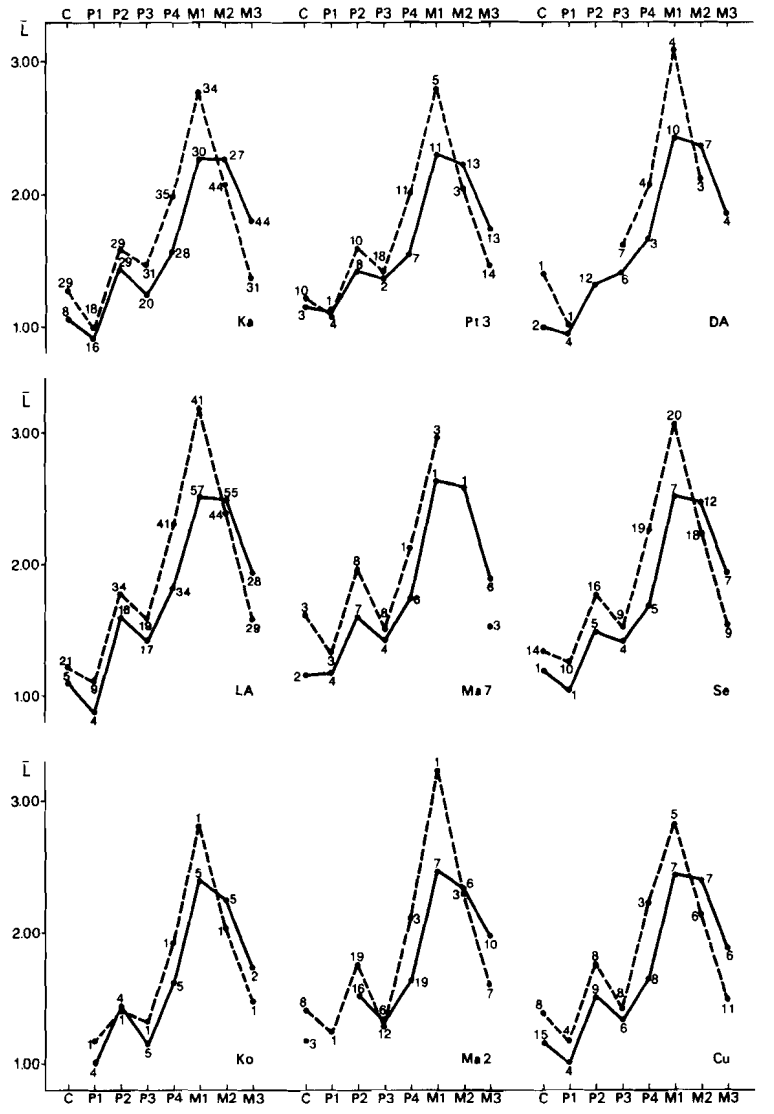


Fig. 46 Tooth length diagrams of some *Dibolia* assemblages. The solid line connects the dots giving the mean length values of the lower teeth, the dashed line those of the upper teeth. The numbers give the number of specimens measured.
DA = Dinar Akçaköy: *Dibolia bifida*
Pt3 = Ptolemais 3; Ka = Kardia: *Dibolia dekkersi*
Se = Sète: *Dibolia brailloni*
Ma7 = Masada del Valle 7: *Dibolia major*
LA = Aljezar B: *Dibolia adroveri*
Cu = Cubla; Ma2 = Masada del Valle 2: *Dibolia turolense*
Ko = Kohfidisch: *Dibolia vinea*

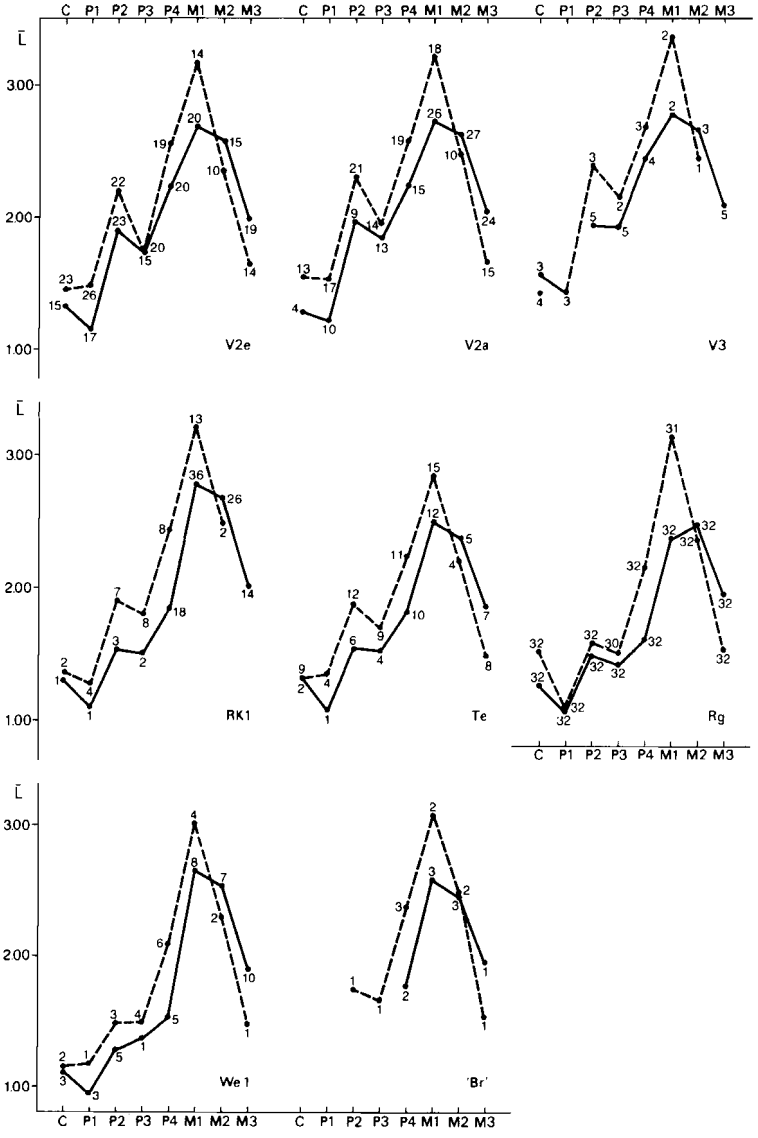


Fig. 47 Tooth length diagrams of some *Galemys* assemblages (lower two rows) and *Desmana* assemblages (uppermost row). The solid line connects the dots giving the mean length values of the lower teeth, the dashed line those of the upper teeth. The numbers give the number of specimens measured.
V3, V2a, V2e = Valdeganga: *Desmana inflata*
Rg = extant *Galemys: Galemys pyrenaicus*
Te = Tegelen, RK1 = Rebielice Królewskie 1; 'Br' = Beremend: *Desmana kormosi*
We1 = Weze 1: *Galemys sulimskii*

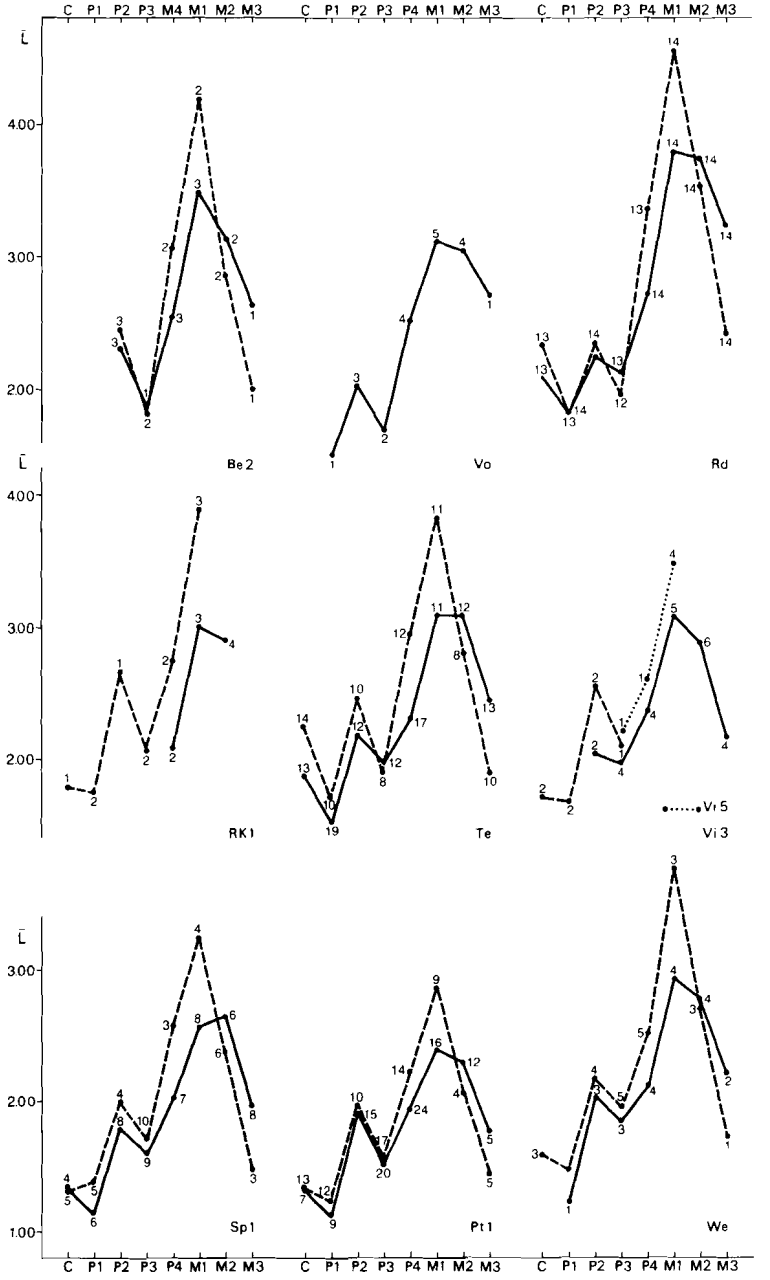


Fig. 48 Tooth length diagrams of some *Desmana* assemblages. The solid line connects the dots giving the mean length values of the lower teeth, the dashed line those of the upper teeth. The numbers give the number of specimens measured.
Rd = extant *Desmana: Desmana moschata*
Vo = Voigtstedt: *Desmana* sp.
Be2 = Betfia 2; Te = Tegelen: *Desmana thermalis*
Vi3, Vi5 = Villany; RK1 = Rebielice Królewskie 1: *Desmana nehringi*
We = Weze 1: *Desmana kowalskae*
Pt1 = Ptolemais 1; Sp1 = Spilia 1: *Desmana verestchagini*

The diagrams show that the proportions of the length of certain teeth are similar in all assemblages, while those of others vary considerably. The proportions belonging to the first category are apparently constant within the subfamily, possibly even in higher taxonomic units. This is the case for:

(a) the relation of the P3, the P4 and the M1 of an assemblage. The dots representing the P3, P4 and M1 fall on a more or less straight line, signifying that the lengths of the teeth are strongly correlated: the mean length of the P4 is about equal to the value of $\frac{P3+M1}{2}$. In the *Dibolia* assemblages the value of $P4/\frac{P3+M1}{2}$ fluctuates around 0.94 (s = 0.038), for *Galemys* the mean value lies somewhat higher – around 0.97 (s = 0.028). In the *Desmana* assemblages there is more variation in the length of the P4 relative to the P3 and the M1 (mean value 0.99, s = 0.053) than in the other genera (see fig. 49).

(b) the same kind of relation exists mutatis mutandis between the M1, the M2 and the M3 of an assemblage.

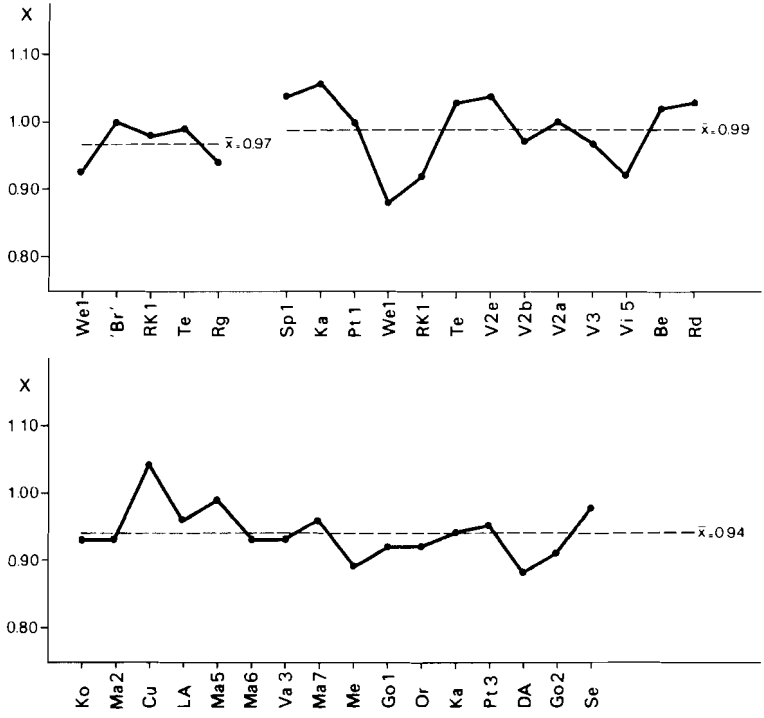


Fig. 49 The relation $X = P4/\frac{P3+M1}{2}$. For the explanation of the abbreviations used for the localities see table 1.

The proportion of the length of the C, the P2 and the P4 is variable. In *Dibolia* assemblages the lengths of these three teeth are strongly correlated, with the mean length of the P2 fluctuating around the value of $\frac{C+P4}{2}$, with a mean value of 0.99 (s = 0.035). In assemblages of *Galemys* and *Desmana* no correlation seems to exist (see fig. 50).

When comparing the tooth length diagrams of assemblages included in one genus, it is striking to note that the length of some elements differ much more than that of others. In the lower jaw the teeth in the middle part of the dentition – p2, p3 and to a lesser extent p4 – show greater differences in size than those of the anterior and posterior parts. In the upper jaw the variable teeth are situated slightly further anteriorly, here C–P3 are most liable to change. Most conspicuous are the differences in the lengths of the p3 and the P3: both the absolute length and the length relative to that of the adjacent teeth vary.

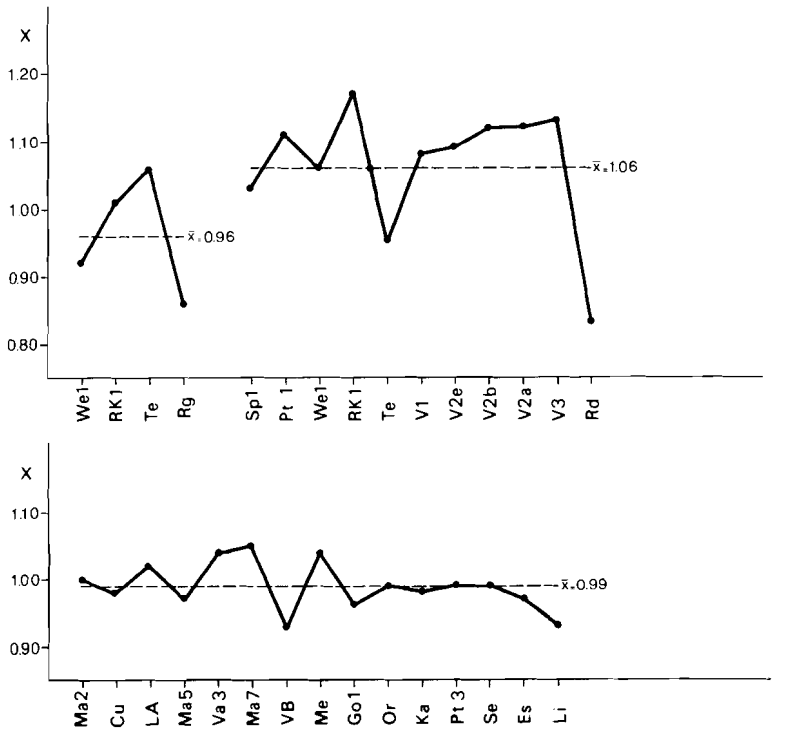


Fig. 50 The relation $X = P2/\frac{C+P4}{2}$. For the explanation of the abbreviations used for the localities see table 1.

In *Dibolia* the p2/p3 ratio decreases with time, and the P2/P3 ratio shows a general tendency to become smaller too. In *Galemys* both the p2/p3 and the P2/P3 ratios remain fairly constant through time. In *Desmana* assemblages the p2/p3 and P2/P3 ratios fluctuate without showing a trend.

The ratios p2/p3 and P2/P3 are here regarded as characteristic on the species level.

Conclusions

From the length – width as well as from the minimum – maximum diagrams it is apparent that two size groups, viz. a small sized and a medium to large sized group can be distinguished. The small sized group is heterogenous regarding the morphology of i1 and I1. Analysis of the tooth length diagrams shows that three groups, based on ratios of the mean lengths of the p2 and the p3 and of the P2 and the P3 can be distinguished. The three groups, c.q. genera are:

Dibolia n.g.

Contains small sized species. The p2/p3 ratio varies from 0.94 to 1.27; the P2/P3 ratio varies from 1.07 to 1.37.

Galemys Kaup, 1829

Contains small sized species. The p2/p3 ratio varies from 0.94 to 1.05; the P2/P3 ratio varies from 1.00 to 1.11.

Desmana Gueldenstaedt, 1777

Contains medium to large sized species. The ratio p2/p3 varies from 1.01 to 1.26; the P2/P3 ratio varies from 1.11 to 1.36.

Chapter 6

PROPOSED CLASSIFICATION

Introduction

In chapter 5 it has been shown that some elements vary in length more than others. Of the variable elements, which are situated in the middle of the lower and upper jaw, six have been selected to serve as a basis for the newly proposed classification. The subdivision of the genera is based primarily on the ratio of the length of the p2 and the p3 (p2/p3) and the ratio of the length of the P2 and P3 (P2/P3) [see p. 84], but the absolute length of the selected teeth has also been taken into account. For reasons that have been explained in chapter 4, morphological features have seldom been used.

The studied genera and species will be discussed in the following sections. A diagnosis will be given for each taxonomic unit; for more complete information, including a morphological description of the teeth, the reader is referred to chapter 9. Tables 3, 4 and 5 give the mean length of the selected teeth and the p2/p3 and P2/P3 ratios of each assemblage.

One of the problems I encountered in attempting to give the classification of the Desmaninae a sound basis was how to incorporate previously described species into the new system. Recently described species like *"Desmana" pontica vinea* Storch, 1978 and *Desmana bifida* Engesser, 1980, which are based on sufficiently large assemblages, fit into the scheme well. But most of the species that have been established before 1970 are based on fewer than 12 teeth, and sometimes on material from several localities. The species that were described before 1984 – with their type localities and the type material – are listed in table 2.

Diagnoses of the genera and species

Dibolia n.g. (table 3)

Derivatio nominis: the name, meaning weapon with two points, refers to the peculiar two-lobed I1.

Diagnosis: a small sized desmanine water-mole. The length of the m1 varies from 2.05 to 2.75 mm, the length of the M1 from 2.40 to 3.40 mm. The I1 is short and straight with a bifid tip; in the i1 the crown does not overhang the root anteriorly.

genus/species	type locality	type material
Desmana bifida Engesser, 1980	Dinar-Akçaköy	dentition nearly complete (68)
D. crassidens Kretzoi, 1953	Kisláng	p2, p4; P2, P3 (4)
D. getica Terzea, 1980	Ciuperceni	p2–p4, m2–m3 (5)
D. kormosi Schreuder, 1940	Beremend 4	P4–M3 (4)
D. nehringi Kormos, 1913	Beremend 1–3	p4–m1 (4)
D. pontica Schreuder, 1940	Polgárdi	c–p2, m2; C–P2, M1 (10)
D. pontica vinea Storch, 1978	Dorn-Dürkheim	dentition nearly complete (63)
D. tegelensis Schreuder, 1940	Tegelen	–
D. thermalis Kormos, 1930	Betfia 2	p2–m3; P2–M3 (25)
D. verestchagini Topachevski, 1963	Kosyakin	p2–m3 (6)
Desmanella quinquecuspidata Mayr & Fahlbusch, 1975	Hammerschmiede	p3–m3; P4–M1 (16)
Galemys semseyi Kormos, 1913	Betfia 2	p4–m3 (4)
Mygalinia hungarica (Kormos, 1913)	Polgárdi	p2, p4–m3 (16)

Table 2 The extinct species of *Desmana, 'Desmanella', Galemys* and *Mygalinia* which were described before 1984 with their type localities and the type material. The figures between brackets give the number of teeth found at the type locality.

Remarks: *Desmana crassidens* and *D. tegelensis* are synonymous with *Desmana thermalis.*

Desmana getica is synonymous with *Desmana bifida* (= *Dibolia bifida*).

Although *Desmana kormosi* (= *Galemys kormosi*), *Desmana nehringi, Desmana pontica* (= *Dibolia pontica*) and *Desmana verestchagini* are each based on a a few teeth only, the names have been retained. Emended diagnoses, based on assemblages that appear to be similar to the type material, will be given.

Desmanella quinquecuspidata and *Mygalinia hungarica* are know from the type locality only and nothing can be added to the original descriptions. For a discussion of these two species see chapter 2.

The p2 is usually longer – rarely of the same length or slightly shorter – than the p3; the p2/p3 ratio varies from 0.94 to 1.27. The P2 is always longer than the P3; the P2/P3 ratio varies from 1.07 to 1.37.

Differential diagnosis: Dibolia differs from *Galemys* and *Desmana* by its two-lobed I1, which is unique in the Desmaninae.

Type species: Dibolia dekkersi n.sp.

Remarks: nine species have been distinguished. Three of these are restricted to central and eastern Europe and Asia, five occur exclusively in Spain and the south of France and one is found in both areas.

Dibolia dekkersi n.sp.

Diagnosis: the mean length of the p2 is about 1.44 mm, the mean length of the p3 is about 1.24 mm, the mean length of the p4 is about 1.58 mm; the p2/p3 ratio is about 1.16. The p1 is single-rooted.

The mean length of the C is about 1.28 mm, the mean length of the P2 is about 1.59 mm, the mean length of the P3 is about 1.46 mm; the P2/P3 ratio is about 1.09. The P1 is double-rooted.

localities	p2/p3	p2	p3	p4	P2/P3	C	P2	P3
		Dibolia bifida (Engesser, 1980)						
Limni 6	1.03	1.35	1.31	1.55	1.07	1.48	1.71	1.60
Ciuperceni	1.03	1.35	1.31	1.53	–	–	–	–
Dinar-Akçaköy	0.94	1.32	1.40	1.66	–	1.40	–	1.61
		Dibolia dekkersi n.sp.						
Ptolemais 3	1.04	1.42	1.36	1.55	1.13	1.22	1.59	1.41
Kardia	1.16	1.44	1.24	1.58	1.09	1.28	1.59	1.46
Gorafe 1	1.16	1.41	1.24	1.58	1.09	1.20	1.53	1.41
Maramena	1.10	1.48	1.34	1.62	1.15	1.27	1.67	1.45
		Dibolia brailloni n.sp.						
Escorihuela	0.99	1.44	1.45	1.73	1.12	1.48	1.76	1.57
Sète	1.06	1.49	1.41	1.68	1.17	1.34	1.77	1.51
Gorafe 2	–	–	–	–	1.16	–	1.76	1.52
Orrios	1.05	1.53	1.46	1.68	1.12	1.41	1.81	1.61
		Dibolia pontica (Schreuder, 1940)						
Polgárdi	–	1.64	–	–	–	1.38	1.79	–
		Dibolia major n.sp.						
Masada d.Valle 7	1.13	1.60	1.42	1.73	1.31	1.62	1,97	1.50
Valdecebro 3	1.04	1.51	1.45	1.72	1.24	1.54	1.89	1.53
		Dibolia luteyni n.sp.						
Villalba Baja 1	–	–	–	1.65	1.12	1.39	1.54	1.38
Masada d.Valle 6	–	–	1.25	–	1.15	–	1.68	1.46
		Dibolia adroveri n.sp.						
Aljezar B	1.13	1.60	1.41	1.82	1.13	1.21	1.78	1.58
		Dibolia turolense n.sp.						
Masada d.Valle 5	1.19	1.53	1.29	1.74	1.28	1.45	1.76	1.37
Los Mansuetos	1.16	1.52	1.31	–	–	–	1.76	–
Cubla	1.14	1.51	1.33	1.65	1.26	1.39	1.77	1.41
Masada d.Valle 2	1.15	1.52	1.32	1.63	1.37	1.41	1.76	1.28
		Dibolia vinea (Storch, 1978)						
Dorn-Dürkheim	1.27	1.45	1.14	1.63	1.20	–	1.51	1.26
Kohfidisch	1.25	1.44	1.15	1.60	1.07	–	1.40	1.31

Table 3. The p2/p3 and the P2/P3 ratios and the mean lengths of the teeth which are used in the classification of *Dibolia*. The type localities of the proposed species are in italics.

Type locality: Kardia, Greece.

Remarks: the localities Maramena 1 (Late Turolian), Kardia (Early Ruscinian) and Ptolemais 3 (Middle Ruscinian), all situated in the north of Greece, have yielded assemblages in which the tooth length patterns are essentially similar. The small assemblage from Gorafe 1 (south of Spain, Early Ruscinian) also fits into this pattern. *Dibolia dekkersi* is characterized by an average value for the p2/p3 ratio, a low value for the P2/P3 ratio and a short C (see table 3).

Dibolia vinea (Storch, 1978)

Emended diagnosis: the mean length of the p2 is about 1.45 mm, the mean length of the p3 is about 1.14 mm, the mean length of the p4 is about 1.63 mm; the p2/p3 ratio is about 1.27. The p1 is double-rooted.

The mean length of the P2 is about 1.51 mm, the mean length of the P3 is about 1.26 mm; the P2/P3 ratio is about 1.20.

Type locality: Dorn-Dürkheim, West Germany.

Remarks: the oldest *Dibolia* assemblages known so far are from the Early Turolian localities Kohfidisch, Austria and Dorn-Dürkheim, West Germany. Both assemblages are included in *Dibolia vinea,* described by Storch as *"Desmana" pontica vinea. Dibolia vinea* is characterized by the high P2/P3 ratio and the very short p3 and P3 (see table 3).

Dibolia turolense n.sp.

Diagnosis: the mean length of the p2 is about 1.52 mm, the mean length of the p3 is about 1.32 mm, the mean length of the p4 is about 1.63 mm; the p2/p3 ratio is about 1.14. The p1 is double-rooted.

The mean length of the C is about 1.41 mm, the mean length of the P2 is about 1.76 mm, the mean length of the P3 is about 1.28 mm; the P2/P3 ratio is about 1.26. The P1 is double-rooted.

Type locality: Masada del Valle 2, Province of Teruel, Spain.

Remarks: four assemblages for which the tooth length diagrams are almost identical have been found in the Middle Turolian of the Teruel basin, Spain. The localities are – in stratigraphical order – Masada del Valle 2, Cubla, Los Mansuetos and Masada del Valle 5. *Dibolia turolense* is characterized by an average p2/p3 ratio and a high P2/P3 ratio (see table 3).

Dibolia adroveri n.sp.

Diagnosis: the mean length of the p2 is about 1.60 mm, the mean length of the p3 is about 1.41 mm, the mean length of the p4 is about 1.82 mm; the p2/p3 ratio is about 1.13. The p1 is double-rooted.

The mean length of the C is about 1.21 mm, the mean length of the P2 is about 1.78 mm, the mean length of the P3 is about 1.58 mm; the P2/P3 ratio is about 1.13. The P1 is double-rooted.

Type locality: Aljezar B, Province of Teruel, Spain.

Remarks: this species of Middle Turolian age has hitherto only been found in Aljezar in the Teruel basin, Spain, where it occurs in large quantities. *Dibolia adroveri* is characterized by a very long p4 and a very short C (see table 3).

Dibolia luteyni n.sp.

Diagnosis: the mean length of the p4 is about 1.65 mm. The p1 is single-rooted.

The mean length of the C is about 1.39 mm, the mean length of the P2 is about 1.54 mm, the mean length of the P3 is about 1.38 mm; the P2/P3 ratio is about 1.12. The P1 is double-rooted.

Type locality: Villalba Baja 1, Province of Teruel, Spain.

Remarks: A *Dibolia* species with low, heavy teeth is known from the Late Turolian sites Masada del Valle 6 and Villalba Baja 1, both situated in the Teruel basin. It is probable that the few teeth found in La Fontana 1a, which is situated in the same area as the two first mentioned localities and is of the same age, also belong to this species. *Dibolia luteyni* is characterized by its bulbous teeth.

Dibolia major n.sp.

Diagnosis: the mean length of the p2 is about 1.60 mm, the mean length of the p3 is about 1.42 mm, the mean length of the p4 is about 1.73 mm; the p2/p3 ratio is about 1.13. The p1 is single-rooted.

The mean length of the C is about 1.62 mm, the mean length of the P2 is about 1.97 mm, the mean length of the P3 is about 1.50 mm; the P2/P3 ratio is about 1.31. The P1 is double-rooted.

Type locality: Masada del Valle 7, Province of Teruel, Spain.

Remarks: the Late Turolian species found in the Teruel basin is the largest species known hitherto. Some of the teeth found in Valdecebro 3, also situated in the Teruel basin, are of the same size as those of *D. major* from Masada del Valle 7, others have a size that is comparable to similar teeth of *D. turolense* from Cubla. However, since the assemblage from Valdecebro has more in common with *D. major* than with *D. turolense,* the assemblage has been included in *D. major. Dibolia major* is characterized by an average p2/p3 ratio and a high P2/P3 ratio in combination with a long p2 and a very long P2 (see table 3).

Dibolia pontica (Schreuder, 1940)

Emended diagnosis: the mean length of the p2 is about 1.64. The p1 has 2 roots.

The mean length of the C is about 1.38 mm, the mean length of the P2 is about 1.79 mm. The P1 has two roots.

Type locality: Polgárdi, Hungary.

Remarks: the larger water-mole from Polgárdi (Late Turolian) was described as *Desmana pontica.* Since the only antemolars found were c–p2 and C–P2 and the i1 and I1 are not known either, an important part of the elements on which our classification is based is missing. Since the teeth of *"Desmana" pontica* are much smaller than those of the oldest true *Desmana* assemblages from Spilia 1 and Kardia, Greece (Early Ruscinian), it seems reasonable to assume that the Polgárdi material belongs to the genus *Dibolia.*

The teeth from Polgárdi fit reasonably well into the tooth length pattern of Ruscinian *Dibolia* assemblages from the Teruel basin in Spain and from the south of France. However, for reasons explained above the material from Orrios, Gorafe 2, Sète and Escorihuela have not been allocated to *D. pontica.*

Dibolia pontica is characterized by a long P2 (see table 3).

Dibolia brailloni n.sp.

Diagnosis: the mean length of the p2 is about 1.49 mm, the mean length of the p3 is about 1.41 mm, the mean length of the p4 is about 1.68 mm; the p2/p3 ratio is about 1.06. The p1 is single-rooted.

The mean length of the C is about 1.34 mm, the mean length of the P2 is about 1.77 mm, the mean length of the P3 is about 1.51 mm, the P2/P3 ratio is about 1.17. The P1 is double-rooted.

Type locality: Sète, south of France.

Remarks: see *Dibolia pontica.*

Dibolia bifida (Engesser, 1980)

Emended diagnosis: the mean length of the p2 is about 1.32 mm, the mean length of the p3 is about 1.40 mm, the mean length of the p4 is about 1.66 mm; the p2/p3 ratio is about 0.94. The p1 is either single- or double-rooted.

The mean length of the C is about 1.40 mm, the mean length of the P3 is about 1.61 mm. The P1 is double-rooted.

Type locality: Dinar-Akçaköy, Turkey.

Remarks: the lower jaw with p2–m3 from Ciuperceni, Roumania (Early

Ruscinian), described by Terzea (1980) as *Desmana getica* and the assemblage from Limni 6, Euboea, Greece (Early Villanyian) are included in *Dibolia bifida.* The species was originally described by Engesser as *Desmana bifida* from the Middle Ruscinian locality Dinar-Akçaköy. It is possible that the *Dibolia* assemblage from Ivanovce, Czechoslovakia (Middle Ruscinian), characterized by an I1 of the AN type (Fejfar, pers. comm.), belongs here too. *Dibolia bifida* is characterized by a low p2/p3 ratio, a small p2 in combination with a p3 of roughly the same size and a very long P3 (see table 3).

Galemys Kaup, 1829 (table 4)

Emended diagnosis: a small sized desmanine water-mole. The length of the m1 varies from 2.20 to 3.00 mm, the length of the M1 from 2.45 to 3.35 mm. The I1 is curved with a pointed tip; in the i1 the crown overhangs the root anteriorly.

The p2 is of roughly the same length as the p3; the p2/p3 ratio varies from 0.94 to 1.05. The P2 is slightly longer or of the same length as the P3; the P2/P3 ratio varies from 1.00 to 1.11.

Differential diagnosis: Galemys differs from *Dibolia* by its curved, pointed I1 and from *Desmana* by its smaller size.

Type species: Galemys pyrenaicus (Geoffroy, 1811).

localities	p2/p3	p2	p3	p4	P2/P3	C	P2	P3
		Galemys pyrenaicus (Geoffroy, 1811)						
various loc.	1.05	1.49	1.42	1.61	1.05	1.51	1.58	1.50
		Galemys semseyi Kormos, 1913						
Betfia 2	–	–	–	2.10	–	–	–	–
		Galemys sp. (Moyà-Solà et al, 1981)						
Venta Micena	–	140		1.66	–	–	1.80	–
		Galemys kormosi (Schreuder, 1940)						
Tegelen	1.01	1.54	1.52	1.81	1.11	1.32	1.88	1.70
Baza	–	1.65	–	1.94	–	1.35	–	–
Reb. Król. 2	0.98	1.57	1.61	1.76	–	–	–	–
Reb. Król. 1	1.02	1.53	1.50	1.84	1.06	1.36	1.91	1.80
'Beremend'	–	–	–	1.77	1.05	–	1.74	1.66
		Galemys sulimskii n.sp.						
Weze 1	0.94	1.29	1.37	1.54	1.00	1.15	1.49	1.49

Table 4. The p2/p3 and the P2/P3 ratios and the mean length of the teeth which are used in the classification of *Galemys.* The type localities of the proposed species are in italics.

Remarks: the small desmanine species found in Weze 1 (Poland), the Beremend fissures (Hungary) and Rebielice Królewskie 1 and 2 (Poland) has been described as *Desmana kormosi* Schreuder, 1940. These assemblages show a close resemblance to the small species from Tegelen (the Netherlands), *"Desmana"* I from Venta Micena (Spain), *Galemys semseyi* from Betfia 2 (Roumania) and the living species *Galemys pyrenaicus* (Spain, France, Portugal). All are of a size comparable to that of the genus *Dibolia.* In all assemblages the p2/p3 and the P2/P3 ratios fluctuate around 1.00.

It thus appears that these small water-moles form a very homogeneous group from the Late Ruscinian onwards; this is in contrast with the contemporaneous assemblages of large forms, which show marked changes during the same interval. Since the genus name *Galemys* has been in use for the small living species for such a long time, all the small sized assemblages are included in this genus.

Since *Galemys* is characterized by more or less fixed p2/p3 and P2/P3 ratios, the species are based on differences in the absolute length of the selected teeth, i.e. p2–p4, C and P2–P3. There are four species.

Galemys pyrenaicus (Geoffroy, 1811)

Emended diagnosis: the mean length of the p2 is about 1.49 mm, the mean length of the p3 is about 1.42 mm, the mean length of the p4 is about 1.61 mm; the p2/p3 ratio is about 1.05. The p1 is single-rooted.

The mean length of the C is about 1.51 mm, the mean length of the P2 is about 1.58 mm, the mean length of the P3 is about 1.50 mm; the P2/P3 ratio is about 1.07. The P1 is single-rooted.

Remarks: this extant species is known from the Pyrenees and the Cantabrian Mountains. The teeth are narrow and sharp. *Galemys pyrenaicus* is characterized by a long C and short P2 and P3 (see table 4). It is the only known *Galemys* species with a single-rooted p3.

Galemys sulimskii n.sp.

Diagnosis: the mean length of the p2 is about 1.29 mm, the mean length of the p3 is about 1.37 mm, the mean length of the p4 is about 1.54 mm; the p2/p3 ratio is about 0.94. The p1 is single-rooted.

The mean length of the C is about 1.15 mm, the mean length of the P2 is about 1.49 mm, the mean length of the P3 is about 1.49 mm; the P2/P3 ratio is about 1.00. The P1 is double-rooted.

Type locality: Weze 1, Poland.

Remarks: this species occurs only in Weze 1 (Late Ruscinian). Originally

the material was described as *Galemys* ? by Sulimski (1959); later the same material was included partly in *Desmana pontica,* partly in *D.* cf. *kormosi* by Sulimski (1962) and in its entirety in *D. kormosi* by Rzebik-Kowalska (1971). *Galemys sulimskii* is characterized by low p2/p3 and P2/P3 ratios and its very small size (see table 4).

Galemys kormosi (Schreuder, 1940)

Supplementary diagnosis based on material from Tegelen: the mean length of the p2 is about 1.54 mm, the mean length of the p3 is about 1.52 mm, the mean length of the p4 is about 1.81 mm; the p2/p3 ratio is about 1.01. The p1 is double-rooted.

The mean length of the C is about 1.32 mm, the mean length of the P2 is about 1.88 mm, the mean length of the P3 is about 1.70 mm; the P2/P3 ratio is about 1.11. The P1 is double-rooted.

Type locality: Beremend 4, Hungary.

Remarks: the species is known from several Beremend localities (4, 5, "Kormos", 1936) which have yielded 19 teeth in total. The holotype, the only specimen found at the type locality Beremend 4, is a fragmentary maxilla with P4–M3, which Kormos (1938) included in *Galemys semseyi.* In 1940 Schreuder described *Desmana kormosi* on the basis of this specimen – which she chose for the holotype – and a number of specimens from other Beremend localities and from Czarnota. *Galemys kormosi* is characterized by its large p2, p3, P2 and P3 (see table 4).

Galemys semseyi Kormos, 1913

In Betfia 2 two water-moles have been found, the smaller of which was described as *Galemys semseyi* (Kormos 1913, 1938). Only two fragmentary lower jaws with p4–m3 have been found, one of which has since disappeared. The specimens apparently belong to a rather large *Galemys* species. Apart from the very long p4 the lengths of the teeth fall within the variation of *Galemys kormosi.*

Galemys sp.

A few teeth were described by Gibert (Moyà-Solà et al, 1981) from Venta Micena, Spain (Early Biharian). In addition to a short description Gibert gives the following information:

"Desmana" 1: p1 L = 1.20 mm; p2 or p3 L = 1.40 mm; p4 L = 1.66 mm

"Desmana" 2: P2 L = 1.80 mm; M2 L = 2.66 mm; M3 L = 1.90 mm

It is possible that the P2 attributed to *"Desmana"* 2 by Gibert belongs to *"Desmana"* 1, as it is normal that a p4 is of roughly the same size as the associated P2. If that is indeed the case, we may well have a *Galemys* species which fits into the gap between *Galemys kormosi* (Early–Late Villanyian) and *Galemys pyrenaicus* (Recent) (see table 4).

Desmana Gueldenstaedt, 1777 (table 5)

Emended diagnosis: a medium to large sized desmanine water-mole. The length of the m1 varies from 2.25 to 4.00 mm, the length of the M1 from 2.75 to 4.80 mm. The I1 is curved with a pointed tip; in the i1 the crown shows an anterior overhang over the root.

The p2 is usually longer than the p3; the p2/p3 ratio varies from 1.01 to 1.26. The P2 is always longer than the P3; the P2/P3 ratio varies from 1.11 to 1.36.

Differential diagnosis: Desmana differs from *Dibolia* by its larger size and by its curved, pointed I1, and from *Galemys* by its larger size.

Type species: Desmana moschata (Linnaeus, 1758)

Remarks: the teeth show a considerable variation in size: from the Early Villanyian onwards the overall size of the animals increased steadily. The p2/p3 and P2/P3 ratios vary to roughly the same extent as in *Dibolia,* but there is no pronounced trend from high to low values.

Six species have been distinguished. The sub-species of *Desmana moschata* have not been studied.

Desmana moschata (Linnaeus, 1758)

Emended diagnosis: the mean length of the p2 is about 2.24 mm, the mean length of the p3 is about 2.12 mm, the mean length of the p4 is about 2.71 mm; the p2/p3 ratio is about 1.06. The p1 is single-rooted.

The mean length of the C is about 2.33 mm, the mean length of the P2 is about 2.35 mm, the mean length of the P3 is about 1.96 mm; the P2/P3 ratio is about 1.20. The P1 is single-rooted.

The teeth are inflated and relatively low.

Remarks: from the tooth length diagram it is apparent that in *Desmana moschata* the c–p3 and the C–P3 are relatively small compared to the p4–m3 and the P4–M3, which makes the tooth length pattern an unusual one. It would be interesting to study the sub-species of *D. moschata* and work out the tooth length diagrams, but such a study falls outside the scope of this paper.

Desmana moschata is characterized by low and bulbous teeth, a long p4 and a very large C (see table 5).

localities	p2/p3	p2	p3	p4	P2/P3	C	P2	P3
			Desmana moschata (Linnaeus, 1758)					
various loc.	1.06	2.24	2.12	2.71	1.20	2.33	2.35	1.96
			Desmana sp.					
Voigtstedt	1.19	2.03	1.70	2.52	–	–	–	–
			Desmana inflata n.sp.					
Valdeganga 4	1.04	1.94	1.87	2.46	–	–	–	1.83
Valdeganga 3	1.01	1.95	1.94	2.45	1.11	1.57	2.40	2.16
Valdeganga 2a	1.07	1.97	1.84	2.24	1.18	1.55	2.31	1.95
Valdeganga 2b	1.08	1.96	1.81	2.40	1.11	1.60	2.40	2.16
Valdeganga 2e	1.10	1.90	1.73	2.24	1.26	1.46	2.20	1.75
Valdeganga 1	–	–	–	–	–	1.51	2.37	–
			Desmana thermalis Kormos, 1930					
Betfia 2	1.25	2.32	1.86	2.55	1.36	–	2.47	1.82
Kisláng	–	2.25	–	2.32	1.20	–	2.32	1.94
Tegelen	1.11	2.19	1.98	2.30	1.29	2.25	2.46	1.90
			Desmana nehringi Kormos, 1913					
Villany 5	–	2.08	–	2.39	–	–	–	2.20
Villany 3	1.04	2.04	1.97	2.38	1.22	1.71	2.56	2.10
Reb. Król. 1	–	–	–	2.09	1.29	1.79	2.66	2.07
Hajnácka	1.14	2.07	1.82	2.24	–	–	–	–
'Beremend'	–	–	2.06	2.41	–	–	–	–
			Desmana kowalskae n.sp.					
Weze 1	1.10	2.03	1.84	2.11	1.11	1.59	2.17	1.95
			Desmana verestchagini Topachevski, 1961					
Kosyakin	1.16	1.80	1.55	2.10	–	–	–	–
Ptolemais 1	1.26	1.90	1.51	1.94	1.26	1.34	1.97	1.56
Kardia	1.19	1.72	1.44	2.01	1.20	–	1.96	1.64
Spilia 1	1.12	1.79	1.60	2.02	1.17	1.32	2.00	1.71

Table 5. The p2/p3 and the P2/P3 ratios and the mean length of the teeth which are used in the classification of *Desmana*. The type localities of the proposed species are in italics.

Desmana verestchagini Topachevski, 1961

Emended diagnosis: the mean length of the p2 is about 1.80 mm, the mean length of the p3 is about 1.55 mm, the mean length of the p4 is about 2.10 mm; the p2/p3 ratio is about 1.16.

Supplementary diagnosis based on the material from Spilia 1: the mean length of the C is about 1.32 mm, the mean length of the P2 is about 2.00 mm, the mean length of the P3 is about 1.71 mm; the P2/P3 ratio is about 1.17. The p1 and the P1 are single-rooted.

Type locality: Kosyakin quarry, Caucasia, U.S.S.R.

Remarks: the oldest assemblage in which the first upper incisor of the *Desmana* type – curved, with a single pointed tip – has been found is the one from Spilia 1, Greece (Early Ruscinian). Similar assemblages, but with the I1 missing, have been found in Kardia and Ptolemais 1, north-west Greece (Early Ruscinian). The fragmentary lower jaw with p2–m2 from Kosyakin, (Early–Middle Ruscinian), described by Topachevski as *Desmana verestchagini,* fits well into the tooth length patterns of these three Greek assemblages, which are allocated to *Desmana verestchagini.* The small collection from Spilia 3, which is somewhat younger, does not fit into this species.

Desmana verestchagini is characterized by its small size.

Desmana kowalskae n.sp.

Diagnosis: the mean length of the p2 is about 2.03 mm, the mean length of the p3 is about 1.84 mm, the mean length of the p4 is about 2.11 mm; the p2/p3 ratio is about 1.10. The p1 is single-rooted.

The mean length of the C is about 1.59 mm, the mean length of the P2 is about 2.17 mm, the mean length of the P3 is about 1.56 mm; the P2/P3 ratio is about 1.11. The P1 is double-rooted.

Type locality: Weze 1, Poland.

Remarks: this species is known from Weze 1, Poland (Middle Ruscinian), only and is presumably ancestral to *Desmana nehringi.* The lengths of the lower teeth fall within the range of variation of *Desmana nehringi* although the p3 and the p4 are smaller than in most assemblages allocated to *D. nehringi.* The upper teeth, in particular the C and the P2, are much smaller than similar teeth from Rebielice Królewskie 1 and Villany 3, which are the only assemblages of *Desmana nehringi* that contain upper teeth.

Desmana kowalskae is characterized by the low p2/p3 and P2/P3 ratios in combination with the small size of the p4 and the P2 (see table 5).

Desmana nehringi Kormos, 1913

Emended diagnosis: the mean length of the p3 is about 2.06 mm, the mean length of the p4 is about 2.41.

Supplementary diagnosis based on the material from Villany 3: the mean length of the p2 is about 2.04; the p2/p3 ratio is about 1.04.

The mean length of the C is about 1.71 mm, the mean length of the P2 is about 2.56 mm, the mean length of the P3 is about 2.10 mm; the P2/P3 ratio is about 1.22. The P1 is double-rooted.

Type locality: Beremend 1–3, Hungary.

Remarks: this large *Desmana* species is known from several localities of Villanyian age, but none of them has yielded a sufficiently large collection for the species to be described in a satisfactory way. In the type locality, Beremend 1–3, a mandibular fragment with p4–m1 (the holotype) and a mandibular fragment with p3–p4, m2–m3 have been found; the holotype has since been lost. Villany 3 has yielded the best collection of this species. *Desmana nehringi* is characterized by a relatively large p3 and P2 (see table 5).

Desmana thermalis Kormos, 1930

Emended diagnosis: the mean length of the p2 is about 2.32 mm, the mean length of the p3 is about 1.86 mm, the mean length of the p4 is about 2.55 mm; the p2/p3 ratio is about 1.25. The p1 is single-rooted.

The mean length of the P2 is about 2.47 mm, the mean length of the P3 is about 1.82 mm; the P2/P3 ratio is about 1.36. The P1 is single-rooted.

Type locality: Betfia 2, Roumania.

Remarks: Schreuder (1940) mentions that all the material from Betfia 2, allocated by Kormos to *Desmana thermalis,* is stored in Budapest and Basle. However, during our investigations Dr. J. Reumer found two of the specimens mentioned by Kormos – which had disappeared between 1930 and 1940 – in the collections of the British Museum in London. One of these specimens is a mandibular fragment with p2, p4–m1 (Kormos' co-type no. 4), the other is a maxillary fragment with P2–M2 (Kormos' co-type no. 1). This brings the total number of teeth from the type locality to 25.

Kretzoi (1953) described two new taxa from Kisláng: *Desmana crassidens* and *Desmagale pannonica. Desmana crassidens* was based on a mandibular fragment with p2 and p4 (the holotype) and a maxillary fragment with P3–P4. *Desmagale pannonica* was based on a mandibular fragment with the alveoles of the i3–m3 and the trigonid of the m1. Kretzoi was of the opinion that the p2 belonging to the last mentioned mandible must have been single-rooted, and he based his new genus on this feature.

When visiting Dr. Kretzoi in Budapest I had the opportunity to study the fragments as well as an unidentified mandibular fragment with the p2 from the same locality. It appeared that the teeth in the maxillary fragment were not the P3 and the P4, but the P2 and the P3. Comparison of the Kisláng material with jaws from Tegelen proved the Kisláng specimens to be similar to the Tegelen species. The material from Kisláng is figured on Plate 4 and fig. 80.

The Dutch locality Tegelen contains two water-moles. Schreuder (1939,

1940, 1941) first described the larger form as *Desmana thermalis tegelensis,* a determination which was based on a fragmentary femur only. Later she reconsidered the specimen in the light of a lower jaw with p2, found in a drilling core from western Holland, and included both specimens in a new species, *Desmana tegelensis.* Collections made by Freudenthal et al. (1971–1975) yielded large assemblages from both water-moles and proved that the large form fits reasonably well into the variation of *Desmana thermalis* from Betfia 2. Since there seems to be no reason to regard the Tegelen assemblage as a separate species, both the Tegelen and the Kisláng assemblages are allocated to *Desmana thermalis.*

Desmana thermalis is characterized by high p2/p3 and P2/P3 ratios (see table 5).

Desmana inflata n.sp.

Diagnosis: the mean length of the p2 is about 1.97 mm, the mean length of the p3 is about 1.84 mm, the mean length of the p4 is about 2.24 mm; the p2/p3 ratio is about 1.07. The p1 is single-rooted.

The mean length of the C is about 1.55 mm, the mean length of the P2 is about 2.31 mm, the mean length of the P3 is about 1.95 mm; the P2/P3 ratio is about 1.18. The P1 is either single- or double-rooted.

The teeth are bulbous and relatively wide.

Type locality: Valdeganga 2a, province of Albacete, Spain.

Remarks: this species has been described as *Desmana nehringi* by Mein (1978) from the Valdeganga section (Late Villanyian). *Desmana inflata* is characterized by its low and wide, inflated teeth (see table 5).

Desmana sp.

Jánossy (1965) has described *Desmana* remains from Voigtstedt (East Germany) as *Desmana* cf. *thermalis.* The material from this locality is rather scanty: with the exception of the I1 and the P3 the upper teeth are unknown. The lower teeth are better represented; the p2 is very small, the p3 is extremely variable.

Since Jánossy does not give descriptions of the teeth and the measurements are probably not comparable we have no opinion concerning the identity of the material.

Chapter 7

PHYLOGENY

Introduction

Desmanine moles are known in Europe and Asia from the Turolian (Late Miocene) onwards. Apart from *"Desmanella" quinquecuspidata* Mayr & Fahlbusch, 1975 from Hammerschmiede and *Mygalea antiqua* Schreuder, 1940 from Sansan (see p.9) no related taxa of Vallesian or older age are known.

Possible ancestors of the Desmaninae

The main characteristics of the subfamily are:
(1) complete dentition
(2) a two-lobed I1 in the oldest genus, *Dibolia*
(3) an enlarged i2 and I1
(4) an enlarged p2 and P2, that is to say larger or at least as large as the p3 and the P3
(5) a rather narrow humerus.

Starting from these characteristics we tried to decide which of the pre-Turolian talpids may be ancestral to the Desmaninae.

Five subfamilies are included in the Talpidae:

(a) Uropsilinae Dobson, 1883

The subfamily is found in North America, Europe and Asia from the Middle Miocene onwards. Characteristics of the Uropsilinae are the incomplete dentition and the narrow humerus.

Although Hutchison (1968) believes the Desmaninae to be possible descendants of the Uropsilinae – an opinion based on the adaptations of the humerus – the fact that the dentition is incomplete and that the p2 is smaller than the p3 (in *Mydecodon* it is even single-rooted) makes it difficult to adhere to this viewpoint.

(b) Gaillardinae Hutchison, 1968

The subfamily is found in North America from the Middle Pliocene onwards. Representatives are adapted to an aquatic life.

(c) Proscalopinae Reed, 1961

The subfamily is known from North America from the Early Oligocene to the Middle Miocene. The dentition is incomplete; the humerus is wide.

(d) Desmaninae Thomas, 1912

(e) Talpinae Fischer von Waldheim, 1817

(I) Tribe Scaptonychini van Valen, 1967

The tribe is known from Europe and Asia from the Middle Miocene onwards. Van Valen placed "ancestral burrowing moles and their relatively unmodified descendants" in this tribe. The wide humerus and the enlarged p1 and C are characteristic features.

(II) Tribe Talpini Fischer von Waldheim, 1817

The tribe is known from Europe and Asia from the Early Miocene onwards. This tribe comprises burrowing moles with a wide humerus. The p1 and C are enlarged.

(III) Tribe Urotrichini Dobson, 1883

The tribe is known from Europe, Asia and North America from the Oligocene onwards. Representatives have a narrow humerus and incomplete dentition. The genus *Paratalpa* – sometimes regarded as related to the Desmaninae – is allocated to this tribe. *Paratalpa* is characterized by a small C and P2 and a somewhat larger P3, which may have one or two roots. The p2 is larger than the p3.

(IV) Tribe Condylurini Dobson, 1883

The tribe stands isolated among the Talpinae. Representatives are restricted to North America and are of the Pleistocene or younger age. The humerus is of medium width.

(V) Tribe Scalopini Dobson, 1883

The tribe is known from Europe, Asia and North America from the Middle Miocene onwards. Genera allocated to the tribe possess several characteristics which are also found in the Desmaninae, such as incomplete dentition, an enlarged I1 and i1 or I1 and i2 and a divided mesostyle in the upper molars. The fact that the humerus is moderately to very wide points to a fossorial way of life. The best known genus is *Proscapanus* (? = *Alloscapanus*); the p1 in this genus is slightly larger than the p3, while the p2 is smaller than either the p1 or the p3. The p1–p3 are small compared to the p4 and are single- or double-rooted.

Several European genera of Oligocene–Middle Miocene age have been described as Talpidae incertae sedis:

(1) *Myxomygale* Filhol, 1890

The genus is known from the Oligocene. The lower premolars p1–p3 are single-rooted, the upper premolars are unknown. The mesostyle of the upper molars is not divided. The humerus is not known.

taxa	complete dentition	p1>p2<p3	mode of life fossorial	found in: Eur.	Asia	N.Am.
Uropsilinae	–	–	–	+	+	+
Gaillardinae	?/+	?	–			+
Proscalopinae	–	–	+			+
Desmaninae	+	–	–/(+)	+	+	
Talpinae						
Scaptonychini	+/–	+	+	+	+	
Talpini	+	+	+	+	+	
Urotrichini	–	–	–	+	+	+
Condylurini	+	–	+			+
Scalopini	+/–	+	+	+	+	+
Talpidae i.s.						
Myxomygale	?/+	?	?	+		
Mygatalpa	+	+	–	+		
Teutonotalpa	?	?	?	+		
Desmanodon	?	+	+		+	

Table 6. Synopsis of some characteristic features and the geographical distribution of the Talpidae.

(2) *Mygatalpa* Schreuder, 1940

The genus is known from the Oligocene to the Early Miocene. The p2 is the smallest of the lower premolars, as the p1 is enlarged. The p3 is much smaller than the p4; the mesostyle of the upper molars is divided. The humerus is roughly as wide as in the Desmaninae.

(3) *Teutonotalpa* Hutchison, 1974

The genus is known from the Middle Miocene. The p3 is much smaller than the p4 and has one root. The morphology of the P4 is different from that of the P4 of the Desmaninae. The mesostyle of the upper molars is divided. The humerus is not known.

(4) *Desmanodon* Engesser, 1980

The genus is known from the Middle Miocene. The p1 (or the c?) is slightly larger than the p3 and has two roots; the p2 is smaller than the p3 and probably has one root. The p3 is small compared to the p4 and has either one or two roots. The mesostyle of the upper molars is divided. The humerus is wide and adapted to a fossorial mode of life.

Table 6 gives a synopsis of some characteristic features as well as the geographical distribution of the taxa of the Talpidae.

If we exclude those taxa that have (1) incomplete dentition, (2) an enlarged p1 and (3) an exclusively North American dispersal, only *Myxomygale*

and *Teutonotalpa* remain as potential ancestors. Until such time as more material of these two genera and of *"Desmanella" quinquecuspidata* and *Mygalea antiqua* becomes available, it is impossible to establish a relationship between these taxa and the true Desmaninae.

Previous authors believed that the origin of the subfamily must be sought in a primitive stock of talpid insectivores which are thought to have lived in Eocene or earlier times. Even so it is surprising that no clear indications of older desmanine moles have been found in Europe. The only explanation seems to be that the ancestors of *Dibolia* lived in (north-west?) Asia and reached Europe during the Middle or early Late Miocene.

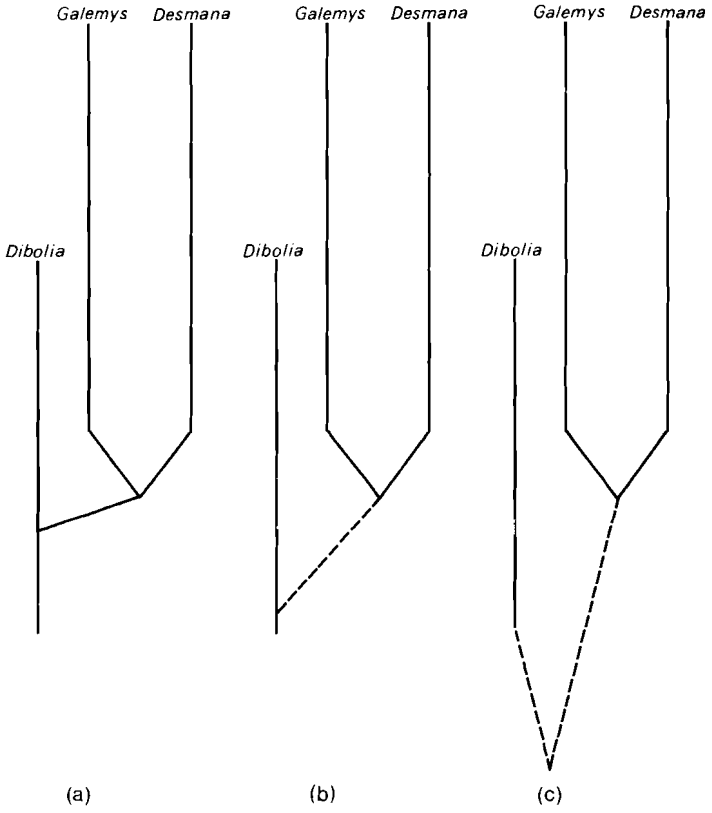


Fig. 51 Three hypothetical phylogenetic reconstructions showing the relationships between the genera allocated to the Desmaninae.

Phylogeny of the Desmaninae

The morphology of the I1 of the genera assigned to the Desmaninae suggests that *Desmana* and *Galemys* are closely related, *Galemys* (first known appearance in the late Middle Ruscinian) being a descendant of a *Desmana*-like form (first known appearance in the Early Ruscinian). If we assume that *Desmana* is related to *Dibolia,* it may be either a direct descendant of *Dibolia* [see fig. 51 (a)] or a descendant of an unknown taxon closely related to *Dibolia* [fig. 51 (b)]. A third possibility is that *Dibolia* and *Desmana* are both descendants of a common stock [fig. 51 (c)]. The material available seems to favour the third hypothesis.

In Turkey and Greece many assemblages of insectivores – not necessarily published – are known from the Oligocene upwards (Ünay, Doucas, pers. comm.), but it is not until the Late Turolian that the first *Dibolia* appears (Maramena 1). The oldest *Desmana* assemblage from this area is of earliest Ruscinian age (Spilia 1). The collections vary considerably in size, a factor which tends to influence their faunal contents, but all things considered the distribution seems to support the conclusion that *Dibolia* and *Desmana* arrived at about the same time in this area, *Dibolia* possibly coming from central Europe and *Desmana* perhaps from (south-west?) Asia.

Table 7 shows the distribution of the species allocated to the Desmaninae. The following observations can be made concerning the possible connection between the species.

In *Dibolia* the p2/p3 ratio diminishes from *Dibolia vinea* through *D. turolense, D. major* and *D. brailloni.* The P2/P3 ratio does not show a trend: it is moderate in *Dibolia vinea,* high in *D. turolense* and *D. major* and again moderate in *D. brailloni.* In addition to this main lineage represented by the four species several contemporary, short living species – which in all likelihood originated as a result of adaptations to a different kind of environment – are present in the same area, though not in the same localities. *Dibolia adroveri* and *D. luteyni* are two examples. *Mygalinia hungarica* from Polgárdi may be another one.

In eastern Europe and Turkey another lineage, represented by *Dibolia dekkersi* and *D. bifida* occurs. The teeth of the species allocated to the eastern lineage are slightly smaller than those of the taxa of the western lineage. In the eastern species the p2/p3 and P2/P3 ratios reach their lowest values. Probably this lineage can also be traced back to *Dibolia vinea.*

That all species must have been closely related shows the trend in the reduction of the number of roots of the p1 and the P1. In the Early and Middle Turolian species both p1 and P1 have always two roots. In the Upper

Turolian and in nearly all known Early and Middle Ruscinian assemblages the p1 is single-rooted and the P1 double-rooted. In the Upper Ruscinian assemblages the p1 has always one root and the P1 one or two root(s). In the only known Villanyian assemblage the p1 has one root; the tooth seems to be missing in one mandibular fragment.

In *Galemys* the p2/p3 and P2/P3 ratios remain the same throughout. It is assumed that *Galemys sulimskii, G. kormosi, Galemys* sp. from Venta Micena (see p. 93) and *Galemys pyrenaicus* represent one lineage, while *G. semseyi* represents a side-line.

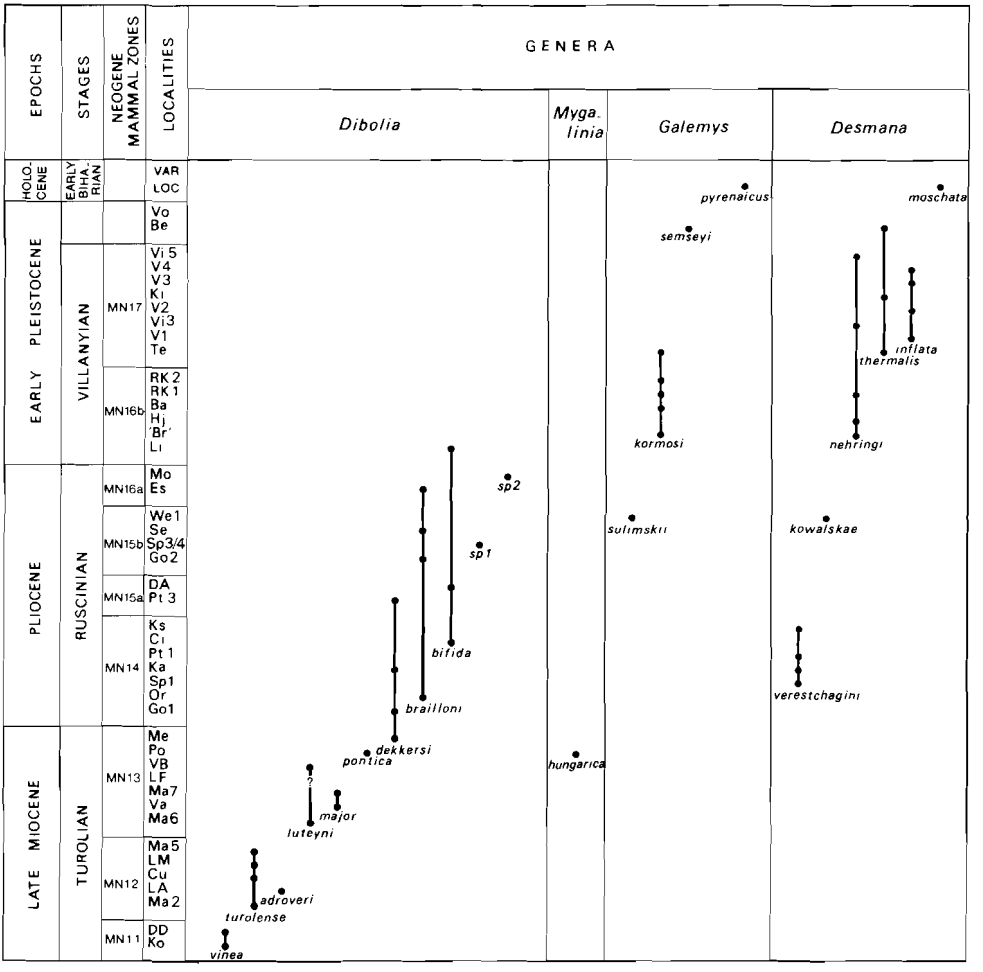


Table 7 Distribution of the species allocated to the Desmaninae.

All *Galemys* assemblages have a single-rooted p1. The Middle Ruscinian species has a double-rooted P1. In Early Villanyian assemblages the P1 has either one or two root(s). In *Galemys pyrenaicus* the P1 is always single-rooted. The assemblage from Tegelen – with a double-rooted p1 and P1 – does not fit into this reduction pattern.

In *Desmana* species the p2/p3 ratio is moderate to low; variations are randomly distributed. The P2/P3 ratio is moderate to high.

Desmana verestchagini can be regarded as ancestral to both the younger *Desmana* species and to *Galemys* (see figs. 41–45). *Desmana kowalskae* and *D. nehringi* seem to represent one lineage, with *D. inflata* as an offshoot. *Desmana thermalis* and *D. moschata* represent another lineage. The material from Voigtstedt is too scanty for species determination and cannot be allocated to any of the lineages.

All *Desmana* assemblages have a single-rooted p1. In the Ruscinian and Villanyian assemblages P1 has either one or two root(s). The P1 of *Desmana thermalis* is always single-rooted, as is the P1 of the extant species *Desmana moschata.*

Chapter 8

FUNCTIONAL MORPHOLOGY AND ECOLOGY

Introduction

Most paleontologists have assumed that fossil Desmaninae had a mode of life similar to that of the extant species. However, since the biotope of *Galemys pyrenaicus* differs considerably from that of *Desmana moschata* – fast mountain streams for the first, slow shallow rivers and lakes for the second – one cannot speak of one biotope.

In many localities yielding fossil water-moles there are two species present, suggesting that the biotopes of these co-occurring species were not as different as those of the two living species. Anatomical characteristics of the fossil representatives of the subfamily support the view that the biotope of fossil Desmaninae was in general closer to that of *Desmana moschata* than of *Galemys pyrenaicus.*

The humerus (Pl. 1, figs. 1–5)

Very few humeri were found. All known specimens are similar to the ones of the extant *Galemys* and *Desmana;* this means that fossil species, including species of *Dibolia,* were also non-fossorial.

Chevron bones (Pl. 1, figs. 6–9) *)

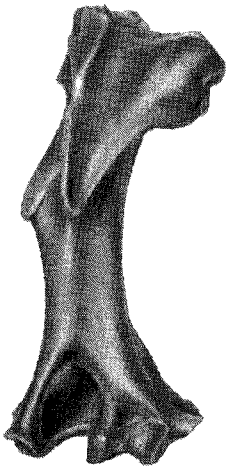
The tails of some rodents and insectivores have modified chevron bones. These oval or roughly H-shaped bones are situated on the ventral side of the vertebrae, overlapping two centra and pressing against the metapophyses of the distal vertebra. One very small chevron occurs in *Talpa europaea* reinforcing the connection between the first and second caudal vertebrae. The laterally flattened tail of the musk rat *(Ondatra zibethicus)* has at least nine chevrons which are better developed than in *Talpa europaea.* In *Galemys pyrenaicus* and *Desmana moschata* the chevrons are H-shaped and so large that they cover most of the ventral side of the caudal vertebrae. Moreover they occur along the full length of the tail. The proximal chevrons are relatively wide and short becoming gradually longer and narrower distally. Their ventral as well as their dorsal side are grooved longitudinally. These grooves,

*) It was M. Hugueney who kindly drew my attention to the chevron bones of *Galemys pyrenaicus.*

Plate 1

1. humerus (sin) of *Desmana thermalis,* Tegelen, anterior view.
2. humerus (sin) of *Galemys kormosi*, Tegelen, anterior view.
3. humerus (sin) of *Desmana verestchagini*, Spilia 1, distal end, anterior view.
4. humerus (sin) of *Dibolia dekkersi*, Kardia, distal end, anterior view.
5. humerus (sin) of *Desmana verestchagini*, Kardia, anterior view.
6. chevron bone of *Desmana verestchagini,* Spilia 1, a) ventral view; b) dorsal view.
7. chevron bone of *Dibolia dekkersi*, Maramena 1, a) ventral view; b) dorsal view.
8. chevron bone of *Dibolia turolense*, Cubla, dorsal view.
9. caudal vertebrae and chevron bones of *Desmana moschata,* side view.

Figs. 1–5, 9 × 2.5 figs. 6–8 × 5.



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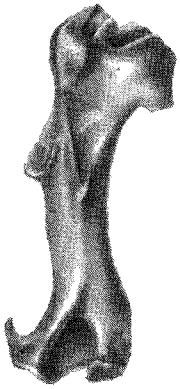

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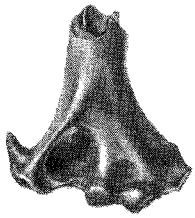

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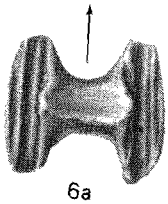

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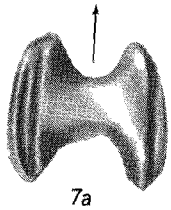

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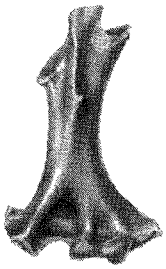

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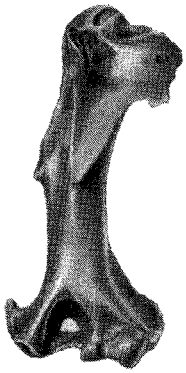

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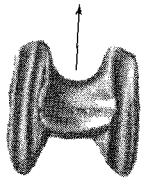

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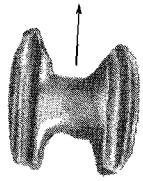

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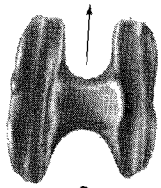

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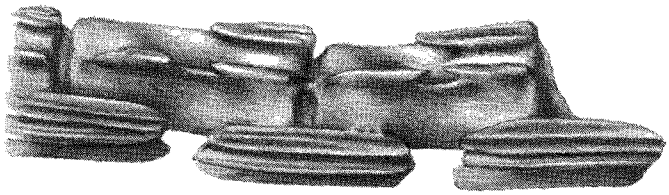


9

through which tendons pass, are less pronounced in the proximal chevrons; they bifurcate – becoming deeper in the middle part of the tail – and shift to the sides of the chevrons near the end of the tail. As far as I have been able to ascertain from the literature the size as well as the number and the shape of the chevrons of the Desmaninae are unique among mammals. Since *Desmana moschata, Galemys pyrenaicus* and *Ondatra zibethicus* with their (partly) laterally flattened tails are among the best swimming smaller mammals, there seems little doubt that their strong chevrons are an adaptation to their subaquatic mode of life.

Chevron bones which are strikingly similar, but smaller than those of *Desmana moschata* and *Galemys pyrenaicus* have been found in several localities that yielded fossil Desmaninae. These chevrons attributed to *Dibolia, Galemys* and *Desmana* suggest that all the representatives of these genera were adapted to a subaquatic mode of life.

The lower jaw (figs. 52.1 to 52.6)

When the fragmentary lower jaws shown in figs. 52.1 to 52.6 and the specimens figured by Kormos (1913, 1938) and by Schreuder (1940) are compared, it becomes apparent that there are striking differences. The shape and the direction of the coronoid, the length and height of the angulare and the shape of the area for muscle attachment on this process and the position of the condyle relative to the occlusal surface are quite different in the various taxa. The skulls of extant *Galemys* and *Desmana* show differences of a similar nature.

The relation between shape and function of the lower jaw has been studied extensively in larger mammals, but not in smaller ones. It is generally accepted that a high position of the condyle relative to the occlusal surface of the teeth – as seen in large herbivores – allows lateral movement of the lower jaw and serves to distribute the biting force evenly over the tooth row. A condyle that is situated at about the level of the occlusal surface – a feature occurring in carnivores – restricts lateral movement of the mandible and serves to increase the biting force, particularly between the rear molars (Crompton and Hiiemäe, 1969).

In *Galemys pyrenaicus* the jaw joint lies somewhat above the tooth row (fig. 52.1) and the dentition is narrow, high and sharp. The C is higher than the upper premolars and the P4 bears a sharp crest. In *Desmana moschata* the jaw joint lies well above the tooth row (fig. 52.2). The dentition is bulbous, low and blunt. The C is only slightly higher than the upper premolars and the P4 is strongly molarized. This means that – should the above mentioned theory be applicable to the Desmaninae – *Galemys* is carnivorous and *Desmana* herbivorous.

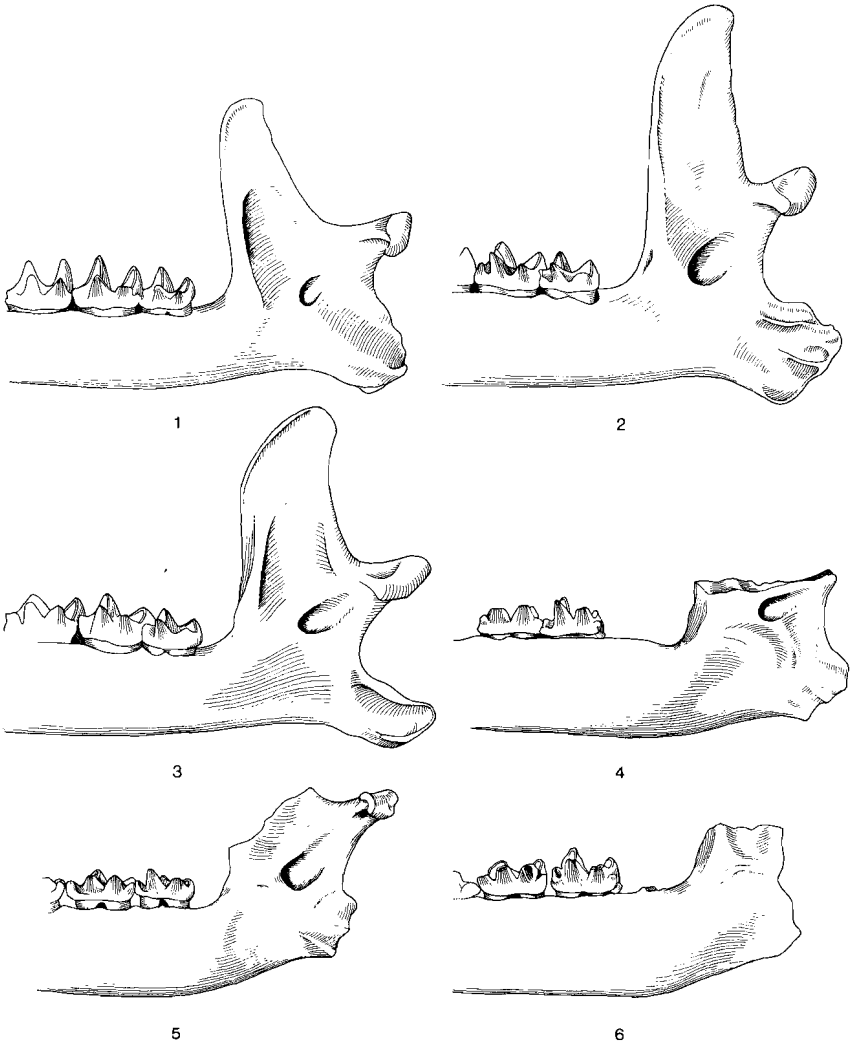


Fig. 52
1. mandibular fragment of *Galemys pyrenaicus*
2. mandibular fragment of *Desmana moschata*
3. mandibular fragment of *Dibolia brailloni*, Sète
4. mandibular fragment of *Desmana verestchagini*, Ptolemais 1
5. mandibular fragment of *Dibolia dekkersi*, Kardia
6. mandibular fragment of *Desmana verestchagini*, Kardia

not to scale

The natural food of these species has been studied in detail (Barabasch-Nikiforow, 1975). *Galemys* feeds mainly on aquatic invertebrates, such as larvae, small gastropods and worms, occasionally on fish. In captivity the animal will eat new-born mice and meat (Niethammer, 1970). *Desmana* is polyphagous, but its main food is animal, such as insect larvae, worms, gastropods and more rarely bivalves. Fish and crustaceans are hardly ever caught. However, in spring and winter *Desmana* also eats water-plants. The food differs according to the season and the geographical area. In captivity the desman will eat fish, but it prefers meat.

The overall impression is that the food of *Desmana* is more varied than that of *Galemys,* but that the animal is rather more omnivorous than herbivorous. It seems probable that its tendency to be herbivorous is due to the absence of suitable prey in its habitat during part of the year.

Fossil forms can be classified as follows:

"carnivorous"	"Omnivorous"
Dibolia pontica from Sète	*Desmana thermalis* from Betfia 2
	Galemys semseyi from Betfia 2
	Desmana nehringi from Villany 3
	Desmana nehringi from Beremend
	Mygalinia hungarica from Polgárdi
	Dibolia dekkersi from Kardia

It is clear that nearly all the species of which the mandible is known show the type of jaw joint found in *Desmana moschata.* It therefore seems reasonable to assume that the food of these species was similar to that of the living *Desmana.* It is surprising that both species from Betfia 2 were "omnivorous".

Ecological niches

Many localities contain the remains of two water-moles, a larger and a smaller one. The oldest known locality in which two species occur is Polgárdi (*Mygalinia hungarica,* a small form, and *Dibolia pontica,* a larger one). From the Ruscinian onwards the situation is similar in a number of central and eastern European localities. In Spain only one locality is known in which two Desmaninae were found (Venta Micena). The following table gives the distribution of the genera of desmanine moles through time.

It is remarkable that *Dibolia* first occurs as the larger member of a pair, but later takes the role of the smaller member. This switch may have influenced the mode of life of *Dibolia,* as representatives of the eastern lineage can be distinguished from those of the western lineage: *Dibolia brailloni* is slightly larger than the contemporary *D. dekkersi* and *D. bifida* and it has an

I1 of morphotype AW, while the eastern species have an I1 of morphotype AN (see p. 57).

	western Europe	central and eastern Europe
Recent	*Galemys*	*Desmana*
Biharian	*Desmana/Galemys*	*Desmana/Galemys*
Ruscinian	*Dibolia*	*Desmana/Galemys* *Desmana/Dibolia*
Turolian	*Dibolia*	*Dibolia/Mygalinia* *Dibolia*

Conclusions

All known representatives of the Desmaninae were good swimmers. Most taxa seem to have been polyphagous, although it is possible that some of the smaller forms were more carnivorous. It is concluded that all taxa lived in shallow quiet water, an ecological niche comparable to that of living *Desmana moschata,* and that the niche of *Galemys pyrenaicus* deviates from the situation that is regarded as "normal" for desmanine moles.

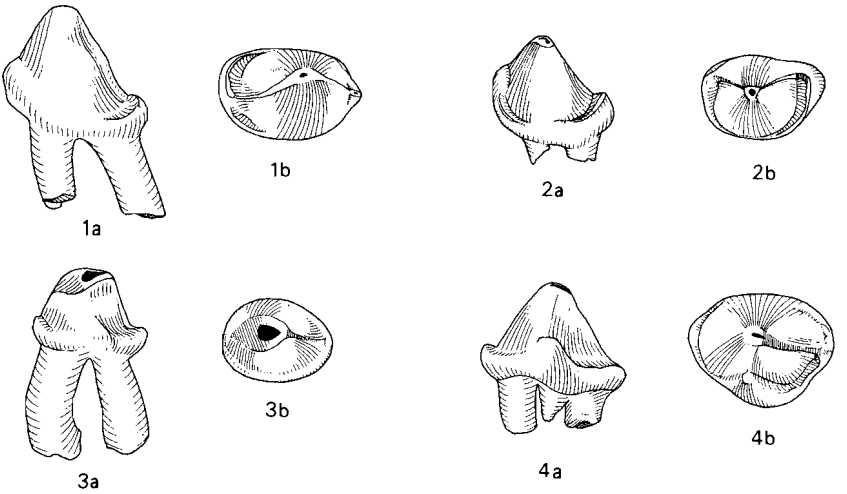


Fig. 53 *Dibolia dekkersi* n.sp.
1. p2 (dext), Ka-615
   a) lingual view b) occlusal-labial view.
2. p3 (dext), Ka-646 (holotype)
   a) lingual view b) occlusal-labial view.
3. C (sin), Ka-964
   a) lingual view b) occlusal-lingual view.
4. P3 (sin), Ka-1056
   a) lingual view b) occlusal-lingual view.

Chapter 9

DESCRIPTIONS

Introduction

Descriptions are given of the following teeth: the i1 and the I1 since they are regarded as characteristic on the generic level; the p2, p3, p4, C, P2 and P3 since these teeth are regarded as characteristic on the species level and the P4 since the morphology of this tooth is regarded as a standard for the degree of molarization of the teeth.

Readers who are interested in the descriptions of the teeth not included here are invited to write to the author for these descriptions.

Dibolia n.g.

For the diagnosis and the differential diagnosis the reader is referred to chapter 6.

Dibolia dekkersi n.sp.

Derivatio nominis: the species is named after Mr. Th.J. Dekkers, former financial administrator of the Institute of Earth Sciences, Utrecht.

Diagnosis: the mean length of the p2 is about 1.44 mm, the mean length of the p3 is about 1.24 mm, the mean length of the p4 is about 1.58 mm; the p2/p3 ratio is about 1.16. The p1 has one root.

The mean length of the C is about 1.28 mm, the mean length of the P2 is about 1.59 mm, the mean length of the P3 is about 1.48 mm; the P2/P3 ratio is about 1.09. The P1 has two roots.

Differential diagnosis: the combination of a p2/p3 ratio with an average value, a P2/P3 ratio with a low value and a short C differentiates *Dibolia dekkersi* from all other *Dibolia* species.

Holotype: p3 (dext), Ka-646 (fig. 53.2), stored in the collection of the Institute of Earth Sciences, Rijksuniversiteit Utrecht, Utrecht, the Netherlands.

Type locality: Kardia, Macedonia, Greece. For a description of the locality see van de Weerd, 1979.

Age of the locality: Early Ruscinian (MN 14).

Other localities with Dibolia dekkersi: Maramena (Late Turolian) and Ptolemais 3 (Early Ruscinian), both situated in the north of Greece and Gorafe 1 (Early Ruscinian) in the Province of Granada, Spain.

Measurements: see table 8 (a) for the lower teeth and table 8 (b) for the upper teeth.

Description of the assemblage from the type locality.

The four mandibular fragments available show the following positions for the foramina mentale: one under the p1, one under the p2–p3 and one under the m1.

The p3 is positioned straight in the lower jaw in two out of three specimens; in the third specimen the position of the tooth is oblique relative to the axis of the jaw, with the anterior root placed lingually.

i1 (22) Fig. 5.7 The crown is wide and low. The central rib is strong but short. The pronounced posterior projection is bordered medially by a short cingulum. The enamel-dentine boundary is slightly curved upwards on the medial side.

p2 (29) Fig. 53.1 The crown is high and sharp and has an elliptical cross-section. Many specimens are relatively narrow. The enamel-dentine boundary rises towards the anterior end of the tooth. A flat or concave postero-lingual face is present. The postero-lingual basin is narrow and deep. The paraconid may be weak or strong. The short postero-lingual cingulum is very wide and may form a small bulge at the base of the posterocristid. The postero-labial and anterior cingula are weak or missing.

p3 (20) Figs. 11.2 and 53.2 The morphology and the outline of the crown are variable. The lingual side is more convex than the labial side. A flat or concave postero-lingual face and sometimes a narrow talonid basin are present. The antero-labial flattening of the crown is indistinct. A weak paraconid may be present. The postero-lingual cingulum may widen at the base of the posterocristid. The labial cingula are inconspicuous.

p4 (28) Fig. 12.2 The anterior end of the crown is often symmetrical. The postero-lingual face is concave; the talonid valley is closed lingually by a high rim formed by the continuation of the posterocristid. The crown overhangs the root labially.

A paraconid and a more or less distinct metaconid are present. Short and narrow postero-labial and anterior cingula are present.

I1 (22) The crown is of medium height. The medial lobe is relatively long and wide. The depth of the indentation in the upper edge is variable. The inner side of the crown is narrow and deeply concave; the medial crest merges into the heavy but short internal cingulum. The enamel-free area is high.

C (29) Figs. 21.3 and 53.3 The crown is small and low, with an elliptical cross-section. The labial side is more convex than the lingual side. An ill-de-

fined postero-lingual face is present in most specimens. The anterior and posterior cingula are rather long and are usually connected lingually. At the base of the posterocrista the cingulum may be inflated.

P2 (29) The crown has an elliptical cross-section. Labial, posterior and lingual sides are convex, a flat posterior face is always present lingually and often labially. A lingual extension is missing in most specimens. The posterior cingula are long and wide, the anterior cingula are short and wide. Along the lingual side a cingulum or an inflated zone is found. Most specimens have two roots, an accessory rootlet is seldom found.

P3 (31) Figs. 24.3 and 53.4 The crown is somewhat variable. Most specimens have an elliptical or a rounded cross-section. Labial, anterior and lingual sides are convex. A long flat postero-lingual face is always present, an ill-defined postero-labial face and a postero-lingual basin are found in many specimens. The lingual extension usually bears a cingular spur or bulge. The posterior cingula are high and heavy and lingually longer than labially; the anterior cingula are short and narrow. Small anterior and posterior cingular bulges are found in most specimens. The tooth has two or three roots.

P4 (35) A high tooth with a sharp tip. The crown is bivonvex with flat or concave posterior faces. The postero-lingual depression is rather deep. Anteriorly a short extension, bearing a small cuspule, is present; posteriorly the continuation of the sharp posterocrista forms a small bulge. The lingual lobe is of normal size; the protocone is of medium height, with a low connection to the paracone. The anterior border is concave, the posterior one more or less straight. The anterior and posterior cingula are long and heavy.

Description of the material from Maramena 1.

For a description of the locality see Bouwens & de Bruijn, in prep.

The six mandibular fragments available show two (1 specimen), three (4 specimens) or four (1 specimen) foramina mentale. The anterior one is situated under p1–p2, the posterior one under the m1. If only one foramen is present in the middle, it is situated under the p4; if two are present they are situated under p2–p3 and under p3–p4.

The position of the p3 is either straight (2 specimens) or slightly oblique relative to the length axis of the jaw with the anterior root labially (2 specimens) or lingually (2 specimens).

The P3 is set either straight or obliquely with the anterior root placed lingually.

i1 (7) The crown is of medium height and is symmetrical. The central rib is faint. The backward projection of the crown is situated either centrally

tooth	loc.	N	L		W(2)		W(2)/L	
			range	mean	range	mean	range	mean
c	Pt3	3	1.04–1.23	1.15	0.69–0.77	0.74	0.62–0.66	0.65
	Ka	8	0.97–1.17	1.07	0.73–0.83	0.78	0.68–0.79	0.74
	Go1	2	1.12–1.19	1.15	0.87–0.98	0.88	0.75–0.78	0.76
	Me	3	1.11–1.23	1.16	0.84–0.90	0.88	0.72–0.79	0.76
p1	Pt3	1		1.11		0.91		0.82
	Ka	16	0.83–0.99	0.91	0.75–0.87	0.81	0.82–0.99	0.90
	Go1	1		0.81		0.67		0.83
	Me	4	0.83–1.10	0.97	0.90–0.97	0.94	0.88–1.08	0.98
p2	Pt3	8	1.37–1.50	1.42	0.83–0.93	0.90	0.59–0.68	0.63
	Ka	29	1.31–1.56	1.44	0.82–1.00	0.92	0.57–0.73	0.64
	Go1	5	1.28–1.50	1.41	0.93–1.02	0.99	0.63–0.79	0.71
	Me	9	1.40–1.54	1.48	0.96–1.04	1.00	0.64–0.74	0.68
p3	Pt3	2	1.34–1.38	1.36	0.90–0.93	0.91	0.65–0.69	0.67
	Ka	20	1.13–1.38	1.24	0.85–0.97	0.90	0.64–0.81	0.73
	Go1	2	1.23–1.26	1.24	0.85–0.85	0.85	0.67–0.69	0.68
	Me	7	1.22–1.47	1.34	0.90–1.03	0.98	0.70–0.82	0.73
p4	Pt3	7	1.47–1.63	1.55	1.03–1.11	1.07	0.66–0.73	0.69
	Ka	28	1.44–1.73	1.58	0.93–1.16	1.08	0.63–0.77	0.69
	Go1	1		1.58		1.19		0.75
	Me	9	1.48–1.69	1.62	1.04–1.20	1.11	0.63–0.75	0.69
m1	Pt3	11	2.24–2.37	2.31	1.66–1.95	1.79	0.72–0.83	0.78
	Ka	30	2.08–2.38	2.27	1.58–1.87	1.74	0.71–0.81	0.77
	Go1	–		–		–		–
	Me	10	2.26–2.46	2.37	1.68–1.98	1.85	0.73–0.88	0.78
m2	Pt3	13	2.14–2.28	2.22	1.65–1.77	1.71	0.75–0.81	0.77
	Ka	27	2.09–2.39	2.26	1.50–1.79	1.63	0.68–0.80	0.72
	Go1	1		2.23		1.75		0.78
	Me	6	2.21–2.33	2.28	1.68–1.75	1.72	0.73–0.78	0.75
m3	Pt3	13	1.68–1.82	1.75	1.18–1.33	1.25	0.65–0.76	0.71
	Ka	44	1.62–2.03	1.80	1.10–1.35	1.21	0.63–0.73	0.67
	Go1	2	1.74–1.96	1.85	1.19–1.28	1.23	0.65–0.68	0.66
	Me	8	1.68–1.80	1.75	1.16–1.31	1.25	0.65–0.77	0.71

Table 8 (a) Measurements of *Dibolia dekkersi* n.sp., lower teeth.

or postero-medially and is bordered by a cingulum. The enamel-dentine boundary is curved upwards in the middle of the medial side.

p2 (9) The long crown has an elliptical outline, usually without an antero-labial flattening. A flat or slightly concave postero-lingual face with or without a talonid basin at its base is present. The paraconid is distinct. The posterior cingula are moderately strong and long; the anterior cingula are faint

tooth	loc.	N	L		W		W/L	
			range	mean	range	mean	range	mean
C	Pt3	10	1.16–1.28	1.22	0.82–0.92	0.86	0.68–0.72	0.70
	Ka	29	1.13–1.41	1.28	0.84–1.00	0.92	0.67–0.77	0.71
	Go1	1		1.20		0.87		0.72
	Me	7	1.17–1.39	1.27	0.86–0.96	0.90	0.65–0.76	0.71
P1	Pt3	4	1.04–1.14	1.09	0.74–0.85	0.80	0.65–0.80	0.73
	Ka	18	0.88–1.13	0.98	0.84–0.96	0.90	0.85–1.01	0.92
	Go1	1		1.01		0.82		0.81
	Me	8	0.91–1.11	1.00	0.90–1.09	0.98	0.87–1.07	0.98
P2	Pt3	10/11	1.52–1.66	1.59	0.93–1.04	1.00	0.61–0.67	0.63
	Ka	29	1.49–1.69	1.59	0.98–1.15	1.06	0.62–0.72	0.67
	Go1	2	1.49–1.57	1.53	1.08–1.12	1.06	0.71–0.72	0.71
	Me	7	1.56–1.76	1.67	1.06–1.32	1.17	0.66–0.78	0.70
P3	Pt3	18	1.29–1.54	1.41	1.05–1.24	1.14	0.74–0.88	0.81
	Ka	31	1.32–1.56	1.46	1.07–1.32	1.18	0.72–0.90	0.81
	Go1	3	1.32–1.50	1.41	1.02–1.12	1.06	0.74–0.77	0.75
	Me	8	1.29–1.53	1.41	1.11–1.37	1.25	0.80–1.05	0.89
P4	Pt3	11/12	1.95–2.10	2.01	1.55–1.72	1.65	0.77–0.85	0.82
	Ka	35	1.89–2.11	1.99	1.55–1.79	1.69	0.79–0.92	0.85
	Go1	2	1.98–2.13	2.05	1.62–1.70	1.66	0.80–0.82	0.81
	Me	6	1.88–2.02	1.95	1.67–1.89	1.74	0.86–0.97	0.89
M1	Pt3	5/6	2.70–2.92	2.81	2.31–2.62	2.44	0.79–0.93	0.87
	Ka	34	2.57–2.95	2.79	2.10–2.49	2.31	0.74–0.93	0.83
	Go1	1		3.05		2.26		0.74
	Me	7	2.80–3.00	2.91	2.47–2.67	2.58	0.83–0.94	0.89
M2	Pt3	3	2.00–2.11	2.04	2.41–2.58	2.50	1.19–1.25	1.22
	Ka	44	1.80–2.16	2.07	2.40–2.71	2.57	1.16–1.34	1.24
	Go1	–		–		–		–
	Me	3/4	2.05–2.11	2.08	2.69–2.79	2.73	1.30–1.33	1.32
M3	Pt3	14	1.35–1.53	1.46	1.75–2.01	1.89	1.24–1.40	1.30
	Ka	31	1.25–1.44	1.36	1.83–2.11	1.99	1.40–1.56	1.46
	Go1	2	1.32–1.42	1.37	1.83–2.02	1.92	1.39–1.42	1.40
	Me	7	1.45–1.54	1.51	2.04–2.27	2.10	1.33–1.47	1.39

Table 8 (b) Measurements of *Dibolia dekkersi* n.sp., upper teeth.

and often short. The roots are slightly or not at all divergent. In one specimen the roots are partly fused.

p3 (7) The crown is variable: some specimens are relatively long, others are rounded. The enamel-dentine boundary rises steeply towards the anterior end of the crown. The postero-lingual face is concave or flat; the talonid basin varies from deep to indistinct. The antero-labial flattening is distinct

in most specimens; the paraconid is individualized. The posterior cingulum is wide, the labial one is faint.

p4 (9) Fig. 54.1 The crown is compact and low with a sub-rectangular cross-section. The anterocristid ends in the antero-lingual corner of the tooth, the posterocristid either in the postero-labial corner or in the middle of the straight posterior border. The postero-lingual face may be flat or concave; the talonid valley at its base may be distinct or inconspicuous and is usually closed lingually. The paraconid is an individualized cusp; a metaconid or a metaconal rib are present. The strong posterior cingulum may form a minuscule hypoconid and/or entoconid. A narrow cingulum may surround the entire crown, but may be partly missing.

I1 (10) Fig. 17.2 The crown is high. The medial lobe is thick and short. The indentation in the upper edge is deep. The inner side of the crown is

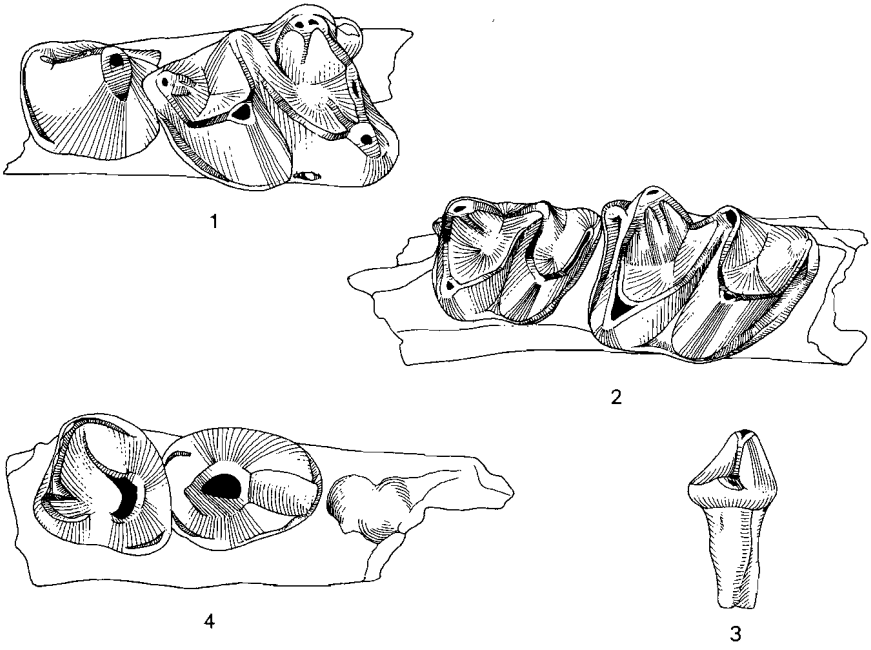


Fig. 54 *Dibolia dekkersi* n.sp.
1. mandibular fragment with p4—m1 (sin), Me-345 occlusal-labial view.
2. mandibular fragment with m2—m3 (dext), Me-389 occlusal-labial view.
3. P1 (sin), Me-65 posterior view.
4. maxillary fragment with P2—P3 (dext), Me-87 occlusal-lingual view.

concave with a sharp medial crest. The narrow internal cingulum is sometimes interrupted. It is connected to the crest. The enamel-free zone is low.

C (7) The crown is small but rather high and has a sharp tip. The outline of the crown is elliptical. The labial side is strongly convex, the lingual side is more or less flat. A postero-lingual face is absent. The anterior cingulum is short; the posterior cingulum is strong and may form a small bulge at the base of the posterocrista. Lingual and labial cingula are missing.

P2 (7) Fig. 54.4 The long crown has an oval cross-section. Both the labial and the lingual sides are convex. A flat postero-lingual face and often a postero-labial face are found. The wide posterior cingulum is lingually longer than labially; a posterior bulge is missing. In most specimens the posterior widening of the crown is hardly more pronounced lingually than labially and a lingual bulge or spur is absent. The long anterior cingulum is narrow. The tooth has two – rarely three – roots.

P3 (8) Fig. 54.4 The compact tooth has a sub-triangular outline; some specimens are wider than they are long. The crown is biconvex with a flat or concave postero-lingual face and a narrow depression at its base. The lingual extension is pronounced. The anterior and in particular the posterior cingula are wide; the postero-lingual cingulum ends in a high spur on the lingual extension. The antero-lingual cingulum may also be connected to this spur. Nearly all specimens have three roots, in one specimen the posterior root is widened to support the lingual extension.

P4 (6) Fig. 25.2 A compact tooth. The outline of the crown is sub-triangular. The tooth is biconvex, with pronounced posterior faces and a posterior depression of variable size and depth. A large cusp may lie at the base of the posterocrista. The lingual lobe is variable; the protocone is high and well separated from the paracone. The anterior border of the lobe is concave, the posterior border is straight. The high postero-lingual cingulum is often interrupted in the middle; it forms in some specimens a small hypocone. The antero-lingual cingulum ends at the base of the protocone. Labial cingula are present.

Description of the material from Gorafe 1.

For a description of the locality see de Bruijn, 1974.

i1 (1) The crown is of medium height and bears a long and strong central rib. The backward projection is distinct. The postero-medial cingulum is long and wide but does not form a posterior bulge. The enamel-dentine boundary curves upwards in the middle of the medial face.

p2 (5) The morphology of the crown is variable. The tooth is strong and rather high, with a sub-triangular outline and a somewhat flattened antero-

labial corner. The enamel-dentine boundary rises towards the anterior end of the crown. A flat or concave postero-lingual face and a depression are present. The paraconid is weakly developed. The short posterior cingula are rather wide, the anterior cingula very narrow. The two roots are straddling. In one specimen the two roots are fused.

p3 (2) The tooth is small compared to the p2. The crown is narrow with an elliptical outline. The lingual side is convex with a flat posterior face, the labial side is flat. An indistinct talonid basin is present. The paraconid is very weakly developed. The crown is surrounded by a narrow cingulum that widens along the posterior end where it forms a pronounced bulge.

p4 (1) The crown is high and has a sub-triangular cross-section. The postero-lingual face is wide and concave; the long and wide talonid valley is lingually closed. A small paraconid and a minuscule metaconid are present. The postero-lingual cingulum is strong, the labial cingula are weakly developed.

I1 (3) The shape of the crown is variable. Two specimens are very wide and compressed, with a short thick medial lobe. In these specimens the inner side of the crown is flat, with a short blunt medial edge and a strong long internal cingulum, which are not connected. One specimen is high and narrow with a high medial lobe. Here the inner side is strongly concave and the medial crest somewhat sharper than in the other specimens. The lower part of the crown has been broken off. The enamel-free zone is rather low.

C (2) Fig. 21.1 The crown is small but high, with an elongated elliptical cross-section. The labial side is strongly convex, the lingual side is flat. A narrow lingual cingulum is present.

P2 (2) A rounded crown with a blunt posterocrista. Its cross-section is oval. Both the labial and the lingual side are convex and may have a flat posterior face. The cingula are narrow and of variable length. Very small anterior and posterior cingular bulges are present.

P3 (3) The crown has a rhombic outline. The lingual side is less convex than the labial side and features a flat postero-lingual face. The lingual extension is wider than in the P2. A labial cingulum and anterior and posterior cingular bulges may be present. The anterior cingulum ends in a spur at the lingual extension. There are two or three roots: the very thin accessory root merges into the wide posterior one.

P4 (2) Both the labial and the lingual sides are convex with a flat or concave posterior face and small posterior basins. The long anterior extension bears a small cusplet; the shorter posterior extension shows an inconspicuous bulge formed by the continuation of the posterocrista. The lingual lobe is wide, the protocone is low with a low connection to the paracone. The ante-

rior and posterior borders of the lingual lobe are more or less straight. The crown is surrounded by a cingulum that is interrupted for a short distance along the base of the protocone and in the middle of the labial side only.

Description of the material from Ptolemais 3.

For a description of the locality see van de Weerd, 1979.

A foramen mentale is present under the m1.

The position of the p3 is slightly oblique relative to the length axis of the lower jaw.

i1 (3) The crown is high and relatively narrow, with a weak and short central rib. The heavy backward projection is bordered by a rather long medial cingulum. The enamel-dentine boundary curves upwards in the middle of the medial side.

p2 (8) Figs. 10.4 and 55.2 The long and relatively narrow tooth has an elongated elliptical cross-section with an inconspicuous antero-labial flattening. The dentine-enamel boundary rises steeply towards the anterior end of the crown. A long talonid basin lies at the base of a flat postero-lingual face. The heavy postero-lingual cingulum forms a small bulge at the base of the posterocristid. The postero-labial cingulum is short. Anterior cingula, if present at all, are very narrow.

p3 (2) Figs. 55.3 and 55.4 The crown is relatively narrow; the enamel-dentine boundary rises steeply towards the anterior end of the crown. The crown is biconvex but for a concave postero-lingual face. The talonid valley is

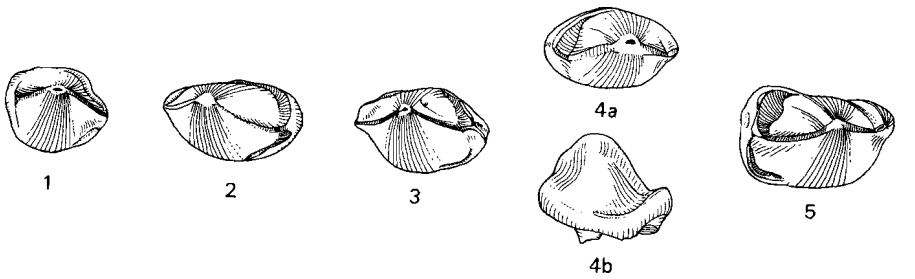


Fig. 55 *Dibolia dekkersi* n.sp.
1. p1 (dext), Pt3-641
occlusal-labial view.
2. p2 (sin), Pt3-656
occlusal-labial view.
3. p3 (sin), Pt3-661
occlusal-labial view.
4. p3 (dext), Pt3-662
a) occlusal-labial view b) lingual view.
5. p4 (dext), Pt3-675
occlusal-labial view.

long and deep. The antero-labial corner of the tooth is slightly flattened. The tooth has a small paraconid and a minuscule metaconid. The postero-lingual cingulum is very heavy but low and forms a distinct bulge at the posterior end. The postero-labial cingulum is weak.

p4 (7) Fig. 55.5 The tooth has a sub-rectangular cross-section with straight anterior and posterior borders. The crown overhangs the root slightly on the labial side. A talonid valley, closed posteriorly by the continuation of the posterocristid, lies at the base of the postero-lingual face. A paraconid and a metaconal rib are present. The postero-labial and anterior cingula are weak.

I1 (7) A rather low tooth with a long thick medial lobe. The deep indentation in the upper edge is situated strongly off-centre. The inner side of the crown is concave, with a blunt medial crest merging into a long and heavy inner cingulum. The enamel-free area is moderately high.

C (10) Fig. 56.1 The tooth is small, but nevertheless rather high. The labial side is more convex than the lingual side. An ill-defined postero-lingual face is present. The weak antero- and postero-lingual cingula are sometimes connected by an inflated zone.

P2 (11) Figs. 23.3 and 56.3 The crown has an elongated elliptical outline and is hardly wider posteriorly than anteriorly. The labial side is more

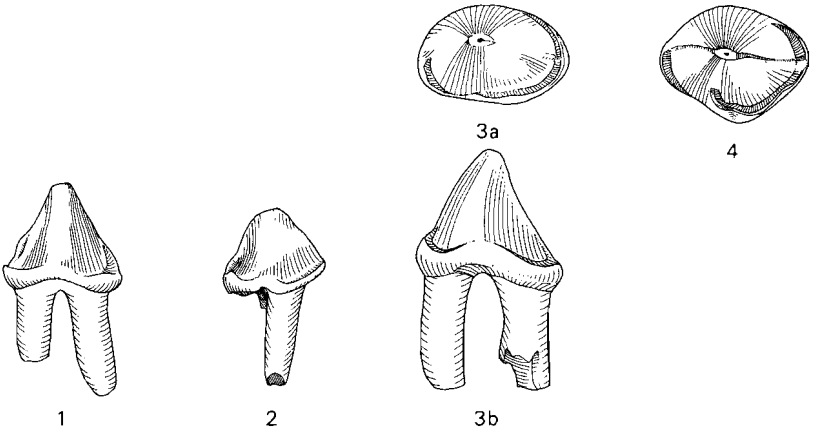


Fig. 56 *Dibolia dekkersi* n.sp.
1. C (sin), Pt3-758
lingual view.
2. P1 (dext), Pt3-761
lingual view.
3. P2 (sin), Pt3-778
a) occlusal-lingual view b) lingual view.
4. P3 (sin), Pt3-804
occlusal-lingual view.

strongly convex than the lingual side. A flat postero-lingual face and in some specimens an ill-defined postero-labial face are present. The antero-lingual cingulum may be connected to the long and wide posterior cingulum.

P3 (18) Fig. 56.4 A rather heavy tooth with an irregular cross-section. The labial, lingual and posterior sides are strongly convex; the flat or concave postero-lingual face is not always distinct. The lingual extension is either wide or narrow and may lie far posteriorly. A postero-lingual basin is usually found. The posterior cingula are long and rather heavy; the antero-lingual cingulum is always short. The tooth has usually two roots, the posterior one of which is wide. More rarely an accessory rootlet is present.

P4 (12) The rather long tooth has a small lingual lobe. The labial and lingual sides are convex with flat or concave posterior faces. The postero-lingual basin is deep. The anterior end is somewhat elongated and may bear a small bulge. The posterocrista is extended and forms a small ill-defined cusp. The lingual lobe is small; the protocone is low, with a low connection to the paracone. The anterior border of the lobe is concave, the posterior one is straight. The long heavy posterior cingulum ends lingually about halfway round the protocone. The anterior cingulum is fairly strong but not very long.

Dibolia vinea (Storch, 1978)

Original reference: "Desmana" pontica vinea in Storch (1978): Die turolische Wirbeltierfauna von Dorn-Dürkheim, Rheinhessen (SW-Deutsland) 2, Mammalia: Insectivora. Senckenbergiana lethaea, *58,* pp. 421–449.

Original diagnosis: p1 mit 2 Wurzeln, die in getrennten Alveolen stehen. Zahn-Masse klein.

Emended diagnosis: the mean length of the p2 is about 1.45 mm, the mean length of the p3 is about 1.14 mm, the mean length of the p4 is about 1.63 mm; the p2/p3 ratio is about 1.27. The p1 is double-rooted.

The mean length of the P2 is about 1.51 mm, the mean length of the P3 is about 1.26 mm; the P2/P3 ratio is about 1.20.

Differential diagnosis: the very small p3 and P3 and the high p2/p3 ratio differentiate *Dibolia vinea* from all other *Dibolia* species.

Holotype: fragmentary mandible with p1–p2, p4–m2.

Type locality: Dorn-Dürkheim, Rheinhessen, West Germany. For a description of the locality see Franzen & Storch, 1975.

Age of the locality: Early Turolian (MN 11).

Other localities with Dibolia vinea: Kohfidisch, Austria (Early Turolian).

Measurements: see table 9.

Description of the material from the type locality, based on the description of Storch and the figured specimens.

The dentition is heavy and rather low with rounded cusps. The premolars are without sharp crests. The position of the p1 is strongly oblique relative to the length axis of the mandible, with the anterior root situated labially. The p3 is set straight or somewhat obliquely in the jaw.

tooth	loc.	N	L		W(2)		W(2)/L	
			range	mean	range	mean	range	mean
p1	DD	2	0.88–0.92	0.90	0.68–0.72	0.70	0.77–0.78	0.77
	Ko	4	0.97–1.06	0.99	0.78–0.89	0.84	0.74–0.92	0.85
p2	DD	6	1.40–1.52	1.45	0.92–1.00	0.94	0.64–0.66	0.65
	Ko	4	1.40–1.47	1.44	0.99–1.02	1.00	0.67–0.71	0.69
p3	DD	2	1.12–1.16	1.14	0.88–0.92	0.90	0.79–0.79	0.79
	Ko	5	1.07–1.21	1.15	0.94–0.96	0.95	0.78–0.89	0.83
p4	DD	13	1.52–1.76	1.63	1.04–1.20	1.14	0.64–0.76	0.70
	Ko	5	1.49–1.67	1.60	1.07–1.23	1.13	0.66–0.74	0.70
m1	DD	6	2.28–2.40	2.33	1.60–1.72	1.67	0.69–0.74	0.72
	Ko	5	2.31–2.51	2.40	1.66–1.79	1.74	0.66–0.75	0.72
m2	DD	9	2.20–2.36	2.30	1.52–1.68	1.61	0.67–0.71	0.70
	Ko	5	2.19–2.32	2.25	1.44–1.74	1.62	0.65–0.79	0.77
m3	DD	6	1.76–1.92	1.83	1.12–1.24	1.17	0.61–0.69	0.64
	Ko	2	1.62–1.82	1.72	1.15–1.34	1.24	0.71–0.74	0.72
P1	DD	–		–		–		–
	Ko	1		1.17		1.00		0.85
P2	DD	6	1.48–1.56	1.51	1.00–1.12	1.05	0.66–0.73	0.70
	Ko	1		1.40		1.15		0.82
P3	DD	2	1.24–1.28	1.26	1.12–1.12	1.12	0.87–0.90	0.88
	Ko	1		1.31		1.10		0.84
P4	DD	(4)		–		–		–
	Ko	1		1.92		1.69		0.88
M1	DD	1		3.08		2.28		0.74
	Ko	1		2.82		2.58		0.91
M2	DD	5	2.08–2.24	2.13	2.60–2.72	2.67	1.20–1.29	1.26
	Ko	1		2.03		2.64		1.30
M3	DD	5	1.36–1.44	1.41	2.04–2.24	2.09	1.44–1.56	1.48
	Ko	1		1.47		2.00		1.36

Table 9. Measurements of *Dibolia vinea* (Storch, 1978).

There are two foramina mentale: one is situated under the p1 and a double foramen is present under the trigonid of the m1.

i1 (1) The crown is high with a moderately strong central rib. The backward projection is strong; the postero-medial cingulum long and strong.

p2 (6) The antero-labial corner of the crown is somewhat flattened. The paraconid and the talonic basin are indistinct. The heavy posterior cingulum forms a small bulge. A cingulum is present except along the labial side.

p3 (2) The antero-labial corner of the crown is flattened. A small talonid is present. The paraconid is similar to the one in the p2. Cingula are of the same kind as found in p2.

p4 (13) The talonid valley is closed lingually by the cingulum. A distinct paraconid is present. The posterior cingulum is short and weak; antero-labial and -lingual cingula are present.

I1 (1) The medial lobe is low and very wide: the indentation between the two lobes lies nearly in the centre. The tooth has a wide and nearly flat inner side with a weak cingulum and a short medial crest.

P2 (6) The crown has a sub-rectangular cross-section. The lingual extension is extremely wide; the lingual cusp is either a cingular bulge or a small cuspule. The anterior cingulum is short and wide. The tooth has three roots.

P3 (2) The crown has a rounded cross-section. The lingual extension is smaller than it is in the P2, but the protocone is strongly individualized. The posterior cingula are long and strong, the anterior cingula weak or non-existing. The tooth has three roots.

P4 (4) The crown has an irregular triangular cross-section. The strong lingual lobe is situated far anteriorly, with a long and straight postero-lingual border and a short and slightly concave antero-lingual one. A weak parastyle and a large mesostyle are present. The anterior and posterior cingula are strong and rather long.

Description of the material from Kohfidisch, based on the descriptions of Bachmayer & Wilson (1970, 1978) and the figured specimens.

For a description of the locality see Bachmayer & Zapfe, 1964.

The premolars – lower as well as upper ones – are low and heavy, rounded teeth. The cingula are weak or absent. The positions of the p1 and the p3 are slightly oblique relative to the length axis of the jaw; the position of the P3 is strongly oblique with the anterior root situated labially.

There are two foramina mentale: one under the p1, the other one under the trigonid of the m1.

p1–p4 (18) The p1 has a labial cingulum. The tooth is double-rooted. The talonid basin of the p4 is of variable depth; its posterior rim may bear one or two cuspules. A paraconid is present.

P2 (1) A weak lingual extension, bearing a small cuspule, is present.

P3 (1) The tooth has a lingual extension of moderate size, situated far posteriorly.

P4 (1) The tooth is larger than the P2 and the P3. The lingual lobe is small but distinct. The anterior cingulum is strong, the posterior one encloses ill-defined postero-lingual and postero-labial basins.

Dibolia turolense n.sp.

Derivatio nominis: the species is named after the town of Teruel, Spain.

Diagnosis: the mean length of the p2 is about 1.51 mm, the mean length of the p3 is about 1.33 mm, the mean length of the p4 is about 1.65 mm; the p2/p3 ratio is about 1.14. The p1 is double-rooted.

The mean length of the C is about 1.39 mm, the mean length of the P2 is about 1.77 mm, the mean length of the P3 is about 1.41 mm; the P2/P3 ratio is about 1.26. The P1 is double-rooted.

Differential diagnosis: the average p2/p3 ratio in combination with the rather short p3 and the high P2/P3 ratio distinguishes *Dibolia turolense* from all other *Dibolia* species.

Holotype: p3 (dext), Ma2-3061, (Fig. 57.1). The specimen will be stored according to the indication of the Comisión Nacional de Geología, Madrid.

Type locality: Masada del Valle 2, Province of Teruel, Spain. For a description of the locality see van de Weerd, 1976.

Age of the locality: Middle Turolian (MN 12).

Other localities with Dibolia turolense: Cubla, Los Mansuetos and Masada del Valle 5, all situated in the Teruel basin, Spain, and of Middle Turolian age.

Measurements: see table 10 (a) for the lower teeth and 10 (b) for the upper teeth.

Description of the material from the type locality.

The dentition is rather heavy with rounded cusps. From the four mandibular fragments available the following information has been extracted.

The two roots of the p1 are set side by side in three specimens, oblique relative to the length axis of the jaw in one specimen (antero-labial to postero-lingual).

The position of the p2 is slightly oblique in three specimens, strongly oblique in one specimen (antero-labial to postero-lingual).

The position of the p3 is straight in the mandible in one specimen, slightly oblique in one specimen (antero-lingual to postero-labial) and strongly oblique in two specimens.

There are three foramina mentale: one is situated under the p1 or under the anterior root of the p2, one under the p4 or between p4–m1 and a third one under the trigonid or the middle part of the m1.

i1 (3) The crown is rather high with a long and strong central rib. The backward projection is distinct. The postero-medial cingulum is faint.

p2 (17) The relatively wide crown has an ill-defined postero-lingual face. The enamel-dentine boundary rises steeply towards the anterior end of the crown. A faint paraconid is present. The postero-lingual cingulum is long, the postero-labial one is short. A small cingular bulge is present posteriorly. The roots are strongly divergent.

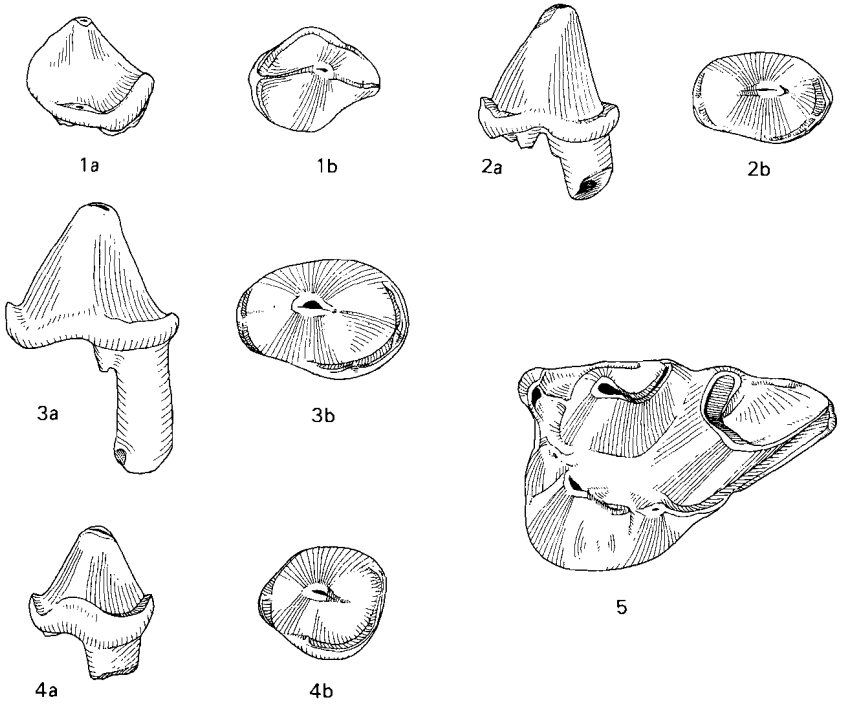


Fig. 57 *Dibolia turolense* n.sp.
1. p3 (dext), Ma2-3061 (holotype)
a) lingual view b) occlusal-labial view.
2. C (sin), Ma2-3151
a) lingual view: b) occlusal-lingual view.
3. P2 (sin), Ma2-3171
a) lingual view b) occlusal-lingual view.
4. P3 (sin), Ma2-3194
a) lingual view b) occlusal-lingual view.
5. M1 (sin), Ma2-3221
occlusal-lingual view.

p3 (6) Fig. 57.1 The crown is short and wide, strongly flattened antero-labially less so postero-lingually. An ill-defined postero-lingual face is present. A faint paraconid is found in some specimens. The postero-lingual cingulum is long and strong, the postero-labial one is short or missing.

p4 (19) Figs. 12.1 and 60.2. The tooth is short and wide, with a flattened antero-labial corner and an ill-defined postero-lingual face. A usually strong

tooth	loc.	N	L		W(2)		W(2)/L	
			range	mean	range	mean	range	mean
c	Ma5	2	1.18–1.20	1.19	0.94–0.95	0.94	0.78–0.81	0.79
	LM	–		–		–		–
	Cu	15	1.06–1.23	1.16	0.77–0.92	0.85	0.65–0.80	0.73
	Ma2	3	1.17–1.18	1.17	0.90–0.94	0.92	0.76–0.80	0.78
p1	Ma5	2	0.98–1.05	1.01	0.87–0.91	0.89	0.83–0.93	0.88
	LM	–		–		–		–
	Cu	4	0.93–1.04	1.00	0.79–0.81	0.81	0.78–0.87	0.81
	Ma2	–		–		–		–
p2	Ma5	6	1.43–1.65	1.53	0.95–1.15	1.04	0.65–0.73	0.68
	LM	1		1.52		0.95		0.62
	Cu	9	1.42–1.55	1.51	0.78–1.05	0.97	0.52–0.70	0.64
	Ma2	16/17	1.40–1.59	1.52	1.02–1.16	1.11	0.68–0.76	0.73
p3	Ma5	2	1.27–1.31	1.29	0.95–1.01	0.98	0.73–0.80	0.76
	LM	1		1.31		1.06		0.81
	Cu	6	1.19–1.45	1.33	0.96–1.05	1.00	0.68–0.86	0.76
	Ma2	6	1.20–1.40	1.31	1.01–1.10	1.06	0.75–0.90	0.81
p4	Ma5	3	1.67–1.82	1.74	1.01–1.19	1.12	0.60–0.66	0.64
	LM	–		–		–		–
	Cu	8	1.53–1.73	1.65	1.15–1.23	1.18	0.66–0.77	0.72
	Ma2	19	1.53–1.73	1.63	1.15–1.33	1.26	0.72–0.81	0.77
m1	Ma5	1		2.31		1.64		0.71
	LM	–		–		–		–
	Cu	7	2.30–2.62	2.45	1.65–1.77	1.71	0.67–0.73	0.70
	Ma2	7	2.39–2.57	2.47	1.73–1.90	1.78	0.69–0.76	0.72
m2	Ma5	1		2.42		1.71		0.71
	LM	1		2.38		1.66		0.70
	Cu	7/6	2.29–2.53	2.40	1.59–1.79	1.71	0.66–0.77	0.71
	Ma2	6	2.18–2.39	2.33	1.62–1.75	1.70	0.72–0.74	0.73
m3	Ma5	–		–		–		–
	LM	–		–		–		–
	Cu	6	1.76–1.96	1.87	1.19–1.30	1.26	0.62–0.72	0.68
	Ma2	10	1.86–2.05	1.96	1.19–1.38	1.31	0.62–0.70	0.67

Table 10 (a) Measurements of *Dibolia turolense* n.sp., lower teeth.

paraconid, a small metaconid or an inflated metaconal rib varying from faint to very strong, and a large hypoconid are present. The narrow talonid gully is closed by the extension of the posterocristid and/or the postero-lingual cingulum. Narrow anterior cingula are present.

I1 (6) The indentation of the upper edge is moderately deep. A weakly inflated basal zone is present on the outside. The medial edge along the inside

tooth	loc.	N	L		W		W/L	
			range	mean	range	mean	range	mean
C	Ma5	5	1.31–1.53	1.45	0.93–1.00	0.96	0.64–0.71	0.66
	LM	–		–		–		–
	Cu	8	1.31–1.45	1.39	0.84–0.91	0.88	0.60–0.69	0.64
	Ma2	8	1.31–1.47	1.41	0.87–0.99	0.94	0.62–0.74	0.67
P1	Ma5	1		1.21		0.88		0.73
	LM	–		–		–		–
	Cu	4	1.05–1.25	1.16	0.80–0.97	0.87	0.74–0.78	0.75
	Ma2	1		1.23		0.89		0.72
P2	Ma5	4	1.74–1.78	1.76	1.19–1.29	1.23	0.68–0.73	0.70
	LM	1		1.76		1.31		0.74
	Cu	8	1.68–1.87	1.77	1.12–1.38	1.26	0.66–0.77	0.71
	Ma2	19	1.65–1.89	1.76	1.19–1.38	1.29	0.70–0.77	0.73
P3	Ma5	5	1.27–1.45	1.37	1.00–1.14	1.10	0.78–0.84	0.80
	LM	–		–		–		–
	Cu	8	1.30–1.53	1.41	1.10–1.24	1.16	0.79–0.87	0.82
	Ma2	12	1.15–1.36	1.28	1.07–1.26	1.20	0.89–0.98	0.94
P4	Ma5	6	2.11–2.34	2.18	1.67–1.89	1.75	0.78–0.84	0.80
	LM	1		2.06		1.69		0.82
	Cu	3	2.19–2.24	2.22	1.77–1.83	1.80	0.81–0.82	0.81
	Ma2	3/4	2.03–2.24	2.11	1.72–1.99	1.84	0.83–0.91	0.88
M1	Ma5	1		3.06		2.35		0.77
	LM	1		3.12		2.24		0.72
	Cu	5	2.44–3.01	2.85	2.25–2.52	2.36	0.75–1.03	0.84
	Ma2	1		3.25		2.33		0.72
M2	Ma5	3	2.17–2.31	2.24	2.47–2.90	2.68		1.20
	LM	–		–		–		–
	Cu	6	2.08–2.20	2.14	2.63–2.86	2.72	1.23–1.33	1.27
	Ma2	3	2.25–2.35	2.29	2.84–2.86	2.85	1.21–1.26	1.24
M3	Ma5	5	1.40–1.58	1.48	1.95–2.07	2.01		1.36
	LM	–		–		–		–
	Cu	11	1.33–1.57	1.47	1.98–2.17	2.07	1.35–1.39	1.41
	Ma2	7	1.52–1.63	1.59	2.13–2.27	2.20	1.36–1.41	1.39

Table 10 (b) Measurements of *Dibolia turolense* n.sp., upper teeth.

of the crown is sharp; the short internal cingulum is weak. The enamel-free area is very low.

C (8) Fig. 57.2 The crown is high with a convex labial side and a flat lingual one. The enamel-dentine boundary curves upwards in the middle of the lingual and the labial sides. The strong anterior and posterior cingula continue for some distance along the lingual side. Most specimens have a very small antero-lingual cingular bulge.

P2 (10) Figs. 23.1 and 57.3 The high and sharp crown has an egg-shaped cross-section. An ill-defined postero-lingual face is present. The lingual extension bears no bulge since the cingulum ends level with the enamel-dentine boundary. Both the anterior and posterior cingula are long and strong; a small cingular bulge is sometimes present anteriorly. The tooth has two roots the anterior one of which is enlarged.

P3 (12) Figs. 24.1 and 57.4 The crown has a rounded cross-section with a rather straight posterior border. The labial side is strongly convex. A flat postero-lingual face and a narrow basin are present. The lingual extension bears a small bulge. The anterior cingulum is wide but short; the posterior cingulum is heavy. The tooth has two roots.

P4 (4) Fig. 25.1 The crown is rather wide and short with a weak anterior extension. A postero-lingual face and an elongated – usually deep – basin at its base are present. The lingual lobe is relatively small and bears a low protocone, which is connected to the paracone by a low ridge. The anterior border of the lobe is strongly concave, the posterior one less so. The heavy anterior and posterior cingula are connected to the tip of the protocone, labially they are connected.

Description of the material from Cubla.

For a description of the locality see Besems & van de Weerd, 1983.

The dentition is rather low, with rounded cusps. The premolars have sharp cristae. The position of the P1 is oblique relative to the length axis of the jaw, with the anterior root situated lingually.

i1 (12) Fig. 58.1 The crown has a strong central rib. The backward projection is pronounced. The postero-medial cingulum is short and weak.

p2 (9) The enamel-dentine boundary rises towards the anterior end of the crown. A pronounced postero-lingual face and a narrow talonid basin are present. The tooth features a slight antero-labial flattening, a weak paraconid and a small hypoconid. The two roots are strongly divergent.

p3 (6) The cross-section is rounded or elliptical. A postero-lingual face and a small talonid basin are usually present. The paraconid is weak, the hypoconid small. The postero-lingual cingulum is long but weak, the postero-labial one, if present, is short.

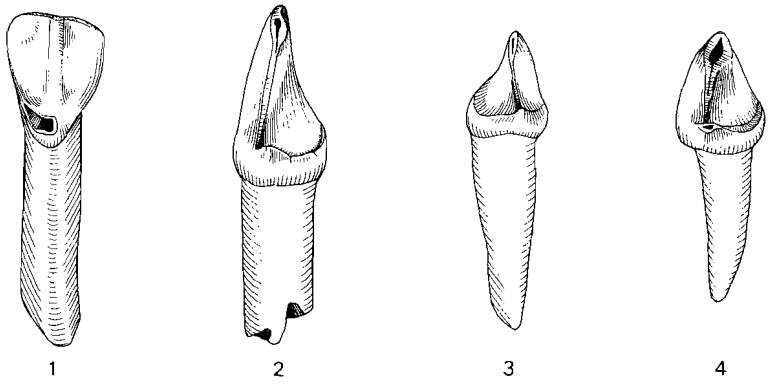


Fig. 58 *Dibolia turolense* n.sp.
1. i1 (dext), Cu-10 posterior view.
2. i2 (sin), Cu-22 posterior view.
3. i3 (dext), Cu-32 posterior view.
4. c (sin), Cu-48 posterior view.

p4 (8) The crown is relatively narrow. The postero-lingual face is concave. The shallow talonid depression is partly closed by the cingulum. The paraconid is well developed. An inflated metaconal rib or a minuscule metaconid are present. The hypoconid is inconspicuous or missing. The posterior and anterior cingula are narrow or may be missing.

I1 (9) Fig.17.1 The crown is flat and wide with a deep indentation in the upper edge. The medial lobe is of modal size. Some specimens have an inflated zone on the outside. The inner side is slightly concave; the medial edge is short, the inner cingulum is short and weak. The enamel-free area is low.

C (8) Fig. 59.1 The tooth is robust and high; both the labial and the lingual side are convex. The enamel-dentine boundary curves upwards in the middle of the lingual and the labial side. The anterior and posterior cingula are moderately long. A few specimens have a minuscule antero-lingual cingular bulge.

P2 (8) Figs. 23.2 and 59.2 The narrow crown has an oval cross-section. The postero-lingual face is somewhat concave. The lingual extension is pronounced: the postero-lingual cingulum ends here in small bulge. The anterior and posterior cingula are well developed. Most specimens have three free roots one of which supports the lingual extension.

P3 (8) Fig. 59.2 The relatively narrow crown has an oval cross-section.

The postero-lingual face is concave. The pronounced lingual extension bears a cingular bulge. Both the anterior and posterior cingula are strong. Most specimens have three free roots.

P4 (3) The crown is long with a very long anterior extension. An ill-defined basin lies at the base of the lingual face. The lingual lobe is rather small; the low protocone is strongly connected to the paracone. The short posterior extension bears a small bulge. The rather heavy cingulum is absent only along the base of the protocone; the protocone and the cingulum are not connected.

Description of the material from Los Mansuetos.

For a description of the locality see van de Weerd, 1976.

p2 (1) The cross-section of the crown is irregular elliptical due to the flattening of the antero-labial corner. A postero-lingual face and a very small talonid basin are present. The paraconid is distinct. The enamel-dentine boundary rises towards the anterior end of the crown. The posterior cingulum is short and lingually more strongly developed than labially. The roots are strongly divergent.

p3 (1) The tooth has a short and wide crown. A postero-lingual face and a small talonid are present. The paraconid is small. A cingulum is missing. The talonid valley is closed posteriorly by a large bulge.

P2 (1) The heavy crown has an elliptical cross-section with nearly straight

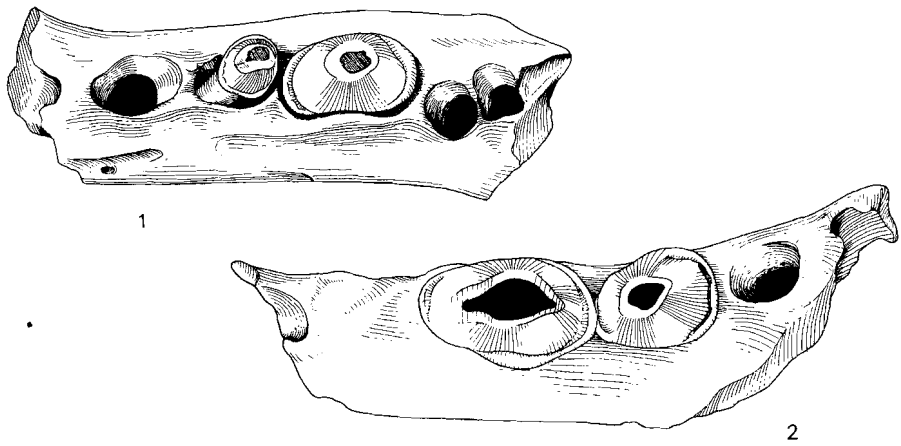


Fig. 59 *Dibolia turolense* n.sp.
1. maxillary fragment with I3–C (sin), Cu-151 occlusal-lingual view.
2. maxillary fragment with P2–P3 (sin), Cu-188 occlusal-lingual view.

anterior and posterior borders. A flat postero-lingual face is present. The lingual extension is rather wide. The anterior and posterior cingula are short and narrow.

P4 (1) The crown has an elliptical outline. Although the lingual lobe is rather small the protocone is high with a fairly high connection to the paracone. The anterior border of the lobe is concave, the posterior one is straight. The postero-lingual cingulum ends at the base of the protocone; the postero-labial cingulum is short.

Description of the material from Masada del Valle 5.

For a description of the locality see van de Weerd, 1976.

p2 (6) Fig. 61.1 The enamel-dentine boundary rises towards the anterior end of the tooth. A postero-lingual face and a small talonid basin may be present. In some specimens the crown is slightly flattened at the antero-labial corner. The paraconid is of variable size. The postero-lingual cingulum is short and bears a small bulge; the postero-labial cingulum is weak.

p3 (2) The crown has a rounded or an elliptical cross-section. A postero-lingual face and a small talonid valley are present. The paraconid as well as the posterior cingular bulge are small. The moderately strong posterior cingulum is of variable length.

p4 (3) Fig. 61.2 The tooth is relatively long and strongly molarized. Flat postero-lingual and antero-lingual faces are present. The paraconid is very well developed; a hypoconid is sometimes present. The talonid basin is long and deep; it is closed by the heavy extension of the posterocristid. The posterior cingula are short, the anterior cingula very narrow or missing.

I1 (3) The medial lobe is fairly thick and wide; the indentation in the upper edge is deep. The inner medial edge is short and sharp; an inner cingulum is missing. The enamel-free area is low.

C (5) Fig. 21.1 The sturdy tooth has an elliptical outline. The enamel-dentine boundary is slightly curved upwards between the roots on both the lingual and the labial side. The crown is strongly biconvex. The rather strong anterior and posterior cingula are of medium length. A minuscule posterior bulge is present in most specimens.

P2 (4) The narrow crown has an elliptical cross-section. The postero-lingual face is slightly concave. The lingual extension is narrow; the cingulum ends level without forming a bulge. The anterior cingulum is short and narrow, the posterior one is wide and heavy. The tooth probably has two sturdy roots and an accessory rootlet supporting the lingual extension.

P3 (5) Fig. 60.1 The crown has an elliptical cross-section with a flat postero-lingual face. The lingual extension is wider than in the P2; the cingulum ends in a high spur. The narrow anterior and posterior cingula are (very) short. A third rootlet may have been present under the lingual extension.

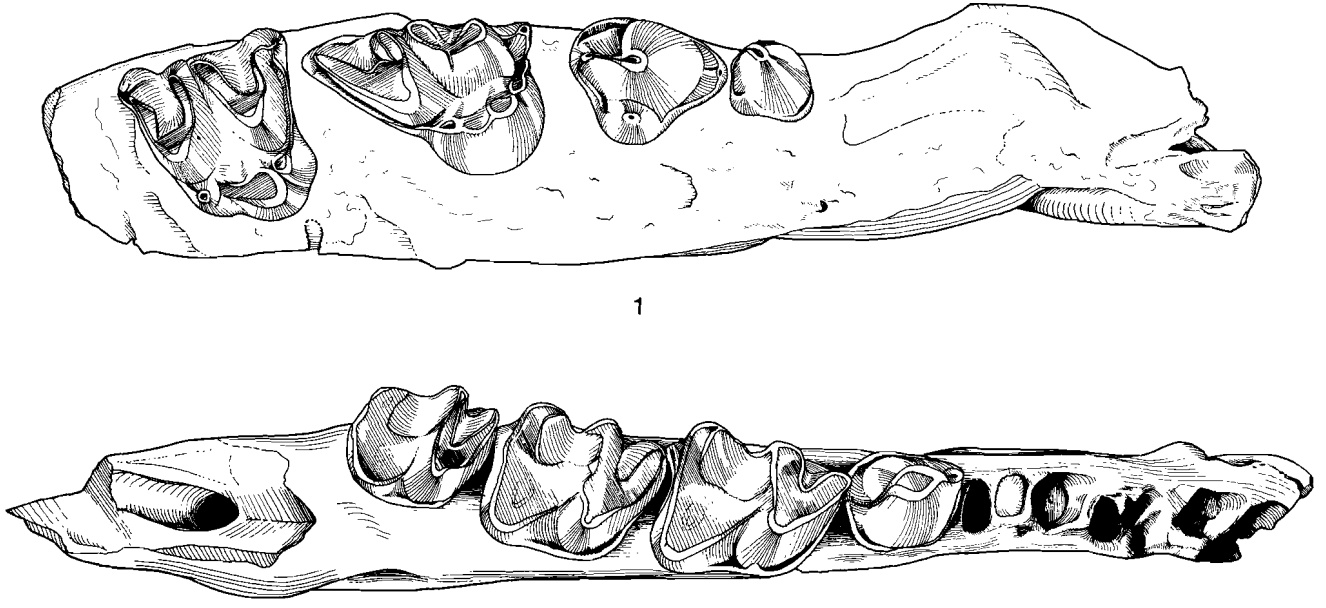


Fig. 60 *Dibolia turolense* n.sp.
1. maxillary fragment with P3—M2 (dext), Ma5-1083 occlusal-lingual view.
2. mandibular fragment with p4—m3 (dext), Ma2-3080 occlusal-labial view.
X 9.4

P4 (6) Fig. 60.1 The crown is long with strong anterior and posterior extensions. In most specimens the cingulum forms a pronounced parastyle. The posterocrista ends in a wide lingual curve that ends in a vague bulge. A moderately large and deep postero-lingual basin with a low rim and a small postero-labial basin are present. The lingual lobe is small with concave anterior and posterior borders. The anterior and posterior cingula are short but wide.

Dibolia adroveri n.sp.

Derivatio nominis: the species is named after Frère Dr. Raphael Adrover, who worked for many years in the Teruel area.

Diagnosis: the mean length of the p2 is about 1.60 mm, the mean length of the p3 is about 1.41 mm, the mean length of the p4 is about 1.82 mm; the p2/p3 ratio is about 1.13. The p1 is double-rooted.

The mean length of the C is about 1.21 mm, the mean length of the P2 is about 1.78 mm, the mean length of the P3 is about 1.58 mm; the P2/P3 ratio is about 1.13. The P1 is double-rooted.

Differential diagnosis: the extremely long p4 and the very short C distinguish *Dibolia adroveri* from all other *Dibolia* species.

Holotype: mandibular fragment with p4–m3 (sin), LA-131, (Pl 2, Fig. 2). The specimen will be stored according to the indication of the Comisión Nacional de Geología, Madrid.

Type locality: Aljezar B, Province of Teruel, Spain. For a description of the locality see Moissenet, Adrover & Aguirre, 1974.

Age of the type locality: Middle Turolian (MN 12).

Measurements: see table 11.

Description of the material from the type locality.

The teeth are rather heavy.

There are two foramina mentale, one is situated below the p2 or between the p1 and the p2, the second one lies below the p4 and the trigonid of the m1 or slightly further backwards.

The position of the p1 is straight relative to the length axis of the mandible. The two roots stand side by side, one in front of the other or the anterior one placed labially and the posterior one lingually.

The position of the p3 is straight or very slightly oblique with the anterior root situated lingually and the posterior one labially.

The position of the P1 is oblique with the anterior part of the crown placed lingually.

The position of the P3 is oblique with the anterior part of the crown placed lingually.

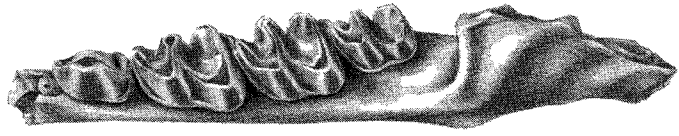
Plate 2 *Dibolia adroveri* n.sp.

1. mandibular fragment with i1–p2 (sin), LA-1 lingual view.
2. mandibular fragment with p4–m3 (sin), LA-131 (holotype) occlusal – labial view.
3. maxillary fragment with I2–P1 (sin), LA-301 occlusal – labial view.
4. maxillary fragment with P2–P3 (sin), LA-381 occlusal – lingual view.

Dibolia brailloni n.sp.

5. skull with I1–I2, C–M3 (dext) and I1, C–P2, P4–M2 (sin) (holotype), Sète.

× 9.6



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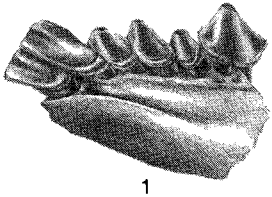

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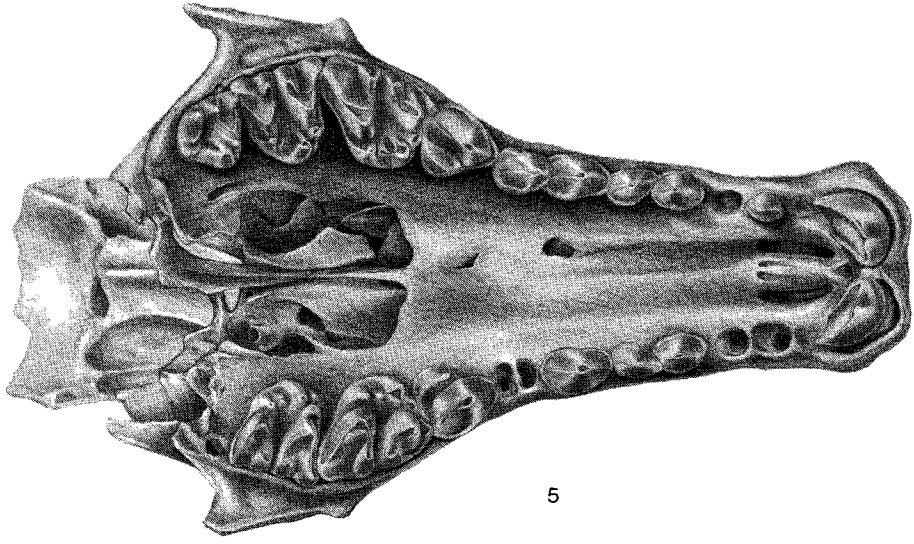

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i1 (13) Fig. 7.1 and Pl. 2, fig. 1 The high asymmetrical crown has a long and strong central rib. The backward projection is situated in the middle of the posterior side. The postero-medial cingulum is very weak.

p2 (17) Fig. 7.1 and Pl. 2, fig. 1 The tooth is sturdy and much larger than the p1. The crown is biconvex with an elliptical cross-section. A narrow flat

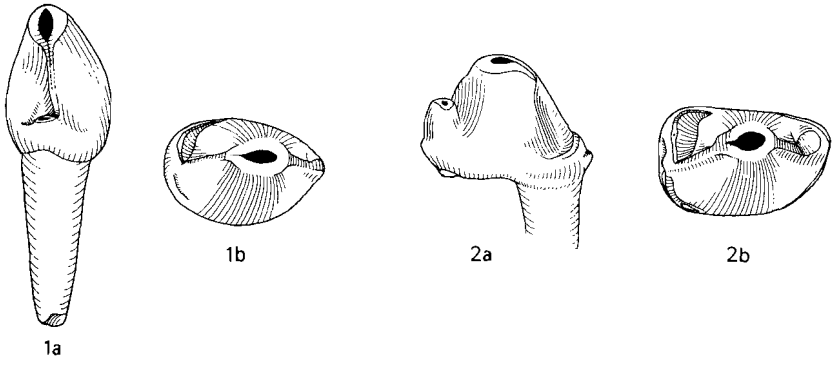


Fig. 61 *Dibolia turolense* n.sp.
1. p2 (dext), Ma5-1023
a) posterior view b) occlusal-labial view.
2. p4 (dext), Ma5-1032
a) lingual view b) occlusal-labial view.

tooth	N	L		W(2)		W(2)/L	
		range	mean	range	mean	range	mean
c	5	1.07–1.13	1.10	0.73–0.81	0.78	0.68–0.74	0.71
p1	4	0.80–0.96	0.86	0.88–0.91	0.89	0.94–1.11	1.04
p2	16/17	1.54–1.65	1.60	1.03–1.22	1.08	0.64–0.74	0.68
p3	17	1.26–1.52	1.41	0.95–1.06	1.00	0.64–0.79	0.71
p4	34	1.64–1.96	1.82	1.06–1.27	1.19	0.61–0.70	0.65
m1	57/58	2.38–2.64	2.51	1.64–1.80	1.73	0.65–0.75	0.69
m2	55	2.35–2.62	2.49	1.61–1.87	1.72	0.64–0.74	0.69
m3	28	1.82–2.02	1.92	1.17–1.32	1.26	0.62–0.70	0.66
C	21	1.14–1.29	1.21	0.90–1.00	0.94	0.70–0.84	0.78
P1	9	1.00–1.22	1.10	0.86–0.95	0.90	0.75–0.91	0.83
P2	34	1.63–1.93	1.78	1.15–1.28	1.22	0.63–0.72	0.69
P3	19	1.45–1.66	1.58	1.18–1.36	1.28	0.76–0.86	0.81
P4	41	2.14–2.37	2.29	1.75–1.95	1.83	0.76–0.85	0.80
M1	41/44	3.01–3.38	3.19	2.06–2.44	2.20	0.65–0.81	0.69
M2	44	2.18–2.54	2.39	2.45–3.00	2.72	1.07–1.19	1.14
M3	29	1.49–1.65	1.57	2.00–2.26	2.12	1.29–1.43	1.36

Table 11 Measurements of *Dibolia adroveri* n.sp. from Aljezar B.

postero-lingual face and a minute talonid basin – closed by the hypoconid – are present. The paraconid is small and inconspicuous. Cingula are either vague or missing. The roots diverge.

p3 (17) The tooth strongly resembles the p2 apart from its greater width. The antero-labial corner is flattened to a certain extent. The crown is biconvex with an ill-defined flat postero-lingual face and a small talonid basin which is closed by the hypoconid. The paraconid is small. Cingula are faint and very short.

p4 (34) Pl. 2, fig. 2 The heavy crown is strongly molarized. At the base of the flat or concave postero-lingual face lies a deep talonid basin which is closed posteriorly by a high ridge – the continuation of the posterocristid – and is open lingually. A strong paraconid is present. The posterior cingulum is usually narrow and short; a faint antero-labial cingulum may be present.

I1 (23) The medial lobe is strong and moderately high. The indentation in the upper edge is of variable depth. The inside of the crown is concave. The sharp medial crest is rather long and merges into a weak and interrupted cingulum. The enamel-free zone is low.

C (21) Pl. 2, fig. 3 The short and wide crown is high; both sides are strongly convex. The enamel-dentine boundary is curved upwards in the middle of the labial and the lingual side. The strong postero-lingual cingulum forms a small platform; the postero-labial and antero-lingual cingula are short and narrow.

P2 (34) Pl. 2, fig. 4 The crown has an elongated elliptical outline and is biconvex with a flat postero-lingual face and a pronounced lingual extension. A wide cingulum runs along the posterior end of the crown, ending at the base of the extension. A short cingulum or a cingular bulge are found at the antero-lingual corner. Wide specimens possess an accessory rootlet that is partly fused with the posterior root; narrow forms have two roots only, the posterior one of which is lingually widened.

P3 (19) Pl. 2, fig. 4 The tooth is heavy and rounded with a pronounced lingual extension and a flat postero-lingual face. The strong postero-lingual cingulum ends slightly above the enamel-dentine boundary and often forms a small bulge. The postero-labial and antero-lingual cingula are short. A free accessory rootlet is nearly always present.

P4 (41) The outline of the crown is sub-triangular. The anterior extension is pronounced and bears a bulge. Posteriorly the crista either ends in a small bulge or it curves to the lingual side. The lingual lobe is strong but short and bears a high protocone. The postero-lingual basin is surrounded by a strong cingulum that ends at the base of the protocone. The anterior and posterior borders of the lobe are concave. The posterior cingulum is wide; the anterior cingula are weak and short.

Dibolia luteyni n.sp.

Derivatio nominis: the species is named after Mr Jaap Luteyn, who made the illustrations for this monograph.

Diagnosis: the mean length of the p4 is about 1.65 mm. The p1 has 1 root.

The mean length of the C is about 1.39 mm, the mean length of the P2 is about 1.54 mm, the mean length of the P3 is about 1.38 mm; the P2/P3 ratio is about 1.12. The P1 is double-rooted.

Differential diagnosis: the small P2 distinguishes *Dibolia luteyni* from *D. turolense, D. adroveri, D. major, D. pontica, D. brailloni* and *D. bifida;* the moderately long P3 distinguishes the species from *D. vinea* and *D. bifida* and the rather long C from *D. dekkersi.*

Holotype: P3 (dext), VB 221, Fig. 62.5. The specimen will be stored according to the indication of the Comisión Nacional de Geología, Madrid.

Type locality: Villalba Baja 1, Province of Teruel, Spain. For a description of the locality see van de Weerd, 1976.

Age of the type locality: Late Turolian (MN 13).

Other localities with Dibolia luteyni: Masada del Valle 6 and probably

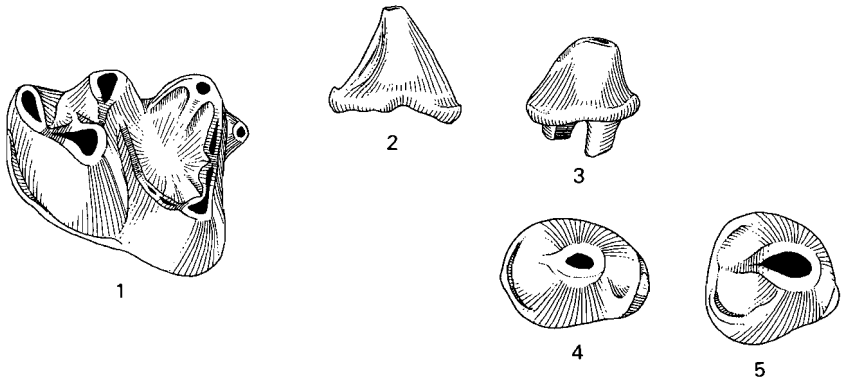


Fig. 62 *Dibolia luteyni* n.sp.
1. m1 (sin), VB-206 occlusal-labial view.
2. C (dext), VB-214 lingual view.
3. P1 (dext), VB-217 lingual view.
4. P2 (dext), VB-220 occlusal-lingual view.
5. P3 (dext), VB-221 (holotype) occlusal-lingual view.

La Fontana 1a, both situated in the Teruel basin, Spain and both of Late Turolian age.

Measurements: see table 12 (a) for the lower teeth and table 12 (b) for the upper teeth.

Description of the material from the type locality.

P4 (1) A thick smooth tooth with a narrow but strongly concave postero-lingual face and a small talonid valley. A metaconid and a paraconid are missing. Except for the posterior cingulum, cingula are faint or lacking.

I1 (1) Fig. 29.2 The medial lobe is small but heavy. The indentation between the lobes is shallow. The inner side of the crown is somewhat concave. The medial edge is rather sharp and connected to the long and heavy inner cingulum. The enamel-free zone is moderately high.

C (2) Fig. 62.2 The tooth has a high and relatively narrow crown. Its cross-section is oval. The enamel-dentine boundary is curved upwards on both the lingual and labial sides. The tooth is biconvex with a slight postero-lingual extension. The postero-lingual cingulum is longer and stronger than the postero-labial one. A short and narrow antero-lingual cingulum is present.

tooth	loc.	N	L		W(2)		W(2)/L	
			range	mean	range	mean	range	mean
c	VB	–		–		–		–
	Ma6	1		1.12		0.79		0.71
p1	VB	1		0.92		0.81		0.88
	Ma6	–		–		–		–
p2*)								
p3	VB	–		–		–		–
	Ma6	1		1.25		1.00		0.80
p4	VB	1		1.65		1.22		0.74
	Ma6	–		–		–		–
m1	VB	1		2.44		1.88		0.77
	Ma6	–		–		–		–
m2	VB	2	2.25–2.38	2.31	1.82–1.83	1.83	0.77–0.81	0.79
	Ma6	–		–		–		–
m3	VB	1		1.74		1.27		0.73
	Ma6	–		–		–		–

*) p2 has not been found

Table 12 (a) Measurements of *Dibolia luteyni* n.sp., lower teeth.

P2 (2) Fig. 62.4 The smooth crown is rather low and has an oval cross-section. It is biconvex without a lingual extension: it is as wide labially as it is lingually. A short but wide antero-lingual cingulum and a long posterior cingulum are present. The roots have not been preserved, but as two pulpa cavities are visible it seems likely that the tooth had two roots.

P3 (2) Fig. 62.5 An extremely heavy low tooth with a sub-triangular outline. A prominent postero-lingual extension bears a high spur formed by the postero-lingual cingulum. A basin is enclosed by this cingulum. The postero-labial and postero-lingual cingula are hardly connected. A very short and wide cingulum is present anteriorly. The tooth has a broad posterior root and a round anterior one.

P4 (1) The tooth is very stout with a sub-triangular cross-section. The posterocrista ends in a cuspule and is not connected to the posterior cingulum.

tooth	loc.	N	L		W		W/L	
			range	mean	range	mean	range	mean
C	VB	2	1.38–1.41	1.39	0.99–1.01	1.00	0.72–0.72	0.72
	LF*)	–		–		–		–
	Ma6	–		–		–		–
P1	VB	1		1.18		1.01		0.86
	LF	–		–		–		–
	Ma6	1		1.28		0.95		0.74
P2	VB	2	1.52–1.57	1.54	1.16–1.26	1.21	0.76–0.80	0.78
	LF	–		–		–		–
	Ma6	1		1.68		1.27		0.76
P3	VB	2	1.37–1.39	1.38	1.39–1.40	1.39	1.01–1.01	1.01
	LF	1		1.47		1.20		0.82
	Ma6	1		1.46		1.41		0.97
P4	VB	1		1.91		1.84		0.96
	LF	1		1.99		1.75		0.88
	Ma6	2	2.04–2.10	2.07	1.95–1.97	1.96	0.93–0.97	0.95
M1	VB	–		–		–		–
	LF	–		–		–		–
	Ma6	1		2.99		2.39		0.80
M2**)								
M3	VB	2	1.46–1.51	1.48	1.91–2.06	1.98	1.31–1.36	1.33
	LF	1		1.47		2.17		1.48
	Ma6	2	1.41–1.46	1.43	1.97–1.98	1.97	1.35–1.40	1.37

*) No lower teeth have been found in La Fontana 1a. **) M2 has not been found.

Table 12 (b) Measurements of *Dibolia luteyni* n.sp., upper teeth.

The lingual lobe is very wide with nearly straight anterior and posterior borders. The strong protocone has a high connection to the paracone. A deep and wide postero-lingual basin is present. The posterior cingulum ends in a small cuspule at the base of the protocone. The postero-labial cingulum is narrow but rather long.

Description of the material from Masada del Valle 6.

For a description of the locality see van de Weerd, 1976.

p3 (1) The heavy biconvex tooth is symmetrical, as the antero-labial corner is not flattened. The postero-lingual cingulum is short but fairly strong; the postero-labial cingulum is short and very narrow. The tooth has two strongly compressed roots.

I1 (1) The medial lobe is heavy; the indentation in the upper edge is deep. An interrupted cingulum is present. The inner side of the crown is rather flat. The blunt medial crest is not connected to the strong and long inner cingulum. In the single fragment available the enamel-free zone is not visible.

P2 (1) The tooth has a very wide and sturdy symmetrical crown with an oval outline. Both cristae are rounded. There is no lingual extension: the crown widens symmetrically towards the posterior end. A rather strong but interrupted cingulum is present posteriorly and antero-lingually. An accessory lingual rootlet is present.

P3 (1) The heavy tooth has a rounded outline with a pronounced lingual extension. The postero-lingual cingulum ends in a high spur on this extension. The postero-labial cingulum is very short and vague; an anterior cingular bulge is present. The tooth has two main roots and one accessory one.

P4 (2) A rounded tooth with a very convex labial border. The rather long anterior extension – bearing a small bulge – merges into short anterior cingula. The protocone is high and sharp with a high connection to the paracone. The anterior border of the lingual lobe is convex, the posterior one is straight. The postero-lingual valley is closed by the posterior cingulum that forms a small but distinct cuspule at the base of the protocone.

Description of the material from La Fontana 1a.

For a description of the locality see van de Weerd, 1976.

I1 (1) A large, wide and flat tooth with an extremely wide flat root. The medial lobe is small compared to the labial one. The indentation is shallow. The inner side of the crown is flat; the medial edge is sharp and connected to the long and rather weak inner cingulum. The enamel-free zone is fairly high.

P3 (1) The stout tooth has a rounded – oval cross-section with a short antero-lingual extension. The postero-lingual cingulum encloses a narrow basin before it ends in a high bulge. The postero-labial and anterior cingula

are narrow. A thin – but well separated – accessory rootlet is present lingually.

P4 (1) A stout tooth with a sub-triangular outline. The anterior extension is short. The posterocrista ends in a faint bulge and is not connected to the cingulum. The lingual lobe is wide with a high connecting crest to the paracone. Both the anterior and the posterior borders of the lingual lobe are concave. A narrow basin is situated postero-lingually. The anterior and posterior cingula are short and not connected to the protocone.

Dibolia major n.sp.

Derivatio nominis: the name refers to the large size of some of the teeth.

Diagnosis: the mean length of the p2 is about 1.60 mm, the mean length of the p3 is about 1.42 mm, the mean length of the p4 is about 1.73 mm; the p2/p3 ratio is about 1.13. The p1 is single-rooted.

The mean length of the C is about 1.62 mm, the mean length of the P2 is about 1.97 mm, the mean length of the P3 is about 1.50 mm; the P2/P3 ratio is about 1.31. The P1 is double-rooted.

tooth	loc.	N	L		W(2)		W(2)/L	
			range	mean	range	mean	range	mean
c	Ma7	2	1.14–1.19	1.16	0.92–0.93	0.92	0.77–0.82	0.79
	Va3	–		–		–		–
p1	Ma7	4	1.10–1.22	1.17	0.98–1.02	1.01	0.83–0.92	0.86
	Va3	–		–		–		–
p2	Ma7	6	1.59–1.70	1.60	1.07–1.16	1.11	0.63–0.79	0.69
	Va3	4	1.44–1.58	1.51	1.02–1.10	1.05	0.68–0.71	0.69
p3	Ma7	4	1.35–1.53	1.42	1.16–1.26	1.20	0.78–0.93	0.85
	Va3	3	1.38–1.56	1.45	1.04–1.17	1.12	0.73–0.85	0.77
p4	Ma7	6	1.65–1.79	1.73	1.09–1.32	1.26	0.66–0.77	0.72
	Va3	6	1.65–1.79	1.72	1.12–1.37	1.28	0.68–0.81	0.74
m1	Ma7	1		2.63		2.06		0.76
	Va3	2	2.55–2.59	2.57	1.86–2.00	1.93	0.72–0.78	0.75
m2	Ma7	1		2.59		1.94		0.75
	Va3	2	2.40–2.50	2.45	1.68–1.86	1.77	0.70–0.74	0.72
m3	Ma7	6	1.82–1.98	1.88	1.18–1.31	1.27	0.64–0.71	0.67
	Va3	3	1.82–1.91	1.85	1.36–1.40	1.38	0.72–0.77	0.75

Table 13 (a) Measurements of *Dibolia major* n.sp., lower teeth.

Differential diagnosis: the average p2/p3 ratio and the high P2/P3 ratio, in combination with the long p2 and the very long P2 distinguish *Dibolia major* from all other *Dibolia* species.

Holotype: p3 (dext), Ma7-537, (Fig. 63.2). The specimen will be stored according to the indication of the Comisión Nacional de Geología, Madrid.

Type locality: Masada del Valle 7, Province of Teruel, Spain. For a description of the locality see van de Weerd, 1976.

Age of the type locality: Late Turolian (MN 13).

Other localities with Dibolia major: Valdecebro 3, situated in the Teruel basin, Spain and of Late Turolian age.

Measurements: see table 13 (a) for the lower teeth and table 13 (b) for the upper teeth.

Description of the material from the type locality.

i1 (1) The wide tooth was probably high. It features a prominent central rib. The centrally situated backward projection is inconspicuous. The postero-medial cingulum is high and short. The enamel-dentine boundary may be slightly curved upwards in the middle of the medial side.

tooth	loc.	N	L		W		W/L	
			range	mean	range	mean	range	mean
C	Ma7	3	1.59–1.63	1.62	0.99–1.05	1.01	0.61–0.64	0.62
	Va3	3	1.47–1.64	1.54	1.00–1.13	1.05	0.66–0.70	0.68
P1	Ma7	3	1.27–1.34	1.31	1.05–1.07	1.06	0.79–0.83	0.81
	Va3	4	1.08–1.23	1.17	0.91–1.00	0.94	0.78–1.93	0.81
P2	Ma7	8	1.89–2.01	1.97	1.17–1.31	1.25	0.60–0.67	0.63
	Va3	8	1.73–2.11	1.89	1.29–1.45	1.36	0.63–0.77	0.72
P3	Ma7	8	1.29–1.60	1.50	1.22–1.38	1.31	0.80–1.07	0.87
	Va3	5	1.48–1.57	1.53	1.15–1.49	1.29	0.75–0.96	0.84
P4	Ma7	1		2.14		1.86		0.87
	Va3	4	2.03–2.26	2.11	1.71–1.98	1.80	0.83–0.88	0.85
M1	Ma7	3	2.73–3.10	2.97	2.57–2.79	2.65	0.83–1.03	0.90
	Va3	4	2,91–3.05	3.01	2.44–2.58	2.52	0.81–0.86	0.84
M2	Ma7	–		–		–		–
	Va3	2	2.19–2.30	2.24	2.63–2.82	2.72	1.14–1.29	1.21
M3	Ma7	3	1.47–1.58	1.52	2.17–2.21	2.19	1.38–1.48	1.44
	Va3	4/3	1.44–1.57	1.50	2.04–2.24	2.14	1.33–1.43	1.42

Table 13 (b) Measurements of *Dibolia major* n.sp., upper teeth.

p2 (6) Fig. 63.1 A stout tooth with sharp cristae. The crown is biconvex with a flat postero-lingual face and a small talonid basin. A minuscule paraconid may be present. The short posterior cingulum may form a bulge; other cingula are weak or missing.

p3 (4) Figs. 11.1 and 63.2 A rounded heavy tooth with a sharp tip. The outline is rhombic due to strong antero-labial and postero-lingual flattening. A postero-lingual face and a talonid basin are missing. There is a weak paraconid. The posterior cingulum is narrow and the posterior bulge is small.

p4 (6) Fig. 63.3 A sturdy, strong tooth. Due to the presence of an inflated metaconal rib a concave postero-lingual sulcus may be present. The talonid valley, which is open lingually, is deep and narrow. The paraconid is pronounced. The posterocristid continues as a crest around the postero-lingual border which closes the talonid basin. An entoconid is present in most specimens. The posterior and postero-labial cingula are wide; the anterior cingula – if present – are very narrow.

I1 (3) Fig. 17.3 The crown is wide and low with a thick medial lobe. The indentation in the upper edge is shallow. An inflated zone runs along the external base of the crown. The inner side is flat but for the concave junction of the two lobes. The blunt medial crest is merging into the inner cingulum. The enamel-free zone is rather high.

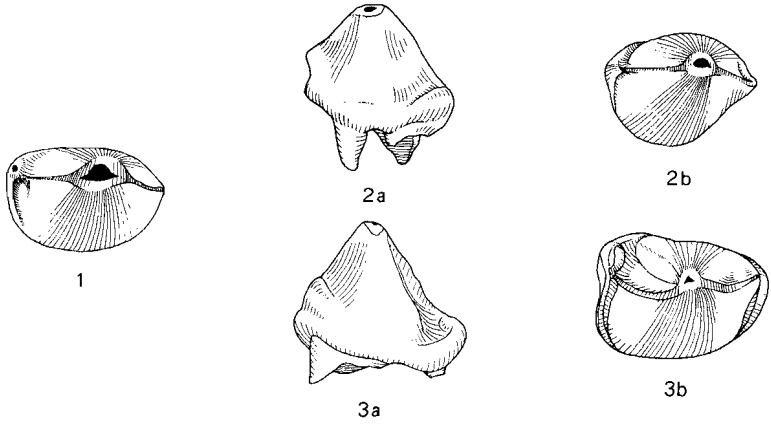


Fig. 63 *Dibolia major* n.sp.
1. p2 (dext), Ma7-522
occlusal-labial view.
2. p3 (dext), Ma7-537 (holotype)
a) lingual view b) occlusal-labial view.
3. p4 (dext), Ma7-541
a) lingual view b) occlusal-labial view.

C (3) The crown is high and relatively narrow with an elliptical or oval cross-section. The enamel-dentine boundary curves upwards in the middle of the labial and the lingual sides. A vague flat postero-lingual face is present. The posterior cingulum is very heavy, in particular along the postero-lingual corner of the crown. The anterior cingulum is short.

P2 (8) Fig. 64.1 The crown has an elongated elliptical outline. The cristae, in particular the anterocrista, are blunt. A faint lingual extension may be present. The anterior and posterior cingula are moderately wide and long. The crown slightly overhangs the root along the labial side. Most specimens have two roots, others have an accessory rootlet or feature a widening of the posterior root.

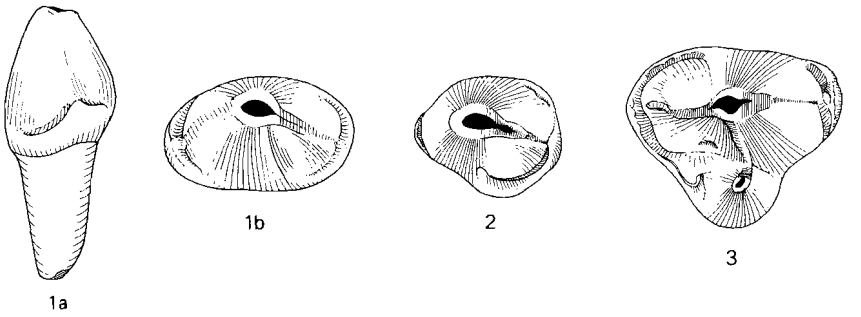


Fig. 64 *Dibolia major* n.sp.
1. P2 (sin), Ma 7-586
a) posterior view b) occlusal-lingual view.
2. P3 (sin), Ma7-597
occlusal-lingual view.
3. P4 (dext), Ma7-601
occlusal-lingual view.

P3 (8) Fig. 64.2 A thick tooth with a rounded – irregular cross-section. A flat postero-lingual face is present. The lingual extension is pronounced. The posterior cingulum is long and ends lingually in a high spur on the lingual extension. The anterior and postero-labial cingula are short and sometimes interrupted. The tooth has two strong roots and one thin accessory rootlet.

P4 (1) Fig. 64.3 The crown is high with a rounded-triangular cross-section. An anterior and a posterior extension are missing. At the base of the posterocrista an ill-defined cuspule – the metacone – is found. The lingual extension is of medium width with a high connecting ridge to the paracone. The anterior border of the lobe is strongly concave, the posterior one is nearly straight. The postero-lingual depression is pronounced, postero-labially a small basin is present. The posterior cingulum is not connected to either the posterocrista or the metacone; it ends at the base of the protocone

in an elongated cuspule. The anterior cingulum is short but wide and forms a bulge at the end of the anterocrista.

Description of the material from Valdecebro 3.

For a description of the locality see van de Weerd, 1976.

There are at least two foramina mentale, one of which is situated below the p1 and the other one below the middle part of the m1.

The position of the p1 and of the p3 are straight relative to the length axis of the jaw.

i1 (1) The single specimen available is worn down to such an extent that the central rib is not visible. The pronounced backward projection is situated in the middle of the posterior border. The postero-medial cingulum is strong and long. The enamel-dentine boundary is not curved upwards in the middle of the medial side.

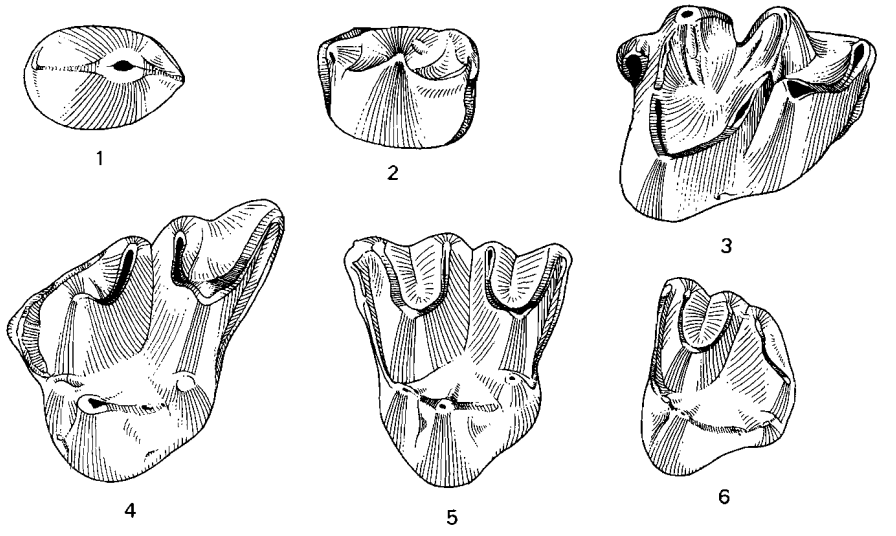


Fig. 65 *Dibolia major* n.sp.
1. p2 (dext) Va3-1012 occlusal-labial view.
2. p4 (sin), Va3-1024 occlusal-labial view.
3. m1 (dext), Va3-1031 occlusal-labial view.
4. M1 (sin), Va3-1088 occlusal-lingual view.
5. M2 (sin), Va3-1092 occlusal-lingual view.
6. M3 (sin), Va3-1096 occlusal-lingual view.

p2 (4) Figs. 10.1 and 65.1 A stout tooth. The enamel-dentine boundary rises steeply towards the anterior and the posterior end of the crown. A postero-lingual face and a minuscule talonid basin may be present. The antero-labial corner of the crown is not flattened. A very weak paraconid is present on the anterocristid. The antero-lingual and posterior cingula are weak; the posterior cingular bulge is very small. The roots are parallel.

p3 (3) A stout tooth. The crown features an antero-labial and a postero-lingual flattening. A postero-lingual face and a talonid basin are present in one of the three specimens. A very small paraconid is present. The cingula are narrow and are found along the labial side only. The posterior cingular bulge is minuscule.

p4 (6) Fig. 65.2 A wide tooth with a sub-rectangular outline. The postero-lingual face is concave; the talonid basin at its base is deep and lingually open. The paraconid is strongly individualized. Some specimens have an indistinct metaconid or a metaconal rib. The posterocristid merges into a crest that continues along the posterior margin of the crown. It partly closes the talonid basin and forms a small entoconid. The posterior cingulum is weak; narrow anterior cingula may be present.

I1 (2) The medial lobe is small compared to the labial one. The indentation in the upper edge of the crown is shallow. Apart from the junction between the lobes the inner side is flat. The medial edge is short and rather sharp; the inner cingulum is long and weak. The enamel-free area is very low.

C (3) A heavy, low tooth with an elliptical outline. The enamel-dentine boundary curves slightly upwards in the middle of the lingual and the labial sides. Weak and sometimes interrupted cingula are present anteriorly and posteriorly.

P2 (8) The high crown has a sharp tip. In some specimens the crown overhangs the root along the labial side. The cross-section may vary, but an elongated or oval outline is most common. An ill-defined postero-lingual face with a small depression at its base is present. The lingual extension is narrow but prominent. The anterior and posterior cingula are moderately long and wide. An accessory rootlet may be present lingually.

P3 (5) The shape of the P3 is variable. The outline may be rounded, elongated or irregular. A flat postero-lingual face with a narrow shallow basin at its base is present in most specimens. The lingual extension varies from small to large; a protocone is lacking. The postero-lingual cingulum ends in a high spur. The anterior and posterior cingula are rather strong and of varying length. The tooth has either two or three roots.

P4 (4) The crown has a sub-triangular outline with a wide lingual lobe. The tooth is weakly molarized and no accessory cuspules are present. A con-

cave postero-lingual face with a basin at its base and in one specimen a flat postero-labial face are present. Both the posterior and anterior borders of the lingual lobe are concave. The anterior and posterior cingula are wide and of medium length.

Dibolia pontica (Schreuder, 1940)

Original reference: Schreuder (1940): A revision of the fossil water-moles (Desmaninae). Extrait des Archiv. Néerl. Zool., *IV*, pp. 202–333.

Original diagnosis: size about that of *Gal. pyrenaicus.* Dentition not high. P1 not oppressed by canine. The latter, with considerable post. talon, is merely a trifle larger than P1, but smaller than P2. P2 and P3 are three-rooted. Protoconule and metaconule of M1 equally strong; hypocone much weaker than protocone; strong cingulum along outer side of paracone. . . . Mental foramen most probably two, ant. one in front of p2. i2 not much stronger than i1; i3 small. Lower canine not incisiform. p1 and p3 so much oppressed by the large, clumsy p2 that the roots of p1 stand transversely side by side and those of the p3 obliquely from the front backwards. Great extent of cingulum at lower molars, absent only at base of hypoconid and along post. half of the inner side.

Emended diagnosis based on the type material: the mean length of the p2 is about 1.64 mm. The p1 is double-rooted.

The mean length of the C is about 1.38 mm, the mean length of the P2 is about 1.79 mm. The P1 is double-rooted.

Holotype: a maxillary fragment with C–P2 (dext).

Type locality: Polgárdi, Hungary. For a description of the locality see Kormos, 1911.

Age of the type locality: Late Turolian (MN 13).

Measurements: see table 14.

tooth	loc.	N	L		W(2)		W(2)/L	
			range	mean	range	mean	range	mean
c	Po	1		1.16		0.92		0.79
p1		1		1.15		1.04		0.90
p2		1		1.64		1.22		1.74
m2		3	2.41–2.52	2.45	1.66–1.95	1.76	0.67–0.81	0.72
C		1		1.38		0.97		0.74
P1		1		1.29		0.95		0.74
P2		1		1.79		1.28		0.72
M1		1		3.02		2.94		0.97

Table 14 Measurements of *Dibolia pontica* (Schreuder, 1940).

Description of the material from the type locality.

There is one foramen mentale present in the single mandible available. It is situated under the p1.

The position of the p1 is oblique relative to the length axis of the jaw with the anterior root placed labially.

p2 (1) A heavy form. The enamel-dentine boundary rises steeply towards the anterior end of the crown. The labial side is convex, the lingual side less so. The postero-lingual face and the paraconid are faint. The rather strong but short posterior cingulum forms a small bulge. The roots diverge slightly.

C (1) The heavy crown is of medium height and has an oval cross-section. The lingual side is as convex as the labial side, apart from an ill-defined flat postero-lingual face. The antero-lingual cingulum is connected to the postero-lingual one.

P2 (1) A stout, rather low crown with an elongated-oval cross-section. A flat postero-lingual face is present. The lingual extension is not prominent; the postero-lingual cingulum forms a vague spur. The anterior and posterior cingula are lingually connected by a narrow stretch. On the lingual side an accessory root is present.

Dibolia brailloni n.sp.

Derivatio nominis: the species is named in honour of Dr. Jean Braillon, who collected and prepared the unique specimens from Sète.

Diagnosis: the mean length of the p2 is about 1.49 mm, the mean length of the p3 is about 1.41 mm, the mean length of the p4 is about 1.68 mm; the p2/p3 ratio is about 1.06. The p1 is single-rooted.

The mean length of the C is about 1.34 mm, the mean length of the P2 is about 1.77 mm, the mean length of the P3 is about 1.51 mm; the P2/P3 ratio is about 1.17. The P1 is double-rooted.

Differential diagnosis: the combination of a low p2/p3 ratio and an average P2/P3 ratio with a long P2 and P3 is not found in any other *Dibolia* species.

Holotype: skull with I1–I2, C–M3 (dext) and I1, C–P2, P4–M2 (sin) (Pl. 2, Fig. 5). Stored in the collection of Dr. Braillon, Beauvais, France.

Type locality: Sète, southern France. For a description of the locality see Michaux, 1969.

Age of the type locality: Middle Ruscinian (MN 15b).

Other localities with Dibolia brailloni: Orrios (Province of Teruel, Spain) of Early Ruscinian age (MN 14), Gorafe 2 (Province of Granada, Spain) of Middle Ruscinian age (MN 15b) and Escorihuela (Province of Teruel, Spain) of Late Ruscinian age (MN 16a).

Measurements: see table 15 (a) for the lower teeth and table 15 (b) for the upper teeth.

Description of the material from the type locality.

The ten mandibular fragments available show that the foramina mentale vary in number (2–5) and position. Fixed positions are under c–p1 and under m1.

tooth	loc.	N	L		W(2)		W(2)/L	
			range	mean	range	mean	range	mean
c	Es	2	1.20–1.21	1.20	0.76–0.77	0.76	0.63–0.64	0.63
	Se	1		1.19		0.85		0.71
	Go2	1		1.23		0.82		0.67
	Or	4	1.11–1.25	1.17	0.84–0.90	0.86	0.72–0.76	0.74
p1	Es	2	0.87–0.90	0.88	0.81–0.81	0.81	0.90–0.93	0.91
	Se	1		1.03		0.90		0.87
	Go2	–		–		–		–
	Or	–		–		–		–
p2	Es	3	1.42–1.47	1.44	1.01–1.08	1.05	0.71–0.76	0.73
	Se	5	1.31–1.59	1.49	0.97–1.11	1.04	0.65–0.72	0.70
	Go2	–		–		–		–
	Or	3	1.42–1.63	1.53	1.08–1.13	1.10	0.66–0.80	0.72
p3	Es	3	1.35–1.54	1.45	0.94–1.19	1.07	0.70–0.77	0.73
	Se	4	1.24–1.50	1.41	0.94–1.09	1.01	0.63–0.77	0.72
	Go2	–		–		–		–
	Or	3	1.42–1.53	1.46	1.03–1.17	1.12	0.72–0.82	0.76
p4	Es	3	1.70–1.75	1.73	1.25–1.30	1.28	0.74–0.75	0.74
	Se	5	1.61–1.75	1.68	1.20–1.32	1.27	0.70–0.80	0.76
	Go2	–		–		–		–
	Or	1		1.68		1.36		0.81
m1	Es	2	2.49–2.50	2.49	1.83–1.91	1.87	0.73–0.76	0.74
	Se	7	2.33–2.64	2.52	1.85–2.08	1.97	0.73–0.85	0.78
	Go2	–		–		–		–
	Or	1		2.64		1.91		0.72
m2	Es	2	2.46–2.55	2.50	1.72–1.79	1.75	0.70–0.70	0.70
	Se	12	2.33–2.58	2.47	1.70–1.94	1.82	0.68–0.81	0.74
	Go2	–		–		–		–
	Or	1		2.45		1.95		0.80
m3	Es	3	1.83–1.97	1.92	1.15–1.34	1.24	0.60–0.75	0.65
	Se	7	1.81–2.02	1.93	1.18–1.39	1.29	0.59–0.73	0.67
	Go2	1		1.80		1.25		0.69
	Or	1		1.91		1.36		0.71

Table 15 (a) Measurements of *Dibolia brailloni* n.sp., lower teeth.

In one specimen the p1 is apparently missing.

In 5 out of 7 specimens the position of the p2 is slightly oblique relative to the length axis of the jaw with the anterior root placed either lingually (in three specimens) or labially (in two specimens).

The position of the p3 is straight in the mandible in two specimens, oblique with the anterior root lingually in four specimens and oblique with the anterior root labially in one specimen.

tooth	loc.	N	L		W		W/L	
			range	mean	range	mean	range	mean
C	Es	2	1.45–1.52	1.48	0.98–0.98	0.98	0.64–0.68	0.66
	Se	14	1.27–1.43	1.34	0.95–1.13	1.01	0.68–0.82	0.76
	Go2	–		–		–		–
	Or	1		1.41		0.99		0.70
P1	Es	2	1.10–1.10	1.10	0.90–0.94	0.92	0.82–0.85	0.83
	Se	10	1.13–1.35	1.25	0.84–1.03	0.93	0.68–0.87	0.74
	Go2	–		–		–		–
	Or	2	1.20–1.28	1.24	0.98–1.01	0.99	0.79–0.82	0.80
P2	Es	4	1.65–1.91	1.76	1.09–1.29	1.16	0.61–0.68	0.66
	Se	16	1.63–1.89	1.77	1.14–1.29	1.19	0.66–0.70	0.68
	Go2	1		1.76		1.32		0.75
	Or	1		1.81		1.26		0.70
P3	Es	5	1.41–1.64	1.57	1.26–1.37	1.33	0.81–0.91	0.85
	Se	9	1.40–1.62	1.51	1.12–1.31	1.21	0.76–0.91	0.80
	Go2	1		1.52		1.32		0.87
	Or	3	1.59–1.65	1.61	1.33–1.37	1.35	0.82–0.86	0.84
P4	Es	1		2.15		1.85		0.86
	Se	19	2.12–2.37	2.25	1.83–2.10	1.93	0.82–0.89	0.86
	Go2	1		2.17		1.81		0.83
	Or	1		2.25		1.85		0.82
M1	Es	–		–		–		–
	Se	20	2.78–3.36	3.07	2.37–3.01	2.63	0.74–1.00	0.86
	Go2	1		3.25		2.27		0.70
	Or	1		3.29		2.53		0.77
M2	Es	2	2.29–2.41	2.35	2.76–2.82	2.79	1.15–1.23	1.19
	Se	18	2.05–2.39	2.22	2.53–2.86	2.71	1.10–1.29	1.22
	Go2	1		2.26		2.72		1.20
	Or	1/0		2.36		–		–
M3	Es	1		1.43		2.02		1.41
	Se	9	1.46–1.63	1.52	1.95–2.13	2.01	1.21–1.41	1.32
	Go2	–		–		–		–
	Or	5	1.56–1.70	1.61	2.11–2.24	2.19	1.32–1.40	1.36

Table 15 (b) Measurements of *Dibolia brailloni* n.sp., upper teeth.

The position of the P1 is straight in 6 out of 13 specimens; in the other 7 specimens its position is oblique with the anterior root situated labially.

The position of the P3 is straight in the jaw in 6 out of 16 specimens, oblique with the anterior root placed lingually in the other 10 specimens.

i1 (1) The crown is symmetrical. The central rib is very faint. The centrally situated backward projection is moderate with a strong postero-medial cingulum. The enamel-dentine boundary is medially slightly curved upwards.

p2 (5) The tooth is rather heavy with a symmetrical elliptical cross-section. The enamel-dentine boundary slopes upwards antero-labially; an antero-labial flattening is rarely found. A weak paraconid may be present. The posterior cingula are moderately wide and long; a minuscule posterior bulge is usually present. Anterior cingula are weak or missing. The roots diverge.

p3 (4) The crown has a rhombic outline due to the strong antero-labial and postero-lingual flattening. The enamel-dentine boundary rises steeply towards the anterior end of the crown. A flat or concave postero-lingual face with a depression at its base is present. The paraconid is weakly individualized. The postero-lingual cingulum is long but weak; the postero-labial cingulum is short.

p4 (5) The crown has a sub-rectangular cross-section and a somewhat inflated tip. The anterior border is straight as the anterocristid ends in the antero-lingual corner of the crown. At the base of the flat or concave postero-lingual face lies a narrow shallow talonid depression which is closed lingually by the cingulum. A weak paraconid is present. The posterior cingula are moderately long and wide; the anterior cingula are faint or missing.

I1 (2) Pl. 2, fig. 5 The crown is of medium height. The medial lobe is small and rather low; the indentation in the upper edge is shallow. The inner side of the crown is narrow and flat with a low, rather blunt, medial edge. The inner cingulum is weak but long. The enamel-free zone is probably fairly high.

C (14) Pl. 2, fig. 5 The crown is relatively small, but may be high. The cross-section is elliptical. The labial side is strongly convex; the lingual side is rather flat. The enamel-dentine boundary curves upwards in the middle of the lingual side. Some specimens are surrounded by a faint cingulum, in others the cingulum is interrupted along the labial side.

P2 (16) Pl. 2, fig. 5 A heavy tooth with a sharp tip. The crown has an oval outline. Both the labial and the lingual sides are convex with a flat posterior face. A lingual extension is missing; instead the posterior part of the crown widens lingually and labially to the same extent. The posterior and anterior cingula are lingually connected. The tooth has two roots with a rounded cross-section.

P3 (9) Pl. 2, fig. 5 The outline of the crown varies. It may be elliptical or rounded. Both the labial and the lingual sides are convex and feature flat posterior faces. The posterior part of the crown widens lingually as well as labially. The posterior cingula are rather weak, but may be bulbous. The anterior cingula are usually faint and short. Most specimens have two roots, some teeth have three.

P4 (19) Pl. 2, fig. 5 A stout and high tooth. The outline of the crown is sub-triangular with a convex labial border. The long and flat postero-lingual and postero-labial faces are separated by the sharp and high posterocrista. The postero-lingual depression may be large and deep or narrow and shallow. The anterior extension is moderately long and bears a small bulge; the posterior cingular bulge is even smaller. The lingual lobe is narrow, the protocone is low with a high connection to the paracone. The anterior border of the lobe is concave, the posterior one somewhat convex or straight. The postero-lingual cingulum is connected to the protocone. The labial cingula may merge; the antero-lingual cingulum is short and wide.

Description of the material from Orrios.

For a description of the locality see van de Weerd, 1976.

p2 (3) Fig. 10.2 The crown is strongly molarized. The enamel-dentine boundary curves upwards towards the anterior end of the crown. The labial side is strongly convex, the lingual side less so. A flat or concave postero-lingual face and a (deep) talonid valley are present. The antero-labial corner of the crown is somewhat flattened. A pronounced paraconid is present. The posterior and anterior cingula are narrow and short. There is a posterior cingular bulge. The roots diverge.

p3 (3) Fig. 66.1 The wide tooth has a rounded or a rhombic outline. Both the labial and the lingual sides are convex. A flat postero-lingual face and a (deep) talonid valley are present. The antero-labial corner of the crown is

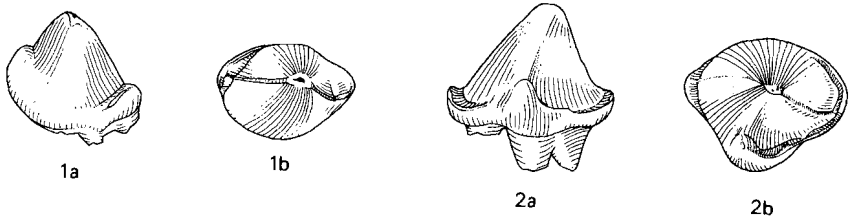


Fig. 66 *Dibolia brailloni* n.sp.
1. p3 (dext), Or-1019
a) lingual view b) occlusal-labial view.
2. P3 (sin), Or-1066
a) lingual view b) occlusal-lingual view.

somewhat flattened. The paraconid is well developed. The short postero-lingual cingulum forms a small cuspule; the anterior cingula are weak or lacking.

p4 (1) The outline of the crown is sub-rectangular. The anterocristid ends in the antero-lingual corner instead of near the middle of the anterior border. At the base of the wide flat postero-lingual face is a wide talonid valley that is closed lingually. The paraconid is strongly individualized. An ill-defined metaconal rib is present. The postero-lingual cingulum is high, but does not form a bulge. The postero-labial and the anterior cingula are low and short.

I1 (2) The two specimens are badly damaged. The medial lobe seems to have been rather heavy and high. The inner side of the crown is concave with a blunt medial rib and a strong but short internal cingulum. The enamel-free zone is probably high.

C (1) A short high tooth with an elliptical outline. A strongly convex labial and a slightly convex lingual side, featuring a flat postero-lingual face, are present. The enamel-dentine boundary curves upwards in the middle of the lingual and labial sides. Anteriorly a short and wide bulbous cingulum is present.

P2 (1) The tooth has an irregular elliptical outline. It has a sharp tip and a sharp posterocrista that ends far lingually in a small cuspule. Distinct postero-lingual and postero-labial faces are lacking. The lingual extension is a mere widening of the paracone. A posterior cingulum is not present. A large anterior cingular bulge is part of the narrow antero-lingual cingulum.

P3 (3) Figs. 24.2 and 66.2 The crown is stout and high and has a sub-triangular outline. Both sides are convex, apart from the flat or slightly concave posterior faces. The postero-lingual cingulum ends in a high spur that forms the pronounced lingual lobe. The borders of the lobe are straight or somewhat concave. The posterior cingula are wide and long; the antero-lingual cingulum is wide but short. The tooth has three roots; the lingual and posterior ones are partly fused.

P4 (1) The heavy tooth is strongly molarized. The long postero-lingual face is flat, the short postero-labial one is concave. The postero-lingual basin is wide and deep; the postero-labial depression is indistinct. Anteriorly a very strong cingular cuspule is present; the posterocrista ends in a faintly individualized but large bulge. The protocone is heavy with a probably high connection to the paracone. The anterior and posterior borders of the lingual lobe are convex. The narrow postero-lingual cingulum ends at the base of the protocone in a small hypocone. The labial and antero-lingual cingula are long and rather high.

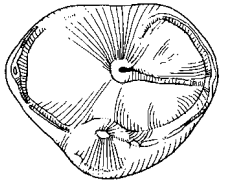
Description of the material from Gorafe 2.

For a description of the locality see de Bruijn, 1974.

P2 (1) A large wide tooth with a wide-elliptical outline and a vague postero-lingual face. The cristae are blunt. The lingual extension is ill-defined. The strong posterior cingulum ends in a high spur. The antero-labial cingulum is wide and heavy but short. The tooth has two roots.

P3 (1) The crown has a sub-triangular outline. The labial side is strongly convex, the lingual side less so. A vague postero-lingual face is present. The lingual extension is very pronounced, but bears no cuspule or cingular bulge. Postero-labially a cingulum is present, a postero-lingual one is missing. The anterior cingulum ends at the base of the lingual extension. The extension is supported by an accessory rootlet.

P4 (1) Figs. 25.3 and 67.1 The crown has a rounded outline without anterior or posterior extensions or cuspules. A concave postero-lingual and a flat postero-labial face are present. The postero-lingual basin is indistinct. The lingual lobe is small; the protocone is low with a high connection to the paracone. The posterior border of the lobe is convex, the anterior one is straight. Both the anterior and posterior cingula end at the base of the protocone. The tooth has three roots, the lingual one of which is thinner than the other two.



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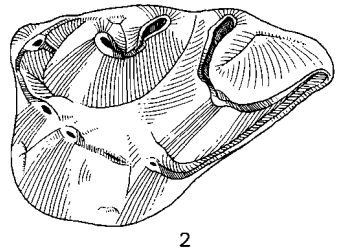


2

Fig. 67 *Dibolia brailloni* n.sp.
1. P4 (sin), Go2-517 occlusal-lingual view.
2. M1 (sin), Go2-518 occlusal-lingual view.

Description of the material from Escorihuela.

For a description of the locality see van de Weerd, 1976.

i1 (1) The tooth has a symmetrical, very high and narrow crown. The central rib is long and pronounced. The centrally situated backward projection is rather faint without a cuspule or a cingulum. The enamel-dentine boundary is slightly curved upwards on the medial side.

p2 (3) Fig. 68.1 The stout biconvex tooth has an elliptical outline. The

enamel-dentine boundary rises towards the anterior end of the crown. The postero-lingual face, the talonid basin, the antero-labial flattening and the paraconid are missing. The very short posterior cingulum does not form a bulge at the base of the posterocristid. The anterior cingulum is short and faint. The roots diverge.

p3 (3) Fig. 68.2 The biconvex crown is not so stout as that of the p2. The outline is rhombic due to a strong antero-labial and postero-lingual flattening. The enamel-dentine boundary rises towards the antero-labial corner of the crown. An ill-defined postero-lingual face is present; a paraconid is missing. The postero-lingual cingulum is short and bulgy.

p4 (3) Fig. 68.3 The crown is stout but short, with a sub-rectangular cross-section. A flat or concave postero-lingual face with a small talonid basin at its base is present. The talonid is lingually open. The antero-labial flattening is pronounced; the anterocrista ends in the lingual corner of the crown. A paraconid and a metaconal rib are present. The inflated posterior cingulum is very short. The postero-labial cingulum and the anterior cingula are narrow, short and weak.

C (2) Fig. 68.4 The high crown has a narrow elliptical outline. The labial side is convex, the lingual side less so. A postero-lingual face is missing.

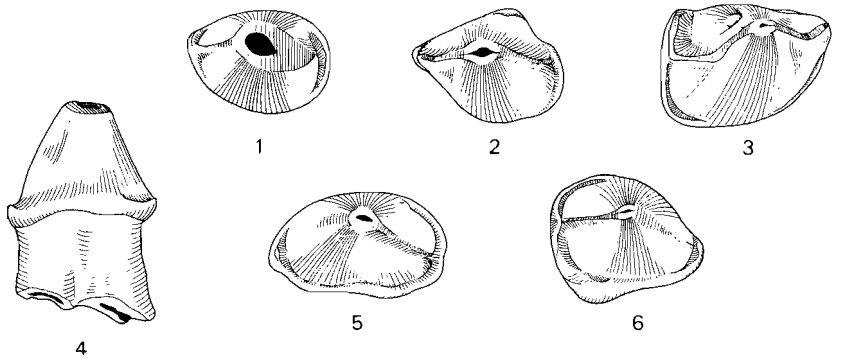


Fig. 68 *Dibolia brailloni* n.sp.
1. p2 (dext), Es-7023 occlusal-labial view.
2. p3 (sin), Es-7028 occlusal-labial view.
3. p4 (dext), Es-7031 occlusal-labial view.
4. C (sin), Es-7063 lingual view.
5. P2 (sin), Es-7073 occlusal-lingual view.
6. P3 (dext), Es-7077 occlusal-lingual view.

The posterior and anterior cingula are very short and rather weak. The two roots are fused all the way down on the lingual side, at the labial side they are fused at the crown-base only.

P2 (4) Fig. 68.5 The crown has an elliptical or an oval cross-section. The labial side is more strongly convex than the lingual one. An ill-defined postero-lingual face is present in some of the specimens. The lingual extension – when present – is not pronounced. The posterior cingulum is long and strong, but a bulge or cuspule is missing at the base of the posterocrista. The anterior cingulum is short. There are two roots, the posterior one of which may be somewhat widened.

P3 (5) Fig. 68.6 The biconvex crown has an irregular outline. Both the lingual and the labial sides have a flat posterior face, the lingual one of which is the largest. The rather pronounced lingual extension is situated far posteriorly. The posterior cingulum is always strong and may form a spur on the lingual extension; the other cingula vary much in length and width. The tooth has two roots, the posterior one of which is wide.

P4 (1) The tooth is weakly molarized. The crown is biconvex with a vague postero-labial and a long slightly convex postero-lingual face. A deep basin is situated at the base of the lingual face. A short anterior extension, bearing a cingular cuspule, is present; the posterior extension is formed by a large bulge at the base of the posterocrista. The lingual lobe is long; the protocone is low with a high connection to the paracone. The anterior and posterior borders of the lobe are straight. The postero-lingual cingulum is connected to the protocone; the shorter antero-lingual cingulum ends at the base of the protocone.

Dibolia bifida (Engesser, 1980)

Original reference: Engesser, 1980: Insectivora und Chiroptera (Mammalia) aus dem Neogen der Türkei. Schweizer. Pal. Abh., *102,* pp. 47–149.

Synonymy: Desmana getica Terzea, 1980

Original diagnosis: Kleiner Desman von der Grösse von *Galemys pyrenaicus* mit nicht gekrümmtem I1, dessen schaufelförmige Krone zwei Spitzen aufweist. P4 deutlich länger als breit mit relativ schwach entwickeltem Innenhügel und schwacher Kante an der Vorderseite des Haubthügels, p3 dreiwurzelig. *) p4 ohne Innenhügel, jedoch mit deutlichem Vorderhügelchen. C/c und P/p relativ grazil, kaum aufgedunsen; p2 etwas kleiner als p3. Wur-

*) This should be either p3 is double-rooted or P3 has three roots.

zeln von p3 nicht schräggelstellt; p1 meist mit einer nicht transversal verbreiterten Wurzel. M1 mit kurzem Lingualteil (Metaconulus kaum nach hinten vorstehend) und relativ gestrecktem Winkel zwischen den beiden Metaconus-Schenkeln. M2 sehr kurz. Untere Molaren ohne Lingualsporn zwischen Proto- und Hypoconid, jedoch mit Schmelzrunzeln im Talonid. Die Crista obliqua von m3 verbindet sich etwa in der Zahnmitte mit dem Protoconid-Metaconid Verbindungsgrat. i2 nicht viel grösser als i1, mit Lingualcingulum. Foramina mentale sehr variabel, meist deren 4.

Emended diagnosis: the mean length of the p2 is about 1.32 mm, the mean length of the p3 is about 1.40 mm, the mean length of the p4 is about 1.66 mm; the p2/p3 ratio is about 0.94. The p1 has one or two roots.

The mean length of the C is about 1.40 mm, the mean length of the P3 is about 1.61 mm. The P1 has two roots.

Differential diagnosis: the low p2/p3 ratio in combination with the small p2 and p3 and a very long P3 distinguishes *Dibolia bifida* from the other *Dibolia* species.

Holotype: M1 (sin)

Type locality: Dinar-Akçaköy, west Turkey. For a description see Becker-Platen et al, 1975.

Age of the type locality: Early Ruscinian (MN 14).

Other localities with Dibolia bifida: Ciuperceni in Roumania, of Early Ruscinian age and Limni 6 on the island Euboea, Greece, of Early Villanyian age.

Measurements: see table 16 (a) for the lower teeth and table 16 (b) for the upper teeth.

Description of the material from the type locality, based on Engesser's description, figures and the casts Dr. Engesser kindly sent me.

The number of foramina mentale is variable, usually four are present. Foramina are located under the p1, under the p3–p4 and under the p4–m1; the location of the fourth one is not indicated by Engesser.

i1 (3) The symmetrical crown shows a central rib. The postero-medial projection is not pronounced; the postero-medial cingulum is wide. The enamel-dentine boundary rises slightly towards the posterior end of the crown.

p2 (12) A strong relatively short and high tooth. The enamel-dentine boundary rises steeply towards the anterior end of the crown. Both the labial and the lingual side are convex; an ill-defined posterior face and a narrow talonid basin are present. The paraconid is small and not individualized. The wide posterior cingula are connected to the faint anterior ones. A hypoconid is present at the base of the posterocristid. The two roots diverge.

p3 (6) The crown has a rounded cross-section. The enamel-dentine boundary rises slightly towards the anterior end of the crown. Both the labial and the lingual side are convex; the lingual side features a flat posterior face. The talonid gully is short and indistinct. A strong antero-labial flattening is apparent. The faint paraconid is not individualized. The posterior cingulum is heavy and labially shorter than lingually. A hypoconid is found at the base of the posterocristid.

p4 (3) The tooth is molarized to a certain extent. The enamel-dentine boundary is curved upwards in the middle of the labial side. The crown is biconvex with a large concave postero-lingual face. The wide and long talonid valley is open lingually. The posterocristid merges into a high crest which ends in an extremely high and strong entoconid. The paraconid is

tooth	loc.	N	L		W(2)		W(2)/L	
			range	mean	range	mean	range	mean
c	Li6	–		–		–		–
	Ci	–		–		–		–
	DA	2	0.92–1.08	1.00	0.84–0.86	0.85		0.85
p1	Li6	1		0.91		0.78		0.86
	Ci	–		–		–		–
	DA	4	0.92–1.04	0.95	0.84–0.90	0.87		0.92
p2	Li6	4	1.31–1.39	1.35	0.97–1.08	1.00	0.73–0.79	0.75
	Ci	1		1.35		1.00		0.75
	DA	12	1.20–1.40	1.32	0.90–1.00	0.94		0.71
p3	Li6	1		1.31		0.96		0.73
	Ci	1		1.31		0.98		0.75
	DA	6	1.34–1.52	1.40	0.92–0.98	0.95		0.68
p4	Li6	1		1.55		1.22		0.79
	Ci	1		1.53		1.05		0.69
	DA	3	1.64–1.68	1.66	1.06–1.16	1.11		0.67
m1	Li6	2	2.71–2.72	2.71	1.99–2.00	1.99	0.73–0.74	0.73
	Ci	–		–		–		–
	DA	10	2.24–2.52	2.43	1.64–2.06	1.80		0.74
m2	Li6	1/2		2.56	1.71–1.80	1.75		0.70
	Ci	1		2.20		1.67		0.76
	DA	7	2.30–2.40	2.37	1.64–1.76	1.68		0.71
m3	Li6	2	1.88–1.92	1.90	1.12–1.23	1.17	0.60–0.64	0.62
	Ci	1		1.65		1.30		0.79
	DA	4	1.84–1.88	1.85	1.24–1.28	1.26		0.68

Table 16 (a) Measurements of *Dibolia bifida* (Engesser, 1980), lower teeth.

variable: weak and hardly individualized in some specimens, strong and distinctly individualized in others. The postero-labial cingulum is wide; the anterior cingula are fairly weak.

I1 (2) A low crown with a long thin medial lobe. The indentation in the upper edge is wide. A long external cingulum is present. The strongly concave inner side of the crown features a long medial cutting edge which merges into the inner cingulum. The enamel-free area is rather high.

C (1) The crown has a oval cross-section. The labial side is more convex than the lingual side. The posterior cingulum is wide and forms a small bulge at the base of the posterocrista. The anterior cingulum is narrow; along the lingual border a weak cingulum is present.

P3 (7) A long tooth with a rhombic outline that is due to an antero-labial and a postero-lingual flattening. Both the labial and the lingual sides are convex with flat posterior faces. An indistinct postero-lingual basin and a postero-lingual extension are present. The posterocrista forms a small cuspule at its base. The crown is surrounded by a cingulum which is missing along the

tooth	loc.	N	L		W		W/L	
			range	mean	range	mean	range	mean
C	Li6 Ci*)	3	1.35–1.56	1.48	0.98–1.08	1.04	0.68–0.73	0.71
	DA	1		1.40		0.88		0.63
P1	Li6	–		–		–		–
	DA	1		1.00		0.88		0.88
P2	Li6	2	1.69–1.74	1.71	1.13–1.20	1.16	0.65–0.71	0.68
	DA	–		–		–		–
P3	Li6	3	1.54–1.70	1.60	1.13–1.22	1.18	0.72–0.77	0.74
	DA	7	1.56–1.68	1.61	1.08–1.24	1.14		0.71
P4	Li6	2	2.05–2.32	2.18	1.77–1.83	1.80	0.79–0.86	0.82
	DA	4	1.92–2.16	2.06	1.52–1.68	1.63		0.79
M1	Li6	–		–		–		–
	DA	4	3.04–3.14	3.09	2.40–2.50	2.45		0.75
M2	Li6	–		–		–		–
	DA	3	2.08–2.14	2.11	2.48–2.58	2.53		1.20
M3	Li6	2	1.51–1.53	1.52	2.07–2.08	2.07	1.36–1.37	1.36
	DA	–		–		–		–

*) from Ciuperceni only lower teeth are known.

Table 16 (b) Measurements of *Dibolia bifida* (Engesser, 1980), upper teeth.

middle of the labial side only. The accessory rootlet is partly fused with the posterior root.

P4 (4) A rather long tooth. Both the labial and the lingual sides are convex with long posterior faces. Anteriorly the crown is somewhat elongated, bearing a small bulge which is formed by the cingulum. Posteriorly the extension of the posterocrista forms a distinct bulge. The lingual lobe is of medium size; the protocone is rather low with a high connecting ridge to the paracone. The anterior and posterior borders of the lobe are straight. The postero-lingual basin is deep and long. The crown is surrounded by a strong cingulum that is connected to the protocone. In some specimens it widens around the postero-labial corner.

Description of the material from Ciuperceni, based on Terzea's description and figures.

For a description of the locality see Terzea, 1980.

In the mandible from Ciuperceni, described by Terzea as *Desmana getica,* one foramen mentale is present. It is situated under the m1.

The position of the p3 is slightly oblique relative to the length axis of the jaw with the anterior root placed lingually.

p2 (1) A plump tooth. The labial and lingual sides are convex without either a postero-lingual face or an antero-labial flattening. The very small paraconid is not individualized. The cingulum is interrupted along the middle of the labial side only. Around the posterior end of the crown the cingulum is high and wide.

p3 (1) A plump tooth. The crown is biconvex and does not seem to possess a postero-lingual face or a talonid valley. A strong antero-labial flattening is apparent. The paraconid is similar to that found in the p2. Cingula are as those in p2; a distinct strengthening of the cingulum is notable at the base of the posterocristid.

p4 (1) A plump tooth. The crown is biconvex with a flat postero-lingual face and a long flat talonid. The paraconid is strongly individualized. The anterior and posterior cingula are wide.

Description of the material from Limni 6.

For a description of the locality see Katsikatsos et al, 1981.

There are two fragmentary mandibles available; one specimen shows a foramen mentale under the p4–m1, the other a foramen under p3 and two under p4–m1. In both fragments the p3 is situated straight relative to the length axis of the jaw.

From the alveoles present in one of the mandibles it is apparent that the p2 and the p3 were both single-rooted, while it seems that the p1 was missing.

i1 (1) The crown is narrow and may have been high. The central rib is wide. The postero-medial extension is indistinct and situated in the middle of the posterior side. It is bordered by a long and strong cingulum. The root is heavy.

p2 (4) Figs. 10.3 and 69.1 A moderately strong tooth. The enamel-dentine boundary rises steeply towards the antero-labial corner of the crown. The labial side is convex, the lingual side is flat with an ill-defined postero-lingual face. The antero-labial corner is flattened. The paracone varies from small to large. The posterior cingulum is wide, forming a small bulge; a long antero-labial cingulum may be present. The roots are variable: one specimen has two free-standing roots placed in front of each other; of two specimens the roots are fused lingually and one specimen has a single – laterally compressed – root.

p3 (1) Figs. 11.3 and 69.2 The crown has a rhombic cross-section with fairly pronounced antero-labial and postero-lingual flattenings and a postero-labial flange. The enamel-dentine boundary rises steeply towards the antero-labial corner of the tooth. The crown overhangs the root postero-labially. The lingual side is less convex than the labial side. The paraconid is of moderate size. The posterior cingula are strong; anterior cingula are missing. The tooth has either one – laterally compressed – root or two roots.

p4 (1) Fig. 69.3 A rather plump tooth which shows a labial overhang of the crown over the roots. Both the labial and the lingual sides are strongly

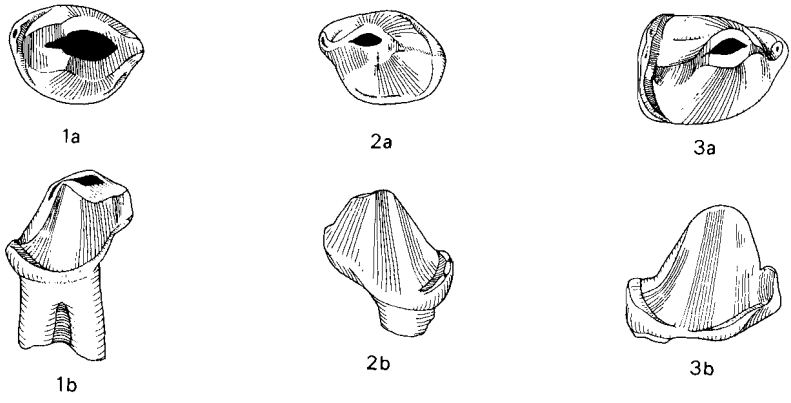


Fig. 69 *Dibolia bifida* (Engesser, 1980)
1. p2 (dext), Li6-1006
   a) occlusal-labial view b) labial view.
2. p3 (sin), Li6-1008
   a) occlusal-labial view b) labial view.
3. p4 (dext), Li6-1010
   a) occlusal-labial view b) labial view.

convex and have a flat posterior face. A shallow narrow talonid valley is present. The antero-labial corner of the crown is flattened. The paraconid is stout; the metaconal rib is weak. The posterior cingulum is fairly wide, the antero-labial one is narrow.

I1 (1) A low and very heavy crown with a long straight root. Both the medial and the labial lobe are extremely thick. The medial lobe is short; the indentation in the upper edge is deep. The inner side of the crown is strongly concave; the medial crest merges into the high and wide but short inner cingulum. The enamel-free zone is not visible since the only specimen available is damaged.

C (3) The lingual side of the crown is slightly less convex than the labial side. An ill-defined flat postero-lingual face is present. The enamel-dentine boundary is slightly curved upwards in the middle of the labial and the lingual sides. The tooth is surrounded by a cingulum that is interrupted along the middle of the labial side only.

P2 (2) The crown has an elongated oval cross-section. The labial and lingual sides are convex with flat posterior faces. The labial one of these is the most conspicuous, due to the fact that the posterocrista ends near the postero-lingual corner of the crown. The lingual extension is rather pronounced and bears a high cingular spur. The crown is surrounded by a strong cingulum that is interrupted along the labial side only. The tooth has two roots.

P3 (3) A long crown with a rhombic outline. The labial and lingual sides are convex with flat posterior faces. The labial face is more distinct than the lingual one. As in the P2 the posterocrista ends near the postero-lingual corner of the crown. The lingual extension is distinct and bears a heavy cingular spur. The posterior cingula are long and wide; the anterior cingula are very wide – in particular lingually – but short. They are not connected to the lingual spur. The cingulum forms a bulge at the base of the anterocrista.

P4 (2) An elongated tooth with a strong lingual lobe. The labial and lingual sides are convex with flat or concave posterior faces. An anterior extension is present in one specimen. The low protocone is not connected to the paracone. The anterior border of the lingual lobe is concave, the posterior one more or less straight. The postero-lingual basin is deep. The posterior and anterior cingula are wide but short and not connected to the protocone. The labial and lingual posterior cingula are not connected at the base of the posterocrista.

Dibolia sp.

The assemblage extracted from several isolated blocks of fissure material, collected near the main fissure at Moreda (Late Ruscinian; Spain), includes 9 teeth, three of which are damaged. This makes it impossible to allocate the assemblage to one of the described species of *Dibolia*. The small C and P2 suggest that the material represents *Dibolia dekkersi*, the only species that has similar teeth of this size.

For the measurements see table 17.

Description of the material from Moreda.

For a description of the locality see Gmelig-Meyling and Michaux, 1973.

I1 (1) Figs. 17.4 and 29.3 A high tooth with a very deep indentation between the two lobes. The medial lobe is high and thin. The inner side is strongly concave with a medial cutting edge which merges into the heavy and long inner cingulum. The labial edge too forms a sharp cutting blade. The enamel-free area is high.

C (1) The tooth is distinctly smaller than the P2. Both the lingual and the labial sides are convex. The posterior cingulum is short, forming a cuspule. The tooth has one very large laterally compressed root. It is not possible to establish whether it is one root all the way down or that only the upper part is fused while the tips are straddling.

P2 (2) The P2 is large relative to the preceding teeth. The crown has a high and sharp tip. The lingual side is less convex than the labial one; on both sides flat posterior faces are present. The inconspicuous lingual extension is situated far posteriorly. The strong but short posterior and anterior cingula form high bulges at the base of the anterocrista and the posterocrista. The tooth has two roots.

tooth	loc.	N	L	W	W/L	
p1	Mo (1971)	1	0.92	0.81	0.88	single-rooted
C	Mo (1973)	1	1.15	0.75	0.66	
P1	Mo (1971)	1	0.85	0.65	0.76	double-rooted
	Mo (1973)	1	0.75	0.60	0.80	double-rooted
P2	Mo (1971)	1	1.62	1.08	0.67	
	Mo (1973)	1	1.55	1.05	0.68	
M1	Mo (1973)	1	3.26	2.44	0.75	
M2	Mo (1971)	1	2.18	2.71	1.24	

Table 17 Measurements of *Dibolia* sp. from Moreda.

Galemys Kaup, 1829

For the emended diagnosis and the differential diagnosis of the genus the reader is referred to p. 93.

Galemys pyrenaicus (Geoffroy, 1811)

Emended diagnosis: the mean length of the p2 is about 1.49 mm, the mean length of the p3 is about 1.42 mm, the mean length of the p4 is about 1.61 mm; the p2/p3 ratio is about 1.05. The p1 is single-rooted.

The mean length of the C is about 1.51 mm, the mean length of the P2 is about 1.58 mm, the mean length of the P3 is about 1.50 mm; the P2/P3 ratio is about 1.07. The P1 is single-rooted.

Differential diagnosis: the long C in combination with the short P2 and P3 distinguishes *Galemys pyrenaicus* from the other *Galemys* species.

Measurements: see table 18.

Description, based on 16 complete dentitions from specimens collected at various localities in the south of France and in Spain.

The maximum number of foramina mentale encountered is five, but four or three are more common. Two foramina have a more or less fixed position,

tooth	N	L		W(2)		W(2)/L	
		range	mean	range	mean	range	mean
c	32	1.13–1.36	1.26	0.77–0.90	0.84	0.59–0.75	0.65
p1	32	0.97–1.19	1.06	0.82–0.90	0.86	0.71–0.87	0.81
p2	32	1.37–1.60	1.49	0.87–0.99	0.93	0.57–0.67	0.63
p3	32	1.30–1.57	1.42	0.81–0.93	0.86	0.55–0.67	0.61
p4	32	1.50–1.75	1.61	0.91–1.10	1.01	0.54–0.68	0.63
m1	32	2.23–2.51	2.37	1.67–1.81	1.74	0.67–0.79	0.73
m2	32	2.35–2.60	2.48	1.58–1.74	1.64	0.62–0.70	0.66
m3	32	1.75–2.11	1.95	1.03–1.21	1.15	0.49–0.66	0.59
C	32	1.35–1.65	1.51	0.81–1.02	0.90	0.54–0.73	0.60
P1	32	0.98–1.28	1.09	0.75–0.86	0.81	0.63–0.83	0.75
P2	32	1.49–1.70	1.58	0.84–0.98	0.92	0.55–0.62	0.58
P3	30	1.39–1.60	1.50	0.82–0.99	0.90	0.54–0.65	0.60
P4	32	2.00–2.41	2.16	1.41–1.66	1.57	0.67–0.79	0.73
M1	31/30	3.03–3.27	3.13	2.22–2.89	2.51	0.69–0.95	0.80
M2	32	2.27–2.57	2.36	2.81–3.05	2.92	1.11–1.29	1.24
M3	32	1.41–1.67	1.53	2.08–2.29	2.16	1.30–1.52	1.42

Table 18 Measurements of *Galemys pyrenaicus* (Geoffroy, 1811) from several localities in France and Spain.

i.e. the anterior one under c–p1 and the posterior one under the m1 (this one is missing in several specimens). Apart from these two, foramina may be found (1) under the p2; (2) under the p2–p3; (3) under the p3; (4) under the p3–p4; (5) under the p4 and (6) under the p4–m1.

The position of the p1 and the p2 is slightly oblique relative to the length axis of the jaw, those of the p3 and the p4 more strongly oblique, with the anterior (part of the) root placed lingually.

The position of the P1, the P3 and the P4 is very oblique, with the anterior (part of the) root placed lingually.

i1 (32) A small and high tooth with a moderate anterior overhang of the crown. The labial part is thin, the medial part is thicker. The medial face is situated in the same plane as the root. A medial extension is missing; the posterior face is flat.

p2 (32) A long narrow tooth. The enamel-dentine boundary rises steeply towards the anterior end of the crown. The labial side is convex; the lingual side is more or less flat. An ill-defined flat postero-lingual face is present. The antero-labial flattening of the crown is strong. The paraconid – if present – is weakly developed. A short and narrow postero-lingual cingulum is present. The roots diverge.

p3 (32) A long and narrow tooth with an inflated tip. The labial side is strongly convex; the lingual side is more or less flat. The antero-labial and postero-lingual corners of the crown are flattened. A long but weakly developed paraconid is present. The inflated posterior cingulum is very short. The tooth is single-rooted.

p4 (32) The tooth has a relatively small crown which is long and narrow with an inflated tip. The labial side is strongly convex; the lingual side is more or less flat. The postero-lingual face is ill-defined. The antero-labial and postero-lingual corners of the crown are flattened. The paraconid is long, but not individualized. A short inflated posterior cingulum is present.

I1 (32) A narrow, compressed tooth. The curved labial and the straight medial face meet under a sharp angle. The tip of the tooth is sharp. The inner side of the crown is concave with a short blunt medial crest. The internal cingulum is missing.

C (32) A large high tooth that is long and relatively narrow. The labial side is convex; the lingual side is more or less flat. The tip of the crown is situated far anteriorly. A short anterior cingular extension is present. Postero-lingually there is a small bulge or a short cingulum.

P2 (32) The crown is very similar to that of the C, but not as high as the canine. The labial side is strongly convex, the lingual side less so. There is no postero-lingual face. The lingual extension is either indistinct or missing. Short cingula are present anteriorly and posteriorly.

P3 (30) The crown is long and narrow with cingular extensions bearing small bulges anteriorly and posteriorly. The lingual side is convex with an ill-defined flat posterior face; the labial side is less convex, with a more pronounced posterior face and an indistinct but long basin. A lingual extension is missing, but there is a weak bulge in the middle of the lingual side. The postero-labial cingulum is long and narrow.

P4 (32) The crown is long and narrow. Anteriorly it is extended by a small cusp that is formed by the continuation of the anterocrista; the posterior end is formed by the long continuation of the posterocrista which curves towards the lingual corner. The lingual lobe is small; the protocone is low and hardly connected to the paracone. The anterior border of the lobe is concave, the posterior one is straight. The shallow postero-lingual basin is edged by a very low and weak cingulum.

Galemys sulimskii n.sp.

Derivatio nominis: the species is named after Dr. Andrzej Sulimski, who was the first to describe the Weze 1 assemblages.

Diagnosis: the mean length of the p2 is about 1.29 mm, the mean length of the p3 is about 1.37 mm, the mean length of the p4 is about 1.54 mm; the p2/p3 ratio is about 0.94. The p1 is single-rooted.

The mean length of the C is about 1.15 mm, the mean length of the P2 is about 1.49, the mean length of the P3 is about 1.49 mm; the P2/P3 ratio is about 1.00. The P1 is double-rooted.

Differential diagnosis: the small size distinguishes *Galemys sulimskii* from all other *Galemys* species.

Holotype: mandibular fragment with i3–p2 (dext), no. 304/8, (Fig. 70.1), stored in the Paleozoological Laboratory, Polish Academy of Sciences, Warsaw, Poland.

Type locality: Weze 1, Poland. For a description of the locality see Sulimski, 1959.

Age of the type locality: Late Ruscinian (MN 15b).

Measurements: see table 19.

Description of the material from the type locality.

There are at least two foramina mentale present. The anterior one is situated under the c–p1, the posterior one under the m1. Between these two, small foramina are found under the p1–p2 and under the p2–p4.

The position of the p3 is either straight or very slightly oblique relative to the length axis of the jaw. In the last case the anterior root is placed lingually.

tooth	N	L		W(2)		W(2)/L	
		range	mean	range	mean	range	mean
c	3	1.04–1.17	1.12	0.83–0.89	0.86	0.73–0.80	0.77
p1	3	0.92–0.97	0.94	0.84–0.88	0.86	0.89–0.94	0.91
p2	5	1.25–1.35	1.29	0.87–1.00	0.94	0.66–0.80	0.73
p3	1		1.37		0.95		0.69
p4	5	1.50–1.62	1.54	1.01–1.21	1.10	0.67–0.80	0.72
m1	8	2.56–2.78	2.65	1.78–2.04	1.92	0.69–0.77	0.72
m2	7	2.36–2.63	2.54	1.76–1.92	1.82	0.68–0.78	0.72
m3	10	1.77–1.99	1.89	1.26–1.50	1.34	0.65–0.79	0.71
C	2	1.12–1.19	1.15	0.87–0.95	0.91	0.78–0.80	0.79
P1	1		1.18		1.00		0.85
P2	3	1.37–1.61	1.49	1.06–1.19	1.12	0.70–0.87	0.76
P3	4	1.45–1.55	1.49	1.10–1.22	1.14	0.75–0.79	0.76
P4	6	1.96–2.24	2.09	1.79–2.00	1.89	0.86–0.94	0.90
M1	4	2.95–3.17	3.01	2.39–2.71	2.53	0.75–0.92	0.84
M2	2	2.27–2.31	2.29	2.66–2.74	2.70	1.17–1.19	1.18
M3	1		1.48		1.94		1.31

Table 19 Measurements of *Galemys sulimskii* n.sp. from Weze 1.

The position of the P3 is slightly oblique.

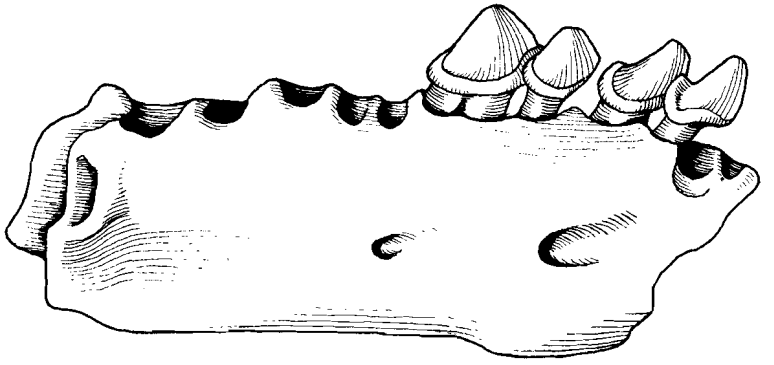
p2 (5) Fig. 70.1 A relatively short tooth. The outline is somewhat triangular since the posterior end of the crown is wider than the anterior end. The enamel-dentine boundary rises steeply towards the anterior end of the crown. The lingual side is less convex than the labial one. The tooth is surrounded by a wide cingulum. The two roots may be partly fused.

p3 (1) The tooth resembles the p2 apart from its rounded-rhombic cross-section. The crown slightly overhangs the root labially. The lingual side is rather flat; the labial side is convex with a flattened anterior corner.

p4 (5) Fig. 70.2 A high, moderately molarized tooth with a concave postero-lingual face and a short talonid. The posterocristid may end far lingually near the postero-lingual corner. The paraconid is heavy; a metaconid or a metaconal rib are present. The cingulum either surrounds the entire crown or is missing along the lingual side only.

I1 (3) The top of the crown is fairly wide with a shallow indentation in the edge. The inner side is somewhat concave due to the presence of a medial ridge.

C (2) The crown has an elliptical outline. The lingual side is flat or concave and wider than the convex labial side. Along the lingual side runs a cingulum; along the anterior and posterior ends and the labial side an inflated zone is present.



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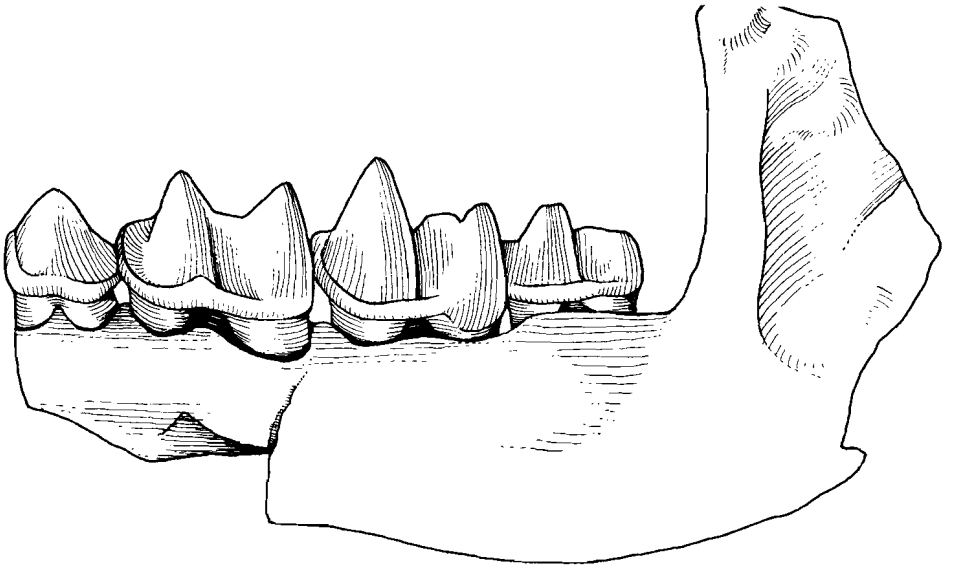


2

Fig. 70 *Galemys sulimskii* n.sp. from Weze 1.
1. mandibular fragment with i3–p2 (dext), no. 304/8 (holotype) labial view (redrawn).
2. mandibular fragment with p4–m3 (sin), no. 304/5 labial view (redrawn).
× 11

P2 (3) The crown is relatively long and narrow with an indistinct lingual extension. A heavy cingulum surrounds the crown. A very small accessory rootlet supports the lingual extension.

P3 (4) The tooth features a concave postero-lingual face and a vague postero-labial face. The postero-lingual basin is pronounced. The lingual extension bears a cingular bulge. The tooth has either two roots, the posterior one of which is wide, or two main roots and a thin accessory rootlet.

P4 (6) The tooth is elongated anteriorly and may bear a small anterior cingular bulge. The crown is surrounded by a heavy cingulum that may be connected to the protocone.

Galemys kormosi (Schreuder, 1940)

Original reference: Schreuder (1940): A revision of the fossil water moles (Desmaninae). Extrait des Archiv. Néerl. Zool., *IV*, pp. 202–333.

Original diagnosis):* Size as *Gal. semseyi* K., thus slightly larger than recent *Galemys* . . . Dentition somewhat higher than in *D. nehringi.* Cingulum slightly more extended than in all water-moles, sharply defined. Premolars not elongated. [P2, P3 and] P4 three-rooted. P4 short, the rounded main cusp and the inner cusps rather independent of each other. At M2 the strong cingulum round the parastyle forms a fifth outer cusplet. [Mental foramen usually 4 . . . p3 somewhat reduced, but only a triffle obliquely set. p2 not much enlarged. Metaconid of p4 indicated only by a ridge or a bulge, thus trigonid not distinct. At m1 and m2 cingulum also present along the posterior side.]

*) the parts of the diagnosis that are not based on material from the type locality are placed between brackets.

Supplementary diagnosis based on material from Tegelen: the mean length of the p2 is about 1.54 mm, the mean length of the p3 is about 1.52 mm, the mean length of the p4 is about 1.81 mm; the p2/p3 ratio is about 1.01. The p1 is double-rooted.

The mean length of the C is about 1.32 mm, the mean length of the P2 is about 1.88 mm, the mean length of the P3 is about 1.70 mm; the P2/P3 ratio is about 1.11. The P1 is double-rooted.

Differential diagnosis: the large size of the p3, the C, the P2 and the P3 distinguishes *Galemys kormosi* from the other *Galemys* species.

Holotype: maxillary fragment with P4–M3 (dext).

Type locality: Beremend 4, Hungary. For a description of the locality see Kormos, 1913, 1938.

Age of the type locality: Early Villanyian (MN 16b).

Other localities with Galemys kormosi: "Beremend" and Beremend 5 (Hungary), Rebielice Królewskie 1 and 2 (Poland) and Baza (Spain), all of Early Villanyian age and Tegelen (the Netherlands) of Late Villanyian age.

Measurements: see table 20 (a) for the lower teeth and table 20 (b) for the upper teeth.

Description of the material from the type locality.

P4 (1) The tooth is of medium size. The labial and lingual sides are convex with flat posterior faces. The postero-lingual basin is narrow and shallow. Anteriorly a short extension – but no bulge – is formed by the cingulum. The lingual lobe is of moderate size with a protocone of medium height well separated from the paracone. Both the anterior and posterior borders of the lobe are concave. The lingual cingula are long, as they end halfway round the base of the protocone. The labial cingula are shorter. The posterior cingula are not connected at the base of the posterocrista.

Description of the material from "Beremend" (= Kormos' specimens 2 and 3; specimen no. 61/1576; specimen no. 61/2199).

p4 (2) The crown is either strongly or moderately elongated. The crown overhangs the root at the postero-lingual corner. The lingual and labial sides are convex with slightly concave posterior faces. The talonid basin may be short or long, shallow and lingually open or closed. The antero-labial corner of the crown is flattened. A heavy paraconid and a rather strong metaconal rib are present. The high and strong postero-lingual cingulum is a continuation of the posterocristid. A hypoconid is present in one of the two specimens. The postero-labial cingulum borders the flange that is formed by the labial overhang and merges into the anterior cingulum.

Description of the material from Beremend 5 (= the material collected by Noszky in 1952).

For a description of the locality see Jánossy, 1979.

No descriptions are available of the P2 and the P3.

P4 (2) The crown has a rounded cross-section. The anterior end is slightly extended; a small cingular bulge may be present. The tooth is biconvex with a long, flat or concave posterior face on both sides. A small and shallow postero-lingual basin is situated lingually. The lingual lobe is wide and bears a high protocone that is connected to the paracone by a low ridge. Both borders of the lobe are strongly concave. The tooth is surrounded by a cingulum that may be interrupted along the antero-labial part of the crown and along the middle of the protocone. A pronounced cingular bulge is present postero-labially.

tooth	loc.	N	L		W(2)		W(2)/L	
			range	mean	range	mean	range	mean
c	Te	2	1.30–1.34	1.32	0.88–0.88	0.88	0.66–0.68	0.67
	RK2	–		–		–		–
	RK1	1		1.30		0.85		0.65
	Ba	–		–		–		–
	'Br'	–		–		–		–
	Br4/5*)							
p1	Te	1		1.07		0.86		0.80
	RK2	–		–		–		–
	RK1	1		1.10		0.91		0.83
	Ba	–		–		–		–
	'Br'	–		–		–		–
p2	Te	6	1.49–1.57	1.54	0.92–1.04	0.97	0.59–0.68	0.63
	RK2	1		1.57		0.94		0.60
	RK1	3	1.50–1.56	1.53	0.93–1.03	0.99	0.60–0.67	0.65
	Ba	1		1.65		1.07		0.65
	'Br'	–		–		–		–
p3	Te	4	1.46–1.56	1.52	0.86–0.97	0.93	0.55–0.66	0.61
	RK2	1		1.61		0.95		0.59
	RK1	2	1.50–1.51	1.50	0.91–0.92	0.91	0.61–0.61	0.61
	Ba	–		–		–		–
	'Br'	–		–		–		–
p4	Te	10	1.71–1.94	1.81	1.01–1.23	1.10	0.58–0.66	0.61
	RK2	3	1.72–1.79	1.76	1.09–1.19	1.13	0.62–0.69	0.64
	RK1	18	1.66–1.99	1.84	1.02–1.30	1.16	0.55–0.78	0.63
	Ba	2	1.92–1.96	1.94	1.20–1.27	1.23	0.62–0.65	0.63
	'Br'	2	1.71–1.83	1.77	1.06–1.10	1.08	0.58–0.64	0.61
m1	Te	12	2.38–2.60	2.50	1.78–1.96	1.86	0.70–0.78	0.74
	RK2	3	2.46–2.62	2.56	1.73–1.85	1.80	0.70–0.71	0.70
	RK1	36	2.63–3.00	2.78	1.86–2.08	1.97	0.67–0.75	0.71
	Ba	2	2.82–2.84	2.83	2.02–2.09	2.05	0.72–0.74	0.73
	'Br'	3	2.37–2.80	2.59	1.85–1.97	1.89	0.70–0.78	0.73
m2	Te	5	2.28–2.44	2.38	1.68–1.85	1.75	0.71–0.78	0.74
	RK2	1		2.63		1.71		0.65
	RK1	26	2.54–2.85	2.68	1.69–1.98	1.83	0.64–0.74	0.68
	Ba	2	2.78–2.82	2.80	1.98–1.99	1.98	0.70–0.72	0.71
	'Br'	3	2.39–2.50	2.46	1.72–1.89	1.80	0.72–0.76	0.73
m3	Te	7	1.80–1.91	1.85	1.08–1.34	1.24	0.60–0.73	0.67
	RK2	–		–		–		–
	RK1	14	1.93–2.09	2.01	1.22–1.41	1.29	0.60–0.70	0.64
	Ba	1		2.11		1.35		0.64
	'Br'	1		1.95		1.37		0.70

*) in Beremend 4 and Beremend 5 only upper teeth were found.

Table 20 (a) Measurements of *Galemys kormosi* (Schreuder, 1940), lower teeth.

tooth	loc.	N	L		W		W/L	
			range	mean	range	mean	range	mean
C	Te	9	1.18–1.46	1.32	0.90–0.99	0.94	0.65–0.79	0.71
	RK2	–		–		–		–
	RK1	2	1.26–1.46	1.36	0.90–0.95	0.92	0.65–0.71	0.68
	Ba	1		1.35		0.97		0.72
	Br5	–		–		–		–
	Br4	–		–		–		–
	'Br'*)							
P1	Te	4/5	1.29–1.38	1.35	0.93–1.06	1.02	0.75–0.82	0.76
	RK2	–		–		–		–
	RK1	4	1.17–1.42	1.27	0.85–1.00	0.93	0.68–0.78	0.73
	Ba	1		1.15		0.89		0.77
	Br5	–		–		–		–
	Br4	–		–		–		–
P2	Te	12	1.75–1.99	1.88	1.09–1.34	1.20	0.59–0.71	0.64
	RK2	–		–		–		–
	RK1	7	1.83–2.09	1.91	1.16–1.32	1.22	0.61–0.67	0.64
	Ba	–		–		–		–
	Br5	1		1.74		1.32		0.76
	Br4	–		–		–		–
P3	Te	9	1.58–1.77	1.70	1.16–1.26	1.21	0.66–0.78	0.71
	RK2	–		–		–		–
	RK1	8	1.70–1.98	1.80	1.18–1.28	1.30	0.66–0.78	0.72
	Ba	1		1.46		1.25		0.86
	Br5	1		1.66		1.47		0.89
	Br4	–		–		–		–
P4	Te	11	2.20–2.29	2.24	1.77–1.96	1.88	0.79–0.88	0.84
	RK2	1		2.29		1.87		0.82
	RK1	8	2.34–2.62	2.44	1.91–2.16	2.04	0.80–0.91	0.84
	Ba	1		2.46		1.97		0.80
	Br5	2	2.34–2.44	2.39	1.98–2.11	2.04	0.85–0.86	0.85
	Br4	1		2.33		1.87		0.80
M1	Te	15	2.49–3.06	2.84	2.28–2.75	2.45	0.78–0.98	0.86
	RK2	1		3.23		2.56		0.79
	RK1	13	3.03–3.35	3.21	2.48–3.12	2.76	0.76–1.01	0.86
	Ba	2	3.14–3.31	3.22	2.91–3.15	3.03	0.88–1.00	0.94
	Br5	1		2.97		3.04		1.02
	Br4	1		3.17		2.51		0.79
M2	Te	4/5	2.11–2.27	2.20	2.73–2.89	2.79	1.23–1.35	1.27
	RK2	1		2.63		2.82		1.07
	RK1	2	2.46–2.52	2.49	2.79–3.00	2.89	1.13–1.19	1.16
	Ba	–		–		–		–
	Br5	1		2.54		2.86		1.13
	Br4	1		2.43		2.62		1.08
M3	Te	8	1.38–1.57	1.48	1.94–2.20	2.07	1.32–1.48	1.40
	RK2	–		–		–		–
	RK1	–		–		–		–
	Ba	1		1.87		2.39		1.28
	Br5	–		–		–		–
	Br4	1		1.54		2.02		1.31

*) in 'Beremend' only lower teeth were found.

Table 20 (b) Measurements of *Galemys kormosi* (Schreuder, 1940), upper teeth.

Description of the material from Baza.

For a description of the locality see de Bruijn, 1974.

i1 (1) A high narrow crown with a very long root. The crown strongly overhangs the root anteriorly. The median side is flat. A central rib, an inflated tip and a backward projection are missing. The root is curved backwards.

p2 (1) The tooth is relatively long and narrow. The enamel-dentine boundary rises steeply towards the anterior end of the crown. The lingual side is less convex than the labial side; both sides have a flat posterior face and a shallow posterior basin. The antero-labial corner of the crown is strongly flattened. The paraconid is well developed. The heavy but short posterior cingula widen conspicuously at the base of the posterocristid.

p4 (2) Figs. 12.5 and 71.2 The heavy crown is molarized to a certain extent. The crown overhangs the root postero-labially and forms a kind of flange. The postero-lingual face is concave; the wide talonid basin is moderately deep and lingually open. The paraconid is individualized. The metaconal rib is heavy. The posterocristid continues into a wide and high postero-lingual rim that borders the talonid basin. The short posterior cingulum runs along the flange.

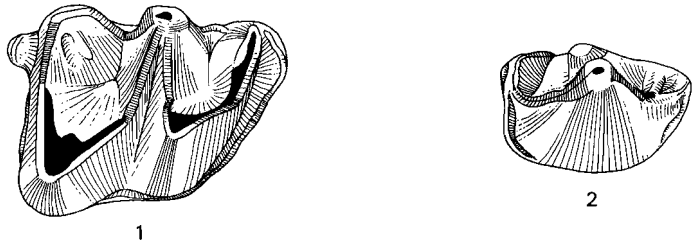


Fig. 71 *Galemys kormosi* (Schreuder, 1940)
1. m2 (dext), Ba-28
occlusal-labial view.
2. p4 (dext), Ba-17
occlusal-labial view.

C (1) The tooth has a small, relatively high crown. The lingual side is less convex than the labial one. The anterior and posterior cingula are heavy but very short; anteriorly the cingulum forms a short extension. Along the labial side is a wide cingulum. The lingual border is broken off.

P3 (1) Fig. 72.3 A small, blunt and rounded tooth. The tip of the crown is situated rather far anteriorly. The crown is biconvex with an ill-defined flat postero-lingual face and a shallow posterior basin. The lingual extension is inconspicuous, recognizable by a high cingular spur. The posterior cingula

and the antero-lingual cingulum are fairly weak and narrow. The tooth has two roots.

P4 (1) Fig. 72.2 A large, long and relatively narrow tooth. The postero-lingual and postero-labial faces are long and flat, the postero-lingual depression is shallow. The long anterior extension is partly formed by a continuation of the anterocrista. The posterocrista merges into the postero-lingual cingulum. The lingual lobe is wide; the protocone is long and heavy with a high connection to the paracone. Its anterior border is concave, the posterior border is straight. The postero-lingual cingulum runs to the tip of the protocone and is not connected to the narrow postero-labial cingulum. The anterior cingula are very short and wide; the protocone is bordered by an indistinct cingulum.

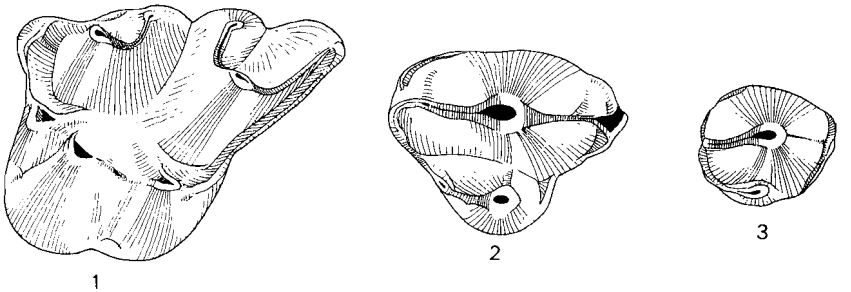


Fig. 72 *Galemys kormosi* (Schreuder, 1940)
1. M1 (sin), Ba-51
occlusal-lingual view.
2. P4 (dext) Ba-47
occlusal-lingual view.
3. P3 (dext), Ba-42
occlusal-lingual view.

Description of the material from Rebielice Królewskie 1.

For a description of the locality see Kowalski, 1960, 1964.

There are two foramina mentale with a fixed position, i.e. one under the c–p1 and another under the m1. Two foramina have a variable position under the p1–p2 and the p2–p4.

The position of the p3 is straight relative to the length axis of the jaw.

The P1 may be set slightly obliquely, the P3 more strongly obliquely in the maxilla.

p2 (3) A long and relatively narrow tooth. A slightly concave postero-lingual face and a talonid valley are present. The paraconid is weakly developed. The labial cingulum is wide and long and forms a small anterior bulge. Lingually the cingulum is missing.

p3 (2) The outline of the crown is rhombic due to an antero-labial and a postero-lingual flattening. The crown slightly overhangs the root postero-labially. This overhang forms a low flange. Postero-lingually a slightly concave face and a small talonid basin are present. The paraconid is well developed. A strong cingulum borders the flange.

p4 (18) The crown is large and high and has a postero-lingual overhang and a flange. At the base of the postero-lingual face is a long talonid basin that is lingually open. The paraconid is individualized. A small metacone or a metaconal rib is present in most specimens. The anterocristids ends in the lingual corner of the crown; the posterocristid merges into a high posterior rim that encloses the talonid basin. The cingulum is wide and missing along the lingual side only.

I1 (3) The top of the crown is either pointed or wide. The presence or absence of an antero-medial face depends on this feature. A weakly developed inner medial crest is present.

C (2) The small tooth has an elliptical outline. The cingulum is interrupted in the middle of the labial side only. A small cingular bulge is present anteriorly.

P2 (7) A large, rather symmetrical form. A flat postero-lingual face is present. The lingual extension is inconspicuous; it bears a weak cingular spur. The cingulum is interrupted in the middle of the labial and/or the lingual side. The tooth has two main roots and may have in addition a thin accessory rootlet.

P3 (8) In most specimens the crown shows a distinct lingual extension with a heavy cingular spur or a small bulge. A postero-lingual face is present; a basin is missing. The cingulum is similar to that in P2. A third root or a fused accessory rootlet is present in all specimens.

P4 (8) A wide tooth. The posterior faces are long, in particular the lingual one. Labially as well as lingually a posterior basin is present. The crown is somewhat elongated anteriorly. The lingual lobe is long and situated far anteriorly. Its short anterior border is concave; the long posterior border is straight. The protocone is well developed and individualized. The heavy cingulum surrounds the crown except for a short stretch along the anterior part of the lingual lobe.

Rebielice Królewskie 2.

No description is available of the small collection from Rebielice Królewskie 2.

Description of the material from Tegelen.

For a description of the locality see Freudenthal et al, 1976.

Two foramina mentale have a fixed position, i.e. the anterior one under c–p1 and the posterior one under the m1. Most specimens have a third foramen under the p4.

The position of the p3 is straight (3) or slightly oblique (1) relative to the length axis of the jaw. In the last case the anterior root is situated lingually.

i1 (5) Fig. 5.2 The narrow crown widens towards the cutting edge. The crown overhangs the root anteriorly. The labial side has a rather high crest; the medial crest is somewhat inflated. The postero-medial extension ends far posteriorly. The curved root is strongly compressed and medially grooved.

p2 (6) Fig. 10.5 A long and narrow tooth with a sub-rectangular outline. The enamel-dentine boundary rises towards the anterior end of the crown and is slightly curved upwards in the middle of the labial and the lingual sides. The crown is biconvex with a flat postero-lingual face and a short ill-defined talonid basin. The antero-labial flattening is pronounced. The paraconid varies from weak to strong and is situated far lingually. The fairly heavy posterior cingulum forms a small bulge at the base of the postero-cristid; the anterior cingulum is weak and short. The roots do not diverge.

p3 (4) Figs. 11.4 and 73.1 The very narrow crown has an elongated rhombic cross-section. The enamel-dentine boundary rises steeply towards the anterior end of the crown. The labial and lingual sides are convex; a vague postero-lingual face may be present. The antero-labial flattening is pronounced; an indistinct antero-lingual flattening may be present. The paraconid is well developed. The very short but strong posterior cingulum forms a small bulge.

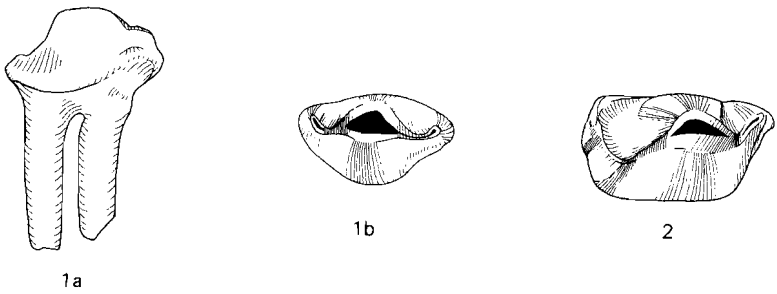


Fig. 73 *Galemys kormosi* (Schreuder, 1940)
1. p3 (reversed, sin), Te-561
a) labial view b) occlusal-labial view.
2. p4 (dext), Te-581
occlusal-labial view.

p4 (10) Figs. 14.2 and 73.2 A narrow tooth. The lingual side is less convex than the labial one; a flat or concave postero-lingual face is present. The deep and narrow talonid valley is open lingually. The paraconid is individualized. A metaconid or metaconal rib is present in some specimens, but missing in others. The extension of the posterocristid forms a high rim around the talonid, ending in an entoconid. Narrow anterior and posterior cingula are present.

I1 (4) Fig. 74 A strongly compressed tooth with a relatively short but high crown. The external anterior face is flat; the edge between the anterior and the labial faces is sharp and acute: the anterior tip of the crown is situated labially. The inner side is concave; a medial crest is present.

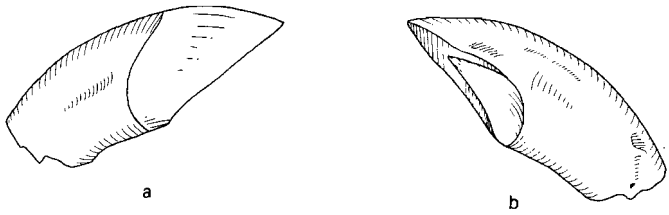


Fig. 74 *Galemys kormosi* (Schreuder, 1940)
I1 (reversed, sin), Te-661
a) labial view b) medial view.

C (9) Fig. 21.4 The crown is small and rather short, but wide. The labial side is convex, the lingual side slightly convex or flat; an ill-defined postero-lingual face is present in most specimens. The crown is surrounded by a wide cingulum or inflated zone that may be interrupted along the lingual side.

P2 (12) Figs. 23.4 and 75.2 A heavy, fairly long and narrow tooth with an elliptical or rounded outline. Both the labial and the lingual side are convex. Posterior faces are nearly always present, lingual and labial posterior basins less often. The lingual extension ranges from pronounced to missing; a low cingular spur is often found. The heavy but short anterior and posterior cingula are not connected. Some specimens have a small accessory rootlet, in others the posterior root is widened.

P3 (9) Figs. 24.4 and 75.3 The crown is relatively long and narrow; it has an irregular rhombic outline due to the flattening of the antero-labial and postero-lingual corners. The lingual and labial sides are convex with (rather) long posterior faces. The narrow lingual extension bears a cingular spur or an indistinct bulge. A posterior extension is either formed by the continuation of the posterocrista, which ends in a very small cuspule, or by the cingulum. The anterior cingulum is restricted to a lingual stretch that is often very wide

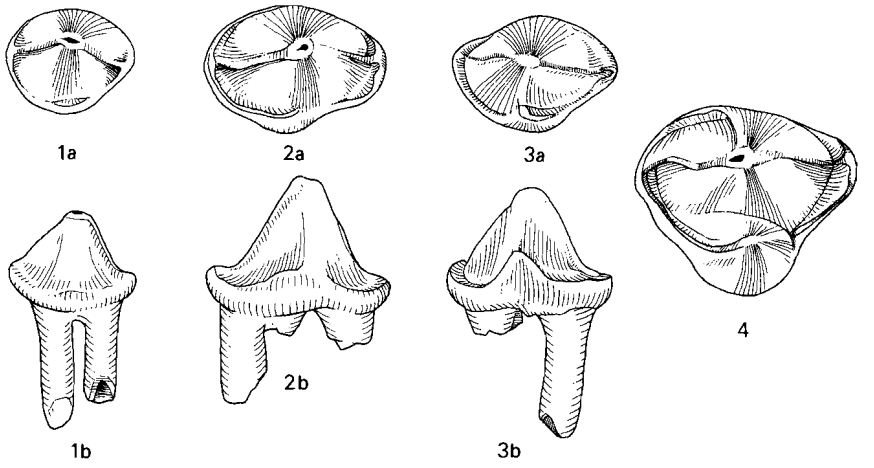


Fig. 75 *Galemys kormosi* (Schreuder, 1940)
1. P1 (reversed, sin), Te-741
a) occlusal-lingual view b) lingual view.
2. P2 (dext), Te-764
a) occlusal-lingual view b) lingual view.
3. P3 (sin), Te-782
a) occlusal-lingual view b) lingual view.
4. P4 (dext), Te-806
occlusal-lingual view.

and that may be connected to the spur. The posterior cingulum is long and of variable width.

P4 (11) Figs. 25.4 and 75.4 The labial side of the tooth is convex with a flat posterior face; the lingual side has a long concave posterior face and a short flat anterior one. The postero-lingual basin is rather small but deep. An anterior extension is formed by the cingulum, a posterior extension by the continuation of the posterocrista which often forms a small bulge. The lingual lobe, the protocone and the connecting ridge between the protocone and the paracone are modal. The anterior border of the lobe is concave, the posterior one more or less straight. The antero-lingual cingulum is heavy but short, ending at the base of the protocone. The postero-lingual cingulum is connected to the tip of the protocone. The labial cingula are short.

Galemys semseyi Kormos, 1913

Description of the material from Betfia 2, based on Kormos' (1913) description and the figures of the holotype.

For a description of the locality see Kretzoi, 1956.

p4 (1) A strongly molarized tooth. The enamel-dentine boundary rises towards the anterior end of the crown. A pronounced posterior face and a talonid basin are present. The paraconid and the metaconid are heavy and well individualized. The posterior cingulum is wide but short.

tooth	N	L	W	W/L
p4	1	2.10	1.10	0.52
m1	1	2.75	1.90	0.69
m2	1	2.50	1.80	0.72
m3	1	2.00	1.30	0.65

Table 21 Measurements of *Galemys semseyi* Kormos, 1913.

Desmana Gueldenstaedt, 1977

For the emended diagnosis and the differential diagnosis the reader is referred to pp. 96–97.

Desmana moschata (Linnaeus, 1758)

Emended diagnosis: the mean length of the p2 is about 2.24 mm, the mean length of the p3 is about 2.12 mm, the mean length of the p4 is about 2.71 mm; the p2/p3 ratio is about 1.06. The p1 is single-rooted.

The mean length of the C is about 2.33 mm, the mean length of the P2 is about 2.35 mm, the mean length of the P3 is about 1.96 mm; the P2/P3 ratio is about 1.20. The P1 is single-rooted.

The teeth are inflated and relatively low.

Differential diagnosis: the long p3, p4 and C distinguish *Desmana moschata* from the other *Desmana* species.

Measurements: see table 22.

Description, based on 7 specimens from various localities in the south western Republics of the U.S.S.R.

The usual number of foramina mentale is four. They have a variable position. Single foramina are found under c, p1, p3, p4 and m1, double foramina under p3 and m1.

The position of the p3 is oblique relative to the length axis of the jaw. The anterior root is situated lingually.

The position of the P3 is slightly oblique with the anterior root situated lingually.

i1 (13) The tooth is much smaller and lower than the very large i2. The

low crown does not feature a central rib or an inflated upper edge. The medial face is high and has a triangular outline. It shows a moderately high enamel-free area. The enamel of the crown strongly overhangs the anterior part of the root. The inner side of the crown bears an inconspicuous medial ridge.

p2 (14) The inflated crown has an egg-shaped cross-section. The enamel-dentine boundary curves upwards towards the anterior end of the crown. The inconspicuous posterior cingulum forms a small bulge. There is a narrow antero-lingual cingulum. The two roots diverge.

p3 (13) A low inflated crown with a somewhat rhombic cross-section, due to the postero-lingual flattening. The enamel-dentine boundary rises steeply towards the anterior end and less steeply towards the posterior end of the crown. An inconspicuous posterior cingulum forms, together with the posterocristid, an ill-defined bulge. There is a narrow antero-lingual cingulum.

p4 (14) The crown is plump and inflated. The posterior face is slightly concave. The enamel-dentine boundary curves upwards in the middle of the lingual and the labial side and rises towards the anterior end of the crown. A narrow, shallow talonid valley, which is open lingually, is present. There is usually a posterior cingulum. Anterior cingula are found in some specimens.

I1 (14) A large and high tooth. The antero-medial face is flat, the antero-labial face is very gently curved; the two faces meet under an obtuse angle.

tooth	N	L		W(2)		W(2)/L	
		range	mean	range	mean	range	mean
c	13	2.00–2.20	2.09	1.53–1.77	1.65	0.74–0.83	0.79
p1	13	1.69–1.89	1.82	1.50–1.68	1.61	0.86–0.94	0.89
p2	14	2.14–2.38	2.24	1.64–1.76	1.69	0.71–0.78	0.76
p3	13	1.95–2.23	2.12	1.68–1.85	1.75	0.78–0.88	0.83
p4	14	2.53–2.84	2.71	1.77–2.05	1.92	0.64–0.78	0.71
m1	14	3.58–3.98	3.79	2.71–3.10	2.98	0.74–0.84	0.79
m2	14	3.43–3.98	3.75	2.57–2.96	2.84	0.72–0.79	0.76
m3	14	3.09–3.36	3.23	1.96–2.23	2.04	0.59–0.68	0.63
C	13	1.86–2.67	2.33	1.64–1.86	1.75	0.62–0.92	0.75
P1	14	1.62–1.92	1.81	1.54–1.79	1.64	0.85–0.99	0.91
P2	14	2.18–2.48	2.35	1.70–1.97	1.85	0.77–0.81	0.79
P3	12	1.74–2.14	1.96	1.81–2.11	1.99	0.93–1.12	1.02
P4	13	3.12–3.53	3.36	2.79–3.05	2.91	0.84–0.96	0.87
M1	14	4.18–4.74	4.54	3.95–4.50	4.19	0.86–0.98	0.92
M2	14	3.35–3.69	3.56	4.48–5.04	4.68	1.22–1.38	1.31
M3	14	2.31–2.63	2.42	3.37–3.85	3.58	1.39–1.58	1.48

Table 22 Measurements of *Desmana moschata* (Linnaeus, 1758).

The tip of the crown is situated labially. A short medial ridge has been present on the inside of the crown, but has been worn away in most specimens. The enamel-free area on the medial face is high.

C (13) The crown is blunt and inflated, with an elliptical cross-section. The labial side is strongly convex, the lingual side less so. Weak and short anterior and posterior cingula may be present. The two strong roots are slightly divergent.

P2 (14) The crown is low, distinctly lower than the crown of the **C**. The tooth is of the same size or somewhat smaller than the **C**, otherwise the two teeth resemble each other strongly. The P2 has an oval or an elliptical cross-section. Both the labial and the lingual sides are convex, but they may feature an indistinct posterior face. The lingual extension is indistinct or missing. The anterior and posterior cingula are narrow and ill-defined. A small cingular bulge is present åt the postero-labial corner of the tooth. The two roots may be partly fused.

P3 (12) A short wide tooth with an irregular outline. The labial side is strongly convex, the lingual side is convex apart from a wide concave posterior face and an ill-defined flat anterior face. Cingular spurs are present at the postero-lingual and the postero-labial corner of the crown; there is a cingular bulge at the antero-lingual corner. The posterior cingulum is narrow. The two roots are (partly?) fused.

P4 (13) The tooth is strongly molarized. The crown is plump and rather low. There is a wide postero-lingual face and the basin at its base is large and deep. The anterior end of the crown is elongated by the cingulum. The posterocrista ends near the labial border of the crown in a very pronounced cusp. This means that the most posterior point of the crown is not situated at the base of the posterocrista, but further lingually. The cingulum – that partly encloses the basin – forms a low bulge. The lingual lobe is strongly connected to the paracone; the protocone is wide but very low. The tooth has three firm roots.

Desmana verestchagini Topachevski, 1961

Original reference: Topachevski (1961): Novyi pliotsenovykh vid vykhukholi iz predkavkazva (A new water-mole from the Pliocene). Paleontolocheskii Zhurnal, 4, pp. 131–137.

Emended diagnosis: The mean length of the p2 is about 1.80 mm, the mean length of the p3 is about 1.55 mm, the mean length of the p4 is about 2.10 mm; the p2/p3 ratio is about 1.16.

Supplementary diagnosis based on the material from Spilia 1: the p1 is single-rooted.

The mean length of the C is about 1.32 mm, the mean length of the P2 is about 2.00 mm, the mean length of the P3 is about 1.71 mm; the P2/P3 ratio is about 1.17.

The P1 is single-rooted.

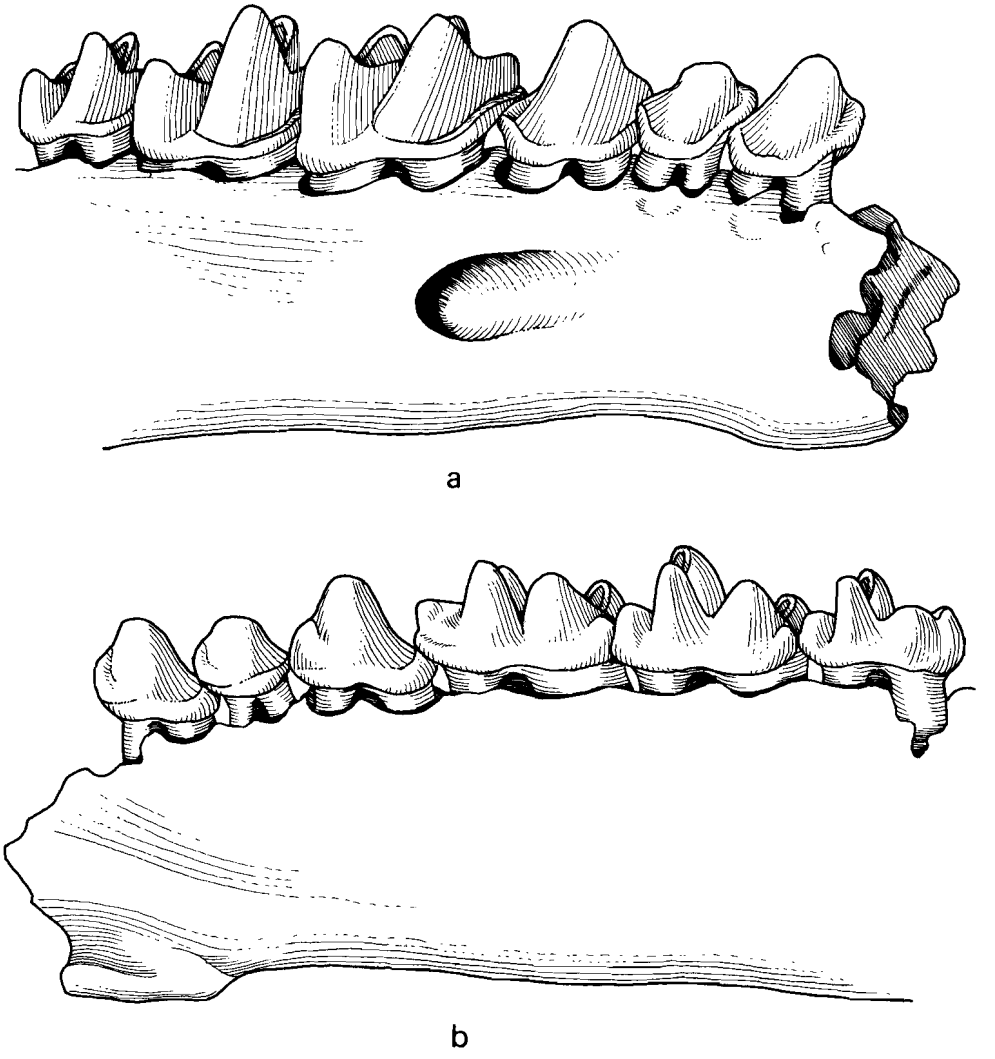


Fig. 76 *Desmana verestchagini* Topachevski, 1961
mandibular fragment with p2–m3 (dext), no. 26967, from Kosyakin Quarry (holotype). After Topachevski, 1961.
a) labial view b) lingual view.
X9

Differential diagnosis: the small size of all the selected teeth, in particular the p3 and the P3, distinguishes *Desmana verestchagini* from all other *Desmana* species.

Holotype: mandibular fragment with p2–m3 (Fig. 76).

Type locality: Kosyakin Quarry, Stavropol, U.S.S.R. For a description of the locality see Belyaeva in Gromova, 1968.

tooth	loc.	N	L		W(2)		W(2)/L	
			range	mean	range	mean	range	mean
c	Ks	–		–		–		–
	Pt1	7	1.23–1.38	1.32	0.82–0.92	0.88	0.62–0.70	0.67
	Ka	1		1.29		0.89		0.68
	Sp1	4	1.32–1.36	1.34	0.90–0.98	0.95	0.68–0.73	0.70
p1	Ks	–		–		–		–
	Pt1	9	1.03–1.22	1.11	0.81–0.91	0.88	0.75–0.83	0.80
	Ka	–		–		–		–
	Sp1	6/7	1.08–1.18	1.13	0.91–1.03	0.97	0.79–0.89	0.85
p2	Ks	1		1.80		1.35		0.75
	Pt1	15	1.81–2.01	1.90	1.05–1.17	1.10	0.54–0.61	0.58
	Ka	5	1.66–1.79	1.72	1.11–1.19	1.14	0.63–0.69	0.66
	Sp1	8	1.74–1.86	1.79	1.10–1.19	1.15	0.62–0.66	0.64
p3	Ks	1		1.55		1.15		0.74
	Pt1	20	1.40–1.64	1.51	1.00–1.23	1.12	0.68–0.83	0.74
	Ka	2	1.41–1.48	1.44	1.14–1.21	1.17	0.81–0.82	0.81
	Sp1	9	1.53–1.68	1.60	1.05–1.29	1.19	0.69–0.79	0.74
p4	Ks	1		2.10		1.40		0.67
	Pt1	24	1.85–2.02	1.94	1.14–1.37	1.26	0.61–0.71	0.65
	Ka	5	1.89–2.07	2.01	1.25–1.51	1.39	0.65–0.73	0.69
	Sp1	7	1.92–2.08	2.02	1.14–1.45	1.32	0.56–0.70	0.65
m1	Ks	1		2.75		2.10		0.76
	Pt1	16/17	2.29–2.48	2.39	1.89–2.15	2.01	0.80–0.91	0.84
	Ka	7	2.45–2.63	2.51	1.92–2.05	1.97	0.73–0.82	0.78
	Sp1	8	2.47–2.63	2.57	1.75–2.11	1.95	0.68–0.82	0.76
m2	Ks	1		2.55		1.95		0.76
	Pt1	12	2.21–2.37	2.30	1.72–1.87	1.80	0.75–0.82	0.78
	Ka	8	2.34–2.56	2.45	1.76–1.94	1.84	0.73–0.80	0.75
	Sp1	6	2.61–2.67	2.64	1.80–2.02	1.92	0.69–0.76	0.73
m3	Ks	1		1.80		1.40		0.78
	Pt1	5	1.70–1.84	1.77	1.30–1.37	1.32	0.72–0.77	0.75
	Ka	8	1.79–1.94	1.86	1.13–1.30	1.21	0.60–0.70	0.65
	Sp1	8	1.85–2.03	1.97	1.21–1.45	1.30	0.61–0.73	0.66

Table 23 (a) Measurements of *Desmana verestchagini* Topachevski, 1961, lower teeth.

Age of the type locality: Early Ruscian (MN 14).

Other localities with Desmana verestchagini: Spilia 1, Kardia and Ptolemais 1, all situated in northern Greece and of Early Ruscinian age.

Measurements: see table 23 (a) for the lower teeth and table 23 (b) for the upper teeth.

Description of the material from the type locality, based on the figured holotype in Topachevski, 1961, 1962.

The mandibular fragment shows a foramen mentale under the m1.

The position of the p3 is very slightly oblique relative to the length axis of the jaw with the anterior root situated lingually.

tooth	loc.	N	L		W		W/L	
			range	mean	range	mean	range	mean
C	Ks*)							
	Pt1	13	1.28–1.49	1.34	0.87–0.97	0.91	0.63–0.76	0.68
	Ka	–		–		–		–
	Sp1	5	1.21–1.45	1.32	0.94–1.00	0.96	0.69–0.79	0.73
P1	Pt1	12	1.17–1.30	1.23	0.91–1.04	0.97	0.74–0.84	0.79
	Ka	–		–		–		–
	Sp1	5	1.32–1.44	1.39	0.94–1.09	1.02	0.67–0.83	0.74
P2	Pt1	10	1.82–2.11	1.97	1.22–1.38	1.30	0.62–0.70	0.66
	Ka	2	1.91–2.01	1.96	1.20–1.30	1.25	0.63–0.65	0.64
	Sp1	4	1.92–2.07	2.00	1.26–1.55	1.42	0.66–0.75	0.71
P3	Pt1	17	1.42–1.70	1.56	1.26–1.50	1.41	0.77–1.01	0.91
	Ka	1		1.64		1.42		0.87
	Sp1	10	1.49–1.82	1.71	1.35–1.74	1.57	0.87–1.01	0.92
P4	Pt1	14	2.16–2.30	2.22	1.85–2.13	2.04	0.84–0.97	0.92
	Ka	1		2.58		2.13		0.83
	Sp1	3	2.53–2.59	2.57	2.07–2.17	2.11	0.83–0.84	0.83
M1	Pt1	9	2.79–3.00	2.87	2.39–2.72	2.55	0.82–0.96	0.89
	Ka	4	3.17–3.30	3.23	2.63–2.84	2.71	0.82–0.86	0.84
	Sp1	4	3.19–3.28	3.25	2.90–3.19	3.07	0.88–0.98	0.94
M2	Pt1	4	1.95–2.15	2.06	2.47–2.68	2.60	1.24–1.28	1.27
	Ka	3	2.35–2.48	2.40	2.87–3.10	2.99	1.22–1.28	1.25
	Sp1	6	2.28–2.46	2.37	2.83–3.18	3.03	1.24–1.32	1.28
M3	Pt1	5	1.39–1.49	1.44	1.86–2.05	1.95	1.31–1.39	1.36
	Ka	5	1.45–1.52	1.48	1.98–2.13	2.08	1.37–1.45	1.40
	Sp1	3	1.43–1.50	1.48	2.10–2.17	2.14	1.40–1.52	1.45

*) in Kosyakin only lower teeth have been found.

Table 23 (b) Measurements of *Desmana verestchagini* Topachevski, 1961, upper teeth.

p2 (1) Fig. 76 A heavy, rather low tooth. The enamel-dentine boundary rises towards the antero-labial corner of the crown. The tooth is biconvex with flat posterior faces and shallow posterior basins. Possibly the antero-labial corner is flattened. The paraconid is distinct but faintly individualized. The posterior and antero-lingual cingula are heavy and short. The roots are divergent.

p3 (1) Fig. 76 The tooth is shorter and lower than the p2. The enamel-dentine boundary rises steeply towards the antero-labial corner of the crown. The tooth is biconvex with flat posterior faces. Possibly the antero-labial corner is flattened. The paraconid is small and hardly individualized. The tooth is surrounded by a cingulum.

p4 (1) Fig. 76 A large and rather high tooth. The biconvex crown shows flat posterior faces and small posterior basins. The paraconid is strongly individualized. The anterior and posterior cingula are wide and long.

Descriptions of the material from Spilia 1

For a description of the locality see Armour Brown et al, 1977.

The mandible fragments available show that only two foramina mentale are present, i.e. one under the p1 and one under the m1.

In seven mandibles the position of the p3 is straight relative to the length axis of the jaw, in one specimen it is oblique, with the anterior root situated lingually.

i1 (6) The crown is small and narrow compared to the heavy, long root. The crown overhangs the root anteriorly. There is no central rib or inflated cutting edge. The posterior face is more or less flat, with a weak backward projection. The postero-medial cingulum is faint or missing.

p2 (8) Pl. 3, fig. 2 A large and high tooth. The enamel-dentine boundary is slightly curved upwards in the middle of the lingual and labial sides and rises faintly towards the anterior and posterior ends of the crown. Narrow, ill-defined posterior faces are present. A paraconid is usually missing. A small cusplet is formed at the base of the posterocristid. The anterior cingula are narrow, the posterior cingula wide and heavy.

p3 (9) Pl. 3, fig. 2 The heavy tooth features an overhang of the crown over the root on the labial side. The crown has a rhombic outline with an antero-labial and a postero-lingual flattening. The crown is biconvex with a short and flat postero-lingual face. The paraconid is high. The short wide posterior cingulum becomes heavier at the base of the posterocristid. The antero-lingual cingulum is faint or missing.

p4 (7) Pl. 3, fig. 2 The morphology of the crown is variable, but most specimens are strongly molarized. The straight posterior border is the widest

part of the crown. A concave postero-lingual face is always present, an ill-defined labial face is found in some specimens. The postero-lingual basin is a rather deep gully that may be open or closed lingually. A shallow basin may be present labially. The paraconid is fairly small; a metaconal rib is seldom present. The posterocristid merges into a high rim that may form a hypoconid and/or an entoconid. The cingula are short and weak.

I1 (4) Figs. 19.2 and 29.5/6 The tooth is moderately compressed. The external-anterior face is flat. The tip of the crown is situated medially. The inner side is flat or slightly concave; a medial crest is probably present. The inner enamel-dentine boundary is sharp.

C (5) The crown is small but high and sharp. The lingual side is less convex than the labial one. The enamel-dentine boundary curves upwards in the middle of the labial and the lingual sides. Some specimens feature a vague, flat postero-lingual face; a postero-lingual flange is present. The posterior and anterior cingula are weak and ill-defined.

P2 (4) A strongly molarized tooth with an elliptical cross-section. The labial side is more strongly convex than the lingual one. A concave postero-lingual face and a very small depression are present. The lingual extension is distinct in most specimens. The posterior cingulum is rather wide, labially longer than lingually, where it ends at the base of the lingual extension. The anterior cingula are extremely wide. The tooth has two main roots and an accessory rootlet on the lingual side.

P3 (10) A strongly molarized tooth with a sub-triangular cross-section. The labial side is more strongly convex than the lingual side. A concave or

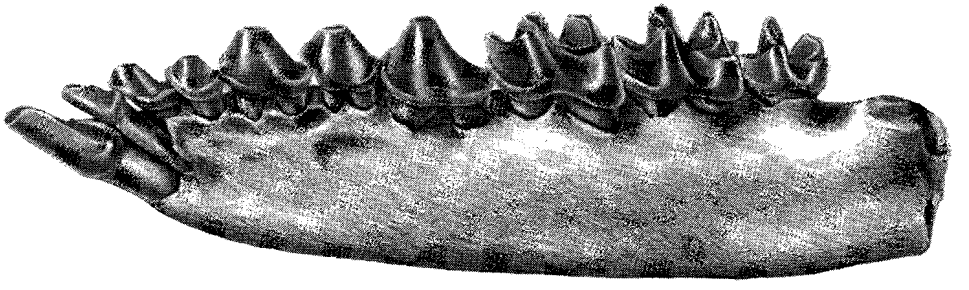


Plate 3 *Desmana verestchagini* Topachevski, 1961
mandibular fragment with i2–m3 (sin), Sp1–221
labial view. X 7

flat postero-lingual face is present. In some specimens the very pronounced lingual extension bears a high spur. The posterior cingula are long and heavy, the anterior cingula – which often bear a minuscule bulge – are short and heavy. The tooth has three roots, the lingual one of which is slightly weaker than the other two.

P4 (3) A strongly molarized tooth. The labial side is convex with a short concave posterior face, the lingual side is a little convex with a long flat posterior face. The postero-lingual basin is open posteriorly. The crown has a pronounced anterior extension that bears a large bulge. Posteriorly the posterocrista forms a distinct bulge. The lingual lobe is wide with a concave anterior border and a straight posterior border. The protocone is of medium height with a high connection to the paracone. The anterior and posterior cingula are wide, lingually shorter than labially. The postero-lingual cingulum forms two bulges before it ends at the base of the protocone.

Description of the material from Kardia.

For a description of the locality see van de Weerd, 1979.

There are two foramina mentale: the anterior one is situated under the c–p1, the posterior one under the m1.

The position of the p3 is either straight or very slightly oblique relative to the lenght axis of the jaw, with the anterior root placed lingually.

i1 (2) The crown of the narrow and low tooth overhangs the root anteriorly. A vague central rib is present. The posterior face is flat. The medial crest merges into a postero-medial extension.

p2 (5) The crown has a sub-rectangular cross-section with a straight posterior end. The enamel-dentine boundary rises steeply towards the anterior end of the crown. The crown overhangs the root labially. The lingual and labial sides are convex, apart from an ill-defined flat or concave face. There is a talonid basin. A faint paraconid is present. The posterior cingula are wide but short. The roots do not diverge.

p3 (2) The tooth has an irregular triangular outline, with a pointed anterior end and a wide, curved posterior border. The enamel-dentine boundary rises very steeply towards the anterior end of the crown. The tooth is biconvex with a flat postero-lingual face and a narrow talonid basin. The posterior cingulum is of variable width; a small bulge may be present.

p4 (5) Fig. 77.1 The tooth is strongly molarized. It has a subrectangular outline with a straight wide posterior border. The crown overhangs the roots labially, ending in a posterior flange. Both sides are convex with indistinct, flat or concave posterior faces. The shallow long talonid basin is divided by the posterocristid. The posterocristid continues as a wide crest that makes a

lingual curve and ends in the postero-lingual corner of the crown. It bears one or two cuspules, the hypoconid and the entoconid. The large paraconid is strongly individualized. Short posterior and antero-labial cingula are found in most specimens.

P2 (2) Fig. 77.2 The crown has an elongated oval cross-section. Both sides are convex, the lingual side shows a flat posterior face. A small basin is present at the base of the face. The lingual extension is inconspicuous: it bears no bulge and is not bordered by a cingulum. The cingula are wide, longer lingually than labially. The roots have not been preserved.

P3 (1) Fig. 24.3 The molarized tooth has a sub-triangular outline. Both sides are convex, the lingual side has a long, flat posterior face. The basin at its base is inconspicuous. The lingual extension is very strong – like the lobe of a P4 – and bears a high and heavy spur. Wide but rather short cingula are present posteriorly and antero-lingually. The tooth has three roots.

P4 (1) Figs. 25.5 and 77.3 A very large, distinctly molarized tooth. Both the anterior and posterior ends are strongly extended, but bear very inconspicuous cingular bulges. The labial and lingual sides are convex with flat posterior faces, the labial one of which is more distinct than the lingual one. The postero-lingual basin is long and deep. The lingual lobe is wide with a very large protocone. Its anterior border is strongly concave, the posterior border is straight. The posterior and anterior cingula are very heavy but

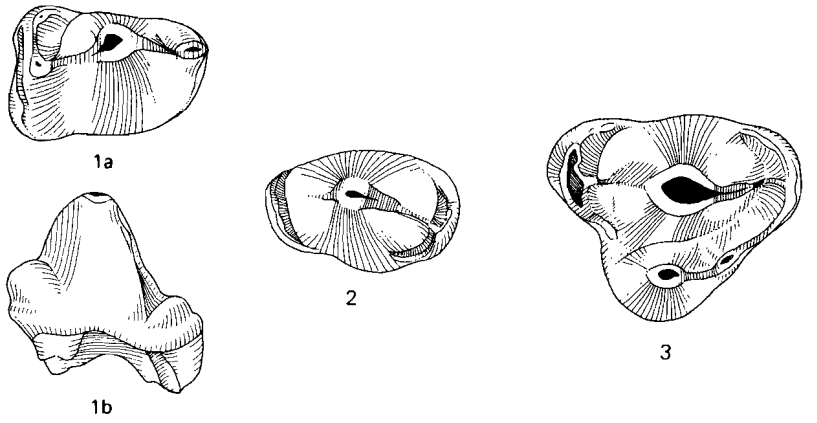


Fig. 77 *Desmana verestchagini* Topachevski, 1961
1. p4 (dext), Ka-1569
a) occlusal-labial view b) lingual view.
2. P2 (sin), Ka-1641
occlusal-lingual view.
3. P4 (sin), Ka-1661
occlusal-lingual view.

short. An exception is the postero-lingual cingulum, that is connected to the protocone. It forms a small bulge at the base of the protocone.

Description of the material from Ptolemais 1.

For a description of the locality see van de Weerd, 1979.

There are two or three foramina mentale present, one is situated under the p1, one under the p4 and the posterior one under the m1.

In the only mandibular fragment that shows the alveoles of the p3, the position of the tooth is straight relative to the length axis of the jaw.

i1 (5) A low tooth. The crown overhangs the root anteriorly. The central rib is faint but long. The posterior face is flat. It features a high medial crest that merges into a heavy bulge which is situated in the middle of the posterior border.

p2 (15) A long and relatively very narrow tooth. The enamel-dentine boundary rises steeply towards the anterior end of the crown. Both sides are somewhat convex. A small talonid valley is present at the base of the ill-defined, concave postero-lingual face. The posterior cingula are short, the anterior cingula short and weak or missing.

p3 (20) Fig. 11.5 A short and relatively wide tooth with an irregular outline. The crown overhangs the roots labially. The enamel-dentine boundary rises very steeply towards the anterior end of the crown. Both sides are convex; a concave postero-lingual face is present. A talonid basin is rarely found, as the postero-lingual corner is flattened in most specimens. The cingula are

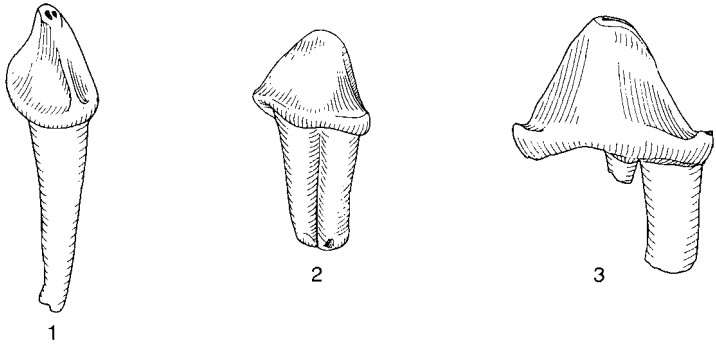


Fig. 78 *Desmana verestchagini* Topachevski, 1961
1. c (dext), Pt1-634
posterior-lingual view.
2. P1 (sin), Pt1-804
lingual view.
3. P2 (sin), Pt1-823
lingual view.

variable: the postero-lingual cingulum is fairly wide – otherwise they are narrow or missing.

p4 (24) Fig. 12.4 The outline of the crown is somewhat variable, but most specimens have a sub-rectangular cross-section. The tooth is molarized to a certain extent, with a weak paraconid, a sharp metaconal rib and a strong entoconid formed independently of both the continuation of the posterocristid and the cingulum. The labial side is convex; the lingual side features a strongly concave posterior face and a flat or concave anterior face. The very deep talonid basin may be open or closed lingually. The posterior cingulum is wide, the anterior cingula are narrow and short.

C (13) The crown is relatively narrow and strongly symmetrical. The enamel-dentine boundary is curved upwards in the middle of both sides. The lingual and labial sides are convex with flat posterior faces. The anterior and posterior cingula are ill-defined and (rather) short.

P2 (10) Figs. 23.5 and 78.3 A long and narrow crown with a sharp tip. Both the labial and the lingual sides are convex; the lingual side has a flat posterior face. There is no postero-lingual basin as the posterocrista ends rather far lingually. The lingual extension is distinct, bordered by a vague inflated zone. The posterior cingulum is longer and wider than the anterior one. The two roots are set wide apart; a thin accessory rootlet is present in most – probably in all – specimens.

P3 (17) The tooth is high and heavy with a very pronounced lingual lobe, which gives the crown a sub-triangular outline. The labial side is strongly convex; the lingual side is convex with an ill-defined flat posterior face. The posterocrista ends far lingually. The lingual lobe bears a very high lingual spur that ends on the slope of the paracone. In most specimens the wide and short posterior cingulum is situated labially of the base of the posterocrista. The anterior cingulum is wide and short. The tooth has three roots.

P4 (14) Fig. 25.6 The tooth has a very wide crown due to the large lingual lobe. The anterior extension is long, but the cingular bulge is low and ill-defined. The flat postero-lingual face is long, as is the deep valley at its base. The postero-labial face is somewhat concave. The protocone is low and strongly connected to the paracone. The anterior border of the lobe is concave, the posterior border more or less straight. In some specimens the postero-lingual cingulum, though low, forms a small bulge at the base of the protocone before it merges into this cusp. The postero-labial cingulum is short but high.

Desmana kowalskae n.sp.

Derivatio nominis: the species is named after the Polish paleontologist Barbara Rzebik-Kowalska.

Diagnosis: the mean length of the p2 is about 2.03 mm, the mean length of the p3 is about 1.84 mm, the mean length of the p4 is about 2.11 mm; the p2/p3 ratio is about 1.10. The p1 is single-rooted.

The mean length of the C is about 1.59 mm, the mean length of the P2 is about 2.17 mm, the mean length of the P3 is about 1.95 mm; the P2/P3 ratio is about 1.11. The P1 is double-rooted.

Differential diagnosis: the small C and P2 distinguish *Desmana kowalskae* from *D. nehringi,* the small p4 and P2 from *D. inflata,* and the overall size from the other *Desmana* species.

Holotype: mandibular fragment with p2–m3 (dext), no. 1204, (Fig. 79), stored in the Paleozoological Laboratory, Polish Academy of Sciences, Warsaw.

Type locality: Weze 1, Poland. For a description of the locality see Sulimski, 1959.

Age of the type locality: Middle Ruscinian (MN 15b).

Measurements: see table 24.

Description of the material from the type locality.

A small foramen mentale is present under the p2, and a larger one under the m1.

tooth	N	L		W(2)		W(2/L)	
		range	mean	range	mean	range	mean
c	–		–		–		–
p1	1		1.23		1.09		0.89
p2	3	1.98–2.11	2.03	1.24–1.31	1.27	0.62–0.63	0.62
p3	3	1.78–1.88	1.84	1.20–1.33	1.25	0.66–0.71	0.68
p4	4	1.83–2.24	2.11	1.23–1.46	1.37	0.62–0.67	0.65
m1	4	2.87–3.03	2.94	2.07–2.43	2.27	0.72–0.82	0.77
m2	4	2.63–2.95	2.77	2.04–2.24	2.08	0.73–0.78	0.75
m3	2	2.11–2.31	2.21	1.51–1.53	1.52	0.66–0.72	0.69
C	3	1.49–1.66	1.59	1.04–1.12	1.08	0.64–0.75	0.68
P1	2	1.44–1.52	1.48	1.18–1.25	1.21	0.82–0.82	0.82
P2	4	1.94–2.32	2.17	1.52–1.69	1.60	0.68–0.86	0.74
P3	5	1.86–2.01	1.95	1.50–1.73	1.62	0.79–0.88	0.83
P4	5	2.40–2.62	2.51	2.25–2.35	2.30	0.87–0.98	0.92
M1	3	3.70–3.85	3.78	2.68–3.53	3.11	0.71–0.95	0.82
M2	3	2.64–2.81	2.71	3.12–3.40	3.27	1.18–1.23	1.21
M3	1		1.73		2.46		1.42

Table 24 Measurements of *Desmana kowalskae* n.sp. from Weze 1.

The position of the p3 is straight or nearly straight relative to the length axis of the jaw.

The position of the P1 is straight, the position of the P3 strongly oblique.

p2 (3) Fig. 79 The tooth is relatively long and narrow and has a rhombic outline due to an antero-labial and a postero-lingual flattening. The lingual side is less convex than the labial one. A postero-lingual face is present. A cingulum is missing only along the labial side.

p3 (3) Fig. 79. The crown has a rounded outline with a slight postero-lingual flattening. The enamel-dentine boundary rises steeply towards the posterior and in particular the anterior end of the crown. The lingual side is rather convex and shows a concave posterior face; the labial side is strongly convex. The paraconid is under-developed. A postero-labial cingulum is present.

p4 (4) Fig. 79 The enamel-dentine boundary rises towards the anterior end of the crown. The tooth is biconvex with a concave postero-lingual face and a short talonid. The paraconid is indistinct; there is no metaconid or metaconal rib. The anterior and posterior cingula are rather wide.

I1 (2) A wide tooth with sharp anterior and posterior edges. The anterior face is slightly concave; the medial face is flat. The inner side is faintly concave and is bordered by a medial crest.

C (3) The crown is relatively long and narrow. The labial side is convex,

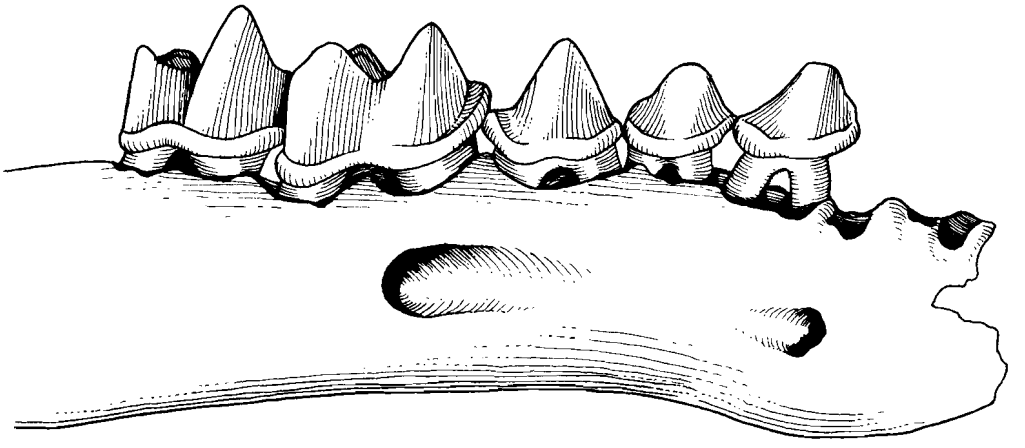


Fig. 79 *Desmana kowalskae* n.sp.
mandibular fragment with p2–m2 (dext), no. 1204 (holotype)
labial view. (redrawn).
X 9

the lingual side more or less flat. The anterior and posterior cingula are lingually connected. A postero-lingual bulge is present.

P2 (4) A relatively long and narrow crown with a faintly concave postero-lingual face. The lingual extension bears a cingular spur. The tooth has two roots.

P3 (5) The tooth has a sub-triangular outline – due to the distinct lingual lobe – with a convex labial border. A concave postero-lingual face is present. The protocone is low but well developed. A small bulge is formed by the anterior cingulum at the base of the anterocrista. The tooth has three roots.

P4 (5) The tooth is large and sturdy. The wide anterior cingulum is divided by the anterocrista, the posterior extension by the posterocrista. The lingual lobe is wide; the protocone is large with a high connection to the paracone. The postero-lingual cingulum is low.

Desmana nehringi Kormos, 1913

Original reference: Kormos, 1913: Trois nouvelles espèces fossiles des desmans en Hongrie. Ann. Mus. Nat. Hung., *XI,* pp. 135–145.

Original diagnosis: la p4 est grosse et trapue . . . Sur cette dent il se trouve devant la cuspide principale une petite élévation visible à la loupe: derrière la cuspide il y a une sorte de talon qui entourne la partie postérieure de la dent en forme d'arc. La molaire m1, de forme caractéristique, possède en avant deux, et en arrière quatre cuspides. . . . A côté de la deuxième cuspide antérieure et la quatrième cuspide postérieure on remarque un petit tubercle (1^{e} et 5^{e} cuspide); à partie de ces tubercles le collet de la dent est entouré sur ses parties antérieure et postérieure d'un bord en émail aigu. . . . Les 3^{e} et 4^{e} cuspides postérieures et la deuxième cuspide antérieure forment les pointes d'un triangle aigu qui contourne une petite cavité . . . .

Supplementary diagnosis based on material from Villany 3: the mean length of the p2 is about 2.04 mm, the mean length of the p3 is about 1.97 mm, the mean length of the p4 is about 2.38 mm; the p2/p3 ratio is about 1.04.

The mean length of the C is about 1.79 mm, the mean length of the P2 is about 2.56 mm, the mean length of the P3 is about 2.10 mm; the P2/P3 ratio is about 1.22. The P1 is double-rooted.

Differential diagnosis: the length of the C and the long P2 and P3 distinguish *Desmana nehringi* from all other *Desmana* species.

Holotype: mandibular fragment with p4–m1 (dext). The specimen – together with a second mandibular fragment with p4–m1 (sin), probably belonging to the same specimen as the holotype – was originally stored in the

tooth	loc.	N	L		W(2)		W(2)/L	
			range	mean	range	mean	range	mean
p2*)	Vi5	2	2.08–2.09	2.08	1.36–1.44	1.40	0.65–0.69	0.67
	Vi3	2	1.90–2.18	2.04	1.24–1.38	1.31	0.63–0.65	0.64
	RK1	–		–		–		–
	Hj	1		2.07		1.40		0.67
	'Br'	–		–		–		–
	Br1–3	–		–		–		–
p3	Vi5	–		–		–		–
	Vi3	4	1.90–2.05	1.97	1.28–1.30	1.29	0.63–0.68	0.66
	RK1	–		–		–		–
	Hj	1		1.82		1.47		0.82
	'Br'	1		2.06		1.34		0.65
	Br1–3	–		–		–		–
p4	Vi5	1		2.39		1.50		0.63
	Vi3	4	2.09–2.50	2.38	1.45–1.60	1.53	0.62–0.69	0.65
	RK1	2	1.99–2.20	2.09	1.47–1.53	1.50	0.67–0.77	0.72
	Hj	2	2.22–2.26	2.24	1.69–1.76	1.72	0.75–0.79	0.77
	'Br'	1		2.52		1.52		0.60
	Br1–3	1		2.30		1.50		0.65
m1	Vi5	–		–		–		–
	Vi3	5	2.84–3.21	3.09	2.30–2.55	2.39	0.72–0.83	0.78
	RK1	3	2.91–3.08	3.01	2.18–2.34	2.24	0.72–0.76	0.74
	Hj	1		3.23		2.87		0.89
	'Br'	–		–		–		–
	Br1–3	1		3.00		2.50		0.83
m2	Vi5	1		2.86		1.98		0.69
	Vi3	6	2.74–3.00	2.89	2.05–2.20	2.13	0.70–0.76	0.73
	RK1	4	2.75–2.97	2.90	1.91–2.06	2.02	0.69–0.70	0.69
	Hj	–		–		–		–
	'Br'	1		3.08		2.21		0.72
	Br1–3	–		–		–		–
m3	Vi5	–		–		–		–
	Vi3	4	2.14–2.20	2.17	1.39–1.60	1.48	0.65–0.73	0.68
	RK1	–		–		–		–
	Hj	–		–		–		–
	'Br'	1		2.31		1.47		0.64
	Br1–3	–		–		–		–

*) c and p1 are unknown.

Table 25 (a) Measurements of *Desmana nehringi* Kormos, 1913, lower teeth.

Natural History Museum in Vienna, but is apparently missing since some time.

Type locality: Beremend 1–3, Hungary. For a description see Kormos, 1913.

Age of the type locality: Early Villanyian (MN 16b).

Other localities with Desmana nehringi: "Beremend" (Hungary), Hajnácka (Czechoslovakia) and Rebielice Królewskie 1 (Poland), all of Early Villanyian age; Villany 3 and Villany 5 (Hungary), of Late Villanyian age.

Measurements: see table 25 (a) for the lower teeth and table 25 (b) for the upper teeth.

Description of the material from the type locality (the holotype), based on the descriptions and the figures given by Kormos, 1913.

A foramen mentale is present under the m1.

tooth	loc.	N	L		W		W/L	
			range	mean	range	mean	range	mean
C	Vi5	–		–		–		–
	Vi3	2	1.70–1.72	1.71	1.20–1.29	1.24	0.71–0.75	0.73
	RK1	1		1.79		1.35		0.75
	Hj*)							
	'Br'*)							
	Br1–3*)							
P1	Vi5	–		–		–		–
	Vi3	2	1.60–1.76	1.68	1.23–1.25	1.24	0.70–0.78	0.74
	RK1	2	1.69–1.81	1.75	0.99–1.30	1.14	0.59–0.72	0.65
P2	Vi5	–		–		–		–
	Vi3	2	2.55–2.58	2.56	1.75–1.80	1.77	0.68–0.71	0.69
	RK1	1		2.66		1.72		0.65
P3	Vi5	1		2.20		1.88		0.85
	Vi3	1		2.10		1.80		0.86
	RK1	2	2.07–2.08	2.07	1.60–1.74	1.67	0.77–0.84	0.80
P4	Vi5	1		2.60		2.25		0.87
	Vi3	–		–		–		–
	RK1	2	2.72–2.78	2.75	2.18–2.21	2.19	0.78–0.81	0.79
M1**)	Vi5	4	3.34–3.78	3.48	2.85–3.21	3.05	0.84–0.94	0.88
	Vi3	–		–		–		–
	RK1	3	3.78–4.09	3.90	3.12–3.59	3.33	0.81–0.88	0.85

*) from Hajnácka, 'Beremend' and Beremend 1–3 only lower teeth are known.
**) M2 and M3 are unknown.

Table 25 (b) Measurements of *Desmana nehringi* Kormos, 1913, upper teeth.

p4 (2) A heavy tooth. The crown overhangs the root labially. The labial side is strongly convex, the lingual side is flat with a concave posterior face. The talonid basin seems to be small and is lingually closed. The paraconid is inconspicuous; there is a small bulge at the base of the anterocristid. The posterior and antero-labial cingula are heavy.

Material from "Beremend"

The mandibular fragment with p3–p4, m2–m3 (sin), no. 61/1577 (3952) from an unspecified Beremend locality, mentioned by Kormos (1938), has been measured but not described by the author. The jaw is figured in Schreuder (1940): pl. IX, fig. 9.

Description of material from Villany 3, based on descriptions of Kormos and Schreuder and on figured specimens.

For a description of the locality see Jánossy, 1979.

Foramina mentale are present under the p1, under the p3–p4 and under the m1.

The position of the p3 and the P3 are oblique relative to the length axis of the jaw. The anterior root of the p3 is situated labially, the anterior root of the P3 lingually.

i1 (1) A small tooth.

p2 (2) A long tooth. A paraconid, though very small, is present. The posterior cingulum is well developed.

p3 (4) The small tooth has a narrow and low crown, the antero-labial corner of which is flattened. The enamel-dentine boundary rises somewhat towards the anterior end of the crown. The paraconid is moderately strong. The posterior cingulum is of variable length and width.

p4 (4) The heavy crown is biconvex with a concave postero-lingual face and a short talonid. The crown slightly overhangs the root postero-labially. The paraconid is well developed; a faint metaconid, an entoconid and a hypoconid are present. The posterior and antero-labial cingula are long and distinct.

C (2) The crown is small but high. The posterior and in particular the anterior cingula are distinct.

P2 (2) A long and heavy tooth that widens towards its posterior end without forming a distinct lingual extension. The cingulum, especially the posterior cingulum, is strong. The tooth has three roots, the accessory one being thin.

P3 (1) The tooth is more strongly molarized than the P2. The outline of the crown is sub-triangular due to the well developed lingual lobe which bears a protocone. A strong cingulum surrounds the crown and is interrupted in the middle of the labial side only. A cingular bulge is found at the base of the posterocrista. The tooth has three roots.

Description of material from Hajnácka, based on the description of Fejfar and the figured specimens.

For a description of the locality see Fejfar, 1964.

There are two foramina mentale; the anterior one is situated under the p1, the posterior one under the m1.

The position of the p3 is slightly oblique relative to the length axis of the jaw, with the anterior root situated lingually.

p2 (1) The rather heavy tooth has an elliptical outline. The enamel-dentine boundary rises towards the anterior end of the crown. The anterior and posterior cingula are long. The roots diverge.

p3 (1) The small but sturdy tooth has a sub-triangular outline with a wide posterior end. The enamel-dentine boundary rises somewhat towards the anterior and posterior ends of the crown. The antero-labial corner is flattened. A minuscule bulge may be present at the base of the posterocristid. The posterior cingulum is of normal width, lingually very long, labially shorter.

p4 (2) The small crown has a wide posterior end. A concave postero-lingual face and a talonid basin are present. The basin is lingually open. The posterocristid continues as a rim around the talonid and ends in a small entoconid in the postero-lingual corner of the crown. The paraconid is indistinct. A cingulum borders the low postero-labial corner. An antero-labial cingulum is present.

Description of the material from Rebielice Królewskie 1.

For a description of the locality see Kowalski, 1960, 1964.

In general two foramina mentale are present, the anterior one of which is situated under the p2 and the posterior one under the m1.

The position of the p3 is oblique relative to the length axis of the jaw, with the anterior root placed lingually.

The position of the P1 is straight or very slightly oblique, that of the P3 strongly oblique.

p4 (2) A heavy tooth. The crown is biconvex with a concave postero-lingual face. A paraconid and a metaconid are missing. The anterior cingulum is long and wide, but it forms only an inconspicuous bulge. The talonid is of medium length and is bordered by the long and strong posterior cingulum.

C (1) A small tooth. The crown is of the same size as that of the P1. The outline is elliptical. The labial side is more convex than the lingual side. The crown is surrounded by a cingulum that is interrupted in the middle of the labial side.

P2 (1) The tooth is relatively long and narrow, but possesses a distinct lingual extension of the crown. The outline is elongated-oval. The posterior cingulum is lingually connected to the anterior one. The tooth has two main roots and a well developed accessory one under the lingual extension.

P3 (2) The tooth is strongly molarized. It is rather long with a sub-triangular cross-section due to the wide lingual lobe. The lobe bears a small protocone and has a concave anterior border and a straight posterior one. The lingual cingulum is not connected to the protocone. The labial cingula are short.

P4 (2) The tooth is of moderate strength without an anterior extension or bulge. Both the lingual and the labial sides have flat or concave posterior and anterior faces. A long, shallow postero-lingual basin and a small postero-labial one are present. The lingual lobe is moderately wide, with a distinct protocone that is well connected to the paracone. The anterior border of the lobe is concave, the posterior border straight. The cingula are rather long; the lingual lobe is bordered by a weak cingulum that is not connected to the protocone.

Description of the material from Villany 5.

For a description of the locality see Jánossy, 1979.

The position of the p3 is oblique relative to the length axis of the jaw, with the anterior root situated labially.

p2 (2) A large and heavy but low tooth, which is only slightly smaller than the p4. The enamel-dentine boundary rises towards the anterior end of the crown. The antero-labial border is flattened. The talonid valley is fairly long. The anterocristid ends far lingually and consequently the paraconid is situated near the lingual corner. There is a small bulge at the base of the posterocristid. A short posterior cingulum is present. The two roots strongly diverge.

p4 (1) A very heavy, wide tooth. The labial side is very convex, the lingual side is flat. The narrow posterior face is slightly concave; the inconspicuous talonid basin is lingually open. The paraconid is moderately individualized. The posterocristid continues as a low lingual crest. The very short posterior cingulum is distinct, the antero-labial one narrow and short.

I1 (1) The tooth is long and narrow, more strongly curved dorsally than ventrally. The tip of the crown is blunt. The inner side of the crown is concave with a blunt medial crest. The enamel-free zone on the medial face is very high.

P3 (1) A sturdy, rather large and high tooth. Both sides are convex without a posterior face. The lingual extension is pronounced, but bears no bulge or cingular spur. The crown is surrounded by a strong cingulum that is missing along the middle of the labial side only.

P4 (1) Both the labial and the lingual sides are convex. The labial side features a short and flat posterior face, the lingual side a long and concave face. The posterocrista is faintly inflated at its base. The lingual lobe is wide, the protocone heavy but low, with a high connection to the paracone. The anterior and posterior borders of the lobe are concave. The anterior and posterior cingula are strong, longer lingually than labially, but not connected to the protocone.

Desmana thermalis Kormos, 1930

Original reference: Kormos, 1930: *Desmana thermalis,* n.sp., eine neue präglaziale Bisamspitzmaus aus Ungarn. Ann. Mus., Nat., Hung., *XXVII,* pp. 1–19.

Synonymy: *Desmana tegelensis* Schreuder, 1940
Desmana crassidens Kretzoi, 1953
Desmagale pannonica Kretzoi, 1953

Original diagnosis (Schreuder, 1940): . . . Height of dentition as in *D. m. moravica,* but cingulum more extended and sharply defined. Premolars rel. larger than in the latter. Single root of P1 vertically grooved, sometimes also the post. root of P2. P3 quadratic, the two roots more or less fused, in the latter case the post. root may show a groove. P4 more trenchant than in subspecies of *D. moschata.* M1 with rather long cutting edge. Lower jaw somewhat more slender and flat than in *D. moschata* and its fossil subspecies. . . . Mental foramina two. i1 slender. Paraconid of p2 absorbed in main cusp. Roots of p3 obliquely set, or straight in the row, but then compressed from before backward. p4 more trenchant than in the other forms, with vestigial paraconid and broad heel. . . .

Emended diagnosis: the mean length of the p2 is about 2.32 mm, the mean length of the p3 is about 1.86 mm, the mean length of the p4 is about 2.55 mm; the p2/p3 ratio is about 1.25. The p1 is single-rooted.

The mean length of the P2 is about 2.32 mm, the mean length of the P3 is about 1.94 mm; the P2/P3 ratio is about 1.36. The P1 is single-rooted.

Supplementary diagnosis based on material from Tegelen: the mean length of the C is about 2.25 mm.

Differential diagnosis: the long p2 and the short P3 distinguish *Desmana thermalis* from *D. nehringi,* the short p3 and p4 from *D. moschata.* The long P2 distinguishes the species from *D. inflata.*

Holotype: maxillary fragment with P2–M3 (sin), (Fig. 80).

Type locality: Betfia 2 (formerly named Püspökfürdö), Roumania.

Age of the type locality: Early Biharian (Early Pleistocene).

Other localities with Desmana thermalis: Tegelen (the Netherlands) and Kisláng (Hungary), both of Late Villanyian (MN 17) age.

Measurements: see table 26 (a) for the lower teeth and table 26 (b) for the upper teeth.

Description of the material from the type locality.

For a description of the locality see Kretzoi, 1956.

There are two foramina mentale present, one under the i3 and one under the m1.

The position of the p3 is straight or very slightly oblique relative to the length axis of the mandible.

The position of the P3 is slightly oblique with the anterior root situated labially.

tooth	loc.	N	L		W(2)		W(2)/L	
			range	mean	range	mean	range	mean
c	Be	–		–		–		–
	Ki	–		–		–		–
	Te	13	1.63–2.02	1.86	1.24–1.50	1.35	0.67–0.78	0.73
p1	Be	–		–		–		–
	Ki	–		–		–		–
	Te	19	1.37–1.70	1.52	1.20–1.47	1.37	0.79–0.99	0.90
p2	Be	3	2.20–2.40	2.32	1.57–1.60	1.59	0.67–0.71	0.69
	Ki	2	2.21–2.29	2.25	1.52–1.52	1.52	0.66–0.69	0.67
	Te	12	1.92–2.31	2.19	1.33–1.54	1.47	0.63–0.72	0.67
p3	Be	1		1.86		1.84		0.99
	Ki	–		–		–		–
	Te	12	1.86–2.18	1.98	1.37–1.67	1.54	0.68–0.89	0.78
p4	Be	3	2.41–2.63	2.55	1.73–1.81	1.76	0.66–0.72	0.69
	Ki	1		2.32		1.71		0.74
	Te	17/16	1.99–2.50	2.30	1.48–1.87	1.65	0.67–0.80	0.72
m1	Be	3	3.37–3.61	3.49	2.48–2.63	2.55	0.73–0.74	0.73
	Ki	–		–		–		–
	Te	11	2.67–3.38	3.10	2.11–2.76	2.52	0.75–0.88	0.81
m2	Be	2	2.98–3.31	3.14	2.34–2.59	2.46	0.78–0.79	0.78
	Ki	–		–		–		–
	Te	12	2.80–3.47	3.09	2.10–2.60	2.39	0.72–0.82	0.77
m3	Be	1		2.63		1.95		0.74
	Ki	–		–		–		–
	Te	13	2.24–2.62	2.45	1.37–1.77	1.59	0.61–0.70	0.65

Table 26 (a) Measurements of *Desmana thermalis* Kormos, 1930, lower teeth.

i1 (1) The tooth is at the cutting edge slightly wider than at the base.

p2 (3) A large tooth, hardly smaller than the p4, with a sub-triangular outline due to the wide and straight posterior border. The enamel-dentine boundary rises somewhat towards the anterior end of the crown. Both sides are convex with an ill-defined flat posterior face. There is no paraconid. The posterior cingulum is of moderate width, the anterior one is weak. The roots are divergent.

p3 (1) A rather small, compact tooth. The cross-section is rhombic. The posterior and lingual cingula are strong. The two roots are set close together.

p4 (3) A heavy compact tooth with a wide posterior border. The crown slightly overhangs the root postero-labially, resulting in a low flange. Both sides are convex, the lingual side featuring a narrow concave posterior face.

tooth	loc.	N	L		W		W/L	
			range	mean	range	mean	range	mean
C	Be	–		–		–		–
	Ki	–		–		–		–
	Te	14	1.98–2.49	2.25	1.39–1.63	1.49	0.61–0.78	0.66
P1	Be	–		–		–		–
	Ki	–		–		–		–
	Te	10	1.60–1.83	1.71	1.41–1.65	1.56	0.77–1.03	0.91
P2	Be	2	2.40–2.56	2.47	1.66–1.90	1.77	0.65–0.78	0.72
	Ki	1		2.32		1.88		0.81
	Te	10	2.32–2.61	2.46	1.59–1.79	1.69	0.61–0.71	0.69
P3	Be	2	1.75–1.90	1.82	1.71–1.80	1.75	0.90–1.03	0.96
	Ki	1		1.94		1.89		0.97
	Te	8	1.69–2.04	1.90	1.60–2.01	1.75	0.85–0.99	0.92
P4	Be	2	3.04–3.10	3.07	2.48–2.75	2.61	0.82–0.89	0.85
	Ki	–		–		–		–
	Te	12	2.68–3.27	2.95	2.25–2.50	2.37	0.76–0.85	0.81
M1	Be	2	4.18–4.20	4.19	3.43–3.70	3.56	0.82–0.88	0.85
	Ki	–		–		–		–
	Te	11	3.66–4.02	3.83	3.04–3.47	3.26	0.76–0.91	0.85
M2	Be	2	2.85–2.87	2.86	3.70–3.99	3.84	1.30–1.39	1.34
	Ki	–		–		–		–
	Te	8/9	2.60–3.10	2.80	3.27–3.87	3.60	1.21–1.38	1.29
M3	Be	1		2.00		2.90		1.45
	Ki	–		–		–		–
	Te	10	1.68–2.12	1.89	2.45–2.91	2.70	1.34–1.50	1.44

Table 26 (b) Measurements of *Desmana thermalis* Kormos, 1930, upper teeth.

The talonid basin is inconspicuous and lingually open. The paraconid may be individualized. A vague metaconal rib is present. The posterocristid continues along the postero-lingual border without forming a hypoconid or an entoconid. The posterior cingulum is of moderate width, the anterior cingula are weaker and stronger labially than lingually.

P2 (3) Fig. 80.1 A stout and smooth tooth with an elongated elliptical outline. The labial side is convex, the lingual side convex with a flat posterior face. The lingual extension is inconspicuous, without a cingular spur or bulge. Short but very pronounced lingual cingula are present. The tooth has two roots, the posterior one of which is widened.

P3 (2) Fig. 80.1 The heavy crown has a rounded cross-section. The tooth is biconvex with a rather long, flat postero-lingual face. The lingual extension is more pronounced than in the P2 and bears a heavy cingular spur. The patchy postero-labial cingulum is connected to this spur. The antero-lingual cingulum is long and narrow. It is not possible to see whether the tooth has a very wide posterior root or one round root and a thin accessory one. The latter seems more probable.

P4 (2) Fig. 80.1 The tooth is strongly molarized, in contrast to the smooth P2 and P3. The anterior extension is extremely long but low. It bears a cingular rim but no bulge. A postero-labial extension of the crown is formed by a large cuspule which is part of the continuation of the postero-crista. The lingual lobe is wide; the large but low protocone is strongly connected to the paracone. The anterior border of the lobe is long and either straight or concave; the posterior border is short and convex. At the base of the long and flat postero-lingual face is a deep basin that is bordered by a high and heavy rim. There is a narrow and steep gully situated postero-labially. The anterior cingula are long and of medium width; the posterior cingula are shorter and wider.

Description of material from Tegelen.

For a description of the locality see Freudenthal et al, 1976.

There are two foramina mentale, the anterior one being situated under the c–p1, the posterior one under the m1.

The position of the p3 is straight relative to the length axis of the mandible in two specimens, slightly oblique in two specimens and strongly oblique in one specimen. In the last three cases the anterior root is situated lingually.

p2 (12) Fig. 10.6; Pl. 4, fig. 5 A large, smooth tooth. The enamel-dentine boundary rises towards the anterior end of the crown. The lingual side is less convex than the labial side and features a flat posterior face in some specimens. The posterior cingulum is short and narrow; anterior cingula – if present – are inconspicuous. The roots are divergent.

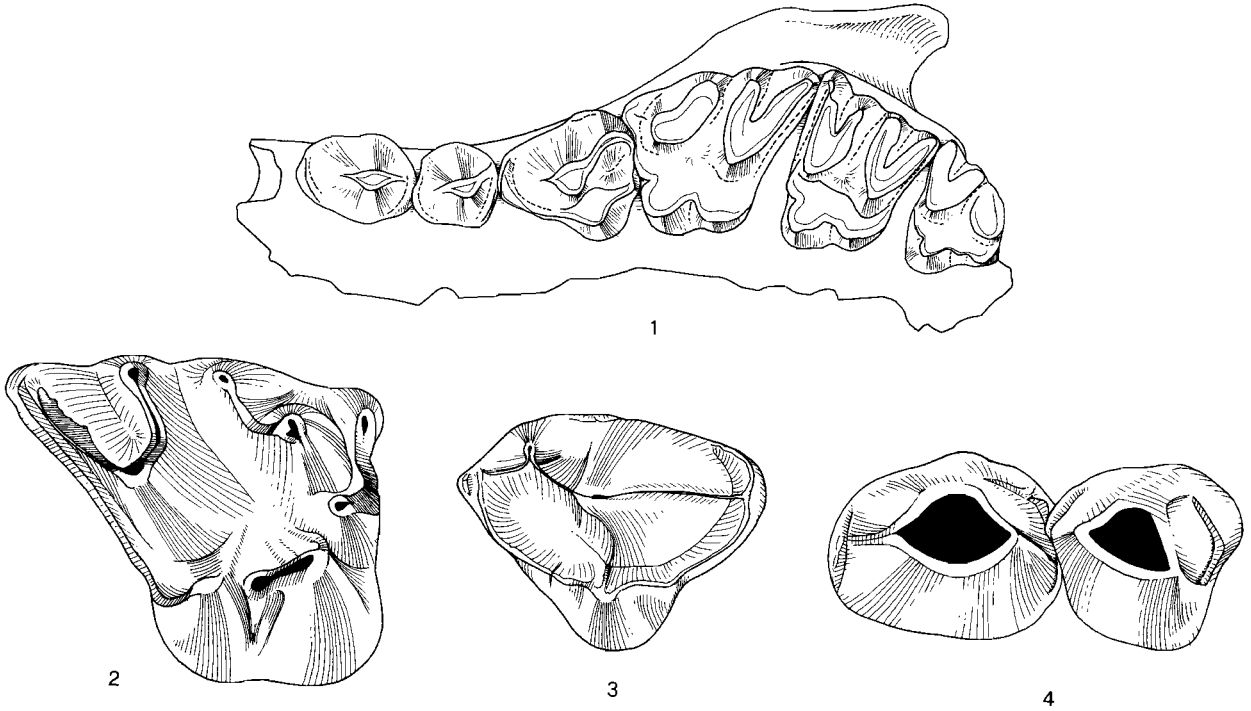


Fig. 80 *Desmana thermalis* Kormos, 1930
1. P2–M3 (sin), Betfia 2 (no. ob/4742) (holotype) occlusal-lingual view.
2. M1 (dext), Te-384 occlusal-lingual view.
3. P4 (dext), Te-396 occlusal-lingual view.
4. P2–P3 (dext), Kisláng occlusal-labial view.
(fig. 80.1 by J.W.F. Reumer, X 6.3).

p3 (12) Fig. 81.2; Pl. 4, fig. 5 The tooth is heavy and smooth and has usually a rhombic outline due to an antero-labial and a postero-lingual flattening of the biconvex crown. The enamel-dentine boundary rises steeply towards the anterior end of the crown. The crown slightly overhangs the root along the labial side. The short postero-lingual face is flat or concave. The postero-lingual cingulum is short and high, otherwise the cingula are similar to those found in the p2.

p4 (17) Fig. 81.3; Pl. 4, fig. 5 The smooth tooth is of variable size; in general the shape resembles that of the p2. The lingual side is less convex than the labial one and features a narrow, strongly concave posterior face. The talonid basin is narrow and lingually open. An ill-defined metaconal rib is present. The posterocristid may continue as a high rim that borders the talonid valley and ends near the lingual corner. An entoconid is nearly always present. The posterior cingulum is narrow and short; anterior cingula – if present – are indistinct.

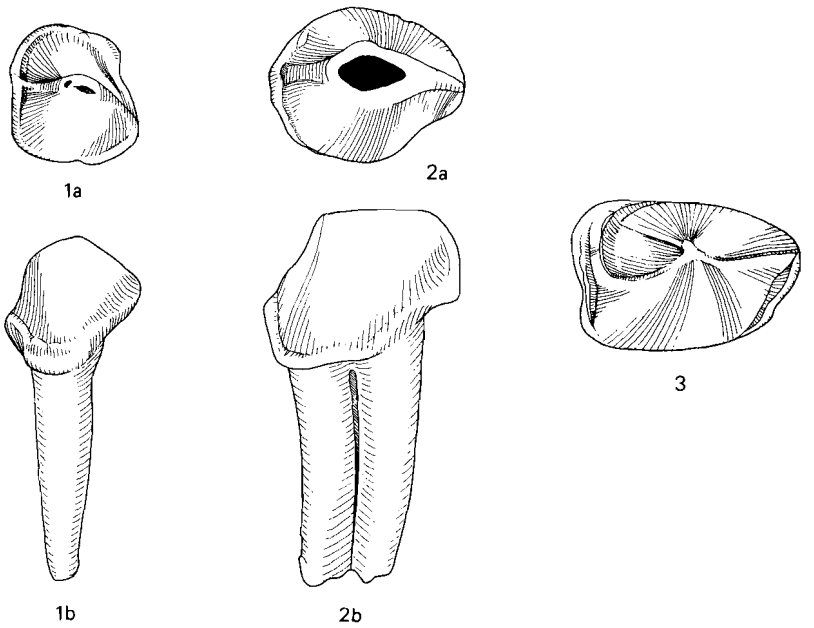


Fig. 81 *Desmana thermalis* Kormos, 1930
1. p1 (dext), Te-81
a) occlusal-labial view b) labial view.
2. p3 (dext), Te-121
a) occlusal-labial view b) labial view.
3. p4 (dext), Te-144
occlusal-labial view.

I1 (10) Figs. 19.3, 29.7 and 82.1/2 A large flat tooth. The dorsal border is strongly curved, the ventral border less so. The narrow anterior face is flat with rounded borders. The inner side of the crown is concave with a high but rather short medial crest. The enamel-free area on the medial face is very high.

C (14) Figs. 21.6 and 82.3 A variable tooth. In general the crown is high

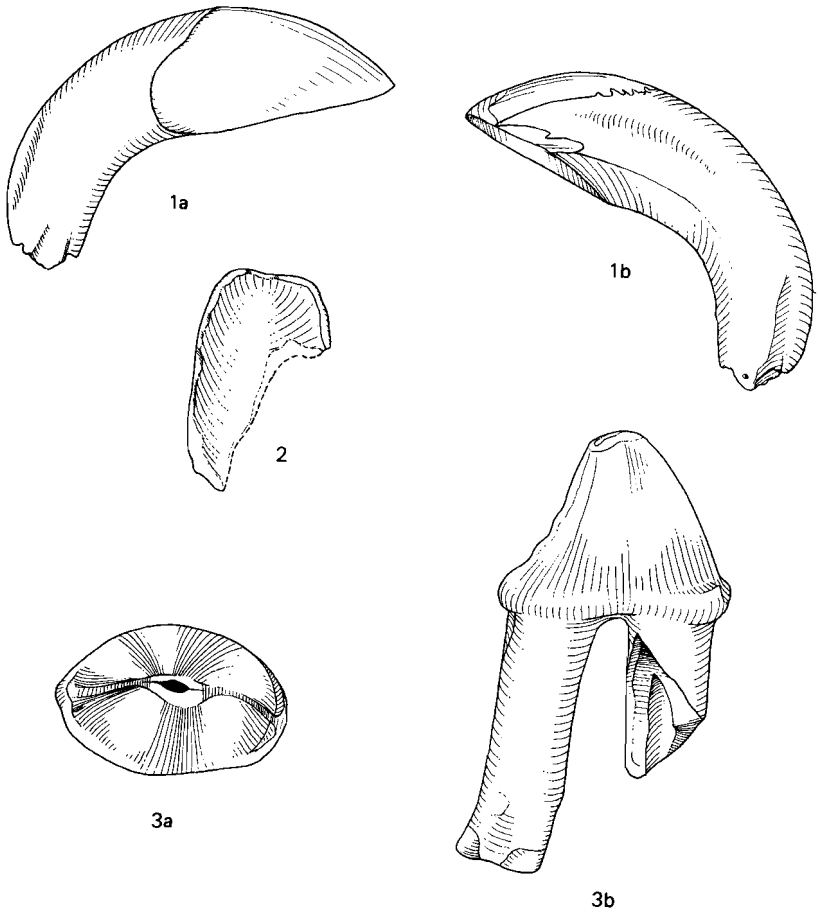


Fig. 82 *Desmana thermalis* Kormos, 1930
1. I1 (dext), Te-221 (X9)
a) labial view; b) medial view.
2. I1 (sin), Te-230
inner view.
3. C (dext), Te-282
a) occlusal-lingual view b) lingual view.

and long – but relatively narrow – with an elliptical outline. The labial side is strongly convex, the lingual side is flat. The short anterior and posterior cingula are usually indistinct.

P2 (10) Fig. 23.6 A heavy tooth that is molarized to a certain extent. The crown widens towards its posterior end without forming a distinct lingual extension; one specimen bears a cingular spur. A concave posterior face is always present lingually, postero-labially a flat face is found in many specimens. A round lingual basin is present. The anterior and posterior cingula are of medium length and width. The tooth has usually two roots, the posterior one of which may be broad. Two specimens have an accessory rootlet which is partly fused to the posterior root.

P3 (8) Figs. 24.6 and 83.3 The very sturdy low tooth has an irregular outline. Both sides are convex, with an ill-defined posterior face lingually and sometimes labially as well. Although the lingual extension is not distinct, a heavy cingular spur is present postero-lingually; in some specimens there is a second – labial – spur. Cingula border the posterior extension; the anterior cingula are faint and short. The tooth has three roots, the lingual one of which varies in strength.

P4 (12) Figs. 25.8 and 80. A rather narrow, high tooth. The postero-lingual face is long and straight; the anterior faces are flat. Anteriorly the crown is extended by the cingulum, which may form a large bulge. The posterocrista turns to the labial side and forms a large isolated metacone. The lingual extension is wide with a low protocone which is strongly connected to the paracone. The anterior border of the lobe is concave, the posterior one straight. The posterior cingulum is not connected to the metacone, but forms a small bulge at its base; lingually the cingulum is connected to the protocone. On the labial side there is a small cingular bead at the base of the gully between the paracone and the metacone. The anterior cingulum, though very wide, is rather short.

Description of the material from Kisláng (see Kretzoi, 1953).

There are at least two foramina mentale, the anterior one of which is situated under p1–p2, the posterior one under p4–m1. A third one may be present under p3–p4.

The p1 is single-rooted. The position of the p3 is straight relative to the length axis of the mandible.

The position of the P3 is slightly oblique with the anterior root situated lingually.

p2 (2) Pl. 4, figs. 2 and 3 A short and relatively wide tooth. The enamel-dentine boundary may curve upwards in the middle of the labial side. Both

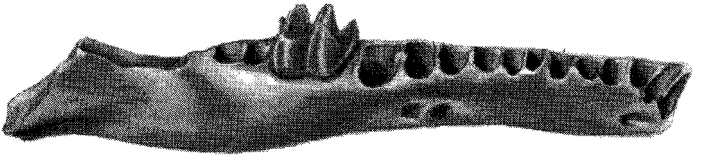
Plate 4 *Galemys kormosi* (Schreuder, 1940)

1. mandibular fragment with m2 (dext), Te-625, labial view

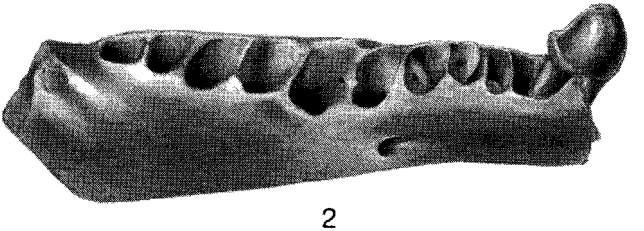
Desmana thermalis Kormos, 1930

2. mandibular fragment with p2 (sin, reversed), Kisláng, labial view
3. mandibular fragment with p2, p4 (dext), Kisláng, labial view
4. mandibular fragment with trigonid of m1 (dext), Kisláng, labial view
5. mandibular fragment with p2–m3 (dext), Te-106, occlusal-labial view

X 4.5



1



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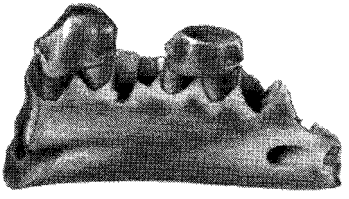

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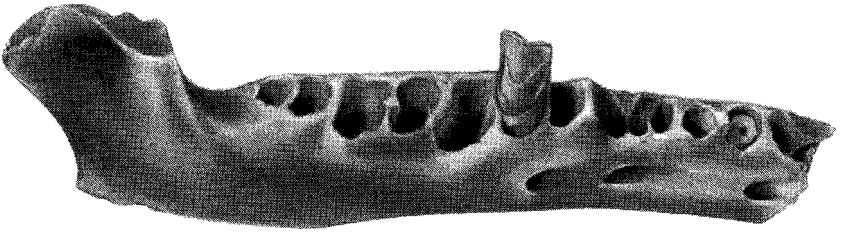

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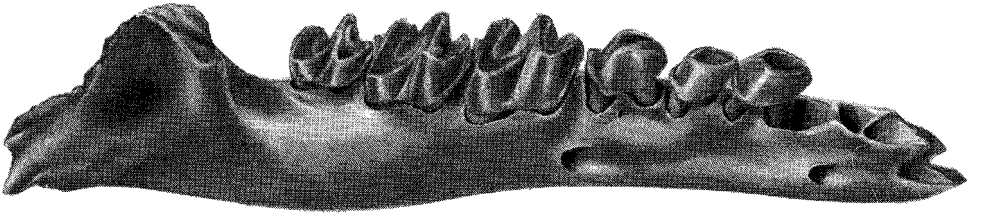

5

the labial and the lingual sides are convex; the lingual side features a flat posterior face. The posterior cingulum is high and wide, in particular at the base of the posterocristid. The anterior cingulum is short and narrow. The two roots diverge.

p4 (1) Pl. 4, fig. 3 A short and relatively wide tooth. The labial side is convex with a concave posterior face. There is a talonid valley. The cingulum, which partly encloses the talonid basin, is of medium height. The anterior cingulum is narrow and rather low.

P2 (1) Fig. 80.4 A stout tooth with an irregular outline. Both the labial and the lingual sides are strongly convex with flat anterior and posterior faces. There is no lingual extension, but the crown widens towards its posterior end. A short but heavy cingulum is present anteriorly. The long postero-lingual cingulum is very high and wide; the postero-labial cingulum is short and narrow. In all probability the tooth has three roots.

P3 (1) Fig. 80.4 The stout tooth is short and wide and has an irregular outline. Both the labial and the lingual side are strongly convex. There is a long, concave postero-lingual face with a narrow basin at its base. There is no lingual extension, instead the very wide posterior border features a lingual and a labial extension. The postero-lingual cingulum is wide and strong; the antero-lingual cingulum is shorter. In all probability the tooth had three roots.

Desmana inflata n.sp.

Original reference: Desmana nehringi in Mein et al, 1978: Les formations continentales du Néogène supérieur des Vallées du Júcar et du Cabriel au NE d'Albacete (Espagne). Biostratigraphie et environnement. Docum. Lab. Géol. Fac. Sci. Lyon, *72*, pp. 99–147.

Derivatio nominis: the name refers to the inflated teeth which are characteristic for the species.

Diagnosis: the mean length of the p2 is about 1.97 mm, the mean length of the p3 is about 1.84 mm, the mean length of the p4 is about 2.24 mm; the p2/p3 ratio is about 1.07. The p1 is single-rooted.

The mean length of the C is about 1.55 mm, the mean length of the P2 is about 2.31 mm, the mean length of the P3 is about 1.95 mm; the P2/P3 ratio is about 1.18. The teeth are low and inflated. The P1 has one or two roots.

Differential diagnosis: Desmana inflata differs from *D. verestchagini* by its lower p2/p3 ratio; from *D. kowalskae* by its long p4 and P2; from *D. nehringi* by its shorter p2, C and P2; from *D. thermalis* by its shorter p2 and C and from *D. moschata* by its overall smaller size.

Holotype: a maxillary fragment with P2–P3 (sin), V2a-271, (Fig. 86.2), stored in the collections of the Department of Earth Sciences, University Claude Bernard, Lyon 1, France.

Type locality: Valdeganga 2a, Province of Albacete, Spain. For a description of the Valdeganga section see Mein et al, 1978.

Age of the type locality: Late Villanyian (MN 17).

Other localities with Desmana inflata: Valdeganga 1, Valdeganga 2b, Valdeganga 2e, Valdeganga 3 and Valdeganga 4, all situated in the same section and of Late Villanyian age.

Measurements: see table 27 (a) for the lower teeth and table 27 (b) for the upper teeth.

Description of the material from the type locality.

The position of the p3 and the P3 is slightly oblique, with the anterior root placed lingually.

i1 (5) Fig. 84.1 The tooth has a very small crown and a heavy, long root.

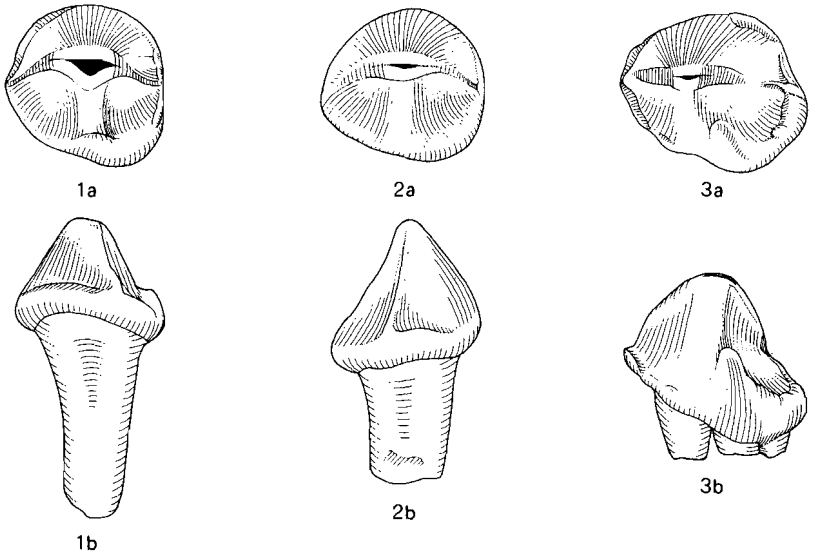

Fig. 83 *Desmana thermalis* Kormos, 1930
1. P1 (sin), Te-302
a) occlusal-lingual view b) antero-labial view.
2. P1 (sin), Te-304
a) occlusal-lingual view b) posterior view.
3. P3 (sin), Te-347
a) occlusal-lingual view b) lingual view.

tooth	loc.	N	L		W(2)		W(2)/L	
			range	mean	range	mean	range	mean
c	V4	1		1.42		1.10		0.77
	V3	4	1.39–1.47	1.43	1.05–1.16	1.11	0.73–0.79	0.77
	V2a	4/5	1.23–1.35	1.29	0.95–1.16	1.09	0.77–0.88	0.84
	V2b	1		1.31		1.14		0.87
	V2e	15	1.24–1.41	1.33	0.93–1.15	1.07	0.70–0.88	0.80
	V1	1		1.34		1.11		0.83
p1	V4	–		–		–		–
	V3	–		–		–		–
	V2a	10	1.11–1.34	1.22	1.07–1.18	1.13	0.84–0.99	0.92
	V2b	2	1.12–1.24	1.18	1.02–1.13	1.07	0.91–0.91	0.91
	V2e	17	1.04–1.26	1.14	1.01–1.15	1.10	0.88–1.05	0.97
	V1	1		1.24		1.14		0.92
p2	V4	1		1.94		1.44		0.74
	V3	5	1.80–2.06	1.95	1.29–1.43	1.36	0.66–0.75	0.70
	V2a	9	1.84–2.11	1.97	1.30–1.50	1.39	0.66–0.75	0.71
	V2b	2	1.96–1.96	1.96	1.41–1.42	1.41	0.71–0.72	0.72
	V2e	23	1.77–1.99	1.90	1.23–1.43	1.31	0.65–0.74	0.69
	V1	–		–		–		–
p3	V4	1		1.87		1.40		0.75
	V3	5	1.79–1.99	1.94	1.37–1.49	1.43	0.71–0.77	0.74
	V2a	13	1.77–1.92	1.84	1.27–1.48	1.36	0.70–0.80	0.74
	V2b	3	1.72–1.89	1.81	1.20–1.43	1.35	0.70–0.79	0.75
	V2e	15	1.59–1.85	1.73	1.16–1.35	1.26	0.66–0.79	0.73
	V1	–		–		–		–
p4	V4	4	2.32–2.59	2.46	1.55–1.69	1.63	0.64–0.69	0.66
	V3	4	2.39–2.54	2.45	1.52–1.70	1.59	0.63–0.67	0.65
	V2a	15	2.12–2.38	2.24	1.51–1.74	1.62	0.65–0.77	0.72
	V2b	2	2.34–2.47	2.40	1.73–1.79	1.76	0.72–0.74	0.73
	V2e	20	2.10–2.38	2.24	1.41–1.70	1.56	0.64–0.75	0.70
	V1	–		–		–		–
m1	V4	1		2.72		2.20		0.81
	V3	2	2.75–2.81	2.78	2.06–2.24	2.15	0.75–0.80	0.77
	V2a	26	2.59–2.87	2.73	1.95–2.36	2.20	0.74–0.84	0.81
	V2b	1		2.86		2.28		0.80
	V2e	20	2.61–2.82	2.70	2.05–2.24	2.14	0.75–0.84	0.79
	V1	2	2.74–2.75	2.74	2.11–2.27	2.19	0.77–0.83	0.80
m2	V4	1		2.61		2.15		0.82
	V3	3	2.56–2.72	2.66	2.07–2.13	2.09	0.77–0.81	0.79
	V2a	27	2.50–2.74	2.63	1.95–2.19	2.05	0.75–0.82	0.78
	V2b	–		–		–		–
	V2e	15	2.53–2.64	2.59	1.91–2.14	2.03	0.75–0.83	0.78
	V1	2	2.68–2.77	2.72	2.11–2.16	2.13	0.78–0.79	0.78
m3	V4	–		–		–		–
	V3	5	1.98–2.14	2.09	1.31–1.47	1.39	0.62–0.70	0.67
	V2a	24	1.89–2.18	2.05	1.27–1.50	1.39	0.63–0.72	0.68
	V2b	–		–		–		–
	V2e	19	1.88–2.10	1.99	1.23–1.49	1.36	0.63–0.72	0.68
	V1	4	2.05–2.15	2.09	1.33–1.50	1.40	0.65–0.70	0.67

Table 27 (a) Measurements of *Desmana inflata* n.sp., lower teeth.

tooth	loc.	N	L		W		W/L	
			range	mean	range	mean	range	mean
C	V4	–		–		–		–
	V3	3	1.46–1.71	1.57	1.30–1.33	1.31	0.78–0.90	0.84
	V2a	13	1.42–1.66	1.55	1.21–1.51	1.33	0.82–1.00	0.86
	V2b	2	1.56–1.64	1.60	1.37–1.38	1.37	0.84–0.88	0.86
	V2e	23	1.26–1.60	1.46	1.10–1.35	1.26	0.72–0.96	0.86
	V1	1		1.52		1.40		0.92
P1	V4	–		–		–		–
	V3	3	1.42–1.46	1.44	1.27–1.33	1.29	0.89–0.91	0.90
	V2a	17	1.41–1.69	1.54	1.31–1.52	1.40	0.84–0.95	0.91
	V2b	4	1.35–1.52	1.45	1.28–1.41	1.36	0.93–0.95	0.94
	V2e	26	1.27–1.67	1.48	1.27–1.49	1.38	0.85–1.06	0.93
	V1	–		–		–		–
P2	V4	–		–		–		–
	V3	3	2.15–2.47	2.40	1.54–1.71	1.63	0.66–0.69	0.68
	V2a	21/22	2.08–2.44	2.31	1.47–1.80	1.65	0.67–0.75	0.71
	V2b	2	2.38–2.42	2.40	1.72–1.72	1.72	0.71–0.72	0.71
	V2e	22	2.06–2.30	2.20	1.45–1.75	1.56	0.66–0.76	0.71
	V1	1		2.37		1.68		0.71
P3	V4	1		1.83		1.67		0.91
	V3	2	2.11–2.22	2.16	1.77–1.80	1.78	0.80–0.85	0.82
	V2a	14	1.76–2.09	1.95	1.61–2.00	1.81	0.87–1.03	0.93
	V2b	1		2.16		1.80		0.83
	V2e	20	1.64–1.85	1.75	1.53–1.85	1.71	0.88–1.08	0.98
	V1	–		–		–		–
P4	V4	–		–		–		–
	V3	3	2.68–2.70	2.69	2.35–2.48	2.40	0.87–0.93	0.89
	V2a	19/20	2.40–2.79	2.58	2.17–2.51	2.33	0.86–0.96	0.90
	V2b	1		2.70		2.36		0.87
	V2e	19	2.45–2.67	2.56	2.18–2.49	2.27	0.86–0.94	0.89
	V1	1		2.87		2.56		0.89
M1	V4	–		–		–		–
	V3	2	3.34–3.38	3.36	2.62–2.70	2.66	0.78–0.81	0.79
	V2a	18	2.98–3.40	3.21	2.57–3.05	2.74	0.78–0.95	0.85
	V2b	1		3.43		2.83		0.83
	V2e	14	3.05–3.30	3.17	2.54–2.76	2.63	0.78–0.86	0.83
	V1	1		3.36		2.84		0.85
M2	V4	–		–		–		–
	V3	1		2.42		2.82		1.17
	V2a	10	2.29–2.59	2.48	2.59–3.03	2.80	1.04–1.17	1.13
	V2b	–		–		–		–
	V2e	10	2.25–2.50	2.35	2.77–2.89	2.84	1.14–1.26	1.21
	V1	–		–		–		–
M3	V4	–		–		–		–
	V3	–		–		–		–
	V2a	15/14	1.54–1.77	1.66	1.95–2.28	2.10	1.20–1.37	1.27
	V2b	–		–		–		–
	V2e	14	1.44–1.79	1.65	1.92–2.19	2.09	1.18–1.33	1.26
	V1	1		1.71		2.18		1.27

Table 27 (b) Measurements of *Desmana inflata* n.sp., upper teeth.

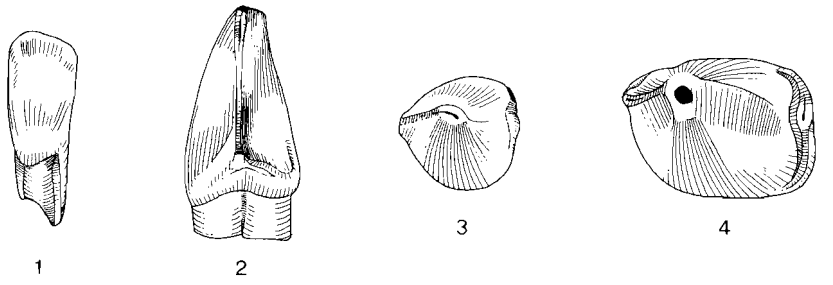

Fig. 84 *Desmana inflata* n.sp.
1. i1 (dext), V2a-10 posterior view.
2. i2 (sin), V2a-17 posterior view.
3. p1 (sin), V2a-41 occlusal-labial view.
4. p2 (sin), V2a-53 occlusal-labial view.

The crown overhangs the root anteriorly. The posterior face is more or less flat and features a slight medial extension. The medial side of the root is grooved.

p2 (9) Figs. 10.7 and 84.4 The strong smooth tooth has a sub-rectangular outline. The lingual border is straight, as both the anterocristid and the posterocristid end far lingually. The labial side is more convex than the lingual one and the crown overhangs the root along this side. The posterior side is flat. The cingulum is narrow, widening slightly in the middle of the posterior border. Faint anterior cingula may be present. The roots diverge strongly.

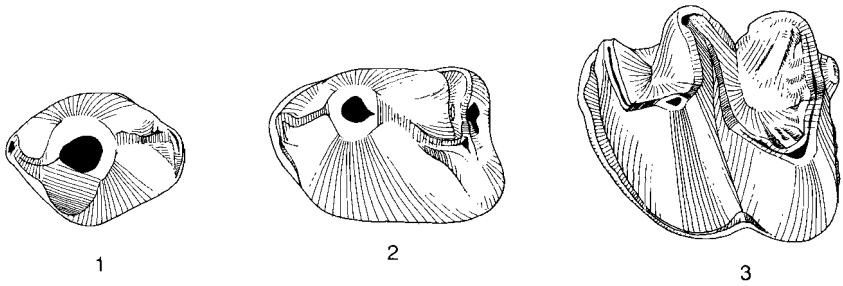

Fig. 85 *Desmana inflata* n.sp.
1. p3 (sin), V2a-62 occlusal-labial view.
2. p4 (sin), V2a-83 occlusal-labial view.
3. m2 (sin), V2a-136 occlusal-labial view.

p3 (13) Fig. 85.1 The tooth has usually a rhombic outline due to an antero-labial and a postero-lingual flattening, but in some specimens the postero-lingual corner is extended into a low flange. The enamel-dentine boundary rises towards the antero-labial corner of the crown. An indistinct paraconid may be present. Faint postero-labial and antero-lingual cingula are present. The anterior root is set diagonally under the crown.

p4 (15) Figs. 12.6 and 85.2 The tooth features a low flange at the postero-labial corner of the crown. The paraconid is small but individualized. The posterocristid continues as a posterior rim that borders the talonid and ends usually in a low entoconid. The postero-lingual face may be concave or flat; the talonid basin at its base is of variable depth and width, but is always open lingually. Faint posterior and antero-labial cingula are present.

I1 (4) The crown is low, with a strongly convex dorsal border. It is moderately compressed laterally. The anterior face is wide and flat, making a very acute angle with the flat labial face. The tip of the crown is situated labially. The inner side of the crown is faintly concave, a medial crest may have been present, but is not found in the fragmentary specimens available.

C (13) A short, very wide crown with a nearly round cross-section. The labial side is strongly convex with an indistinct flat posterior face. The lingual side is less convex. Short and low anterior and posterior cingular bulges are present. The two roots are either separated or lingually fused.

P2 (22) Fig. 86.2 A large sturdy tooth. The lingual side is less convex than the labial side and features an indistinct posterior face. The crown has an egg-shaped cross-section. A lingual extension is not present, the crown widens lingually as well as labially towards its posterior end. The anterior cingulum is short and narrow, it is not more than a slight bulge; the posterior cingulum is longer but very narrow. Most specimens feature a strong lingual accessory rootlet; one specimen possesses a labial rootlet as well.

P3 (14) Fig. 86.2 A plump tooth without sharp cristae, but with a pointed tip. The cross-section is round or sub-triangular. Both the labial and the lingual side are strongly convex. The lingual extension is ill-defined and bears no cuspule or spur. The anterior cingulum – when present – is very short; the posterior cingulum is long but narrow. The tooth has two or three roots.

P4 (20) Figs. 25.7 and 86.3 The crown has a rounded-triangular cross-section. The posterocrista is sharp; the tip of the crown is pointed. Both the labial and the lingual sides are convex with a flat or concave posterior face. The posterior basin is shallow and often narrow and ill-defined. The lingual lobe is wide with straight anterior and posterior borders. The anterior and posterior cingula are of variable length and are usually narrow. A small anterior cingular bulge is present.

Description of the material from Valdeganga 1.

i1 (1) A very small crown. The crown overhangs the root anteriorly. The flat posterior face features a medial backward extension.

I1 (1) The specimen is much worn. The dorsal border of the flat crown is strongly convex; the ventral border is nearly straight. The anterior face is flat. The tip of the crown is situated labially.

C (1) An extremely wide and plump tooth with an elliptical cross-section. The labial side of the crown is strongly convex, the lingual side less so. This side features an ill-defined flat posterior face. The anterior and posterior cingula are very short. The two roots diverge. They are fused over a short distance.

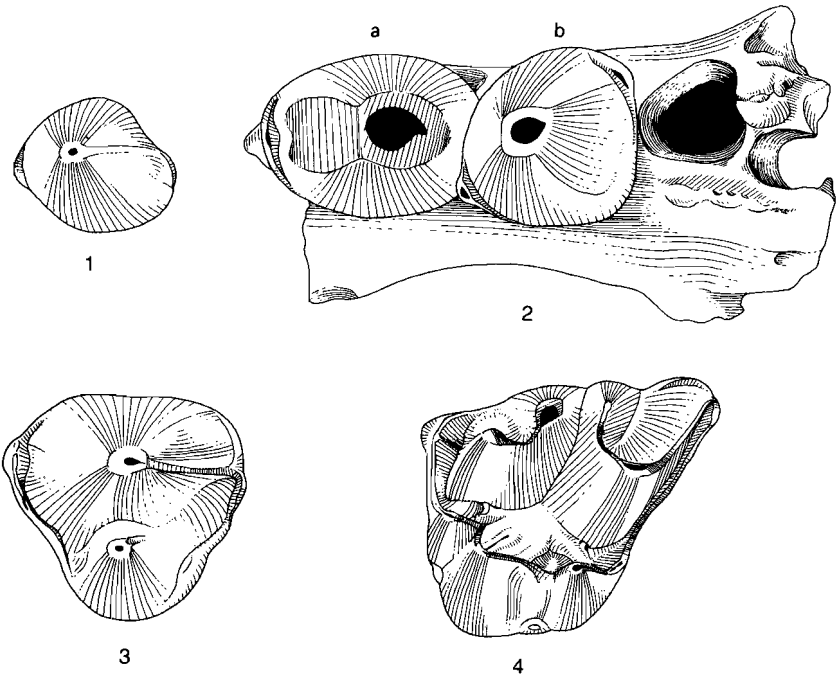

Fig. 86 *Desmana inflata* n.sp.
1. P1 (sin), V2a-243
occlusal-lingual view.
2a P2 (sin), V2a-271 (holotype)
occlusal-lingual view.
2b P3 (sin), V2a-271 (holotype)
occlusal-lingual view.
3. P4 (sin), V2a-317
occlusal-lingual view.
4. M1 (sin), V2e-456
occlusal-lingual view.

P2 (1) A large and long tooth with an egg-shaped outline. Both the lingual and the labial side are convex with a flat posterior face. There is no lingual extension, instead the crown widens gradually towards its posterior end. Short anterior and posterior cingula are present. The single specimen has two roots.

P4 (1) A rounded tooth. The postero-labial face is indistinct, the postero-lingual face is more pronounced. There is no talonid basin. The anterior part of the crown is not extended. At the base of the posterocrista the cingulum forms a small bulge. The lingual lobe is small; the protocone is low and situated far anteriorly. The anterior border of the lobe is convex, the posterior border slightly so. The narrow anterior and posterior cingula are not connected.

Description of the material from Valdeganga 2e.

p2 (23) The smooth tooth often has a sub-rectangular outline. The enamel-dentine boundary rises steeply towards the anterior end of the crown. The labial side is more strongly convex than the lingual side. The posterior side is rather flat. An indistinct paraconid is notable in some specimens. The cingulum widens conspicuously in the middle of the posterior border. Faint anterior cingula may be present. The roots diverge strongly.

p3 (15) The crown has either a rhombic outline – due to an antero-labial and a postero-lingual flattening – or a more symmetrical cross-section caused by a low postero-lingual flange. The crown is biconvex. Usually there is a faint paraconid. The posterior cingulum is (very) short and of variable width. Faint anterior cingula may be present.

p4 (20) The postero-labial corner of the crown ends in a low flange. The lingual side is somewhat convex; the postero-lingual face is variable, but is often concave. The talonid basin is rather narrow but deep and more or less closed lingually. The paraconid is variable is size. The continuation of the – indistinct – posterocristid is high and ends in a strong entoconid. Faint and short labial cingula are present.

I1 (11) Fig. 19.1 The crown is strongly convex dorsally and more or less straight ventrally. The anterior face is flat, making an acute angle with the flat labial side. The tip of the crown is situated labially. The inner side is concave. A high but short medial ridge is present.

C (23) Fig. 21.5 A very plump tooth with a nearly round cross-section. The labial side is strongly convex, the lingual side (much) less so. The anterior and posterior cingula are very short and bulgy. The roots are often fused near their base; in one specimen they are fused all the way on the lingual side.

P2 (22) A stout tooth. The crown has an egg-shaped cross-section. The labial side is strongly convex, the lingual side is more or less flat with – in some specimens – an ill-defined posterior face. A lingual extension is missing; the crown widens symmetrically towards its posterior end. A small cingular bulge is present anteriorly; the posterior cingulum is short and narrow. Most specimens possess a thin lingual rootlet. Rarely there are two accessory rootlets, one of which is situated lingually, the other one labially.

P3 (20) A stout tooth. Both the labial and the lingual side are convex; in some specimens the lingual side is more strongly convex than the labial one. The lingual extension may be either indistinct or pronounced. A lingual cusp is missing, but an ill-defined cingular spur may be present. The posterior cingulum is long but vague and narrow; usually there is no anterior cingulum. The tooth has either two very wide roots or three roots.

P4 (19) The tooth has a rounded-triangular cross-section. The crown is strongly biconvex with a short concave postero-labial face and a very long flat postero-lingual face. The anterior cingulum may form a small cuspule; the posterocrista widens near its end without forming a bulge. The lingual lobe is wide; the protocone is low but plump. The anterior border of the lobe is slightly concave, the posterior border straight. The anterior cingulum may be either interrupted and short, or long. The posterior cingulum ends at the base of the protocone.

Description of the material from Valdeganga 2b.

p2 (2) A wide and heavy tooth with a sub-rectangular cross-section. The anterocristid ends near the lingual corner, as is the case in a p4. The enamel-dentine boundary rises towards the anterior end of the crown. The labial side is more strongly convex than the lingual one; the posterior side is flat. There is a weak paraconid. The cingulum widens in the middle of the posterior border; faint anterior cingula are present.

p3 (3) The tooth is varying in size. The antero-labial corner of the crown is flattened; the postero-lingual corner is either flattened or extended into a low flange. The enamel-dentine boundary rises towards the antero-labial corner. The tooth is biconvex. A distinct postero-labial cingulum is present in all three specimens; an antero-lingual cingulum is found in two specimens.

p4 (2) A high tooth. The crown strongly overhangs the root around the postero-labial corner. The labial side is more convex than the lingual side. A posterior face is missing. The talonid basin is shallow and partly closed lingually. The heavy posterior cingular rim may form an entoconid. Faint anterior cingula are present.

I1 (1) A long tooth with a strongly curved dorsal border and a more or

less straight ventral border. The anterior face is straight. The tip of the crown is situated labially. The inner side of the crown is concave, featuring a strong but blunt medial ridge.

C (2) A strongly inflated tooth with a nearly round cross-section. The labial side is very strongly convex, the lingual side less so. There is a short bulgy posterior cingulum; the anterior cingulum is short and narrow. The tooth has two separate roots.

P2 (2) A large inflated tooth with an egg-shaped cross-section. The labial side is strongly convex, the lingual side less so. The posterior end of the crown is somewhat flattened. The anterior and posterior cingula are short, but both bear a very small bulge. The roots are not preserved in the two specimens available.

P3 (1) The tooth is hardly inflated. The outline has an irregular shape due to the strong lingual lobe. The labial side is convex, the lingual side less so. The anterior cingulum is short, but bearing a very small bulge; the posterior cingulum is more strongly developed. The lingual lobe features a high spur which is not connected to the cingulum. The roots are not preserved.

P4 (1) A large tooth with a rounded cross-section. The anterior end bears a cingular bulge; the base of the posterocrista is somewhat inflated without forming a cuspule. The labial side is strongly convex with a short concave posterior face; the lingual side is convex too, with a long and strongly concave posterior face. There is a basin at the base of the postero-lingual face. The lingual lobe is relatively narrow; the protocone is low and well connected to the paracone. The anterior border of the lobe is concave, the posterior border is distinctly convex. The anterior and posterior cingula end at the base of the protocone.

Description of the material from Valdeganga 3.

i1 (1) A small tooth. The crown overhangs the root anteriorly. The flat posterior side has a medial backward extension.

p2 (5) As the anterocristid ends near the lingual corner, the tooth has a sub-rectangular outline. The enamel-dentine boundary rises towards the anterior end of the crown. The labial side is more strongly convex than the lingual one; the posterior side is flat. An indistinct paraconid is present. The posterior cingulum is weak, but widens in the middle of the posterior border in some specimens. A short but distinct antero-lingual cingulum may be present. The roots diverge.

p3 (5) The tooth has a rhombic outline due to an antero-labial and a postero-lingual flattening. The enamel-dentine boundary rises towards the antero-labial corner of the crown. The crown overhangs the root labially.

The tooth is biconvex; some specimens have a flat postero-lingual face. An indistinct paraconid is present. The posterior cingulum, which is labially stronger than lingually, is of varying length and width.

p4 (4) The tooth is biconvex with an extremely long talonid and a postero-labial flange. The posterior face is either flat or concave. The posterocristid may be pronounced or inconspicuous. The shallow talonid basin is wide; posteriorly it is closed by the entoconid, lingually it is open. The paraconid is strong. A very wide but low cingulum borders the flange. The anterior cingulum is faint.

C (3) The wide, inflated tooth has a rounded cross-section. The labial side is very convex, the lingual side less so. The anterior and posterior cingula are short and bulgy. The tooth has either one or two roots.

P2 (3) A large plump tooth with an egg-shaped cross-section. The labial side is very convex, the lingual side less so. There is no lingual extension. The short and narrow anterior and posterior cingula each form a small bulge. The tooth has two main roots and two accessory rootlets, one of which is situated lingually, the other one labially.

P3 (2) The tooth has a rhombic cross-section due to an antero-labial and a postero-lingual flattening. The lingual extension is inconspicuous and a lingual spur or bulge is missing. The anterior and posterior cingula are narrow and short; both form a minuscule bulge. The roots are not preserved in the two specimens available.

P4 (3) The tooth is not or hardly inflated. The crown is biconvex and features a short flat postero-labial face and a long concave postero-lingual face. In one out of the three specimens a pronounced posterior basin is present. The crown is anteriorly elongated due to a bulge formed by the cingulum. The posterocrista ends in a swelling. The lingual lobe is wide, with straight or slightly concave anterior and posterior borders. The protocone is low but sturdy. The narrow anterior and posterior cingula are not connected to the tip of the protocone.

Description of the material from Valdeganga 4.

p2 (1) As the anterocristid ends far lingually, the tooth has a sub-rectangular outline. The labial side is more convex than the lingual one; the posterior side is flat. The cingulum widens in the middle of the posterior border. A short but distinct antero-lingual cingulum is present.

p3 (1) The tooth has a rhombic outline due to an antero-labial and a postero-lingual flattening. The crown overhangs the root labially. The enamel-dentine boundary rises towards the antero-labial corner. The crown is biconvex. There is a vague paraconid. The posterior cingulum is faint.

p4 (4) The shape of the tooth varies. Some teeth are long and high, with a very long, low postero-labial flange, other specimens are compact with a less pronounced flange. The talonic valley is shallow and narrow. It is posteriorly closed by the entoconid and lingually open. The paraconid is faintly individualized. The posterior cingulum may be well developed or weak; the antero-labial cingulum is faint.

P3 (1) The tip of the crown is situated far anteriorly. The tooth features a slight postero-lingual flattening and a postero-labial extension. The lingual extension is inconspicuous. The posterior cingulum is high and long, ending in a high spur on the lingual extension. The roots are not preserved in the fragmentary specimen available.

Desmana sp. from Voigtstedt (see p. 98).

tooth	N	L		W(2)		W(2)/L	
		range	mean	range	mean	range	mean
p1	1		1.50		1.40		0.93
p2	3	1.90–2.10	2.03	1.50–1.70	1.60	0.71–0.84	0.79
p3	3	1.50–1.90	1.70	1.70–1.80	1.75	0.95–1.13	1.04
p4	4	2.50–2.60	2.52	1.70–2.00	1.85	0.68–0.80	0.73
m1	5	3.00–3.30	3.12	2.70–3.00	2.86	0.85–0.97	0.92
m2	4	3.00–3.20	3.05	2.50–2.80	2.62	0.83–0.93	0.86
m3	1		2.70		2.10		0.78

Table 28 Measurements of the material from Voigtstedt, allocated to *Desmana* cf. *thermalis* by Jánossy, 1965.

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Appendix

THE AGE OF THE ASSEMBLAGES FROM WHICH DESMANINAE HAVE BEEN STUDIED

The relative age of the localities has been estimated on their rodent content (see table 29). The stratigraphic position is better established for some localities than for others. In the following review the degree of certainty of the stratigraphic position of each locality is discussed. Selected references are given for each locality.

Mein's zonal scheme for the continental Neogene, as accepted by the International Symposium of Mammalian Stratigraphy of the European Tertiary, held in Munich in 1975, is followed here with the exception of:

1) The biozonation of the Pliocene, based on the supposed sequence of *Promimomys* and *Mimomys* species, as proposed by van de Weerd in 1982. In van de Weerd's zonation the Middle Ruscinian (MN 15) starts with the appearance of the first true *Mimomys,* i.e. *M. davakosi,* a form which is more primitive than *M. occitanus.* Thus MN 15 is split into two zones: MN 15a characterized by the presence of *Mimomys davakosi* and MN 15b characterized by *M. occitanus.* The Middle Ruscinian as a whole is marked by the presence of species of *Paraethomys, Trilophomys, Dolomys* and *Stephanomys* (southwest Europe) of a specific evolutionary stage.

2) Most paleontologists working with mammal remains place the boundary between the Pliocene and the Pleistocene at the base of the first cool period, i.e. between the zones MN 16a and MN 16b. This custom is followed in this study.

The co-occurrence of *Eliomys* species, *Myoglis meini, Megacricetodon* aff. *debruijni* and *Anomalomys gaudryi* in Hammerschmiede makes an Early Vallesian (MN 9) age most probable for this locality. *Ref.* Mayr & Fahlbusch, 1975; Mayr, 1979.

The Early Turolian (MN 11) is characterized in particular by the presence of *Parapodemus lugdunensis* and *Eozapus intermedius.*

In Kohfidisch *Parapodemus* cf. *lugdunensis* and *Eozapus intermedius* are present, so an Early Turolian age for this assemblage is most probable although the presence of *Progonomys woelferi* may suggest it to be slightly older. *Ref.* Bachmayer & Zapfe, 1974; Bachmayer & Wilson, 1970, 1978, 1980; van de Weerd, 1976.

The presence of *Parapodemus lugdunensis* and *Eozapus* in Dorn-Dürkheim places this fauna too in the Early Turolian. *Ref.* Franzen & Storch, 1975; van de Weerd, 1976; Storch, 1978.

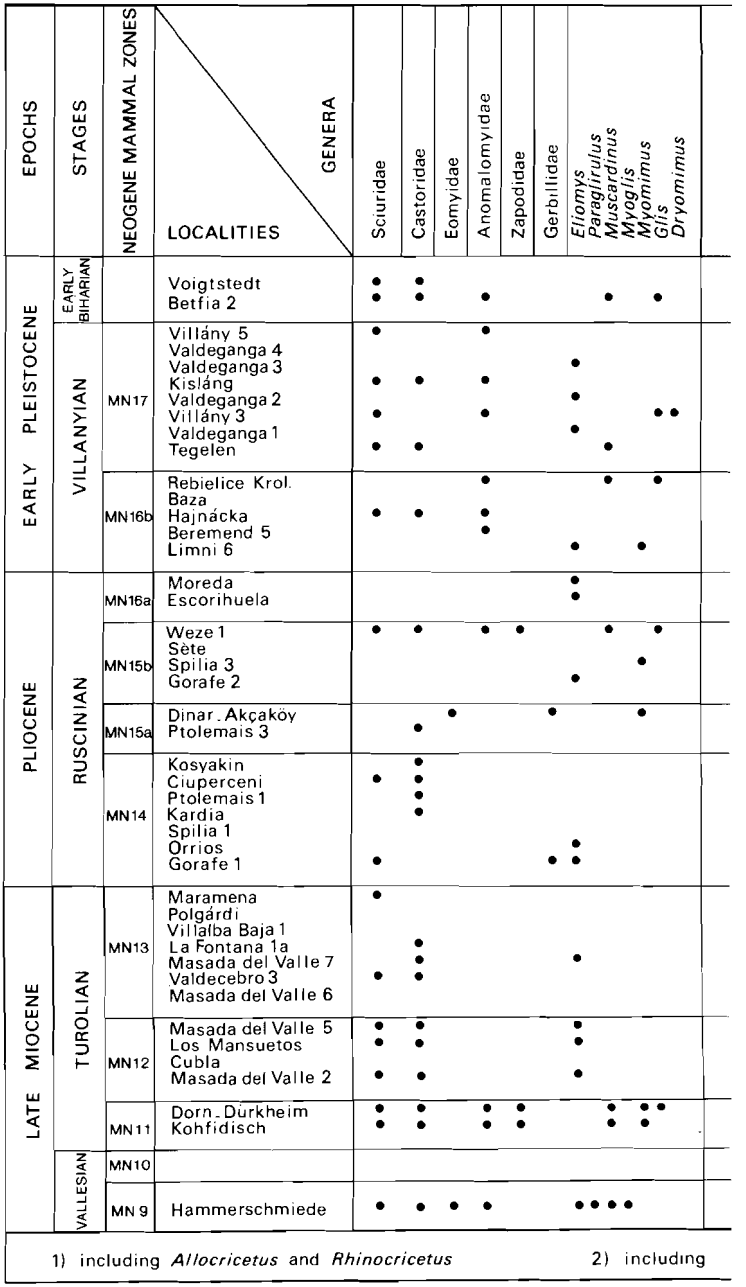

Table 29 Rodent content of the localities of which fossil Desmaninae have been studied.

Anomalomys
Democricetodon
Megacricetodon
Microtocricetus
Kowalskia
Epimeriones
Collimys
Cricetulodon
Hispanomys
Ruscinomys
Cricetus 1)
Trilophomys
Blancomys
Baranomys 2)
Progonomys
Parapodemus
Valerymys
Occitanomys
Stephanomys
Apodemus
Paraethomys
Castillomys
Rhagapodemus
Micromys
Orientalomys
Rattus
Promimomys
Mimomys s.str
Dolomys
Ungaromys 3)
Cseria
Mimomys (Kislangia)
Pliomys
Mimomys (Microtomys)
Villanyia
Clethrionomys
Lagurus
Microtus (Allophaiomys)
Microtus (Pitymys)
Microtodon
3) including Germanomys and Stachomys

The Middle Turolian (MN 12) of Spain and the south of France is characterized by the association of *Occitanomys adroveri, Valerymys turoliensis* and *Parapodemus gaudryi barbarae. Ruscinomys schaubi* occurs in the Middle and Late Turolian.

In Masada del Valle 2 the three first-named species are found; in Cubla, Los Mansuetos, Aljezar B and Masada del Valle 5 all four species occur. All these faunas are considered to be approximately of the same age. *Ref.* van de Weerd, 1976; van de Weerd & Daams, 1978; Adrover, 1983.

The Late Turolian (MN 13) is marked by the occurrence of *Parapodemus gaudryi gaudryi, Cricetus kormosi* and a murid with *Parapodemus* as well as *Apodemus* morphotypes. In southwest Europe the occurrence of *Stephanomys ramblensis* is characteristic.

Masada del Valle 6, Valdecebro 3, Masada del Valle 7, La Fontana 1a and Villalba Baja 1 all contain *Stephanomys ramblensis.* The occurrences of *Parapodemus gaudryi barbarae* and *Valerymys turoliensis* in Masada del Valle 6, of *Valerymys turoliensis* and *Occitanomys adroveri* in Valdecebro 3 and of *O. adroveri* in Masada del Valle 7 seem to suggest that these three localities are slightly older than La Fontana 1a and Villalba Baja 1. *Ref.* van de Weerd, 1976; van de Weerd & Daams, 1978.

Polgárdi contains *Parapodemus gaudryi gaudryi* and *Cricetus kormosi* and therefore fits well into the west European zonation. *Ref.* Kormos, 1911, 1913; Schaub, 1930, 1938; Schreuder, 1940; van de Weerd, 1976.

The assemblage from Maramena 1 is rather different from the west European finds, but the presence of true *Cricetus, Occitanomys,* two species of *Apodemus* and a murid transitional between *Parapodemus* and *Apodemus* suggests a Late Turolian age. *Ref.* Armour-Brown et al, 1977; de Bruijn & van der Meulen, 1979; Bouwens & de Bruijn, in prep.

The Early Ruscinian (MN 14) is characterized by the occurrence of *Rhagapodemus hautimagnensis, Castillomys crusafonti gracilis* and *Promimomys insuliferus. Trilophomys* occurs for the first time.

Gorafe 1 and Orrios contain *Castillomys crusafonti gracilis* and *Trilophomys* as well as *Stephanomys* and *Paraethomys.* Arvicolids are absent. Both assemblages are therefore placed at the beginning of the Early Ruscinian. *Ref.* de Bruijn, 1974; van de Weerd, 1976; van de Weerd & Daams, 1978.

In Spilia 1 *Rhagapodemus hautimagnensis* is present. In Kardia and Ptolemais 1 this species occurs associated with *Promimomys insuliferus.* Spilia 1 may be slightly older than Kardia, but the absence of *Promimomys* may also be due to other reasons. *Ref.* Armour-Brown et al, 1977; de Bruijn & van der Meulen, 1979; van de Weerd, 1979.

In Ciuperceni the beds with Desmaninae contain no characteristic rodents, but the presence of *Mimomys occitanus* in the overlying beds suggests an Early Ruscinian age for this locality. *Ref.* Terzea, 1980.

Kosyakin (Stavropol) is difficult to place. According to Belyaeva the assemblage is most likely of Middle Pliocene age, which means that it is as old as – or somewhat younger than – the Odessa Catacombs. As the age of the Catacombs is considered to be Middle Ruscinian, Kosyakin is placed high in zone MN 14. *Ref.* Topachevski, 1962; Belyaeva, 1968.

The *Promimomys* found in Dinar-Akçaköy is larger and more evolved than *P. insuliferus* (MN 14), but less so than *P. cor,* found in Csarnóta 2 (MN 16a) (van der Meulen, pers. comm.). Therefore Dinar-Akçaköy is placed tentatively in MN 15a, but its age may be somewhat younger. *Ref.* Becker-Platen et al, 1975; Engesser, 1980.

In Ptolemais 3 *Mimomys davakosi* is present, which suggests that the assemblage belongs in MN 15a. *Ref.* van de Weerd, 1979.

Gorafe 2 contains *Paraethomys jaegeri, Stephanomys, Trilophomys* and *Dolomys nehringi,* an association which is characteristic for the Middle Ruscinian. *Ref.* de Bruijn, 1974; Montenat & de Bruijn, 1976; van de Weerd et al, 1977.

In Spilia 3 *Mimomys occitanus* and *Occitanomys brailloni* are found. This locality is therefore placed in zone 15b. *Ref.* Armour-Brown et al, 1977; de Bruijn & van der Meulen, 1979.

In Sète two *Paraethomys* species, i.e. *P. meini* and *P. jaegeri* are found together with *Occitanomys brailloni* and the zonal marker *Mimomys occitanus. Ref.* Michaux, 1969; Montenat & de Bruijn, 1976; van de Weerd et al, 1977.

According to Sulimski (1959) a large part of the Pliocene is represented in the cave filling of Weze 1. However, according to Kowalski (pers. comm.) and Rzebik-Kowalska (1971) the age of the entire deposit is "uppermost Pliocene". The occurrence of *Dinaromys hungaricus, Trilophomys pyrenaicus, Mimomys* cf. *stehlini* (a form transitional between *M. occitanus* and *M. stehlini*) and *Cseria praegracilis* is in accordance with the last view as it suggests a late Middle Ruscinian age. Thus Weze 1 is placed in zone MN 15b. *Ref.* Sulimski, 1959, 1962; Kowalski, 1964; Rzebik-Kowalska, 1971.

The Late Ruscinian is characterized by the association of *Trilophomys* and *Stephanomys* (both showing a more advanced stage of development than the species of these genera found in the previous zone), *Castillomys crusafonti crusafonti* and several arvicolids with little or no crown cement such as *Mimomys stehlini* and *Cseria gracilis.*

Escorihuela contains *Stephanomys minor, Castillomys crusafonti* s.l.,

Trilophomys, Mimomys stehlini and *Cseria gracilis.* In Moreda *S. minor, S. donnezani, Castillomys crusafonti crusafonti, M. stehlini* and *Mimomys (Kislangia) cappettai* occur. Both assemblages are therefore placed in the Late Ruscinian (MN 16a). *Ref.* for Escorihuela: van de Weerd, 1976; van de Weerd et al. 1977; van de Weerd & Daams, 1978. For Moreda: Gmelig-Meyling & Michaux, 1973; de Bruijn, 1974; van de Weerd et al, 1977.

From the Early Pleistocene onwards Arvicolidae with cement in the synclines of the crown are abundant. The age determinations of the assemblages are based on certain evolutionary trends in the Arvicolidae, such as the increase of the crown cement, the disappearance of the roots, the increase in hypsodonty, the increase in height of the enamel-free areas along the sides of the crown and the development of differentiation of the thickness of the enamel in the cheek teeth.

In this paper the Villanyian is divided into two parts; a Middle Villanyian is not distinguished. The Early Villanyian (MN 16b) is characterized particularly by the presence of *Mimomys polonicus.*

In Limni 6 *Mimomys* cf. *polonicus, M.* cf. *septimanus* and *Pliomys hungaricus* are found together with the murids *Orientalomys similis, Micromys praeminutus* and *Apodemus dominans. Ref.* de Bruijn & van der Meulen, 1979; Katsikatsos et al, 1981.

Some of the assemblages from the Beremend fissures, especially those which were collected before 1940, are difficult to fit into our biostratigraphic scheme. In Beremend 5, the reference locality for the Early Villanyian, two *Mimomys* species as well as *Dolomys milleri* are found. It is assumed here that the age of Beremend 1–3 (collected by Petenyi), of Beremend 4 and of the material collected by Kormos in 1936 (here called Beremend 1936) does not deviate much from that of Beremend 5. *Ref.* Kormos, 1913, 1938; Kretzoi, 1956; van der Meulen, 1973; Jánossy, 1979.

Hajnácka contains several *Mimomys* species with crown cement and is therefore considered to be of about the same age as Beremend 5. *Ref.* Fejfar, 1964.

Baza contains *Mimomys polonicus* only and is therefore placed in the Early Villanyian. *Ref.* de Bruijn, 1974; van de Weerd & Daams, 1978.

In Rebielice Królewskie *Mimomys polonicus* occurs together with several other arvicolid species such as *Lemmus* (an indicator for a relatively cold climate). The fauna seems to be younger than that of Osztramos 7 (also containing *Lemmus*) which is of the same age as – or slightly younger than – Beremend 5. For this reason Rebielice Królewskie is considered to be somewhat younger than Beremend 5 (van der Meulen, pers. comm.). *Ref.* Kowalski, 1960, 1964; Rzebik-Kowalska, 1971; Freudenthal et al, 1976).

The Late Villanyian (MN 17) is recognized by the occurrence of *Mimomys pliocaenicus* (a species evolved from *M. polonicus*), and certain evolutionary stages in several arvicolid lineages, such as *Mimomys (Kislangia)* and *M. (Microtomys)*.

Mein placed the Valdeganga section in the Villanyian, i.e. Valdeganga 1 and 2 in the Early Villanyian (MN 16b) and Valdeganga 3 and 4 in the Late Villanyian (MN 17). This age determination is based on the evolutionary stages of *Stephanomys, Castillomys crusafonti* and *Mimomys*. However, considering the presence of *Mimomys (Kislangia) rex* as well as a representative of the *M. (Microtomys) pussilus-readi* group, a Late Villanyian age for the entire section seems more probable. *Ref.* Mein et al., 1978.

The assemblages from Tegelen, Villany 3, Kisláng and Villany 5 resemble each other closely. Tegelen contains *Mimomys pliocaenicus, M. newtoni* and *M. (Microtomys) reidi*. Villany 3 contains the same three species together with *M. (Kislangia) rex* and *Lagurus arankae*. Kisláng contains *Mimomys* cf. *newtoni, M. (Microtomys) reidi* and *Lagurus arankae* together with *Kislangia* and other *Mimomys* species. Villany 5 contains *Mimomys pliocaenicus, M. newtoni, M. (Microtomys) reidi, M. (Kislangia) rex* and the oldest known *Microtus* species, i.e. *Microtus (Allophaiomys) deucalion*. A Late Villanyian age for all four localities with Tegelen as the older and Villany 5 as the younger one seems most probable. *Ref.* for Tegelen: Schreuder, 1940; van der Meulen, 1974; Freudenthal et al, 1976; Reumer, in press. For Villany 3 and Villany 5: Kormos, 1938; Kretzoi, 1956; van der Meulen, 1974; Freudenthal et al, 1976; Mayhew, 1979. For Kisláng: Kretzoi, 1953; Freudenthal et al, 1976; Jánossy, 1979.

The Early Biharian assemblages are characterized by the dominance of *Microtus* species. *M. (Allophaiomys) pliocaenicus* appears for the first time at the base of the Lower Biharian. *Mimomys savini*, a descendant of *M. pliocaenicus*, is a zone marker.

Betfia 2 contains *Microtus (Allophaiomys) pliocaenicus;* the assemblage is placed at the beginning of the Early Biharian. *Ref.* Kormos, 1913, 1930; Kretzoi, 1956; van der Meulen, 1973, 1974.

Voigtstedt contains *Mimomys savini* together with several *Microtus* species. The age of the assemblage is estimated as late Early Biharian. *Ref.* Kahlke et al, 1965; Jánossy, 1965; van der Meulen, 1973.

Addendum

Just after my manuscript was finished, Mr. Mein drew my attention to a paper by Topachevski and Pashkov in Vestnik Zoologii of May–June 1983. In this paper the authors propose a tentative subdivision of the genus *Desmana* into five subgenera. These subgenera are defined on the basis of the relative length of the p2, p4, C, P1 and the P2 and on the morphology of those areas of the mandible where the masticatory muscles insert. The species included in the subgenera are partly known from the literature, such as *Desmana pontica* Schreuder, *Desmana nehringi* Kormos, *Desmana thermalis* Kormos and *Desmana moschata* (Linnaeus), and partly new. These latter are neither described not figured and are therefore to be regarded as nomina nuda at this moment.

Table A gives the subgenera of Topachevski and Pashkov with their type species, the list of allocated species (the names in parenthesis are those used here), the ratios used by Topachevski and Pashkov and the ratios according to the measurements in this paper.

According to Topachevski and Pashkov the genus *Desmana* consists of three lineages, i.e. the main lineage *Desmana Archaeodesmana – Desmana Praedesmana – Desmana Desmana* and two parallel lineages with the species included in *Desmana Pliodesmana* and *Desmana Galemodesmana.*

On fig. a the p2/p4, P1/C and P2/C ratios of *Dibolia, Galemys* and *Desmana* are shown. The p2/p4 ratio is more or less the same for all three genera and is therefore apparently unsuitable as a criterium for classification. The P1/C and P2/C ratios show a normal distribution in *Dibolia* and a bimodal distribution in *Galemys* and *Desmana.* In *Galemys* the low values are caused by a short P1 or P2, in *Desmana* by the extremely long C. In the case of *Desmana* this grouping endorses the lineages that I propose in chapter 7. It should be noted that these lineages are not the same as those proposed by Topachevski and Pashkov.

It is clear that the P2/C ratio may be quite useful to distinguish lineages if more material will become available. For the moment there is no reason to adopt the subdivision proposed by Topachevski and Pashkov.

Ref. Topachevski, V.A. & A.V. Pashkov (1983). Nadvidovaya sistematica vykhukholei roda *Desmana* (Insectivora, Talpidae). (The supraspecific systematics of the water-moles of the genus *Desmana* (Insectivora, Talpidae)). Vestnik Zoologii, *3*, p. 39–45.

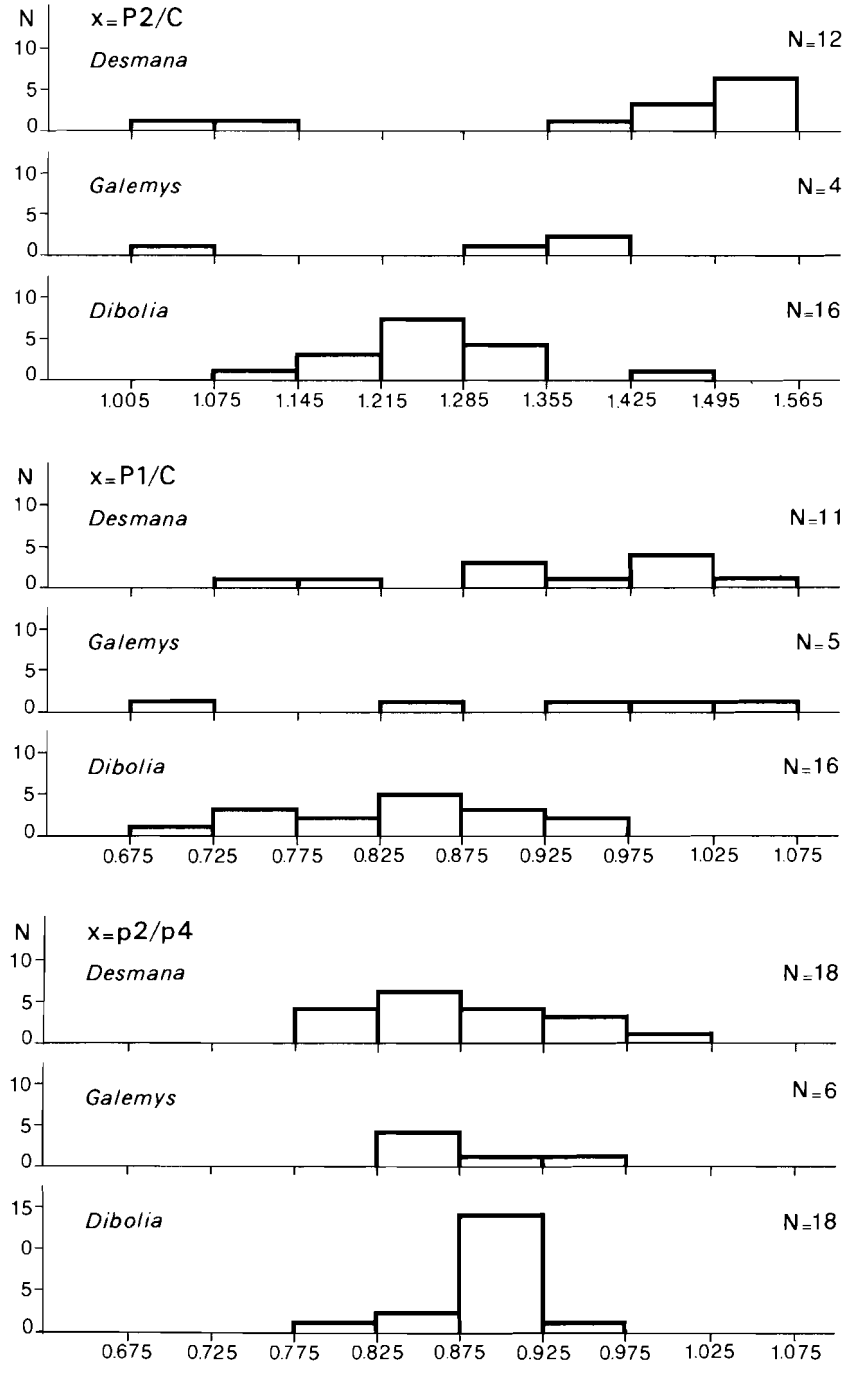

Fig. a For explanations see the text.

subgenus	species	p2 : p4	P1 : C	P2 : C
Desmana s.s.	*Desmana moschata*[1])	p2 < p4	0.76	0.90
		0.83	0.78	1.01[2])
	several subspecies of *D.m.*			
Praedesmana	*Desmana thermalis*[1])	p2 < p4	P1 < C	1.17
		0.91–0.97	0.76	1.09[2])
	D. nogaica nom. nud.[3])			
Pliodesmana	*Desmana jalpugensis* nom. nud.[1])	p2 > p4	–	–
	D. moravica nom. nud			
Archaeodesmana	*Desmana pontica*[1])	p2 < p4	0.93	1.33
	(*Dibolia pontica*)	–	0.93	1.30[2])
	D. verestchagini	0.86–0.98	0.92–1.06	1.47–1.52[2])
Galemodesmana	*Desmana nehringi*[1])	p2 < p4	P1 >> C	1.30–1.50
		0.86–0.92	0.98–0.98	1.49–1.50[2])
	Desmana kormosi (*Galemys kormosi*)	0.83–0.89	0.85–1.02	1.40–1.42[2])
	Desmana semseyi (*Galemys semseyi*)	–	–	–[2])
	Desmana getica (*Dibolia bifida*)	0.80–0.88	0.71	1.16[2])
	Desmana polonica nom. nud			

[1]) type species
[2]) ratios according to the measurements in this paper
[3]) figured and described by Topachevski (1962) as *Desmana thermalis*

Table A For explanation see the text.