

# Dental morphology of *Talpa europaea* and *Talpa occidentalis* (Mammalia: Insectivora) with a discussion of fossil *Talpa* in the Pleistocene of Europe

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A description is given of the last premolar and molars of *T. europaea* from The Netherlands and *T. occidentalis* of Spain. The metrical and morphological differences between the dentitions of the two species are small. A review is given of the literature of fossil *Talpa* in the Pleistocene of Europe. The suggestion that *T. minor* is ancestral to *T. caeca* is rejected. *T. fossilis* is tentatively considered a junior synonym of *T. europaea*.

## Introduction

Knowledge of the extant representatives of a group is important for any palaeontological study. Recent species provide us with information on the ecology and zoological studies may provide phylogenetic trees which can be used as a model to be tested with the fossil record. Equally important is that by studying recent material, we can get an impression of the variation in morphology and size within a species, which may help us in the definition of fossil species. This holds particularly true for smaller mammals, since micromammal palaeontologists usually study the dentition only. Species that are well defined on the basis of the colour of their skin, their karyotypes or other characteristics that do not fossilise, may be indistinguishable on the basis of their dentition. Thus we know, for instance, that the dentitions of the common vole *Microtus arvalis* and the field vole *M. agrestis* differ in the morphology of the M2 only, and cannot be identified on the basis of the other elements when found isolated. This, of course, is important information for the palaeontologist.

Unfortunately, extensive descriptions of the dentitions of recent mammals are rare. Zoologists can use a multitude of characters for describing recent species, and the description of teeth and molars usually plays a minor role in their descriptions. We were first faced with this problem when one of us (JvC) wrote her student thesis on the *Talpa* from the Lower Pleistocene locality Tegelen (The Netherlands). The Tegelen assemblage was compared with the literature on fossil species, but comparison the dentitions of recent species proved difficult in the absence of adequate descriptions. Therefore, it was decided to make a detailed description of the dental morphology of *Talpa europaea*. Since it has been suggested that the small Pleistocene *Talpa* species, *T. minor*, might be related to the small recent European *Talpa* species, we would have included in the thesis a description of the dentition of the blind mole species *Talpa caeca* or *T. occidentalis*. Unfortunately, we did not have any material from these species at the time. Recently, dr. E. Martin-Suarez offered us three skulls from the Iberian blind mole *T. occidentalis* from Andalusia (Spain),

thus allowing a comparison between the dentitions of *T. europaea* and this species.

Robert (1983) noted that comparison between fossil and recent *Talpa* species was difficult, because the measurements used for identifying recent skeletal remains could often not be taken from the fragmentary fossil material. Nonetheless, the measurements commonly used in palaeontological studies can be taken on recent material, making a comparison possible. This is the approach taken in this paper. Here we give full description of the dental elements of *T. europaea* and *T. occidentalis* in the same manner as we describe fossil talpids, focussing on the elements that are commonly retrieved in excavations, viz. the molars and the last premolars. Our objective is twofold. First we wish to explore the differences in the dentitions of well-defined recent species, to discover which characters can be used to distinguish them on the basis of their dentitions. Secondly we want to use these data for the interpretation of the fossil record of *Talpa* in Europe, as known from literature.

### Material and methods

Specimens of *Talpa europaea* were obtained from two garden owners, who had set traps in an effort to protect their lawns from demolition by mole burrows. Thus 22 specimens were collected from Oude Mirrum in the north of The Netherlands, and 10 animals from Bergen op Zoom in the south. The Oude Mirrum specimens were collected and macerated in one bucket. While cleaning the material only 31 mandibles were retrieved. Individual elements were also lost during the process, so that the number of elements available for the description ranges from 25 to 44. The specimens from Bergen op Zoom were macerated separately, and the dentitions from that locality are more complete, with the notable exception of the M3, of which only one specimen was retrieved after cleaning the skulls. The three skulls of *Talpa occidentalis* were obtained from Dr E. Martin-Suarez of the University of Granada, Spain. These animals were collected in Andalusia, southern Spain.

The number in brackets in the descriptions denotes the numbers of specimens available. The various elements are measured according to the methodology of van den Hoek Ostende (1989).

### Recent *Talpa* species of Europe

In Europe five recent species of *Talpa* are recognised, *T. europaea*, *T. caeca*, *T. occidentalis*, *T. romana* and *T. stankovici* (Niethammer, 1990; Hutterer, 1993). Important characters for distinguishing the various species are size, karyotype, eye development and the morphology of the pelvis. Since characters can be variable within one species and have not been recorded sufficiently throughout the range of the various species, the classification is by no means final (Niethammer, 1990).

*Talpa europaea*, the common mole, lives in the temperate regions of Europe including England. The easternmost occurrence of the species lies at the rivers Ob and Irtysh (Russia). In contrast to the other European species the eyes are free. The ischium and sacrum are usually fused, the so-called europoid pelvis. In the caecoid pelvis, which is the most common type in *T. caeca* and *T. romana*, such a fusion is not found (Niethammer, 1990). The dentition of *T. europaea* is relatively small, with the length M1-M3 less than 19% of the condyle base length. A division of the mesostyle of the upper molars can only be observed in unworn specimens.

The Roman mole *Talpa romana* was long considered a subspecies of *T. europaea*. The two species are of similar size. The only difference that can be observed directly are the skin-covered eyes in *T. romana*. *T. romana* usually has a caecoid pelvis. Although the body size of the two species is similar, the dentition of *T. romana* is clearly larger than that of *T. europaea*. This holds true for the length of the tooth row as well as for the individual elements. The mesostyle of the upper molars tends to be divided (Niethammer, 1990). The species is found in the Apennines, Italy, but is also recorded from the extreme southeast of France.

The Balkan mole *T. stankovici* used to be classified as a subspecies of *T. romana*. It was raised to species level on the basis on electrophoretic analysis of enzymes (Filipucci et al., 1987). *T. stankovici* is somewhat smaller than *T. romana*. Both species are macrodont. The species is found in northern Greece, Macedonia, southern Serbia and probably also Albania (Niethammer, 1990).

*Talpa caeca*, the blind mole, and *T. occidentalis*, the Iberian blind mole, were also long considered conspecific. Here too, the electrophoretic enzym research of Filipucci et al. (1987) lead to the conclusion that a division at the species level is warranted. Till than, *occidentalis* was considered a subspecies of *T. caeca*. *T. caeca* differs from all other European species in its karyotype ( $2n = 36$  vs.  $2n = 34$  in the other species). In contrast to *T. occidentalis*, *T. caeca* usually has a caecoid pelvis. Otherwise the two species are morphologically similar. Both are smaller than *T. europaea*, have skin-covered eyes. Subadult specimens show a division of the mesostyle of the upper molars, which may disappear with wear.

Although electrophoretic research shows five distinct gene poles for the European *Talpa* species (Filipucci et al., 1987), only three groups can be recognised on the basis of size and morphology. The large similarity between *Talpa caeca* and *T. occidentalis* on one hand and *T. romana* and *T. stankovici* on the other, makes it highly unlikely that these species could be recognised on the basis of their fossils. Thus for palaeontologists, which are dependant on size and morphology for the description of their species, the classical classification in three species, *T. europaea*, *T. caeca* s.l. (including *T. occidentalis*) and *T. romana* s.l. (including *T. stankovici*), is more suitable. According to Filipucci et al. (1987) this classification is inconsistent with genetic data. The genetic difference between *T. caeca* and *T. occidentalis* is larger than that between *T. caeca* and the other European *Talpa* species. On the basis of genetics Filipucci et al. (1987) assumed that the divergence of the various recent European *Talpa* species took place roughly between three and one million years ago, i.e. in the Upper Pliocene and Lower/Middle Pleistocene.

### Systematic part

#### Talpidae Fisher von Waldheim, 1817

#### *Talpa* Linnaeus, 1758

#### *Talpa occidentalis* Cabrera, 1907

(figs. 1a, 2a, 3a&b, 4a)

Measurements: the measurements are listed in table 1.

Descriptions: p4 (6) The premolar consists mainly of the high, triangular paraconid. The tip of this cusp lies in the centre of the p4. The lingual and posterior sides of the premolar are straight; the labial side is convex. The parastylid lies anterolingually of the paraconid, on a wide cingulum. The talonid is relatively long. It is bordered on the lin-

Table 1. Measurements of *Talpa occidentalis* from Andalusia (Spain).

element	N	Length		Width	
		Range	Mean	Range	Mean
p4	6	1.13-1.30	1.20	0.68-0.85	0.76
m1	6	1.93-2.13	2.03	1.27-1.40	1.34
m2	6	2.25-2.50	2.41	1.30-1.39	1.35
m3	6	2.01-2.28	2.11	1.17-1.33	1.23
P4	6	1.44-1.70	1.56	0.92-1.12	1.01
M1	6	2.67-2.87	2.78	1.61-1.79	1.67
M2	6	2.19-2.33	2.25	2.40-2.72	2.60
M3	6	1.47-1.58	1.53	2.02-2.10	2.06

gual and posterior sides by a low ridge. It is divided by a posterocristid, which runs from the lingual side of the posterior face of the paraconid to the middle of the posterior side.

m1 (6) The trigonid is clearly shorter and narrower than the talonid. The par-alophid is shaped a curved blade, which partly closes the trigonid basin at the lingual side. The paraconid is weakly developed. The protoconid-metaconid crest is straight. The oblique cristid ends against the middle of the protoconid-metaconid crest. The talonid basin is very wide and open. The entocristid and metacristid are absent. The re-entrant valley is deep. The entostylid is small and lies directly behind the entoconid. There are no cingulums.

m2 (6) The trigonid is somewhat wider and somewhat longer than the talonid. In

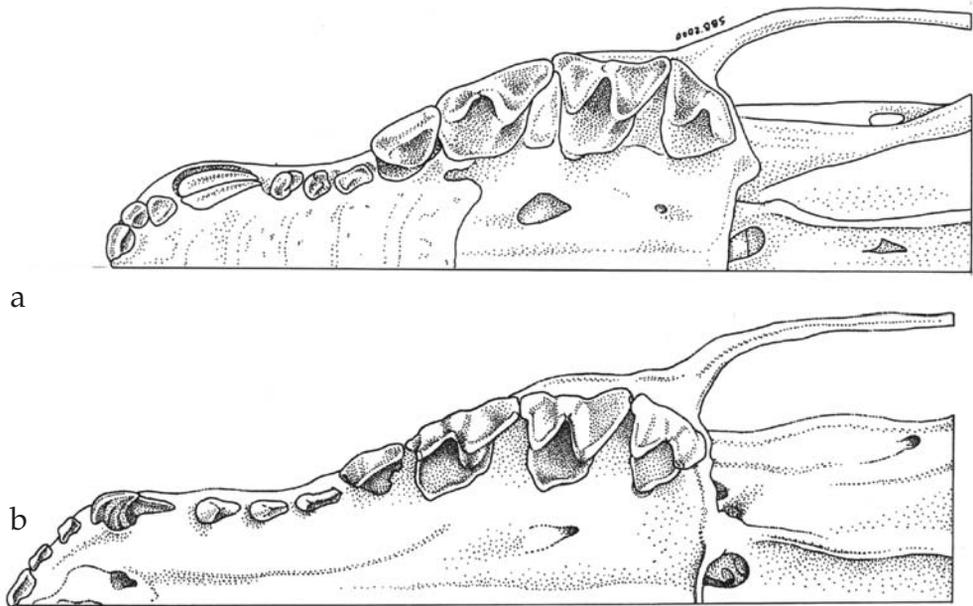


Fig. 1. The upper jaw of *Talpa occidentalis* (a) and *Talpa europaea* (b).

Table 2. Measurements of *Talpa europaea* from Bergen op Zoom (BoZ) and Oude Mirrum (OM), the Netherlands.

element	Locality	N	Length		Width	
			Range	Mean	Range	Mean
p4	BoZ	9	1.26-1.47	1.37	0.58-0.75	0.67
	OM	29	1.16-1.48	1.39	0.55-0.75	0.65
m1	BoZ	10	2.11-2.37	2.26	1.21-1.34	1.30
	OM	28	2.09-2.45	2.32	1.22-1.48	1.33
m2	BoZ	10	2.43-2.60	2.53	1.12-1.41	1.31
	OM	32	2.40-2.71	2.59	1.18-1.45	1.34
m3	BoZ	9	1.92-2.19	2.08	0.99-1.31	1.17
	OM	25	2.01-2.21	2.12	1.03-1.27	1.19
P4	BoZ	10	1.59-1.85	1.72	0.90-1.19	1.05
	OM	44	1.61-2.02	1.76	0.93-1.26	1.03
M1	BoZ	10	2.61-3.08	2.81	1.38-1.68	1.54
	OM	43	2.31-3.18	2.79	1.36-1.73	1.57
M2	BoZ	10	2.10-2.52	2.30	2.30-2.80	2.54
	OM	35	2.19-2.53	2.33	2.27-2.76	2.54
M3	BoZ	1		1.40		2.08
	OM	31	1.27-1.52	1.39	1.76-2.13	1.97

contrast to the m1, the paraconid is developed as a cusp. The protoconid-paraconid crest is slightly bend; the protoconid-metaconid crest is straight. The oblique cristid ends near the base of the metaconid. Thus, the talonid basin is narrower than in the m1 and the re-entrant valley is more open. The talonid basin is bordered by a - very - low entocristid. The parastyloid and entostyloid are small. There are no cingulums.

m3 (6) The trigonid is clearly wider and somewhat longer than the talonid. The trigonid resembles that of the m2. The entoconid and hypoconid are small and low. The oblique cristid ends against the base of the metaconid. The shallow talonid basin is bordered lingually by a very low entocristid. The re-entrant valley is very wide and open. The entostyloid is small. There are no cingulums.

P4 (6) The outline of the occlusal surface is triangular. The paracone is high and large. Its tip lies just in front of the middle of the premolar. The posterocrista is sharp and relatively straight. In front of the paracone lies a tiny parastyle. The lingual flange is little more than a wide cingulum at the base of the paracone. In unworn specimens the flange shows a low ridge at the lingual side (?protocone). There is a narrow cingulum along the labial side of the posterocrista.

M1 (6) The outline of the occlusal surface is quadrangular. The protocone is large and low. Its tip lies lingually of the paracone. The hypocone is a thickening in the posterior arm of the protocone. It lies lingually of the metacone. The anterior arm of the protocone connects to the parastyle, which is very small. In front of the base of the paracone the protoconule appears as a slight thickening in the anterior arm of the protocone. There is a small bulge in the outline of the M1 at the position of the protoconule. The posterior arm of the protocone ends behind the base of the metacone.

The posterior arm of the paracone is rather straight, with a sharp curve just before it reaches the mesostyle. The mesostyle is divided. The two cusplets stand close

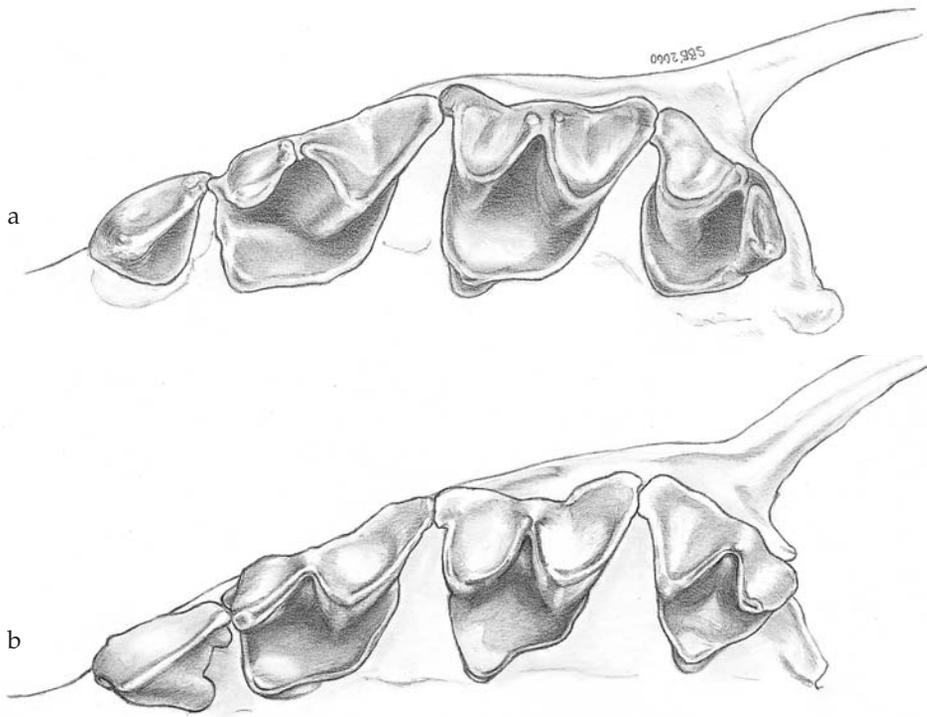


Fig. 2. Detail of the P4-M3 of *Talpa occidentalis* (a) and *T. europaea* (b).

together and may merge with wear. The posterior arm of the metacone is about twice as long as the anterior arm.

M2 (6) The outline of the occlusal surface is triangular. Due to the anterior position of the protocone the molar is slightly askew. The posterolingual side is concave. The protocone lies lingually of the paracone. The protoconule is completely incorporated in the anterior arm of the protocone. The hypocone is a small elevation in the posterior arm of the protocone. It lies lingually of the tip of the metacone.

The lingual cusps are V-shaped, with long, sharp ridges. The arms of the paracone and the anterior arm of the metacone are about the same length. The posterior arm of the metacone is c. 25% longer. The trigon basin is deep. The mesostyle is divided with the two cusplets standing close together. The cusps of the mesostyle can merge with wear. The anterior arm of the paracone is bend near its end and forms a small perastyle. The posterior arm of the metacone is straight.

M3 (6). The outline of the occlusal surface is triangular. The protocone is low. Its anterior arm ends against the anterior side of the paracone. The protoconule is absent. The posterior arm of the protocone runs along the posterolingual side of the molar. It ends just lingually of the base of the metacone, where it shows a slight thickening (?hypocone). The anterior arm of the paracone is somewhat longer than the posterior arm. The end of the anterior arm bends and forms a slightly protruding parastyle. The mesostyle is divided. The two cusplets stand close together and may merge with

Table. 3. Measurements of the humerus of various European *Talpa* species. Data from Niethammer (1990) with the exception of Bergen op Zoom and Oude Mirrum (own measurements).

Species	Locality	N	Length	Width diaphyse	Width epiphyse
<i>europaea</i>	Bergen op Zoom (NL)	10	1.44-1.78	0.36-0.45	0.77-0.91
<i>europaea</i>	Oude Mirrum (NL)	34	1.55-1.78	0.40-0.48	0.83-0.96
<i>europaea</i>	Kleinalm/Nieder Tauern (D)	15	1.31-1.45	0.33-0.39	0.67-0.78
<i>europaea</i>	Ramsau/Dachstein (D)	18	1.36-1.59	0.34-0.42	0.71-0.86
<i>europaea</i>	Rheinland (D)	14	1.45-1.66	0.38-0.46	0.78-0.92
<i>europaea</i>	Spain	16	1.52-1.82	0.43-0.47	0.81-0.99
<i>stankovici</i>	Greece	3	1.52-1.57	0.40-0.43	0.86-0.87
<i>romana</i>	Italy	1	1.61	0.46	0.90
<i>caeca</i>	Tessin (I)	38	1.28-1.46	0.32-0.38	-
<i>caeca</i>	Alpi di S. Benedetti (I)	17	1.14-1.28	0.29-0.35	-
<i>caeca</i>	Pelister (former Yugoslavia)	30	1.15-1.26	0.28-0.34	-
<i>occidentalis</i>	Spain	22	12.1-1.46	0.30-0.41	0.65-0.78

wear. The anterior arm of the metacone is about the same length as the posterior arm of the paracone. There are no cingulums.

*Talpa europaea* Linnaeus, 1758  
(figs. 1b, 2b, 3c&d, 4b)

Measurements: the measurements are listed in table 2.

Descriptions: p4 (38). The premolar consists mainly of the high, triangular paraconid. The tip of the paraconid lies at about 1/3 the length of the premolar. The lingual and posterior sides of the p4 are relatively straight; the labial side is convex. The parastylid lies on the anterolingual side of the paraconid and is strongly protruding. The talonid is relatively long. It is connected to a wide but short cingulum along the posterolingual flank of the paraconid. The talonid is bordered by a low posterior ridge, which continues over the lingual cingulum. The posterocristid runs from the lingual side of the paraconid to the posterolingual corner of the p4.

m1 (38). The trigonid is narrower than the talonid. The trigonid and the talonid are about the same length. The protoconid-paraconid crest is strongly curved; the protoconid-metaconid crest makes a weak curve. Thus the trigonid basin is U-shaped. There is a circular depression lingually of the protoconid-paraconid crest. The oblique cristid ends against the middle of the protoconid-metaconid crest or just labially of that point. The talonid basin is wide and open; the re-entrant valley is small. There is no entocristid, nor a metacristid. The entostylid is well developed. In some specimens there is a small bulge in the anterior face of the paraconid at the position of the parastyle. There are no cingulums.

m2 (42). The trigonid is somewhat wider and somewhat longer than the talonid. The protoconid-paraconid crest is slightly bend; the protoconid-metaconid crest is straight. The trigonid basin is relatively wide. There is a deep, round pit between the

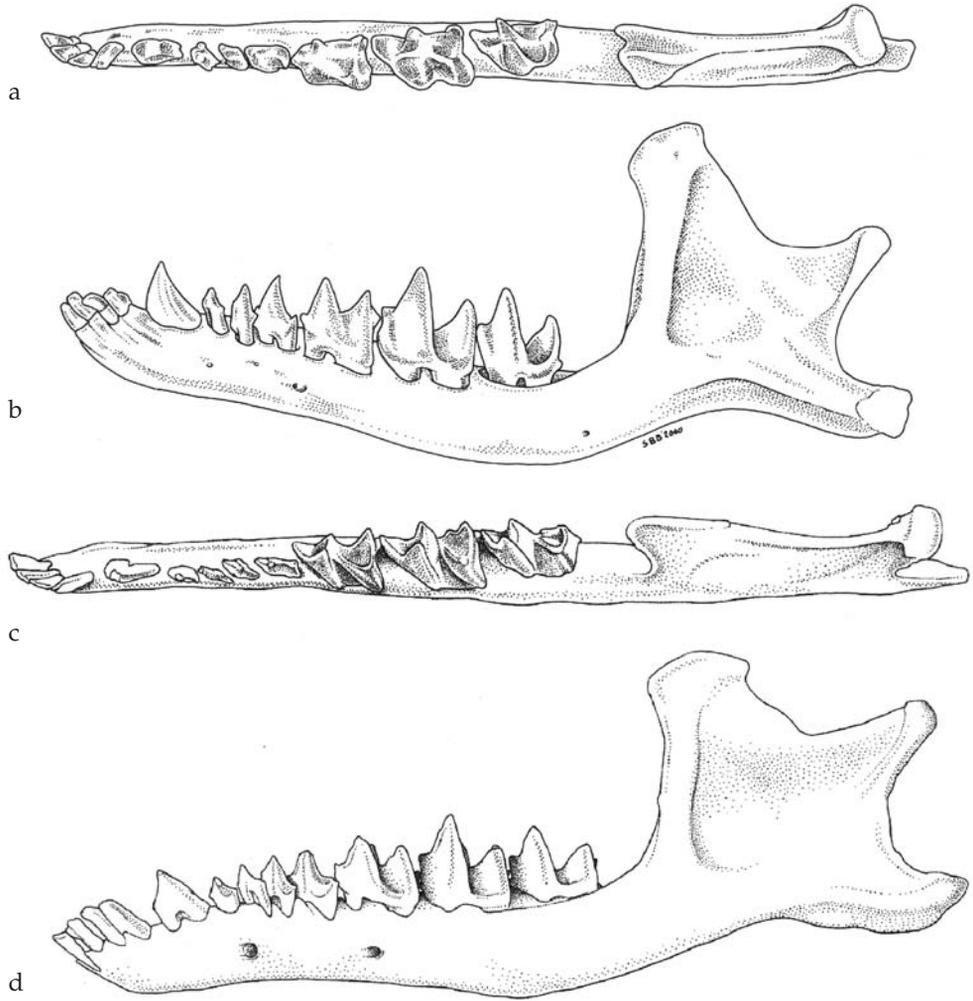


Fig. 3. The mandible of *Talpa occidentalis* (a. occlusal view; b. labial view) and *T. europaea* (c. occlusal view; d. labial view).

paraconid and the metaconid. The oblique cristid ends near the base of the metaconid. The talonid basin is narrow; the re-entrant valley is very open. The talonid basin is bordered by a very low entocristid. The parastylid and entostylid are well developed.

m3 (31). The trigonid is clearly wider and somewhat longer than the talonid. The trigonid resembles that of the m2, but is smaller. The protoconid-paraconid crest is nearly straight. The talonid is strongly reduced. The oblique cristid, posterior arm of the hypoconid and the entocristid form a continuous low ridge circling the talonid basin. The hypoconid and the entoconid are almost completely incorporated in this ridge. The oblique cristid ends against the base of the metaconid. The parastyle is well developed and lies anterolingually of the paraconid. In some specimens there is a very small entostylid. There are no cingulums

Table. 4. Measurements of the humerus of various European *Talpa* species. Data from Niethammer (1990) with the exception of Bergen op Zoom and Oude Mirrum (own measurements).

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<i>caeca</i>	Pelister (former Yugoslavia)	30	1.15-1.26	0.28-0.34	-
<i>occidentalis</i>	Spain	22	1.21-1.46	0.30-0.41	0.65-0.78

P4 (54). The outline of the occlusal surface is triangular. The paracone is high and large. Its tip lies in front of the middle of the premolar. The sharp posterocrista is straight and long. In front of the paracone lies a small, protruding parastyle. The lingual extension appears as a bulge lingually of the tip of the paracone. In some unworn specimens a tiny, ridge-shaped protocone can be observed. The labial cingulum is well developed.

M1 (53). The outline of the occlusal surface is quadrangular. The protocone is large and low, and lies lingually of the paracone. The hypocone appears as a thickening in the posterior arm of the protocone, lingually of the metacone. The anterior arm of the protocone ends against the base of the paracone; the posterior arm ends behind the base of the metacone.

The posterior arm of the paracone is straight to slightly curved. The anterior arm of the metacone is about the same length as the posterior arm of the paracone. Both these arms bend sharply at the undivided mesostyle. The posterior arm of the metacone is about twice as long as the anterior arm, and is straight. In front of the paracone lies a well-developed parastyle.

M2 (53). The outline of the occlusal surface is triangular. Due to the anterior position of the protocone, which lies nearly lingually of the paracone, the molar is askew. The anterolingual and posterolingual sides of the M2 are concave. The protoconule is incorporated in the anterior arm of the protocone in which it forms a small thickening. The development of the hypocone varies. In about 1/3 of the specimens, the hypocone appears as a thickening in the posterior arm of the protocone. In others the hypocone is a low, conical cusp that lies at the end of the posterior arm of the protocone near the base of the metacone. In one specimen the hypocone is isolated.

The lingual cusps are V-shaped. The anterior arm of the paracone either bends outward in a gentle curve or is bend at about 3/4 its length. In either case it forms a relatively long parastyle. The posterior arm of the paracone is about the same length

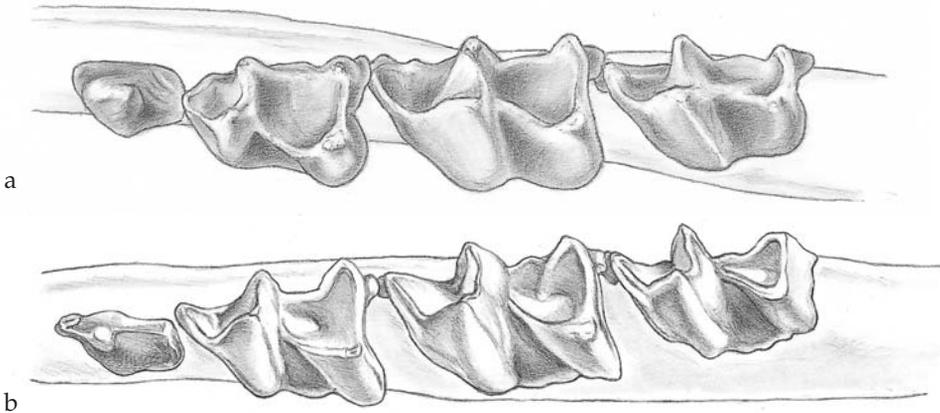


Fig. 4. Detail p4-m3 of *Talpa occidentalis* (a) and *T. europaea* (b).

as the anterior arm or sometimes a bit longer. The mesostyle is undivided. In unworn specimens the two cusps of the mesostyle may be discernible. The anterior arm of the metacone is somewhat shorter than the posterior arm of the paracone. The posterior arm of the metacone is straight. It is 30-50% longer than the anterior arm of that cusp.

M3 (32). The outline of the occlusal surface is triangular. The protocone is low. Its anterior arm ends against the paracone, just in front of the base of that cusp. There is no protoconule. The posterior arm of the protocone runs along the posterolingual side of the molar and connects to the hypocone. The latter is a low bulge directly adjacent to the base of the metacone. In some specimens there is a notch in the outline where the posterior arm of the protocone and the hypocone meet. The paracone is the largest cusp of the M3. Its anterior arm bends outward in a weak curve. It is somewhat longer than the posterior arm. The valley between the two arms of the paracone is wide and shallow. The mesostyle is undivided. In unworn specimens the two cusps of the mesostyle may be discernible. The anterior arm of the metacone is somewhat shorter than the posterior arm of the paracone.

### Discussion

The metrical differences between *Talpa europaea* and *T. occidentalis* are small. In our material the dimensions of the M1 and M2 of *T. occidentalis*, for instance, fall completely in the size variation of *T. europaea*. The only element for which there is a small overlap in size only, is the p4. At first sight the similar size of the dentitions is somewhat surprising. Since the body size of *T. europaea* is larger than that of *T. occidentalis*, one would expect that this size difference is also reflected in the dimensions of the molars. However, as we already noted earlier, *T. europaea* has relatively small molars for its size. We did not include the humeri in our study. Measurements of the humeri of *T. occidentalis* and *T. europaea* as given by Niethammer (1990) show that here too there is an overlap in size, although much smaller than in the dentition (table 3).

Fig. 5 shows the average lengths for the various molars and last premolars. It shows that on average the p4, m1 and m2 are smaller in *T. occidentalis*, whereas the

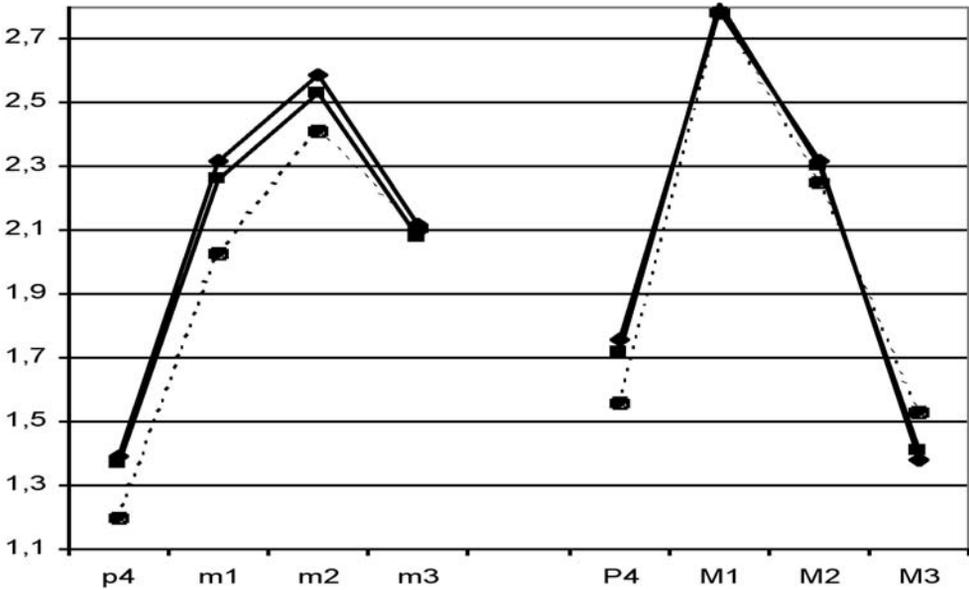


Fig. 5. Length diagram of the p4-m1 and P4-M1 of *Talpa occidentalis* (circles and interrupted lines) and *T. europaea* (continuous lines) from Bergen op Zoom (squares) and Oude Mirrum (rhombics).

m3 is comparable in size. In the upper dentition the P4 of *T. occidentalis* is smaller, M1 and M2 are in size similar to *T. europaea*, and the M3 is even larger in the Spanish species. It is remarkable that the m2 of *T. occidentalis* is smaller than that of *T. europaea*, whereas its counterparts in the upper jaw, the M1 and M2, are comparable in size to those of the common mole. The relatively small p4 and P4 are probably related to the shorter snout of *T. occidentalis* (figs. 1, 3). Robert (1983) found the length of the anterior dentition relative to the length of the molar row could be used to distinguish between species. The total length of the molars in *T. europaea* is comparable to that of *T. caeca* s.l., but the length of the anterior dentition is longer. On the other hand, the length of the anterior dentition of *T. europaea* and *T. romana* s.l. is similar, but the length of the molar row in the latter species is larger. This implies that in fossil material the species can be distinguished on the basis of this character, provided one has complete mandibles at his disposal.

Morphologically the dentitions of *Talpa europaea* and *T. occidentalis* are also very similar. The differences are listed in table 4. In short, the dentition of *T. europaea* shows a better developed trigonid of the m1, a stronger development of the styles and stylids in general, better developed hypocones in the upper molars and an undivided (M1/M2) or at least less divided (M3) mesostyle. Recording these small differences from Recent material is one thing, but the applicability of these characters for distinguishing species on the basis of fossil material quite another. The development of hypocones or styles and stylids can only be determined in suitably large assemblages, which are rare. Even for determining the degree of division of the mesostyle larger assemblages are required, since this character is dependent on wear. An

unworn M2 of *T. europaea* may show the individual cusps of the mesostyle, whereas the mesostyle may appear undivided in a worn molar of *T. occidentalis*.

The relative size of the elements may prove to be a more useful character. The relatively short p4 and the weaker development of the trigonid of the m1 are related to the shorter snout length in *T. occidentalis*. As we noted above, Robert (1983) showed that the snout length is a useful character for distinguishing between species, particularly when one has complete mandibles at ones disposal. We already noted that it is peculiar that the m2 of *T. occidentalis* is relatively short compared to the M1 and M2. This might be related to the development of the styles in the upper molars. Since these are weaker in *T. occidentalis* the gap between M1 and M2 is shorter. Since the m2 occupies this gap in occlusion, it is shorter as well.

In conclusion our data show that metrical and morphological differences between the dentitions of *Talpa europaea* and *T. occidentalis* are small. The two species can probably be only distinguished in fossil material if sufficiently large assemblages are available. The metrical differences of the humeri of the two species are larger and thus more useful.

### Fossil *Talpa* species of the European Quaternary

The genus *Talpa* has a long evolutionary history. The oldest species is *T. tenuidentata* Ziegler, 1990 from the Lower Miocene of southern Germany (Ziegler, 1990). Ziegler suggested that a phylogenetic lineage could be reconstructed from *T. tenuidentata* through the Middle Miocene species *T. minuta* Blainville, 1838, the common mole *T. europaea*. Matters are, however, a bit more complicated than that. A lot of names have been proposed for fossil *Talpa* species, particularly in the Pliocene and Pleistocene. To complicate things further, some of the species have primarily been defined on the basis of the humerus (e.g. *T. gilothi* Storch, 1978; *T. csarnotana* Kretzoi, 1959). Doukas et al. (1995) already indicated that the fossil representatives of *Talpa* are badly in need of a revision.

The names proposed for the Pliocene and Pleistocene species of *Talpa* can roughly be divided in three size categories, middle-sized, small, and large. In this section we discuss the various species accordingly.

#### Middle-sized *Talpa* species ("*T. fossilis*", *T. europaea*)

The middle-sized *Talpa* in Late Pleistocene deposits is usually referred to as *T. europaea*. In older deposits the middle-sized *Talpa* is often classified as *T. fossilis* Petényi, 1864, particularly in German literature. In French literature of Early and Middle Pleistocene localities the middle-sized *Talpa* species is often identified as *T. cf. europaea* (e.g. Mas Rambault and Valerot: Chaline, 1972; Montouse 5: Clot et al., 1976; Saint-Saveur: Crochet & Michaux, 1981). Presumably this split in *T. fossilis* and *T. cf. europaea* presents a linguistic barrier only.

The name *Talpa fossilis* was first used by Pomel (1848). He noted that many talpid remains from caverns and the diluvium were attributed to *T. vulgaris* (= *T. europaea*) although the identifications are by no means certain. He had seen material which was indistinguishable from *T. europaea* and *T. caeca*. Apart from those he had found a species which was somewhat more robust and larger, and particularly differed a bit

in the morphology of the carpals. He named this species *T. fossilis*.

Apparently, Pomels description has gone unnoticed, since the name *Talpa fossilis* is usually attributed to Petényi (1864). His description of *Talpa vulgaris fossilis* from the Hungarian locality Beremend was published in his Hatrahagyott Munkai (Posthumous works). We found this paper to be illusive, but were fortunate to be able to obtain a copy through the help of Dr L. Meskavaros (Budapest). Since the description is in Hungarian, a language not accessible to most, we give a translation of the original description:

“*Talpa vulgaris fossilis* Petényi. The fossil bone material of this animal totally agrees with the corresponding bones of the recent common mole, both in morphology and size; thus this fossil mole does not differ from the recent mole on the specific level, if one does not take into account the only difference noted by me, viz. that in the modern mole the labial side of the mandible has only two foramina mentale, one under the second premolar, the other under the first molar, whereas in the fossil mole three of such foramina are found, one under the first premolar, but two - be it one of them very shallow - under the first molar.”

Petényi (1864) then continues with a listing of the material he found. Notably, he had a large number of humeri, but lacked upper molars.

Thus, according to the original description, *Talpa fossilis* Petényi, 1864, is indistinguishable from *T. europaea*. A mix-up with *T. caeca* s.l. is unlikely, since humeri found by Petényi also fall inside the size variation of the common mole, whereas the humeri of the blind moles are somewhat smaller.

Kormos (1930) described *Talpa praeglacialis* from the Early Pleistocene locality Püspökfürdő (Betfia 2). This species showed on average a larger number of foramina mentale than found in *T. europaea* (more than two in over half of the specimens, whereas Robert (1983) found more than two foramen in c. 8% in Recent *T. europaea*). Later he also placed material of the Austrian late Middle Miocene locality Hundsheim in *T. praeglacialis* (Kormos, 1937). The Hundsheim material had earlier been described as *T. europaea* var. *major* by Freudenberg (1914). Kretzoi (1938) placed *T. praeglacialis* in the synonymy of *T. fossilis*.

Rabeder (1972) placed the material from Hundsheim in *T. europaea*. He suggested that some small morphological and size differences between *T. fossilis* and *T. europaea* may exist, but that this would rather indicate a possible distinction at the subspecies level. Von Koenigswald (1970) stated in his discussion on the talpids from the coeval German locality Petersbuch 1 that there are no morphological or size differences between *T. fossilis* and *T. europaea*. We tentatively concur with Rabeder and von Koenigswald in considering *T. fossilis* Pétenyi, 1864, a junior synonym of *T. europaea*. A revision of the material from the type locality is needed to confirm that the two are indeed conspecific.

Robert (1983) proposed to retain the name *T. fossilis* as a chronospecies, since she observed a gradual increase in size in the Pleistocene and possibly also a gradual development of the division of the mesostyle from invariably divided in the older assemblages to mostly undivided in *T. europaea*. The latter observation was primarily based on Crochet & Michaux (1981), who found that the mesostyle was invariably undivided

in *Talpa* cf. *europaea* from the Middle Pleistocene of Saint-Saveur, France. However, since this identification was not confirmed by humeri, the Saint-Saveur talpid may be referable to *T. caeca* s.l., which is similarly sized and in which the mesostyle is divided. Thus there is no basis for the evolutionary trend proposed by Robert (1983).

Considering *Talpa fossilis* a junior synonym of *T. europaea* does not mean that all the material previously assigned to *T. fossilis* can be automatically transferred to the recent species. This needs to be checked for every assemblage separately. Given the close similarity between *T. europaea* and *T. caeca* s.l. the two can be easily confused, particularly when no humeri have been found. Furthermore, older assemblages previously assigned to *T. fossilis* (the name has been used for various Pliocene and even an Upper Miocene assemblage) could also belong to a fossil species, which is now extinct.

#### Small-sized *Talpa* species (*T. minor*)

Next to *Talpa fossilis*, and often in the same locality, a smaller species of *Talpa* is found. The first reference to this small talpid is given by Pétenyi (1864), who in a footnote mentioned that one of the humeri from Beremend was much smaller than the others. However, he thought that it might belong to a young animal. The species was named by Freudenberg (1914). He named the smaller species from the Austrian late Middle Pleistocene locality Hundsheim *Talpa europaea* var. *minor*. He specifically mentioned that this species is not referable to *T. caeca*, since the m1 and m2 are of similar size, whereas the m1 is smaller than the m2 in *T. caeca*.

When Kormos (1937) revised the Hundsheim material, he referred the smaller *Talpa* to *T. gracilis*, a small species he had described from Püspökfürdő (Betfia 2) (Kormos, 1930). Here too the largest morphological difference with *T. europaea* lied in the morphology of the lower molars. According to Kormos the m1 lacked the paraconid. Kretzoi (1938) concluded that *T. minor* and *T. gracilis* were synonymous.

The smaller talpid from Csarnota (Hungary) was described by Kretzoi (1959) as *Talpa csarnotana*. This species is of the size of *T. minor*, but differs in a stronger development in the proximal area of the humerus and a shorter shaft. The name has remained relatively unnoticed. Storch (1978) used it in his comparison of the Turolian *T. gilothi* with other *Talpa* species, and in doing so gave the first illustration of the species. Since it is unlikely that Csarnota contain a different smaller *Talpa* species that other Hungarian localities of similar age, we assume that *T. csarnotana* is a junior synonym of *T. minor*.

*Talpa minor* has been found in numerous European localities. The oldest occurrence is in the Pliocene Polish locality Podlesice (Kowalski, 1956), the youngest in the German late Middle Pleistocene locality Petersbuch 1 (von Koenigswald, 1970). As in the middle-sized talpids, there was initially also a linguistic split in the naming of the small talpids. Whereas in Central Europe the smaller talpid was commonly referred to as *Talpa minor*, French assemblages were assigned to *T. caeca* (Mas Rambault: Chaline, 1972), *T. cf. caeca* (Les Valerots: Chaline, 1972), or *T. caeca-minor* (Montousse 5: Clot et al. (1976). Robert (1983) included all these Lower and Middle Pleistocene assemblages in *T. minor*. Reumer (1996) found *T. minor* in the French Middle Pleistocene locality Aventignan.

Kurtén (1968) suggested that *Talpa caeca* could be derived from *T. minor*. He also indicated that fossils of the recent species had been found in the Late Pleistocene of

Italy, without, however, giving any references to literature. According to Robert (1983) *T. minor* evolved into *T. caeca* by enlargement. This conclusion was based on measurements of the humerus and radius taken from literature. We reject this suggestion. Although the humeri of *T. minor* and *T. caeca* s.l. are similarly sized, the dentitions are not. The molars of *T. caeca* s.l. are in size comparable to *T. europaea*, whereas the molars of *T. minor* are much smaller. If *T. minor* gave rise to *T. caeca* s.l., one would expect to find dentitions of intermediate size in the Upper Pleistocene. As it is, no small talpid has been found in these strata, in spite of a sufficient number of microvertebrate studies on that interval.

#### Large-sized *Talpa* (*T. episcopal*is, *T. magna*)

The first record of a large-sized *Talpa* was given by Pomel (1848). He made mention of *T. magna*, a name was based on a single mandible. Pomel attributed the name to Owen (*Geospalax magna* Owen), but we could not find any original description by that author and therefore assume this was an unpublished name.

Kormos (1930) assigned some of the large postcranial elements from Püspökföld (Betfia 2) to a separate species, *Talpa episcopal*is. Robert (1983) tentatively assigned some of the bones from the Middle Pleistocene French locality Mas Rambault to the same species. Kormos had already noted that it is strange to have three species of *Talpa* in one single locality (*T. fossilis* and *T. minor* are also known from Betfia 2) and assumed that the find of the corresponding dental elements would help solve the riddle. Kretzoi (1938) also considered the presence of three *Talpa* species in Betfia 2 an absurdity, and proposed to give them different generic names. To date, no dental elements of *Talpa episcopal*is have been found. The presence of three talpids of the same genus in one locality is still unique. The only other case in which such a co-occurrence was assumed, was that of three *Geotrypus* species in the Oligocene French locality Cournon (Lavocat, 1951). This was, however, shown to be based on a misinterpretation of the material (Crochet, 1995; van den Hoek Ostende, 2001). We assume that this is also the case in Betfia 2. The matter can, however, only be resolved by reviewing the original material.

Large *Talpa* specimens can also be encountered in the Late Pleistocene. Although most of the material from this period is included in *T. europaea*, Storch (1974) argued that the larger elements should be assigned to a separate species, *T. magna* Woldrich, 1893 (non Pomel, 1848). Niethammer (1990) suggested that the relationships of this species with the Middle Pleistocene *T. episcopal*is Kormos, 1930, and the recent *T. altaica* Nikolsky, 1883, should be examined. Given its present distribution in the Taiga zone of Siberia between the rivers Ob and Lena, the latter species could very well have survived in the cold conditions of the European Weichselian.

### General conclusions

Doukas et al. (1995) indicated that the fossil representatives of the genus *Talpa* are badly in need of revision. The descriptions of the dentition of two recent species, and the following review of the literature given in this paper are a first contribution to such a revision. In summary, we came to the following conclusions:

*Talpa europaea* and *T. occidentalis* differ little in the size and morphology of their

dentitions, but more so in the dimensions of the humeri.

There is no ground for the suggestion that *T. minor* was ancestral to the recent blind moles *T. caeca* and/or *T. occidentalis*.

*Talpa fossilis* Petényi, 1864, is tentatively considered a junior synonym of *T. europaea*. Reassessment of the material from the type locality is needed to confirm this.

Many questions remain unanswered. Knowledge of the dentitions of the remaining European *Talpa* species (*T. caeca*, *T. romana* and *T. stankovici*), as well as of *Talpa* species outside of Europe (e.g. *T. altaica*) is needed. This knowledge can then be used to re-evaluate the fossil *Talpa* assemblages.

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