
**Insectivore faunas from the Lower Miocene of Anatolia.
Part 4: The genus *Desmanodon* (Talpidae) with the description of a
new species from the Lower Miocene of Spain**

Lars W. van den Hoek Ostende

*Instituut voor Aardwetenschappen, Postbus 80 021, 3508 TA Utrecht, The Netherlands and
Nationaal Natuurhistorisch Museum, Postbus 9517, 2300 RA Leiden, The Netherlands*

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ABSTRACT

A review is given of the literature on *Desmanodon* and *Paratalpa*. These two talpid genera can only be identified on the basis of the morphology of the humerus. Two species of *Desmanodon*, *D. ziegleri* n. sp. and *D. burkarti* n. sp., are described from the Lower Miocene of Anatolia. These species are considered ancestral to the Middle Miocene species of Anatolia. *D. ziegleri* is also a likely ancestor for the European species of *Desmanodon*. *Desmanodon daamsi* n. sp. is described from the Lower Miocene of Spain. The *Desmanodon/Paratalpa* finds from the Calatayud-Teruel basin (Spain) are discussed.

The tribal classification of *Desmanodon* is problematic, since some species resemble Urotrichini, whereas other are morphologically closer to Scalopini. This suggests that the distinction between the two tribes should be re-evaluated.

The stratigraphic and geographic distribution of *Desmanodon* indicates that the genus immigrated into Europe sometime during the Early Miocene.

INTRODUCTION

Our knowledge of fossil micromammals is primarily based on the study of teeth. In some rare cases skulls or even whole skeletons have been found, but as a rule the postcranial remains cannot be associated with the teeth. An exception to this rule are the talpids. Their fossorial mode of life is reflected in the skeleton, in particular in the humerus. The morphology of the humerus plays an important role in the taxonomy of the fossil Talpidae. In Europe species of the genera *Desmanodon* and *Paratalpa* can only be distinguished on the basis of the humerus (van den Hoek Ostende, 1989).

In this paper two new species of *Desmanodon* from the Lower Miocene of

Anatolia are described. The species provide new insights in the evolutionary history of this genus. The Middle Miocene species of *Desmanodon* from Anatolia and some recently collected material from the Lower Miocene of Spain will be discussed. The paper forms part of a series on the insectivores from the Lower Miocene of Anatolia. These insectivores were collected by the Mineral Research and Exploration Institute of Turkey (M.T.A.) in cooperation with Utrecht University in the project 'Reconstruction of the changes in the continental Neogene of Anatolia', supported by NATO grant CRG 910750. Earlier papers in the series dealt with the Erinaceidae (van den Hoek Ostende, 1992), Heterosoricidae (van den Hoek Ostende, 1995a) and Dimylidae (van den Hoek Ostende, 1995b).

Fig. 1 shows the various Lower Miocene localities in Anatolia in which *Desmanodon* has been found. Papers on the muroid genera *Eumyarion*, *Mirabella*, *Deperetomys*, *Cricetodon* and *Enginia* and on the Gliridae from these localities have appeared in another series (de Bruijn and Saraç, 1991, 1992; de Bruijn *et al.*, 1993; de Bruijn and von Koenigswald, 1994; Ünay, 1994).

METHODS AND COLLECTION

The nomenclature for parts of molars and the method of measuring follow van den Hoek Ostende (1989). The lingual bulge on the posterior flank of the protoconid of the p4 was called the 'Metaconidknospe' by Ziegler (1985). We do not consider this bulge homologous with the metaconid. True metaconid cusplets are present on the p4 of some insectivores (e.g. *Galerix uenayae*, see van den Hoek Ostende, 1992, plate 4, fig. 13), but these are situated on the lingual

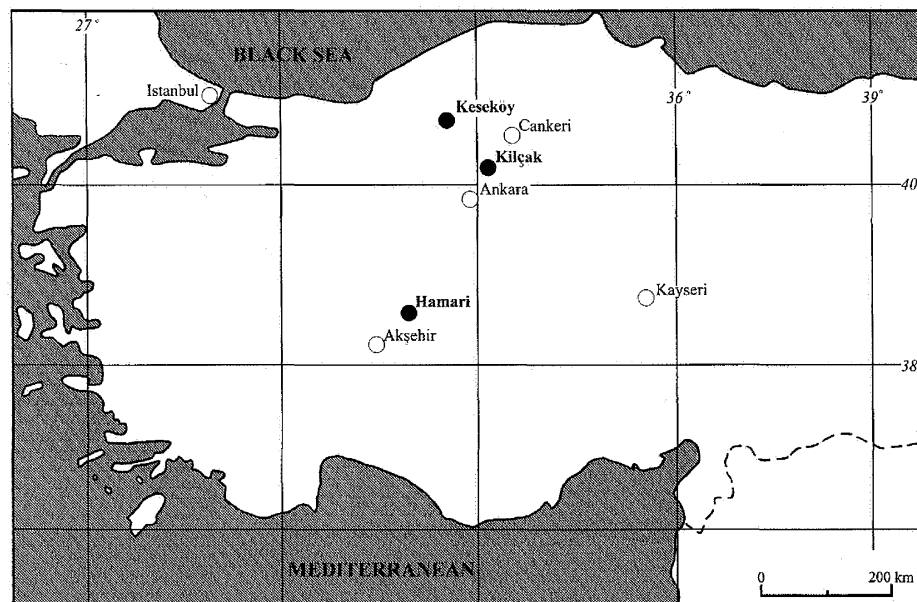


Fig. 1. Lower Miocene mammal localities in Anatolia.

flank of the protoconid. The posterior bulge on the protoconid of the p4 is called the protocristid in analogy with the metacristid.

The width given for lower molars is always the width of the talonid. All measurements are in millimetres. The numbers of specimens upon which the descriptions are based are given in brackets. We follow Hutchison (1974) for the nomenclature of the parts of the humerus. The magnification used on the plates for (pre-)molars is 17×, for humeri 8×.

The material from Harami (Ha 1 and Ha 3), Kilçak (Ki 0, Ki 0", Ki 3A and Ki 3B) and Keseköy (Ke) was collected during joint fieldwork in the period 1987–1993 by Engin Ünay, Gerçek Saraç (both from the Mineral Research and Exploration General Directorate of Turkey (M.T.A.)) and Hans de Bruijn from Utrecht University. The material will be stored in the collections of the M.T.A. (Ankara). The Çandır material was collected by Erksin Güleç from the D.T.C. Fakültesi in Ankara, Hans de Bruijn and Gerçek Saraç in 1992–1993.

The material from the Daroca-Calamocha area of the Calatayud–Teruel Basin was collected by a team of specialists of the Museo Nacional de Ciencias Naturales in Madrid (Remmert Daams, now Complutense University, Madrid), the Utrecht University (Albert van der Meulen) and the National Museum for Natural History in Leiden (Matthijs Freudenthal) during a joint project in the late seventies/early eighties. Since 1991 sampling was continued by the first two participants. Sampling still continues and every year more localities in the area are discovered. The material from the localities San Roque 1 (SR 1), Moratilla 1 (Mor 1), Vargas 1 (VRG 1A), Bañon 2 (Ban 2) and Ramblar 1 (Ram 1) is stored in the National Museum for Natural History in Leiden. The material from La Col C (Col-C), La Col D (Col-D), San Roque 3 (SR 3), San Roque 4A (SR 4A), San Roque 4B (SR 4B), San Roque 5 (SR5), San Marco (SAM), Olmo Redondo 4A (OR 4A), Fuente Sierra 2 (FTE 2), Fuente Sierra 3 (FTE 3), Fuente Sierra 4 (FTE 4), Vargas 2B (VRG 2B), Vargas 4A (VRG 4A), Vargas 4BB (VRG 4BB), Agreda (Agr), Ramblar 5 (Ram 5), Ramblar 7 (Ram 7), Valhondo 1 (VH 1) and Navarete del Rio (Nav) is stored in the Museo de Ciencias Naturales in Madrid.

The material from Rubielos de Mora (RM) was collected by Hans de Bruijn and Coja Rümke (Utrecht University) in the early seventies. The *Desmanodon* from this locality was described by Gibert (1974) under the name *Paratalpa micheli*. Part of the Rubielos de Mora collection is stored at Utrecht University.

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REVIEW OF THE LITERATURE

The *Desmanodon*/*Paratalpa* problem

In this section the literature data on both *Desmanodon* and *Paratalpa* are discussed. The reason for including the latter genus is that without humeri some species of *Desmanodon* and *Paratalpa* cannot be distinguished (van den Hoek Ostende, 1989). This leads to identifications which may seem peculiar to scho-

lars not working with talpids. For instance Ziegler (1990) described a talpid from Stubersheim 3 under the heading '*Paratalpa meyeri* vel *Desmanodon antiquus*'. Thus Ziegler suggests that he could not identify the genus but that, if he would know the genus, he could identify the species. This seems strange, but is correct. On the basis of the dentition, the mole from Stubersheim 3 can neither be distinguished from *Paratalpa meyeri*, which occurs in levels somewhat older than Stubersheim, nor from *Desmanodon antiquus*, which is found in younger levels. The two species do differ in the morphology of the humerus. These differences are large enough to warrant a distinction at the genus level (Engesser, 1980; van den Hoek Ostende, 1989; Ziegler, 1990). Without the humerus, however, one is faced with the unsatisfactory and even somewhat frustrating situation, that species cannot be identified further than '*Paratalpa* or *Desmanodon*'.

Given the fact that the dentitions of *Paratalpa* and *Desmanodon* are so similar, one might wonder whether undue emphasis is placed on the morphology of the humerus. Should the two genera be merged into one? The answer to this question is 'No'. The differences in humerus morphology are too clear cut. In this paper we recognize two species of *Paratalpa* and six species of *Desmanodon*. All of the latter have a humerus characterized by a long teres tubercle. The teres tubercle is short in both *Paratalpa* species. No intermediate forms have been found. Furthermore, the humerus of *Paratalpa* is clearly more slender than it is in *Desmanodon*. The differences between the humeri of *Paratalpa* and *Desmanodon* are larger than those between the humeri of the extant genera *Urotrichus* and *Neurotrichus* (fig. 4b and 4d).

How can we explain the similarity between the dentitions of species which are placed in different genera? In an earlier paper (van den Hoek Ostende, 1989) I suggested that the European species of *Paratalpa* and *Desmanodon* were part of one evolutionary lineage. *Desmanodon* would have evolved from *Paratalpa* when the locomotory system evolved to one adapted to a more fossorial way of life. Within this lineage there would be no changes in the morphology of the dentition. This hypothesis can, however, no longer be maintained. In this paper *Desmanodon* species are described which show that this genus was already present in Anatolia at the same time that *Paratalpa* lived in Europe.

We think that the explanation for the similarity between *Paratalpa* and *Desmanodon* is far more practical. We simply do not have clear-cut characters to distinguish between the two genera. Species within this group of talpids can primarily be distinguished on size. Morphological characters used in the taxonomy are variable (the degree of division of the mesostyle, the degree of development of the protoconule and of the hypocone) and more or less dependent on wear. This makes it difficult to distinguish between dentitions of similar size. *Paratalpa* and *Desmanodon* are by no means unique among talpids in this respect. Rümke (1985) stated that the morphology of the molars of the three genera of Desmaninae described in her review are remarkably similar. So similar that she did not give descriptions of the molars of the various species, but concentrated on the incisors, canines and premolars.

The literature on *Desmanodon* and *Paratalpa*

The genus *Desmanodon* was defined by Engesser (1980) in his work on the insectivores of Anatolia. Engesser recognized two species, *D. major* from Yeni Eskihisar (MN 7/8) and *D. minor* from Sariçay (MN 7/8). He described the humerus as well as the dentition of these species. These associations of humerus and dentition seems certain, since the humeri clearly do not belong to *Desmanella*, the only other mole he recognized in these localities. In addition to *Desmanodon major* and *D. minor* Engesser described an M1 and M3 from Paşalar (MN 6) (*Desmanodon* cf. *minor*) and two small m1 from Sariçay, which I identified as *Myxomygale* sp., but which are probably referable to a hitherto undescribed Uropsiline genus (van den Hoek Ostende, in preparation).

Doukas (1986) described *Desmanodon meuleni*, from the Lower Miocene (MN 4) locality Aliveri (Evia, Greece). In his unpublished thesis (Doukas, 1983), he recognized two morphotypes in the upper molars: morphotype A, characterized by the presence of a protoconule, an incompletely divided mesostyle and a pointed lingual outline, and morphotype B, lacking the protoconule, with a well-divided mesostyle and a rather rounded lingual outline. However, in 1986 he considered the differences part of a gradual variation. The humerus of *D. meuleni* has never been found, and therefore one cannot be certain that the species belongs to *Desmanodon*. For two reasons, however, it is likely that it is indeed a species of *Desmanodon*. The P4 is of a type that is known from Anatolian *Desmanodon* species but is not found in *Paratalpa*, and the Aliveri species is considerably younger than the last certain occurrence of *Paratalpa*. According to Doukas (1986) the *Desmanodon* specimens from Paşalar belong to the Aliveri species.

Ziegler (1985) described *Desmanodon antiquus* from southern Germany. His description was based on a few dental elements and humeri from Rembach, Rauschenröd (MN 4) and Puttenhausen (MN 5). Later more material was found (Ziegler and Fahlbush, 1986; van den Hoek Ostende, 1989). Ziegler suggested that the *Desmanodon* specimens from Paşalar should be allocated to *D. antiquus*. He reconstructed a lineage from *D. antiquus* to *D. minor* and *D. major*.

Van den Hoek Ostende (1989) discussed the differences between *Paratalpa*, *Teutonotalpa* and *Desmanodon*. Because *Paratalpa* and *Desmanodon* have a different type of humerus generic separation is warranted. However, the dental elements of *Paratalpa micheli*, *Teutonotalpa meyeri* and *Desmanodon antiquus* cannot be distinguished. I therefore placed *Teutonotalpa meyeri*, of which the humerus is not known, in the synonymy of *Paratalpa micheli*. Ziegler (1990) agreed to consider *Teutonotalpa* a junior synonym of *Paratalpa*, but pointed out that the species *meyeri* cannot be a junior synonym of *micheli*, since it was described earlier. According to Ziegler *P. meyeri* and *P. micheli* are two distinct species differing in the humerus, which is somewhat more robust in *P. meyeri*.

Van den Hoek Ostende (1989) distinguished three morphotypes of P4 in the *Desmanodon/Paratalpa* group, based on the development of the parastyle and the protoconal flange (fig. 2). *D. meuleni*, *D. minor* and *D. major* all have mor-

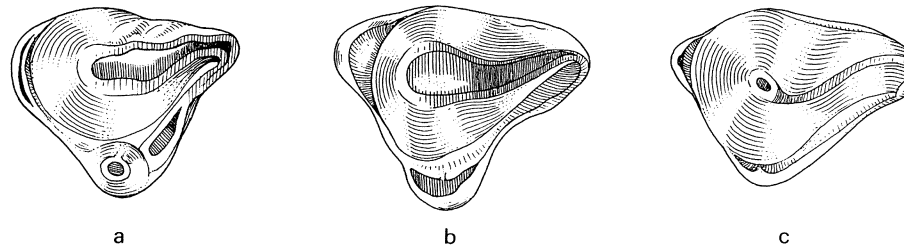


Fig. 2. The three morphotypes of P4 found in *Desmanodon* and *Paratalpa*. a: type A, b: type B, c: type C.

phototype A, characterized by a small parastyle and a large conical protocone. Since these species share the same type of P4, I suggested that they formed part of one evolutionary lineage. Morphotype B, characterized by a large parastyle and large protoconal flange, and morphotype C, in which the parastyle and protoconal flange are small, are both found in *D. antiquus* and in the *Paratalpa* species. The occurrence of similar P4 morphotypes in the European species of *Desmanodon* and in *Paratalpa* was one of the reasons for my suggestion that the two genera are part of a single evolutionary lineage.

The genus *Paratalpa* was described by Lavocat (1951) from the Upper Oligocene locality Cournon. The genus is primarily known from the extensive description given by Huguenev (1972), in her review of the talpids from the Upper Oligocene locality Coderet. Huguenev placed *Paratalpa* in the Urotrichini on the basis of the similarity in both molar morphology and dental formula between this genus and the Recent *Urotrichus*. Ziegler (1990) described material of *Paratalpa* from the Upper Oligocene and Lower Miocene of southern Germany. He distinguished three species: *Paratalpa micheli*, *P. brachy chir* and *P. meyeri*. These three species have similar dentitions, but differ in the robustness of the humerus, which is slender in the Upper Oligocene (*P. micheli*) and more robust in the Lower Miocene (*P. brachy chir* and *P. meyeri*). *P. brachy chir* is known from Tomerdingen (MN 1), Weisenau, Budenheim and Budenheim/Heßler (all MN 2). *P. meyeri* is known from Haslach, Eggingen and Ulm-Westtangente (MN 2). Later Ziegler and Werner (1994) also noted the presence of *Paratalpa* sp. in Lautern 2 (MN 1). Biologically it seems unlikely that two species of one genus that are of similar size and morphology live in the same region at the same time. Since Ziegler gives no criteria to distinguish the two Lower Miocene species of *Paratalpa*, I propose to place *P. meyeri* (Schlosser, 1887) in the synonymy of *Paratalpa brachy chir* (Meyer, 1847).

Ziegler (1990) also described a mole from the MN 3 locality Stuberheim 3, which, due to the absence of humeri, was identified as *Paratalpa meyeri* vel *Desmanodon antiquus*. Various insectivores, like the erinaceid *Galerix*, and the talpids *Myxomygale hutchisoni* and *Desmanella* aff. *engesseri*, have their first occurrence in southern Germany in Stuberheim 3, which suggests an immigration wave. In many aspects the insectivore assemblage of Stuberheim 3 resembles those of the MN 4 localities, in which *Desmanodon* is certainly

present. Therefore Ziegler (1990) suggested that Stubersheim 3 might also represent the oldest record of *Desmanodon*, which would have immigrated together with the other insectivores.

SYSTEMATIC PART

Talpidae Fisher von Waldheim, 1817

***Desmanodon* Engesser, 1980**

Type species: *Desmanodon major* Engesser, 1980

Other species included: *Desmanodon minor* Engesser, 1980
Desmanodon meuleni Doukas, 1986
Desmanodon antiquus Ziegler, 1985
Desmanodon ziegleri n.sp.
Desmanodon burkarti n.sp.
Desmanodon daamsi n.sp.

***Desmanodon ziegleri* n.sp.** (plate 1, figs. 1–8)

Derivatio nominis: This species is named in honour of Dr. Reinhard Ziegler (Stuttgart), who published several important papers on the insectivores from the Lower Miocene of S. Germany.

Diagnosis: *Desmanodon ziegleri* is a medium-sized species of *Desmanodon* (M2 = 1.74). The mesostyle of the upper molars is incompletely to well divided with the two cusplets standing closely together. The talonid of the m1 is only somewhat wider than the trigonid. The protoconule on the M1 and M2 is always present. The pectoral process of the humerus is pronounced.

Differential diagnosis: *D. ziegleri* is clearly smaller than *D. minor* and *D. major*. It is somewhat larger than *D. meuleni* and comparable in size to *D. antiquus*. The width of the talonid of the m1 relative to the trigonid is less than in *D. minor* and *D. major*. *D. ziegleri* differs from all the other species of *Desmanodon* in always having a protoconule on the M1 and M2.

Type locality: Harami 1

Other localities with *Desmanodon ziegleri*: Ki 0, Ki 0'', Ki 3A, Ki 3B, Ha 3.

Type level: MN 2

Holotype: M2 sin. (Ha1 4049) (plate 1 fig. 6)

Description of the holotype: The outline of the occlusal surface is slightly

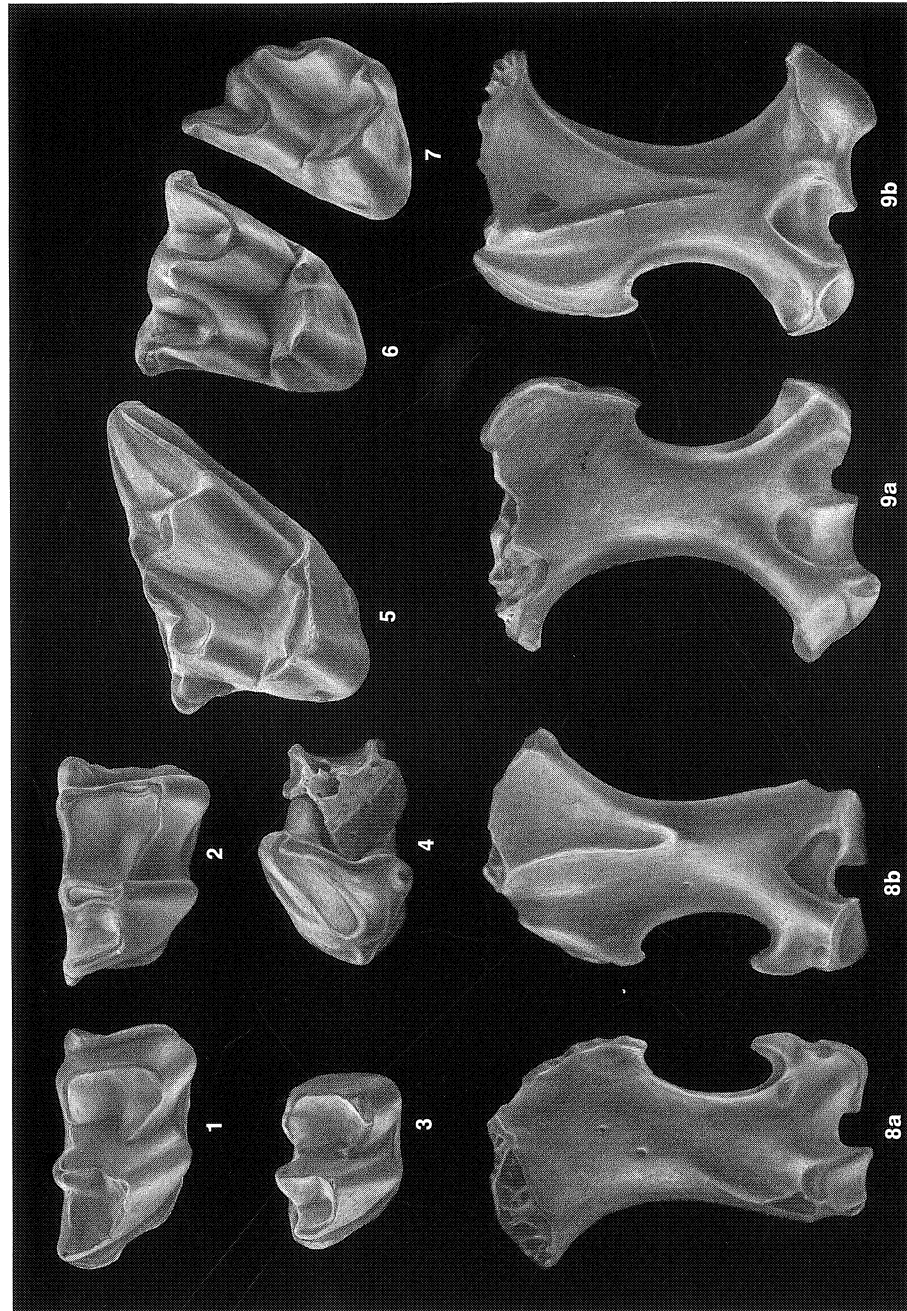


Plate 1. *Desmanodon zieglerei* n. sp. from Harami 1. 1. m3 (Ha 1 3931); 2. P4 (Ha 1 3983); 3. M1 (Ha 1 4011); 4. M2 (holotype) (Ha 1 4049); 5. M3 (Ha 1 4084) (all 17×); 6. humerus (Ha 1 4129) a. posterior view, b. anterior view; *Desmanodon burkartii* from Keseköy; 7. humerus (Ke 6800) a. posterior view, b. anterior view (8×).

asymmetrical. The protocone lies far to the anterior side of the molar. Directly in front of the protocone lies a small but distinct protoconule. The posterior arm of the protocone connects with the hypocone. The latter is a small cusplet just lingually of the metacone. The metacone is only somewhat higher and somewhat larger than the paracone. The anterior arm of the paracone bends near its end and forms a slightly protruding parastyle. The posterior arm of the paracone connects to the mesostyle. The division of the mesostyle is incomplete. The posterior arm of the metacone bends near its end and forms a small metastyle. The very narrow posterior cingulum connects the posterior arm of the hypocone to the metastyle. There is a short anterior cingulum that runs from the parastyle to the anterior flank of the paracone. There is a small lingual cingulum between the base of the protocone and the base of the hypocone.

Measurements: The measurements are listed in table I.

Table Ia. Measurements of the lower elements of *Desmanodon ziegleri* (Kilçak and Harami localities) and of *Desmanodon burkartii* (Kecseköy).

tooth	loc	N	Length		Width	
			range	mean	range	mean
p4	Ke	6	1.20-1.37	1.30	0.73-0.93	0.82
	Ha3	-				
	Ha1	-				
	Ki3A	-				
	Ki0''	1		1.10		0.66
	Ki0	-				
m1	Ke	10	1.86-1.98	1.93	1.14-1.35	1.26
	Ha3	-				
	Ha1	-				
	Ki3A	1		1.79		1.16
	Ki0''	1		1.77		1.18
	Ki0	-				
m2	Ke	6	1.93-2.14	2.08	1.20-1.44	1.29
	Ha3	1		1.91		1.13
	Ha1	-				
	Ki3A	-				
	Ki0''	-				
	Ki0	-				
m3	Ke	8	1.47-1.63	1.56	0.85-1.00	0.91
	Ha3	1		1.48		0.83
	Ha1	6	1.37-1.48	1.43	0.78-0.99	0.86
	Ki3A	-				
	Ki0''	1		1.51		0.89
	Ki0	1		1.52		0.84

Table Ib. Measurements of the upper elements of *Desmanodon ziegleri* (Harami and Kılçak localities) and of *D. burkarti* (Keseköy).

tooth	loc	N	Length		Width	
			range	mean	range	mean
P4	Ke	3	1.49–1.65	1.60	1.33–1.36	1.35
	Ha3	–				
	Ha1	1		1.31		1.01
	Ki3A	–				
	Ki0''	–				
	Ki0	–				
M1	Ke	6	2.32–2.68	2.53	1.49–1.69	1.55
	Ha3	–				
	Ha1	6	2.23–2.73	2.51	1.34–1.64	1.49
	Ki3A	–				
	Ki3B	1		2.34		1.53
	Ki0''	–				
M2	Ke	26	1.73–1.98	1.85	2.02–2.34	2.14
	Ha3	4	1.55–1.79	1.67	1.87–2.13	2.00
	Ha1	11	1.66–1.81	1.74	1.82–2.07	1.96
	Ki3A	–				
	Ki3B	1		1.64		2.06
	Ki0''	2	1.61–1.72	1.67	2.08–2.13	2.11
M3	Ke	9	1.06–1.56	1.18	1.62–1.78	1.72
	Ha3	2	1.13–1.17	1.15	1.63–1.75	1.69
	Ha1	6	1.04–1.16	1.10	1.46–1.74	1.61
	Ki3A	1		1.15		1.75
	Ki0''	–				
	Ki0	–				

Description

m3 (6) The outline of the molar surface is trapezoid. The trigonid is of the same length as the talonid and only somewhat wider. The protoconid is the highest cusp. The metaconid is somewhat lower than the protoconid. The paraconid is clearly lower than the metaconid.

The entoconid has about the same height as the paraconid. The hypoconid is somewhat lower than the entoconid. The oblique cristid ends against the middle of the protoconid-metaconid crest. There is a large entocristid, which is fused with the entoconid, giving the latter a blade-like appearance. The anterior cingulum is well developed. It runs along the base of the paraconid and continues as a very short lingual cingulum. There is a short labial cingulum between the base of the hypoconid and the base of the protoconid. In five out of

the six specimens there is also a very weak posterior cingulum at the base of the hypoconid.

P4 (3) The outline of the occlusal surface is sub-triangular. The labial side is convex; the anterior side is straight and the postero-lingual side is concave. The paracone is a large and very high cusp which makes up most of the P4. Its posterocrista is slightly S-curved. In worn specimens it becomes straight. In the posterolingual corner the posterocrista bends and continues as the posterolingual cingulum. Directly in front of the paracone lies a very small parastyle. The protocone is very low. It lies lingually of the tip of the paracone. In one specimen it is a distinct, cone-shaped cusplet (morphotype A). It appears as a ridge on the lingual cingulum in the second specimen (morphotype C). In the third specimen the protocone is broken off. There is an anterior cingulum connecting the protocone to the parastyle. The posterolingual cingulum connects the protocone to the posterocrista of the paracone. The labial cingulum is narrow.

M1 (7) The outline of the occlusal surface is subtriangular. The protocone lies far to the lingual side. The anterior arm is short and ends against the base of the paracone. The protoconule is a thick bulge in the anterior arm of the protocone. The posterior arm of the protocone connects to the small hypocone, which lies near the base of the metacone. The posterior arm of the hypocone connects to the posterior cingulum. The paracone is of the same height as the protocone. In four specimens the parastyle is preserved. It is a small cusplet which lies on a sharply protruding extension antero-labially of the paracone. The curved posterior arm of the paracone connects to the mesostyle. The division of the mesostyle is incomplete. The posterior arm of the metacone is 50% longer than the anterior arm. It extends to the postero-labial corner of the molar.

The posterior cingulum is the best developed cingulum of the M1. It runs from the hypocone all along the base of the posterior arm of the metacone. There is a weak labial cingulum. In two out of the seven specimens it only runs along the metacone. In one out of the seven it is present only along the base of the paracone. In two specimens it runs all along the labial side. The other specimens are too damaged to observe the development of the cingulum. A very weak cingulum is present between the base of the protocone and the base of the hypocone. In two out of the seven specimens there is also a weak cingulum between the base of the protocone and the protoconule.

M2 (14) The remaining M2 from Harami 1 differ from the holotype mainly in the degree of division of the mesostyle and the development of the cingulums. The mesostyle is well divided in eight specimens; the division is incomplete in the other six. The posterior cingulum is interrupted in three out of the fourteen specimens. Nine out of the fourteen specimens have a short patch of cingulum between the base of the protocone and the base of the metacone. A short cin-

gulum between the protocone and the protoconule is present in three out of the fourteen specimens.

M3 (6) The outline of the occlusal surface is subtriangular. The protocone is the largest cusp; it occupies the entire lingual part of the molar. Its anterior arm ends at the base of the paracone, from which it is separated by a small valley. The protoconule is a small widening of the anterior arm of the protocone. The posterior arm ends at the base of the hypocone. The latter is a distinct, cone-shaped cusplet. The paracone is of the same height as the protocone. The end of the anterior arm of the paracone bends forward to form a small parastyle. The two arms of the paracone have about the same length. The mesostyle is well divided in three specimens. The division is incomplete in the other three. The metacone is somewhat lower than the protocone and the paracone. There are no cingulums.

Humerus (1) The humerus is relatively slender. It has the long teres tubercle which is typical for the genus *Desmanodon*. The areas around the caput and the capitulum are damaged. In anterior view the pectoral process stands out. It is surrounded by a ridge. Pectoral process and teres tubercle both reach to about halfway the shaft. The supratrochlear fossa is deep. On the posterior side there is a strong ridge which runs from the ectepicondyle in the direction of the teres tubercle. The olecranon fossa is relatively shallow.

Other localities

The available material of *Desmanodon zieglerei* from the other localities is indicated in table II. The p4, m1 and m2 have not been found in the type locality and are described in full. The variation within the other elements is discussed.

p4. The outline of the occlusal surface is elliptical. The premolar consists mainly of the very high protoconid. This cusp is triangular in occlusal view. The posterior and lingual flanks are straight, the labial side is slightly convex. Behind the protoconid lies a short talonid, which is bordered posteriorly by a high cingulum. The labial cingulum is well developed, there is no cingulum on the lingual side.

Table II. Elements and their numbers of *Desmanodon zieglerei* n.sp. from localities other than the type locality.

	p4	m1	m2	m3	P4	M1	M2	M3	humerus
Kilçak 0	1	–	–	1	–	–	–	–	–
Kilçak 0''	–	1	–	1	–	2	2	1	1
Kilçak 3A	–	1	–	–	–	–	–	1	–
Kilçak 3B	–	–	–	–	–	1	1	–	–
Harami 3	–	–	1	1	–	–	5	2	–

m1. The outline of the occlusal surface is trapezoidal. The talonid is clearly wider than the trigonid. In the specimen from Kilçak 0'', the trigonid and talonid have the same length. The talonid of the m1 from Kilçak 3A is shorter than the trigonid. The cusps are high and pointed. The two arms of the protoconid are straight. The trigonid basin is narrow. The entoconid and the hypoconid have about the same height. There is neither a metacristid nor an entocristid. The oblique cristid ends against the middle of the protoconid-metaconid crest. Directly behind the entoconid lies a very strong entostylid. There is no parastylid. The posterior cingulum is strong. The labial and anterior cingulums are well developed.

m2. The outline of the occlusal surface is trapezoidal. The cusps are high and pointed. The trigonid and talonid have about the same length and width. The protoconid is the highest cusp. The arms connecting the protoconid to the metaconid and paraconid are straight. The entoconid and the hypoconid are of about the same height, somewhat higher than the paraconid, but lower than the metaconid. The well-developed entocristid is completely fused with the entoconid, giving this cusp a blade-like appearance. There is no metacristid. The oblique cristid ends against the middle of the protoconid-metaconid crest. The parastylid and the entostylid are well developed, but only slightly protruding. The anterior cingulum is very wide. The posterior cingulum and the labial cingulum are well developed.

m3. A posterior cingulum is found in the specimens from Kilçak 0 and Kilçak 0'', but not in the specimen from Harami 3. The latter has a very short lingual cingulum.

The division of the mesostyle is incomplete in one of these specimens. The mesostyle is well divided in the other, as well as in the M1 from Kilçak 3B. None of these specimens has lingual cingulums; one of the M1 from Kilçak 0'' has a labial cingulum which runs from the parastyle to the mesostyle.

M2. The division of the mesostyle of the M2 from Harami 3 and Kilçak 0'' is incomplete. The specimen from Kilçak 3B is too worn to assess the original division of the mesostyle. The two specimens from Kilçak 0'' have a weak but continuous posterior cingulum. This cingulum is interrupted in Harami 3 and Kilçak 3B. Lingual cingulums are only found in two M2 from Harami 3.

M3. The mesostyle is well divided in the specimen from Kilçak 3A. The division is incomplete in the other M3. The specimens from Kilçak 0'' and Kilçak 3A lack the protoconule. One of the M3 from Harami 3 has lingual cingulums on both sides of the protocone.

Humerus. The humerus from Kilçak 0'' agrees well with the humerus from the type locality. Unfortunately this humerus is also damaged in the region

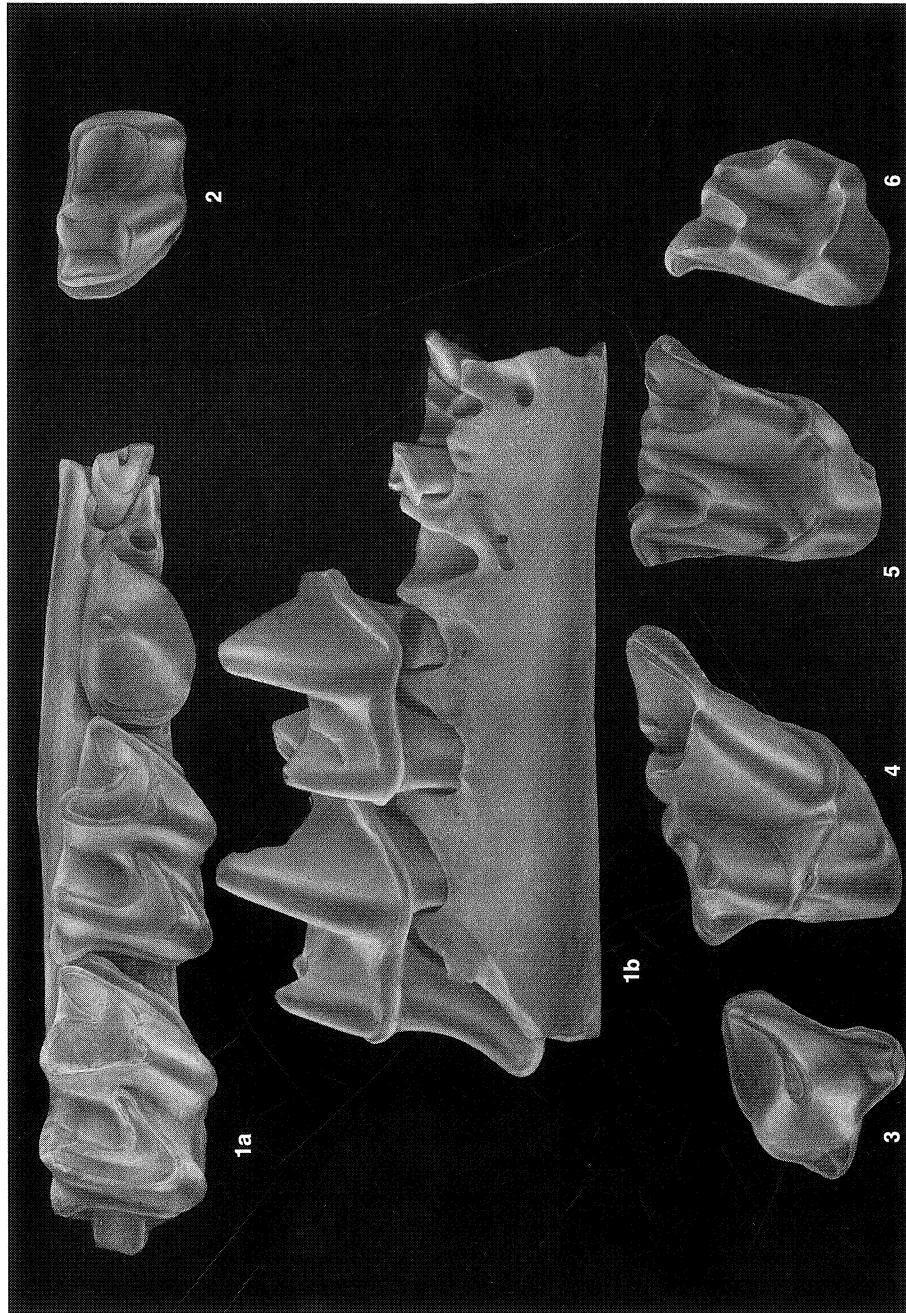


Plate 2. *Desmanodon burkarti* n. sp. from Keseköy. 1. mandible with p4-m2 (Ke 6742); a. occlusal view; b. lingual view (p4 was lost between SCAN sessions). 2. m3 (Ke 6757); 3. P4 (Ke 6761); 4. M1 (Ke 6765); 5. M2 (holotype) (Ke 6771); 6. M3 (Ke 6791) (all 17×).

around the caput and the capitulum, so that it does not provide additional information.

***Desmanodon burkarti* n. sp.** (plate 1 fig. 9; plate 2 figs. 1–6)

Derivatio nominis: This species is named in honour of Dr. Burkart Engesser (Basel), who described the first species of *Desmanodon*.

Diagnosis: *Desmanodon burkarti* is a medium-sized species of *Desmanodon* (M2 = 1.85). The talonid of the m1 is only somewhat wider than the trigonid. The mesostyle of the upper molars is clearly divided. The protoconule is usually present on the M2, rarely on the M1. The cingulums on the p4 and P4 are well developed.

Differential diagnosis: *D. burkarti* is smaller than *D. minor* and *D. major*. Furthermore, it differs from these species in the width in the talonid of the m1 with respect to the trigonid, which is less in *D. burkarti* than in *D. minor* and *D. major*. *D. burkarti* is somewhat larger than *D. meuleni* and *D. zieglerei*. It differs from all other species of *Desmanodon* except *D. zieglerei* in usually having a protoconule on the M2. *D. burkarti* differs from *D. zieglerei* in the absence of a protoconule on the M1 and a stronger division of the mesostyle on the upper molars.

Type locality: Keseköy

Type level: MN 3

Holotype: M2 sin. (Ke 6771) (plate 2 fig. 5)

Description of the holotype: The outline of the occlusal surface is slightly asymmetrical. The width of the molar is much larger than its length. The protocone lies closely to the anterior side. It has a short anterior arm, which ends near the base of the paracone. The protoconule is a weak cusplet, which is incorporated in the anterior arm of the protocone. The posterior arm of the protocone connects to the hypocone. The hypocone is very small. It lies at the base of the metacone.

The anterior arm of the paracone and posterior arm of the metacone bend near their ends to form the parastyle and metastyle respectively. The posterior arm of the paracone and the anterior arm of the metacone connect to the mesostyle. The mesostyle is clearly divided. A very weak posterior cingulum connects the hypocone to the metastyle. A short but wide anterior cingulum runs from the parastyle to halfway the anterior arm of the paracone. There is a small patch of cingulum between the base of the protocone and the base of the hypocone.

Measurements: The measurements are listed in table I.

Description

p4 (6) The outline of the occlusal surface is sub-elliptical. The premolar consists mainly of the very large and high protoconid. The tip of this cusp lies in the middle of the premolar. The anterior face of the protoconid is rounded, the posterior flank is rather flat. There runs a weak posterocristid along the postero-lingual side of the protoconid. There is a very small cusplet on the antero-lingual side of the protoconid. Behind the protoconid lies a large flattening (talonid) which is bordered by a strong posterior cingulum. The labial cingulum is continuous in four out of the six specimens. All of these also have a continuous lingual cingulum. The two other specimens have a small cingulum along the antero-lingual flank of the protoconid only.

m1 (10) The outline of the occlusal surface is quadrangular. The talonid is clearly wider than the trigonid. Talonid and trigonid have the same length. The molar has high cusps. The protoconid is the highest cusp. The two arms of this cusp are straight. The tip of the protoconid lies labially of the metaconid, which is somewhat lower than the former cusp. The paraconid is much lower than the metaconid. The entoconid and the hypoconid are of about the same height as the metaconid. The oblique cristid ends against the middle of the protoconid-metaconid crest. In some specimens there is a weak entocristid; in other specimens the entocristid is absent. There is no metacristid. The anterior and labial cingulums are well developed; the posterior cingulum is strong. Directly behind the entoconid lies a well-developed entostylid, which protrudes slightly. There is no parastylid.

m2 (6) The outline of the occlusal surface is trapezoidal. The cusps are high and pointed. The talonid is only somewhat longer than the trigonid. Talonid and trigonid are of the same width. The protoconid is the highest cusp. Its tip lies labially of the tip of the metaconid. The arms connecting the protoconid to the metaconid and paraconid are straight. The paraconid is lower than the metaconid. The hypoconid and the entoconid are of about the same height as the paraconid. The entocristid is well developed; the metacristid is absent. The oblique cristid ends just lingually of the middle of the protoconid-metaconid crest. The re-entrant valley is wide and deep. The anterior cingulum is very strong. The labial cingulum and the posterior cingulum are well developed. The parastylid and the entostylid protrude slightly.

m3 (8) The outline of the occlusal surface is trapezoidal. The talonid is only slightly narrower than the trigonid. The latter is shorter than the talonid. The protoconid is the highest cusp. The arms connecting the protoconid to the metaconid and the blade-like paraconid are straight. The hypoconid and the entoconid are low. There is a weak entostylid. The oblique cristid ends against the middle of the protoconid-metaconid crest. The anterior cingulum is strong. There is a short labial cingulum which borders the re-entrant valley.

P4 (3) The outline of the occlusal surface is sub-triangular. The antero-lingual and postero-lingual sides are strongly concave. The premolar consists mainly of the very large paracone. The tip of this cusp lies in front of the middle of the P4. The posterocrista is slightly curved. In front of the paracone lies a low parastyle on a rather large anterior flattening. The protocone lies on a large flange lingually of the tip of the paracone. It is a very low cusplet. The cingulums are well developed. They surround the entire P4 and are only interrupted at the labial side of the paracone. In one out of the three specimens the cingulum is also interrupted at the antero-lingual side of the paracone.

M1 (5) The outline of the occlusal surface is sub-triangular. The protocone forms the antero-lingual corner of the molar. Its short anterior arm ends against the base of the paracone. In unworn specimens a small protoconule may appear as a slight thickening of the anterior arm. The posterior arm of the protocone runs along the base of the metacone and continues as the posterior cingulum. The weak hypocone is completely incorporated in this arm.

The paracone is of the same height as the protocone. The well-developed parastyle lies directly in front of the paracone. The posterior arm of the paracone is slightly curved and connects to the mesostyle. The mesostyle is clearly divided. The posterior cusplet of the mesostyle connects to the straight anterior arm of the metacone. The posterior arm of the metacone is about 50% longer than the anterior arm. It extends to the postero-labial corner of the M1. The posterior cingulum is well developed. It runs along the posterior arm of the metacone and continues as a short labial cingulum. In one out of the five specimens there is a small patch of lingual cingulum between the base of the protocone and the base of the hypocone.

M2 (15) The other M2 differ from the holotype in the development of the protoconule and the cingulums. The protoconule is absent in three out of the fifteen specimens. The posterior cingulum runs along the flank of the metacone in six out of the fifteen specimens. This cingulum is interrupted or even absent in the other specimens. A short patch of postero-labial cingulum is present in four out of the fifteen specimens.

M3 (9) The outline of the occlusal surface is sub-triangular. The protocone occupies the complete lingual part of the molar. Its anterior arm ends near the base of the paracone from which it is separated by a narrow valley. In one out of the nine specimens a protoconule appears as a small widening of the anterior arm of the protocone. The posterior arm of the protocone ends at the base of the hypocone. The hypocone is a small cusplet which lies lingually of the metacone. The two arms of the paracone are about of the same length. The anterior arm bends to form a protruding parastyle. The posterior arm connects to the mesostyle, which is clearly divided. The posterior part of the mesostyle connects to the anterior arm of the metacone. In some specimens there is a

small patch of cingulum between the parastyle and the anterior arm of the paracone.

Humerus (1) The humerus of *Desmanodon burkarti* is clearly longer and more robust than that of *D. ziegleri*. It is particularly wide at its distal end. The area around the caput is damaged. The teres tubercle is very long. The pectoral process is not as pronounced as in *D. ziegleri*. Instead it lies in one plane with the rest of the shaft and is separated from it by a faint ridge. In contrast to *D. ziegleri*, the pectoral process reaches further distally than the teres tubercle. The posterior ridge is also much less developed in *D. burkarti* than in *D. ziegleri*. In contrast to the latter species the ridge lies more to the side of the humerus and ends about halfway the shaft. The olecranon fossa is deep.

Desmanodon minor Engesser, 1980 (plate 3 figs. 1–7)

Type locality: Sariçay

Locality: Çandır

Measurements: The measurements are listed in table III.

p4 (1) The outline of the occlusal surface is sub-rectangular. The premolar consists mainly of the large protoconid. The tip of the protoconid lies close to the lingual side. The lingual flank of the protoconid is straight; the labial side is convex. A faint ridge runs along the posterolingual edge of the cusp. Behind the protoconid is a very short talonid, which is bordered by a high posterior cingulum. A short longitudinal ridge connects the posterior cingulum to the posterior flank of the protoconid.

m1 (3) The talonid is much wider than the trigonid. Talonid and trigonid have the same length. Two out of three specimens have a weak entocristid. There is

Table III. Measurements of *Desmanodon minor* from Çandır.

tooth	N	Length		Width	
		range	mean	range	mean
p4	1		0.93		0.62
m1	3	1.86–1.92	1.89	1.33–1.43	1.40
m2	1		2.09		1.30
m3	3	1.46–1.59	1.54	0.75–0.92	0.85
P4	1		1.76		1.35
M1	3	2.48–2.95	2.72	1.60–1.86	1.74
M2	12	1.82–2.18	2.02	2.12–2.52	2.36
M3	3	1.19–1.24	1.22	1.72–1.92	1.81

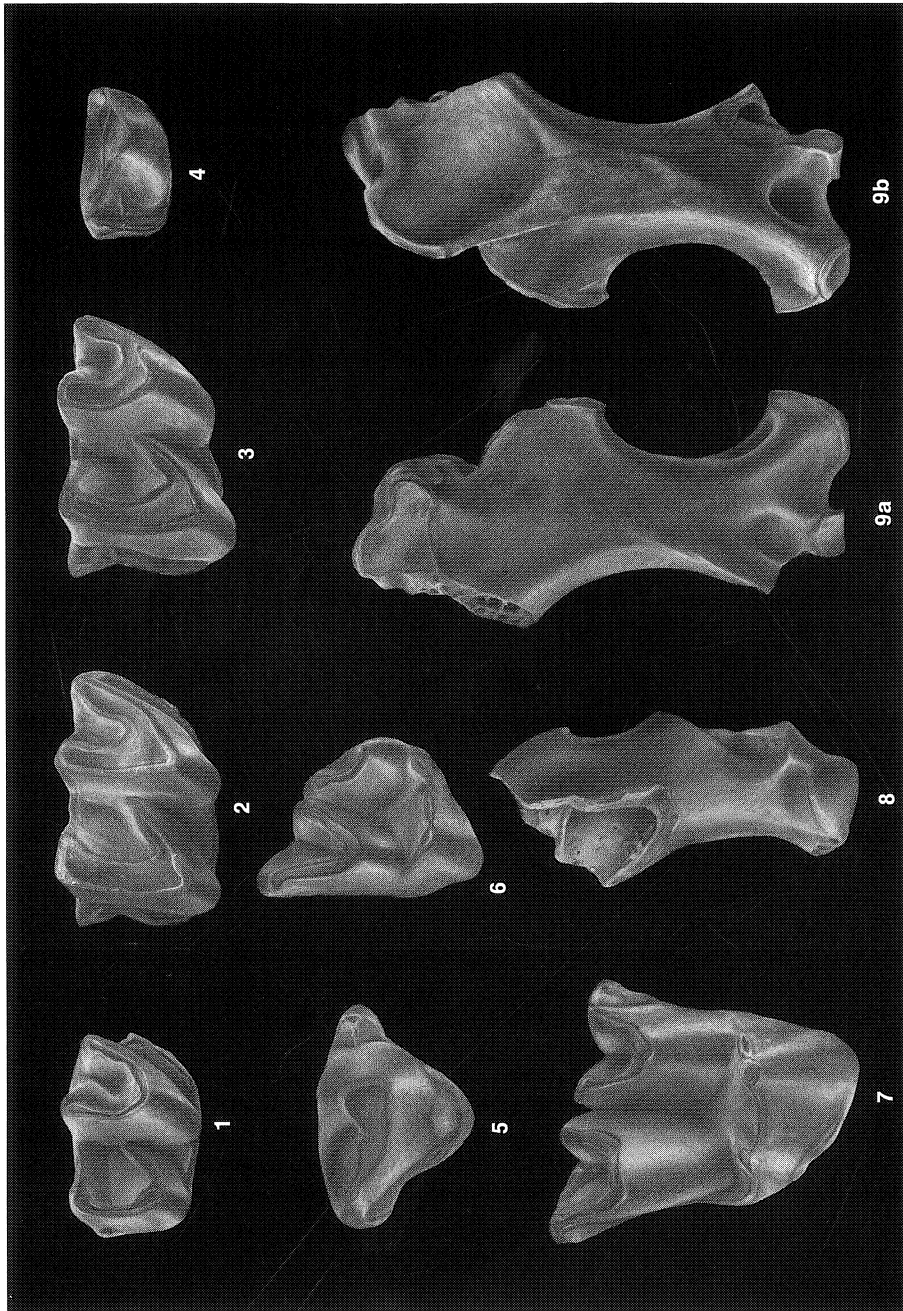


Plate 3. *Desmanodon minor* from Çandır (specimens unnumbered). 1. m3; 2. m2; 3. m1; 4. p4; 5. P4; 6. M2 (17×); 7. humerus fragm. anterior view. *Desmanodon daamsi* n. sp.; 8. humerus (RM 585) a. posterior view, b. anterior view (8×).

no metacristid. The oblique cristid ends against the middle of the protoconid-metaconid crest. The labial cingulum, which borders the re-entrant valley, and the posterior cingulum are well developed. The anterior cingulum is narrow.

m2 (1) The talonid is as wide as the trigonid, but somewhat shorter. The cusps are high and pointed. The talonid basin is bordered by a well-developed entocristid. There is no metacristid. The oblique cristid ends against the middle of the protoconid-metaconid crest. The re-entrant valley is wide and deep. The cingulums are well developed.

m3 (3) The talonid is slightly more narrow and longer than the trigonid. The cusps of the talonid are very low. The oblique cristid ends lingually of the middle of the protoconid- metaconid crest. The anterior cingulum is strong. The re-entrant valley is bordered by a labial cingulum. In two out of three specimens there is a small bulge in the flank of the entoconid at the position of the entostylid.

P4 (1) The outline of the occlusal surface is triangular. The premolar consists mainly of the large paracone. The posterocrista runs from the tip of the paracone backwards and is slightly curved. The parastyle is small. The protocone is a low, conical cusp which lies on the rather large lingual extension. The only cingulum is the well-developed postero-lingual cingulum.

M1 (3) The outline of the occlusal surface is quadrangular rather than triangular. The hypocone is formed by a small widening of the posterior arm of the protocone. The protoconule is absent. The two cusplets of the mesostyle stand far apart and a wide valley separates the paracone and metacone. The posterior cingulum is well developed. There is a short cingulum at the base of the protocone.

M2 (14) The M2 has a rather robust appearance. The hypocone is distinct but poorly individualised. Two of the unworn specimens have a very small protoconule. The mesostyle is clearly divided with a deep valley separating the paracone and metacone. In twelve of the fourteen specimens there is a short cingulum directly behind the protocone. Three of these also have a short cingulum in front of the protocone. The two remaining specimens have no lingual cingulums.

M3 (3) The hypocone of the M3 is a strongly individualised cusplet, just lingually of the metacone. The anterior arm of the protocone is very short. The protoconule is absent. The mesostyle is clearly divided.

Humerus (1) Only a fragment of a humerus has been found. The proximal part and the entepicondyle are broken off. The teres tubercle is long. The trochlea is rather shallow.

Remarks on the Anatolian species of *Desmanodon*

The finds of *Desmanodon* in the Lower Miocene of Anatolia extend the strati-

graphic range of this genus considerably downwards. So far, the oldest certain occurrences were from MN 4 (*D. antiquus* in several southern German localities), although, as we noted in the section 'review of literature', the genus may have already been present in Stubersheim 3 (MN 3), a locality which did not yield any humeri. Fortunately, we know the humerus of both *D. ziegleri* (Harami 1 and Kilçak 0") and of *D. burkarti* (Keseköy). The oldest occurrence of *Desmanodon* described in this paper is *D. ziegleri* from Kilçak 0 (MN 2). *Desmanodon*-like molars have been found in localities in the Kargi section (MN 1). No humeri have been found in these localities.

Desmanodon ziegleri and *D. burkarti* provide good structural ancestors to the Middle Miocene species of *Desmanodon*. A lineage *D. ziegleri*–*D. burkarti*–*D. minor*–*D. major* would be characterized by an increase in size, a gradual reduction of the protoconule and a widening of the mesostyle on the upper molars. In the lower molars the talonid of the m1 becomes wider with respect to its trigonid. The humerus becomes more robust. The pectoral process and tubercle process extend more distally: in *D. ziegleri* both processes reach to the middle of the shaft. In *D. burkarti* and *D. minor* the pectoral process reaches further than the tubercle teres. In *D. major* the tubercle teres nearly extends to the same height as the pectoral process. *D. burkarti*, *D. minor* and *D. major* have a P4 with a small parastyle and a large protoconal flange which bears a conical protocone. This type of P4 (morphotype A) is not known from Europe, where morphotype B and C are found (van den Hoek Ostende, 1989). Morphotype A is also found in one of the P4 of *D. ziegleri* from Harami 1, but the other complete P4 is clearly of morphotype C.

Since the, otherwise European, morphotype C is found in *D. ziegleri*, this species can also be considered ancestral to *D. antiquus*. This species has completely lost the protoconule, and often has a protocristid on the p4. The teres tubercle and the pectoral process extend far to the distal end. The humerus of *D. antiquus* resembles in this respect that of *D. major*. Ziegler's (1985) suggestion that *D. antiquus* may have been ancestral to *D. minor* has become unlikely, because a lineage *D. ziegleri*–*D. antiquus*–*D. minor* would imply a number of evolutionary reversals. The protoconule of the upper molars would be lost and reappear, the protocristid of the p4 would develop and be lost, and the teres tubercle would become longer and than again shorter. Assuming that *D. major* descends from *D. minor* it would become longer again.

On the basis of the strong similarity between the dentitions of the Central European species of the two genera, I suggested that *Desmanodon* descended from *Paratalpa*. The finds of *Desmanodon*, in the Lower Miocene of Anatolia show that the genus developed elsewhere, and thus this suggestion is falsified. Nevertheless, the two genera seem closely related. *Desmanodon* may have originated from an Oligocene species of *Paratalpa*, or the two genera could share a common ancestor. One of the reasons for placing the European species of *Desmanodon* and *Paratalpa* in one lineage, was that the species of these genera have similar morphotypes of P4 (morphotype B and C). Morphotype C is now considered a synplesiomorphic character, found in the oldest species of both

genera. The morphotype A, which is found in Anatolia and the Greek locality Aliveri, is derived. The oldest record of this type is in *Desmanodon zieglerei* (MN 2), a species which may also still have the primitive type C. Morphotype B is also considered a derived character, which developed separately in *Paratalpa* and *Desmanodon* (see discussion).

The *Desmanodon* from Paşalar, classified by Engesser (1980) as *D. cf. minor*, has later been attributed to *D. antiquus* by Ziegler (1985) and to *D. meuleni* by Doukas (1986). The presence of *D. minor* in the locality Çandir, which is of about the same age as Paşalar, supports the original identification of Engesser.

***Desmanodon/Paratalpa* in Spain**

***Desmanodon daamsi* n. sp.** (plate 3 fig. 9; plate 4 figs. 1–8)

Derivatio nominis: This species is named after Prof. Dr. Remmert Daams (Madrid), who collected most of the material in the Daroca–Calamocha area (Calatayud–Teruel Basin).

Diagnosis: *Desmanodon daamsi* is a medium sized species of *Desmanodon* ($M2 = 1.93$). The cusps tend to be somewhat inflated. The division of the mesostyle of the upper molars is incomplete. The hypocone is poorly developed and may be absent. The humerus has a relatively long and slender shaft.

Differential diagnosis: *Desmanodon daamsi* is smaller than *D. minor* and *D. major*, and larger than *D. meuleni* and *D. zieglerei*. It differs from all other species of *Desmanodon* in its poorly developed hypocone on the M1 and M2, the somewhat inflated cusps and the incomplete division of the mesostyle. The humerus has a shaft which is relatively longer than in other species of the genus.

Type locality: Rubielos de Mora

Type level: MN 4

Holotype: M2 dext. (RM 562) (plate 4 fig. 4)

Description of the holotype: The outline of the occlusal surface is slightly asymmetrical. The protocone is large and somewhat bulbous. Its anterior arm ends at the base of the paracone. The protoconule is absent. The hypocone is a weak cusplet which lies at the end of the posterior arm of the protocone, just lingually of the base of the metacone. The labial part of the M2 is wider than the lingual part. The labial cusps are of about the same size. The metacone is somewhat higher than the paracone. The anterior arm of the paracone bends near its end and forms a small parastyle. The division of the mesostyle is incomplete. The posterior cingulum runs from the metastyle to halfway the flank

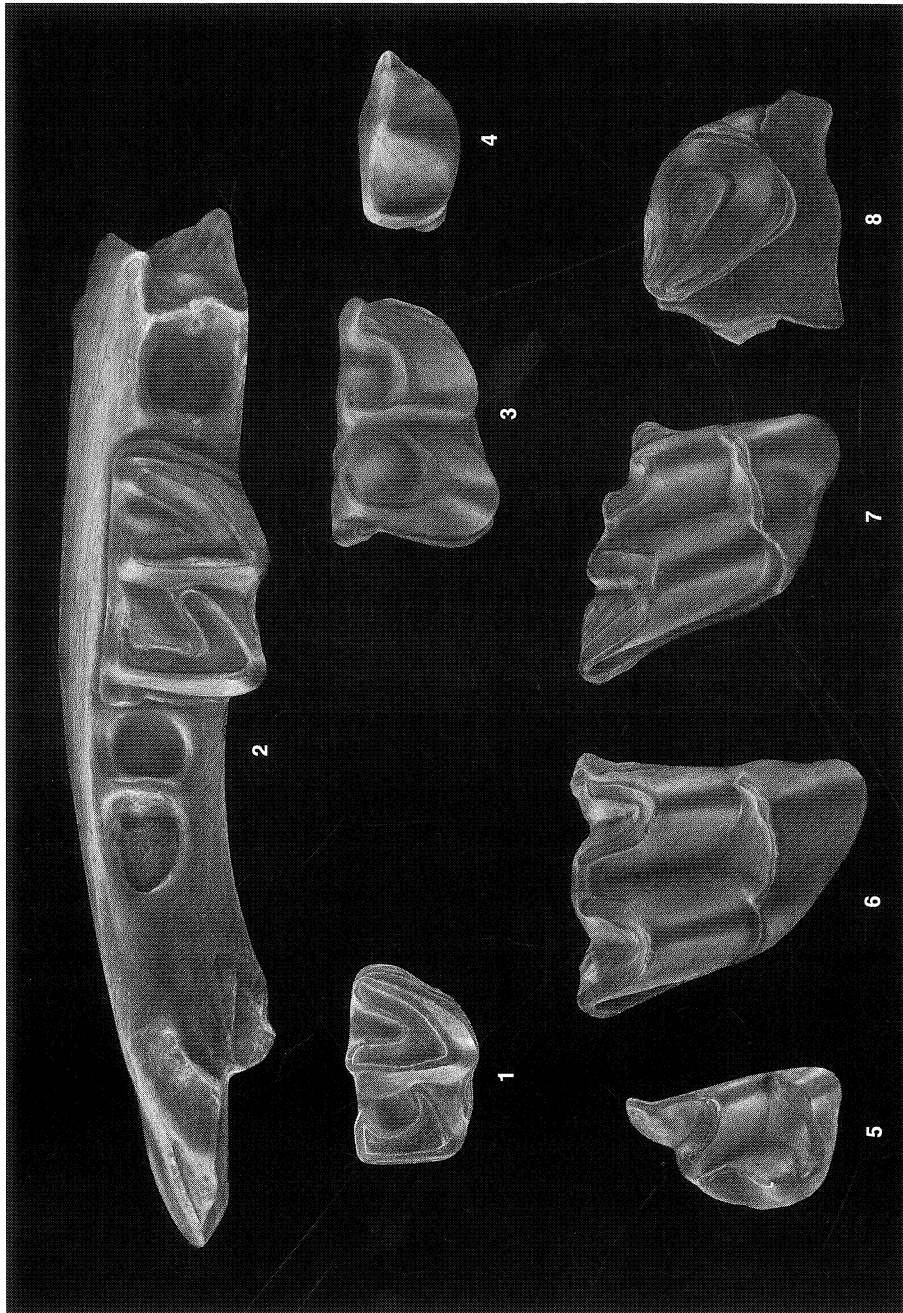


Plate 4. *Desmanodon daamsi* n. sp. from Rubielos de Mora. 1. m3 (RM 531); 2. mandible with m2 (RM 522); 3. m1 (RM 514); 4. p4 (RM 512); 5. M3 (RM 583); 6. M2 (holotype) (RM 562); 7. M1 (RM 557); 8. P4 with part of maxillary (RM 542) (all 17 \times).

of the metacone. There is a short anterior cingulum near the parastyle. There are no lingual cingulums.

Measurements: The measurements are listed in table IV.

Table IV. Measurements of *Desmanodon daamsi* n.sp. from Rubielos de Mora.

tooth	N	Length		Width	
		range	mean	range	mean
m1	2	1.95–1.99	1.97	1.34–1.40	1.37
m2	3	2.00–2.09	2.04	1.20–1.30	1.26
P4	1		1.71		1.27
M1	7	2.52–2.84	2.66	1.46–1.80	1.68
M2	5	1.80–1.98	1.93	2.22–2.42	2.32
M3	13	1.03–1.27	1.19	1.54–1.89	1.77

Description

p4 (2) The last lower premolar is a simple tooth which consists mainly of the large, triangular protoconid. There is a small bulge on the anterior side of the protoconid. Behind the protoconid lies a very short talonid which is bordered by a posterior cingulum.

m1 (2) The talonid is somewhat wider and shorter than the trigonid. The paraconid lies at the end of a long paralophid. The entoconid and protoconid are somewhat inflated. The entocristid is well developed; there is no metaacristid. The oblique cristid ends against the middle of the protoconid-metaconid crest. The entostylid is well developed but protrudes only moderately. There is no parastylid. The posterior cingulum and anterior cingulum are well developed. The narrow labial cingulum is interrupted at the base of the protoconid.

m2 (5) The talonid is somewhat shorter than the trigonid. The talonid and trigonid are of the same width. The paralophid is long. Entoconid and protoconid are somewhat inflated. The entocristid is well developed; the metaacristid is absent. The oblique cristid ends just lingually of the middle of the protoconid-metaconid crest. The entostylid is small and protrudes slightly. The parastylid is a blade-like cusplet on the anterior cingulum. The cingulum is well developed on the anterior and posterior side. The labial cingulum is weak.

m3 (5) The talonid is of the same length as the trigonid in three specimens, longer in the other two. It is only slightly more narrow than the trigonid. The oblique cristid ends against the middle of the protoconid-metaconid crest. The entocristid is strong. The anterior cingulum is very well developed. The re-entrant valley is bordered by a weak labial cingulum.

P4 (1) The only P4 is very worn. It consists mainly of the large and bulbous

paracone, which is flanked lingually by a small, blade-like protocone and in front by an even smaller parastyle (morphotype C).

M1 (7) The outline of the occlusal surface is quadrangular. The lingual part is poorly developed: the protocone is relatively small, the protoconule is absent. The hypocone can be seen in unworn specimens only. The division of the mesostyle is incomplete. The posterior arm of the metacone is only somewhat longer than the anterior arm (ca. 25%). The parastyle is small and the only cingulum is the well-developed posterior cingulum.

M2 (6) The other M2 resemble the holotype, though the lingual part is generally even more narrow. The hypocone may disappear with wear. The mesostyle is well divided in one of the M2, the division is incomplete in the other five. The posterior cingulum is continuous in one out of the six specimens.

M3 (3) In occlusal view the outline of the M3 is a semi-circle. The anterior arm of the paracone is only slightly longer than the posterior arm. The hypocone is small to very small and partly fused with the metacone. The division of the mesostyle is incomplete.

Humerus (2) Two nearly complete humeri and three distal fragments have been preserved. The area around the caput is damaged in both specimens. The teres tubercle is long. The pectoral crest is very high and pronounced. The pectoral process is large. Pectoral ridge and pectoral tubercle are poorly developed. The shaft is relatively long and slender. The supratrochlear fossa is deep, the olecranon fossa rather shallow.

***Desmanodon/Paratalpa* from the Daroca–Calamocha area
(Calatayud–Teruel Basin)**

A number of Ramblian-lower Middle Aragonian (MN 2–MN 5) localities in the Daroca–Calamocha area yielded teeth which belong to either *Desmanodon* or *Paratalpa*. Since no humeri have been encountered, the molars cannot be identified to genus. The material of the largest assemblage, that of La Col C, is described below in detail. The differences between the material from the other localities (table V) and that of La Col C is discussed afterwards, and the P4, which is not present in La Col C, is described. The measurements of the Daroca–Calamocha mole are given in table VI.

La Col C (plate 5, figs. 1–7)

p4 (7) The premolar consists mainly of the large, triangular protoconid. There is a small bulge on the anterior side of the protoconid. The rear of the p4 is bordered by a posterior cingulum. In one out of the seven specimens there is a small flattening (talonid) between the posterior ridge and the protoconid. This specimen also has a small protocristid.

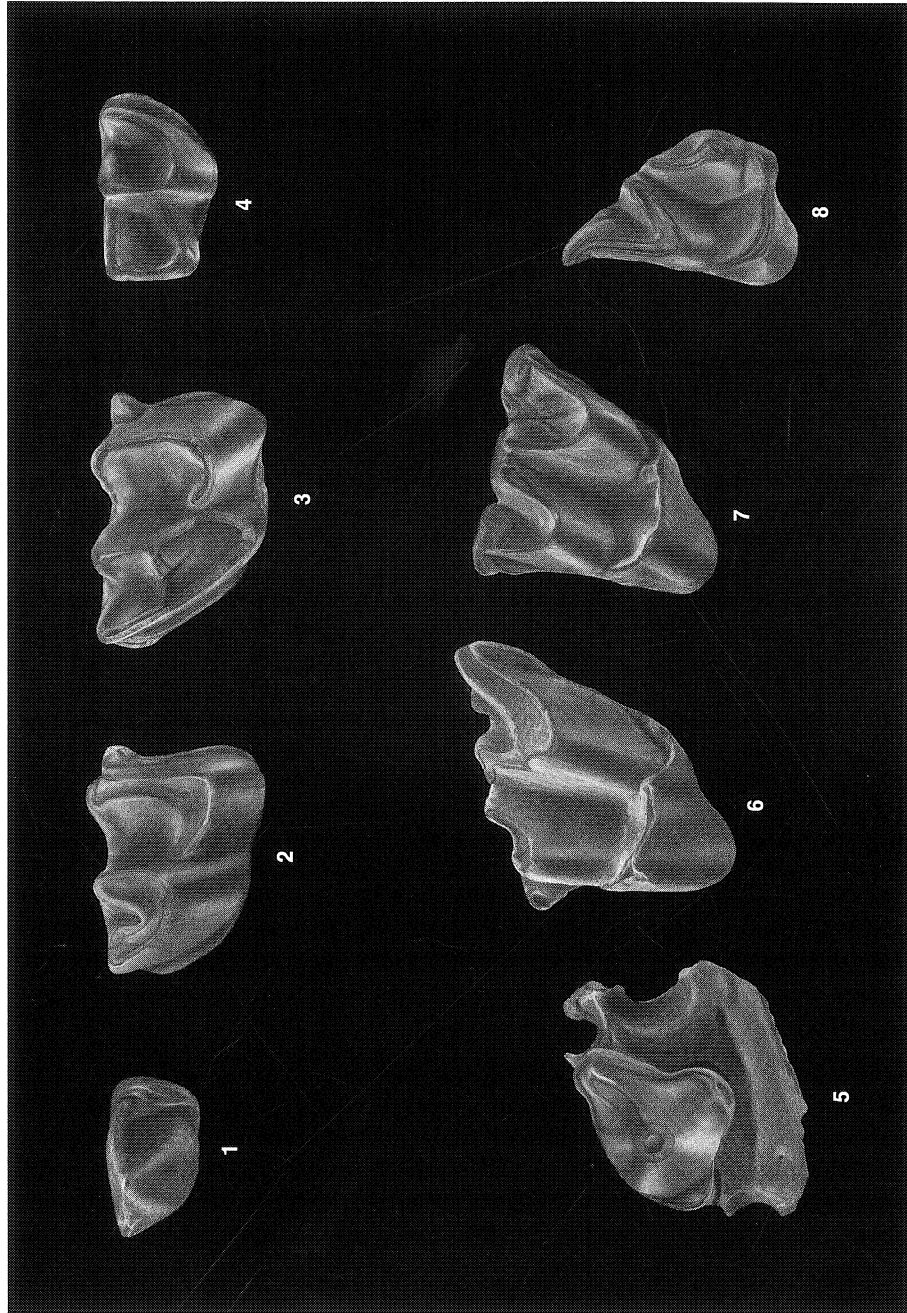


Plate 5. *Desmanodon/Paratalpa* from La Col C. 1. p4 (Col C 147); 2. m1 (Col C 116); 3. m2 (Col C 123); 4. m3 (Col C 141); 5. M1 (Col C 153); 6. M2 (Col C 166); 7. M3 (Col C 177) (all 17 \times).

m1 (7) The talonid is as long as the trigonid, and only somewhat wider. The entocristid is well developed in six of the seven specimens. The oblique cristid ends against the middle of the protoconid-metaconid crest or somewhat la-

Table V. Elements and their numbers of *Desmanodon/Paratalpa* recovered from the various localities in the Daroca–Calamocha area.

	p4	m1	m2	m3	P4	M1	M2	M3
La Col D	6	7	5	–	–	4	1	–
La Col C	7	7	16	7	–	12	9	5
Fuente Sierra 4	–	3	–	3	–	–	3	–
Fuente Sierra 3	2	1	–	–	–	1	2	2
Fuente Sierra 2	–	–	–	–	–	2	2	–
Vargas 2B	–	–	–	–	–	5	1	2
Olmo Redondo 5	–	–	–	1	–	–	–	–
Vargas 1A	–	1	–	1	–	4	6	3
Vargas 4BB	–	2	–	–	1	3	3	7
Vargas 4A	2	–	1	–	–	5	2	4
Olmo Redondo 4A	–	–	1	–	–	–	–	1
San Roque 3	–	–	1	–	–	–	–	2
San Roque 5	–	1	–	–	–	1	2	–
San Marco	–	–	–	–	–	3	3	2
San Roque 1	–	1	–	–	–	1	1	–
San Roque 4B	–	–	–	–	–	1	1	–
San Roque 4A	–	–	2	1	–	1	1	–
Moratilla 1	2	4	1	5	–	2	1	–
Bañon 2	–	–	–	–	–	2	3	2
Agreda	2	3	1	2	–	3	10	6
Ramblar 5	–	–	–	–	–	–	1	–
Ramblar 7	1	1	1	–	1	1	1	–
Ramblar 3B	–	–	–	3	–	–	–	–
Valhondo 1	3	4	3	2	1	4	5	10
Ramblar 1	–	4	2	3	–	1	1	10
Navarete del Rio	–	–	1	–	1	3	–	3

bially of that point. There is no parastylid. The entostylid is small to well developed. The posterior and labial cingulums are well developed. In some specimens the labial cingulum is interrupted at the base of the protoconid.

m2 (16) The talonid and trigonid are of the same length and width. The entocristid is well developed. The oblique cristid ends against the middle of the protoconid-metaconid crest. The parastylid is almost completely incorporated in the anterior cingulum. The entostylid is small. The labial cingulum is weak. The anterior cingulum is weak to well developed. The posterior cingulum is well developed.

m3 (7) The talonid is narrower than the trigonid. Talonid and trigonid are of the same length. The entocristid is well developed. The oblique cristid ends against the middle of the protoconid-metaconid crest. The anterior cingulum is well developed. It bears the low, blade-like parastylid. The labial cingulum is weak.

Table VIa. Measurements of the lower dentition of *Desmanodon/Paratalpa* from the Daroca-Calamocha area.

element	loc	N	Length		Width	
			range	mean	range	mean
p4	Col D	5	1.04–1.25	1.18	0.70–0.83	0.75
	COL C	7	1.09–1.24	1.17	0.64–0.74	0.77
	FTE 3	1		1.19		0.70
	VRG4A	2	1.17–1.22	1.20	0.71–0.72	0.72
	Mor 1	1		1.27		0.87
	Agr	2	1.21–1.27	1.24	0.76–0.76	0.76
	Ram 7	1		1.25		0.81
	VH 1	3	1.23–1.36	1.31	0.76–0.84	0.79
m1	COL D	5	1.73–1.97	1.84	1.19–1.40	1.26
	FTE 4	3	1.77–1.83	1.79	1.22–1.26	1.24
	COL C	8	1.63–1.93	1.80	1.14–1.32	1.23
	VRG 1A	1		1.68		1.21
	VRG 4BB	2	1.83–1.85	1.84	1.29–1.34	1.32
	SR 5	1		1.70		1.05
	SR 1	1		1.96		1.23
	Mor 1	2	1.70–1.89	1.80	1.27–1.29	1.28
	Agr	3	1.90–2.02	1.95	1.24–1.36	1.31
	Ram 7	1		1.87		1.26
	VH 1	4	1.75–2.01	1.90	1.14–1.28	1.23
	Ram 1	4	1.70–1.83	1.80	1.14–1.22	1.17
	m2	COL D	5	1.92–2.02	1.98	1.18–1.38
COL C		14	1.79–2.03	1.90	1.02–1.32	1.15
VRG 4A		1		2.00		1.26
SR 3		1		1.80		1.23
OR 4A		1		1.87		1.22
Mor 1		4	1.89–1.97	1.92	1.23–1.25	1.24
Ram 7		1		2.08		1.18
VH 1		3	1.96–1.98	1.97	1.21–1.24	1.22
Ram 1		2	1.89–1.94	1.92	1.14–1.29	1.22
Nav		1		1.83		1.27
m3		FTE 4	3	1.35–1.40	1.37	0.78–0.80
	COL C	6	1.39–1.53	1.46	0.75–0.84	0.77
	VRG 1A	1		1.50		0.87
	SR 4A	1		1.48		0.76
	Mor 1	5	1.36–1.61	1.50	0.78–0.90	0.85
	Agr	2	1.49–1.57	1.53	0.81–0.90	0.86
	VH 1	2	1.40–1.45	1.43	0.71–0.75	0.73
	Ram 1	3	1.36–1.46	1.41	0.77–0.81	0.79

M1 (12) The outline of the occlusal surface is triangular. One out of the twelve M1 bears a protoconule. The hypocone is a poorly individualised cusp that lies on the posterior arm of the protocone. The hypocone may disappear

Table VIb. Measurements of the upper dentition of *Desmanodon/Paratalpa* from the Daroca-Calamocha area.

element	loc	N	Length		Width	
			range	mean	range	mean
P4	Ram 7	1		1.66		1.12
	VH 1	1		1.51		1.03
	Nav	1		1.60		1.28
M1	COL D	3	2.33-2.46	2.39	1.61-1.72	1.66
	COL C	12	2.33-2.64	2.48	1.52-1.67	1.57
	FTE 3	1		2.63		1.71
	FTE 2	32	2.42-2.59	2.50	1.56-1.70	1.63
	VRG 2B	2	2.37-2.51	2.44	1.53-1.67	1.59
	VRG 1A	3	2.27-2.51	2.40	1.62-1.71	1.66
	VRG4BB	2	2.23-2.58	2.41	1.61-1.71	1.66
	VRG 4A	4	2.28-2.54	2.38	1.58-1.68	1.62
	SR 1	1		2.57		1.53
	SR 4A	1		2.33		1.66
	Mor 1	2	2.51-2.56	2.54	1.52-1.58	1.55
	Ban 2	1		2.42		1.55
	Agr	2	2.61-2.64	2.63	1.53-1.58	1.56
	Ram 7	1		2.63		1.57
	VH 1	3	2.45-2.61	2.53	1.52-1.61	1.55
	Ram 1	1		2.60		1.61
	Nav	3	2.39-2.41	2.40	1.49-1.70	1.59
M2	COL D	1		1.86		2.25
	FTE 4	3	1.62-1.69	1.66	1.96-2.03	2.00
	COL C	5	1.64-1.83	1.73	1.93-2.08	2.01
	FTE 3	1		1.75		2.04
	FTE 2	2	1.76-1.83	1.79	2.01-2.02	2.02
	VRG 1A	4	1.59-2.03	1.81	1.92-2.29	2.14
	VRG 4BB	3	1.73-1.96	1.85	2.16-2.35	2.27
	VRG 4A	2	1.91-1.92	1.92	2.18-2.18	2.18
	SR 1	1		1.98		2.10
	SR 4B	1		1.76		1.98
	SR 4A	1		1.74		1.87
	Mor 1	1		1.92		2.24
	Ban 2	2	1.78-1.83	1.81	2.05-2.06	2.06
	Agr	8	1.75-1.99	1.91	1.76-2.21	2.09
	Ram 5	1		1.75		2.01
	Ram 7	1		1.74		2.15
	VH 1	5	1.58-1.81	1.71	2.00-2.19	2.07
Ram 1	1		1.78		2.08	

with wear, but is also absent in one of the unworn specimens. The mesostyle is divided, the division is incomplete in five of the twelve specimens. The parastyle is small. The posterior cingulum is well developed. There is a short labial cingulum along the base of the metacone. There are no lingual cingulums.

Table VIb (continued).

element	loc	N	Length		Width	
			range	mean	range	mean
M3	COL D	2	1.15–1.15	1.15	1.66–1.74	1.70
	COL C	4	0.98–1.06	1.03	1.53–1.69	1.61
	FTE 3	1		0.98		1.53
	VRG 2B	2	1.07–1.08	1.08	1.41–1.55	1.48
	VRG 1A	2	0.98–1.09	1.04	1.59–1.64	1.62
	VRG 4BB	7	1.11–1.26	1.18	1.48–1.66	1.61
	VRG 4A	4	1.13–1.26	1.20	1.58–1.68	1.63
	OR 4A	1		1.18		1.72
	SR 3	1		1.22		1.78
	Ban 2	2	1.03–1.04	1.04	1.50–1.55	1.53
	Agr	5	1.05–1.22	1.11	1.50–1.79	1.64
	VH 1	8	0.94–1.10	1.03	1.59–1.73	1.65
	Ram 1	5	0.93–1.08	1.02	1.45–1.58	1.52
	Nav	3	1.05–1.12	1.09	1.58–1.63	1.61

M2 (9) The outline of the occlusal surface is sub-triangular. The lingual side is rather pointed. The protoconule is invariably absent. The hypocone is a small cusplet which lies directly lingually of the metacone. The mesostyle is divided, but the division is incomplete in five of the nine specimens. The parastyle is very small. It lies on a short patch of anterior cingulum. There is also a short posterior cingulum near the end of the posterior arm of the metacone.

M3 (5) The occlusal surface has a trapezoidal outline. The anterior arm of the paracone is clearly longer than the posterior arm. The hypocone is well developed and lies against the metacone. The mesostyle is well divided in three of the five specimens. In the other two the division is incomplete.

***Desmanodon/Paratalpa* from other localities in the Daroca–Calamocha area**

Lower dentition

Usually the p4 lacks the talonid; the posterior cingulum lies directly behind the protoconid. The only p4 from La Col C which has a short talonid also bears a protocristid. This combination is also found in the specimen from Ramblar 7. A short talonid is, apart from these specimens, only found in one of the specimens from La Col D. A protocristid is also found in one of the two specimens from Fuente Sierra 3.

The m1 seems to be the most variable element of the lower molars. Specimens which lack the entocristid are found in Ramblar I, Moratilla 1 and La Col D. The latter assemblage is remarkable in the direction of the oblique cristid, which always ends lingually of the middle of the protoconid-metaconid crest, and not labially as in La Col C. Most assemblages agree in this character with

La Col C, although a more lingual direction of the oblique cristid is also found in one of the m1 of Valhondo 1 and one specimen from Moratilla 1. The m2 and m3 from the various localities fall within the variation of La Col C.

Upper dentition

Only six P4 have been found. All of these clearly belong to morphotype C, with an S-curved postero-crista and very small protocone and parastyle. The labial cingulum is weak. The postero-lingual cingulum may be very strong (one of the P4 from Valhondo 1, the specimen from Ramblar 7 and from Vargas 4BB) in which case the postero-lingual side is straight. In the other two specimens from Valhondo 1 and in the Navarete specimen (plate 5, fig. 5), the development of the postero-lingual cingulum is somewhat less and the postero-lingual side is slightly concave.

The hypocone of the M1 is totally absent in two of the larger assemblages, Agreda (3 specimens) and Vargas 1A (four specimens), but is usually present in other assemblages (not including the assemblages mentioned above ten out of forty M1 lack this cusp). The division of the mesostyle is incomplete in twenty-two of the forty-four M1. The degree of division of the mesostyle in the M2 seems to be less than in the M1 (thirty-five out of fifty M2 have an incompletely divided mesostyle). Twenty-four of the fifty-three M3 have an incomplete division of the mesostyle (this character could not be observed in three damaged specimens). The anterior arm of the paracone of the M3 in La Col C is longer than the posterior arm. This character is only rarely seen in the other localities, in which the two arms are of about the same length.

Remarks on the Spanish finds of *Desmanodon*

Gibert (1974) assigned the moles of Rubielos de Mora, described here as *Desmanodon daamsi*, to *Paratalpa micheli*. However, the humerus with its long teres tubercle, makes it clear that the species should be placed in *Desmanodon*. At first glance the teres tubercle seems to be shorter than in other species of *Desmanodon*. However, this is due to an elongation of the shaft rather than to shortening of the teres tubercle. The typical humerus distinguishes *D. daamsi* from other species of *Desmanodon*. Characteristics in the dentition are the tendency of some cusps to become inflated, the very poorly developed hypocone and the mesostyle which is, in contrast to other species of *Desmanodon*, poorly divided. These features also distinguish the dentition of *D. daamsi* from that of *Paratalpa micheli*.

The age of the Rubielos de Mora locality has been the subject of debate (Lopez-Martinez, 1989; Alvarez, 1987). Currently it is placed in MN 4 (de Bruijn *et al.*, 1992), probably in the lowermost part of the zone (Daams, pers. comm., 1996). The position in MN 4 is primarily based on a single element of the cricetid *Neocometes*, the only fossil of this genus ever found in Spain. Other elements in the fauna make clear that it is certainly older than those of Rauscheröd and Rembach, the localities which yielded the oldest humeri of

Desmanodon in Europe hitherto. Thus the occurrence of *Desmanodon* in Rubielos is considered now the oldest certain record of the genus in Europe.

The various localities in the Daroca–Calamocha area containing *Desmanodon/Paratalpa* cover a large timespan (MN 2–MN 5). There are some differences between assemblages, e.g. the absence of a hypocone on the M1 in Agreda and Vargas 1A, but there is no pattern in changes in morphology or size indicating local evolution or replacement. Therefore all assemblages are assigned to the same species. The identification of the species from Daroca–Calamocha is hampered by the absence of humeri. The dentition differs from that of *D. daamsi* in being smaller. This is particularly apparent in the width of the upper molars (fig. 3), which is larger in *D. daamsi* due to the longer arms of the labial cusps. Furthermore, the hypocone is better developed and the mesostyle is somewhat more divided in the assemblages from the Calatayud–Teruel Basin than in that from Rubielos de Mora.

The absence of humeri in the Daroca–Calamocha area makes it impossible to identify the genus. The assemblages could belong to *Paratalpa* or *Desmanodon*. If the Daroca species belongs to *Desmanodon* (and there are indications that this is indeed the case, see discussion), this would imply that two middle-sized species of *Desmanodon* were present in Spain during MN 4. The presence of two similar species can only be explained if the two occupied different ecological niches. This seems to be the case. The Rubielos de Mora locality represents a humid biotope (de Bruijn and Moltzer, 1974), in which *Desmanodon*

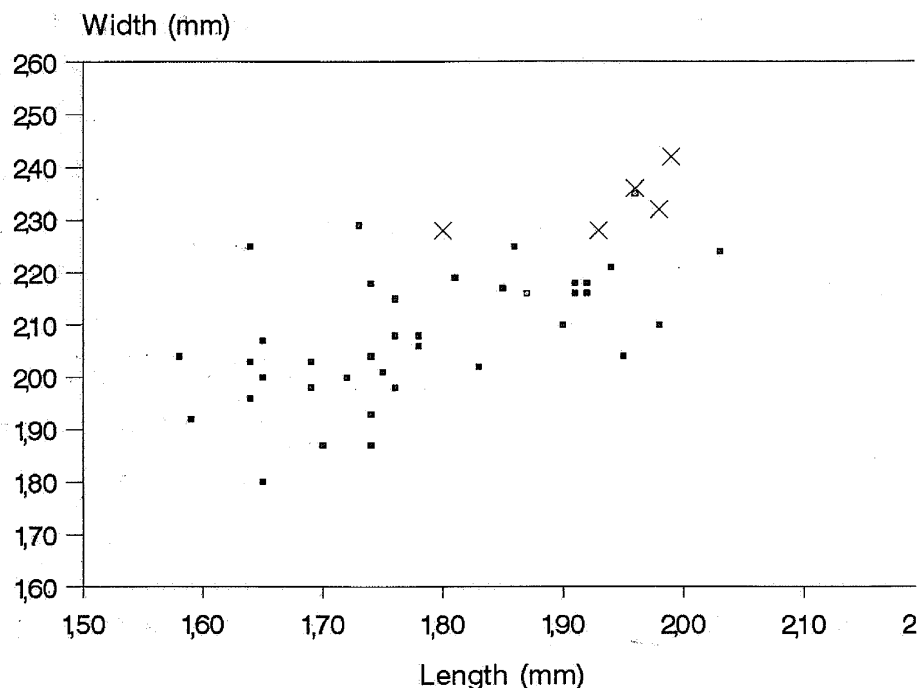


Fig. 3. Length/Width diagram of the M2 of *Desmanodon daamsi* from Rubielos de Mora (X) and *Desmanodon/Paratalpa* from the Teruel–Calatayud Basin (●).

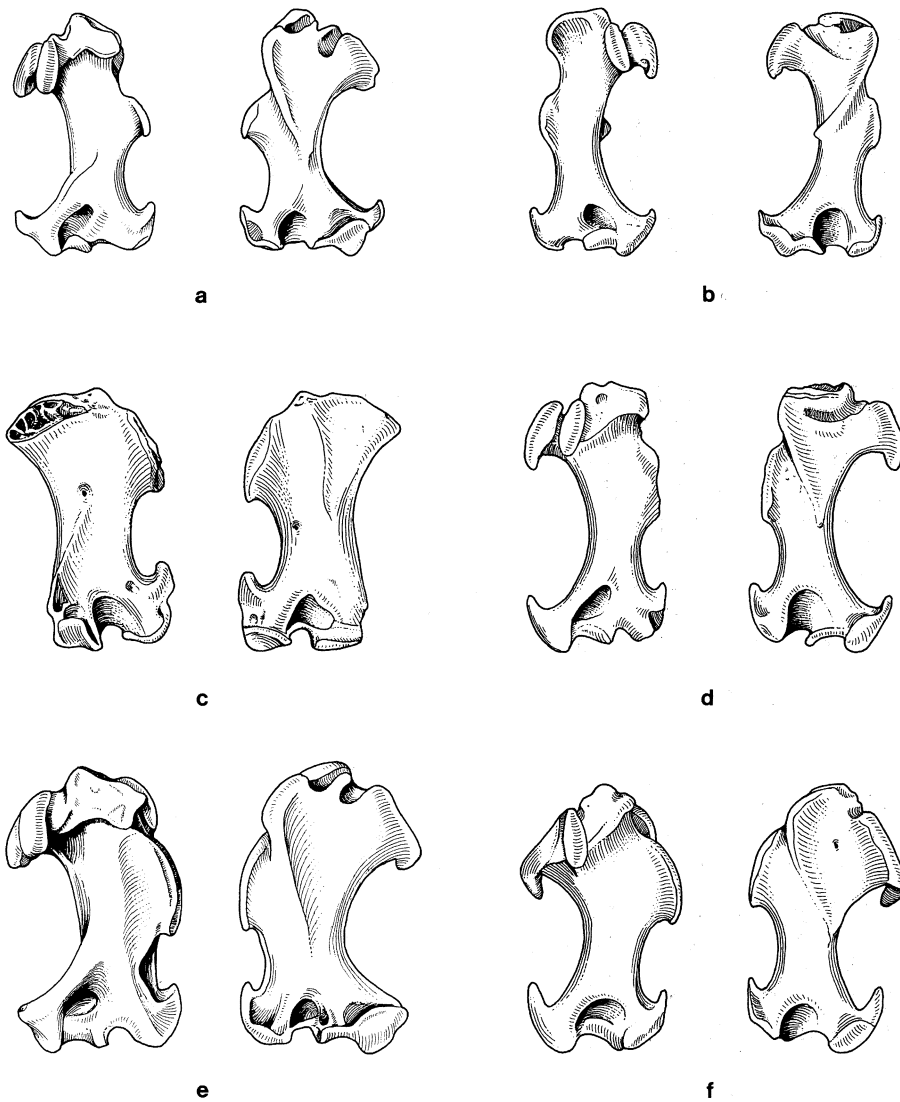


Fig. 4. Humeri of fossil and recent talpidae. a. *Paratalpa micheli*; b. *Urotrichus pilirostris*; c. *Desmanodon zieglerei*; d. *Neurotrichus gibbsi*; e. *Desmanodon major* f. *Scapanulus owensi*.

may have taken to a more malacophagous diet, as is indicated by the somewhat inflated cusps of *D. daamsi*.

Classification of *Desmanodon*

When Engesser (1980) described *Desmanodon*, he classified the genus as Talpidae inc. sedis. Engesser noted the resemblance with *Paratalpa*, and assumed that both genera originated from a common ancestor. He suggested that finds from the Lower Miocene of Anatolia would clarify the relationship between the

two genera. Although the exact evolutionary relationships between *Desmanodon* and *Paratalpa* are not yet clear, the close resemblance between the Lower Miocene representatives of the two genera indicates that they are indeed closely related. Since *Paratalpa* was included by Hugueney (1972) in the Urotrichini sensu Hutchison (1968), it seems logical that *Desmanodon* should be placed in this tribe as well.

Hugueney placed *Paratalpa* in the Urotrichini on the basis of the resemblance in dental morphology and dental formula of *P. micheli* and the Recent *Urotrichus talpoides*. She did not discuss the humerus of *Paratalpa*, apart from saying that its morphology did not contradict a classification as Urotrichini. Comparison between the humerus of *U. pilirostris* (fig. 4a) and that of *P. micheli* (fig. 4b) shows that the two are fairly similar. Both are slender and have a short teres tubercle. The most apparent difference is in the position of the pectoral tubercle. The resemblance between the humerus of *Desmanodon zieglerei* (fig. 4c) and that of *Neurotrichus gibbsi* (fig. 4d) is even more striking. Both are slender (though more robust than in *P. micheli* or *U. pilirostris*), both have a long teres tubercle and a similar position of the pectoral tubercle.

The older representatives of *Desmanodon* indicate that the genus should be included in the Urotrichini. The younger species, however, have a humerus which is far more robust than in any of the other Urotrichini. The humerus of *D. major* (fig. 4e), for instance, shows a strong resemblance to that of the Recent *Scapanulus owensi* (fig. 4f). *Scapanulus* was included in the Scalopini by Hutchison (1968), but was considered a Urotrichine by Van Valen (1967). The division between the Scalopini and Urotrichini is unclear, as is shown by the discrepancy between the classifications of Van Valen (1967) and Hutchison (1968). Van Valen only included the Recent genera *Scalopus* and *Scapanus* in the Scalopini and included a large number of fossil genera in the Urotrichini. Hutchison, on the other hand, chose for a more narrow definition of the Urotrichini, including only *Urotrichus* and *Neurotrichus* in this tribe and transferring most of the Urotrichini sensu Van Valen to the Scalopini.

Genetic evidence has shown that Scalopini and Urotrichini are sister groups (Yates and Moore, 1990), which makes the difficulties in separating the two groups understandable, certainly where fossil forms are concerned. With respect to the development of the humerus *Desmanodon* takes a somewhat intermediate position between the two tribes. This means that the tribal distinction between Scalopini and Urotrichini needs to be re-evaluated. Possibly the two tribes should be merged.

DISCUSSION

The geographical and stratigraphical distribution of the various species of *Paratalpa* and *Desmanodon* in Central Europe, Greece, Anatolia and Spain is given in fig. 5. Within each region the various localities have been given in stratigraphical order. Within one zone the relative position of localities from different regions does not have any stratigraphical significance. For instance,

MN-zone	Greece and Anatolia					Central Europe				Spain		
	Localities	<i>Desmanodon ziegleri</i>	<i>Desmanodon burkarti</i>	<i>Desmanodon neulenti</i>	<i>Desmanodon minor</i> <i>Desmanodon major</i>	Localities	<i>Paratalpa micheli</i>	<i>Paratalpa brachychir</i>	<i>Paratalpa/Desmanodon</i>	<i>Desmanodon antiquus</i>	Localities	<i>Paratalpa/Desmanodon</i>
MN 7/8	Yeni Eskihsisar											
	Sarıçay											
MN 6	Çandır											
	Pasalar				?							
MN 5						Puttenhausen			?	La Col-C	?	
MN 4						Rembach/ Forsthart			B	Vargas 1A	?	
	Aliveri			A		Rauscheröd			C	Rubielos de Mora		
MN 3						Stubersheim 3			C	Agreda	?	
	Keseköy			A						Valhondo 1	C	
MN 2	Harami 1+3			A						Navarete	C	
	Kilçak 3A+3B	?				Budenheim/ Hessler		?				
	Kilçak 0+0"					Ulm-West- tangente			B			
MN 1	Kargi	?				Tomerdingen			?			
						Saulcet			B			
MP 30						Coderet			C			

Fig. 5. The distribution of the various types of P4 and of humeri in *Paratalpa* and *Desmanodon*. The letters A, B and C refer to the morphotypes of P4 in figure 2. Question marks indicate that the P4 is not known. The different types of hatching refer to the type of humerus found. The absence of hatching indicates that no humerus has been found in a locality.

we do not know whether the Harami assemblages are younger than those from Ulm-Westtangente, as the figure might suggest. We do know, however, that the southern German localities in MN 2 are all placed in the lower part of that zone (Werner, 1994) and that Navarete del Rio is placed in the uppermost part of MN 2 (van der Meulen and Daams, 1992). Steininger *et al.* (1990) suggested that MN2 covers a timespan of almost two million years, which means that the German localities may well be over a million years older than Navarete del Rio.

Figure 5 shows that *Paratalpa* and *Desmanodon* do not co-occur in Central Europe. The youngest occurrence of *Paratalpa* is in the lower part of MN 2; *Desmanodon* is in Europe only known from MN 4 and MN 5. The European representatives of the two genera may have either the B or the C morphotype of P4. The similarity in dentitions and the succession in time led me to suggest that *Desmanodon* developed from *Paratalpa* in Europe some time during the Early Miocene (Van den Hoek Ostende, 1989). This hypothesis is, however, obviously incorrect, because we know now that *Desmanodon* was already present in Anatolia during the period that *Paratalpa* lived in Europe. The Anatolian Lower Miocene species of *Desmanodon* provide good ancestors for the European species. Our present working hypothesis is that *Desmanodon* immigrated from Anatolia into Europe sometime in the Early Miocene, replacing *Paratalpa*. The suggestion that *Desmanodon* is an immigrant is not new. It was already made by Ziegler (1990), who noted that the locality Stubersheim 3 contains several immigrants. Ziegler could not prove his hypothesis, since due to the absence of humeri, the *Paratalpa/Desmanodon* species from Stubersheim 3 cannot be identified to genus. Assuming that *Desmanodon* replaced *Paratalpa* in the European faunas, the immigration must have taken place after the youngest occurrence of *Paratalpa* (*i.e.* lower part MN 2) and the oldest certain occurrence of *Desmanodon* (lowermost MN 4). The material from the Calatayud-Teruel Basin largely covers this time span, but, since no humeri have been found in this area, it does not give a direct answer to the question when the migration took place.

Although it is not possible to determine the time of immigration of *Desmanodon*, we can hypothesize on it, using the morphology of the P4. In Europe the oldest assemblages of both *Paratalpa* (Coderet) and *Desmanodon* (Rubielos de Mora) yielded P4 of morphotype C, whereas the P4 from the younger assemblages are of morphotype B (Saulcet and Ulm–Westtangente for *Paratalpa*, Rembach and Forsthart for *Desmanodon*). Therefore, morphotype B seems to have developed independently in both *Paratalpa* and *Desmanodon*. Morphotype C is the primitive type, which is also apparent from the P4 of *D. ziegleri*. One of the P4 from Harami 1 is still of this type, whereas the other belongs to morphotype A, which is also found in all younger Anatolian species of *Desmanodon*. Assuming that *D. ziegleri* is ancestral to both the Anatolian lineage and the European *Desmanodon*-species, the European lineage must have split off before morphotype A developed in Anatolia (*i.e.* sometime during MN 1 or 2). Following this assumption, the talpid from the MN 3 locality Stubersheim 3 is most likely a *Desmanodon*. If this species belonged to *Paratalpa*, one would

expect it to have a morphotype B P4, like the Miocene *Paratalpa* assemblages of Saulcet and Ulm–Westtangente. The same holds true for the mole from the Daroca–Calamocha area, where only morphotype C P4 have been found. Since the oldest locality in this area, Navarete del Rio, is placed in the uppermost part of MN 2, the immigration of *Desmanodon* must have taken place during the later part of MN 2.

If the Daroca–Calamocha mole is indeed referable to *Desmanodon*, this implies that two species of this genus were present in Spain during the Early Miocene. *Desmanodon* from the Daroca–Calamocha area is probably closely related to *D. daamsi* from Rubielos de Mora, as is indicated by the reduction of the hypocone of the M1 and the high percentage of incompletely divided mesostyles. These features are even more apparent in *D. daamsi*. The fact that two closely related species could co-exist in Spain can partly be explained on geographical grounds. We assume however, that the two species also occupied different ecological niches. *D. daamsi* has slightly inflated cusps. In insectivores, inflation of the cusps is primarily found in mollusc-eaters, such as the semi-aquatic family Dimylidae. This suggests that *D. daamsi* was specialised to thrive in more humid environments, as were found at the time in Rubielos de Mora (de Bruijn and Moltzer, 1974).

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