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THE MIDDLE PLEISTOCENE INSECTIVORES (ORDER EULIPOTYPHLA) FROM MIESENHEIM I (GERMANY)

THIJS VAN KOLFSCHOTEN[1,2]

[1] Faculty of Archaeology, Leiden University, Einsteinweg 2, 2333 CC Leiden, The Netherlands; e-mail: t.van.kolfschoten@arch.leidenuniv.nl.
[2] Joint International Research Laboratory of Environmental and Social Archaeology, Shandong University, Qingdao; Institute of Cultural Heritage, Shandong University, 72 Binhai Highway, Qingdao, Shandong, 266237, China.

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Abstract: The locality of Miesenheim I has yielded a rich assemblage of smaller mammals (Eulipotyphla, Lagomorpha, and Rodentia) comprising 28 taxa. Insectivores (Order Eulipotyphla), with over 2,000 identifiable remains, are well represented. The fauna includes four species from the family Soricidae (*Neomys* cf. *newtoni*, *Sorex minutus*, *S. subaraneus*, and *Sorex* (*Drepanosorex*) *savini*) and three taxa from the family Talpidae (*Talpa europaea*, *T. minor*, and *Desmana* sp.). *Sorex subaraneus* and *Neomys* cf. *newtoni* are the most commonly found species, whereas *Desmana* sp. is rare. The fauna originates from the early Toringian and is associated with the later part of the early Middle Pleistocene (pre-Elsterian/Cromerian IV/Marine Isotope Stage 13). The composition of the Miesenheim I insectivore assemblage is typical of late Biharian and early Toringian faunas; it contrasts with that of the late Toringian faunas. Furthermore, morphological differences have been observed between the remains from Miesenheim I and those from younger faunas.

Key words: Soricidae, Talpidae, Middle Pleistocene, late Cromerian, biostratigraphy, Neuwied Basin

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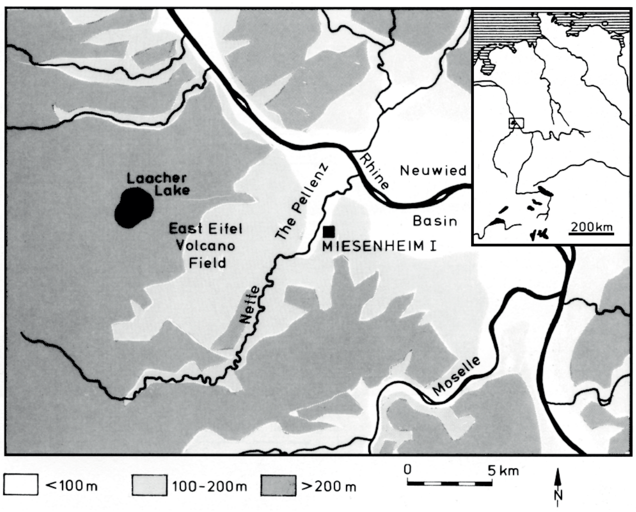
Introduction

The German locality Miesenheim I is in the Neuwied Basin, on a small spur of land on the eastern bank of the Nette Stream, a tributary of the River Rhine, just east of the village of Miesenheim (Text-fig. 1). The first stone artefacts and bone fragments were discovered here following pumice extraction in 1982, leading to a series of archaeological excavations from 1982 to 1990 (Boscheinen et al. 1984, Bosinski et al. 1988, Turner 1989, 2000, van Kolfschoten 1990).

The first small mammal remains, including beaver remnants, humerus bones from moles, and teeth from voles, were recovered during preliminary investigations conducted shortly after the site's discovery in the summer of 1982. Large sediment samples have been processed, and the residues have been screened for fossils using binocular microscopes to enhance the recovery of small vertebrate remains. This method yielded thousands of small mammals remains, alongside finds collected during the archaeological excavations from 1982 to 1986. The small mammal remains come from lithostratigraphic Units C, F, and G (with the vast majority from the archaeological find horizons in Units F and G). Although the finds originate from different layers, the assemblages are considered a single faunal unit (van Kolfschoten and Turner 1996).



Text-fig. 1. Geographical location of Miesenheim I (Germany).

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Preliminary results of the investigation into these small mammal remains have been published in several papers (van Kolfschoten in Boscheinen et al. 1984, van Kolfschoten in Bosinski et al. 1988, van Kolfschoten 1990, van Kolfschoten and Turner 1996). However, the previously published literature lacks more detailed information about the recorded small mammal taxa. This paper provides an overview of the recorded taxa and detailed information on the insectivores (Order Eulipotyphla) that are well-represented in the fossil small mammal assemblage.

The paper is dedicated to the late Oldřich Fejfar, a prominent Czech palaeontologist and one of the founders of the current Quaternary biostratigraphical subdivision based on the small mammal record of Central Europe. He was a great scientist and a source of inspiration for me and many of my colleagues.

The geological setting of the small vertebrate assemblage

The Miesenheim I section that yielded the small mammal assemblage consists of seven superimposed lithostratigraphic units. At the base are alternating lenses of sand and loamier material (Unit I), covered by loamy deposits (Unit H), upon which a weakly developed palaeosol has formed. Above the truncated remains of this soil, a colluvial horizon (Unit G) has formed. During a break in this sedimentation phase, a dark layer of autochthonous organic material has been deposited, alternating with allochthonous silty and clayey sediments, leading to the development of a hydromorphic soil (Unit F). The hydromorphic soil (Unit F) and the underlying colluvium (Unit G) represent the archaeological find horizons. These are covered by loamy colluvium (Unit C), gravel deposits (Unit B), and reworked loess (Unit A). For a more detailed description of the geological setting of the site, the reader is referred to Brunnacker in Boscheinen et al. (1984), Turner (1989), and Müller in Turner (2000). Detailed taphonomic analyses indicate that most of the faunal remains excavated at Miesenheim I were in situ (Turner 2000).

Material and methods

The Miesenheim I fossil assemblage includes over 6,000 small mammal remains. The fossil material is generally well-mineralised, but only partially preserved. The assemblage consists almost entirely of individual teeth and bone fragments.

Most of the Miesenheim I small mammal remains were extracted from residues created by wet-sieving bulk sediment samples through a 0.5 mm mesh. Additionally, larger remains from taxa such as *Talpa europaea*, *T. minor*, and *Desmana* sp. were recovered and hand-picked during the archaeological excavations. Thus, these species are slightly overrepresented in the assemblage.

The Miesenheim I small mammal assemblage includes representatives of the orders Eulipotyphla, Lagomorpha, and Rodentia. This paper presents an overview of the collected Eulipotyphla remains. The abundant fossils assigned to the orders Lagomorpha and Rodentia will be presented in another paper (van Kolfschoten in prep.).

For the presentation of the Eulipotyphla, the measurement protocol and dental terminology adhere to Reumer (1984) for the mandibles and teeth of Soricidae, and to Rümke (1985) for the Talpidae. In this paper, the initial letters of all upper jaw teeth are written in capital letters, while those of the lower jaw are denoted with a lowercase letter.

The fossil remains described in this paper are stored in the archaeozoological collection of the Faculty of Archaeology, Leiden University, Leiden, Netherlands.

Systematic palaeontology

Order Eulipotyphla Waddell et al., 1999

Remarks. The order Eulipotyphla (in older literature referred to as the order Insectivora) is well represented in the Miesenheim I small mammal assemblage, comprising two families: Soricidae and Talpidae.

Family Soricidae G. Fischer, 1814

Remarks. Shrew remains have been found in all strata, with over 2,000 individual specimens collected. Unfortunately, the remains are highly fragmented, even though the material is well fossilised. Identifiable skull fragments are absent, and there are no complete mandibles. Teeth almost exclusively occur in isolation and are often preserved in fragments. Some of the teeth display a dark, reddish-brown colour at the tips. This red pigmentation of the outer part of the enamel of the cusps, caused by the presence of iron compounds in the outer part of the enamel of the cusps of the teeth (Moya-Costa et al. 2018), is characteristic of the red-toothed shrews that includes, among others, species from the genera *Sorex* and *Neomys*.

The examined shrew remains were identified based on the morphological characteristics of the lower jaws, along with the upper and lower incisors, and were assigned to two different genera: *Neomys* and *Sorex*. The *Sorex* specimens were further classified into three distinct sizes, representing three different species: *S. minutus*, *S. subaraneus*, and *S.* (*Drepanosorex*) *savini*.

Genus *Neomys* Kamp, 1829

***Neomys* cf. *newtoni* Hinton, 1911**

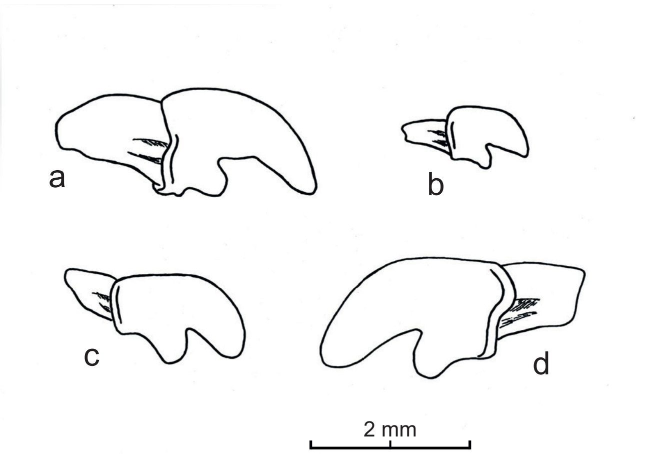
Material. Upper and lower dental elements, including 41 upper and 12 lower incisors, and 14 incomplete mandibles.

Dimensions. Tables 1, 2, Text-figs 2–9.

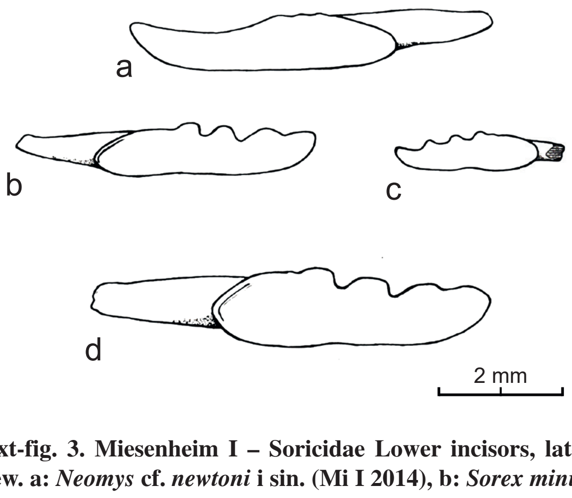
Morphological characteristics. The upper incisors (Text-fig. 2a) are fissident and strongly curved dorsally. The lower incisors possess a single cusp (Text-fig. 3a). The mandible features a sharply pointed coronoid process and exhibits a distinct coronoid spicule on the exterior (Text-fig. 5g–h). The internal temporal fossa is wide and does not extend into the coronoid process. Additionally, the

Table 1. Dimensions (in mm) of the Soricidae remains from Miesenheim I.

element	measurement	*Neomys* cf. *newtoni*			*Sorex minutus*			*Sorex subaraneus*			*Sorex* (*D.*) *savini*		
		N	range	mean	N	range	mean	N	range	mean	N	range	mean
I sup.	lenght	18	17.9 –20.3	19.22	6	5.1–6.3	5.75	12	14.7–18.9	17.22	13	19.7–23.5	22.28
	lenght talon	18	7.0–8.8	7.92	6	9.9–10.8	10.35	12	8.1–10.0	9.70	13	9.8–13.5	11.94
I inf.	length	3	4.2–4.7	4.40	5	2.3–2.4	2.34	11	3.4–3.8	3.57	6	4.3–4.6	4.47
mandibula	lenght m1–m3				2	3.0–3.1	3.05	2	3.6–3.7	3.65	3	4.2–4.4	4.29
ramus	height	12	4.3–4.6	4.46	3	2.8–2.9	28.70	11	3.8–4.5	4.20	6	5.5–6.0	5.80



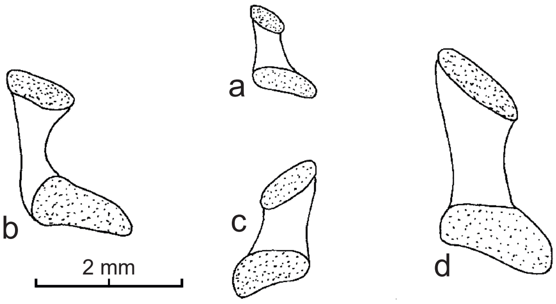
Text-fig. 2. Miesenheim I – Soricidae Upper incisors, lateral view. a: *Neomys* cf. *newtoni* I dext. (Mi I 512), b: *Sorex minutus* I dext. (Mi I 520), c: *Sorex subaraneus* I dext. (Mi I 501), d: *Sorex* (*Drepanosorex*) *savini* I sin. (Mi I 527).



Text-fig. 3. Miesenheim I – Soricidae Lower incisors, lateral view. a: *Neomys* cf. *newtoni* i sin. (Mi I 2014), b: *Sorex minutus* i sin. (Mi I 2088), c: *Sorex subaraneus* i dext. (Mi I 2070), d: *Sorex* (*Drepanosorex*) *savini* i dext. (Mi I 2057).

upper condylar facet (Text-fig. 4b) connects to the longer lower facet via a slender interarticular bone bridge that is prominently concave on the inner side. The mental foramen is situated beneath the m1, positioned between the trigonid and talonid.

The features described above are typical of shrews belonging to the genus *Neomys*. The morphology of the *Neomys* remains found at Miesenheim I differs from



Text-fig. 4. Miesenheim I – Soricidae condyle, caudal view. a: *Sorex minutus* mandibula sin. (Mi I 1881), b: *Neomys* cf. *newtoni* mandibula sin. (Mi I 1702), c: *Sorex subaraneus* mandibula dext. (Mi I 1866), d: *Sorex* (*Drepanosorex*) *savini* mandibula sin. (Mi I 1717).

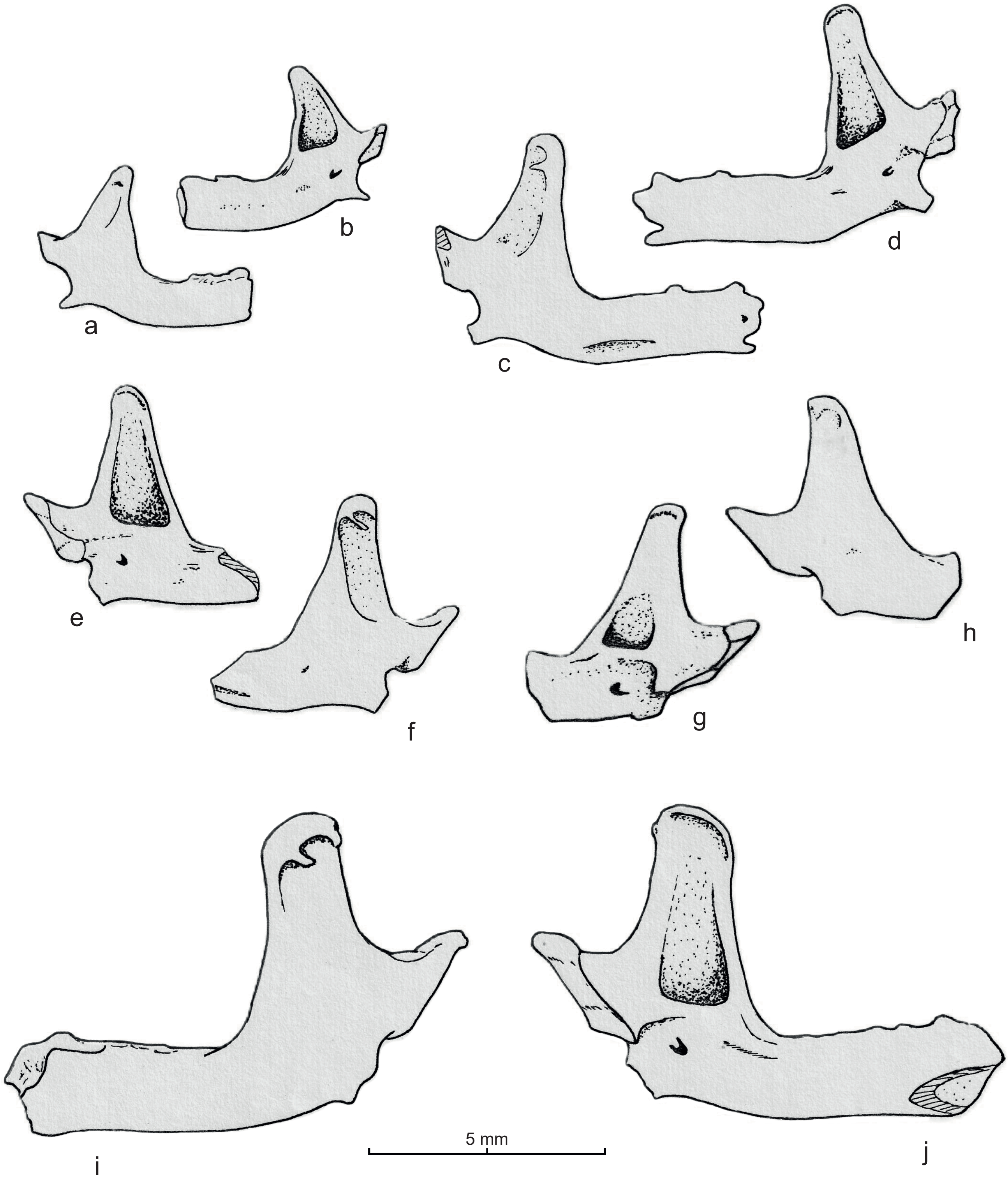
that of the extant species, *Neomys fodiens* (Pennant, 1771), in several respects. For instance, the Miesenheim I specimens are smaller, have a broader internal temporal fossa, and display a more pronounced coronoid spicule. In terms of size (Text-figs 6–8), the remains correspond more closely with *Neomys* species from the Early and Middle Pleistocene of Europe, such as *Neomys newtoni* Hinton, 1911, and *Neomys browni* Hinton, 1911. *N. newtoni* is characterised by a condyloid process featuring a relatively narrow upper articular facet and a deeply incised bone bridge between the upper and lower articular facets (Hinton 1911). These characteristics are also evident in the Miesenheim I material. In contrast, the condylar bone bridges of *N. fodiens* and *N. browni* are generally wider and more inwardly incised, with the upper articular facet being broader in *N. browni*. Additionally, the coronoid height of the Miesenheim I mandible is significantly greater than that of *N. newtoni* from its type locality in West Runton. The dimensions are more consistent with fossils from Mt. Peglia (van der Meulen 1973) and Westbury-sub-Mendip (Bishop 1982), which are referred to as *Neomys* cf. *newtoni*.

Genus *Sorex* Linnaeus, 1758

Sorex minutus Linnaeus, 1766

Material. Upper and lower dental elements, including 9 upper and 5 lower incisors, and 10 incomplete mandibles.

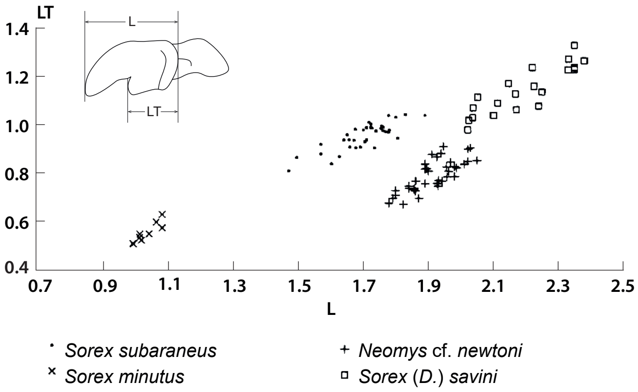
Dimensions. Tables 1, 2, Text-figs 2–9.



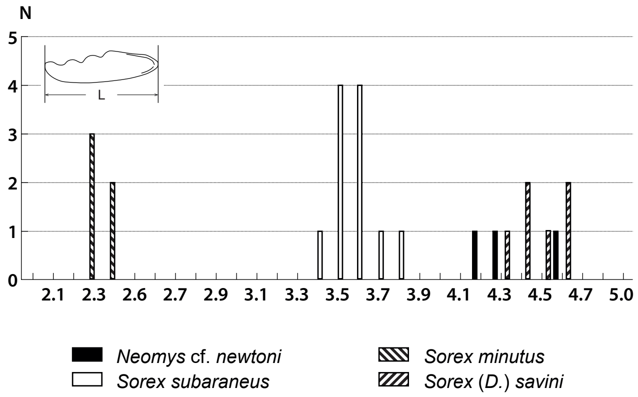
Text-fig. 5. Miesenheim I – Soricidae mandibulae, lateral view (a, c, f, h, i) and lingual view (b, d, e, g, j). a, b: *Sorex minutus* mandibula dext. (Mi I 1813), c–f: *Sorex subaraneus*, c, d – mandibula sin. (Mi 1701), e, f – mandibula dext. (Mi 1709), g, h: *Neomys* cf. *newtoni* mandibula dext. (Mi I 1885), i, j: *Sorex* (*Drepanosorex*) *savini* mandibula sin. (Mi I 1769).

Morphological characteristics. The dimensions of the dental elements are small (Text-figs 6–8). The upper incisors (Text-fig. 2b) have a straight dorsal outline and are strongly fissident. The lower incisors display three distinct cusps (Text-fig. 3b). The coronoid process of the lower jaw (Text-fig. 5a, b) is relatively broad and slightly inclined forwards. The coronoid spicule is small, and the internal fossa temporalis is broad, extending significantly into the coronoid process. The bony bridge between the upper and lower articular surfaces (Text-fig. 4a) is wide. The mental foramen is located below the paraconid of the m1.

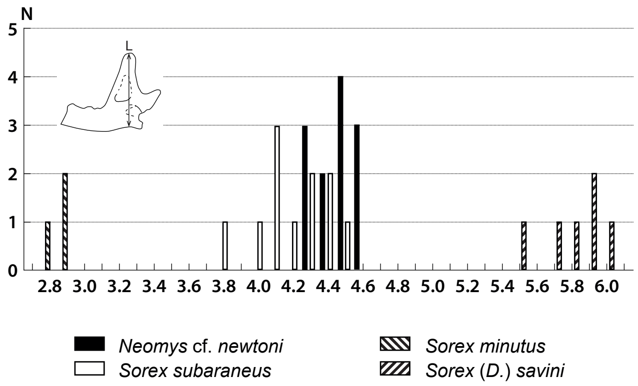
The fossil remains are attributed to *S. minutus*, based on their dimensions and general morphological characteristics.



Text-fig. 6. Miesenheim I – Soricidae. Dimensions (in mm) of the upper incisors. Length (L) and length of the talon (LT).



Text-fig. 7. Miesenheim I – Soricidae. Length (in mm) of the lower incisors.



Text-fig. 8. Miesenheim I – Soricidae. Height (in mm) of the mandibular coronoid process.

The measurements of the materials from Miesenheim I closely align with those from other Middle Pleistocene sites, such as Petersbuch (von Koeningswald 1970) and Maastricht-Belvédère (van Kolfschoten 1985). The dimensions of the Miesenheim I material exceed those of *S. minutissimus* Zimmermann, 1870. The mandibles of the two species can also be distinguished by the position of the mental foramen. In *S. minutissimus*, the mental foramen is located below the m1, approximately between the trigonid and talonid. In contrast, in *S. minutus*, the mental foramen is found further anteriorly, beneath the paraconid of the m1 (Heim de Balsac 1940).

Sorex subaraneus Heller, 1958

Material. Upper and lower dental elements including 32 upper and 35 lower incisors, and 15 incomplete mandibles.

Dimensions. Tables 1, 2, Text-figs 2–9.

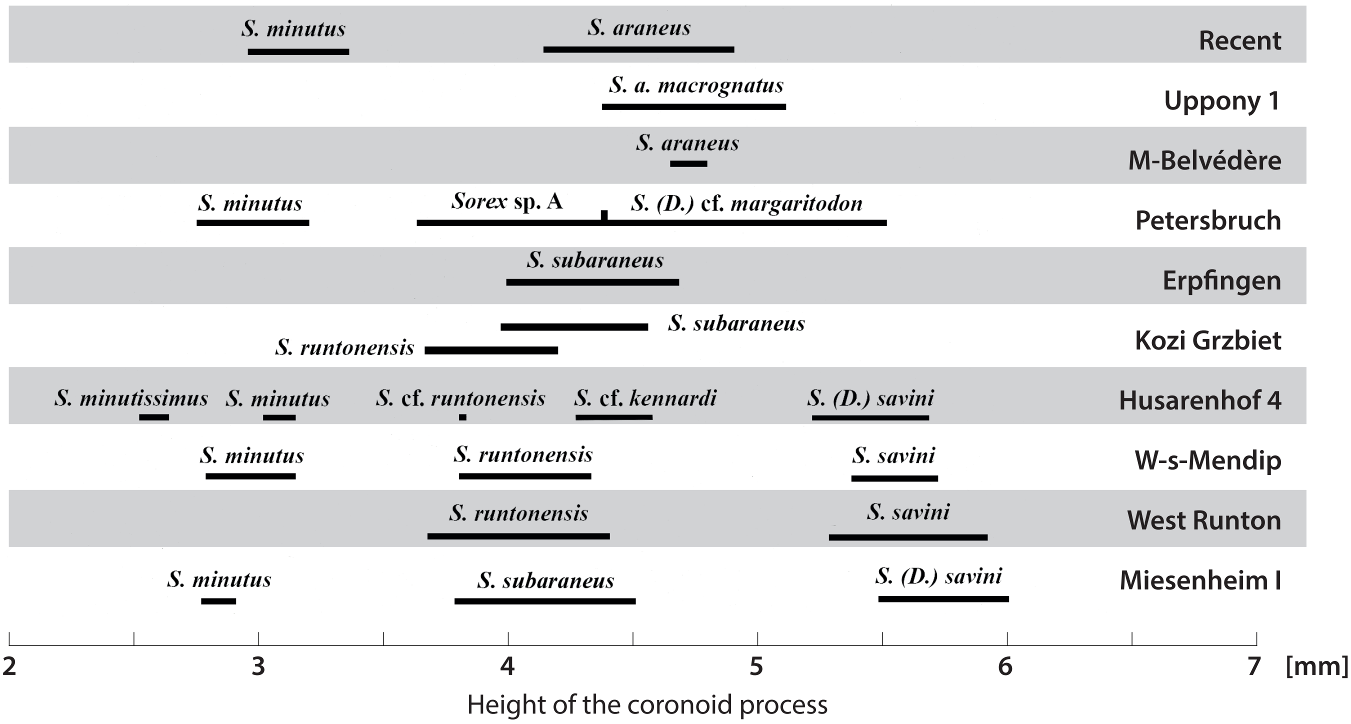
Morphological characteristics. The upper incisors (Text-fig. 2c) exhibit a straight dorsal outline and are only slightly fissident. The lower incisors possess three distinct cusps (Text-fig. 3c). The coronoid process of the lower jaw (Text-fig. 5c–f) is generally somewhat widened in its upper section. The external temporal fossa is typically deep and may be bordered by a sharp edge. The internal temporal fossa is broad and extends far into the coronoid process. The articular facets (Text-fig. 4c) are interconnected by a bone bridge that is concave on the inner side. The mental foramen is situated below the transition between the trigonid and talonid of the m1, or below the posterior edge of the trigonid.

Based on the dimensions, the material is classified as belonging to the group of medium-sized *Sorex* species that are intermediate in size between *Sorex minutus* and *S. araneaus*; a group that includes, among others, *S. runtonensis* Hinton, 1911, *S. kennardi* Hinton, 1911, *S. prealpinus* Heller, 1930 and *S. subaraneus* Heller, 1958 (Rofes et al. 2016). The medium-sized *Sorex* remains from the fauna of Miesenheim I were originally assigned to as *S. runtonensis*, one of the most abundant representatives of the genus in the shrew fauna of the European Pleistocene record (Osipova et al. 2006), and published as such in previous publications reporting on the fossil (small) mammal fauna from Miesenheim I (van Kolfschoten in Boscheinen et al. 1984, van Kolfschoten in Bosinski et al. 1988, van Kolfschoten 1990, van Kolfschoten and Turner 1996).

Rofes et al. (2016) question the distinction between *S. runtonensis* and *S. subaraneus*, wondering if the highly

Table 2. Dimensions (length m1–m3, ramus height) (in mm) of *Sorex subaraneus* from Miesenheim I (this paper), and the dimensions of *S. runtonensis* and *S. subaraneus* from Kozi Grzbiet and *S. subaraneus* from Erpfingen, presented Rzebik-Kowalska and Pereswiet-Soltan (2018).

locality	species	length m1–m3			ramus height		
		N	range	mean	N	range	mean
Miesenheim I	*S. subaraneus*	2	3.60–3.70	3.65	11	3.80–4.50	4.20
Kozi Grzbiet	*S. runtonensis*	16	3.40–3.59	3.49	7	3.66–4.21	3.89
	S. subaraneus	16	3.57–3.95	3.69	15	3.94–4.54	4.21
Erpfingen	*S. subaraneus*	4	3.52–3.80	3.66	18	4.01–4.64	4.32



Text-fig. 9. Miesenheim I – Soricidae, the height of the coronoid process. The range of the height of the coronoid process for the extant *S. minutus* (Bishop 1982) and the extant *S. araneus* (collection Leiden University) and of a number of (sub)species from various localities: Uppony 1 (Jánossy 1965b), Maastricht-Belvédère (van Kolfschoten 1985), Petersbuch (von Koenigswald 1970), Erpfingen and Kozi Grzbiet (Rzebik-Kowalska 2000), Husarenhof 4 (von Koenigswald 1973a), Westbury-sub-Mendip (Bishop 1982), West Runton (Stuart 1981) and Miesenheim I.

polymorphic *S. runtonensis* and *S. subaraneus* could be regarded as a morphological continuum of a single species, *S. runtonensis*. However, Rzebik-Kowalska and Pereswiet-Soltan (2018) do not follow the suggestion of Rofes et al. (2016). The authors convincingly demonstrate that both species, *S. runtonensis* and *S. subaraneus*, are valid species that differ in size and morphological features (Rzebik-Kowalska and Pereswiet-Soltan 2018). *Sorex subaraneus* is larger, and its lower teeth are more massive compared to those of *S. runtonensis*. Moreover, the shape of the interarticular area of the condyloid process is trapezoidal in *S. subaraneus*, while this area is rectangular in *S. runtonensis* (Rzebik-Kowalska and Pereswiet-Soltan 2018).

The measurements of the Miesenheim I material are, in comparison with the data presented by Rzebik-Kowalska and Pereswiet-Soltan (2018) (Tab. 2), more aligned with those of *S. subaraneus* than with *S. runtonensis*. Additionally, the interarticular area's shape in the condyle process of the Miesenheim I specimens (Text-fig. 4c) is more trapezoidal than rectangular. These features justify changing the original identification of the Miesenheim I medium-sized *Sorex* from *S. runtonensis* to *S. subaraneus*.

Sorex (*Drepanosorex*) *savini* Hinton, 1911

Material. Upper and lower dental elements, including 21 upper and 22 lower incisors, and 9 incomplete mandibles.

Dimensions. Tables 1, 2, Text-figs 2–9.

Morphological characteristics. The assemblage includes *Sorex* remains that exhibit the largest dimensions. The upper incisors are slightly fissident, and the dorsal outline is relatively straight (Text-fig. 2d). The lower incisors possess four large, rounded cusps (Text-fig. 3d). The upper portion of the coronoid process is broad (Text-fig. 5i, j), and the coronoid spicule is well developed. The external temporal fossa is large with indistinct borders, while the internal temporal fossa is wide and extends significantly into the coronoid process. The two articular facets (Text-fig. 4d) are nearly identical in size and are connected by a broad bony bridge. The mental foramen is situated below the posterior edge of the p4.

The dimensions of the Miesenheim I *Sorex* remains listed above indicate that the material should be classified as part of the group of large-sized *Sorex* species. Middle Pleistocene shrew remains, larger than those of the extant species *Sorex araneus* Linnaeus, 1758, are classified in the literature under the genus *Drepanosorex* Kretzoi, 1941 (Kretzoi 1965, Jánossy 1969, 1976). Some researchers, including von Koenigswald (1973a) and Bishop (1982), regard *Drepanosorex* as a subgenus of the genus *Sorex*. Reumer (1985) has confirmed that distinguishing between the genera *Drepanosorex* and *Sorex* is unjustified, suggesting instead that it is preferable to consider *Drepanosorex* as a subgenus of the genus *Sorex*. Reumer identifies four species within this classification based on size: *S.* (*D.*) *praearaneus* Kormos, 1934, *S.* (*D.*) *margaritodon* Kormos, 1930, *S.* (*D.*) *savini* Hinton, 1911, and *S.* (*D.*) *austriacus* Kormos, 1937. The four species differ in size and the degree of exoedaenodonty (Reumer 1984, 1985, Rzebik-Kowalska 2000, Rofes and Cuenca-Bescós 2013), with *S.* (*D.*) *praearaneus* being the smallest and most primitive, while *S.* (*D.*) *austriacus* is the largest.

The dimensions of most of the larger shrew specimens found at Miesenheim I overlap with those of *S.* (*Drepanosorex*) *savini* from its type locality at West Runton and from Westbury-sub-Mendip (Text-fig. 9); a few specimens from Miesenheim I are somewhat larger. The dimensions of the Miesenheim I remains are larger than those of *S.* (*D.*) *margaritodon* from the type locality Betfia II, Romania (Betfia-IX: ramus height: 4.82–5.84, mean 5.25, N = 68) (Rzebik-Kowalska 2000) and from Sima del Elefante, Spain (TE9: ramus height: 5.02–5.18, mean 5.1, N = 2) (Rofes and Cuenca-Bescós 2013). Given the morphological similarities and only minor size differences, the larger shrews from Miesenheim I are thus classified as *S.* (*Drepanosorex*) *savini*.

According to Reumer (1985), *S.* (*D.*) *austriacus* is the largest and youngest of these four species, occurring in the faunas of Hundsheim, Erpfingen, and Sudmer-Berg-2. However, the dimensions of the specimens from Erpfingen and Sudmer-Berg-2 are similar to those of *S.* (*D.*) *savini* from the type locality West Runton. The material from Hundsheim, described by Rabeder (1972) as *Drepanosorex austriacus*, is partially larger than the specimens from West Runton. Nevertheless, the considerable overlap in size variation indicates that the differences are too minor to warrant separate species classification. Rabeder compared the specimens from Hundsheim with Hinton's (1911) illustration of a lower incisor of *S.* (*D.*) *savini* from West Runton, and observed that the lower incisors from West Runton appeared more robust. However, this characteristic is not evident in the actual material from West Runton (cf. Reumer 1985: fig. 3). Consequently, the specimens from Hundsheim should be classified as *S.* (*D.*) *savini* and may, at most, be regarded as a subspecies, as originally proposed by Kormos (1937).

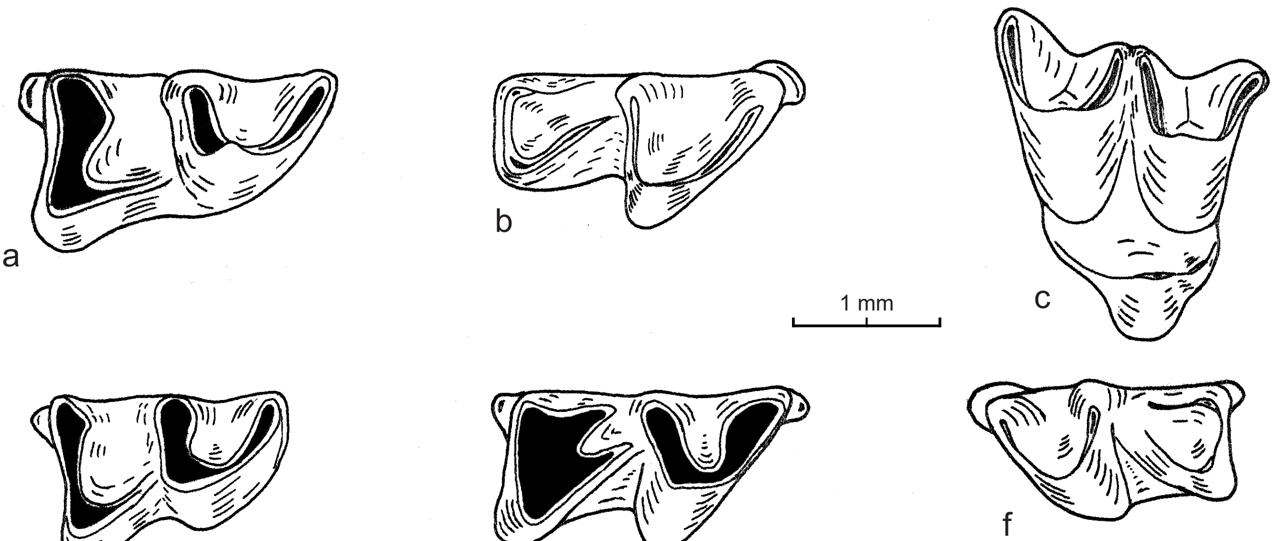
Horáček and Ložek (1988) studied the larger shrew remains from Petersbuch and assigned the material to a new species, *Sorex* (*Drepanosorex*) *postsavini* Horáček et Ložek, 1988, due to its distinctly smaller size when compared to *S.* (*D.*) *savini* and *S.* (*D.*) *austriacus*. Previously, von Koenigswald (1970) had assigned these remains to *S.* (*D.*) cf. *margaritodon*, because of only minor differences compared to the similarly sized but stratigraphically older *S.* (*D.*) *margaritodon*. However, Horáček and Ložek (1988) observed differences in the pigmentation, the shape of the processus articularis and the coronoid process.

Family Talpidae G. Fischer, 1814
Subfamily Talpinae G. Fischer, 1814

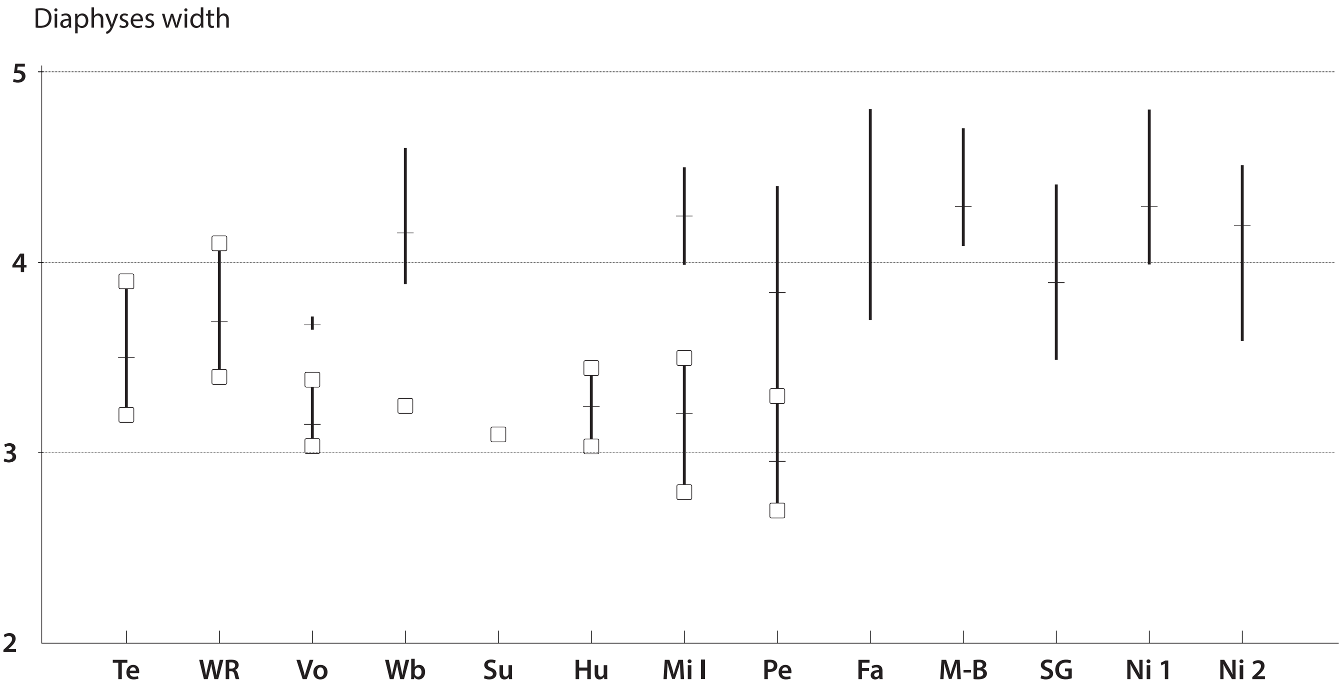
Genus *Talpa* Linnaeus, 1758

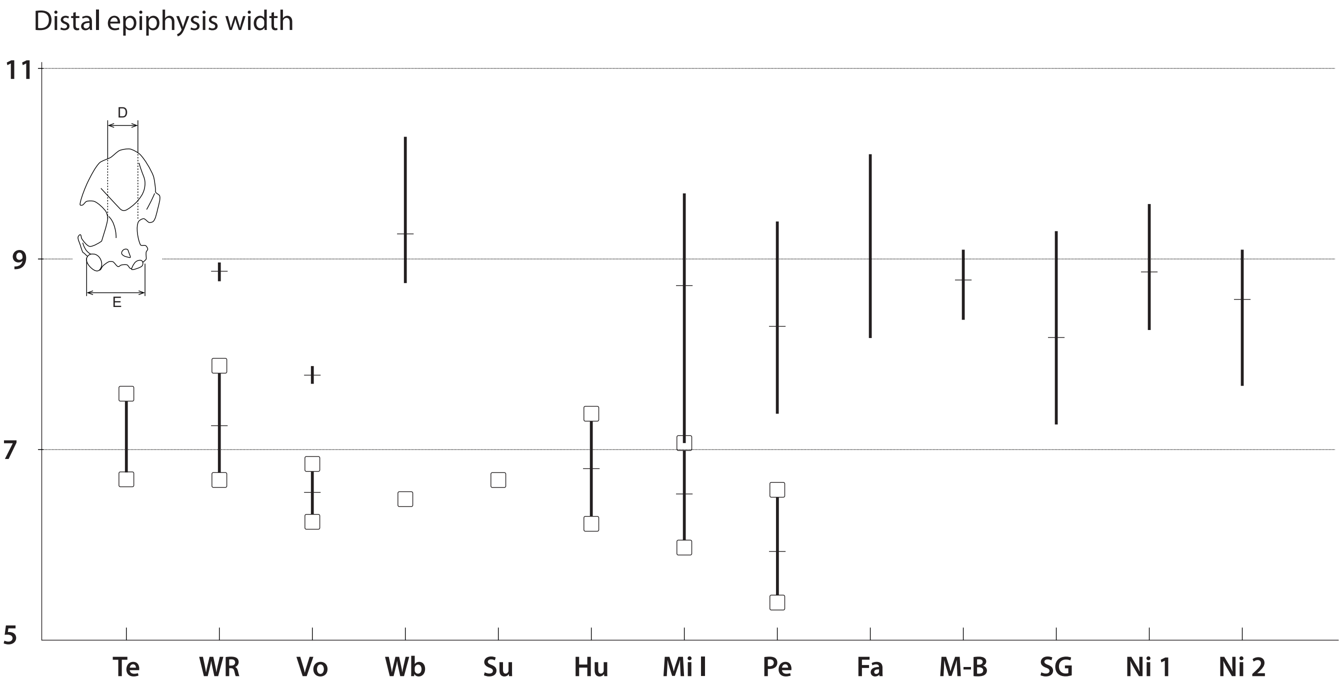
Remarks. Mole remains are well represented in the Miesenheim I fossil assemblage. Most of the humeri were collected during the archaeological excavation, leading to their overrepresentation in the assemblage. However, only one of the thirty-eight humeri is completely preserved; the others are damaged at the proximal end. Additionally, the lower jaws are also incomplete. The morphology and dimensions of the characteristic teeth, jaws, and humeri roughly resemble those of the common mole, *Talpa europaea*. The upper molars exhibit a well-developed protocone, paracone and metacone. The outline of the occlusal surface of the M1 is quadrangular, whereas those of the M2 and M3 are triangular. The lower molars possess a well-developed trigonid and talonid. For detailed information on the dentition of *Talpa europaea*, readers are referred to van Cleef-Roders and van den Hoek Ostende (2001). The humeri are short and stout with a flattened distal end – features regarded as specialised adaptations for digging and burrowing.

In Europe, five extant species of the genus *Talpa* are recognised (van Cleef-Roders and van den Hoek Ostende 2001, Marchetti 2024). Furthermore, several extinct *Talpa* species are documented in the Quaternary fossil record.



Text-fig. 10. Miesenheim I – *Talpa* Upper and Lower molars, occlusal view. *T. europaea*: a: m1 dext. (Mi I 25), b: m3 dext. (Mi I 43). *T. minor*: c: M2 dext. (Mi I 42), d: m1 dext. (Mi I 36), e: m2 dext. (Mi I 14), f: m3 sin. (Mi I 52).





Text-fig. 11. Diagrams showing the range and the mean of the dimensions of the humeri of the extant and the fossil *Talpa europaea*, and the fossil *Talpa minor* (indicated with open squares): Te – Tegelen (Roders 1988), WR – West Runton (Stuart 1981), Vo – Voigtstedt (Stuart 1981), Wb – Westbury-sub-Mendip (Bishop 1982), Su – Sudmer-Berg-2 (von Koenigswald 1972), Hu – Husarenhof 4 (von Koenigswald 1973a), Mi I – Miesenheim I (this paper), Pe – Petersbuch (von Koenigswald 1970), Fa – la Fage (Jammot 1974), M-B – Maastricht-Belvédère, Fauna 4 (van Kolfschoten 1985), SG – Southern Germany, recent (von Koenigswald 1985), Ni 1 – The Netherlands (Oude Mirrum), recent (Roders 1988), Ni 2 – The Netherlands (Bergen op Zoom), recent (Roders 1988).

However, the fossil record of *Talpa* exhibits minimal morphological variation, and significant overlap in size among the recognised *Talpa* species, with several fossil species being based on inadequate remains. The taxonomy of the fossil representatives of the genus *Talpa* is ambiguous (Doukas et al. 1995, van Cleef-Roders and van der Hoek Ostende 2001, Marchetti 2024), and requires revision. Nonetheless, the literature shows a consensus that the living and extinct *Talpa* species can be classified into three size groups: small (e.g., *T. minor* Freudenberg, 1914), middle (e.g., *T. europaea* Linnaeus, 1758, *T. fossilis* Petenyi, 1864), and large (e.g., *T. episcopalis* Kormos, 1930) (van Cleef-Roders and van der Hoek Ostende 2001, Marchetti 2024).

Table 3. Dimensions (in mm) of the dental elements of *Talpa minor* from Miesenheim I.

element	measurement	N	range	mean
P4	length	1		1.45
	width	1		0.92
M1	length	1		2.46
	width			
M2	length	5	1.79–1.97	1.88
	width	5	2.07–2.73	2.24
M3	length	2	1.27–1.30	1.29
	width	2		1.70
p4	length	1		1.26
	width	1		0.50
m1	length	1		1.76
	width trigonid	2	0.90–0.94	0.92
	width talonid	2	1.09–1.19	1.15
m2	length	1		2.15
	width trigonid	2	1.02–1.13	1.08
	width talonid	2	1.09–1.13	1.11
m3	length	1		1.86
	width trigonid	1		0.98
	width talonid	1		0.78

The mole remains from Miesenheim I show clear differences in dimensions and are therefore attributed to two species: *Talpa europaea* and *Talpa minor*. The remains attributed to the two species also display some morphological differences.

Talpa europaea Linnaeus, 1758

Material. 9 dental elements, 2 mandibles, 13 humeri.

Dimensions. Humeri – length: 14.8–16.6 mm, mean 15.47 mm (N = 3); width of the diaphysis: 4.0–4.5 mm, mean 4.25 (N = 12); width of the distal epiphysis: 7.1–9.7 mm, mean 8.75 (N = 10).

The dimensions and morphological characteristics of the teeth (Text-fig. 10a, b) and humeri (Text-fig. 11) closely correspond with data from recent common mole populations in the Netherlands (van Cleef-Roders and van den Hoek Ostende 2001).

A comparison with the comprehensive dataset presented by Marchetti (2024) indicates that the dimensions of the humeri listed above fall within the ranges observed in *T. europaea*. The *Talpa europaea* humeri from Petersbuch, with a mean length of 15.42 (N = 15), a mean diaphyseal width of 3.85 (N = 90), and a mean epiphyseal width of 8.32 (N = 90) (von Koenigswald 1970), exhibit comparable dimensions. However, the diaphyseal and epiphyseal widths of the Miesenheim I humeri are generally larger than those from Petersbuch (Text-fig. 11).

Talpa minor Freudenberg, 1914

Material. 20 dental elements, 2 mandibles, 25 humeri.

Dimensions. Dental elements – see Table 3; humeri – width of the diaphysis: 2.8–3.5 mm, mean 3.21 (N = 25); width of the distal epiphysis: 6.0–7.1 mm, mean 6.56 (N = 13).

Morphological characteristics. The material listed above has smaller dimensions than the remains attributed to *Talpa europaea*. Additionally, there are diagnostic differences in the morphological features. The upper molars, particularly the M2 (Text-fig. 10c) and M3 exhibit a mesostyle divided into two cusps. In contrast, the mesostyle of the upper molars of *T. europaea* is undivided (van Cleef-Roders and van den Hoek Ostende 2001). This distinctive division of the mesostyle can also be seen in the upper molars of *T. minor* from the Early Pleistocene fauna of Tegelen (Netherlands). The lower molars of the two species represented in the Miesenheim I faunal assemblage also display morphological differences. In the lower molars of *T. minor*, the connection between the trigonid and hypoconid is positioned at a more lingual location (Text-fig. 10f) compared to those assigned to *T. europaea* (Text-fig. 10b).

T. minor is represented in numerous Early to Middle Pleistocene faunas. For example, it is known from Husarenhof 4 (von Koenigswald 1973a), Mauer (Heller 1939: the material was identified by Heller as *Talpa gracilis* Kormos, 1930), Mosbach (Bahlo and Malec 1969: described as *Talpa* sp.), Sudmer-Berg-2 (von Koenigswald 1972), Petersbuch (von Koenigswald 1970), and Westbury-sub-Mendip (Bishop 1982). *Talpa gracilis* is regarded as a synonym of *Talpa minor* (Rabeder 1972). During the late Middle Pleistocene and Late Pleistocene, *T. minor* was no longer found in northwestern and central Europe, north of the Alps (von Koenigswald 1973b). In faunas such as La Fage (Jammot 1974), Maastricht-Belvédère Fauna 4 (van Kolfschoten 1985), and Hunas (Heller 1983), moles are represented solely by the larger form *T. europaea*.

Subfamily Desmaninae Thomas, 1912

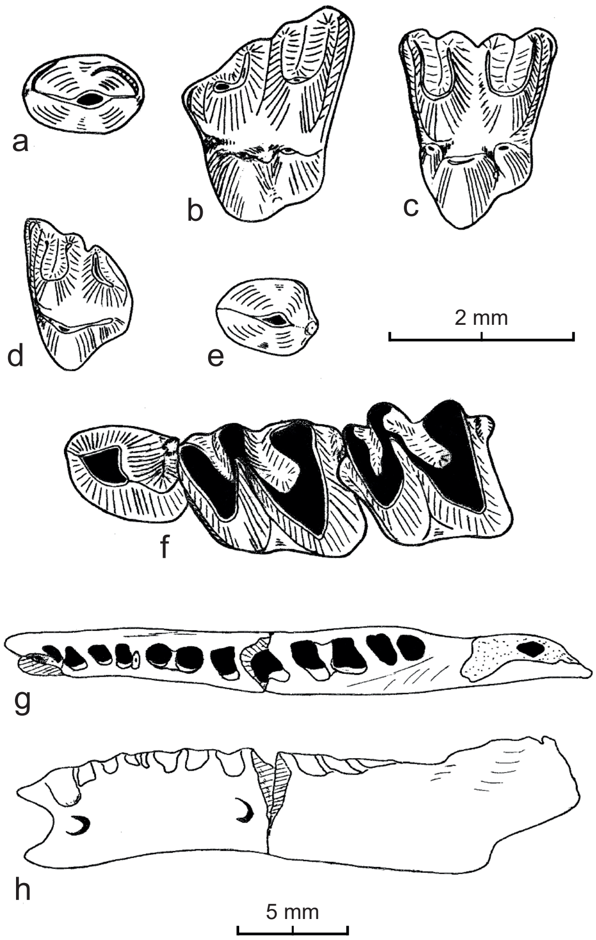
Genus *Desmana* Gueldenstaedt, 1777

Desmana sp.

Material. 35 dental elements, 6 mandibula fragments, 1 humerus.

Measurements. Tables 4, 5.

Morphological characteristics. The P1 has a single root, and the crown exhibits a well-developed posterior-labial cingulum. The P2 has two roots, and the two P2 premolars differ in the development of the lingual cingula. The right P2 (Text-fig. 12a) displays a pronounced lingual cingulum, whereas the left P2 has a poorly developed cingulum. The roots of the P3 molars are not preserved, so the number of roots remains unknown. The P3 presents a narrow posterior cingulum that connects to a relatively well-developed protocone.



Text-fig. 12. Miesenheim I – *Desmana* sp. Upper and Lower molars. a–g: occlusal view, h: lateral view. a: P2 dext. (Mi I 216), b: M1 sin. (Mi I 235), c: M2 sin. (Mi I 245), d: M3 sin. (Mi I 240), e: p2 dext. (Mi I 207), f: p4–m2 sin. (Mi I 237), g, h: mandible sin. (Mi I 232).

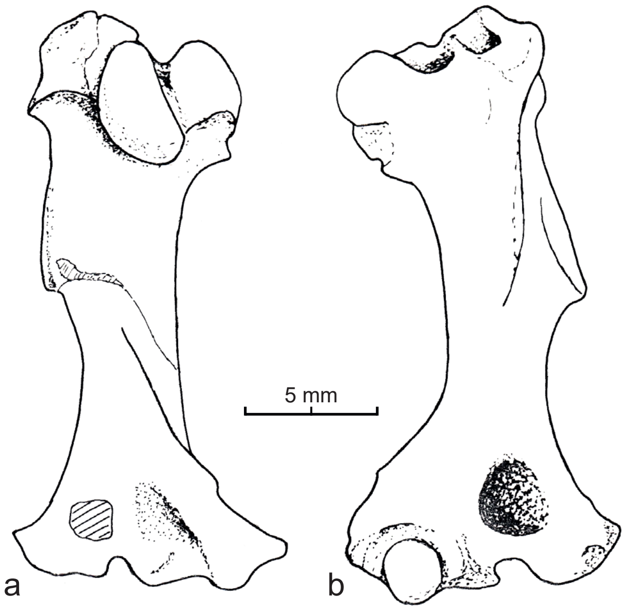
The M1 (Text-fig. 12b) displays a well-developed parastyle, whereas the mesostyle is relatively weak and only slightly broadens the tooth in the labial direction. At the base of the crown, there is a small cingulum situated between the protocone and protoconule. In the somewhat triangular M2 (Text-fig. 12c), the lingual part, which includes the protocone, protoconule, and metaconule, is relatively short. The parastyle is small, and the posterior groove is wide. The M3 (Text-fig. 12d) is short and broad. The parastyle is well-developed and connects to the anterior cingulum. The protoconule is nearly entirely fused with the protocone.

The lower jaws (Text-fig. 12g, h) are only partially documented; the coronoid, condyloid, and angular processes are absent in all specimens. On the labial side, the mandible exhibits two mental foramina of approximately the same size, positioned just below the midline. The anterior one is located beneath the root of p1, while the posterior one is situated under the anterior root of m1. The morphology of the alveoli suggests that the mandibular teeth c and p1 are single-rooted, whereas p2 and p4 are two-rooted. The p3 has either one or two weakly separated alveoli.

The p1 features a cingulum only on the posterior side. Additional cusps are absent on both the lingual and labial sides. In the anterior section of the p2 (Text-fig. 12e), the lingual and labial cingula are weakly developed, while the posterior cingulum is more robust and broader on the postero-lingual side of the tooth. The p4 (Text-fig. 12f) possesses a cingulum on its anterior side; the paraconid is small, whereas the isolated entoconid is well-developed. The hypoconid connects to the protoconid via the posterocristid, and the hypoconid and entoconid are joined by a weakly developed ridge. One of the p4 premolars, which is minimally worn, exhibits an isolated metaconid.

The m1 (Text-fig. 12f) features a well-developed anterior cingulum, with the hypoconid and metaconid connected by an oblique cristid. A parastylid is absent. The m2 (Text-fig. 12f) differs from the m1 by possessing a parastylid and a wider groove between the anterior cingulum and protoconid. Additionally, the m2 exhibits a poorly developed cingulum on the labial side, along with an additional cusp on the lingual side of the paraconid. The m3 displays a weakly developed entostylid. The parastylid of the m3 may be regarded as an extension of the broad anterior cingulum.

The right humerus (Text-fig. 13) is almost complete; only the distal end shows some damage. A flattened shaft characterises the bone.



Text-fig. 13. Miesenheim I – *Desmana* sp. Humerus dext. (Mi I 261). a: posterior view, b: anterior view.

Desmana thermalis and *Desmana moschata*

The dimensions of the material outlined and described above (Tab. 4) are relatively large; therefore, only species from the genus *Desmana* Gueldenstaedt, 1777 are considered for taxonomic assignment. In contrast, the genus *Galemys* Kaup, 1829 includes species that are significantly smaller (Rümke 1985). Rümke (1985) provides detailed information on six different *Desmana* species: *D. verestchagini* Topachevski, 1961, *D. kowalskae* Rümke, 1985, *D. nehringi* Kormos, 1913, *D. thermalis* Kormos, 1930, *D. inflata* Rümke, 1985, and *D. moschata* (Linnaeus,

Table 4. Dimensions (in mm) of the dental elements of *Desmana* sp. from Miesenheim I, *D. thermalis* from Tegelen (Rümke 1985), *D. thermalis* from Betfia (Rümke 1985) and the extant *D. moschata* (Rümke 1985).

element	measurement	Miesenheim I			*D. thermalis* – Tegelen			*D. thermalis* – Betfia			*D. moschata*		
		N	range	mean	N	range	mean	N	range	mean	N	range	mean
I2/3	length	1		1.23									
	width	1		1.17									
C	length				14	1.98–2.49	2.25				13	1.86–2.67	2.33
	width				14	1.39–1.63	1.49				13	1.64–1.86	1.75
P1	length	2	1.85–2.08	1.96	10	1.60–1.83	1.71				14	1.62–1.92	1.81
	width	2	1.65–1.69	1.67	10	1.41–1.65	1.56				14	1.54–1.79	1.64
P2	length	2	2.66–2.69	2.68	10	2.32–2.61	2.46	2	2.40–2.56	2.47	14	2.18–2.48	2.35
	width	2	1.72–1.79	1.76	10	1.59–1.79	1.69	2	1.66–1.90	1.77	14	1.70–1.97	1.85
P3	length	2	1.75–1.86	1.81	8	1.69–2.04	1.90	2	1.75–1.90	1.82	12	1.74–2.14	1.96
	width	2	1.74–1.94	1.84	8	1.60–2.01	1.75	2	1.71–1.80	1.75	12	1.81–2.11	1.99
P4	length				12	2.68–3.27	2.95	2	3.04–3.10	3.07	13	3.12–3.53	3.36
	width				12	2.25–2.50	2.37	2	2.48–2.75	2.61	13	2.79–3.05	2.91
M1	length	1		3.71	11	3.66–4.02	3.83	2	4.18–4.20	4.19	14	4.1.8–4.74	4.54
	width	1		4.22	11	3.04–3.47	3.56	2	3.43–3.70	3.56	14	3.95–4.50	4.19
M2	length	1		3.43	8	2.60–3.10	2.80	2	2.85–2.87	2.86	14	3.35–3.69	3.56
	width	1		4.32	9	3.27–3.87	3.60	2	3.70–3.99	3.84	14	4.48–5.04	4.68
M3	length	3	2.10–2.18	2.14	10	1.68–2.12	1.89	1		2.00	14	2.31–2.63	2.42
	width	2	2.86–3.34	3.10	10	2.45–2.91	2.70	1		2.90	14	3.37–3.85	3.58
i3	length	6	1.36–1.68	1.55									
	width	6	1.30–1.48	1.39									
c	length	3	1.71–1.95	1.81	13	1.63–2.02	1.86				13	2.00–2.20	2.09
	width	4	1.38–1.69	1.55	13	1.24–1.50	1.35				13	1.53–1.77	1.65
p1	length	1		1.81	19	1.37–1.70	1.52				13	1.69–1.89	1.82
	width	1		1.57	19	1.20–1.47	1.37				13	1.50–1.68	1.61
p2	length	1		2.32	12	1.92–2.31	2.19	3	2.20–2.40	2.32	14	2.14–2.38	2.24
	width	1		1.57	12	1.33–1.54	1.47	3	1.57–1.60	1.59	14	1.64–1.76	1.69
p3	length				12	1.86–2.18	1.98	1		1.86	13	1.95–2.23	2.12
	width				12	1.37–1.67	1.54	1		1.84	13	1.68–1.85	1.75
p4	length	2	2.54–2.76	2.65	17	1.99–2.50	2.30	3	2.41–2.63	2.55	14	2.53–2.84	2.71
	width	2	1.80–1.89	1.85	16	1.48–1.87	1.65	3	1.73–1.81	1.76	14	1.77–2.05	1.92
m1	length	1		3.91	11	2.67–3.38	3.10	3	3.37–3.61	3.49	14	3.58–3.98	3.79
	width trigonid	1		2.66									
	width talonid	2	3.02–3.17	3.10	11	2.48–2.63	2.55	3	2.48–2.63	2.55	14	2.71–3.10	2.98
m2	length	2	3.49–3.50	3.50	12	2.80–3.47	3.09	2	2.98–3.31	3.14	14	3.43–3.98	3.75
	width trigonid	2	2.38–2.81	2.60									
	width talonid	2	2.51–2.95	2.73	12	2.10–2.60	2.39	2	2.34–2.59	2.46	14	2.57–2.96	2.84
m3	length	2	2.79–2.93	2.86	13	2.24–2.62	2.45	1		2.63	14	3.09–3.36	3.23
	width trigonid	2	1.68–1.85	2.05									
	width talonid	2	1.90–2.20	1.77	13	1.37–177	1.59	1		1.95	14	1.96–2.23	2.04

1758). The first two species have a Pliocene age, and the remaining four species belong to the Pleistocene fossil record of Europe. The individual species can primarily be distinguished by the sizes of the upper and lower canines, and premolars.

The dimensions of the elements from Miesenheim I align most closely with those of *D. thermalis* and *D. moschata*, as indicated by Schreuder (1940) and Rümke (1985). However, the lower molars of *D. thermalis* from the type locality Betfia 2 (previously known in the older literature as Püspökfürdö) (Rümke 1985) are smaller than those from Miesenheim I (Tab. 4).

D. thermalis can be distinguished from *D. moschata* by its shorter p3 and p4 (Rümke 1985). The p2/p3 ratio (length of p2/length of p3) is approximately 1.25 for *D. thermalis*, whereas it is about 1.06 for *D. moschata*. Furthermore, the P2/P3 ratio is also lower in *D. moschata* (*D. thermalis*: approx. 1.36; *D. moschata*: approx. 1.20). The p3 is absent in the material from Miesenheim I, thus the p2/p3 ratio cannot be computed. The P2 from Miesenheim I (Text-fig. 12a) is exceptionally long, even exceeding the length of the P2 from *D. moschata*. Consequently, based on the average length values, the P2/P3 ratio for the material from Miesenheim I is 1.48, which is quite high, and surpasses the ratio values of all species within the genus *Desmana* (Rümke 1985). Consequently, from the p2/p3 and P2/P3 ratios, the material from Miesenheim I cannot be definitively assigned to either of the two species, *D. thermalis* or *D. moschata*.

If one morphologically compares the elements of Miesenheim I with the teeth of the current *D. moschata* and the elements of *D. thermalis* from Betfia 2, certain differences become apparent. Compared to the morphology of the elements of *D. thermalis* and *D. moschata*, the posterior-labial cingulum of the P1 and the posterior-lingual cingulum in one of the P2 elements are significantly more developed, while the mesostyle of the M1 is smaller, resulting in an M1 that is less expanded on the labial side. In the M2 of Miesenheim I, the cingula are markedly wider, and the lingual section, which includes the protocone, protoconule and metaconule, is relatively underdeveloped.

The mandibles of *D. moschata* generally have four mental foramina, with their positions in the jaw varying (Rümke 1985). In contrast, *D. thermalis* has only two mental foramina: one located beneath the i3 and the other situated below the m1.

The lower premolars and molars from Miesenheim I exhibit features in common with the lower dentition of *D. thermalis*, which are not present in the dental elements of the extant *D. moschata*. The posterior cingulum of the p2 is more strongly developed in both *D. thermalis* and the specimens from Miesenheim I, than in those from *D. moschata*. The p4 from Miesenheim I shows numerous similarities to the p4 from *D. thermalis*, although the entoconid is less prominent in *D. thermalis*. In *D. moschata*, the posterior cingulum of the p4 is small. The m1 and m2 of the extant *D. moschata* lack a labial cingulum, which is present in the molars from Miesenheim I and those of *D. thermalis* from Betfia 2. The connection between the hypoconid and trigonid of the m1 is more labial in *D. moschata*. The anterior cingulum of the m1 is shorter in *D. moschata*, whereas the anterior cingulum of the m2 is broader. Furthermore, *D. moschata* lacks an extra cusp on the lingual side of the paraconid.

In summary, the material from Miesenheim I differs from the dental elements of the existing *D. moschata* and from fossils of *D. thermalis* from the type locality. However, the mandibular teeth from Miesenheim I also display significant morphological similarities to those of *D. thermalis*, yet in terms of size, the material from Miesenheim I aligns more closely with *D. moschata.*

The Middle Pleistocene *Desmana* record

The Middle Pleistocene remains of *Desmana* are classified as either *D.* aff. *thermalis* or *D. moschata*. In the literature, three distinct subspecies of *D. moschata* have been described: *D. moschata magna* (Owen, 1846), based on specimens from the localities of West Runton (Cromer-Forest Bed) and Ostend (UK), *D. moschata moravica* Schreuder, 1940, based on fossils from Stránska skála (Czech Republic), and *D. moschata mosbachensis* (Schmidtgen, 1925), based on remains from the main fauna of Mosbach (Germany).

The characters reported by Schreuder (1940) for *D. m. magna* are based on material from two distinct localities, whose faunas differ significantly in age, contrary to previous assumptions. The type material, a mandible containing p2–m2, comes from Ostend, while the other material originates from the older fauna of West Runton (Cromer Forest-Bed Formation), the type locality for the English Cromerium s.s. Schreuder (1940) notes that the parastyle develops only weakly in the M1 of *D. m. magna*. However, the teeth illustrated by Schreuder (Schreuder 1940: figs 14, 15) indicate that this is true for only one specimen. Fig. 14

Table 5. The dimensions (in mm) of the humerus of *Desmana* sp. form Miesenheim I compared to the dimensions of three humeri of *Desmana moschata moravica* from Stránská skála (Schreuder 1940).

Measurement	Miesenheim I	*D. m. moravica*		
Length	21.2		21.0	19.8
Width of the proximal epiphyse	7.6	7.0	7.4	
Minimal width of the shaft	3.6	3.7	3.8	3.8
Minimal thickness of the schaft	3.1	2.6	2.8	2.6
Width of the distal epiphyse	>10.3	10.7	11.1	11.4
Maximal widt of trochlea	4.2	4.7	4.7	4.7
Maximal height of trochlea	2.4	2.2	2.2	2.3

depicts a tooth with a parastyle as well developed as in the M1 of Miesenheim I.

D. m. moravica can be distinguished from other subspecies by its lower crowns (Schreuder 1940). The crown height of specimens from Miesenheim I is comparable to that of the crown of the extant *D. moschata*, which is significantly higher than that of *D. m. moravica*. The dimensions of the Miesenheim I desman humerus (Tab. 5) correspond closely with those of the humeri attributed to *D. m. moravica*, as presented by Schreuder (1940). Schreuder also notes that the latter can be distinguished from the humeri of the contemporary *D. moschata* due to its smaller size and more flattened shaft, a feature that is also observed in the Miesenheim I humerus.

The lower jaw from Mosbach, classified as *D. m. mosbachensis*, contains three mental foramina: the anterior foramen situated below the p2, the middle foramen below the m1, and the small posterior foramen located below the m2 (Bahlo and Malec 1969). In the Miesenheim I specimens, the anterior foramen is found beneath the p1.

The remains of *Desmana* from Voigtstedt (Germany) are classified as *Desmana* aff. *thermalis* by Jánossy (1965a), primarily due to their dimensions. The dental elements and humeri from Voigtstedt are smaller than those of the Miesenheim I specimens. Rümke (1985) assigned the material as *Desmana* sp., based on the data provided by Jánossy (1965a).

In 1990, Topachevsky and Pashkov published an article describing three new *Desmana* species: *D. meridionalis* (type locality Chihmikioy, Moldova), *D. nogaica* (type locality Cherevichnoe, Ukraine), and *D. gureevi* (type locality Luzanovka, Ukraine), dating from the late Early to Middle Pleistocene. However, the status of these species remains uncertain. The definition of the three species is based on a limited number of dental elements, and aside from a well-developed entoconid on the lower p4, the distinctive diagnostic features of the different species are observable in the *Desmana* fossils from the late Middle Pleistocene fauna of Schöningen (Germany) (Stolk 2007). The morphological differences noted by Topachevsky and Pashkov (1990) in the fossil material from the studied localities likely reflect morphological variation within a single species.

The information presented above indicates that the taxonomy of the late Early and Middle Pleistocene fossil representatives of the genus *Desmana* is ambiguous and requires revision. The Miesenheim I fossil desman remains differ significantly from those of the two well-defined species, *D. thermalis* and *D. moschata*, making it impossible to assign them to either species. Therefore, an assignment to *Desmana* sp. is preferable.

Table 6. Fauna composition of the small mammal assemblages from Miesenheim I, layers G, F, and C. The Eulipotyphla record is presented in this paper; the Lagomorpha and Rodentia will be published in another paper (van Kolfschoten in prep.).

Miesenheim I	Layer		
	G	F	C
Eulipotyphla			
Neomys cf. *newtoni*	×	×	×
Sorex minutus		×	
Sorex subaraneus	×	×	
Sorex (*Drepanosorex*) *savini*	×	×	
Talpa europaea	×	×	
Talpa minor	×	×	
Desmana sp.	×	×	
Lagomorpha			
Lepus sp.	×		
Rodentia			
Trogontherium cuvieri	×	×	
Castor fiber	×	×	
Sciurus sp.		×	
Eliomys quercinus	×	×	
Muscardinus avellanarius	×	×	
Sicista sp.		×	
Cricetus major		×	
Allocricetus bursae		×	
Lemmus lemmus		×	
Pliomys episcopalis	×	×	
Clethrionomys glareolus	×	×	×
Arvicola terrestris cantiana	×	×	×
Microtus (*Terricola*) *arvalidens*	×	×	×
Microtus (*Terricola*) *gregaloides*		×	
Microtus arvalis/*M. agrestis*	×	×	×
Alexandromys oeconomus		×	×
Microtus (*Stenocranius*) *gregalis*		×	×
Apodemus sylvaticus/ *A.* aff. *maastrichtiensis*	×	×	

The Miesenheim I and its small mammal assemblage

Faunal composition and taphonomy

The fossil small mammal assemblage from Miesenheim I is rich. However, only layers G, F, and C yielded small mammal remains (Tab. 6). Most of the remains originate from layer F; layer G is also relatively rich in fossils, whereas only a few teeth and bones have been discovered in layer C. Insectivores are well represented in the Miesenheim I small mammal assemblage, comprising 40 % of the more than 6,000 identifiable small mammal remains. *Sorex runtonensis* and *Neomys* cf. *newtoni* are the most common species, whereas *Desmana* sp. is rare. *Arvicola terrestris cantiana* is the best-represented rodent species. *Trogotherium* and *Castor fiber* are represented by both dental and skeletal material. However, it is noteworthy that Lagomorpha, such as the European hare (*Lepus*) are rare, and that hedgehogs (*Erinaceus*) and bats (Chiroptera) are absent from the fauna.

The fossil assemblage of small mammals consists almost exclusively of single teeth and bone fragments. A significant portion of the fossil remains was most likely accumulated as pellets and mixed with the remains of (semi-)aquatic animals. Only a small proportion of the material exhibits etching traces, suggesting that the pellets did not originate from diurnal birds of prey but from nocturnal owls (Mayhew 1977). The rarity of Lagomorpha and the absence of the hedgehog (*Erinaceus*) may suggest that the pellets originate from a relatively small owl rather than, for example, the eagle owl (*Bubo bubo*). Bats are generally found in very small numbers within pellets. Of a total of 38,651 small mammals from pellets in Belgium, only 17 (0.044 %) were identified as bats (Asselberg 1971). Although bats are more commonly found in the barn owl's diet (*Tyto alba*), their proportion typically remains below 0.1 % (Uttendörfer 1939, 1952). The relative frequency of Soricidae within the overall fauna of Miesenheim I aligns with the high proportion of Soricidae found in the pellets of the recent barn owl. The diet of other owls, such as the little owl (*Athene noctua*), tawny owl (*Strix aluco*), long-eared owl (*Asio otus*), and short-eared owl (*Asio flammeus*), exhibits a significantly lower proportion of Soricidae (Uttendörfer 1939, 1952, Asselberg 1971, Van der Straeten 1972). Unlike other owls and birds of prey, barn owls deposit their pellets close to the nest rather than regurgitating them at a greater distance than other owls (Uttendörfer 1939). This behaviour may account for the notably high occurrence of small mammal remains in the deposits of Miesenheim I. However, attributing the pellets to the barn owl remains questionable, as recent barn owls tend to favour nesting in buildings or suitable cavities in rock faces rather than in partially wooded, swampy, relatively flat areas lacking rocks in the immediate vicinity, such as the Miesenheim I site. This contradicts the assumption that the pellets originate from a barn owl, which has feeding and breeding habits similar to modern owls.

Palaeoenvironmental reconstruction

Semi-aquatic animals such as *Neomys* cf. *newtoni*, *Desmana* sp., *Trogontherium cuvieri*, *Castor fiber*, and *Arvicola terrestris cantiana* are relatively common in the small mammal fauna of Miesenheim I (Tab. 6). In contrast, other species such as *Sciurus* sp., *Eliomys quercinus*, *Muscardinus avellanarius*, *Clethrionomys glareolus*, and *Apodemus sylvaticus*, prefer forest or forest-edge habitats. The presence of these species indicates that the biotope was predominantly forested. *Sorex* (*D.*) *savini* preferred moist environments, such as deciduous forests, marshes or even open water (Reumer 1984). The pygmy shrew, *Sorex minutus*, and most probably also *S. subaraneus* prefer moist and cool to temperate environments, with dense ground cover. *Microtus arvalis* and *Microtus agrestis* tend to avoid dense forest areas and prefer open biotopes. Indicators of a steppe biotope include *Cricetus major*, *Allocricetus bursae* and *Lasiopodomys* (*Stenocranius*) *gregalis*.

The composition of the small mammal fauna indicates that the site is a wetland biotope, and the surrounding area is a wooded landscape with large clearings. The presence of forest dwellers such as *Muscardinus avellanarius* and *Eliomys quercinus*, whose current distribution barely extends beyond northern Germany, demonstrates that the fauna of Miesenheim I is interglacial. The presence of *Lemmus lemmus* within the fauna supports the assumption (von Koenigswald 1972) that this species did not occupy the same ecological niche during the Early and Middle Pleistocene as it does today.

The larger mammal record, primarily characterised by the remains of roe deer, red deer, and horses, also suggests a locally mixed biotope, predominantly wooded but featuring some open glades at the edges of the floodplain (Turner 2000).

The fossil herpetofauna collected at Miesenheim I indicates a (semi)aquatic environment. It includes the remains of at least one salamander (*Triturus vulgaris*), five anurans (*Bufo calamita*, *Rana arvalis*, *Rana lessonae*, *Rana ridibunda*, *Rana temporaria*), two lizards (*Lacerta* cf. *L. vivipara*, *Anguis fragilis*) and one snake (*Natrix* sp.). All these species are currently living, and all are found in the vicinity of Miesenheim, Germany. The diverse herpetofauna indicates the presence of an aquatic habitat, such as a marsh or a small pond, surrounded by a relatively moist terrestrial environment with adequate low vegetation and ground cover (Holman and van Kolfschoten unpubl.).

The Miesenheim I deposits also yielded a rich malacological fauna, with 73 identified taxa representing land and freshwater molluscan species (Roth in Turner 2000). The malacological data from the depositional sequence suggest a progressive climatic deterioration following an interglacial phase. The molluscan record indicates that layers H, G, and the base of F were deposited during the latter part of an interglacial phase, characterised by a more continental climate than today. In comparison to the lower part of the section, the malacological record from Layer C suggests cooler climatic conditions. Similar changes can be observed in the composition of the small mammal fauna (Tab. 6). The glirids *Eliomys quercinus* and *Muscardinus avellanarius* are primarily found in the lowermost fossiliferous levels (Units G and F). In the upper horizon (Unit C), there is a decline in the abundance of *Clethrionomys glareolus* and an increase in *Microtus* species.

The stratigraphical age of the Miesenheim I fauna

The Miesenheim I fauna includes *Arvicola terrestris cantiana*, and consequently, it can be concluded that the fauna post-dates the *Mimomys*-*Arvicola* transition. This transition marks the change from Biharian water voles with rooted molars of the genus *Mimomys* to the more advanced Toringian water voles with unrooted molars, assigned to the genus *Arvicola*. This transition marks the boundary between the Biharian-Toringian stages as defined by Fejfar and Heinrich (1981) and Fejfar et al. (1998).

The *Arvicola* molars from Miesenheim I, assigned to *Arvicola terrestris cantiana*, show primitive features such as high "Schmelzband-Differenzierungs-Quotient" (SDQ) values (ranging from 180–126; mean 152.03; N = 78). Comparable values are also observed in the *Arvicola* molars from the Central and Western European localities such as Kärlich Gb, Mosbach-2 (main fauna), Mauer, Bilzingsleben, Hundsheim, Erpfingen 1 and 3, Jockrim, Petersbuch, Sudmer-Berg-2, Tarkö, Boxgrove, Westbury-sub-Mendip, Sprimont (Belle Roche) and Neede (Heinrich 1987, van Kolfschoten 1990).

As von Koenigswald (1973b) demonstrated, it is possible to divide the Central European faunas containing “primitive” *Arvicola* representatives assigned to *A. terrestris cantiana* into two groups, distinguished by the association of different species. The first group includes faunas such as Hundsheim, Mosbach-2, and Miesenheim I, characterised by “primitive” forms like *Sorex runtonensis*, *S.* (*Drepanosorex*) *savini*, and *Pliomys episcopalis* (= Arvicola faunas type 1 as defined by von Koenigswald 1973b). These species are absent in the faunas of the second group, which includes those from Bilzingsleben, Neede, and Swanscombe, classified as von Koenigswald’s Arvicola faunas type 2.

The *Arvicola terrestris cantiana* zone, as described by Fejfar and Heinrich (1981) corresponds to Biozone Q 3, as classified by Horáček and Ložek (1988) for the Central European Quaternary. The latter authors proposed subdividing their biozone Q 3 into three subzones: Q 3-1 to Q 3-3. The species spectrum characterising subzone Q 3-1 closely aligns with that of Miesenheim I, differing from subzone Q 3-2 due to the presence of *Sorex* (*Drepanosorex*) *savini* and *Pliomys episcopalis*.

The Kärlich clay pit, located on the southern edge of the Neuwied Basin, approximately 5 km southeast of Miesenheim I, has also yielded rich mammalian faunal assemblages (van Kolfschoten 1990). Rooted water vole molars assigned to the genus *Mimomys* have been retrieved from the loess deposits of Kärlich F, while the overlying Kärlich Gb yielded primitive *Arvicola* molars. The small mammal assemblages of Kärlich Gb and Miesenheim I are very similar in composition; therefore, both are correlated with Bio-subzone Q 3-1 and von Koenigswald’s Arvicola faunas type 1.

Middle Pleistocene deposits in the Middle and Lower Rhine region demonstrate a distinct change in heavy mineral composition, shifting from a dominance of brown hornblende to a predominance of pyroxenes (augite). This transition occurred at the end of Glacial C or the beginning of Interglacial IV of the “Cromerium complex” (Zagwijn 1985). The Miesenheim I deposits exhibit a heavy mineral spectrum predominantly characterised by augite. In contrast, the fauna of Kärlich Gb originates from sediments featuring a heavy mineral dominance of brown hornblende, indicating that this fauna is older than that of Miesenheim I (van Kolfschoten 1990, van Kolfschoten and Turner 1996). Both warm stage faunas, Kärlich Gb and Miesenheim I, postdate the Kärlich F loess deposits, which are correlated with the Don-glaciation and with Marine Isotope Stage (MIS) 16, and predate the Elsterian, correlated with MIS 12. Therefore, it is assumed that the fauna of Kärlich Gb correlates with MIS 15 and that of Miesenheim I with MIS 13.

Discussion and conclusions

The Miesenheim I small mammal record offers insights into several insectivores (Order Eulipotyphla) that inhabited the Middle Rhine region and beyond during the early Middle Pleistocene (MIS 13). Four species from the family Soricidae and three taxa from the family Talpidae are represented. The remains attributed to *Neomys* cf. *newtoni* differ in certain characteristics, including size, from elements of the Eurasian water shrew, *Neomys fodiens*. The smaller dimensions of the Miesenheim I specimens align more closely with *Neomys* species from the Early and Middle Pleistocene. The smallest shrew in the Miesenheim I assemblage is *Sorex minutus*; the medium-sized shrew *Sorex runtonensis* is, on average, smaller than the extant common or Eurasian shrew, *Sorex araneus*. Additionally, the lower jaws of *Sorex runtonensis* differ morphologically from those of *Sorex araneus*. The larger shrew remains are assigned to the extinct *Sorex* (*Drepanosorex*) *savini*. The mole dental remains and humeri from Miesenheim I are attributed to two species due to clear differences in dimensions: the European mole, *Talpa europaea*, and the smaller, extinct *Talpa minor*. Some molars of these two species exhibit differences in morphological features. The desman remains from Miesenheim I could not be assigned to a specific species. The fossil desman remains from Miesenheim I differ significantly from those of the well-defined species, *D. thermalis* and *D. moschata*.

The Miesenheim insectivore assemblage indicates a late Biharian to early Toringian age for the fauna. However, a Biharian age is excluded due to the occurrence of unrooted water vole remains from the genus *Arvicola*. The Miesenheim I fauna differs from late Toringian faunas in the composition of the insectivore guild. *Sorex* (*Drepanosorex*) and *Talpa minor* became extinct during the Middle Pleistocene. Both taxa are present in the fauna from Petersbuch (Germany) (von Koenigswald 1970), which is assumed to have a Holsteinian/MIS 11 age. The Reinsdorf Interglacial (MIS 9) deposits exposed at the locality of Schöningen (Germany) (van Kolfschoten 2014) yielded a rich vertebrate record that includes rare remains of *Sorex* (*Drepanosorex*), while *Talpa minor* is absent from the assemblage. These data suggest that both taxa continued to exist in Central and Western Europe after the Elsterian/Anglian (MIS 12) glaciation. However, they became extinct in the region during the later phase of the late Middle Pleistocene. The Miesenheim I small mammal fauna is characteristic of faunas from the later phase of the early Middle Pleistocene. The small mammal assemblage differs in composition from post-Elsterian faunas, and some of the insectivore species exhibit morphological differences from stratigraphically younger relatives.

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