

Redescription of *Macrobiotus xerophilus* (Dastych, 1978) comb. nov., with some phylogenetic notes (Tardigrada, Macrobiotidae)

(mit 34 Abbildungen und 1 Karte)

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Abstract: *Macrobiotus xerophilus* (Dastych, 1978) comb. nov., a semiterrestrial tardigrade new for the German fauna is redescribed and transferred from the family Calohypsibiidae into the family Macrobiotidae. Redescription includes light and SEM observations, as well as previously unknown eggs. Phylogenetic status of this taxon and a relation between the soil habitat and a reduction of claws and legs in Eutardigrada are discussed.

Keywords: Tardigrada, *Macrobiotus xerophilus* comb. nov., taxonomy

Introduction

Invertebrate fauna of Sandhausener Dune, a small sandy nature reserve near Heidelberg (SW Germany) has been investigated. The study revealed a large number of *Parhexapodibius xerophilus* Dastych, 1978. Additional sampling of this area resulted in many more specimens and egg of this species. Until now *P. xerophilus* has been recorded from a few localities in eastern Poland (Fig. 35). Analysis of the German material, supported by SEM observations, shed a new light on the taxonomic status of *Parhexapodibius xerophilus*. The data consistently indicate a need to transfer this taxon into the genus *Macrobiotus*, Macrobiotidae, from the family Calohypsibiidae where it was originally assigned to.

Material and methods

The nature reserve "Sandhausener Düne, Pflege Schönau-Galgenbuckel" is located about 5 km SW of Heidelberg and covers an area of 18 ha. The reserve includes a dune of postglacial origin that has undergone relatively little change since its formation. The dune is scarcely covered by xerothermic vegetation (*Corynephorus canescens* [L.]) which includes mosses and lichens. These mosses

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and lichens are present in numerous scattered patches on sandy soil. Physiographic information on the reserve, its flora and fauna is given in Horn (1980).

The field samples of moss, lichens and soil were collected into paper envelopes. Tardigrades were extracted in the laboratory by the method described by Dastych (1985). The light microscope examinations (phase and interference contrast) were conducted out on living specimens and on specimens mounted either in Faure's medium or in polyvinyl-lactophenol. All drawings and micrographs are based on the material from Sandhausener Düne. For comparison purposes the type material of *Parhexapodibius xerophilus* and other specimens collected in Poland (Dastych 1978, 1988) were used.

For SEM observations animals were transferred from water into hot Bouin's medium, dehydrated in graded ethanols, critical-point-dried, arranged on double-stick tape and coated with gold to the thickness of 45 nm. Observations and micrographs were made using electron microscope Philips SEM 505 and Cambridge S4 10.

Material examined: 102 specimens and one egg extracted from 11 moss, lichen and soil samples collected from dry, sandy sites at the reserve "Sandhausener Düne", Heidelberg (SW Germany); 27 February and 25 May, 1986. Comparative material: 17 paratypes of *Parhexapodibius xerophilus* from Siedlce (Dastych, 1978) and 25 specimens from Popowo, Michalowo and Tarnopol (Dastych, 1988); all localities in eastern Poland (Fig. 35).

Repositories: the Zoological Institute and Zoological Museum, University of Hamburg (15 specimens and egg), the Zoological Museum, Copenhagen (10 specimens), the National Museum of Natural History, Washington (9 specimens). Two slides with 12 specimens and several specimens prepared for SEM are in the collection of junior author (G. A.); the remainder of material is in senior author's (H. D.) collection.

Redescription

Macrobiotus xerophilus (Dastych, 1978) comb. nov.

Parhexapodibius xerophilus: Dastych, 1978

Parhexapodibius xerophilus: Schuster et al., 1980

Hexapodibius xerophilus: Maucci, 1981

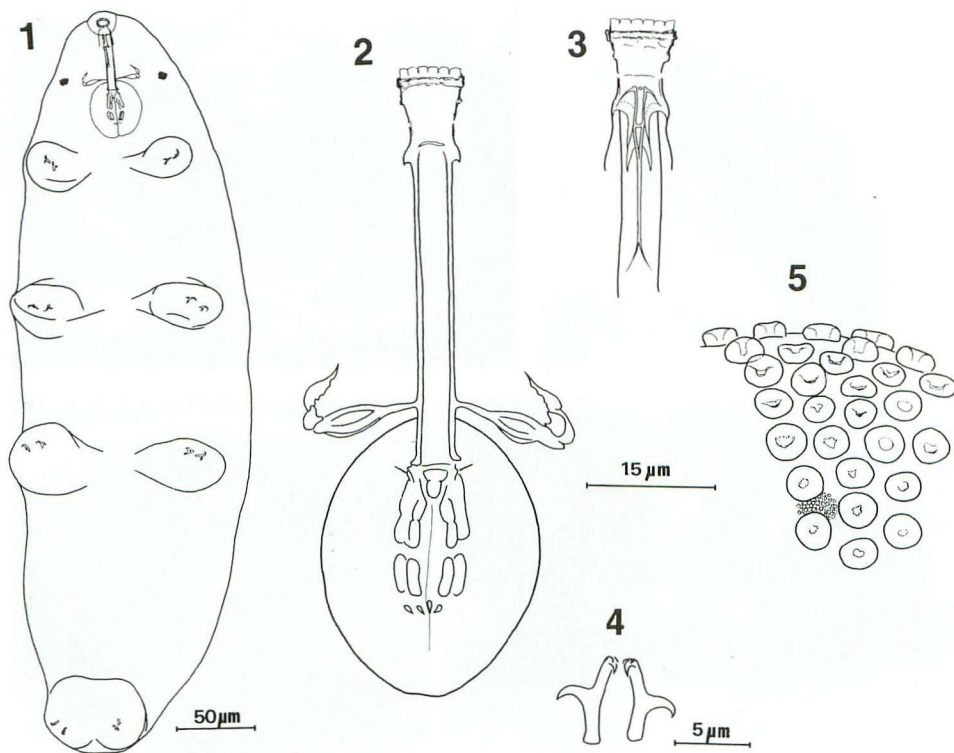
Hexapodibius xerophilus: Ramazzotti & Maucci, 1983

Parhexapodibius xerophilus: Dastych, 1988

Diagnosis: *Macrobiotus* with strongly reduced legs and claws; claws are always the smallest on hind pair of legs. Eyes, two macroplocoids and a microplocoid are present. Eggs with hemispherical, flattened processes. Type locality: eastern Poland (Dastych, 1978).

The body is 196–510 μm long and white in colouration. Most specimens have green intestine contents. Large posterior eye dots are present. In light microscope cuticle is smooth. No distinct granulated pattern could be detected with SEM either (Figs. 9, 13). The cuticle has small and sparsely distributed pores (Fig. 9) with characteristic perforation on the bottom (Fig. 13). A ring of larger pores without such a perforation surrounds the base of mouth cone (Fig. 10). If mouth cone is everted, two rings of larger pores are visible (Figs. 14, 15). They have some irregular perforation at the bottom (Fig. 15).

The mouth opening is subterminal and surrounded by 10 lamellae (Figs. 2, 7, 9, 10). This latter character was overlooked in the original description. The lamellae are poorly visible or sometimes invisible in phase or interference contrast. The area around the mouth opening consists of several characteristic

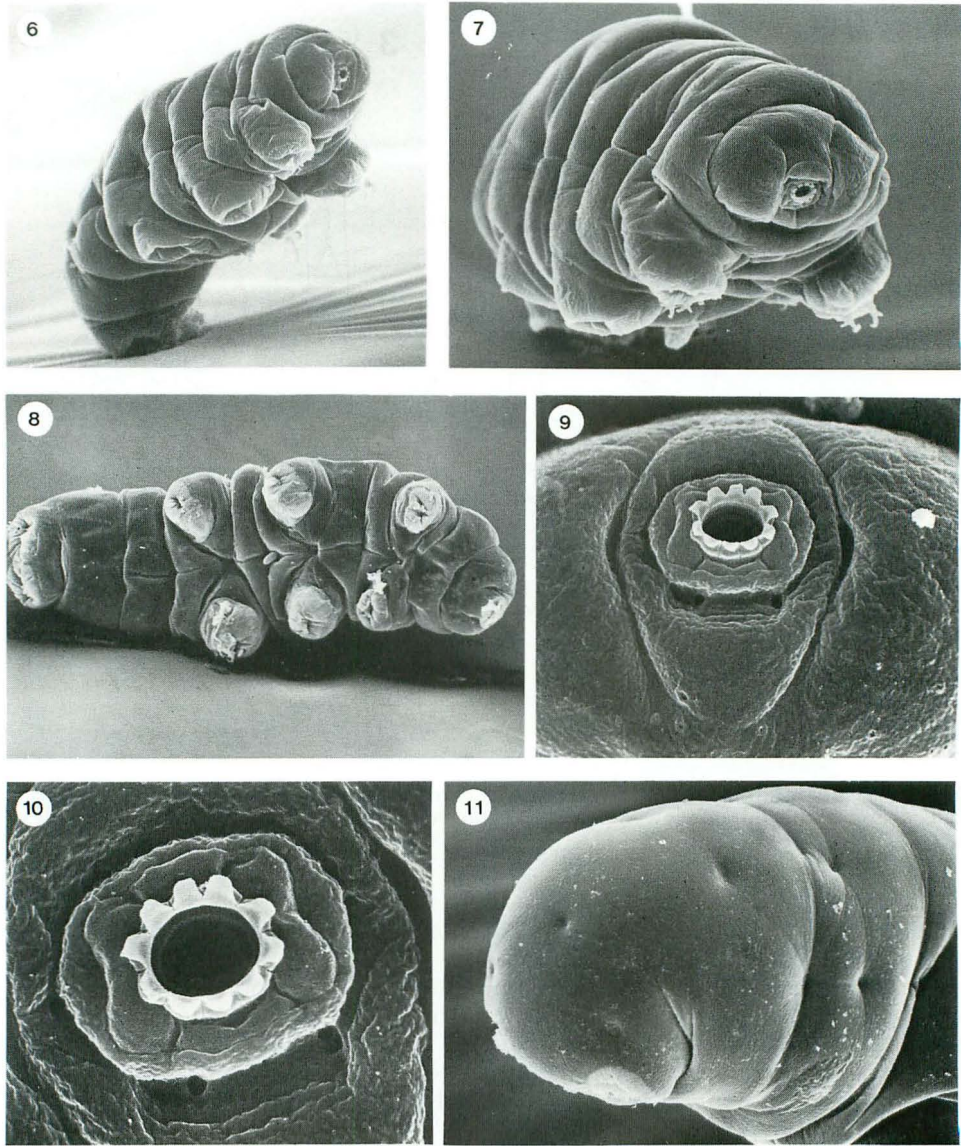


Figs. 1–5: *Macrobiotus xerophilus* (Dastych) comb. nov.: 1 = habitus, ventral view; 2 = buccal apparatus, dorsal view; 3 = mouth tube, ventral view; 4 = claws of the first pair of legs; 5 = fragment of egg.

fields which form a mouth cone. The cone is located centrally on an oval protuberated shield and is surrounded by two large convex fields (“cheeks”) that are lateral parts of the head segment (Fig. 9). The mouth cone consists of four elongated lobes that are slightly constricted in their middle and surround the mouth opening outside the ring of lamellae (Fig. 10). The lobes are developed on a convex approximately round shield. The structure of the mouth region and of the lateral parts of the head segment is similar to that of *Macrobiotus hufelandi* Schultze (cfr. Walz, 1979). The mouth cone is homologous to circum-oral sensory field (COFS) described by Walz (1979). He coined the term anterior-lateral sensory fields (ALSF: 1. c., 1979) for the lateral sides of the head segment (“cheeks”).

The mouth cavity has no transversal bands of granulation. The dorsal ridges (terminology after Pilato, 1972) are shaped as a single transversal bar (Fig. 2). Two ventro-lateral ridges are delicate and have 1–2 tiny granules (medio-ventral ridge) between them (Fig. 3). Some specimens, particularly the younger ones, are without these granules. The mouth tube has a well developed reinforcement bar.

The pharynx is oval or egg-like, with two macroplacoids and a microplacoid. The first macroplacoid is almost twice as long as the second and is constricted in its middle; the microplacoid is conspicuous (Figs. 2, 25, 26). Between apophyses and the first macroplacoid there are two small and thin rods directed upwards.

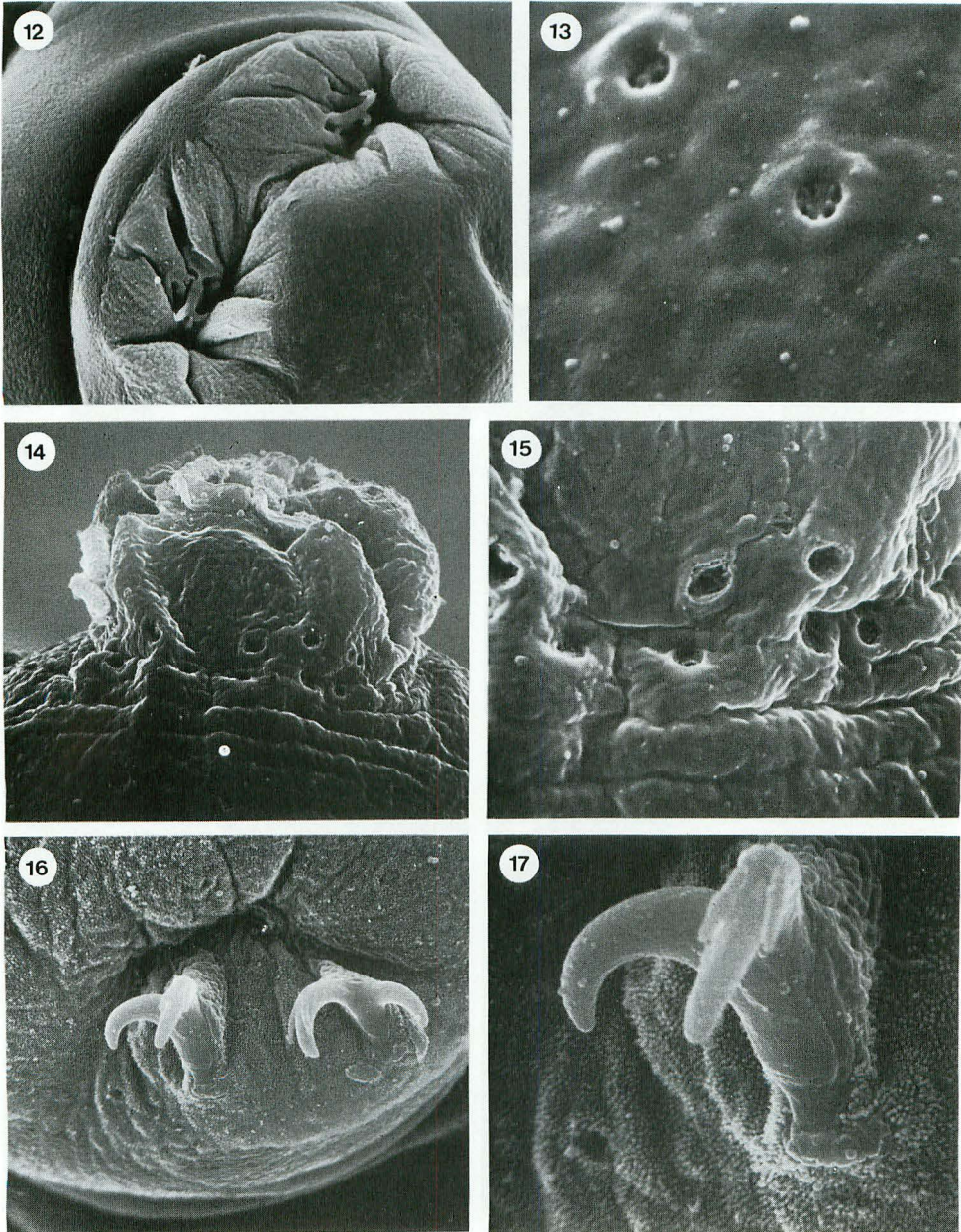


Figs. 6–11: *Macrobiotus xerophilus* (Dastych) comb. nov.: 6 = habitus, lateral view (550 ×); 7 = habitus, frontal view (775 ×); 8 = habitus, ventral view (428 ×); 9 = mouth region (3400 ×); 10 = mouth cone, frontal view (5600 ×); 11 = terminal segments of the body, dorso-lateral view (5600 ×)

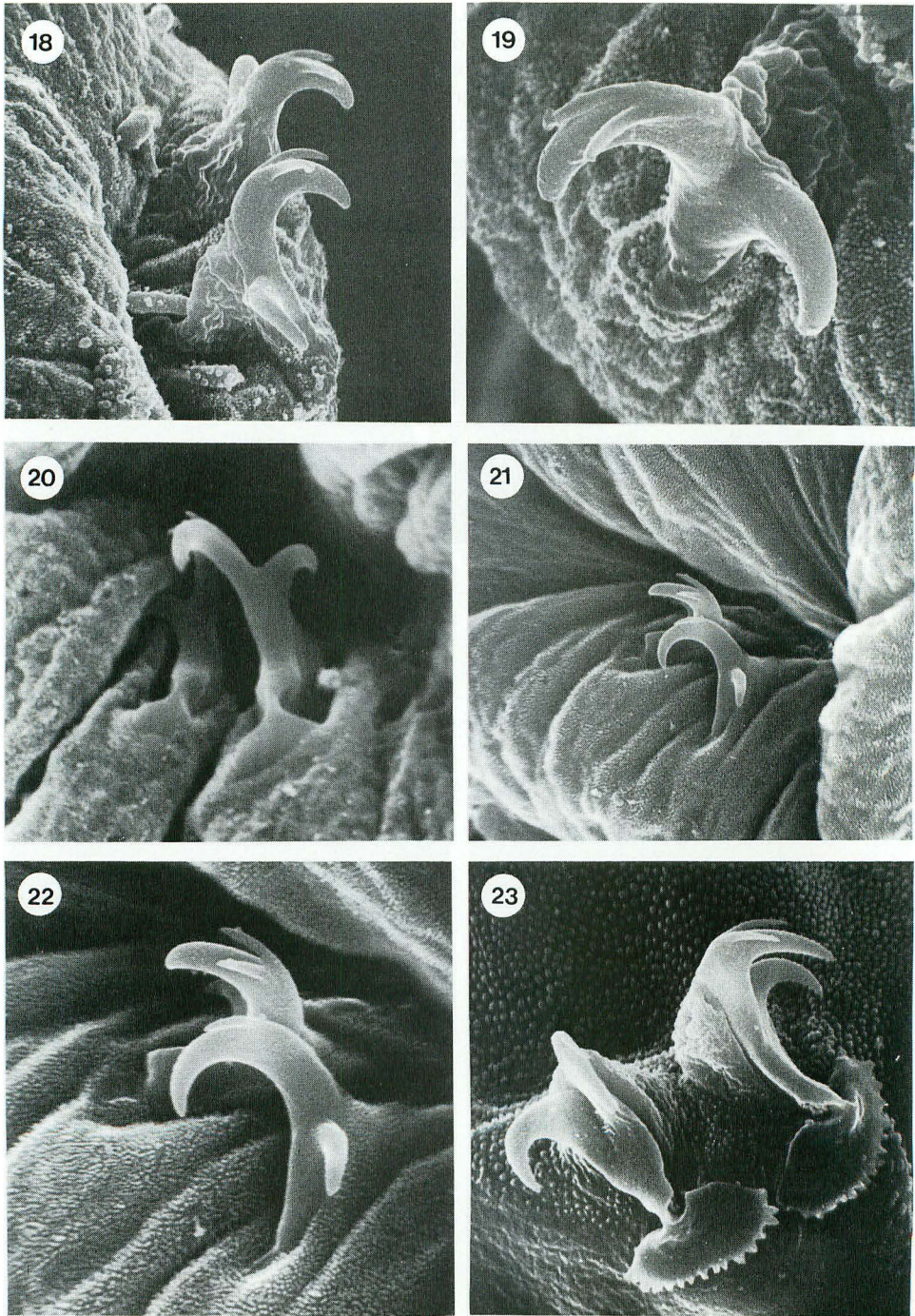
Legs of the three anterior pairs (I–III) are short and reduced; the fourth pair is rudimentary (Figs. 1, 8). Each leg of the pairs I–III has a characteristic small swelling on its anterior side (Figs. 7, 24). The hind legs are developed as two very small and flat swellings. They are located close to each other on a common “plate” on the ventrum of the terminal segment (Figs. 1, 12, 29).

All claws are reduced and relatively small. Their size slightly increases from the first to the third pair of legs. External claws are slightly larger than the internal ones. The claws on the hind legs are always the smallest (Fig. 1). Their absolute size is variable (Fig. 33) and their length is 25–82 % of the length of

claws on the third pair of legs (Fig. 34). The main branches of the claws have minute accessory spines (Figs. 16–22), usually undetectable on hind legs by light microscopy. The bases of claws from the first to the third pair of legs have no lunules, but a small rigid plate is present. This plate is formed by a small constriction of the basal part of the claw (Figs. 19, 20). On the hind legs these constrictions are more developed and the basal plates are relatively larger.



Figs. 12–17: *Macrobiotus xerophilus* (Dastych) comb. nov.: 12 = the fourth pair of legs, ventral view (1930 ×); 13 = pores in the cuticle (34000 ×); 14 = everted mouth cone, dorsal view (7000 ×); 15 = detail of Fig. 14, large pores (14000 ×); 16 = claws of the first pair of legs (6250 ×); 17 = external claw of the first pair of legs (17800 ×)



Figs. 18–23: *Macrobiotus xerophilus* (Dastych) comb. nov., Figs. 18–22 = claws of the third pairs of legs, lateral view (7800 ×); 19 = internal claw of the third pair of legs (15000 ×); 20 = claws of the fourth pair of legs (7050 ×); 21 and 22 = claws of the fourth pair of legs (6700 × and 13400 ×); Fig. 23 = *Macrobiotus richtersi* Murray: claws of the fourth pair of legs (5000 ×)

Although they are similar in shape to lunules, they are more rigid relative to the flexibility of the main part of the claw. Most probably they are homologues of the "normal" lunules occurring in all representatives of the genus *Macrobiotus*, e. g. *M. richtersi* Murray (fig. 23). Judging from the SEM micrographs, the size of these plates is variable (Fig. 20, 22). They are undetectable by light microscopy (Figs. 27–29). The claws of the hind legs are rudimentary in one specimen. They are reduced to small (1.5 μm) and elongated plates. In another specimen the base of claws on this pair of legs has been broken off (Fig. 22).

Below we provide measurements taken on a specimen 502 μm long: the length of buccal tube is 45 μm , its external diameter is 5.5 μm . Pharynx size is 36 \times 30 μm . The length of the first macroplacoid is 10 μm , the second one is 5.5 μm long; their width is 2.4 μm . The microplacoid is 2.5 μm long. The claws on the first pair of legs (measurements of internal claws are in brackets) are 6.6 μm (5.7) long, on the second pair 7.4 μm (6.7) and on the third pair they are 7.7 (7.1) μm long. The length of claws on the fourth pair is 5.5 μm (4.9); their min-max length is 1.5–5.8 μm .

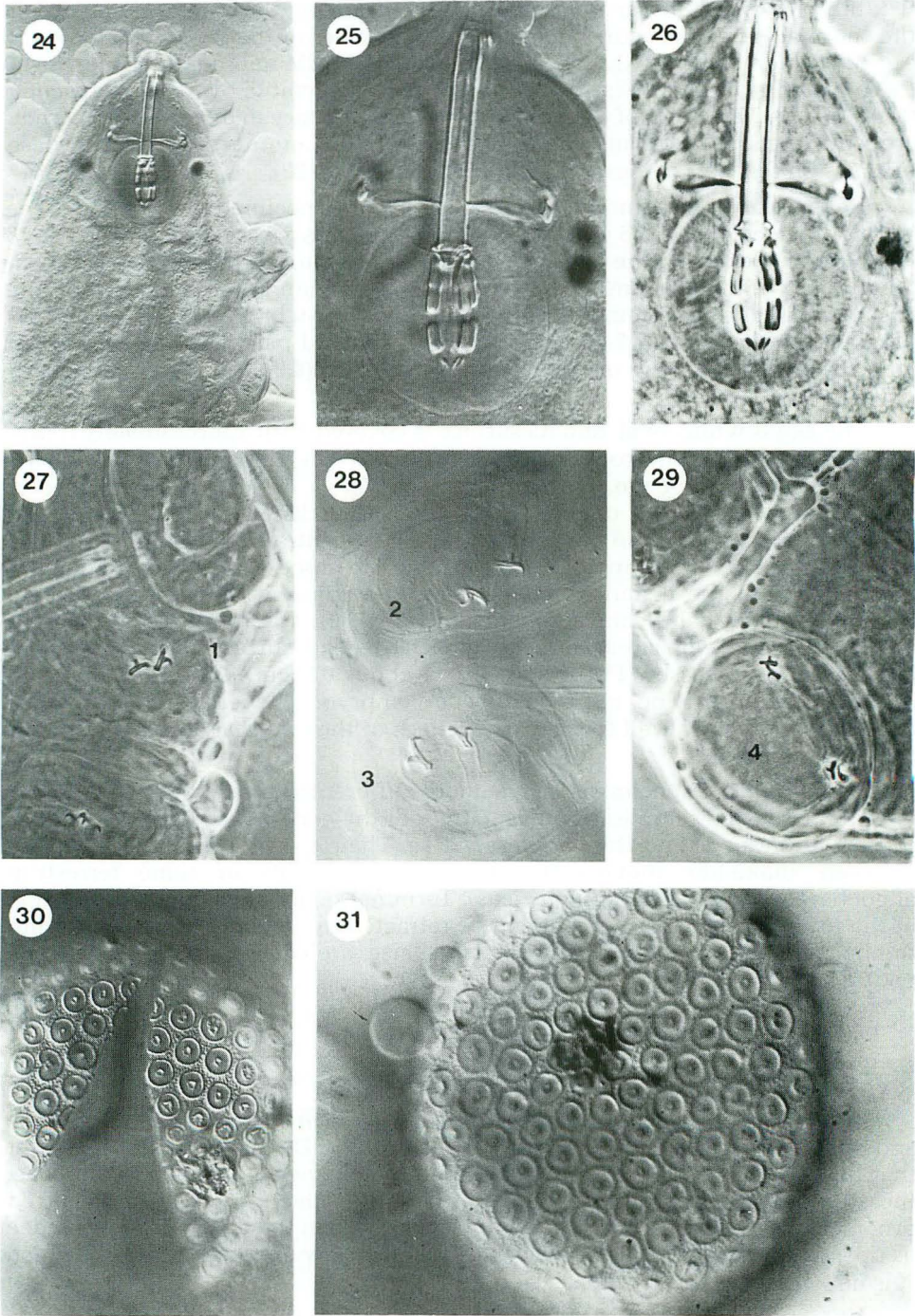
The egg is white, oval, and its surface is covered with approximately round and strongly flattened processes (Figs. 5, 30, 31). The egg size inclusive of the processes is 74 \times 64 μm , without processes 71 \times 60 μm . The diameter of processes is 3.5–5.8 μm , usually about 4 μm ; their length is 1.4–2.1 μm . The processes are smooth and with a characteristic, central structure inside. This structure resembles a funnel-like depression. The processes are located close to each other and the distance between any two adjacent processes is usually smaller than the half of their diameter (Figs. 5, 30). The number of processes counted on the egg circumference is 35. The egg surface is perforated in between the processes. Pore diameter is about 0.3 μm . The pores form an irregular network. The egg contains an embryo. The embryo has buccal apparatus and claws well formed. The length of the external claws on the first pair of leg is 4.0 μm .

M. xerophilus specimens move more differently than other tardigrades found in the same samples (representatives of the genera *Macrobiotus*, *Ramaz-zottius*, *Milnesium*) and they are less active. Their locomotion is intermediate between snake-like movements and the movements of some terrestrial oligochaets (e. g. the genus *Lumbricus*). Terminal segment plays important role in the locomotion. This segment can be retracted up to a half of its length into the body. Also the claws, due to the small size, are easily retracted inside the body during locomotion.

Discussion

The specimens from Sandhausener Dune agree in all details with paratypes and other specimens of *Parhexapodibius xerophilus* Dastyh. There is no doubt that both known populations are conspecific. Presence of ten buccal lamellae, the strengthening bar, the sequence of claw branches "2112", and free-layed ornamented eggs place this species univocally within the family Macrobiotidae as opposed to Calohypsibiidae, where it was originally assigned and from which it is now transferred.

At present the family Macrobiotidae contains five genera (*Macrobiotus* Schultze, *Pseudodiphasco* Ramazzotti, *Dactylobiotus* Schuster, *Minibiotus* Schuster and *Adorybiotus* Maucci & Ramazzotti) but little is understood of their phylogenetic relationships. The species discussed in this paper is placed into the genus *Macrobiotus* because of the features of its buccal apparatus, mouth



Figs. 24–31: *Macrobiotus xerophilus* (Dastyh) comb. nov.: 24 = front of the body; 25 and 26 = buccal apparatus; 27 = claws of the first and the second pair of legs; 28 = claws of the second and the third pair of legs; 29 = claws of the fourth pair of legs; 30 and 31 = surface of egg (Figs. 24, 25, 28, 30, 31 = interference contrast; Figs. 26, 27 and 29 = phase contrast. 1–4: successive pair of legs)

region, and general similarities in the claw structure to those of other Macrobiotidae. On the other hand, *M. xerophilus* (Dastych) comb. nov. exhibits a unique reduction of claws, particularly on hind legs. This character might warrant its elevation to at least subgeneric level. At present however, its tentative status within the genus *Macrobiotus* is retained for the sake of taxonomic stability and until more data become available to justify a revision of the genus.

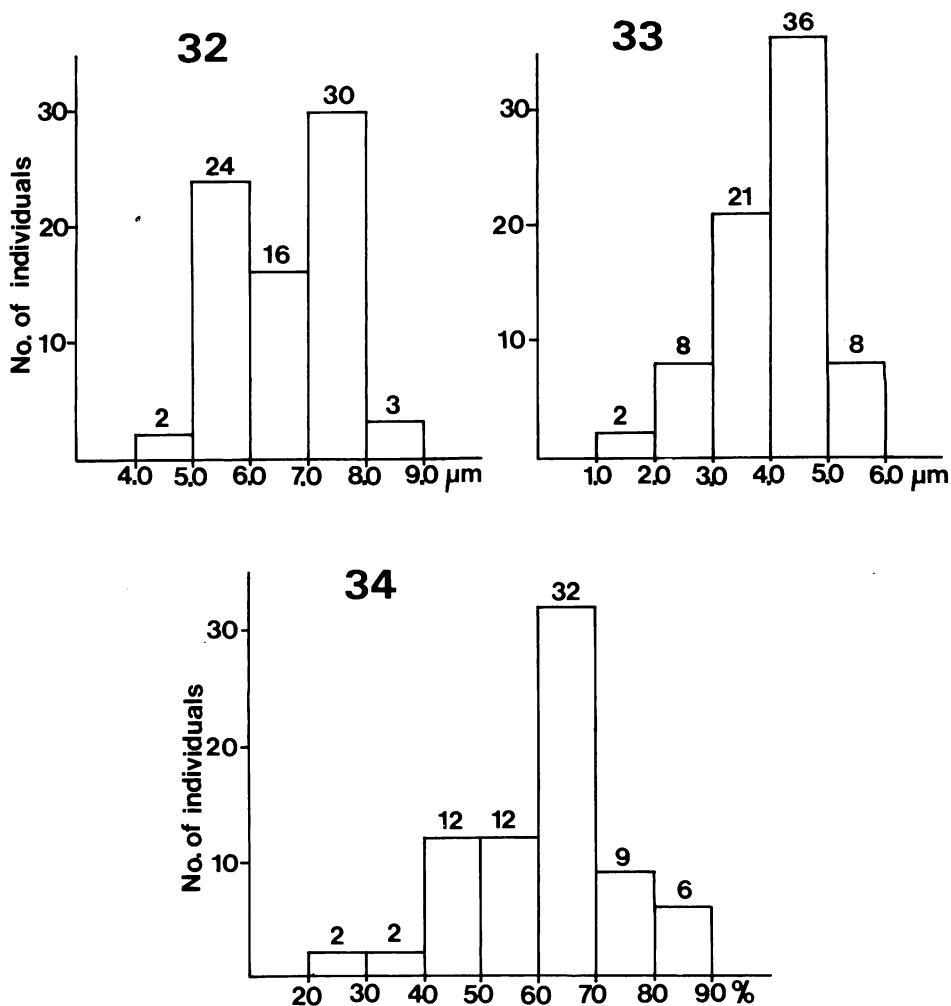
Macrobiotus xerophilus (Dastych) comb. nov. has probably originated from any form with two macroplacoids, claws of *Macrobiotus*-type, that is with fully developed lunules and egg processes of hemispherical shape. Presumably its separation from an ancestral stock took place late relative to other congenics and both, the reduction of lunules and the claw size gave rise to the specialized and apomorphic claw formation. Interestingly, the transformation of the dorsal ridges in the mouth cavity into a single transversal bar present in this species has been already found in *Macrobiotus sapiens* Binda & Pilato. It was then recognized as a feature unique to this genus (Binda & Pilato, 1984). In *M. xerophilus* and *M. sapiens* the character must have originated independently. This conclusion is stronger when one considers the completely different structure of egg processes that indicates their distant yet recognizable affinity.

In Eutardigrada two distinct evolutionary trends can be distinguished on the basis of claw systems, particularly in their presence and size. The first trend is represented by forms with increasing size of claws from the first to the fourth pair of legs and with relatively well separated and long legs. This trend prevails in the whole class. It occurs in every major phyletic lineage and has to be considered as plesiomorphic, especially that similar development has taken place in the majority of marine forms from which terrestrial tardigrades originate. The second trend, an apomorphic one, is characterized by varying degrees of reduction of claw systems and legs. This reduction progresses anteriorly, i. e. from the fourth (hind) to the first pair of legs. Until now this tendency has been found only in a few taxa within Eutardigrada. The taxa sharing this trend include: two genera of the Calohypsibiidae (the genus *Parhexapodibius* Pilato and *Hexapodibius* Pilato), two genera of unclear systematic status, i. e. *Apodibius* Dastych and *Necopinatum* Pilato, recently described *Doryphoribius pilato* Bertolani, 1983 of the Hypsibiidae, and *Macrobiotus xerophilus* (Dastych) comb. nov. of the Macrobiotidae.

In *Parhexapodibius* (three species known) the claws of hind legs are always the smallest and in *Hexapodibius* (three species) the claws are present only on the legs of the first to the third pairs and are completely reduced (absent) on the hind pair of legs. *Apodibius* (two species) is characterized by the absence of claws from all legs. In the monotypic genus *Necopinatum* only the first pair of legs has unique and single pincer-like structures while remaining three pairs of legs are free, i. e. deprived of any of such structures.

Parhexapodibius and *Hexapodibius* represent a common phyletic lineage (Pilato, 1969 a) as inferred from the *Calohypsibius*-type of claws and from the *Doryphoribius*-type of buccal apparatus. One can therefore speculate that *Apodibius* with its similar type of buccal apparatus also belongs to this assemblage. However, highly autapomorphic reduction (absence) of all claws in this genus conceals information about their structure and, as consequence, their type, which is a character of uttermost importance in phylogenetic considerations. Thus, placement of the genus *Apodibius* in the family Calohypsibiidae has to be considered a tentative solution.

Doryphoribius pilato Bertolani and *Macrobiotus xerophilus* (Dastych) comb. nov. are characterized by the type of the claw reduction identical to that described for the genus *Parhexapodibius*. This type is defined by occurrence of



Figs. 32-34: *Macrobiotus xerophilus* (Dastych) comb. nov.: 32 = length of external claws on the third pair of legs (min-max. = 4.7-8.2 μm); 33 = length of external claws on the fourth pair of legs (min-max. = 1.5-5.8 μm); 34 = the length ratios (in %) of external claws on the third and the fourth pair of legs (min-max. = 25-82 %: for all diagrams $n = 75$)

the smallest claws on hind pair of legs. Since this striking similarity occurs between representatives of three divergent lineages, it is concluded that this character arose independently and at least three times in Eutardigrada. The resemblance is thus a result of convergent evolution which presumably is a response to similar selective forces.

Almost nothing is known about biology and ecology of all these "aberrant" taxa and about conditions that could have led to their origin. Our knowledge of soil tardigrades is meager and the potential existence of morphotypes strictly adopted to soil habitats has to be studied. Although data about habitat preferences of the discussed forms are fragmentary (Pilato 1969 b, 1969 c, 1971, 1982; Bernard, 1977; Dastych, 1978, 1983; Bertolani, 1983), they indicate that the reduction of the claw systems can be interpreted as an adaptation to the soil environment. One can envision soil capillary systems acting as a strong selective

factor that gives an evolutionary advantage to forms with reduced claws and legs. Similarities in the development of claw systems among remote phyletic lineages support this view. Almost all of these representatives show more or less predilection to the sandy soil or to cryptogames growing on this substrate.

Interestingly, they usually occur at dry sites. Thus, one can expect the existence of other such forms, particularly in "dry psammon", that is, among terrestrial communities of cryptobiotic metazoans that inhabit capillar systems of sandy soils, and are active during wet periods only.

A similar adaptation exists in *Pseudodiphascon bindae* Christenberry & Higgins, 1979, which has been described from soil mosses growing in rather dry and warm locality, judging from the original description (l. c., 1979). Its legs and claws are diminished (the latter, however, are all of equal size). Lunules are also missing. Another example is *Macrobiotus pseudohufelandi* Iharos, 1964. It has claws of "aberrant" shape on the three anterior pairs of legs. Lunules are absent from the claw bases and developed only at the bases of "normally" shaped claws of the hind pair of legs. This species is considered a xerothermic form (Dastyh, 1988). One should stress that Kristensen (1982) considered the diminished legs and claws as an adaptation in the only known limnic interstitial tardigrade, *Eohypsibius nadjae*, from Greenland's homothermal springs. He also attributed the same status to small leg size and thin claws in the genus *Microhypsibius* Thulin, found by him in the same region, predominantly in soil and detritus. A recent discovery of the genus *Hexapodibius* in gravel of maritime Antarctic (Usher & Dastyh, 1987) and occurrence of *Apodibius* in Europe (Dastyh, 1983), southern Africa (Mozambique: Binda, 1984) and Australia (unpublished: specimens kindly sent by Miss L. Nicholls) indicate that the claw reduction in Eutardigrada is a common and world-wide phenomenon.

We can expect that all the known "aberrant" tardigrades, found in recent years and characterized by varying degrees of reduction in claw and leg size, are probably only a small fraction of the actual tardigrade fauna. The prospective

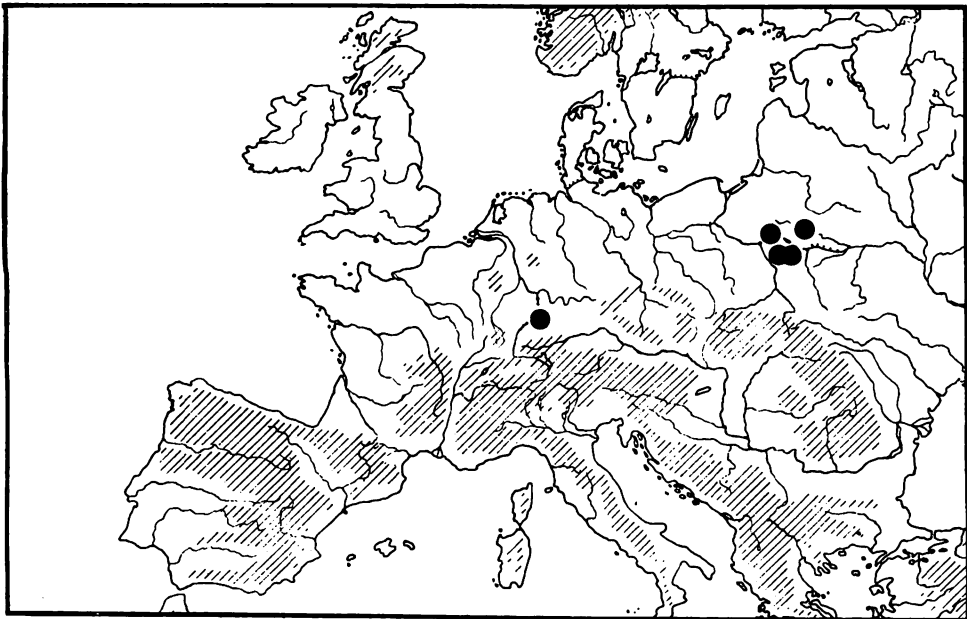


Fig. 35: Localities of *Macrobiotus xerophilus* (Dastyh) comb. nov.

knowledge that can be accumulated through further taxonomical and ecological studies will be of great importance to the advancement of our understanding of evolution of Eutardigrada. Given the incompleteness of that understanding more research on soil tardigrades is urgently needed.

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Zusammenfassung

In der vorliegenden Arbeit wird die in Deutschland erstmals nachgewiesene semiterrestrische Art, *Macrobiotus xerophilus* (Dastych, 1978) comb. nov., neu beschrieben. Die zunächst in die Calohypsibiidae eingeordnete Art wird aufgrund der neuen licht- und rasterelektronenmikroskopischen Befunde nun in die Macrobiotidae gestellt. Der phylogenetische Status des Taxons und die mögliche Beziehung zwischen dem spezifischen Habitat und der Reduktion von Krallen und Extremitäten bei Eutardigraden werden diskutiert.

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