

Phylogeny of the Terrestrial Isopoda (Oniscidea): a Review

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> Abstract

Recent hypotheses on the phylogeny of the Oniscidea are summarized. The position of the Oniscidea in the phylogenetic system of the Isopoda is discussed. Within the Oniscidea, phylogenetic relationships are considered mainly down to „family“ level. Well founded monophyletic clades are discussed and unresolved and problematic regions are pointed out. A list of probable autapomorphies is given for each taxon. The knowledge on the fossil record of Oniscidea is reviewed briefly. Finally it is concluded that we need phylogenetic analyses down to species level in order to construe a robust phylogeny hypothesis for higher oniscidean taxa. An indispensable requirement for this is taxonomic revisions.

> Key words

Isopoda, Oniscidea, characters, phylogeny, review.

1. Introduction

The Oniscidea is a taxon of the Isopoda that comprises mostly terrestrial species. Its monophyly is well supported by numerous morphological apomorphies. According to the most recent catalogue, 3527 species were known by the year 2000 (SCHMALFUSS 2003); an updated electronic version of that catalogue available in the internet counts 3637 species known by the year 2004. A few species of Oniscoidea are extensively studied and well-known, for instance *Armadillidium vulgare*, *Porcellio scaber*, *Porcellionides pruinosus*, and *Ligia oceanica* (complete bibliography in SCHMALFUSS 2003 and SCHMALFUSS & WOLF-SCHWENNINGER 2002).

Oniscidea species are found in various terrestrial habitats, preferably moist ones, but some are even able to live in arid regions. In contrast to other terrestrial crustaceans, the terrestrial isopods are independent from open water, due to the fact that their early ontogeny takes place in a brood pouch (marsupium) on the ventral side of the female. Some species are amphibious at the seashore (e.g. *Ligia*, *Olibrinus*), and very few species have secondarily adapted to aquatic habitats, either in hypersaline (*Haloniscus*) or subterranean waters (e.g. *Typhlotricholigioides*). From an evolutionary point of view, model organisms for the evolution of the adaptations to terrestrial life are found

among the Oniscidea (*Ligia* species) (CAREFOOT & TAYLOR 1995). Most Oniscoidea species feed on decaying plant material and the “microflora” growing on it. They often constitute an important part of the soil fauna, with up to several hundreds of specimens per square meter (DAVIS 1984; ARAUJO & BOND-BUCKUP 2005), consuming up to 12 % of the whole plant detritus (GRÜNWALD 1988). A wide range of predaceous soil arthropods may feed on terrestrial isopods (SUTTON & SUNDERLAND 1980; RAUPACH 2005).

Many papers have been published that contain at least some comments on the phylogeny of Oniscidea. Most of them are taxonomic papers including some considerations on the phylogenetic relationships of the taxa described therein, while articles focused on phylogeny are much less numerous. Until the 1970s, phylogenetic contributions consisted mainly of speculations on relationships between taxa or of evolutionary scenarios based on traditional classification. Application of the principles of phylogenetic systematics (HENNIG 1950, 1982; Ax 1984) led to the construction of testable hypotheses. In particular, hypotheses on the position of Oniscidea within the Isopoda, on the relationships among the 5 principal taxa of Oniscidea (ERHARD 1995, 1996, 1997), on the phylogeny of the oniscidean

subgroup *Crinocheta* (SCHMIDT 2002, 2003) and on the phylogenetic relationships within some low-rank subgroups have been published (e.g. *Orthometopon*: SCHMALFUSS 1993; *Ischioscia*: LEISTIKOW & SCHMIDT 2002; *Androdeloscia*: LEISTIKOW 1999 and SCHMIDT & LEISTIKOW 2005). The latest comprehensive work summarizing the information from previously published literature is by WÄGELE (1989), who proposed a cladogram including all families of Oniscidea.

Most of the papers on the phylogeny of the Oniscidea have been published after WÄGELE (1989). The present review shall give a summary of the progress made since. The most significant contributions in this period are: ERHARD (1995, 1996, 1997) on the skeleto-muscular anatomy of the pleon; SCHMIDT (2002, 2003) on the (mainly) external morphology of *Crinocheta*; SCHMIDT & WÄGELE (2001) on respiratory structures of the pleopods; LEISTIKOW (2001) on the external morphology of South American “*Philosciidae*”. In addition, some molecular studies have been published in recent years (MICHEL-SALZAT & BOUDON 2000; MATTERN & SCHLEGEL 2001; MATTERN 2003).

2. Terminology

For setae, scales and similar structures, I follow the definitions given in SCHMIDT (2002: 283). The description of the relative position of parts and appendages follows RACOVITZA (1923), with exception of the first antennae and the uropods, which are described according to their natural position.

The characters / character states relevant for the phylogenetic reasoning are numbered as (C1)–(C204) to facilitate cross-reference within this paper. Usually apomorphic character states will be listed as potential autapomorphies of taxa, while the respective plesiomorphic states are added in square parentheses. “R” behind the number of a character state indicates that the apomorphy in question concerns a loss or reduction, “?” in that position indicates that the feature is a doubtful autapomorphy of the taxon. For each taxon, it is attempted to provide complete lists of morphological apomorphies.

3. Major lineages and classification of Isopoda and Oniscidea

3.1. Lineages of Isopoda

According to WÄGELE (1989) the Isopoda include 8 principal lineages (“suborders”, Fig. 1) of more or less well supported monophyly. One of these is the **Oniscidea**, while the others are:

The **Phreatoicoidea**, which include ca. 50 species (GRUNER 1993) in freshwater habitats of Australia, New Zealand, South Africa and India.

The **Calabozoidea** consist of a single phreatic species in Venezuela.

The **Asellota** (incl. *Microcerberida*) comprise ca. 1940 mostly benthic species in freshwater and marine habitats, especially in the deep-sea. The monophyly of the Asellota is well founded on complex morphological apomorphies (WÄGELE et al. 2003: 536).

The **Valvifera** include ca. 500 species (GRUNER 1993), predominantly marine, some in freshwater. The 5th pleopods form a characteristic operculum for the remaining pleopods.

The **Anthuridea** comprise ca. 330 species (GRUNER 1993), nearly all of them marine, burrowing or in the interstitial system. All of them seem to be carnivores.

The **Sphaeromatidea** are represented by ca. 900 species (GRUNER 1993), mostly marine, some in freshwater. The group includes species with rolling ability, but a flattened habitus is considered plesiomorphic. The monophyly of this group is less well supported and should be examined further (DREYER & WÄGELE 2002: 231).

The **Cymothoidea** (incl. *Gnathiidea* and *Epicaridea*) are comprised of ca. 1450 species (GRUNER 1993), mostly marine, some in freshwater.

In contrast to this system, BRUSCA & WILSON (1991) after a cladistic analysis based on morphological characters do not include the *Microcerberida* in Asellota, but regard them as sistergroup of the Asellota, and come to a different arrangement of the taxa formerly being classified as “*Flabellifera*”. In their strict consensus tree, the Valvifera, Anthuridea, Epicaridea, *Gnathiidea* and several lineages of “*Flabellifera*” form an unresolved polytomy with 8 branches. In past classifications the *Gnathiidae* and *Bopyridae* were ranked as suborders (as *Gnathiidea* and *Epicaridea*, still retained in the systems of BRUSCA & WILSON 1991 and SCHMALFUSS 1989, Fig. 2), before their subordinate position within the Cymothoidea was proposed by WÄGELE (1989). The Cymothoidea excl. these two taxa, and the Sphaeromatidea had been grouped together as *Flabellifera*, but this group has been found paraphyletic by WÄGELE (1989) and BRUSCA & WILSON (1991).

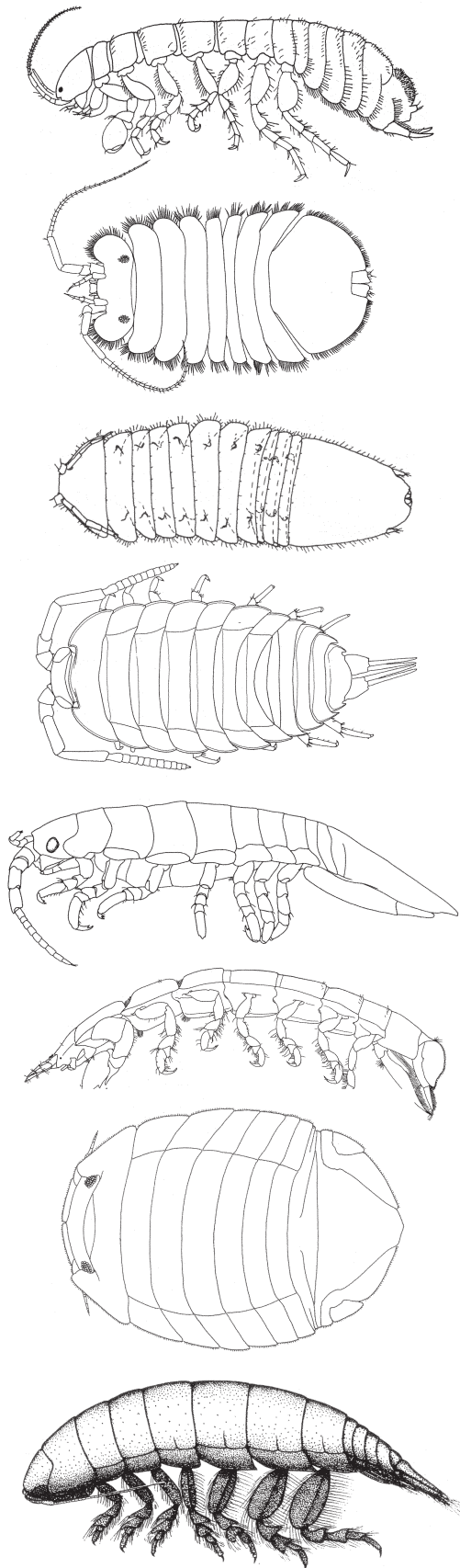


Fig. 1. Representatives of 8 suborders of Isopoda; Phreatoicidae: *Phreatoicus australis* (redrawn after CHILTON 1891); Asellota: *Jaera istri*; Calabozoidea: *Calabozoa pellucida* (from VAN LIESHOUT 1983); Oniscidea: *Ligia oceanica*; Valvifera: *Idotea granulosa*; Anthuridea: *Cyathura carinata*; Sphaeromatidea: (indet.); Cymothoidea: *Cirolana borealis* (from GRUNER 1983).

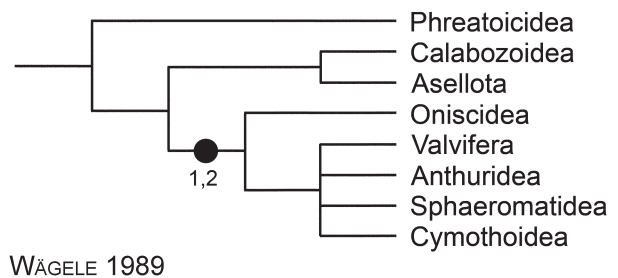
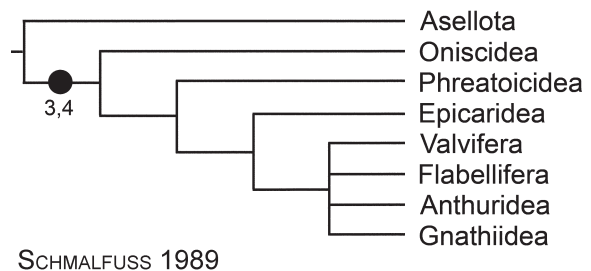
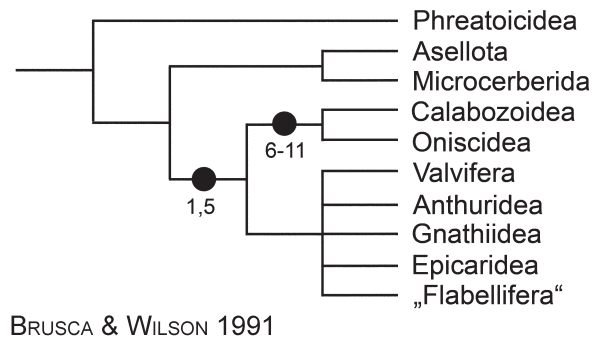


Fig. 2. Hypotheses on basal relationships within the Isopoda.

3.2. Lineages of Oniscidea

The Oniscidea consist of the following five principal lineages:

The **Ligiidae** include the genera *Ligia* and *Ligidium* with ca. 80 species living at the seashore or in terrestrial habitats with a high humidity. Apparently they represent the most primitive Oniscidea. It is assumed that in the evolution of terrestriality, the ancestral Oniscidea passed a stage similar to that of the shore inhabiting species of *Ligia*.

The **Tylidae** are represented by ca. 20 species inhabiting the seashore and 1 in terrestrial habitats. All of them can “conglobate” (“roller”-type habitus, SCHMALFUSS 1984).

The **Mesoniscidae** (*Mesoniscus*) includes only 2 very similar, montane species in the Alps and Carpathians. They lack eyes and pigment.

The **Synocheta** comprise about 630 species. They are mainly small isopods adapted to endogeous or cave habitats. There are no coastal species, and all of them are confined to rather moist environments.

The **Crinocheta** include ca. 2750 species, hence about 80 % of the Oniscidea. Many of them possess more or less complex lungs in the pleopod exopodites, and many are adapted to habitats that are rather dry compared with the habitats of the other terrestrial Isopoda.

An aquatic life habit, as found in various species of Synocheta and a few Crinocheta (summarized by TABACARU 1999), is regarded as a secondary condition that evolved several times within the Oniscidea.

4. Phylogenetic position of Oniscidea within the Isopoda

Earlier hypotheses on the relationships between the higher taxa of Isopoda have been summarized by WÄGELE (1981, 1989). The history of the hypotheses on the phylogenetic position of the terrestrial Isopoda within the Isopoda is complicated by the fact that the Oniscidea were not always regarded as a natural group or monophyletic taxon. Therefore the hypotheses assuming monophyly and non-monophyly are here treated separately.

4.1. Hypotheses assuming non-monophyly of Oniscidea

All morphology-based hypotheses including non-monophyletic Oniscidea are pre-phylogenetic, not derived following the principles of phylogenetic systematics. An independent origin of subgroups of terrestrial isopods from marine ancestors has been proposed first by CHILTON (1901), who divided them into two lineages, one including Ligiidae, Trichoniscidae, Tylidae and Helleridae, the other one including Scyphacidae, Oniscidae and Armadillidae (most of these taxa defined in a broader sense than today). VERHOEFF (1920) assumed an independent origin of the Hypotracheata, Atracheata and Pleurotracheata. VANDEL in numerous contributions discussed phylogenetic relationships and evolutionary scenarios of terrestrial isopods. In several publications from 1943 to 1981, he assumed the non-monophyly of the Oniscidea. VANDEL (1943) came to the conclusion that the Tylidae (“Série tylienne”) are most closely related to the Valvifera; for the Stenoniscidae (based on literature data only) he assumed the same, but argued that they probably had a different origin than Tylidae. For the remaining terrestrial isopods (“Série ligienne”) he proposed an independent origin from marine isopods certainly different from the Valvifera, probably from the Cirolanidae

(Cymothoidea, then “Flabellifera”). Later, VANDEL (1964, 1965) regarded also the Trichoniscidae as having become terrestrial independently from the other Oniscidea, because he believed that in Trichoniscidae the aquatic life habit of *Cantabroniscus* and *Typhlotricholigioides* represented the ancestral condition.

In a study on sequences of the mitochondrial 16S rRNA gene, MICHEL-SALZAT & BOUCHON (2000) found *Ligia* + *Tylos* more similar to Valvifera + Sphaeromatidea than to the remaining Oniscidea. The cladogram was calculated with a neighbor joining algorithm that reveals similarity, so this result is also not based on phylogenetic methodology in the strict sense, and is here considered insufficient to outweigh the complex morphological apomorphies of Oniscidea.

4.2. Hypotheses including monophyletic Oniscidea (Fig. 2)

The Oniscidea were placed as “sistergroup” to Asellota (KOSSMANN 1880; MONOD 1922), or to a taxon formed by Epicaridea, Anthuridea, Gnathiidae and Flabellifera (STROEMBERG 1972), they were regarded as close relatives of Flabellifera and Valvifera (SCHULTZ 1969), or they were placed on an “independent” branch beside other taxa of Isopoda (KUSSAKIN 1973). However, all these hypotheses or classifications are not based on phylogenetic reasoning. BRUCE (1980) placed the Oniscidea as sistergroup of the Valvifera + Phoratopodidae. The Phoratopodidae are closely related to Oniscidea neither in WÄGELE’s (1989) nor in BRUSCA & WILSON’s (1991) cladograms.

In WÄGELE’s (1989) dendrogram the Oniscidea are sistergroup of a taxon consisting of Valvifera, Anthuridea, Sphaeromatidea and Cymothoidea, the relationships among the latter 4 taxa are not further resolved (Fig. 2). The proposed synapomorphies of the Oniscidea and the other mentioned taxa are: (C1) Coxae enlarged to form laterally extended coxal plates; coxal plate of first pereon segment fused to tergite [coxae ring-shaped] (WÄGELE 1989: 232) (Fig. 1). (C2) Anterior filter rims of the stomach with their caudal portion curved laterally [not curved] (WÄGELE 1989: 232) (Fig. 3); the straight condition of the anterior filter rims in the Anthuridea is explained as a secondary condition. The Calabozoidea + Asellota are sister taxon to the former assemblage of “suborders”, and the Phreatoicidea represent the basalmost isopod branch. There are no characters that unite Oniscidea to Valvifera alone.

SCHMALFUSS (1989), in a paper focused on the phylogeny of Oniscidea, proposed a cladogram in which Asellota are the sistergroup of all other Isopoda, and Oniscidea are the sistergroup of the remaining taxa, incl. Phreatoicidea (Fig. 2). He referred to two synapomorphies of the Isopoda excl. Asellota, the (C3) biting

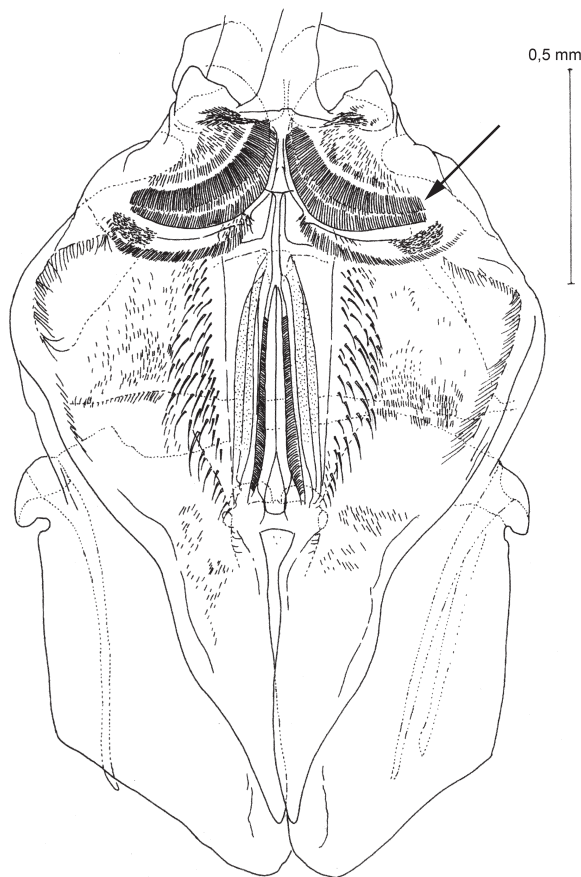


Fig. 3. *Ligia exotica*, stomach in ventral view: anterior filter rims curved laterally (C2).

mandible, derived from a rolling-squeezing mandible (both types of mandibles being dicondylic), and (C4) the presence of frontal arms in the maxillary apodemes (Fig. 4).

BRUSCA & WILSON (1991) in a cladistic analysis of morphological characters, found Calabozoidea as sistergroup of Oniscidea, and Calabozoidea + Oniscidea as sistergroup of the remaining isopod taxa excl. Phreatoicoidea, Asellota and Microcerberidea (Fig. 2). Synapomorphies of the Isopoda excl. Phreatoicoidea, Asellota and Microcerberidea are (C1) lateral coxal plates and (C5) lack of an articulation within the pleopod exopodites. Synapomorphies for Calabozoidea and Oniscidea are (C6) cuticular tricorn sensilla, (C7) “penes on pleomere 1 or on the articulating membrane between pleomere 1 and thoracomere 8”, (C8) endopods of male pleopods 1 and 2 styliform and greatly elongated, (C9)R mandible without palp, (C10) pleopodal exopods broad and opercular and endopods thick and tumescent, and (C11)R maxilliped endite without coupling setae; two of these characters concern reductions. In Calabozoidea, (C1) coxal plates are considered to be absent (WÄGELE 1989) or present (BRUSCA & WILSON 1991), which explains the different composition of the taxon defined by that character state.

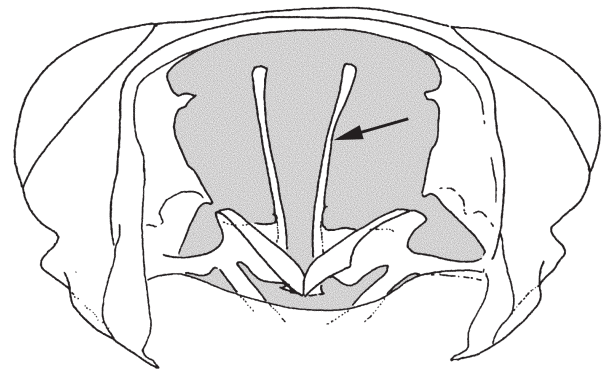


Fig. 4. *Ligia exotica*, cephalothorax caudal, maxillary apodeme with frontal arms (C4).

Regarding the (C6) cuticular tricorn sensilla, SCHMIDT (2002, 2003) rather considers these structures as an apomorphy of an unnamed taxon comprising most of the “higher” Crinocheta.

TABACARU & DANIELOPOL (1996) conducted a cladistic analysis based on 43 morphological characters; the included taxa were Asellota, Valvifera, and the five principal subgroups of the Oniscidea (Tylidae, Ligidae, Mesoniscidae, Synocheta, Crinocheta). They found the Valvifera to be more closely related to the Oniscidea than the Asellota, which is consistent also with the hypotheses proposed by WÄGELE (1989), SCHMALFUSS (1989) and BRUSCA & WILSON (1991). The relationship of Valvifera and Oniscidea is supported by (C12) peduncle of second antenna 5-jointed [6-jointed], (C1) lateral coxal plates, (C13) male genital papillae basally fused, inserting on the articulation membrane between pereion and pleon [inserting on the inner corner of pereopod 7 coxae or on the posterior margin of pereion sternite 7]; but note that the papillae are absent in Oniscidea-Tylidae.

DREYER & WÄGELE (2002) analysed the 18S rRNA gene for reconstruction of isopod phylogeny. Based on the results of this analysis, which confirm the above mentioned hypothesis of WÄGELE (1989), they introduced a new taxon Scutocoxifera (referring to the lateral coxal plates), which includes the Oniscidea, Valvifera, Sphaeromatidea, Anthuridea, and Cymothoidea and is supported also by the abovementioned morphological apomorphies (C1) and (C2). The Phreatoicoidea and Asellota are not in the Scutocoxifera. An analysis of mitochondrial 12S rRNA, 16S rRNA and CoI genes (WETZER 2002), including two species of Oniscidea and representatives of other isopod taxa, did not yield a stable result: The two oniscidean species do not group together and are found in completely different positions in the cladograms depending on gene partition and analytical procedure.

5. Oniscidea as a monophyletic taxon

Now the monophyly of the Oniscidea with the taxonomic content given in 3.2. is well established (SCHMALFUSS 1974, 1989; WÄGELE 1989; BRUSCA & WILSON 1991; ERHARD 1995; TABACARU & DANIELOPOL 1996), and the group is supported by numerous apomorphies.

- (C14) Water conducting system present [absent] (WÄGELE 1989; detailed description in HOESE 1982, 1983) (Fig. 5). This system is composed of scale rows on the ventral side of the coxal plates; it is very complex and thus a very convincing autapomorphy of the Oniscidea.
- (C15) Pleotelson very short, only slightly longer than a pleon segment [pleotelson not reduced in length] (WÄGELE 1989).
- (C16R) First antenna with only 3 articles: 2 peduncular and and 1 flagellar article [3 peduncular and and 1 or more flagellar articles] (WÄGELE 1989) (Fig. 6).
- (C17) First antennae inserting directly between second antennae [first antennae inserting antero-medially to the second antennae] (BRUSCA & WILSON 1991) (Fig. 6).
- (C18) Second antenna: dorsal apodeme present in the first article [absent] (SCHMALFUSS 1974: char. 2).
- (C19R) Mandibular palp absent [present] (WÄGELE 1989).
- (C20) Mandible: a tuft of setae is divided into two parts, one located on the lacinia mobilis, the other one beside it [tuft of setae not divided, entirely beside the lacinia mobilis] (SCHMALFUSS 1974: char. 6) (Fig. 7).
- (C21) Mandible: dorsal adductor (M43) inserts partly on the dorsolateral maxillipedal apodeme [all strands of M43 originate on the dorsal part of the cephalic capsule] (SCHMALFUSS 1974: char. 7).
- (C22) Mandible: muscle M45 originates at the dorsal end of the frontal arm, and inserts on the ventral side of the mandible corpus [M45 originates basally on the frontal arm and inserts laterodorsally on the mandible corpus] (SCHMALFUSS 1974: char. 8).
- (C23) Mandible: muscle M46 consists of 6 strands [M46 consists of only 1 strand] (SCHMALFUSS 1974: char. 9).
- (C24) Hypopharynx: supporting sclerite of the lateral lobes reaching their lateral margin [supporting sclerite ends at the insertion of M50] (SCHMALFUSS 1974: char. 11) (Fig. 8).
- (C25) Hypopharynx: median extension prolonged into a frontal cone [median extension short] (SCHMALFUSS 1974: char. 12).

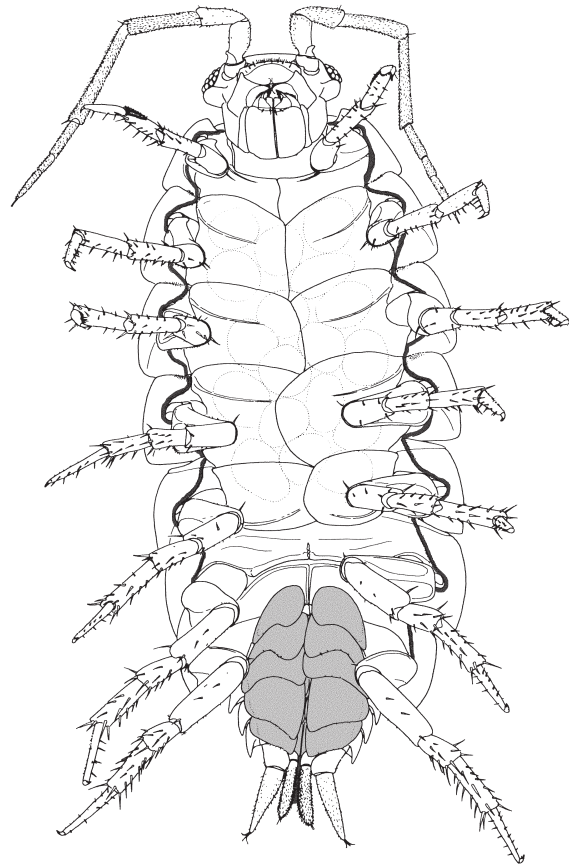


Fig. 5. *Philoscia affinis* (Crinocheta), ventral view of ovigerous female. (C14) Water conducting system, scale rows indicated by bold black line, pleoventral chamber grey.

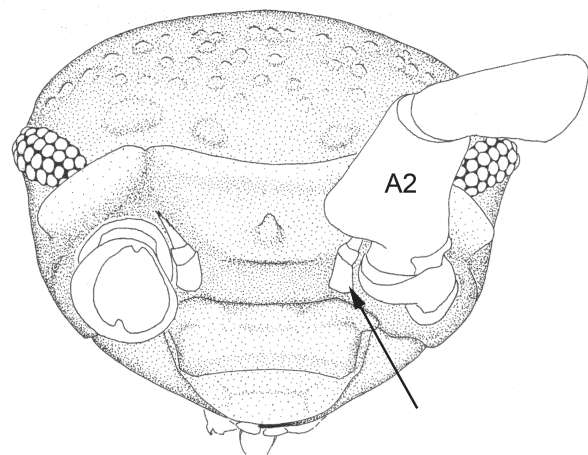


Fig. 6. *Trachelipus trachealis* (Crinocheta, Trachelipodidae), cephalothorax in frontal view: (C16) first antenna with only 3 articles; (C17) first antennae inserting directly between second antennae.

- (C26) Hypopharynx: muscle M50 originates on the maxillipede apodeme [M50 originates on the cephalic capsule] (SCHMALFUSS 1974: char. 13).
- (C27) Second maxilla: endites fused with each other and with "basis"; only two endites, distal "comb"

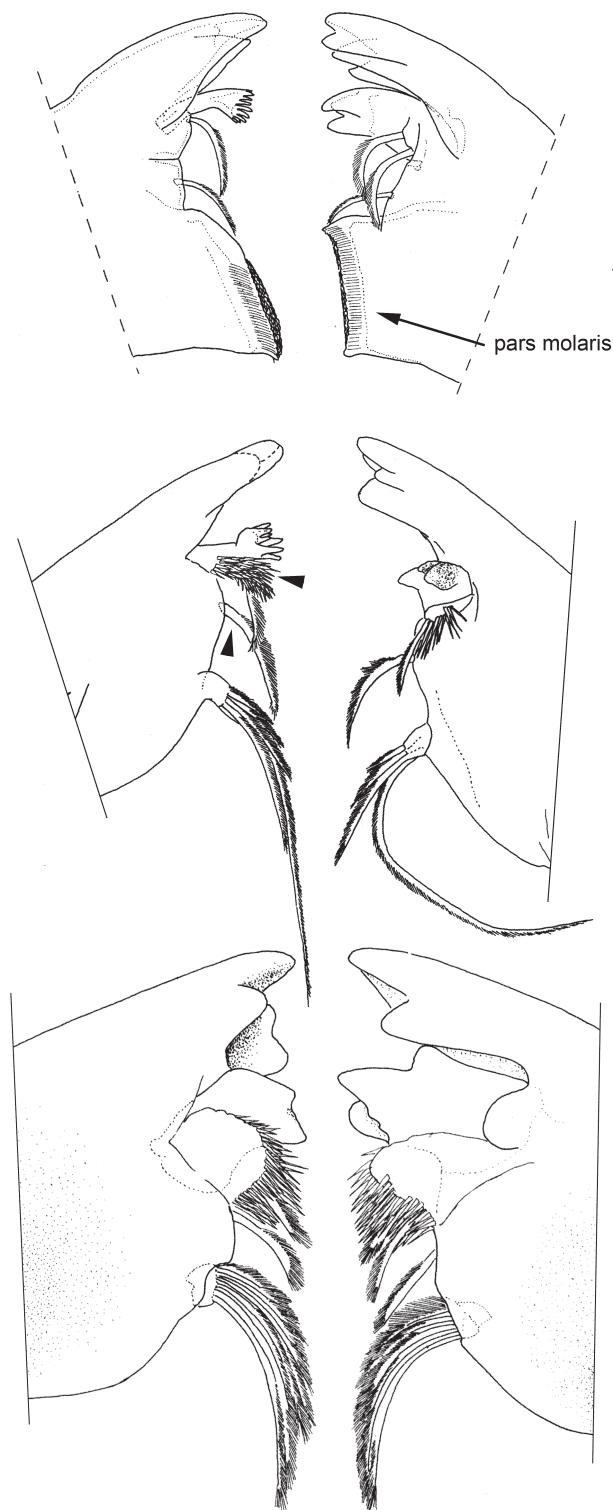


Fig. 7. Mandibles: *Amerigoniscus nicholasi* (Synocheta), above, *Deto marina* (Crinocheta, Detonidae, from SCHMIDT 2002), *Didima humilis* (Crinocheta, «Philosciidae»), below. (C20) Tuft of setae beside the lacinia mobilis is divided into two parts, one is moved on the lacinia (arrowheads). In Crinocheta, (C109) pars molaris replaced by tuft of setae.

setae" absent [second maxilla with three endites bearing setae] (SCHMALFUSS 1974: char. 16, 17; WÄGELE 1989: 232) (Fig. 9).

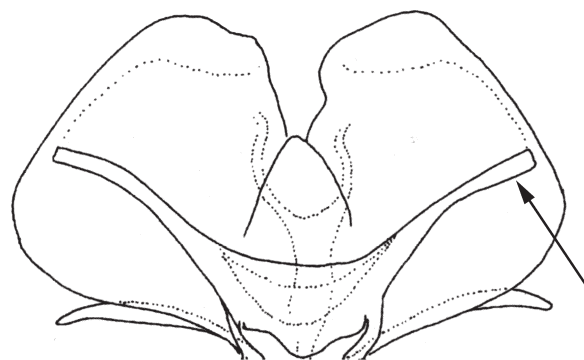


Fig. 8. *Ligia exotica*, hypopharynx. (C24) supporting sclerite of the lateral lobes reaching margin.

- (C28) Second maxilla: at the basis only one moveable sclerite [at the basis 5 moveable sclerites] (SCHMALFUSS 1974: char. 18).
- (C29) Maxilliped: frontal insertion extended distally on the basis [frontal insertion at the proximal end of the maxilliped] (SCHMALFUSS 1974: char. 24).
- (C30) Maxilliped with a single coxal sclerite [Maxilliped with 2 coxal sclerites] (SCHMALFUSS 1974: char. 25) (Fig. 9).
- (C31R) Maxilliped endopodite (= palp): articulation between carpus and propodus absent, muscles M84 and M85 absent [articulation and both muscles present] (SCHMALFUSS 1974: char. 25, 32, 33) (Fig. 9).
- (C32R) Maxilliped endopodite (= palp) reduced relative to basis [as long or longer than basis] (WÄGELE 1989: 232).
- (C33) Maxilliped basal endite without retinacula on inner margin [retinacula present] (SCHMALFUSS 1974: char. 27).
- (C34R) Pereiopod 1 not subchelate [pereiopod 1 subchelate] (WÄGELE 1989: 232).
- (C35) Pleopod 1 sexually dimorphic, in the male the median side of the endopodite somewhat prolonged [pleopod 1 not sexually dimorphic] (WÄGELE 1989: 232).
- (C36) Male pleopod 2 endopodite is reduced to basal article of the appendix masculina [male pleopod 1 endopodite not reduced in size].
- (C37) Uropods stick-shaped [uropods leaf-like] (WÄGELE 1989: 232).
- (C38) Male genital papillae proximally fused, located on intersegmental membrane pereion 7–8 [Male genital papillae fully separated medially, located ventrally on caudal margin of sternite 7] (WÄGELE 1989: 232).
- (C39) Tergites with scale-setae [tergites without scale-setae].
- (C40) "Antennal and uropodal spikes" present, which are complex and compound sensillar structures at

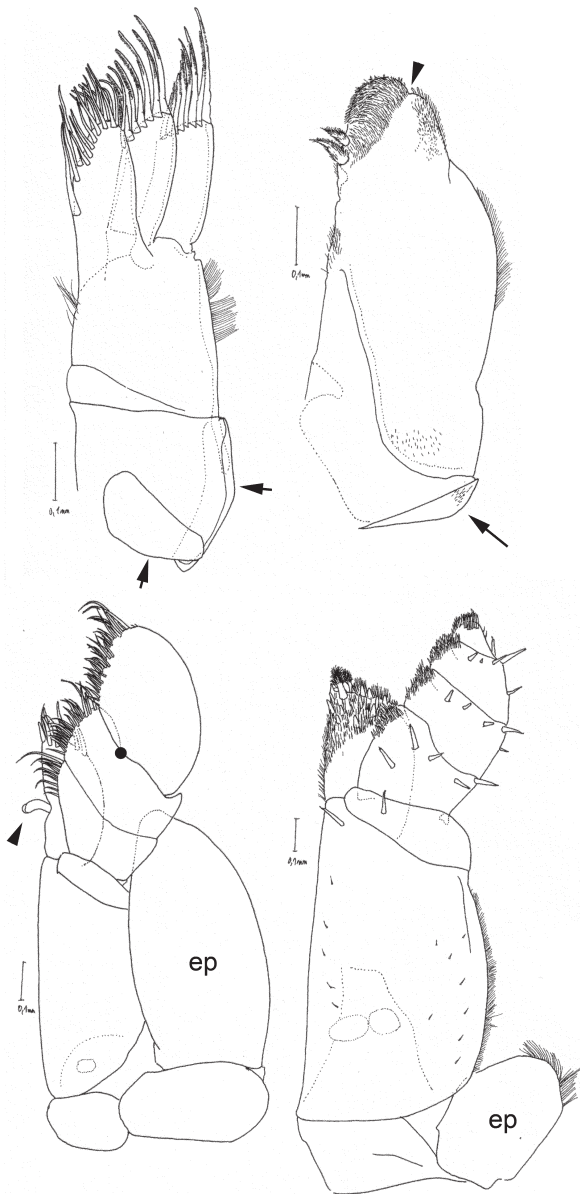


Fig. 9. Above: second maxilla of *Idotea granulosa* (Valvifera) with 3 endites and 2 moveable sclerites, and of *Ligidium formosanum* (Oniscidea) with 2 endites fused to the basis (C27), and 1 moveable sclerite (C28); arrows point to moveable sclerites at basis, arrowhead indicates border between two endites. Below: Maxilliped of *Idotea granulosa* and *Ligia exotica*, showing characters (C29–33).

the tips of antennae and uropodal rami [plesiomorphic state: ?] (BRUSCA & WILSON 1991).

(C41) Sternal calcium deposits present, forming a spherular layer [sternal calcium deposits absent] (ZIEGLER 2002: 300).

All the apomorphies found by SCHMALFUSS (1974) have been demonstrated only for *Tylos* and *Ligia* (Oniscidea) compared with *Mesidotea* (= *Saduria*) (Valvifera); they are tentatively regarded as autapomorphies of the Oniscidea, but should be examined in a broader

oniscidean sample. SCHMALFUSS (1974: char. 1) additionally mentioned the “reduction of the first antenna”. However, in *Tylos* and *Ligia*, the first antenna is more strongly reduced than in other Oniscidea, and the putative condition in the Oniscidea groundpattern is given above (C16). Probably only the reduction of the peduncular articles by 1 (from 3 to 2) is an autapomorphy of Oniscoidea. In *Ligia* and *Tylos* the “reduction” of the first antenna is different and more probably is convergently evolved. SCHMALFUSS’ char. 3–5 concern attachment sites or absence of certain muscles in the second antenna; they are considered as insecure and should be tested by examination of other isopods (SCHMALFUSS 1974); they are not included in the above list. SCHMALFUSS’ char. 10 refers to the reduction of the mandibular muscle M48, which is present in *Mesidotea*. The first maxilla has 1 basal sclerite in *Ligia* and *Tylos* and two basal sclerites in *Mesidotea*. SCHMALFUSS (1974) regards “the fused basal sclerites” (char. 14) as a probable synapomorphy, but points out that it is not sure, because he could not demonstrate that the Isopoda groundpattern had two sclerites. Char. 15 is the reduction of muscle M57 of the first maxilla. Char. 19–23 refer to the absence of certain muscles of the second maxillae, this certainly is correlated with the fusion of sclerites and may be included in the above listed characters (C27) and (C28). The plesiomorphic state of (C30) has been observed in *Mesidotea* and also in *Asellus*. In the maxilliped, several further muscles are absent in the oniscideans: M71, M73, M75 in the coxa or basis and M83 in the palp (SCHMALFUSS 1974: char. 28–31).

According to WÄGELE (1989), the most prominent apomorphies of the Oniscidea are (C14) the water conducting system, (C16) the first antenna of only 3 articles, and (C35, C36) the shape of the male pleopods. BRUSCA & WILSON (1991) found 2 apomorphies supporting the monophyly of Oniscidea, (C17) the position of the insertion of the first antennae and (C40) “antennal and uropodal spikes”. They regarded further structures (C6, C38) and the loss of some structures (C19, C33) as synapomorphies of Calabozoidea and Oniscidea. In Tylidae, the (C60) male genital papillae are entirely absent, so the respective character cannot be directly assessed.

Cuticular calcium carbonate is stored in large deposits between the epithelium and the old cuticle and reused after moult. These deposits consist of up to 3 layers, a proximal “homogeneous layer”, a “proximal spherular layer” in the middle, and a distal “distal spherular layer”. In *Ligia* only the proximal spherular layer has been found (C41), in *Ligidium* both spherular layers are present (C50), and in *Tylos* as well as representatives of Synocheta and Crinocheta all three layers are present (C57) (ZIEGLER 2003). The second layer may be a synapomorphy of all Oniscidea exclud-

ing *Ligia*, while the third layer probably is an apomorphy of all Oniscoidea excluding *Ligia* and *Ligidium* (see below). Data on *Mesoniscus* are not available.

There is so far only one molecular study relevant to the question of Oniscoidea monophyly: that of DREYER & WÄGELE (2002) on nuclear 18S rRNA gene sequences. Therein the 3 sampled species of Oniscoidea group together: *Ligia* and 2 species of Crinocheta. The analysis of MATTERN (2003), which beside 24 species of Oniscoidea included *Asellus aquaticus* as the single outgroup species, cannot be considered as testing the monophyly of Oniscoidea.

6. Prae-phylogenetic classifications of the terrestrial Isopoda

The terrestrial isopods were first regarded as a sub-order of the Isopoda by LATREILLE (1829). The first classification was presented four years later by J.F. BRANDT (1833), who divided the terrestrial isopods into 'Ligieae' and 'Oniscinea', the latter further subdivided into 'Porcellionea' and 'Armadillina'. The Porcellionea included the 'Hexarthrica' (*Trichoniscus* and *Platyarthrus*) and the 'Schizarthrica' (the other non-conglobating species), while the 'Armadillina' included 'Armadillidia' and 'Cubaridea'.

C.L. KOCH (1844) used only two hierarchic levels and classified the terrestrial isopods in 'Armadillidae', 'Oniscidae' and 'Ligiidae'. In MILNE EDWARDS' (1940) classification the 'Ligieae' sensu BRANDT were quoted as 'Cloportes maritimes' and the Oniscinea sensu BRANDT as 'Cloportes terrestres'. The latter included the 'Tylosiens' in addition to the 'Porcellionides' and 'Armadillidiens'.

DANA (1852) was the first author using the name 'Oniscoidea'. He divided them into three families "Armadillidae" (conglobating Oniscoidea), "Oniscidae" (non-conglobating Oniscoidea) and "Asellidae" (now Asellota, not part of the Oniscoidea). In a monograph of all terrestrial isopods known at that time, BUDDE-LUND (1885) distinguished four families, "Onisci", "Ligiae", "Tylidae" and "Syspasti"; the latter include only the genus *Helleria*, which now belongs to the Tylidae. VERHOEFF (1920) tried to classify the terrestrial isopods on the basis of their respiratory structures, and divided them in Hypotracheata (Tylidae, Syspastidae, Stenoniscidae), Atracheata (Ligiidae, Trichoniscidae), and Pleurotracheata (Oniscidae, Porcellionidae, Armadillidae, Armadillidiidae, Eubelidae). VERHOEFF (1936) distinguished 18 families included in the three taxa Protophora, Endophora, and Embolophora, based on the different structure of the genital papilla.

VANDEL considered the terrestrial isopods as polyphyletic, yet he retained "Oniscoidea" as a taxon and rejected to apply his phylogenetic reasoning to the classification. The three lineages he proposed to be derived independently from aquatic forms he classified as the "série tylienne", "série ligienne" and "série trichoniscienne". VANDEL (1957) proposed the taxon Diplocheata, which in the text included only the Ligiidae, but in a figure is implied to include also Mesoniscidae. The classification presented by VANDEL (1960), the Diplocheata is composed of Ligiidae and Mesoniscidae.

LEGRAND (1946) introduced the taxon names Synocheta and Crinocheta, which refer to the taxa named Endophora and Embolophora by VERHOEFF (1936). LEGRAND's names are still in use for monophyletic taxa. VANDEL (1960) instituted two subdivisions of Crinocheta as Atracheata and Pseudotracheata. The name Atracheata had been used by VERHOEFF (1920) for a taxon composed of Ligiidae and Trichoniscidae. For formal reasons VANDEL's subdivisions of Crinocheta received two proposals of renaming. MORRIS (1979) named them Oniscacea and Porcellionioidea. BOWMAN & ABELE (1982), apparently without having seen MORRIS' article, named them Oniscoidea and Armadilloidea.

The classifications by SCHMÖLZER (1965), BOWMAN & ABELE (1982), and HOLDICH et al. (1984) mainly relied on the ideas of VANDEL, and did not provide any progress with regard to phylogeny hypotheses.

7. Morphology based phylogeny hypotheses for Oniscoidea

The subdivision of the Oniscoidea was subject of investigations on morphology and anatomy as well as synthetic work on published data (SCHMALFUSS 1974, 1989; WÄGELE 1989; TABACARU & DANIELOPOL 1996; ERHARD 1995, 1996, 1997).

Each of the five currently distinguished principal lineages – Ligiidae, Tylidae, Mesoniscidae, Synocheta, Crinocheta – is regarded as monophyletic, though with limitations in terms of Ligiidae (see below); however, for their relationships there are still contradictory hypotheses.

A sistergroup relationship between Synocheta and Crinocheta had already been proposed by LEGRAND (1946), and was confirmed by WÄGELE (1989) and ERHARD (1995) (Fig. 10). In contrast, TABACARU & DANIELOPOL (1996) favoured a sistergroup relationship of Synocheta and Mesoniscidae. SCHMALFUSS (1989) postulated the relationships Ligiidae + ((Mesoniscidae + (Synocheta + Crinocheta)), and made the tenta-

tive proposition of a sistergroup relationship between Crinocheta-Actaeciidae and Tylidae, which was based mainly on a similarity of the uropods.

WÄGELE (1989) included Tylidae, Mesoniscidae and Ligiidae in a taxon Diplochaeta, based on the (C42) reduction of the third article of the first antenna, which, however, is different in the three groups, and on the (C43) respiratory fields on the ventral side of the pleopods. WÄGELE's (1989) hypothesis was also accepted by GRUNER (1993) for his textbook. The structure of the first antennae actually is very different in the 3 taxa, and the reduction of the terminal article was later interpreted as a convergency (ERHARD 1995). Respiratory surfaces on the ventral side of the pleopods are present also in many Synocheta and Crinocheta – as a plesiomorphic condition, while dorsal respiratory fields are a derived condition within the Crinocheta (SCHMIDT & WÄGELE 2001).

A phylogenetic analysis based on morphological and anatomical data (ERHARD 1995), mainly from the skeletomuscular system of the pleon, supports the monophyly of the Oniscidea (see above) and favours the monophyly of a taxon including Synocheta, Crinocheta and Mesoniscidae (for which TABACARU & DANIELOPOL 1996 introduced the name Orthogonopoda). This is based mainly on the structure of the male pleopod 1 endopodite and of the uropod endopodite. The relationships between Ligiidae, Tylidae and the taxon including Synocheta, Crinocheta and Mesoniscidae remained unresolved. The main aim of the study by ERHARD (1995) was to test the hypothesis of a sistergroup relationship between the Actaeciidae and Tylidae (see above), which was clearly refuted. A combination with data taken from the literature allowed to assume a sistergroup relationship between the Ligiidae and all remaining Oniscidea, but ERHARD (1995) preferred to propose this only as a preliminary result. ERHARD (1996) added anatomical data on the skeletomuscular system of the pleon of *Mesoniscus alpicola*, and came to the conclusion, that a basal split in the Oniscidea is between Ligiidae and the remaining subgroups, which are split in Tylidae and a taxon including Mesoniscidae, Synocheta and Crinocheta, the relations of the three latter taxa remaining unresolved.

Concerning the relations between Synocheta, Crinocheta and Mesoniscidae, there are two different hypotheses. One assumes a sistergroup relationship between the Synocheta and Mesoniscidae (TABACARU & DANIELOPOL 1996), the other hypothesis favours a sistergroup relationship between Synocheta and Crinocheta (SCHMALFUSS 1989, WÄGELE 1989). These hypotheses are discussed below. The third possibility, a sistergroup relationship between Mesoniscidae and Crinocheta, has never been proposed.

ERHARD (1997) described in detail the anatomy of the skeletomuscular system of the pleon of *Titanethes*

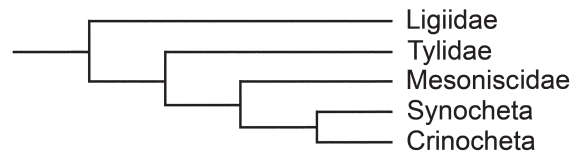


Fig. 10. Phylogenetic relations within the Oniscidea as proposed by ERHARD (1996).

albus, a representative of the Synocheta. A combination with the previous data confirms the relationships of the Ligiidae + (Tylidae + (Mesoniscidae + (Synocheta + Crinocheta))), and a sistergroup relationship between the Synocheta and Crinocheta was clearly favoured over a Synocheta + Mesoniscidae clade.

8. Phylogeny hypotheses based on molecular data

Phylogeny hypotheses based on the evaluation of DNA sequences were proposed by MICHEL-SALZAT & BOUCHON (2000) using the 16S rRNA (mitochondrial LSU rRNA) gene, and MATTERN & SCHLEGEL (2001) and MATTERN (2003) using the 18S rRNA gene sequences (papers on population genetics or on a single species are not considered here).

MICHEL-SALZAT & BOUCHON (2000) analysed partial 16S rRNA gene sequences of 27 species of Oniscidea, 3 Valvifera, 3 Asellota, 3 Sphaeromatidea, 1 Cymothoidea, 1 Anthuridea, 2 Amphipoda, 1 Tanaidacea, 1 Cumacea and 2 Decapoda. They found that the sequences of Tylidae, Ligiidae and Synocheta-Trichoniscidae are similar in length, while those of Crinocheta are significantly shorter than those of the other Oniscidea and also of the other Crustacea included in the study. There is a deletion of 30–54 nucleotides in the Crinocheta and an insertion of 2–3 nucleotides in the Crinocheta-Porcellionidae. The final matrix included 303 nucleotide positions, of which 209 were parsimony-informative. In the resulting cladograms (two cladograms calculated with Neighbour Joining, NJ), some taxa appear as monophyletic, e.g. Synocheta, Crinocheta, and the crinochetan subgroups Armadillidae and Armadillidiidae, but in other parts the cladogram deviates from the morphology-based hypotheses, e.g. *Ligia* + *Tylos* appear more closely related to Valvifera + Sphaeromatidea than to the remaining Oniscidea, and *Ligidium* is obtained as sister to a species of Cymothoidea. However, the latter branches are very short and unstable with regard to changes in taxon composition and reconstruction method. It should be kept in mind that NJ is a dis-

tance-based method that shows similarity (e.g. WÄGELE 2000). Also a ML analysis had been computed but the results are not shown in the paper.

MATTERN & SCHLEGEL (2001) and MATTERN (2003) studied the 18S rRNA gene of various Ligiidae, Synocheta and Crinocheta, while Tylidae and Mesoniscidae are not included. MATTERN & SCHLEGEL (2001) covered only 12 species (10 “families”) of Oniscidea and 1 species of *Asellus* as outgroup, which can hardly be regarded as a representative sample. Within Oniscidea, the phylogeny hypothesized is Ligiidae + (Synocheta + Crinocheta) in the results by all algorithms used (MP, ML, NJ). MATTERN (2003) added sequences of further 12 species to the previous dataset, now covering 24 species (11 “families”). Within Oniscidea, the Ligiidae, Platyarthridae, and Trachelipodidae are not monophyletic. In all different analyses *Oniscus* and *Philoscia* are closest relatives. In an analysis of the entire 18S gene, the Porcellionidae appear as sistergroup of the remaining Crinocheta, which is not compatible with hypotheses derived from morphological data.

9. Current view on Oniscidea phylogeny based on morphology

Ligiidae

The Ligiidae, including the genera *Ligia* and *Ligidium*, are characterized mainly by plesiomorphies. In contrast to all other Oniscidea, the tergite of the maxilliped segment is still delimited from the head by a suture.

Some characters mainly of the pleopods and their muscles may be interpreted as synapomorphies of *Ligia* and *Ligidium*:

- (C44) The insertion area of pleopod 1 endopodite very large, the articulation membrane is developed only dorsally [insertion area narrow, articulation membrane present at dorsal and ventral side] (ERHARD 1997: 34).
- (C45) In the medial region of the pleopod 2 protopodite there is a large, multi-stranded muscle [this muscle absent] (ERHARD 1997: 36).
- (C46R) Pleon muscle M47 is absent [present] (ERHARD 1997: 33, char. 25R).
- (C47R) The distal article of the first antenna (i.e., the only flagellar article, see (C16)) is very small [article not reduced in size] (ERHARD 1995: 106).

If these characters (C44–47) are accepted as autapomorphies of a monophyletic taxon Ligiidae, then

(C48–52) must be interpreted as parallelisms (ERHARD 1997).

Ligidium + Holoverdicata or *Ligidium* + Orthogonopoda

These two groupings are incompatible with the assumption of monophyletic Ligiidae. A relationship of *Ligidium* and the Holoverdicata (= Oniscidea excl. Ligiidae) is indicated by the following similarities.

- (C48R) The presence of only two pairs of well developed midgut glands [three pairs] (ERHARD 1997: 63).
- (C49R) The absence of sclerotized sternal processi [present] (ERHARD 1997: 63).
- (C50) Sternal calcium deposits with a proximal spherular layer, in addition to a distal spherular layer [only one layer, corresponding to the distal spherular layer] (ZIEGLER 2003: 306).

Even arguments for a sistergroup relationship of *Ligidium* with the Orthogonopoda (= Oniscidea excl. Ligiidae and Tylidae) have been proposed:

- (C51) Uropod endopodite weaker than exopodite [equally developed] (ERHARD 1997: 63).
- (C52) Parts of the water conducting system on the dorsal side of pleopod 1 epipodite [on the ventral side of the pleopod 1 epipodite] (ERHARD 1997: 63).

The respective plesiomorphic conditions are found in *Ligia* for characters (C48, 49, 50, 51), and in both *Ligia* and Tylidae for (C52). However, these five characters are either reductive or have low complexity and therefore cannot be regarded as strong evidence. Analysis of sequence data from the 18S rRNA gene led to cladograms with *Ligia* as sistergroup of all remaining Oniscidea and *Ligidium* as sistergroup of the Crinocheta + Synocheta clade, thus supporting the view that Ligiidae is a paraphyletic group (MATTERN 2003; with Tylidae and Mesoniscidae not included).

Holoverdicata (Oniscidea excl. Ligiidae)

The monophyly of a taxon including the Tylidae, Mesoniscidae, Synocheta and Crinocheta was proposed by ERHARD (1996) and further confirmed by ERHARD (1997). The characters supporting this hypothesis are:

- (C53) Remotor muscles of pleopods 3–5 (M9, 11, 13) insert frontally on the dorsal apophyses of the anterior margin of the pleon tergites [remotor muscles

originate posteriorly in the tergites] (ERHARD 1997: 21).

(C54) Distal article of the male pleopod 2 endopodites with medial grooves [with ventral grooves] (ERHARD 1996: 22, 1997: 47).

(C55R) Remotor muscles of pleopods 1–2 (M2 and M6) consist of max. 2 strands [3 strands in *Ligia*] (ERHARD 1997: 23).

(C56) The tergite of the maxilliped segment is completely fused with the cephalon [the tergite of the maxilliped segment is delimited from the cephalon by a suture] (ERHARD 1997: 56).

(C57) Sternal calcium carbonate deposits with a proximal homogeneous layer, in addition to two spherular layers [sternal calcium deposits composed of a proximal spherular layer and a distal spherular layer, or of a proximal spherular layer only] (ZIEGLER 2003: 306).

The (C54) grooves are absent in *Crinocheta*, which can thus not be directly assessed for this character.

Ligiamorpha (Oniscidea excl. Tylidae)

This goes back to VANDEL's idea of a diphyletic origin of the terrestrial isopods, with the Tylidae more closely related to the Valvifera. This hypothesis reappeared in the cladogram of TABACARU & DANIELOPOL (1996) but was supported by only 1 character:

(C58) Coxal plates fused to the tergites [clearly distinct from tergites] (TABACARU & DANIELOPOL 1996: 74).

In Tylidae these plates are moveably separate from the tergites. In *Ligia*, they are demarcated by a suture but immovable. In comparison of the two hypotheses Ligiamorpha and Holoverticata, it is obvious that the Holoverticata is supported by much stronger evidence.

Tylidae

The Tylidae are a well defined monophyletic group with numerous apomorphic characters (ERHARD 1997). These characters are:

(C59) Conglobation ability [no conglobation ability] (ERHARD 1995: 97) (Fig. 11).

(C60R) Male genital papillae absent [present] (ERHARD 1995: 97).

(C61) Pleon epimera forming medially extended plates "phylacomeres" that partly cover the pleopods [no phylacomeres] (ERHARD 1995: 97).

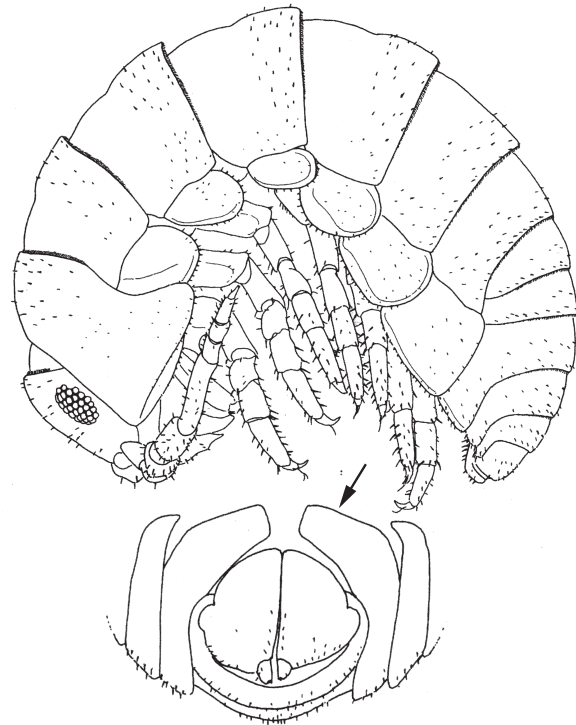


Fig. 11. *Tylos ponticus*, habitus lateral, pleon distal part in ventral view: (C59) conglobation; (C61) pleon epimera forming phylacomeres.

(C62) Pleon segments almost immobile, between the tergites with very narrow and unusually thick membrane [pleon segments mobile, with more extended membranes] (ERHARD 1995: 97).

(C63R) Pleopod 1 exopodites and endopodites as well as the medial parts of the pleopod 1 protopodites and of pleon sternite 1 absent [all these parts present] (ERHARD 1995: 98, 1996: 32).

(C64R) Medial region of protopodite of pleopod 2 and medial region of pleon sternite 2 completely absent [these parts of pleopod 2 present] (ERHARD 1995: 99).

(C65) Ventral side of pleopod 2–5 exopodites differentiated as lungs [not differentiated as lungs] (ERHARD 1995: 99, 1996: 32).

(C66) Uropod protopodite plate-like, ventral of the pleotelson, with two articulation points close to each other on the lateral side [uropod protopodite styliform, inserting terminally on pleotelson, with dorsal and ventral articulation] (ERHARD 1995: 100).

(C67) Dorsal apophysis of pleotelson shifted ventrally [dorsal apophysis of pleotelson situated dorsolaterally on the anterior margin] (ERHARD 1995: 100).

(C68) First antenna reduced to 1 article [first antenna 3-jointed] (ERHARD 1995: 106).

(C69) Pleon muscles M19, 21, 23, 25 double-stranded, inserted caudally on the tergites and directed slightly frontally to the anterior margin of the following

segment, M26a absent [M19, 21, 23, 25, single-stranded, 26a inserted frontally on the tergites and directed caudally to the anterior margin of the following segment] (ERHARD 1997: 24).

(C70) Female brood pouch with internal sac [without internal sac] (TABACARU & DANIELOPOL 1996: 74).

(C71?) Septum separating the pleopods from the anal region [no such septum] (TABACARU & DANIELOPOL 1996: 74).

TABACARU & DANIELOPOL (1996) also regarded the characters (C60, 63, 65, 66, 68, 70, 71) as autapomorphies of Tylidae. However, for character (C71), they neither give an illustration nor a reference to another work in which this is described; it remains uncertain what exactly is meant.

Currently, the Tylidae include the genera *Helleria* (1 species) and *Tylos* (20 species) (SCHMALFUSS 2003). A phylogenetic analysis is not available. *Tylos* species are littoral and have a worldwide distribution in appropriate climate, while *Helleria* is endemic to Corsica and adjacent mainland areas and lives in *Quercus ilex* forests from the coast up to 1200 m altitude (VANDEL 1960).

Orthogonopoda

(Oniscidea excl. Ligiidae and Tylidae)

The monophyly of this group including *Mesoniscus*, *Synocheta* and *Crinocheta* is well founded (ERHARD 1997).

(C72) Male genital papillae partially fused [fully separated] (ERHARD 1996: 5, 1997: 32).

(C73) Muscle M1 in males acts as pleopod 2 locomotor, its posterior insertion is on the posterior margin of the insertion of pleopod 2 [M1 is a flexor of the pleon trunk, its posterior insertion is on a tendon at the sternal segment border between pereionomer 7 and pleomer 1] (ERHARD 1997: 20).

(C74) The two articles of the male pleopod 2 endopodite in line, insertion on the protopodite in extreme medial position [the two articles of pleopod 2 endopodite forming a right angle, insertion on the protopodite distant from its medial margin] (ERHARD 1995: 99, 1996: 21) (Fig. 12).

(C75) Ventral articulation point between male pleopod 2 protopodite and endopodite in medial position [ventral articulation point together with dorsal articulation point on a dorsoventral axis distant from the medial margin of the protopodite] (ERHARD 1995: 99, 1996: 21) (Fig. 12).

(C76) Uropod endopodite smaller than exopodite [uropod endopodite and exopodite of same size] (ERHARD 1997: 55).

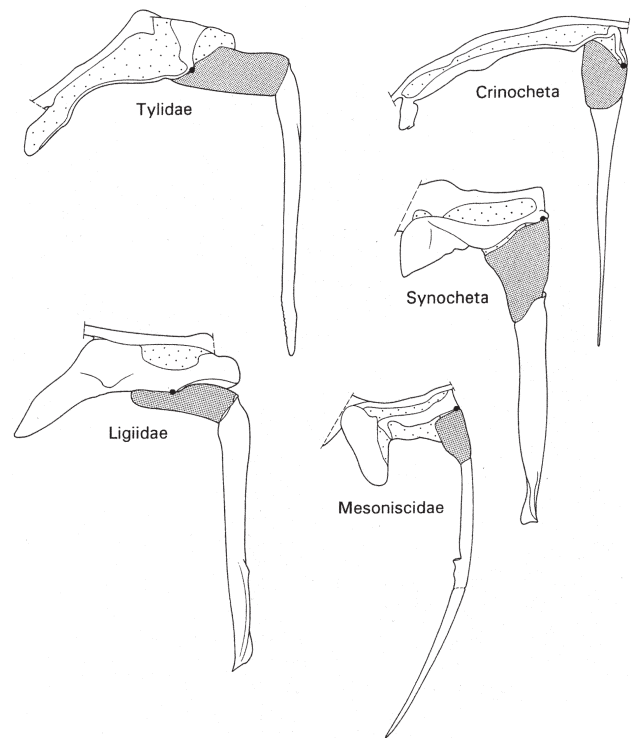


Fig. 12. Male pleopod 2 (exopodites omitted) of representatives of 5 main taxa of Oniscidea: *Ligia oceanica* (Ligiidae), *Tylos* sp. (Tylidae), *Mesoniscus alpicola* (Mesoniscidae), *Hyloniscus riparius* (Synocheta), *Actaecia bipleuria* (Crinocheta). On the left the plesiomorphic state, on the right the apomorphic state (C74, 75) of the Orthogonopoda. From ERHARD (1996: 21).

(C77) Pleon muscles M18, 20, 22, 24, 26 split into two strands each [these muscles with one strand each] (ERHARD 1997: 24).

(C78) Female pleopod 2 endopodite inserted upon the medial end of the protopodite, perpendicular to it [female pleopod 2 endopodite distant from the medial end of the protopodite, parallel to it] (ERHARD 1997: 48).

The (C76) size and insertion of the uropod endopodite relative to the exopodite was proposed to be a synapomorphy of *Oniscus* and *Actaecia* by ERHARD (1995); it is not an autapomorphy of the *Crinocheta*, but of a larger taxon, which could not be detected by ERHARD (1995) due to his restricted sample. ERHARD (1997, 1998) retains only the relative size in (C76), not the subapical insertion of the endopodite as mentioned in ERHARD (1995). (C52) may be an autapomorphy of Orthogonopoda only if it evolved convergently in *Ligidium* and Orthogonopoda. The interpretation of the homology of the muscles enumerated in (C77) was different in ERHARD (1995), and was changed due to additional data (ERHARD 1996).

Euoniscoida (Synocheta + Crinocheta)

A close relationship between the Synocheta and Crinocheta had been assumed already before the introduction of phylogenetic systematics. Later, in phylogenetic analyses, these two taxa appeared as sister-groups, united by the apomorphic (C79) fusion of the genital papillae. ERHARD (1997) found two additional synapomorphies in the musculature of the pleon (C80, 81).

(C79) Complete fusion of the male genital papillae [partial fusion of the genital papillae] (ERHARD 1996: 5, 1997: 32).

(C80) Particular arrangement of the pleon muscles M19, 21, 23 inserting posteriorly on the tergites and directed frontally; muscles 25 and 26a absent [M19, 21, 23, 25, 26a inserted anteriorly on the tergites and directed caudally] (ERHARD 1997: 24, char. 78).

(C81) Pleon muscles M76, 86 and 94, which move the pleopod exopodites 3–5, with 2 strands each [only 1 strand] (ERHARD 1997: 53, char. 89).

The presence of a muscle M47, which moves the pleopod 1 endopodite, had been regarded as a synapomorphy of Synocheta and Crinocheta (ERHARD 1995: char. 25), but later this muscle was found also in *Saduria entomon* (Valvifera) and *Anilocra frontalis* (Cymothoidea), which gives the implication that for Oniscidea it is a plesiomorphy, and that it has been lost in Ligiidae and Tylidae, in the latter together with the entire endopodite 1 (ERHARD 1996, 1997). ERHARD (1997, char. 25R) regarded the (C46) loss of M47 as a probable synapomorphy of *Ligia* and *Ligidium*. If the apically not fused genital papilla of *Namiboniscus* (Crinocheta-Olibrinidae) represents a plesiomorphic condition, then (C79) cannot be retained as an autapomorphy of Euoniscidea.

The (C80) position of the muscles M19, 21, 23 is similar to the position of their homologues in Tylidae (C69); ERHARD (1997: 24) notes that these characters have a low complexity and high probability of convergency; in his final cladogram the position of these muscles is convergent and apomorphic for Tylidae and Crinocheta-Synocheta.

Synocheta + *Mesoniscus*

In contrast to the preceding hypothesis, TABACARU & DANIELOPOL (1996) advocate a sistergroup relationship between *Mesoniscus* and Synocheta, supported by 3 apomorphies:

(C82) Simple spermatophore [double spermatophore



Fig. 13. Pereiopod dactyli of *Ligia baudiniana*, Styloniscidae, *Olibrinus truncatus* (Crinocheta, Olibrinidae), *Didima humilis* (Crinocheta, Oniscoidea, "Philosciidae").

in Ligiidae, Tylidae and Crinocheta] (TABACARU & DANIELOPOL 1996: 74).

(C83R) Pereiopods with simple claw [pereiopods with paired claws] (TABACARU & DANIELOPOL 1996: 74) (Fig. 13).

(C84R) "Compound" eyes with 3 or 1 ommatidium, or entirely absent [with numerous ommatidia] (TABACARU & DANIELOPOL 1996: 74).

ERHARD (1997) argued that the spermatophore actually is formed in a different way, the reduction of eyes is an unspecific reductive trait, and that only the third character, the (C83) single claw in the pereiopods, is a potentially valid argument. The description as "paired" claws is misleading, because Oniscidea never have paired claws; they have either a single claw, or they have an additional claw-like structure ventrally of the claw (here called "inner claw" as in various previous publications). However, given the plesiomorphic situation with the inner claw being present in Ligiidae, Tylidae and Crinocheta and outgroup taxa (Asellota, Valvifera, Sphaeromatidea), the lack of the inner claw is also a reductive trait that is less significant than the characters supporting a Synocheta + Crinocheta clade. The inner claw is also absent in some taxa of the Crin-

ocheta, as *Olibrinus* and *Quelpartoniscus*. This may be interpreted as a convergency, but differences in the structure of the inner claw of Ligiidae and Tylidae on one side, and most Crinocheta on the other side, raise the question, whether the inner claw is homologous between these two groups. It is also possible that the inner claw as present in Ligiidae and Tylidae was lost in the stemline of the Orthogonopoda and that the inner claw present in most Crinocheta is a new structure (SCHMIDT 2002).

Mesoniscus

There is no doubt about the monophyly of the Mesoniscidae (ERHARD 1997), which includes only two species of the genus *Mesoniscus* (Fig. 14). These are endemics of the Alps and Carpathian Mts. and represent rare cases of Oniscidea restricted to high altitudes. Autpomorphies are:

- (C85R) Genital papillae distinctly reduced in length [not reduced in length] (ERHARD 1996: 5).
- (C86) Anterior bridge of pleon sternite 1 fused to ventral wall of pleopod 1 protopodite; muscle M48 absent [pleon sternite 1 and pleopod 1 protopodite not fused, M48 present, connecting these sclerites] (ERHARD 1996: 18).
- (C87) Distal article of male pleopod 2 with incision and dorsolateral lobe [both incision and lobe absent] (ERHARD 1996: 23).
- (C88) Pleopod 3–5 endopodites cleft into 2–3 lobes, one of them directed towards the protopodite in pleopods 4 and 5 [pleopod 3–5 endopodites not cleft into lobes] (ERHARD 1996: 26).
- (C89) Pleopods 3–5: depressor muscles of protopodites (M71+72, 81+82, 89+90) consisting of numerous separate strands [depressor muscles of protopodites undivided] (ERHARD 1996: 26).
- (C90) Muscles M73, 83 and 91 inserting on the dorsal side of pleopod 3–5 protopodites [inserting on ventral or medial side] (ERHARD 1996: 26).
- (C91R) Compound eyes absent [present].
- (C92) Distal article of the first antenna reduced to a small sclerite [article not reduced] (ERHARD 1995: 106).

The reduction of the distal article of the first antenna is different in *Mesoniscus* (C92) and in Ligiidae (C47), therefore it is regarded as non-homologous (ERHARD 1997); the (C96) absence of the inner claw on the pereopods, taken as autapomorphy of *Mesoniscus* (ERHARD 1998: 307) and of Synocheta (ERHARD 1998: 308), in which it evolved convergently (ERHARD 1997), is interpreted differently here (see under *Mesoniscus* + Synocheta).

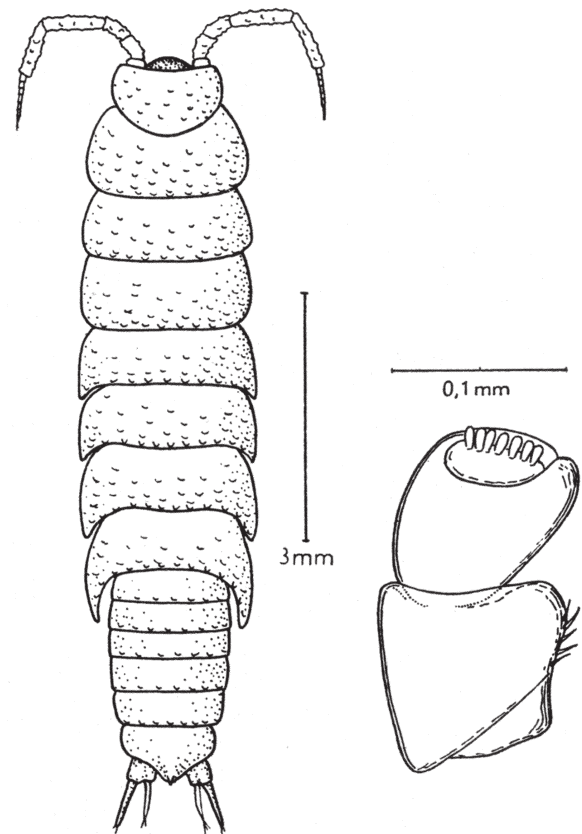


Fig. 14. *Mesoniscus alpicola*, habitus, first antenna (C92) (from GRUNER 1966).

Synocheta

The Synocheta is constituted by several apomorphies:

- (C93) The male genital ducts are distally fused [entirely separated] (SCHMALFUSS 1989: 11; WÄGELE 1989: 118).
- (C94) Eyes with at most 3 ommatidia [numerous ommatidia].
- (C95) Remotor muscles of pleopod protopodites M9, 11, 13 composed of 2 strands each [of 3 strands] (ERHARD 1997: 23).

The (C96) lack of the inner claw of the pereopods, also referred to by ERHARD (1997), is here not regarded as an autapomorphy of the Synocheta (see above).

The Synocheta comprise about 16 % of the Oniscidea species and currently include the families Trichoniscidae (Fig. 15, *Hyloniscus*), Styloniscidae, Titanidiidae and Schoebliidae (SCHMALFUSS 2005). They are mostly small, have simple respiratory fields and are confined to habitats with high humidity. A few species became secondarily aquatic and live in cave waters.

Buddelundiella, formerly classified in family of its own together with *Buchnerillo*, is now included in the Haplophthalminae (Trichoniscidae). *Buchnerillo* seems to belong actually in the Crinocheta (SCHMAL-

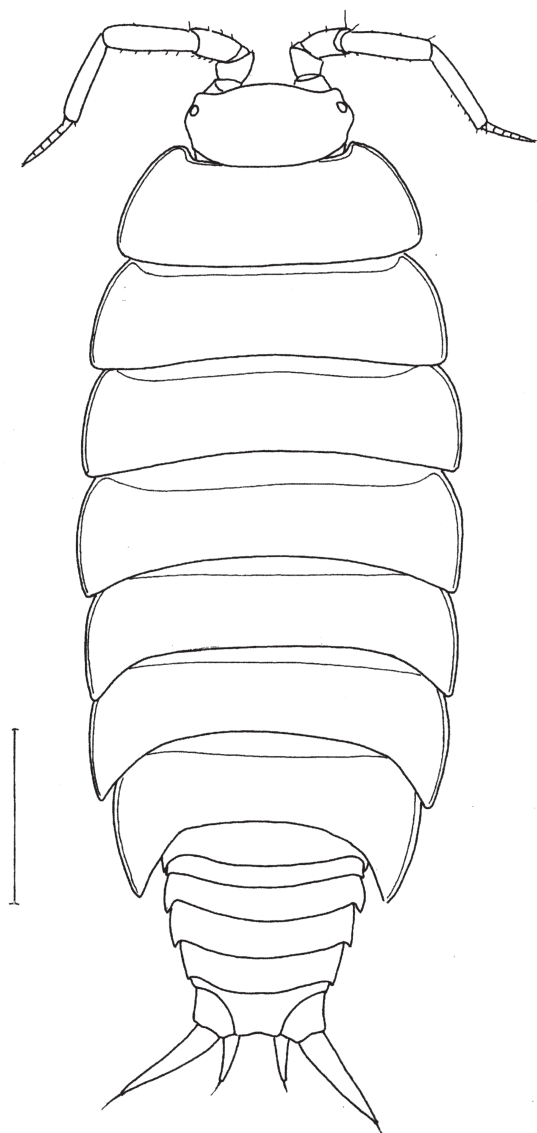


Fig. 15. *Hyloniscus riparius* (Synocheta, "Trichoniscidae", habitus.

FUSS 2005). Among the four above-mentioned families, the Trichoniscidae are a paraphyletic basal group including all species not having the apomorphies of the other families. A phylogenetic analysis of the relationships within the Synocheta is still lacking.

There are several species of Synocheta which have an aquatic mode of life. In contrast to the assumptions of some earlier authors (VANDEL 1964, 1965), this is now regarded as a secondary condition (e.g. SCHMALFUSS 2005). Since all major clades of Oniscidea and almost all species have a water-conducting system consisting of scale-rows, the latest common ancestor (groundpattern) can not have been primarily aquatic, but should have been at least amphibious (see also TABACARU 1999).

The classification of the Synocheta is mainly based on characters of the male pleopods. SCHMALFUSS (2005) distinguished two "different phyletic lines":

1. The male pleopod 1 endopodite is elongated relative to that of the female, and simple without any "individualized setae" or other appendages. The male pleopod 1 exopodite shows specializations thought to be related to the copulation behaviour. This group contains the North American genera *Amerigoniscus*, *Brackenridgia* and *Typhlotricholigioides* and the Palearctic genera *Finaloniscus*, *Escualdoniscus*, *Trichonethes*, *Caucasonethes* and *Psachonethes*.

2. ("Trichoniscidae s.str."): The male pleopod 1 endopodite is elongated and bears an individualized long seta, which in some groups evolved into an apparent second article of this appendage. The male pleopod 1 exopodite is not or only slightly modified (*Hyloniscus*). This group includes the remaining Holarctic genera as well as Haplophthalminae, *Buddelundiella*, "Turanoniscidae", Styloniscidae, Titanidae and Schoebliidae.

Utopioniscus and, according to SCHMALFUSS (2005), *Cantabroniscus* do not belong to one of these groups; both may be the sistertaxon of the remaining Synocheta or of one of the two above mentioned groups. SCHMALFUSS (2005: 18) proposes the relationships *Cantabroniscus* + (lineage 1. + (*Utopioniscus* + lineage 2.)).

The above groups 1. and 2. have been recognised by VANDEL (1953), who, however, did not include the Haplophthalminae, Styloniscidae and the other above-mentioned taxa. in the second group and did not exclude *Cantabroniscus* from the first group (the numbers of the groups seem to be confused by error in SCHMALFUSS 2005: 19). This is mainly due to the fact that VANDEL did not follow strictly phylogenetic reasoning, but accepted paraphyletic groups as taxa in the classification.

Crinocheta

The Crinocheta include ca. 80 % of the described species of the Oniscidea. They form a well supported monophylum. Apomorphies are found in the musculature of the pleon, the conformation of the male copulatory apparatus, marsupium, mouthparts and stomach. A hypothesis on the groundpattern of the Crinocheta is given in SCHMIDT (2002: 313). The stem species of Crinocheta most probably represented the "runner-type" as described by SCHMALFUSS (1984), with smooth tergal surface, slightly enlarged coxal plates, weakly developed pleon-epimera, and slender pereopods and second antennae. Numerous characters provide evidence for a monophyletic origin of the Crinocheta.

(C97) Pleon ventrum 1 with moveable, median apophysis that is tensed up by muscle M4; the ventral longitudinal muscles run over this apophysis

- [pleon ventrum 1 without moveable apophysis] (ERHARD 1997: 16, char. 5).
- (C98R) Medial strand of pleon muscle M3 absent [medial strand present] (ERHARD 1997: 20).
- (C99) Pleon muscles M2 and M6 insert on the dorsal apophyses on the anterior margins of the pleon tergites [M2 and M6 insert caudally or on the middle of the pleon tergites 1 and 2] (ERHARD 1995, 1997: 23).
- (C100) Male pleopod 1 endopodites lanceolate, with dorsomedial spermatic grooves (ERHARD 1995: 98, 1997: 29), with a row of minute setae along the grooves (SCHMIDT 2002: 324, 2001: 129) [endopodite leaf-like, without such grooves, and without row of minute setae].
- (C101R) Pleopod 1 and 2 epipodites vestigial, without water conducting structures [pleopod 1 and 2 epipodites well developed, with structures belonging to the water conducting system] (ERHARD 1997: 29).
- (C102) Linear arrangement of male pleopod 2 protopodite and endopodite, insertion of the endopodite medial; the needle-like male pleopod 2 endopodites are moved in the spermatic grooves of the pleopod 1 endopodites during copulation [male pleopod 2 endopodite and exopodite forming a right angle; the insertion distal to the medial edge of the protopodite; no complex coadaptation of endopodites 1 and 2] (ERHARD 1995: 99, 1997).
- (C103) Medial lamellae of male pleopod 1 endopodite enclose the distal part of the genital papilla [medial lamellae of pleopod 1 endopodites do not enclose distal part of genital papilla] (ERHARD 1995: 100, 1997, char. 49).
- (C104) Genital papilla with a strongly sclerotized ventral shield [without ventral shield] (ERHARD 1997: 32).
- (C105R) Female pleopod 1 endopodites absent [present] (ERHARD 1997).
- (C106R) Pleopod 1 muscle M55 absent [present] (ERHARD 1997).
- (C107) Muscles M74, 84, 92, which move the pleopod endopodites, are present [these muscles absent] (ERHARD 1997: 53).
- (C108) Brooding females with “cotyledons” in the marsupium [cotyledons absent] (WÄGELE 1989: 118; ERHARD 1997: 59).
- (C109) Pars molaris of mandibles replaced by a tuft of hairy setae [pars molaris present] (WÄGELE 1989: 118; ERHARD 1997: 59) (Fig. 7).
- (C110R) Medial endite of second maxilla with 2 penicils [with 3 penicils] (WÄGELE 1989: 118).
- (C111) Male pleopod 1 muscle M49, which moves the endopodite, present [absent] (ERHARD 1995: 98, 1997: 36; SCHMIDT 2002).
- (C112) Stomach: lateralalia are very elongated and bear a curved and chitineous ridge with strong spines

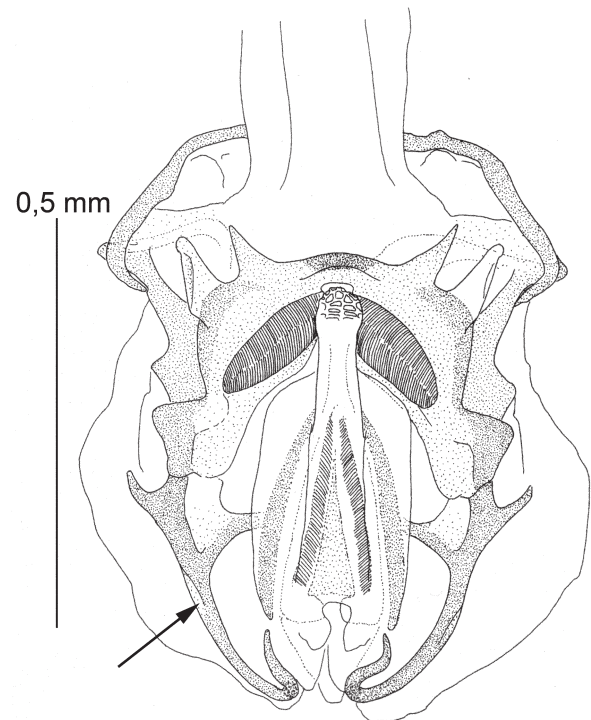


Fig. 16. *Armadillidium nasatum* (Crinocheta, Oniscoidea, Armadillidiidae), stomach in ventral view. Arrow indicates chitinized frame (C116).

- on the dorsal side [less elongated, with tubercles on the ventral face] (TABACARU & GIURGINCA 2003: 80).
- (C113R) Stomach: superomedianum absent [present] (TABACARU & GIURGINCA 2003: 80).
- (C114) Stomach: medial apodema and antero-ventral apodema long and strongly developed [short and weakly developed] (TABACARU & GIURGINCA 2003: 80) (Fig. 16).
- (C115) Stomach: triturating apparatus made up of a dentate plate situated caudo-ventrally on the lateralalia, and a dentate plate lateral and caudal to the clathri setarum anteriores [no triturating apparatus] (TABACARU & GIURGINCA 2003: 80).
- (C116) Stomach: inferolateralalia limited by a strongly chitinized frame and divided into two areas by an oblique bar [this frame and oblique bar absent] (TABACARU & GIURGINCA 2003: 80) (Fig. 16).
- (C117) Stomach: dorsal lamella short, trapezoidal, with strongly chitinized edge [dorsal lamella of other shape, with not strongly chitinized distal edge] (TABACARU & GIURGINCA 2003: 81).

The presence of (C97) moveable apophyses on pleon ventrum 1 was listed as a putative synapomorphy of Synocheta and Crinocheta (ERHARD 1995), as this condition also occurs in the synochetan *Hyloniscus riparius*. Later, however, a detailed investigation revealed that the plesiomorphic condition is found in

the synochetans *Titanethes albus* and *Cantabroniscus primitivus*, and this character was then regarded as an autapomorphy of the Crinocheta only (ERHARD 1997: char. 5).

The (C103) distal part of the genital papilla is enclosed by lamellae of the pleopod 1 endopodites in the groundpattern of the Crinocheta. This is still present in the Olibrinidae and Detonidae, while in the Scyphacidae s.str. + Oniscoidea this condition is further evolved to a permanent interlocking between the ventrolateral lamellae of pleopod 1 endopodites and grooves of the genital papilla (SCHMIDT 2002).

The presence of “cotyledons” seems to be correlated with the closure of the marsupium and its separation from the water-conducting system. The plesiomorphic condition, in which the marsupium is open anteriorly and posteriorly, is found in Ligiidae, Tylidae, and Trichoniscidae, while the closed marsupium was found in several representatives of the Crinocheta (Oniscidae, Porcellionidae, Armadillidiidae) (HOESE 1984) but in no non-crinochetan Oniscoidea. *Mesoniscus* has not been studied. Within Crinocheta, the presence of cotyledons is not yet proven for Olibrinidae due to the lack of sufficient material, and in *Platycytoniscus* (“Philosciidae”) they are secondarily absent (SCHMIDT 2002: 310). In the other taxa of Crinocheta studied by SCHMIDT (2002, 2003), cotyledons are present.

The stomach of the Crinocheta has a structure that is very different from the remaining Oniscoidea and presents a number of putative apomorphies. TABACARU & GIURGINCA (2003) studied the stomach of 13 species of Crinocheta; the most basal branches are not considered, but they refer to a published description of the stomach of *Deto* (BARNARD 1925). In consequence, the above mentioned characters may be apomorphies of the Crinocheta or of subordinate taxa of the Crinocheta. In (C116) and (C117) “strongly chitinized” may refer to a particular thick cuticle or to a sclerotization, or both.

Phylogenetic relationships within the Crinocheta

Within the Crinocheta, ERHARD (1995) stated that the Scyphacidae were a paraphyletic group including species close to the groundpattern of the Crinocheta. Further, he regarded a sistergroup relationship between the Actaeciidae and the remaining Crinocheta (= Oniscoidea sensu SCHMALFUSS 1989, Oniscoidea (SF) in the following) as well-founded by 4 apomorphies. The absence of lungs, however, which ERHARD observed in *Actaecia bipleuria*, is not important in this context, because at the base of the Oniscoidea very probably lungs were absent, and in *Actaecia euchroa*, the presence of lungs, although not visible in whole mounts

of the pleopod exopodites, has been demonstrated by SEM and serial sections (SCHMIDT & WÄGELE 2001).

The phylogenetic relationships among the families of the Crinocheta have been examined in more detail by SCHMIDT (2002, 2003). According to the analysis of morphological characters, the Scyphacidae are paraphyletic, as assumed by ERHARD (1995), and are split into the monophyletic taxa Detonidae, Scyphacidae s.str. and Alloniscidae; the Olibrinidae are found even further basal than the aforementioned taxa. Further “families” found to be paraphyletic are the Philosciidae, Dubioniscidae, Platyarthridae, Trachelipodidae, and Porcellionidae. In the cladogram of Crinocheta (SCHMIDT 2002: fig. 17), the Olibrinidae branch off first, then follow, one after the other, the Detonidae, Scyphacidae s.str., and – as the most basal branch of Oniscoidea (SF) – the Alloniscidae. The rest of the tree represents the great bulk of Oniscoidea (SF); at its base there is a trifurcation with (1) a taxon including Philosciidae, Halophilosciidae and Scleropactidae, (2) the Stenoniscidae, and (3) a taxon including all the rest. Within the latter, there is low resolution; yet, at least a sistergroup relationship between the Armadillidae and Eubelidae can be assumed, and a close relationship between Bathytropidae and Tendosphaeridae seems possible. The Trachelipodidae were divided into the monophyletic Agnaridae and the probably still paraphyletic “Trachelipodidae” s.str. FERRARA & ARGANO (1989) proposed to include the genera with 5 pairs of *Porcellio*-type lungs as ‘Agnara-group’ in the Porcellionidae, not in the Trachelipodidae. The Porcellionidae seem to be paraphyletic with respect to the Armadillidiidae.

In the papers by SCHMIDT, many clades were not yet named because the data supporting their monophyly were considered not sufficient for doing so. The relationships between the “families”, and the assumptions of monophyly or paraphyly are far from being clarified. For most of the “families” only one or few species were so far examined. Below, relatively well supported monophyla are outlined and the respective apomorphies are given; also some important paraphyla and their current situation are mentioned.

An unnamed “Taxon 0” (SCHMIDT 2002: 324) comprising the Crinocheta excl. Olibrinidae, based on the presence of a row of minute setae along the spermatic groove on the male pleopod 1 endopodite (98), cannot be retained. This row of minute setae is more likely to represent an apomorphy of the Crinocheta, being lost in *Olibrinus* (SCHMIDT 2001: 129) but present in other Olibrinidae (see below).

In their study on the 18S rDNA of 12 species of Oniscoidea and *Asellus* as outgroup, MATTERN & SCHLEGEL (2001) found a group including Oniscidae, Philosciidae, Platyarthridae, Cylisticidae and Armadillidiidae; this is part of a more inclusive group together with

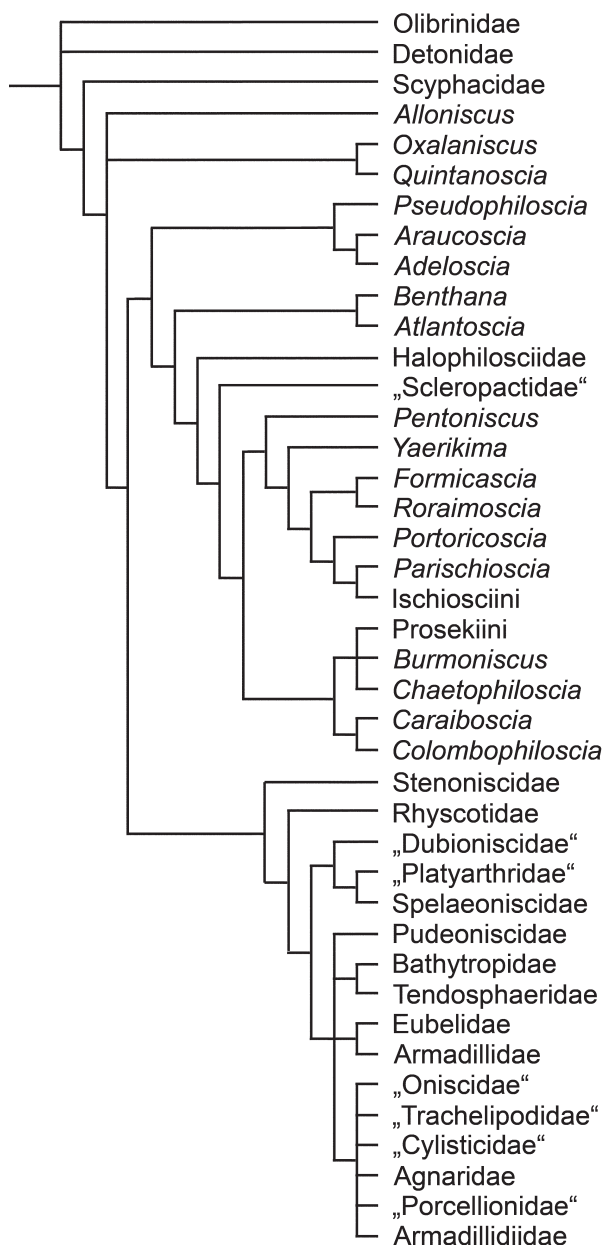


Fig. 17. Phylogenetic relations within the Crinocheta as based on morphological characters. This is a tentative combination of the cladograms proposed by LEISTIKOW (2001) and SCHMIDT (2002) taking into consideration also some new information (which lowers the resolution of the cladogram).

Porcellionidae and Trachelipodidae. The Armadillidae is sistergroup of the remaining Crinocheta. This differs from the cladogram constructed on the basis of morphological characters by SCHMIDT (2002) in the position of the Platyarthridae. However, it is very probable that the cladograms will change when more taxa and/or characters are added, for the reasons given above.

It is important to point out here, that in the MATTERN & SCHLEGEL (2001) study "Philosciidae" is represented by *Philoscia*, which is more closely related to *Oniscus* than to the majority of the "Philosciidae" (LEISTIKOW 2001).

LEISTIKOW (2001) investigated the phylogenetic relationships between the Neotropical "Philosciidae" on genus or species level, and included also representatives of some other taxa.

A tentative combination of the phylogeny hypotheses by LEISTIKOW (2001) and SCHMIDT (2002, 2003) is represented in Fig. 17. Some unpublished additional data required the breakdown of several nodes.

In the following, the crinochetan taxa Olibrinidae, Detonidae and Scyphacidae (s.str.) are outside the taxon Oniscoidea (SF), while the latter taxon comprises all other crinochetans (including the Alloniscidae).

Olibrinidae: This group currently includes 4 genera with ca. 10 species. SCHMIDT (2002: 323) gave putative synapomorphies only for species of *Olibrinus* (Fig. 18), because no specimens of *Adoniscus* were available. The discovery of two new species (*Namiboniscus brevicornis*, Namibian coast, and *Paradoniscus aquaticus*, Socotra) required modification of the apomorphy hypotheses (SCHMIDT 2001: 129; TAITI & FERRARA 2004: 230). (Note: SCHMIDT 2001 was written later but printed earlier than SCHMIDT 2002, 2003 due to technical problems delaying the publication of the latter article.) Now the following characters are considered as autapomorphies of the Olibrinidae:

(C118) Mesal endite of first maxilla with an acute apex covered with "hairs", and 2 very small, vestigial penicils [mesal endite with 2 well developed penicils on mediobasal corner and acute angle on laterodistal corner] (SCHMIDT 2002: 323, 2001: 129).

(C119) Lateral endite of first maxilla with 13 teeth and a "slender stalk". The fact that the 13 teeth are simple and not differentiated among each other, is apomorphic; apical margin strongly oblique; lateral margin without fringe of "hairs" [lateral endite with 5 + 6 teeth, some of the mesal group pectinate or apically cleft, those of the lateral group simple, a pair of small subapical setae and one slender stalk; apical margin weakly oblique; lateral margin with fringe of "hairs"] (SCHMIDT 2002: 323, 2001: 129).

(C120) Maxilliped endite proximally somewhat set off from the mesal margin of the maxilliped basis [mesal margin of endite is in line with the mesal margin of the basis] (SCHMIDT 2001: 129).

Three previously proposed characters cannot be retained as autapomorphies of the Olibrinidae, but probably of subtaxa:

(C121?) Uropod sympodite elongate, cylindrical, longer than the endopodite and much bigger than the pleotelson [uropod sympodite short, cylindrical

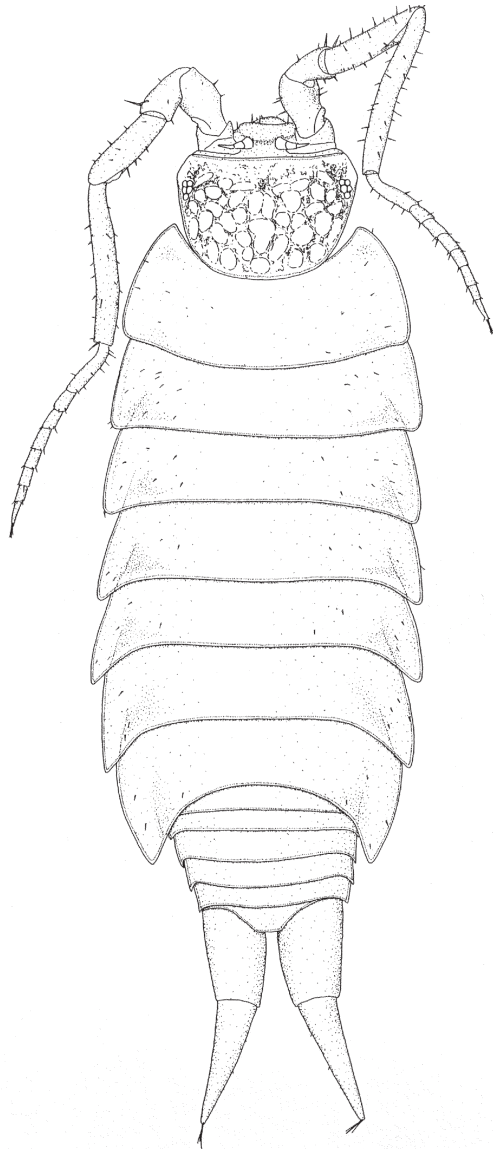


Fig. 18. *Olibrinus truncatus*, habitus (from SCHMIDT 2002).

or slender and smaller than pleotelson] (WÄGELE 1989: 116).

(C122R) Only one transverse line present on the cephalothorax (it either represents the linea frontalis or the linea supraantennalis) [two transverse lines present on the cephalothorax (linea frontalis and linea supraantennalis)] (SCHMIDT 2001: 129).

(C123) Genital papilla with a ventral shield surpassed by a rounded lobe and genital orifices in a sub-apical, lateral position on this lobe [genital papilla with ventral shield surpassed by a long lobe with genital orifices in apical position] (SCHMIDT 2002: 324).

The (C121) size relation of the uropod sympodite to the pleotelson may be interpreted as an autapomorphy of *Olibrinus* rather than Olibrinidae after the discovery of *Namiboniscus* and *Paradoniscus*.

In *Paradoniscus*, the cephalothorax has a linea frontalis and a linea supraantennalis (TAITI & FERRARA 2004: 230).

The (C122) presence of only one transverse line on the cephalothorax may be a synapomorphy of the Olibrinidae excl. *Paradoniscus*.

Character (C123) may be an apomorphy of *Olibrinus* only. *Namiboniscus* shows a genital papilla with a ventral shield surpassed by two separate tips with one terminal orifice each, which also may represent a plesiomorphic condition for Crinocheta. Therefore the character state described for *Olibrinus* is regarded as convergency of the similar situation (C133) in Oniscoidea.

Detonidae (Fig. 19): A part of the former “Scyphacidae”, separated and considered monophyletic by SCHMIDT (2002: 328) on the basis of two putative apomorphies, one of them very weak:

(C124) Cephalothorax with distinct lateral lobes delimited by the linea supraantennalis [lateral lobes absent] (SCHMIDT 2002: 218).

(C125) Tergal surface tuberculate [smooth] (SCHMIDT 2002: 328).

The **Scyphacidae** s.str. include only *Scyphax* and *Actaecia* with ca. 10 species on sandy beaches in Australia and New Zealand. The monophyly of this taxon seems well supported by:

(C126) Seleniform compound eyes of about 80 ommatidia (or more) and the related changes in cephalothorax morphology [oval compound eyes of max. 30 ommatidia] (SCHMIDT 2002: 344).

(C127) The first antenna has the second article longest and the distal article very short [proximal article longest, second article shortest] (SCHMIDT 2002: 328).

The **Oniscoidea** (sensu SCHMALFUSS 1989), include the remaining majority of the Crinocheta. The name was used by earlier authors for the taxon now called Oniscidea. To avoid confusion, in the present text Oniscidea (SF) is used for the taxon discussed here. Several apomorphies have been proposed:

(C128R) Flagellum of second antenna with 3 articles (or less) [flagellum with 4 articles] (SCHMALFUSS 1989).

(C129) ‘Apical organ’ of second antenna with enveloping sheath and 2 lateral free sensilla [apical article with a tuft of free sensilla] (SCHMIDT 2003: 5) (Fig. 20).

(C130) Male pleopod 1 endopodites with muscle M49 divided in lateral and medial portions, endopodite

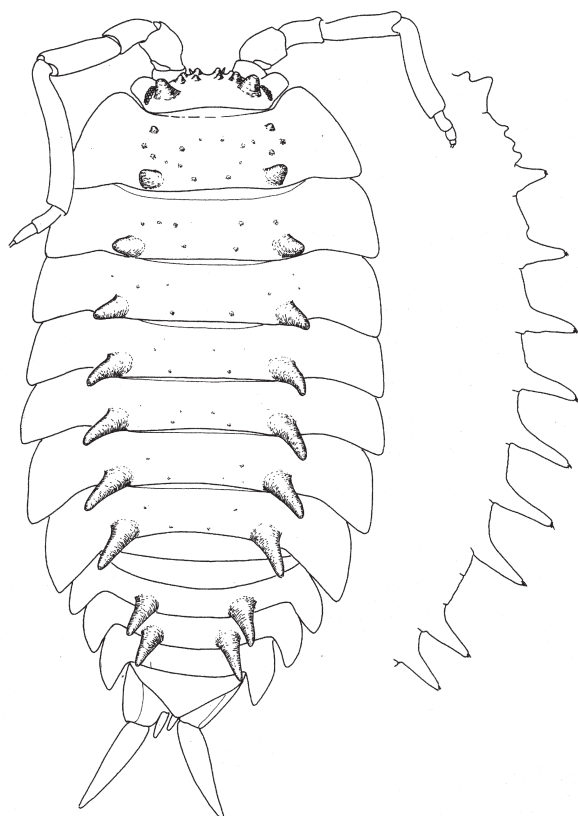


Fig. 19. *Deto echinata*, habitus. On right side the tergal tubercles in profile.

with lateral joint-like structure [only lateral portion of M49 present, endopodite without lateral joint-like structure] (ERHARD 1995).

(C131) Ventromedial edge of male pleopod 2 exopodite with hairy sulcus [without hairy sulcus] (ERHARD 1995).

(C132) Medial edge of male pleopod 5 exopodite with a hairy furrow to fit endopodite 2 [without such furrow] (ERHARD 1995).

(C133?) Male genital orifices in subapical, lateral position on the genital papilla, surpassed by a rounded lobe [orifices in apical position on a long lobe surpassing the ventral shield] (SCHMIDT 2003: 5) (Fig. 12).

(C134R) Maxilliped palp with 3 tufts of sensory setae [with 4 tufts] (SCHMIDT 2003: 5).

(C135) Maxilliped endite broad, rounded, with a small hairy seta ("penicil") [endite narrow, with a large penicil] (SCHMIDT 2003: 5).

(C136) Pereiopod 1 carpus on frontal face with a dense, longitudinal brush of many scales, which is used for grooming the second antennae [brush less dense, composed of few scales only] (SCHMALFUSS 1998).

Character (C132) is disputable. LEISTIKOW (2001: 22) assumes that a straight, hairy medial edge of the

pleopod 5 exopodite, even with a furrow to hold the pleopod 2 endopodite, evolved several times convergently. It is apparently present in all "higher Crinocheta" (i.e. Oniscoidea excl. "Philosciidae", Rhyscotidae and Scleropactidae), and some Philosciidae". The absence of this furrow in many "Philosciidae" thus may be plesiomorphic. A shape of the male genital papilla similar to (C133) is present in Olibrinus. Since this seems to be not part of the groundpattern of Olibrinidae, it is regarded as an independently evolved character (C123) there (see above).

The **Alloniscidae** include only the genus *Alloniscus*. There are few species, all of them littoral. A taxonomic revision is needed to determine the actual number of species. *Alloniscus* is probably the sister-group of all remaining Oniscoidea (SF); at least, it represents an early branch within the Oniscoidea (SF). Putative apomorphies are:

(C137) Dorsal respiratory fields on pleopod exopodites 1–5 [ventral surface respiratory] (SCHMIDT 2003: 13).

(C138) Dactylar seta with enlarged knife-shaped tip [apically not enlarged] (SCHMIDT 2003: 13).

The **Oniscoidea excl. Alloniscidae** may form a monophyletic taxon (unnamed "taxon 2", SCHMIDT 2003: 13), based on the apomorphic situation of the tergal sensilla:

(C139) Tergal sensilla with a sheath of epicuticular scales; one pair (or several pairs?) per pereiontergite differentiated from the others by a more protruding sensory hair [tergal sensilla only loosely associated with a group of epicuticular scales, all tergal sensilla with hairs equally shaped] (SCHMIDT 2003: 14) (see deviating pair of sensilla in Fig. 24).

The deviating pair of sensilla is known as the "noduli laterales", because e.g. in Porcellionidae and Trachelipodidae they are usually located on small depigmented tubercles, which were observed by early researchers of terrestrial isopods. These noduli laterales, especially their position, has been an important character in the traditional classification of the terrestrial Isopoda. There are varying degrees of divergence of noduli laterales and other tergal sensilla; their number (1 to several pairs on each tergite) and their distance to the lateral and posterior margins differs between taxa. It is not yet understood whether the noduli or the other tergal sensilla are more similar to the uniform tergal sensilla in outgroup taxa, i.e. it is not clear what exactly is plesiomorphic and apomorphic.

In many supposedly primitive taxa of the "Philosciidae" the presence of noduli laterales is not docu-

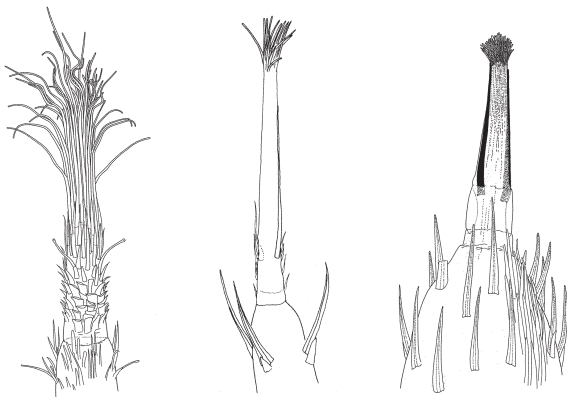


Fig. 20. Second antennae, apical organ (C129); *Detonella papillicornis* (Detonidae), left; *Didima humilis* ("Philosciidae"), middle; *Porcellio alluaudi* (Porcellionidae), right (in part from SCHMIDT 2002).

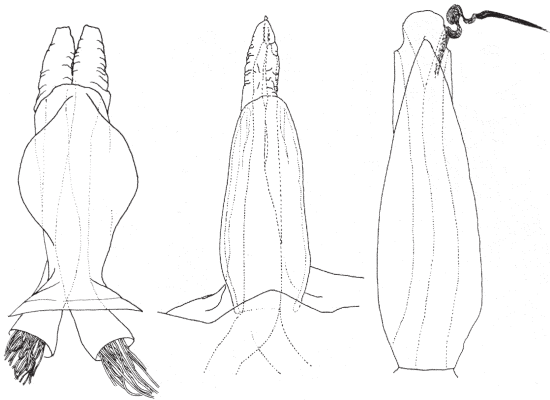


Fig. 21. Genital papillae: *Namiboniscus brevicornis*, left, *Aetaecia euchroa*, middle, *Chaetophiloscia elongata*, right (from SCHMIDT 2001, 2002).

mented or it is unknown, how they differ, if they differ at all, from the remaining tergal sensilla. Accordingly, in addition to Alloniscidae, part of the "Philosciidae" may also have to be excluded from this "taxon 2". More research is needed before a formal taxon definition can be proposed.

The "**Philosciidae**" (ca. 450 species) very probably do not represent a monophylum (see above). In LEISTIKOW's (2001) cladogram the various genera of South American Crinocheta, the "Philosciidae" form a paraphylum, in which Rhyscotidae, Scleropactidae and the "higher Crinocheta" (i.e. Oniscoidea excl. Alloniscidae, "Philosciidae", Rhyscotidae and Scleropactidae) represent subordinate clades. Only few of the clades have been assigned taxon names; a formal splitting into monophyletic taxa that can be named may be done after an analysis including also representatives of "Philosciidae" from other continents. The two taxa defined and named by LEISTIKOW (2001)

are discussed below. Furthermore, LEISTIKOW (2001: 75) found that *Philoscia* is more closely related to *Oniscus* than to most "Philosciidae". Therefore the name "Philosciidae" will have to be used for a much smaller group of species than now and probably will become obsolete at all. Species-level phylogeny hypotheses are available for *Ischioscia* (LEISTIKOW & SCHMIDT 2002) and *Androdeloscia* (SCHMIDT & LEISTIKOW 2005).

The **Ischiosciini** include the Neotropical philosciid genera *Ecuadoroniscus*, *Oreades*, *Tropiscia*, *Ischioscia* and *Mirtana*. Possible synapomorphies are:

- (C140) First antenna with a shield-like protrusion on the distal margin of the proximal article [distal margin of proximal article straight] (LEISTIKOW 2001: 340).
- (C141) Pleotelson with distal semicircular pit on ventral face [pleotelson with distal transverse furrow on ventral face] (LEISTIKOW 2001: 40).

A hypothesis of the phylogenetic relationships between the genera is also presented in LEISTIKOW (2001: 57), and a phylogenetic analysis at species level is available for *Ischioscia* (LEISTIKOW & SCHMIDT 2002).

The **Prosekiini** include 6 "philosciid" genera with 38 species, all of them distributed in the Neotropical region.

- (C142) First antenna with aesthetascs on the medial side not appressed to the article and distant from the apical pair of aesthetascs [aesthetascs on medial side appressed to the article and not clearly distant from the apical pair] (LEISTIKOW 2001: 46) (Fig. 23).
- (C143) First antenna: transverse fold between the two groups of aesthetascs, thus third artical apically concave [third article conical] (LEISTIKOW 2001: 46).
- (C144) Male pleopod 1 with hyaline lamellae near apex [no such lamellae] (LEISTIKOW 2001: 46).

A hypothesis of the phylogenetic relationships between the genera is presented in LEISTIKOW (2001: 57). A phylogenetic analysis at species level is available for *Androdeloscia* (habitus: Fig. 24) (SCHMIDT & LEISTIKOW 2005).

One taxon, the **Halophilosciidae**, had already been separated from other Philosciidae as "subfamily" Halophilosciinae (of the Oniscidae) by KESSELYÁK (1930) due to differences in the male genital system. The ca. 20 species are strictly littoral, and are distributed nearly world-wide with the apparent exception of Australia. Halophilosciids share the following apomorphies:

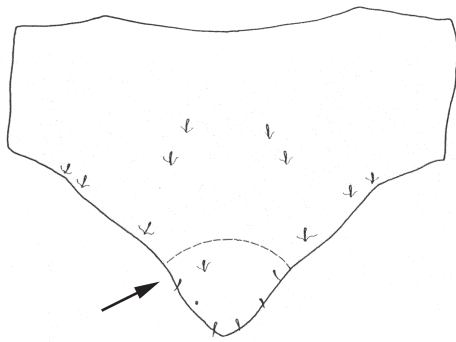


Fig. 22. Pleotelson of *Ischioscia bolivari* (Ischiosciini) (C141).

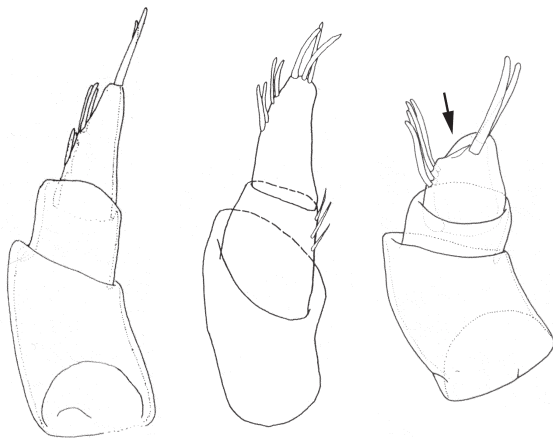


Fig. 23. First antenna of *Didima humilis* ("Philosciidae"), *Ischioscia bolivari* (Ischiosciini) and *Androdeloscia monstruosa* (Prosekiini). In *Ischioscia* (C140) the distal margin of the proximal article is enlarged. *Androdeloscia* has the (C142) aesthetascs on medial side not appressed to distal article, and (C143) a transverse fold between two groups of aesthetascs.

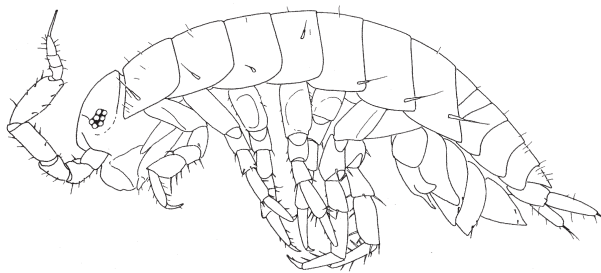


Fig. 24. Prosekiini: *Androdeloscia monstruosa*, male, lateral view.

(C145) Genital papilla with bifurcate tip, which is interconnected with the pleopod 1 endopodites [not bifurcate, the genital orifices in apical or subapical position] (KESSELYÁK 1930: 282).

(C146) Vasa deferentia originate in pereioner 4, are prolonged to pereioner 5 or 6, then abruptly turn anteriorly to reach the middle of pereioner 3, then

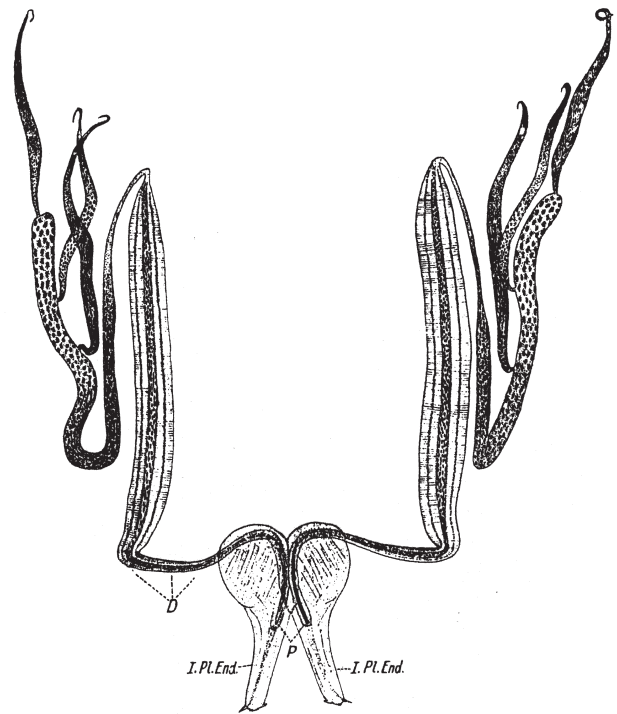


Fig. 25. *Halophiloscia*, male genital apparatus (from KESSELYÁK 1930).

turn back again while tapering extremely, then follows a thickened, straight part leading to the genital papilla [vasa deferentia neither with similar loops nor with strongly thickened part] (KESSELYÁK 1930: 284) (Fig. 25).

(C147) Spermatozoa are arranged in "tortilla-like" clusters coated with mucus, which are not true spermatophores [?] (VANDEL 1962).

(C148) Male pereopod 1 carpus and propodus enlarged and propodus inflated, both bearing prominent brushes composed of cuticular scales [carpus and propodus almost cylindrical, no scale fields] (LEISTIKOW 2001: 35).

(C149) Ungual seta strong, apically spatuliform [seta simple, similar to inner claw] (LEISTIKOW 2001: 35).

(C150) Extreme enlargement of male pleopod 1 and 2 endopodites [Male pleopod 1 and 2 endopodites more slender] (SCHMIDT 2003: 22).

(C151) "Fringed" appearance of the tufts of setae on the maxilliped palp [setae on maxilliped palp in tufts, not in rows] (SCHMIDT 2003: 22).

The bifurcate shape of the male genital papilla (C145) has alternatively been interpreted as the ancestral state, since e.g. the Ligiidae have two genital papillae (see above; VANDEL 1962: 476). The results of a histological investigation suggest that the bifurcate appearance is caused by prolongation of the vasa def-

erentia and thus is a secondary condition (MACCAGNO 1933), which is apomorphic for the Halophilosciidae. The thickened part of the vasa deferentia consists of muscles and does not contain glands (KESSELYAK 1930: 286).

For the **Scleropactidae** SCHMALFUSS (1980) presented the first phylogenetic analysis, which was extended by TAITI et al. (1986). The Asian species of Scleropactidae, included in the Toradjinae, were revised by FERRARA et al. (1995); they could not find any character unique to Toradjinae or Scleropactidae. SCHMIDT (2007) analysed the phylogenetic relationships between the Neotropical species based on morphological characters and produced a taxonomic revision. A clear statement of monophyly could not be made, but *Chileoniscus*, *Sphaerobathytropa* and *Synuropus* were excluded from Scleropactidae. Unfortunately, a plausible new placement of these taxa could not be proposed.

The **Stenoniscidae** is a clearly monophyletic small taxon. The 7 species live in littoral habitats.

- (C152) Elongate body, coxal plates separated from tergites by grooves [at least coxal plates 1 and 5–7 not separated from tergites] (VANDEL 1945) (Fig. 26).
- (C153R) First antenna 2-jointed [first antenna 3-jointed] (VANDEL 1945).
- (C154) Pereion sternites with grooves for basipodites (VERHOEFF 1908) and basipodites with grooves for merus and carpus [sternites and pereiopods without these specializations].
- (C155R) First pleon tergite absent [present] (VANDEL 1945).
- (C156R) First pleopod of female absent [present] (VANDEL 1945).
- (C157) Uropod endopodite conical, exopodite conical and smaller than endopodite [uropod endopodite laterally flattened, exopodite larger than endopodite] (VANDEL 1945).
- (C158) Pleotelson in dorsal view completely covering the uropods [pleotelson short, surpassed by the uropod sympodites] (VANDEL 1945).

The coxal plates are moveably separate from the tergites in the plesiomorphic state, as seen in Tylidae and various marine isopods. If correctly regarded as an apomorphy here, (C152) is a secondary condition, see (C58). The first antenna has the 3rd article more or less reduced also in Ligiidae (C46), and in Tylidae only the proximal article is retained (C68). The situation in Stenoniscidae is regarded as evolved independently.

The **Rhyscotidae**, including ca. 25 species, is an-

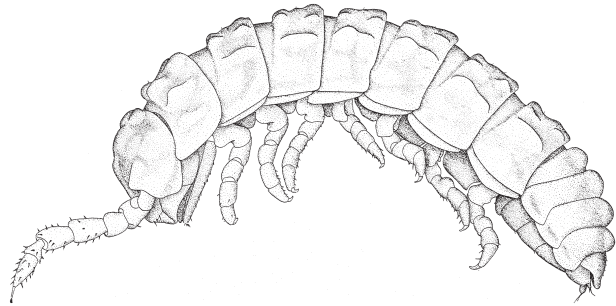


Fig. 26. *Stenoniscus carinatus*, habitus (from SCHMIDT 2002).

other almost certainly monophyletic taxon, constituted by numerous apomorphies:

- (C159) Hermaphroditism [sexes separate].
- (C160) Frons inflated, with muscles coming from the dorsal wall of the oesophagus [frons not inflated] (SCHMIDT 2003: 54).
- (C161) Second maxilla: medial lobe articulated with basal part, lateral lobe reduced in size [both lobes not articulated but confluent with the basal part, lateral lobe usually larger than medial lobe] (SCHMIDT 2003: 53).
- (C162) Maxilliped palp basal article laterally confluent with basis [maxilliped palp delimited from basis] (SCHMIDT 2003: 54).
- (C163) The two distal articles of maxilliped palp bearing a flexible lamina on the frontal margin [no such lamina] (SCHMIDT 2003: 54).
- (C164) Ungual seta vestigial or transformed into a sac-like structure [ungual seta has the normal shape of a seta] (SCHMIDT 2003: 54).
- (C165) Male pleopod 1 endopodite with a slender distal process of at least half the length of the remaining part of the endopodite; the row of small setae (present in most Crinocheta) not extending onto this process [without such process] (SCHMIDT 2003: 54).
- (C166R) Pleopod 3–5 endopodites reduced in size [not reduced in size] (SCHMIDT 2003: 54).
- (C167) Respiratory fields on ventral and dorsal faces of pleopod exopodites [respiratory fields on ventral face of pleopod exopodites] (SCHMIDT 2003: 54) (Fig. 28).
- (C168) Number of eggs and embryos fixed to 2 or 4 [number of eggs more or less variable, usually larger than 4] (SCHMIDT 2003: 54).
- (C169) Marsupial larvae slender, stick-shaped, with long, protruding appendage buds; their size large in relation to the eggs [marsupial larvae retain more or less the ovoid shape, with stout appendage buds; not much larger than eggs] (SCHMIDT 2002: 54) (Fig. 27).

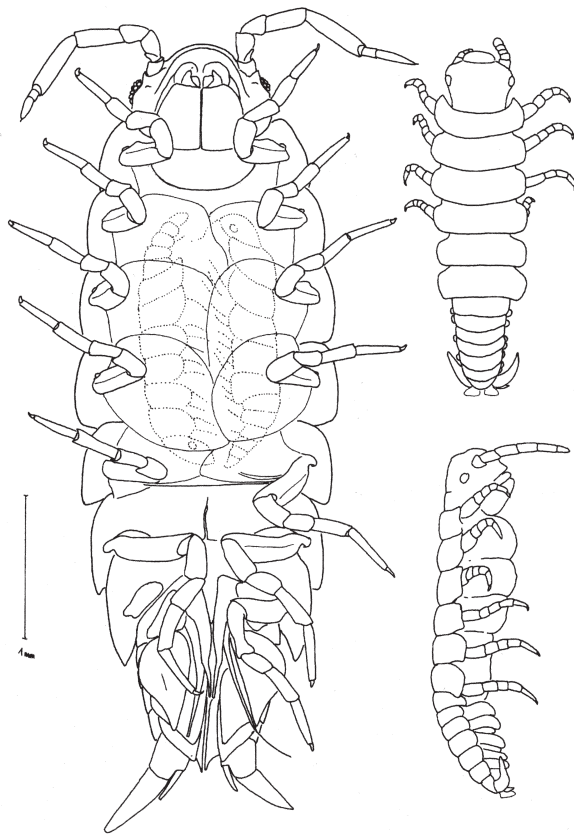


Fig. 27. *Rhyscotus sphaerocephalus*, specimen with marsupium, ventral view; marsupial larva, dorsal and lateral view, same scale (C159, C168, C169).

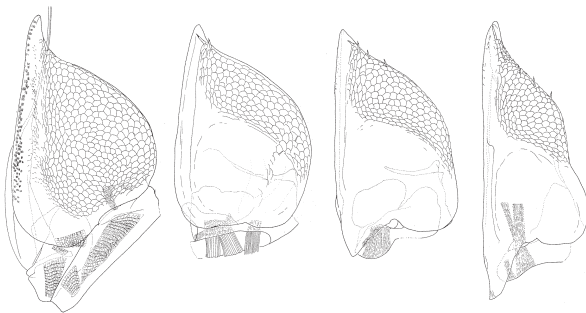


Fig. 28. *Rhyscotoides parallelus*, pleopods 2–5. The portion covered with scales is exposed to the exterior, the proximal field without scales is part of respiratory chambers between the exopodites (C167).

The deviating structure of the mouthparts (C161–163) raises the question whether they are adapted to feed on something different than decaying plant material as usual for almost all Oniscidea. Rhyscotidae were reared in the laboratory, and reported to feed on decaying leaves (JOHNSON 1956); this should be re-examined. Probably the particular development of the marsupial larvae constitutes another apomorphy. This was mentioned in the text by SCHMIDT (2002: 54), but not included in the list of apomorphies therein. The

(C164) ungual seta may be vestigial or transformed in a membraneous sac. The polarity among these two character states present in Rhyscotidae is not known, but both of them are apomorphic in respect to the normal ungual seta of the outgroup taxa.

The **Squamiferae** were redefined to include “Dubioniscidae”, “Platyarthridae”, and Spelaeoniscidae (SCHMIDT 2003: 55).

(C170) Shell shaped tergal scale-setae with narrow base, enlarged distal part and serrate margins [scale-setae with narrow distal part and with non-serrated margins] (SCHMIDT 2003: 55).

(C171) Lateral endite of first maxilla: lateral group of teeth broader than half of the apical margin [inner group of teeth occupies more than half of the apical margin] (SCHMIDT 2003: 55).

(C172R) Distal 2 articles of maxilliped palp fused, number of setae reduced [distal 2 articles of maxilliped palp delimited from each other] (SCHMIDT 2003: 55).

The “**Dubioniscidae**” were based on plesiomorphic or doubtful characters by SCHULTZ (1995). Also the “**Platyarthridae**” were doubted to be monophyletic by SCHMIDT (2003), who examined only *Trichorhina* in detail. MATTERN’S (2003) investigation confirmed this doubt: *Trichorhina* always was in the basal part of the Crinocheta cladogram, while *Platyarthrus* grouped with *Oniscus* and *Philoscia*. This latter relationship may be supported also by morphological evidence (C. Schmidt, unpublished data). In consequence, *Platyarthrus* with some probability will have to be removed from the taxon now known as “Platyarthridae”.

Within the Squamiferae, the **Spelaeoniscidae** represent a clearly monophyletic taxon. Apomorphies are:

(C173) Uropod endopodite dorsoventrally flattened, mesal margin without spines or setae [uropod endopodite laterally compressed and the mesal margin bearing a dense fringe of setae] (SCHMIDT 2003: 79).

(C174R) Compound eyes with max. 3 ommatidia [probably with more than 3 ommatidia] (SCHMIDT 2003: 79).

(C175) Lateral margin of maxilliped endite with broadly convex lobe; except for 1 seta on the caudal face, the endite lacks setae or spines [lateral margin of endite not laterally extended, distal margin bearing several acute lobes] (SCHMIDT 2003: 179).

(C176) Middle article of maxilliped palp with two large setae and another structure of same size and shape between them. The latter may be a seta or

a seta-shaped lobe [middle article with a proximal large seta or a tuft of setae, and a distal tuft of at least 1 large and some smaller setae; the third large «seta» as found in the apomorphic condition is absent] (SCHMIDT 2003: 79).

- (C177) Setae on pereopods more or less serrate [setae simple] (SCHMIDT 2003: 79).
- (C178) Dactylar seta on pereopod dactyli distinctly shorter than outer claw [dactylar seta slightly shorter or longer than outer claw] (SCHMIDT 2003: 79).
- (C179R) Mandibles: lobe basal of lacinia mobilis lacks spines [“hairy lobe” with some hairs or scales] (SCHMIDT 2003: 179).

All the following taxa were provisionally grouped together by SCHMIDT (2003), but no convincing apomorphies could be found. May be the (C184) T- or Y-shape of the tergal sensilla represents a synapomorphy, but this may be not present in the whole group, or it may be plesiomorphic with respect to the shape of the tergal sensilla found in Squamiferae (C170) At least the Eubelidae and Armadillidae probably are more distantly related to the remaining taxa.

The **Eubelidae** and **Armadillidae** may be sister taxa. This relationship is not strongly supported, but there is no indication for assuming a closer relationship of one of them with another taxon. Putative synapomorphies are:

- (C180) With conglobation ability, the second antennae are inside the ball (“endoantennal conglobation”). [No conglobation ability, habitus of the clinger-type] (SCHMIDT 2003: 100).
- (C181) Uropod sympodites flattened, exopodites reduced in size [uropod sympodites not flattened, exopodites larger] (SCHMIDT 2003: 100).
- (C182) Pleopod 1–5 exopodites each with one partly internalized dorsal respiratory field [pleopod 1–5 exopodites each with one fully exposed dorsal respiratory field, described as “*Oniscus*-type” open respiratory field] (SCHMIDT 2003: 100).
- (C183) First maxilla: slender seta on lateral endite much shorter than tooth setae [slender seta as long as tooth setae] (SCHMIDT 2003: 100).

The second antennae are protected inside the ball during (C180) “endoantennal conglobation”; the frons is flat and does not have any structures to hold the antennae, as e.g. in Armadillidae (see below).

PAOLI et al. (2002: 283) postulate a dorsal “semilunar area” near the lateral margin of the pleopod exopodites as the plesiomorphic state of the respiratory structure in Eubelidae, explaining why they do not consider this simply as a reductive structure. This

semilunar area seems to differ from the (C182) *Oniscus*-type open respiratory field mainly in its extension, being restricted only to the dorsal lateromarginal parts of the exopodite. From a functional point of view I consider it more plausible that the stem species of Eubelidae (and Eubelidae + Armadillidae) had these respiratory areas more extended; then there would be no fundamental difference to the *Oniscus*-type respiratory fields.

The **Eubelidae** includes more than 240 species, mostly distributed in the Afrotropical Region (PAOLI et al. 2002). They are thought to be monophyletic, based on two character states:

- (C185) Presence of a curved groove (“sulcus arcuatus”) on the dorsal face of the first coxal plate, at some distance from the lateral margin [absence of such a groove] (Fig. 29).
- (C186) Uropod sympodites enlarged and flattened, with the exopodite reduced in size and inserted on the posterior margin [Uropod sympodites neither enlarged nor flattened, the exopodite normally sized and inserted] (TAITI et al. 1991).

TAITI et al. (1991) also presented a preliminary, poorly resolved cladogram for Eubelidae based on some morphological characters. No further study on the phylogeny of Eubelidae has been published since. The shape of the uropods of Eubelidae may be plesiomorphic, inherited from a common ancestor of Eubelidae and Armadillidae,

In Eubelidae, the insertion of the exopodite on the posterior margin of the sympodite is the same as in non-conglobating Oniscidea, and therefore should not be included in the apomorphic character state. The (C181) enlarged sympodite and the small exopodite are found also in Armadillidae, therefore this may be a synapomorphy of Eubelidae and Armadillidae (SCHMIDT 2003). In consequence it seems improbable that (C186) can be retained as apomorphy of the Eubelidae.

A structure very similar to the sulcus arcuatus is present also in *Buddelundia* and, a bit less similar, in *Venezillo hendersoni*, which according to other characters both belong in the Armadillidae. The probable function of the sulcus arcuatus as part of the water-conducting system was investigated by FERRARA & PAOLI (2003), who also explain why they think that similar structures in *Buddelundia* and *Venezillo hendersoni* evolved convergently. According to PAOLI et al. (2002), various types of pleopodal lungs evolved several times convergently within the Eubelidae.

The **Armadillidae** are the most diverse “family” within the Oniscidea (ca. 590 species). TAITI et al.

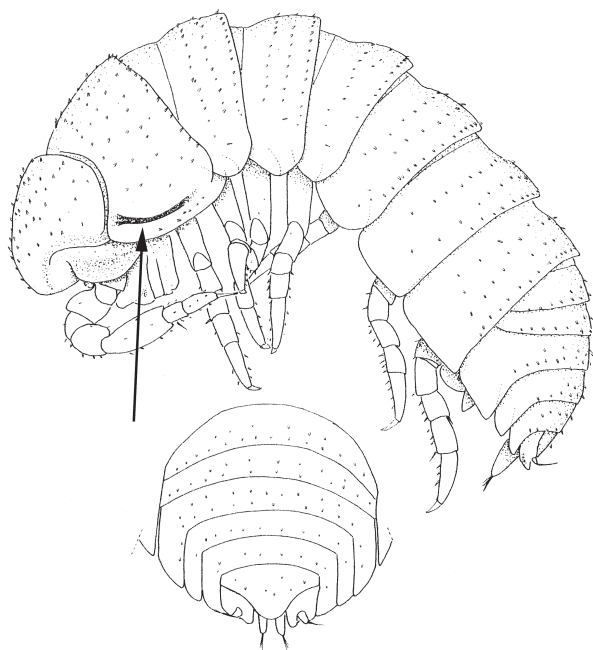


Fig. 29. Eubelidae: *Elumoides* sp., habitus lateral and pleon dorsal. Arrow indicates 'sulcus arcuatus' (C185).

(1998) discussed the characters, and provided a list of genera. Their discussion of the morphological characters allows to make a tentative reconstruction of the groundpattern. A cladistic analysis is still lacking, but the monophyly seems to be indicated by several apomorphies:

- (C187) Uropod medial margin deeply concave, exopodite reduced in size, inserted on the protopodite dorsally near the medial margin of the sympodite, not surpassing the posterior margin (TAITI et al. 1998: 294) [Uropod medial margin not deeply concave, exopodite less reduced in size, inserted on the distal margin].
- (C188) Pereiomer 7 sternite with a bilobed caudal process [seventh sternite with non-bilobed process or with more or less straight posterior margin] (SCHMALFUSS 1996; TAITI et al. 1998: 294) (Fig. 30).
- (C189) Tuft of hairy setae representing pars molaris of mandible: setae densely spaced upon a stalk-shaped socket (the entire structure appearing as a single hairy seta) [setae distinctly discrete and not on a socket] (SCHMIDT 2003: 115).
- (C190) Pleopod 5 exopodite with distal part delimited by a furrow and bent ventrally in a 90° angle [distal part not delimited and not bent ventrally] (SCHMIDT 2004: 115) (Fig. 30).

For (C187) the plesiomorphic state is that found in Eubelidae, the presumed sistergroup of the Armadillidae (SCHMIDT 2002, 2003). The differences between Scleropactidae and Armadillidae, as discussed by TAITI

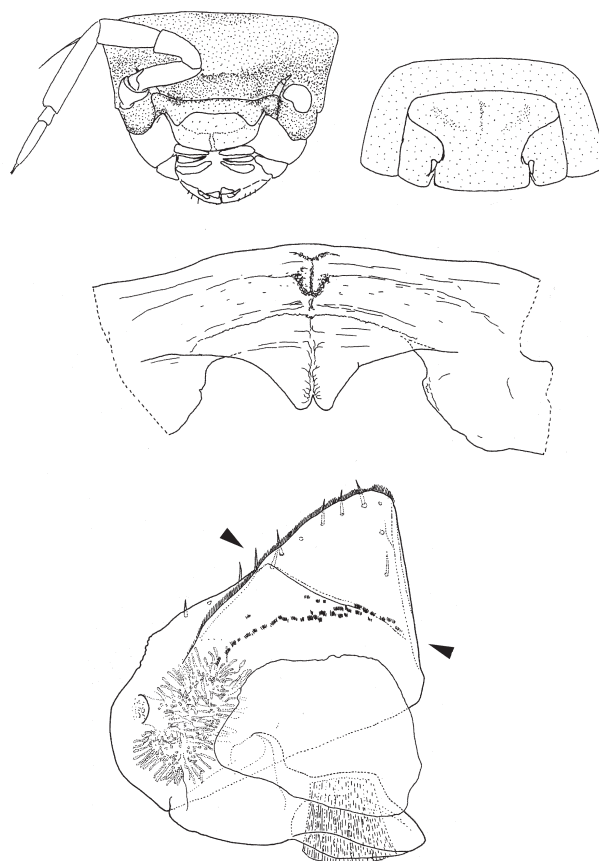


Fig. 30. Armadillidae: *Venezillo* sp., cephalothorax, frontal view, distal part of pleon, dorsal view, and pereion sternite 7; *Australiodillo bifrons*, pleopod 5 (arrowheads indicate the fold) (C187, 188, 190).

et al. (1998) are not used for hypothesizing the plesiomorphic state, because the Scleropactidae most probably are phylogenetically more distant and the adaptations to conglobation thus are not considered homologous between Scleropactidae and Armadillidae.

Then remains an unnamed group including Bathytropidae, Tendosphaeridae, Oniscidae, Trachelipodidae, Cylisticidae, Agnaridae, Porcellionidae, Armadillidiidae. The assumption of its monophyly is highly tentative and may be supported only by the wide occurrence of intersegmental articulation-like structures between the coxal plates or tergites 1–4:

- (C191) Anterior margins of coxal plates 2–4 bearing a transverse, cone-shaped process with a tip that points laterally; the process fits to a furrow on the underside of the preceding tergite/coxal plate [such structures absent] (Fig. 31).

This condition was proposed as a probable synapomorphy of *Porcellio* and Armadillidiidae (SCHMIDT 2003: 156). However, similar structures are present also in clinger-type species of *Porcellium*, *Tracheli-*

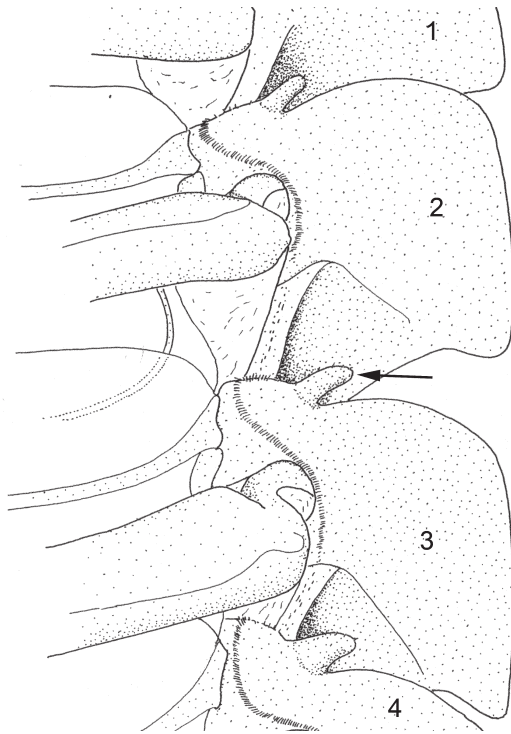


Fig. 31. *Trachelipus ratzeburgii*: ovigerous female, coxal plates 1–4 in ventral view. Arrow points at conical process (C191).

pus, *Oniscus* and *Bathytropa*. In contrast, taxa of Porcellionidae, Trachelipodidae, Agnaridae with runner-type habitus do not have this articulation. The problem of homology of (C191) among the various taxa remains to be investigated. If it is homologous, it would be either an autapomorphy of the unnamed taxon discussed here or of a taxon including the species with clinger or conglobating habitus, but excluding the species with runner habitus. The latter alternative would require a complete rearrangement of the traditional classification, which, however, cannot be regarded as well founded on phylogenetic reasoning. This demonstrates the necessity of thorough phylogenetic analyses of “Bathytropidae”, “Oniscidae”, “Trachelipodidae”, “Cylisticidae”, and the other taxa included in the assemblage here discussed.

The “**Bathytropidae**” include ca. 10 genera and 25 species, but most of them seem to be misplaced, and even the entire family could well be an artificial assemblage. SCHMIDT (2003: 85) regarded only *Bathytropa* as a certain member of “Bathytropidae”

The **Tendosphaeridae** currently include 3 genera with 4 species, all conglobating. *Tendosphaera* (2 species) is certainly monophyletic, and the other 2 genera are probably not closely related with it. *Tendosphaera verrucosa* has a narrow distribution in the western Alps, *T. graeca* in northern Greece. Apomorphies of *Tendosphaera* are:

- (C192) A pair of longitudinal furrows on the cephalothorax that are continued by transverse furrows on pereion tergite 1 [no such furrows] (SCHMIDT 2003: 99).
- (C193) First coxal plate with a cleft (schisma), second and third coxal plates with lobes on their inner face [these coxal plates simple] (SCHMIDT 2003: 99).
- (C194) Lateral endite of first maxilla with simple teeth only [at least several teeth of the medial group are apically cleft] (SCHMIDT 2003: 99).
- (C195) Dactylar seta with spatulate tip [dactylar seta simple] (SCHMIDT 2003: 99).
- (C196) Male pleopod 1 endopodite: distal part with subapically stout, with a very narrow and complicatedly twisted apex [male pleopod 1 endopodite apex moderately acute, neither subapically stout nor with a twisted apex] (SCHMIDT 2003: 99).
- (C197) Uropod exopodite short and styliiform, inserted on the enlarged sympodite in lateral position [uropod exopodite short lanceolate, inserted approximately in the middle of the distal margin of the exopodite] (WÄGELE 1989).

The furrows referred to in (C192) harbour the second antennae while conglobated. They are similar to those of *Triceratosphaera* (Spelaeoniscidae), but as there is no other evidence for such a relationship, this should be a convergency.

The “**Oniscidae**” now are restricted to 3 genera with few species (SCHMIDT 2003: 115) occurring in western and central Europe. The apomorphy proposed for *Oniscus asellus*, (C198) a longitudinal groove with a dense field of scales on the frontal face of each pereopod basipodite (beside the articulation with the coxal plate; SCHMIDT 2003: 123), has been found also in at least 1 species of *Trachelipus* (C. Schmidt unpubl. data). Therefore this feature is now considered quite unlikely to be an autapomorphy of Oniscidae in its present extent, and there is altogether no basis for assuming the monophyly of the Oniscidae.

The “**Trachelipodidae**” in the sense of the older authors are considered as paraphyletic (SCHMIDT 2003). The species with “*Porcellio*-type” lungs have been re-transferred to Porcellionidae by FERRARA & ARGANO (1989), and separated as Agnaridae by SCHMIDT (2003). Currently 6 genera are classified as “Trachelipodidae” (SCHMIDT 2003; TAITI & FERRARA 2004), apparently because of a similar structure of the pleopodal lungs, as in *Nagurus* or *Trachelipus*. The species of “Trachelipodidae” have a runner or clinger habitus. MATTERN (2003) found *Porcellium* closer to *Cylisticus* (“Cylisticidae”) and *Protracheoniscus* than to *Trachelipus*.

The **Agnaridae** include ca. 80 species with internal lungs, formerly classified in the Trachelipodidae, and separated as the *Agnara*-group by FERRARA & ARGANO (1989). The species exhibit the runner-type habitus or are more or less heavily tuberculate. The geographic distribution extends from the Mediterranean to eastern and southern Asia. The only apomorphy proposed up to now is the particular structure of the lungs:

- (C199) Spiracles of the internal lungs located on the lateral edge of the pleopod exopodites, perispiracular area small [spiracles on the caudal face of the exopodites, distant from the lateral edge?, perispiracular area large].

The lack of knowledge on the majority of the nominal genera and species prevents any more elaborate hypotheses on the monophyly of the Agnaridae and on the relationships within the group. In consequence, also this group is considered as weakly supported.

For *Orthometopon*, a morphology-based hypothesis on the phylogenetic relationships among the species is available (SCHMALFUSS 1993). A “population”-level study on the same genus is based on a short (470 bp) fragment of the mitochondrial CoI gene; it includes mainly samples from Greece (POULAKAKIS & SFENTHOURAKIS 2008). The results of these two investigations are incongruent with regard to both species delimitation and phylogenetic relationships.

The “**Cylisticidae**” is another problematic taxon, with 2 or 3 genera including ca. 50 species. They are distributed in the NW-Mediterranean and from eastern Europe to the Caucasus and northern Iran. Obviously they have been grouped together mainly because of the (C201) exoantennal conglobation.

The putative autapomorphies mentioned by SCHMIDT (2003: 138) refer only to *Cylisticus* or probably only to part of *Cylisticus*:

- (C200) Basipodite of male pereopod 6 with a ventral field of numerous large, widely spaced scale-setae [basipodite 6 not with longer and more numerous scale-setae than basipodite 5].
- (C201) Exoantennal conglobation ability [habitus of clinger-type] (Fig. 32: cephalothorax).

SCHMALFUSS (2003: 2) found that (C200) is present only in the larger, epigeal species of *Cylisticus* and lacks in the smaller, endogean species. Also the closely related *Parcylisticus* does not have this sexual dimorphism on pereopod 6. SCHMALFUSS (2003) argues that conglobation ability is a character with high probability for convergency and that there are no other differences to genera of Trachelipodidae.

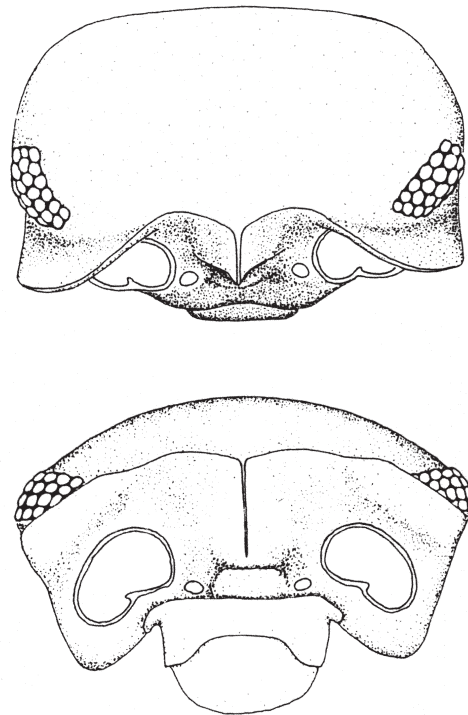


Fig. 32. *Cylisticus convexus*: cephalothorax, dorsal and frontal (from SCHMIDT 2003) (C201).

The **Porcellionidae** were regarded as probably not monophyletic by SCHMIDT (2003), who presumed that the Armadillidiidae might be part of the Porcellionidae. However, MATTERN (2003), based on 18S rRNA data, found monophyletic Porcellionidae, represented by *Porcellio* and *Porcellionides*, and *Armadillidium* does not group together with *Porcellio* in any of the cladograms.

The **Armadillidiidae** are a well-founded monophyletic group. They comprise about 300 species, among them *Armadillidium vulgare*, the “most extensively investigated species of terrestrial isopods” (SCHMALFUSS 2003: 2). They are restricted to the Mediterranean Region, except for 2 synanthropic species. The morphological characters, except for the conglobation ability, resemble very much those of Porcellionidae.

- (C202) Endoantennal conglobation ability, cephalothorax with antennal lobes [no endoantennal conglobation ability, cephalothorax without antennal lobes; clinger-type habitus] (SCHMIDT 2003: 167) (Fig. 33).
- (C203) Uropod exopodites strongly depressed, plate-like, fitting into the gap between the pleotelson and the epimera of the pleon segment 5 [uropod exopodites slightly depressed, conical] (SCHMIDT 2003: 167) (Fig. 33).



Fig. 33. *Armadillidium granulatum*: Cephalothorax and pereopod 1 frontal, pleon dorsal (C202–204).

(C204) Pleotelson without narrowed distal portion (secondary condition) [pleotelson with narrowed, triangular distal part] (SCHMIDT 2003: 167) (Fig. 33).

The assumption that the Armadillidiidae are a sub-taxon of the Porcellionidae (SCHMIDT 2003: 166) is plausible regarding the morphological evidence, but has not found support by the few analyses based on nuclear or mitochondrial rRNA gene sequences.

Furthermore, there are some taxa including one or few species, which are incompletely known and cannot even tentatively be placed in a cladogram of the Oniscidea. This is the case for **Delatorreidae**, for which some characters are illustrated by SCHMIDT (2003) on the basis of few poorly preserved specimens, but no exclusive similarities with any other taxon could be found. The same is true for the **Pudeoniscidae**, which are placed tentatively in an unnamed taxon in the cladogram by SCHMIDT (2002: 309; “taxon 6”), for which no clear apomorphies could be found. The “families” **Hekelidae** and **Irmaosidae** have not been considered in the comprehensive study by SCHMIDT (2002, 2003) due to the lack of material.

9. Fossil record

The oldest known fossils of terrestrial isopods are from the Eocene-Oligocene Baltic Amber. ROGER (1953:

326), in the *Traité de Paléontologie*, writes that these are specimens of Oniscidae, Porcellionidae and Trichoniscidae, but does not give a reference to the original work. The same information was published by MORRIS (1979), again without citation. SCHMALFUSS (1980) refers to descriptions of only two species from Baltic Amber, which cannot be placed in the classification on the basis of the original descriptions by KOCH & BEHRENDT (1854). “*Armadillidium molassicum*” from the Miocene, cited by MORRIS (1979), was described by HEER (1859) as *Armadillo molassicus*; the description and illustration (HEER 1865: 352) are not sufficient to recognize whether it is an isopod or a millipede. MORRIS (1979) described *Eubelum rusingaense* from the lower Miocene of Rusinga Island, Lake Victoria, Kenya. This clearly belongs to the Eubelidae. SCHMALFUSS (1980) described *Protosphaeroniscus tertarius* from the Dominican Amber of Haiti/Hispaniola, with an estimated age of 25–30 million years. A specimen from the Miocene of Kerala (India), described as a species of *Armadillidium* (SRIVASTAVA et al. 2006), does not belong in the Isopoda judging from the photo.

Since the Oniscidea are united in a taxon Scutocoxifera together with Valvifera, Sphaeromatidea, Anthuridea, and Cymothoidea, also fossils of these taxa may be of some interest to determine the age of Oniscidea. Sphaeromatidea are known from the upper and middle Jurassic (POLZ 1998; GUINOT et al. 2005). Cymothoidea were found in Upper Jurassic deposits (Solnhofener Plattenkalke) (POLZ 2004; POLZ et al. 2006); the oldest fossil specimen of Valvifera is in “cementstone” from the early Palaeogene, about 50–60 million years old (POLZ 2007).

10. Evolution of the terrestrial isopods

It is now generally accepted that the terrestrial isopods colonized land from the seashore, without passing through freshwater (CAREFOOT & TAYLOR 1995). Among the extant Oniscidea, most species of *Ligia* are still inhabiting the seashore, and *Ligia* has an amphibic lifestyle, being able to feed and even moult under water (GRUNER 1966: 171). Most Tylidae and a number of Crinocheta are littoral as well. The remaining species of Ligiidae, the Synocheta and *Mesoniscus* are confined to habitats of high humidity, while in the Crinocheta, there is a large number of species living in drier habitats, a few are even occurring in arid regions. There is a vast amount of papers dealing with physiological adaptations to the terrestrial environment (EDNEY 1968; WARBURG 1989, and references therein). *Ligia oceanica* still depends on sufficient salinity. This need can be fulfilled either from the substrate or from

the food; the ability to compensate unsuitable ambient salinity by salt uptake with the food (e.g. marine algae) is seen as an important adaptation to the life above the water level (JÖNS 1965). Adaptations concerning the detection of food sources, feeding and digestion were reviewed in detail by ZIMMER (2002). The structure of mouthparts and digestive tract changed obviously in response to terrestrial food sources. The functional aspect of mouthpart morphology, however, is poorly known.

The so-called water-conducting system, which consists of rows of scales leading from the head to the pleoventral chamber (HOESE 1982, 1983), is evidently a structure of major importance. These rows are able to hold water by capillary forces. The urine secreted by the maxillary nephridia moves backwards to reach the pleoventral chamber via this system. The Oniscidea excl. Crinocheta have also similar rows on the opposing surfaces of pereopods 6 and 7, which enable them to take up water between these two legs, which are then appressed to each other. In the Crinocheta there are at most some scale-rows on the pereopod 7 ischium, which seems to represent a reductive, non-functional state. The Crinocheta are able to dispose of excess liquid or to take up water by the uropod endopodites (DROBNE & FAJGELJ 1993), which form a water-conducting tube when appressed to each other. In contrast, in HOESE'S (1981: 141) experiments, *Porcellio* and *Oniscus* did not take up water via the uropod endopodites.

The median fusion of the genital papillae and the linear arrangement of the male pleopod 2 protopodite and endopodite are seen as key innovations in the evolution of the terrestrial isopods, which enabled the subsequent development of the complex copulatory apparatus of the Crinocheta. This apparatus is believed to make sure a "rapid and precise transfer" of the sperm, which may have contributed to the ability of colonizing less humid microhabitats (ERHARD 1995).

Other characters transformed or developed in correlation to the terrestrial life are the size of the first antennae, which are always extremely small and have at most 3 articles, and the number of flagellar articles of the second antennae. In Ligiidae and some Synocheta the 2nd antennae have numerous flagellar articles, while in the Oniscoidea there are at most 3, and in those taxa adapted to less humid conditions (e.g. Porcellionidae, Armadillidiidae, Armadillidae, Agnaridae) most species have only 2 flagellar articles. The distal sensilla on the apical flagellar article form a loose tuft in the plesiomorphic oniscidean condition, while later they become condensed and shortened to form a compact sensory cone. This transformation may be an adaptation to drier environment, and may also have mechanical reasons.

The mouthparts in general show a reduction in setation towards the more terrestrial forms. The mandible

lost the pars molaris in the stemline of the Crinocheta. Although a functional explanation has not (yet) been found, it seems that this reduction is correlated with changes in the foregut (stomach) structures observed exclusively in Crinocheta (TABACARU & GIURGINCA 2003). In the place of the molar process, the Crinocheta have one setulate seta or a tuft of several such setae. Interestingly, in some species of Scleropactidae, the structure of the mandibles suggests that they have a secondary masticatory surface, formed by the lacinia mobilis of the right mandible and the pars incisiva of the left mandible (SCHMIDT 2007). The maxilliped palp became smaller relative to the basis, and the number of articles decreased from 5 to 3.

Changes seen in the pereopods are the loss of the scale rows on P6 and P7 belonging to the water conducting system at the base of the Crinocheta, the evolution of brushes for grooming antennae (and mouthparts?) on pereopod 1, and the loss of the inner claw in the stemline of Orthogonopoda, followed by the evolution of a secondary inner claw at the base of the Crinocheta. There is a great diversity of processes, tubercles, tufts of setae or scales, etc. that occur only in males, mostly on the pereopod 7. According to their shape, there are numerous cases of parallelisms within the Oniscidea; functional studies are still lacking.

The respiratory structures in the pleopod exopodites had been used as a central character system in the classification by earlier authors (VERHOEFF, VANDEL). More recent studies revealed a multiple convergent evolution of lung structures of various complexity within the Crinocheta (SCHMIDT & WÄGELE 2001) and even within the Eubelidae (PAOLI et al. 2002). The plesiomorphic condition (evolved in a common ancestor of Oniscidea) is a respiratory area with very thin cuticle on the ventral surface of the exopodites; the next step is a shift of the respiratory area to the dorsal surface, where it occupies a more or less extended lateral area that is delimited by a raised fold. While this condition with some probability evolved several times independently, more complicate structures seem to have evolved even more times convergently in various clades.

PAOLI et al. (2002) concluded that in Eubelidae, uncovered lungs and covered (= internal) lungs evolved independently from a comparatively simple structure named "semilunar area", which is similar to the simplest form of dorsal respiratory field with unfolded surface. According to their hypothesis, the uncovered lungs evolved by increasing folding of the surface of the respiratory field, while the covered lungs evolved by tubular invagination of the cuticle, which led independently to the formation of monospiracular and polyspiracular lungs. Further insight can not be achieved without phylogeny hypotheses for the taxa in which the various types of lungs are present. The

evolution of lungs in the Tylidae likely occurred independently from other oniscidean taxa (EBBE 1981; HOESE 1983).

The functional aspects of habitus types different from the “runner-type” with comparatively long legs and antennae and smooth tergites are described by SCHMALFUSS (1984). The “runner-type” is supposed to represent the plesiomorphic state. According to a cladistic analysis of the “families” of Crinocheta, each of the other habitus types evolved several times independently (SCHMIDT 2002, 2003).

11. Conclusion

The present state of knowledge on the phylogeny of the Oniscidea has been outlined. The hypotheses on the phylogenetic relationships among the Ligiidae, Tylidae, *Mesoniscus*, Synocheta and Crinocheta are well founded and supported by numerous apomorphies. Within these 5 groups, there is a phylogeny hypothesis only for the Crinocheta. Important gaps identified are:

1. The lack of a comprehensive taxonomic revision and a phylogenetic analysis of the Synocheta.
2. Lack of comprehensive taxonomic revisions and phylogenetic analyses for many taxa of the Crinocheta, especially for Armadillidae, Armadillidiidae, Philosciidae (other than Neotropical), Porcellionidae, and Agnaridae.
3. Incomplete, and probably not representative sampling for the Crinocheta, which impedes with proving the monophyly and constructing the respective groundpatterns. This may be achieved by successive revisions and phylogenetic analyses of the Crinocheta down to species level.
4. For the majority of morphological characters, the functional aspects have not been studied.
5. Very limited and non-representative sampling of Oniscidea for molecular phylogenetic analyses.

It is obvious that the first problem to solve is the lack of comprehensive taxonomic revisions in many groups. This lack currently prevents access to the majority of species and morphological characters for phylogenetic analysis. Also for DNA sequencing (barcoding) the identification of the species is essential and little progress can be made without having taxonomic revisions.

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Appendix

1. Synonymy list for high-rank taxa in Oniscidea

Crinocheta Legrand, 1946

Embolophora Verhoeff, 1936

Diplochaeta Wägele, 1989

≠ Diplocheta Vandel, 1957

Ligiidae Brandt, 1833

Ligieae Brandt, 1833

Cloportes maritimes Milne Edwards, 1840

Diplocheta Vandel, 1957: 2160

Mesoniscus Carl, 1906

Mesoniscidae Verhoeff, 1908

Microcheta Schmalfuss, 1989: 21

Oniscidea Latreille, 1829

Oniscides Latreille, 1829

Oniscoidea Dana, 1852

Oniscoidea Schmalfuss, 1989

≠ Oniscoidea auct.

Synocheta Legrand, 1946

Endophora Verhoeff, 1936

Tylidae Milne Edwards, 1840

Tylosiens Milne Edwards, 1840

Tylomorpha

Tylida Erhard, 1998: 304

2. Proposed classification of Oniscidea

Oniscidea

Ligiidae

Holoverticata

Tylidae

Orthogonopoda

Mesoniscus

Euoniscoidea

Synocheta

“Trichoniscidae” in part

Haplophthalminae

Styloniscidae

Titanidae

Schoebliidae

Crinocheta

Olibrinidae

Detonidae

Scyphacidae

Oniscoidea sensu SCHMALFUSS (1989)

Alloniscus

“Philosciidae”

“Scleropactidae”

Halophilosciidae

n.n.

Stenoniscidae

n.n.

Rhyscotidae

n.n.

Squamiferae

“Dubioniscidae”

“Platyarthridae”

Spelaeoniscidae

n.n.

n.n.

Eubelidae

Armadillidae

Bathytropidae

Tendosphaeridae

Oniscidae

“Trachelipodidae”

“Cylisticidae”

Agnaridae

“Porcellionidae”

Armadillidiidae