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Phylogeny and Biogeography of South American Crinocheta, traditionally placed in the family "Philosciidae" (Crustacea: Isopoda: Oniscidea)

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Abstract

South America is diverse in climatic and thus vegetational zonation, and even the uniformly looking tropical rain forests are a mosaic of different habitats depending on the soils, the regional climate and also the geological history. An important part of the nutrient webs of the rain forests is formed by the terrestrial Isopoda, or Oniscidea, the only truly terrestrial taxon within the Crustacea. They are important, because they participate in soil formation by breaking up leaf litter when foraging on the fungi and bacteria growing on them.

After a century of research on this interesting taxon, a revision of the terrestrial isopod taxa from South America and some of the Antillean Islands, which are traditionally placed in the family Philosciidae, was performed in the last years to establish monophyletic genera. Within this study, the phylogenetic relationships of these genera are elucidated in the light of phylogenetic systematics. Several new taxa are recognized, which are partially neotropical, partially also found on other continents, particularly the old Gondwanian fragments. The monophyla are checked for their distributional patterns which are compared with those patterns from other taxa from South America and some correspondence was found. The distributional patterns are analysed with respect to the evolution of the Oniscidea and also with respect to the geological history of their habitats.

Species that were probably introduced are marked with an asterisk (*), nomina dubia are marked with an accent (^).

Key words: Crustacea, Isopoda, Oniscidea, Crinocheta, phylogenetical systematics, phylogeny, biogeography, Neotropis, South America

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1 Introduction

The taxon Oniscidea plays an important role in the decomposition of organic material within the terrestrial biota. They can occur in high densities, comprising the bulk of terrestrial detritivores with numbers of up to 500 individuals per square meter (Davis 1984). In South America, they are found in tropical ecosystems where they are both terrestrially and arboreally distributed (Picardo 1913, Paoletti 1989, Nadkarni and Longini 1990). Their contribution to the consumption of decaying plant material may be up to 12% (Grünwald 1988), thus they play an important role in soil formation. Although they are ubiquitous, little is known about their life history and the phylogeny of this interesting suborder of the Isopoda. The Oniscidea is the only truly terrestrial taxon of the Crustacea.

The oniscidean fauna of Europe is well documented; and an identification key for the approximately 1230 nominal species is available (Schmölzer 1965), although new species and even genera are still being discovered (e.g. Schmalfuss 1998a). A survey of African Oniscidea listed 575 species (Ferrara and Taiti 1979). For the Americas, a number of 254 species of terrestrial Isopoda was given by van Name (1936) and several more were listed in subsequent publications (van Name 1940 and 1942). A recent survey led to an increase to up to 521 described nominal species in 1997 (Leistikow and Wägele 1999). But this is only the tip of the iceberg since every expedition to the tropical rain forests reveals new species and even genera.

Up to now, about 4000 species of Oniscidea are known, half of all known isopods (Gruner 1993). Apart from some smaller taxa, the suborder is subdivided into the monophyletic adelphotaxa Synocheta and Crinocheta, the latter comprising the bulk of the species. A summary of the attempts made in the last years to establish a phylogenetic system of the higher taxa of Oniscidea was given by Erhard (1998).

Until recently, the phylogeny within the Crinocheta had been poorly studied, with almost every known family forming a paraphyletic assembly rather than reflecting the natural relationships within this taxon (H. Schmalfuss, pers. comm.). New insight into the phylogeny of this group was provided by Schmidt (1999).

Among the Crinocheta, about one hundred genera are placed in the so-called family "Philosciidae", the phylogeny of it has not been discussed sufficiently yet. This basal group is, besides the Armadillidae, one of the most important groups of Oniscidea in tropical habitats (Schmalfuss 1984a: 12), in South America about one fifth of the nominal species belong to this family (Leistikow and Wägele 1999). It is confined to moist areas whereas the Armadillidae are adapted to drier habitats (Taiti et al. 1998). While we have a considerable understanding of the diversity of "Philosciidae" in Africa (Taiti and Ferrara 1980, Taiti and Ferrara 1982, Ferrara and Taiti 1985), the islands in the Indian Ocean (Barnard 1964, Ferrara and Taiti 1983, Taiti and Ferrara 1984), South and South East Asia (Taiti and Ferrara 1986b, Manicastri and Taiti 1987, Taiti and Manicastri 1988, Green et al. 1990, Taiti et al. 1992) and the Australian region (Herold 1932, Verhoeff 1926, Vandel 1973a, 1973b, 1977), there are only few contributions to the systematics of "Philosciidae" from South America. Particularly, the early works on neotropical "Philosciidae" (Dollfus 1893, Budde-Lund 1893, van Name 1936) did not deal with supra-generic systematics; and even the attempts of Lemos de Castro (1958a, 1958b, 1958c, 1976, 1985b) and Vandel (1952, 1963, 1968, 1972) did not clarify the situation convincingly. In a relatively recent work on Mexican Oniscidea (Mulaik 1960), most "Philosciidae" were simply placed in the genus *Philoscia*, although this genus is in fact confined to the western Palearctic (Schmalfuss 1990b).

This study aims to establish monophyletic taxa for the South American species showing a philosciid facies. The species and genera were described in the past in a very superficial way and many characters have been overlooked. Until very recently, sexual dimorphism for example was thought to be restricted to the pereopods 1 and 7, whereas recent thorough descriptions gave evidence to the fact that almost all pereopods might be affected by sexual differentiation (Schmidt 1998; Leistikow 1999a). The detailed study of the species of all accessible genera from South America are the basis for new definitions of these genera in the last years (Leistikow 1997b, 1998a-c and 1999a-c, 2000a-b, 2001a-f, in press). Additional new species for many taxa could be identified (Leistikow, 1997a, 1999c and d). The question whether all South American representatives of the so-called family "Philosciidae" belong to a single monophylum or whether they represent different monophyletic groups will be discussed. For the taxa recognised, the biogeographic patterns will be traced on an inter- and infracontinental scale. For the higher taxa, the biogeography is discussed with regard to the colonisation of Gondwana in comparison to other biogeographic scenarios presented in the literature (e.g. Vandel 1946). The general infracontinental patterns worked out will be compared with patterns known from other invertebrate and vertebrate taxa. Fortunately, South America is well-studied biogeographically.

In order to make the determination of South American philosciids possible for non-specialists, a key to the genera is included, keys on species level were published for *Androdeloscia* (Leistikow 1999c), *Erophiloscia* (Leistikow 2001a), *Ischioscia* (Leistikow in press) and *Benthana* (Leistikow and Araújo, in press). They should facilitate the recognition of the species and aid in the discrimination of the representatives of this taxon in ecological studies where they are mostly referred to just as "Isopods".

2 History

In this chapter, the history of the exploration of the diversity of South American philosciids is presented in a review of the enhancement of our knowledge from both a taxonomic and faunistic approach over the last 100 years. At the begining of the century, the genus *Philoscia* Latreille, 1804 was a "melting pot" for species which at least have the narrow pleon in common. Budde-Lund (1904, 1908) made some efforts to resolve this genus into more natural groups which led to the establishment of several subgenera, later elevated to generic rank by subsequent authors, e.g. *Aphiloscia* Budde-Lund, 1908, *Benthana* Budde-Lund, 1908, and *Pseudophiloscia* Budde-Lund, 1904. Verhoeff (1908a, b) contributed to the systematics on supra-specific level, he mainly focussed on European representatives of *Philoscia*. From the Americas, the first "philosciid" species were mentioned in the middle of the last century. Dana (1853) described some species from Chile, as did Nicolet (1849); Miers (1877) focussed on the Crustacea of Central America and described *Philougria nitida* Miers, 1877 from Nicaragua, the first species of a taxon now known as *Ischioscia* Verhoeff, 1928. Budde-Lund (1885, 1893) and Dollfus (1890, 1893) added further species of "*Philoscia*" from Venezuela and Chile. Van Name (1936) adopted the subgeneric division of Budde-Lund (1908) but hesitated in raising them to the rank of genera. New species were still described as belonging to *Philoscia* although he recognised the differences in these taxa. It was the merit of Verhoeff (1928, 1939, 1941, 1951) to establish the first new genera of Philosciidae for the neotropical fauna. The works of Vandel on the faunas of Venezuela (1952), Ecuador (1968) and Colombia (1972) enhanced our knowledge on the philosciids of South America, although several genera are described superficially. But in many cases it is not conforming to the rules of the ICZN or simply lacking the phylogenetic background. An example is the establishment of the genus *Ecuadoroniscus* Vandel, 1968 with the single species *E. orientalis* Vandel, 1968 based on female specimens. In many "philosciid" taxa, it is quite impossible to determine the female specimens isopod without the knowledge of the characters of the corresponding male. The females are therefore just determined by the fact that they were found alongside males of this species.

Further information on the isopod fauna of South America was contributed by Lemos de Castro in his revision of several "philosciid" species (1958a), the genus *Benthana* Budde-Lund, 1908 (1958b) and the description of a closely related species which was placed in the new genus *Benthanoscia* (1958c). Subsequently, revisions of *Balloniscus sellowii* (Brandt, 1833) and *Atlantoscia alceui* Ferrara and Taiti, 1981 were published (Lemos de Castro 1976, 1985b).

Most recently, new species of *Prosekia* Vandel, 1968 were described by Lemos de Castro (1984), Lemos de Castro and Souza (1986) and Lima (1997), whereas Araújo and Buckup (1994) described a new species of *Benthana*. The last new genera added to the neotropical fauna were *Paraguascia* Schultz, 1995 and *Alboscia* Schultz, 1995 from Paraguay (Schultz 1995)

For those forms mentioned above, Vandel (1943) coined the term "Oniscidae inférieurs", which coincides with the sub-family Philosciinae of Oniscidae established one decade later by the same author (1952). However, instead of giving a definition, he simply mentioned the term "Philosciinae" in a key of the subfamilies with the following characters: Antennal flagellum three-articulate, genital papilla not bifurcate at the apex, small or medium-sized neopleurae, pleon narrower than pereon. A short definition followed in the work on French Oniscidea (Vandel 1962). Vandel (1962) did not notice that the subfamily Philosciidae was first established by Maccagno (1933) in her work on the Halophilosciinae. The institution of the subfamily Philosciidae by Maccagno (1933) was a proposal to substitute the taxon Halophilosciinae Kesselyák, 1930. And although this doing is not conform to the nomenclatory rules, it is the first time the term Philosciinae was mentioned.

In his work on Ecuadorian Oniscidea, Vandel (1968) dedicated a chapter to the Philosciinae. Here, the evolution of Philosciinae was interpreted as a regressive evolution with the reduction of several features like the linea frontalis, and lateral lobes on the cephalothorax, the simplification of the molar penicil of the mandibles, the setation of the pereopods, or the reduction of neopleurae of the pleonites 3 to 5. Vandel ignored that several of these reductions can be found in other families, too. Vandel (1968) separated the genera *Ischioscia* Verhoeff, 1928, *Proischioscia* Vandel, 1968 and *Oreades* Vandel, 1968 in a "groupe ischioscien" due to the shape of the cephalothorax and compound eyes. All the other forms were lumped in the "groupe philoscien proprement dit" which was regarded as homogenous but he accepted that more research was needed. In two subsequent papers of Australasian Oniscidea (Vandel 1973a, 1973b), several new genera and species of Philosciinae were described and some considerations on the systematics were presented. A new definition for the family comprised the following characters (Vandel 1973a): cephalothorax with linea supra-antennalis, linea frontalis only in primitive species, pleon narrower than pereon, prominent neopleurae present in primitive species, three-articulate antennal flagellum, endite of maxilliped with penicil in primitive forms, genital papilla simple. The following groups were established: 1. "groupe rennelloscien" with excentric noduli laterales on coxal plates II, IV and VII; 2. "groupe plymophiloscien" for which no particular characters were given; 3. "groupe chaetophiloscien" with an excentric position of the nodulus lateralis of coxal plate IV (inherited from their ancestors, the Oniscidae); 4. "groupe paraphiloscien" with elongate, narrow body, noduli laterales close to lateral margin, reduction of teeth of the maxillula to 3+2. The Philosciinae gained the rank of a family Philosciidae due to their abundance and variety in tropical and subtropical habitats (Vandel 1973b), with a definition which was summarized as an uninterrupted regressive evolution. A new group was established: the "groupe eurygastorien" which was considered as beinig intermediate between the Oniscidae and the Philosciidae (*Philoscia*-type of cephalothorax and buccal appendages, prominent neopleurae). From Vandel’s point of view, the most primitive group was the "groupe eurygastorien" from Australia, therefore he assumed that the family originated from this area. This hypothesis was never challenged by subsequent authors although the monophyly of "Philosciidae" was questioned now and then (e.g. Wägele 1989). Schmalfuss (1990a) even found no autapomorphies for well-established genera like *Chaetophiloscia* Verhoeff, 1908. The monophyly of "Philosciidaae" seriously has to be doubted, because autapomorphies never were found, it is set in parenthesis in this work and the species are addressed to as Crinocheta of philosciid facies.

About one hundred genera are united in the family "Philosciidae", most of them are representatives of the so-called "runner-type": long-legged with narrow pleotelson (Schmalfuss 1984b). They try to escape from their predators (spiders etc.) by running away and hiding in the leaf litter or the like. Thus, they have the same protective strategy which can be found in the Ligiidae. Moreover, it is probable that this strategy belongs to groundpattern of Oniscidea. Even with respect to behavioural aspects they show mostly plesiomorphic patterns similar to the Ligiidae (summary in Warburg 1968). In other words, the family "Philosciidae" is a paraphyletic assembly of genera with plesiomorphic habitus (Wägele 1989). This assembly has to be revised to clarify the natural relationships; Schmalfuss (1990b) discussed a close relationship between *Philoscia* Latreille, 1804 and *Oniscus* Linné, 1758 due to several characters in the lung morphology. On the other hand, the separation of the family Balloniscidae Vandel, 1963 has to be reconsidered. Vandel (1963) instituted the family for the genera *Balloniscus* Budde-Lund, 1908 and *Plataoniscus* Vandel, 1963, because the species bear five pairs of pleopodal lungs. As recently demonstrated (Ferrara et al. 1994), the evolution of lung structures can also be found in members of the "Philosciidae", namely the genus *Aphiloscia* Budde-Lund, 1908. Therefore, the presence or lack of lung structures should not exclusively be used as a criterion to establish a taxonomic unit.

To circumscribe the generic boundaries of the taxa of philosciid facies, Taiti and Ferrara (1980) established a set of criteria which seemed appropriate to them for recognition of the genera. The position of the noduli laterales, the presence of cephalic lines or the structure of mouth parts are important characters for taxonomical investigations and to elucidate the phylogeny. However, there are several characters not considered up to now. Moreover, the phylogenetic information was not brought in a wider context. There are many characters which contain information on the phylogeny; the structure of the pereopods, genital papilla and antennae were not investigated in former studies. It is one task of this contribution to describe further characters.

As in other families of Crinocheta, the philosciids most probably originated from the ancient continent Gondwana (Vandel 1946); they are widely distributed in Australia, southern Asia and Africa. The South American fauna of Crinocheta of philosciid facies is especially rich, where about 129 species in 42 genera were described until 1997 (Leistikow and Wägele 1999). 12 species and ten genera are endemic to Cuba. There are few contributions to the Oniscidea of South America, and reviews on distinct faunal regions are particularly scarce. Besides the works of Vandel (1952, 1968 and 1972), a comprehensive study on Mexican Oniscidea was presented by Mulaik (1960), but unfortunately most of the descriptions are incomplete and the taxonomy is not up to date, and it has not been even at the time of publication. The only recent contributions to faunal regions were made by Schultz (1995) on Oniscidea from Paraguay and by Araújo et al. (1996) on terrestrial isopods from southern Brazil. As will be shown in this work, the number of species described is merely the top of the iceberg and further research in South America, especially in the Amazon basin and the Andes will reveal a much higher number of species. Another problem of our understanding of the systematics and biogeography of the Crinocheta is the superficial description of the species; sometimes the descriptions do not allow a recognition of the species without re-examination of the type material. Particularly at the turn of the century it was common practice to lump all the slender Crinocheta in the single genus *Philoscia* Latreille, 1804. Some good attempts were made by Budde-Lund (1908) and Verhoeff (1908) to split off several new genera from this melting pot. But almost 30 years later new species were still described as belonging to *Philoscia* (van Name 1936). Lemos de Castro contributed a couple of papers on several genera of philosciid facies (summary in Leistikow and Wägele 1999) of Brazil, but without a phylogenetic and biogeographic approach.

All the studies on Oniscidea from the New World show that the Gondwanian origin of these taxa can not be doubted. Interestingly, such species are totally absent from the interior of North America, apart from the synanthropic species *Philoscia muscorum* (Scopoli, 1793). Its occurrence is due to human introduction (J. Jass and B. Klausmeier, pers. comm.). Only the littoral species of the genus *Littorophiloscia* Hatch, 1947 are autochthonously distributed along the shores of North America (Schultz 1975,1977a). It seems as if only a few genera have reached the Central American land bridge. Until recently, only two contributions mentioning genera of philosciid facies were published (Schultz 1984; Leistikow 1997a). The author’s own research in Central America revealed the presence of a couple of further genera. Within this study these distributional patterns will be considered in detail, particularly with respect to their northern distributional limits.

3 Material and Methods

For the present study, most of the known South American genera of the so-called "Philosciidae" have been examined using type material of museum collections. Furthermore, the fauna of Venezuela, Peru, Costa Rica and Guatemala were analysed in detail. The material was collected by Prof. Dr. J.W. Wägele, C. Schmidt (Venezuela), Dr. W. Hanagarth (Peru), and several researchers from Costa Rica; it was supplemented by the author’s own collections in Central America. For the reconstruction of phylogeny, additional species of Oniscidea were examined for outgroup comparison. A list of the species examined is given below (table 1).

The material was examined mainly by means of a Wild stereoscope, for the appendages an Olympus light microscope was used. The animals were dissected and the appendages were mounted in glycerine jelly. Line drawings were prepared using a camera lucida. As far as museum material is concerned, microscopic slides of the type material were examined. In cases where it was not possible to elucidate details of the morphology, the structures were examined via scanning electron microscopy (SEM Hitachi S 450). The material was critical point dried with a Balzers Union Critical Point Dryer and then coated with a 30 nm coat of gold with an Anatech Hummer VII sputter.

Lung structures, which can be found in some species, were investigated in detail: in addition to the SEM analysis, the pleon was mounted in unicryl resin and cut with a Leica microtome in 0.25 mm slides which were stained with bromine-toluidine blue and then examined with a light microscope. Ink drawings of some representative slides were prepared.

For the analysis of phylogenetic relationships, the Hennigian principles of outgroup comparison, determination of character homology and polarity, and tree construction using the maximum parsimony method were used. For the analysis of the phylogeny of the taxa examined, groundpatterns were reconstructed for the taxa recognized. Characters that are commonly found within a taxon and particularly in their basal representatives were adopted for the groundpattern, both autapomorphies of the taxon and plesiomorphic characters. In terminal taxa, in this work mainly genera, attention has to be paid to apomorphic characters which evolved within a taxon. Such characters can not belong to the groundpattern. Subsequently, groundpatterns for higher taxonomic hierarchies are reconstructed by comparing the groundpatterns of the subordinate taxa. The groundpatterns were used for the reconstruction of the cladogram presented in chapter 5.2 (fig. 13a-d); the sistertaxon relationships were evidenced by means of synapomorphies, the polarity of character states was fixed by outgroup comparison. All taxa, which do not belong to the taxon under consideration were used as outgroups.

New genera were established to accommodate some species which formerly were included in Philoscia Latreille, 1804, but do not share the autapomorphies of this genus. For the definition of new genera, the characters of the species were compared to those present in existing genera. After a check monophyly of the

Table 1. List of the species examined. Species that were probably introduced are marked with an asterisk (*), nomina dubia are marked with an accent (^).

Ligiidae:

Ligia baudiniana Milne Edwards, 1840, Costa Rica, own collection

Detonidae:

Deto echinata Guérin, 1836, South Africa, NMHU

"Philosciidae":

Adeloscia dawsoni Vandel, 1977, Kermadec Archipelago, MNHN

^*Andenoniscus narcissi* Vandel, 1968, Ecuador, MNHN

Andenoniscus schmalfussi Leistikow, 1999, Panama, SMNS

Andenoniscus silvaticus Verhoeff, 1941, Peru, ZSM

^*Andenoniscus tropicalis* Vandel, 1968, Ecuador, MNHN

Androdeloscia albamaculata (Lima, 1997), Brazil, MNRJ

Androdeloscia conipus Leistikow, 1999, Peru, SMNS

Androdeloscia dalensi Leistikow, 1999, Venezuela, MHNG

Androdeloscia digitata Leistikow, 1999, Brazil, MHNG

Androdeloscia feistae Leistikow, 1999, Peru, SMNS

Androdeloscia ferrarai Leistikow, 1999, Peru, SMNS

Androdeloscia formosa (Mulaik, 1960), Mexico, Guatemala, MUFM

Androdeloscia hamigera (Vandel, 1952), Venezuela, MHNG

Androdeloscia lejeunei (Castro and Souza, 1986), Brazil, MNRJ

Androdeloscia longiunguis Leistikow, 1999, Peru, SMNS

Androdeloscia malleus Leistikow, 1999, Peru, SMNS

Androdeloscia merolobata Leistikow, 1999, Peru, SMNS

Androdeloscia opercularis Leistikow, 1999, Venezuela, MHNG

Androdeloscia plicatipus Leistikow, 1999, Peru, SMNS

Androdeloscia poeppigi Leistikow, 1999, Peru, SMNS

Androdeloscia pseudosilvatica Leistikow, 1999, Venezuela, MHNG

Androdeloscia silvatica (Castro and Souza , 1986), Venezuela, MHNG

Androdeloscia taitii Leistikow, 1999, Peru, SMNS

Androdeloscia tarumae (Lemos de Castro, 1984), Brazil, MNRJ

Androdeloscia valdezi Leistikow, 2000, Guatemala, MNHU

Aphiloscia vilis (Budde-Lund, 1908), Tanzania, own collection

Araucoscia chilenica Verhoeff, 1939, Chile, ZSM

Atlantoscia floridana (van Name, 1940), Brazil, own collection

Atlantoscia rubromarginata Araújo and Leistikow, 1999, Brazil MNRJ, own collection

Balloniscus sellowii (Brandt, 1833), Brazil, Argentina, own collection

Benthana convexa Lemos de Castro, 1958, Brazil, MNRJ

Benthana longicaudata (Lemos de Castro, 1958), Brazil, MNRJ

Benthana taeniata Araújo and Buckup, 1994, Brazil, own collection

**Burmoniscus kohleri* Schmalfuss and Ferrara, 1978, Guatemala, own collection

**Burmoniscus meeusei* (Holthuis, 1949), Venezuela, own collection

Caraiboscia christiani Leistikow, 2001, Venezuela, own collection

Caraiboscia microphthalma Vandel, 1968, Ecuador, MNHN

^*Chaetophiloscia frontalis* Lemos de Castro, 1967, Brazil, MNRJ

^*Chaetophiloscia walkeri* (Pearse, 1915), Colombia, AMNH

Colombophiloscia alticola Vandel, 1968, Ecuador, MNHN

Ecuadoroniscus orientalis Vandel, 1968, Ecuador, MNHN

Erophiloscia acanthifera Leistikow, 2001, Peru, SMNS

Erophilosica longistyla Vandel, 1972, Colombia, MNHN

Erophiloscia recurvata Leistikow, 2001, Peru, SMNS

Erophiloscia waegelei Leistikow, 2001, Colombia, MNHN

Formicascia inquilina (van Name, 1936), Guyana, AMNH

**Halophiloscia couchi* (Kinahan, 1875), Venezuela, own collection

Ischioscia amazonica Lemos de Castro, 1955, Brazil, MNRJ

Ischioscia bolivari Vandel, 1968, Brazil, MNHN

Ischioscia cadoangelis Leistikow, 1999, Costa Rica, MUCR, own collection

Ischioscia debilis (Budde-Lund, 1893), Venezuela, BMNH

Ischioscia elongata Leistikow, 1997, Costa Rica, USNM, own collection

Ischioscia fasciifrons Leistikow, 2001, Venezuela, BMNH

Ischioscia guamae Leistikow, 2001, Venezuela, BMNH, own collection

Ischioscia hanagarthi Schmalfuss, 1980, Peru, SMNH

Ischioscia hirsuta Leistikow, 2001, Venezuela, BMNH, own collection

Ischioscia irmleri Schmalfuss, 1980, Brazil, SMNH

Ischioscia longicauda Schmalfuss, 1980, Peru, SMNH

Ischioscia marmorata Leistikow, 1999, Costa Rica, MUCR

Ischioscia martinae Leistikow, 1997, Costa Rica, USNM, own collection

Ischioscia mineri van Name, 1936, Dominica, AMNH

Ischioscia muelleri Leistikow, 1997, Costa Rica, USNM, own collection

Ischioscia nitida (Miers, 1877), Peru, Guiana, BMNH

Ischioscia panamensis Leistikow, 1999, Panama, SMNS

Ischioscia pariae Leistikow, 2001, Venezuela, BMNH, own collection

Ischioscia plurimaculata Leistikow, 1999, Costa Rica, MUCR, own collection

Ischioscia quadrispinis Leistikow, 1999, Costa Rica, MUCR, own collection

Ischioscia stenocarpa Schmalfuss, 1980, Peru, SMNH

Ischioscia sturmi (Vandel, 1968), Ecuador, MNHN

Ischioscia trifasciata Leistikow, 2001, Venezuela, BMNH, own collection

Ischioscia variegata (Dollfus, 1893), Venezuela, MNHN, own collection

Ischioscia zebricolor Leistikow, 1999, Panama, SMNS, own collection

*_Littorophiloscia denticulata_ (Taiti and Ferrara, 1981), Guatemala, own collection

Littorophiloscia insularis (Castro and Souza, 1986), Venezuela, own collection

Metaprosekia nodilinearis Leistikow, 2000, Venezuela, own collection

Mirtana costaricensis Leistikow, 1997, Costa Rica, MUCR

Oniscophiloscia anomala (Dollfus, 1890), Chile, MNHN

Oniscophiloscia mirifica Wahrberg, 1922, Juan Fernández, own collection

^*Oreades lativentris* Vandel, 1968, Ecuador, MNHN

Oxalaniscus ctenoscoides (Mulaik, 1960), Mexico, MUFM

Parischioscia omissa (van Name, 1936), Brazil, AMNH

^*Pentoniscus exilis* van Name, 1925, Guyana, AMNH

Pentoniscus pruinosus Richardson, 1913, Costa Rica, USNM

Pentoniscus vargasae Leistikow, 1998, Costa Rica, MUCR

^*Philoscia colimensis* Mulaik, 1960, Mexico, MUFM

^*Philoscia demerarae* van Name, 1925, Guyana, AMNH

^ *Philoscia geayi* Paulian de Felice, 1944, uyana, MNHN

^ *Philoscia gracilior* Paulian de Felice, 1944, Guyana, MNHN

^*Philoscia moneaguensis* van Name, 1936, Jamaica, AMNH

Philoscia muscorum (Scopoli, 1793), Germany, Bielefeld, own collection

^*Philoscia diminuta* Budde-Lund, 1893, Venezuela, BMNH

^*Philoscia seriepunctata* Budde-Lund, 1893, Venezuela, BMNH

Plataoniscus borellii (Dollfus, 1897), Argentina, MNHN

Portoricoscia richmondi (Richardson, 1901), Puerto Rico, USNM

Prosekia rutilans (Vandel, 1952), Venezuela, MNHN

Pseudophiloscia inflexa Budde-Lund, 1904, Chile, MNHU

Pulmoniscus insularuminfraventum Vandel, 1952, Venezuela, MNHN

Quintanoscia contoyensis (Mulaik, 1960), Mexico, MUFM

Roraimoscia roraimae (van Name, 1936), Venezuela, AMNH

Tropiscia flagellata Vandel, 1968, Venezuela, MNHN

Xiphoniscus mirabilis Vandel, 1968, Ecuador, MNHN

Yaerikima kartaboana (van Name, 1936), Guyana, AMNH

Scleropactidae:

Scleropactes talamancensis Leistikow, 1997, Costa Rica, USNM

Armadillidae:

Reductoniscus tuberculatus Leistikow, 1997, Borneo, MNHG, MNHU

taxon and if there was sufficient evidence for the separate status of a taxon with respect to those characters commonly thought to show minor interspecific variation, a new genus was established. Characters, which are supposed to be important of a supraspecific level (Vandel 1973a and b, Taiti and Ferrara 1980) are the shape of the cephalothorax and the compound eyes, the presence and position of noduli laterales on the coxal plates, the presence of a sulcus marginalis, the structure of the maxilliped, the arrangement of teeth on the lateral maxillular endite, setal patterns of the pereopods, the shape of pleon and pleotelson, the shape of the male pleopod 5 and the genital papilla. The characters mentioned above leave their mark on the generic diagnosis.

Additionally, a cladistic analysis was performed using the PAUP 3.1.1 software (Swofford 1993). The PAUP analysis was performed as a heuristic search, the bootstrap tree was found by 1000 replicates with simple weighting and simple taxon addition. The unrooted trees were rooted by using the taxon 17 "*Ligia*" as outgroup. Characters were transformed in binary data, which were characterzied as "ordered", with character state "0" the plesiomorphic and "1" the apomorphic character state. Wägele (1994) proposed to weigh characters carefully after an a priori analysis of complexity, variability and gain/loss decisions. It was tried to reduce character weighing to a minimal extent mainly because it takes a "subjectivity" to the analysis which actually is tried to be reduced by the use of mathematical algorithms for reconstruction of the phylogeny. In cases where a convergent acquisition of a character was highly unprobable, the character weight was set "5", in cases, where a reductive character occurred, its weight was set "2", the reduction of noduli laterales was set "1", because it is not clear whether the reduction occurred only one time. The characters, which are new acquisitions (e.g. the shape of the antenna-grooming brush (character 58), are more complex compared to the reductive characters (e.g. loss of the ornamental sensory spine, character 56). Furthermore, Wägele (1996) called attention to a thorough a priori analysis of characters by using Hennig's methodology. The use of "ordered" characters in the analysis reflects the a priori examination of the polarity of a character. The results of the PAUP analysis will not be published, since it appears to the author as if the cladisitc analysis may be over-estimated in comparison to the "brain-work" cladogram. A PAUP analysis of *morphological* data may suffer from some adversities compared with an analysis of *molecular* data. First of all, the ratio of characters to taxa is much higher when dealing with molecular data compared with morphological characters. The analysis of a gene coding e.g. for an rRNA may reveal more than 1000 bases, in other words characters. In contrast, the analysis presented in this study is performed with 75 characters. The probability thus is much higher for each character, to "get lost" in a bootstrap cycle. If it is a phylogenetically informative character, the bootstrap value is lowered by chance. Due to the lower number of characters, some taxa may solely be supported by a single autapomorphy. This character may be rather complex, therefore weighed in the data matrix. But simply by chance, and this is a principle of the bootstrap algorithm, it may not be taken in consideration in a sufficient manner, even when 1000 bootstrap replicates are performed. Carpenter (1992 and 1996) doubted in the reliability of a bootstrap analysis mainly for two reasons: firstly, even most of the molecular data sets do not fulfil the statistical limitations of the bootstrap which needs for about 1000 or even 10000 data to be performed reliably. Secondly, statistically sufficiently supported taxa with a confidence of 0.95 need at least three synapomorphies, a fact wich may not be fulfilled in many morphological data sets (cf. also Felsentein 1985).

List of acronymes used:

AMNH	American Museum of Natural History, New York
BMNH	British Museum (Natural History), London
IPNM	Instituto Politécnico Nacional de México, Ciudad de México
MNHG	Muséum d'Histoire Naturelle de Genève, Genf
MNHN	Muséum National d'Histoire Naturelle, Paris
MNHU	Museum für Naturkunde der Humboldt-Universität, Berlin
MNRJ	Museo Nacional, Rio de Janeiro
MUCR	Museo de la Universidad de Costa Rica, San José
MUFM	Museo de la Universidad Federal de México
SMNS	Staatliches Museum für Naturkunde, Stuttgart
USNM	National Museum of Natural History, Smithonian Institution, Washington
VC	Vandel Collection in the Muséum National d'Histoire Naturelle, microscopic slides
ZSM	Zoologische Staatssammlung, München

4 Taxonomic Section

4.1 Phylogenetically Informative Characters

This chapter deals with the phylogenetically informative characters of the morphology of the oniscidean taxa examined with particular respect to the putative groundpattern of Oniscidea and the groundpattern of the Crinocheta recently worked out by Schmidt (1999).

Although Racovitza (1923a, b) proposed an orientation and nomenclature for the isopod body and its appendages, some modifications are made in this study. The appendages are all orientated towards their plesiomorphic position with respect to the groundpattern of Mandibulata hanging down ventrally regardless their functional orientation in the animal. Hence, the terms "medial", "lateral", "rostral" and "caudal" are used for describing structures on the appendages: the rostral side of both the maxillula or pleopod 1 is the side facing towards the cephalothorax, the lateral side towards the lateral margin.

Each paragraph with the description of character states of every tagma and its appendages is followed by the codes used for the character states in the phylogenetic analysis in chapter 5. These lists of character states do not represent a morphological row, some characters reflect alternative evolutional stages.

The cephalothorax of the Oniscidea and hence the Crinocheta is divided by several cuticular furrows in distinct areas which were described in detail by Jackson (1928): a linea supra-antennalis runs between the antennal sockets and forms their lateral margin, dividing the frons in a *postfrons* ventrally and a profrons dorsally of this line. On the *postfrons*, between the insertions of the antennulae, a small distinct area is demarcated, the "lame frontale" [**Ct3-1**], which was figured by Vandel (1952: 117) for *Ischioscia variegata* (Dollfus, 1893). This contrasts with the observations of Jackson (1928) who reported that the lamina frontalis is fused with the clypeus. In the following, the term "lamina frontalis" is used in the sense of Vandel (1943 and 1952). A detailed examination of the morphology and the anatomy of this region of the cephalothorax is needed to clarify the term lamina frontalis. The linea frontalis separates the profrons from the vertex and the genae. Both lines are missing in some taxa due to reduction. In contrast, the *linea marginalis* between the vertex and the genae is always present, in some taxa ending caudally of the eyes, in others joining the linea frontalis laterally and thus forming lateral lobes. All three lines, linea frontalis, linea supra-antennalis and *linea marginalis* are present in species of the genus *Ligia* Fabricius, 1798, in several Crinocheta and Synocheta and must belong to the groundpattern of Oniscidea [**Ct1-1**]. Vandel (1943) stated that the linea frontalis did not exist primarily although he gave a drawing of *Ligia oceanica* (Linné, 1756) and of *Ligidium hypnorum* (Cuvier, 1792) with indication of a linea frontalis (Vandel 1943: 42, fig 16 and 44/45, fig. 17). Few taxa like *Prosekia rutilans* (Vandel, 1952) show the lines mentioned above and bear lateral lobes [**Ct1-5**]. In the common European species *Philoscia muscorum* (Scopoli, 1793) the linea supra-antennalis is reduced [**Ct1-2**], whereas in the bulk of the South American taxa the linea frontalis is missing [**Ct1-3**]. The genus *Pulmoniscus* gen. n. lacks both linea frontalis and lateral lobes [**Ct1-6**]. In a distinct taxon of northern South America, the cephalothorax is modified with a straight profrons [**Ct1-4**], one well-known genus of this taxon is *Ischioscia* Verhoeff, 1928. The shape of the vertex is arched in most taxa of Crinocheta [**Ct2-1**], in *Oniscophiloscia*, the linea frontalis and part of the profrons form a t-shaped medial lobe [**Ct2-4**]. Some taxa like *Ischioscia* have the vertex flattened and the compoud eyes laterally protruding [**Ct2-2**], the profrons of *Mirtana* Leistikow, 1997 bears two swellings medially of the compound eyes [**Ct2-3**]. The clypeus is in most taxa formed by a broad basal part and a narrower distal part adjacent to the *labrum* [**Ct4-1**], it may be subequal in breadth in both the basal and the distal part [**Ct4-2**].

Ct1-1	Cephalothorax with linea frontalis and linea supra-antennalis, no lateral lobes (plesiomorphic)
Ct1-2	Cephalothorax with linea frontalis and lateral lobes, linea supra-antennalis reduced
Ct1-3	Cephalothorax with linea supra-antennalis and lateral lobes, linea frontalis reduced
Ct1-4	Cephalothorax without lateral lobes, profrons level
Ct1-5	Cephalothorax with *linea frontalis*, linea supra-antennalis and lateral lobes
Ct1-6	Similar to Ct1-3, but lateral lobes reduced

Ct2-1	Cephalothorax more or less rounded in frontal view (plesiomorphic)
Ct2-2	Cephalothorax with flattened vertex and laterally protruding compound eyes
Ct2-3	Similar to Ct2-2, but profrons with two swellings
Ct2-4	Similar to Ct2-1, but with T-shaped medial lobe
Ct2-5	Similar to Ct2-2, but Cephalothorax T-shaped in frontal view

Ct3-1	Lamina frontalis distinct (plesiomorphic)
Ct3-2	Lamina frontalis not clearly demarcated

Ct4-1	Clypeus with basis two times broader than distal part (plesiomorphic)
Ct4-2	Clypeus with basis as narrow as distal part

In *Ligia baudiniana* Milne Edwards, 1840, the **eyes** are composed of several hundred ommatidia [**Ey-1**]. A large numer of ommatidia is considered to be a plesiomorphic condition, because they are present in most isopod taxa. In most Crinocheta, the number is reduced considerably, and the larger species of South American "philosciids" bear up to 30, which are arranged in four longitudinal rows [**Ey-2**]. In the genera *Benthana* Budde-Lund, 1908 and *Balloniscus* Budde-Lund, 1885 from southern South America, the number is reduced to less than 20 ommatidia [**Ey-3**]. In other cases, particularly in the smaller species of about 5 mm body length, the five to ten ommatidia are arranged more randomly [**Ey-4**]. Some endogeous taxa are eyeless [**Ey-6**] or possess few individualized ommatidia [**Ey-5**]. The reduction of the number of ommatidia is considered to have occurred several times convergently, depending on the body size and the life strategy of the taxon dealt with: in taxa of small body size, only a couple of ommatidia may be present; in endogeous or troglobitic taxa, eyes may be useless for orientation and thus are prone to reduction.

Ey-1	Eyes composed of several hundred ommatidia arranges in longitudinal rows (plesiomorphic)
Ey-2	Eyes composed of 20 to 30 ommatidia arranged in four rows
Ey-3	Eyes composed of less than 20 ommatidia arranged in four rows
Ey-4	Eyes composed of about ten ommatidia randomly arranged
Ey-5	Eyes composed of three to four individualized ommatidia
Ey-6	Eyes totally reduced

Both **pereon** and **pleon** bear several distinct characters: In most of the taxa examined the dorsal tegument is smooth with cuticular scales and scattered tricorn-like setae [**Ha1-1**]. These setae are referred to as "tricorn-like" [**Ha3-1**] since they differ from the real tricorns of *Porcellio* Latreille, 1804 which were examined in detail by Holdich (1984). The cuticular plaque is not shaped like an inverted "Y" with a thickened base [**Ha3-3**]. In some taxa, the cuticular plaque of the tricorn-like setae is broadened and forms a leaf-like

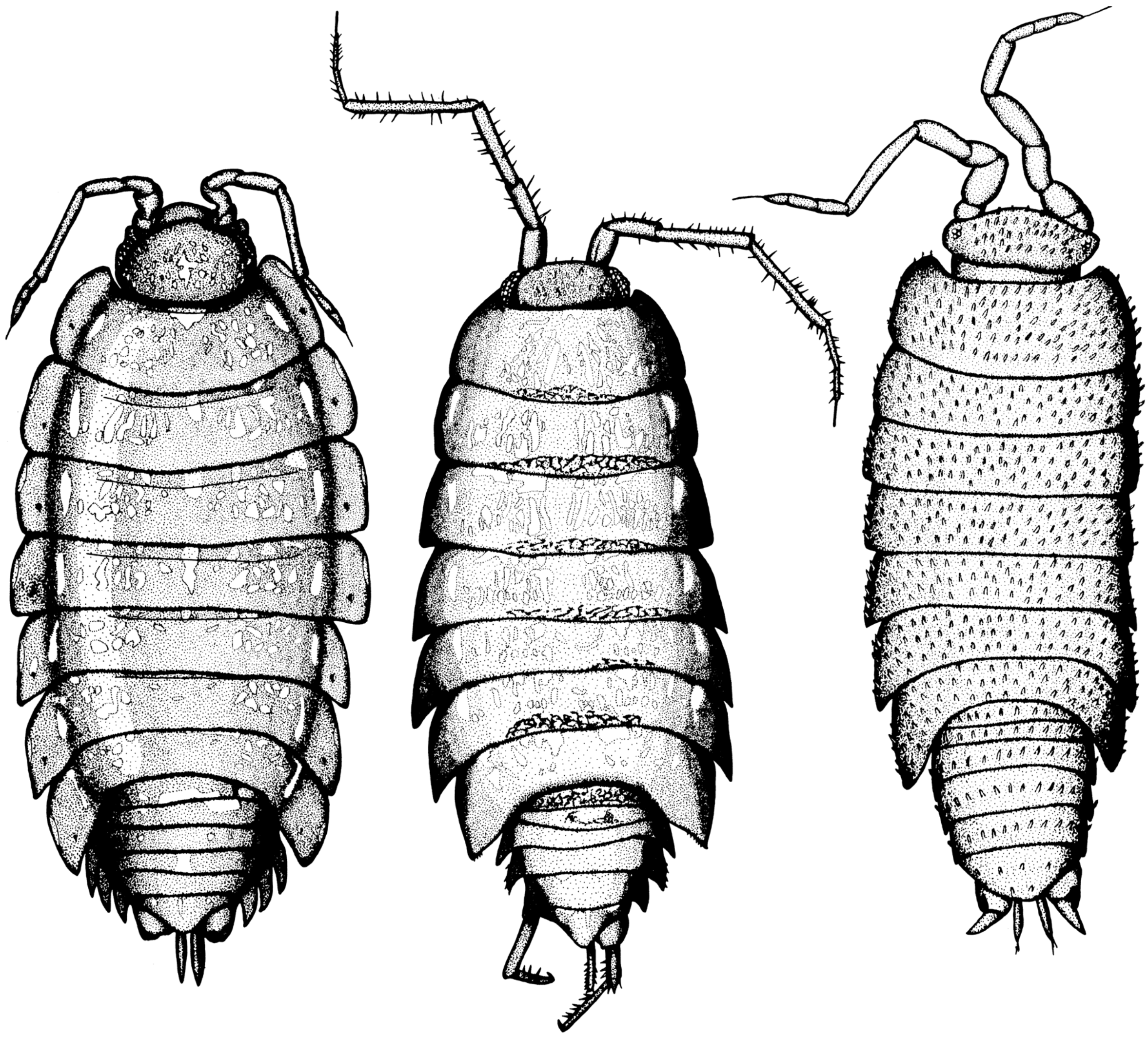

Fig. 1. The different ecomorphological strategies of the Oniscoidea.
Left: *Oniscophiloscia mirifica* Wahrberg, 1922, the clinger type; Middle: *Ischioscia martinae* Leistikow, 1997, the runner type; Right: *Caraiboscia christiani* Leistikow, 2001, the elongate endogeous type

structure with stronger cuticular ridges. The fine structure of these tergal "Blättchenschuppen" was first examined by Schmalfuss (1977) for *Platyarthrus* Brandt, 1833 [**Ha3-2**]. These structures are referred to as "leaflet scales" in this study. The general habitus is influenced by the ratio of the breadths of both the coxal plates and pleonal neopleurae. The plesiomorphic character state is the so-called "runner type" (fig. 1) described by Schmalfuss (1984b) with small neopleurae [**Ha2-1**] and small coxal plates [**Ha5-1**]. In *Ischioscia* these neopleurae, which are found in the pleonites 3 to 5, are quite conspicuous and the pleon is only slightly narrower than the pleon. In several taxa like the genus *Androdeloscia* these neopleurae are much reduced and attached to the lateral pleurites [**Ha2-3**]. Within the Crinocheta, a change in the defensive strategies to the "clinger type" (Schmalfuss 1984b) shows in their shorter pereopods and their prominent neopleurae which lead to an ovate outline of the body [**Ha2-2**], the coxal plates are much broader [**Ha5-3**]. Moreover, their tegument is more or less granulate [**Ha1-2**] as in *Mirtana costaricensis* Leistkow, 1997 or *Benthana longicaudata* (Lemos de Castro, 1958).

The pleotelson is slightly rounded in *Ligia* and the basal Oniscoidea [**Ha4-1**]. It margins are straight in several taxa like *Pseudophiloscia* Budde-Lund, 1904 [**Ha4-2**] or even concave [**Ha4-3**], additionally, *Ischioscia* has a semicircular pit apically [**Ha4-5**]; in the genus *Philoscia*, the Porcellionidae and Onisidae, the distal part of the pleotelson is triangular and much narrower than the proximal part [**Ha4-4**]. In the smaller species, the cuticle is soft, possibly due to a lesser content of calcium carbonate [**Ha6-1r**], similar to the cuticle of *Ligia* [**Ha6-1**]. All Crinochheta with noduli laterales possess a cuticle with deposits of calcium carbonate [**Ha6-2**], which protects the animal from loss of moisture via the cuticle, the derived condition. Since the small genera like *Androdeloscia* evolved from an ancestor within his specific taxon, as can be evidenced from a set of apomorphies, their soft cuticle is a reductive character.

Ha1-1	Dorsum smooth, covered with tricorn-like setae (plesiomorphic)
Ha1-2	Dorsum granulate

Ha2-1	Neopleurae small, pleon narrower than pereon (plesiomorphic)
Ha2-2	Neopleurae broad, continuing outline formed by coxal plates
Ha2-3	Neopleurae almost invisible, pleon much narrower than pereon, coxal plates medium-sized
Ha2-4	Neopleurae almost invisible, pleon much narrower than pereon, coxal plates narrow

Ha3-1	Dorsal sensory receptors "tricorn-like" (plesiomorphic)
Ha3-2	Dorsal receptors with leaf-like cuticular scale
Ha3-3	Dorsal receptors real tricorns: cuticular plaque fused with sensillum, basally thickened, shape of an inverted Y

Ha4-1	Pleotelson caudally rounded (plesiomorphic)
Ha4-2	Pleotelson caudally with straight margins
Ha4-3	Pleotelson caudally with concave margins
Ha4-4	Pleotelson with angled lateral margins, distal part triangular in shape
Ha4-5	Similar to 4-3, with semicircular pit on caudal side of tip
Ha4-6	Pleotelson with two lateral concavities

Ha5-1	Coxal plates medium-sized as in *Philoscia* Latreille, 1804 (plesiomorphic)
Ha5-2	Coxal plates very narrow
Ha5-3	Coxal plates broad as in *Oniscus* Linné, 1958
Ha5-4	Similar to Ha5-1, but coxal plate II distally drawn out in the male

Ha6-1	Cuticle soft with low content of calcite (plesiomorphic)
Ha6-2	Cuticle with deposits of calcium carbonate

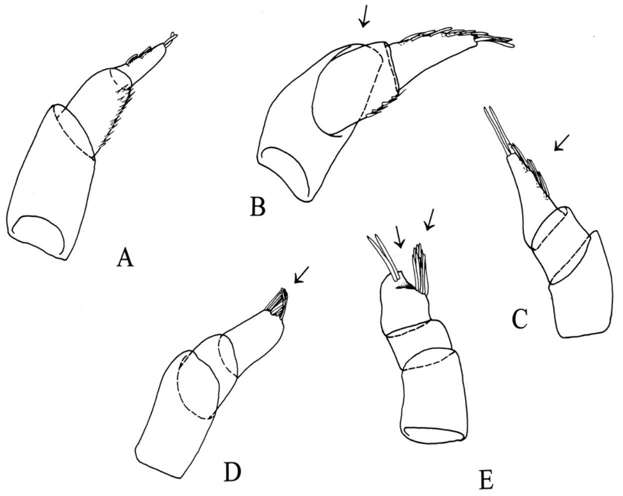

Fig. 2. Some examples of the shape of the antennula in the Crinocheta.
A: *Deto echinata* Guérin, 1836; B: *Ischioscia guamae* Leistikow, 2001, arrow indicating character [A1-3]; C: *Benthana taeniata* Araújo and Buckup, 1994, arrow indicating character [Ae1-1]; D: *Philoscia muscorum* (Scopoli, 1793), arrow indicating [Ae1-4]; E: *Androdeloscia formosa* (Mulaik, 1960), arrows indicating [Ae1-3]

The **antennula** or first antenna (fig. 2) is three-articulate in all examined species. This is the condition in the groundpattern of the Oniscidea. In basal species like *Ligia baudiniana* and *Halophiloscia couchii* (Kinahan, 1875), the articles are elongate and cylindrical [**A1-1**], whereas in other species a derived condition is found: the proximal article is bulky, the distal articles - particularly the medial one - being much shorter [**A1-2**], the members of the genus *Ischioscia* (fig. 2B) have the distal margin of the proximal article drawn out to form a shield-like protrusion [**A1-3**]. On the distal articles, several sets of aesthetascs are inserted, in all cases a set of two aesthetascs apically, the more medio-proximally aesthetascs are inserted in pairs in stepped order (fig. 2B/C) which is certainly the plesiomorphic character state in the Oniscoidea [**Ae1-1**], because it reflects the aesthetasc pattern of formerly unfused flagellar articles as seen in other isopod taxa. These structures may be modified in several ways: the proximal article can be further shortened or enlarged, the sets of medial aesthetascs can be arranged in different positions. In the genus *Prosekia* (fig. 2E), the lateral aesthetascs form a tuft [**Ae1-3**]; in *Philoscia* Latreille, 1804 (fig. 2D), all the aesthetascs are gathered in an apical group [**Ae1-2**]. A further characteristic arrangement is found in the genera *Caraiboscia* Vandel, 1968, *Colombophiloscia* Vandel, 1968 and *Nesophiloscia* Vandel, 1968. Here, the aesthetascs are not attached to the article, they are erected and form a cockscomb-like row [**Ae1-4**].

A1-1	Antennula slender, all articles subequal in length (plesiomorphic)
A1-2	Antennula stout, medial article much shorter than others
A1-3	Antennula with proximal article bearing a shield-like protrusion
A1-4	Similar to A1-3, but protrusion only slight

Ae1-1	Aesthetascs medially in pairs, forming a stepped row (plesiomorphic)
Ae1-2	Aesthetascs gathered apically
Ae1-3	Aesthetascs gathered in a medial tuft separated from an apical pair
Ae1-4	Aesthetascs of cockscomb-like arrangement

The **antenna** is rather uniform in all the examined species: The peduncle is composed of five free articles, a further basal peduncular article is partially fused with the cephalothorax (Schmalfuss 1974). The articles are densely covered with tricorn-like setae and bear a distal sensory spine at least in the distal articles 4+5. The flagellum is composed of far more than ten articles in the Ligiidae [**A2-1**], in the Oniscoidea no taxon has such a multi-articulate flagellum. The number of flagellar articles is reduced to fewer than ten: the Scyphacidae and Detonidae are known to have four flagellar articles [**A2-2**], The three-articulate flagellum [**A2-3**] was one of the characters used by Vandel (1962) to describe the family "Philosciidae". This is however a character of the groundpattern of the Oniscoidea sensu Schmalfuss (1989). Some differences in the flagellum concern the allometry of articles and the position of aesthetascs; they can be found in pairs on the medial and distal articles, sometimes there are two sets on the medial article. Apically on the distal article, there is an apical organ composed of a tuft of sensilla (fig. 3). This apical organ was examined in detail by Mead *et al.* (1976) in *Porcellionides sexfasciatus* (Koch, 1847). The sensilla, which are free in *Ligia* or *Deto* Guérin, 1836 (fig. 3A) [**Ao1-1**] are wrapped in a cuticular sheath with just the tips free, two sensilla pass through the cuticular sheath in the proximal half of the apical organ [**Ao1-2**]. Two different character states can be found: the apical cone is much shorter than the distal article (fig. 3B) with the free sensilla as long as the entire organ [**Ao2-1**], the length ratio is further shifted towards a much shorter apical organ in the "higher" Crinocheta like *Philoscia* (fig. 3D) or *Porcellio* [**Ao2-2**]. In most of the "philosciids"examined and also in the Scleropactidae (fig. 3C), the apical cone is half as long as the flagellum with short free sensilla [**Ao2-3**].

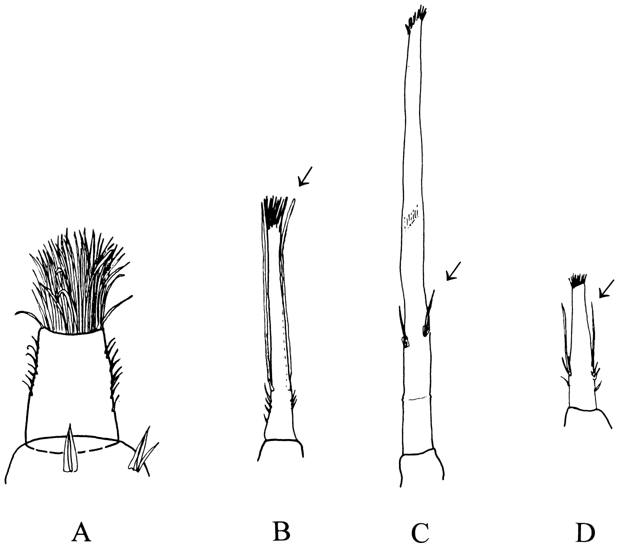

Fig. 3. The different character states of the apical organ of the antenna in the Crinocheta, arrows indicating free sensilla. A: *Deto echinata* Guérin, 1836; B: *Benthana taeniata* Araújo and Buckup, 1994; C: *Ischioscia guamae* Leistikow, 2001; D: *Philoscia muscorum* (Scopoli, 1793)

A2-1	Antennal flagellum multi-articulate (plesiomorphic)
A2-2	Antennal flagellum four-articulate
A2-3	Antennal flagellum three-articulate

Ao1-1	Apical organ a simple tuft of sensilla (plesiomorphic)
Ao1-2	Apical organ covered by cuticular sheath

Ao2-1	Apical organ shorter than distal flagellar article, long free sensilla (plesiomorphic)
Ao2-2	Apical organ less than half the length of the distal flagellar article, long free sensilla
Ao2-3	Apical organ at least half the length of the distal flagellar article, short free sensilla

In all Oniscidea, the **mandibles** lack a palp; and the pars molaris which is present in the Ligiidae and Synocheta [Md**1-1**] is replaced by a molar penicil in the Crinocheta [**Md1-2**]. This molar penicil can consist of more than ten branches e.g. in *Roraimoscia* Leistikow, 2000 [**Md2-1**], about seven to ten partially fused branches in *Ischioscia* [**Md2-2**], up to five partially fused branches in *Andenoniscus* [**Md2-3**] or even a simple penicil as in *Colombophiloscia* [**Md2-4**]. The pars intermedia is identical in its equipment with penicils in all the examined species: the left mandible bears two and the right bears one penicil, and several coniform setae. There are only slight differences in the shape of the asymmetrical laciniae mobiles in the examined species. They are close to the groundpattern as described by Schmalfuss (1974a).

Md1-1	Pars molaris present (plesiomorphic)
Md1-2	Pars molaris replaced by a molar penicil

Md2-1	Molar penicil composed of more than ten free branches (plesiomorphic)
Md2-2	Molar penicil composed of seven to ten basally fused branches
Md2-3	Molar penicil composed of three to five basally fused branches
Md2-4	Molar penicil simple

More differences can be observed in the maxillae 1 or **maxillulae** (fig. 4): In the groundpattern of Oniscidea, the medial endite bears three apical penicils [**Mm1-1**], this number is reduced to two in the Crinocheta, with an apical tip most probably representing the remainder of the third penicil [**Mm1-2**]. There are some taxa like *Benthana* Budde-Lund, 1908 (fig. 4C) or *Atlantoscia* Ferrara and Taiti, 1981, where the apical tip is reduced [**Mm1-3**]. The lateral endite bears a fringe of trichiae latero-distally. In *Ligia*, a set of five strong teeth is inserted laterally on the apex, they are placed in a semi-circle in the middle with a feathery stalk [**Ml1-1**]. The number of teeth is subsequently reduced with the inner set bearing six teeth (fig. 4B) in *Deto* [**Ml1-2**]. In all the other taxa examined herein, there are only four prominent simple teeth laterally, at the base of the rostral tooth a small plaque can be found representing the fifth tooth. Among the teeth, a so-called slender stalk is present in most genera [**Ml2-1**]. This stalk was first observed by Ferrara et al. (1995) on the maxillula of Torajiinae, a Southeast Asian subfamily of Scleropactidae, but can be found in most crinochete taxa (Schmidt 1999). The stalk is the vestigial feathery slender tooth present in *Ligia.* Within the Oniscoidea, it may sometimes be reduced as in *Balloniscus* [**Ml2-2**] or inserted more medially as in *Oxalaniscus* Leistikow, 2000 [**Ml2-3**]. The medially placed set of six smaller teeth is diverse in tooth morphology. The following different conditions have been observed: most of the teeth are ctenate in the genus *Benthana* (fig. 4B) and its allies [**Ml1-3**], or they bear one additional tip (fig. 4A/D), which is called a cleft tooth [**Ml1-4**]. The latter is the most common condition in the South American philosiids. Few taxa have lost the additional tips totally, all the teeth of the maxillula are simple as in *Caraiboscia* Vandel, 1968 (fig. 4E) or *Pseudophiloscia* Budde-Lund, 1904 [**Ml1-5**] or the number of teeth is reduced [**Ml1-6**], particularly in the smaller species. Moreover, in *Pseudophiloscia* Budde-Lund, 1904 the lateralmost tooth is huge compared to the others [**Ml1-8**]. On the rostral surface of the endite, two small subapical teeth can be found. In most species examined, there is only one subapical tooth, if there is any. A particular type of smaller teeth is found in the genus *Pulmoniscus* gen. n.: the apex of the tooth is bearing three points which produce a crown-like appearance [**Ml1-7**].

Mm1-1	Medial maxillular endite with three penicils (plesiomorphic)
Mm1-2	Medial maxillular endite with two penicils and apical tip
Mm1-3	Similar to MM1-2, apical tip reduced

Ml1-1	Lateral maxillular article with 5+7 teeth, plumose slender stalk, inner set ctenate (plesiomorphic)
Ml1-2	Lateral maxillular article with 5+6 teeth, teeth of inner set simple

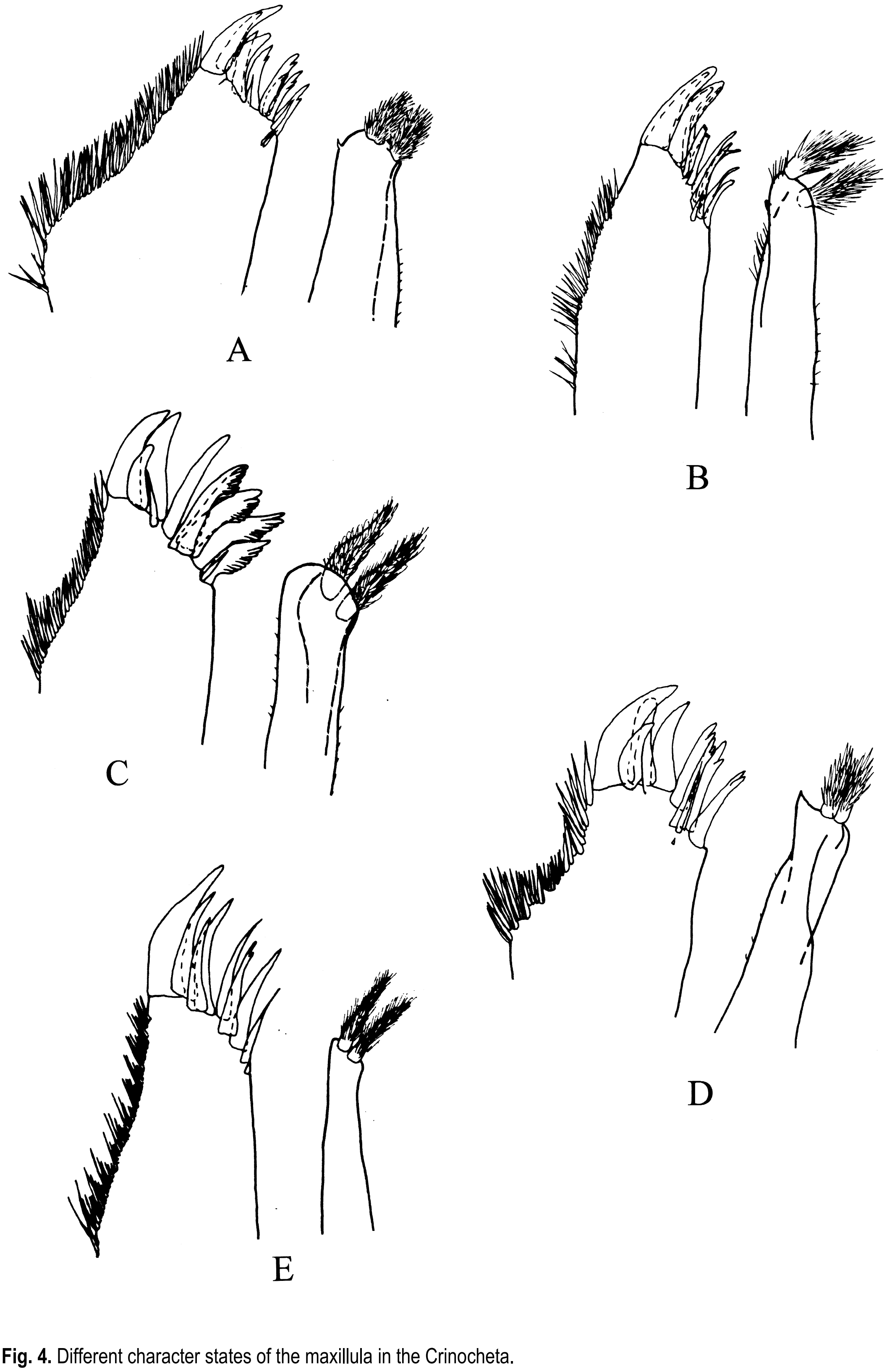

Fig. 4. Different character states of the maxillula in the Crinocheta.
A: *Ischioscia guamae* Leistikow, 2001 [Ml1-4]; B: *Deto echinata* Guérin, 1836 [Ml1-1, with simple teeth]; C: *Benthana taeniata* Araújo and Buckup, 1994 [Ml1-3]; D: *Androdeloscia formosa* (Mulaik, 1960) [Ml1-4/6]; E: *Caraiboscia christiani* Leistikow, 2001 [Ml1-5/6]

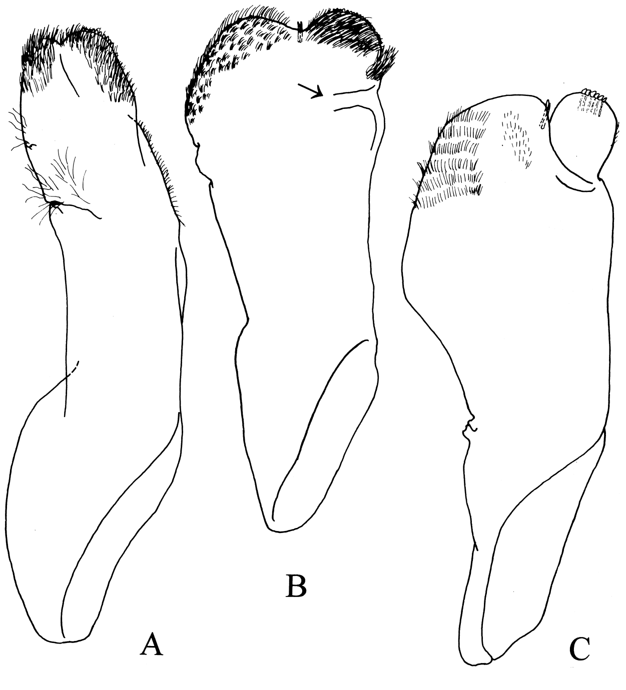

Fig. 5. Three typical maxillae of the Crinocheta.
A: *Deto echinata* Guérin, 1836 [M2-1]; B: *Ischioscia guamae* Leistikow, 2001, arrow indicating [M2-4]; C: *Philoscia muscorum* (Scopoli, 1793)

Ml1-3	Lateral maxillular article with 4+6 teeth, inner set ctenate
Ml1-4	Lateral maxillular article with 4+6 teeth, inner set cleft
Ml1-5	Lateral maxillular article with 4+6 teeth, inner set simple
Ml1-6	Number of teeth of inner set reduced
Ml1-7	Shape of some smaller teeth modified: apex crown shaped
Ml1-8	Lateral tooth huge, remaining teeth subequal in length

Ml2-1	Simple slender stalk present in lateral position (plesiomorphic)
Ml2-2	Slender stalk reduced
Ml2-3	Similar to Ml2-1, but stalk more medially inserted

The **maxilla** (fig. 5) is composed of two endites which are fused over most of their length. In the groundpattern of the Crinocheta, which is similar to the character state found in *Deto* (fig. 5A), both lobes are of equal breadth [**M2-2**], densely covered with small trichiform setae and pectinate scales. This character state is found in several of the genera examined in this work. The bulk of species possess a more derived morphology of the maxilla: the medial lobe is reduced in size and it looks like being embraced by the lateral lobe [**M2-3**]. In other taxa the medial lobe is broader than the lateral, obviously a convergence to the plesiomorphic condition found in *Ligia* [**M2-1**]. Among those taxa, *Ischioscia* is characterized by a strong sclerotized clasp (fig. 5B), proximal to the inner lobe [**M2-4**]. There is a row of small innervated cusps on the apex of the medial lobe, their number ranging from five to about 20.

M2-1	Maxilla with inner lobe broader than outer lobe (plesiomorphic)
M2-2	Maxilla with both inner and outer lobe subequal in breadth
M2-3	Maxilla with inner lobe smaller than outer lobe
M2-4	Maxilla with a slcerotized clasp proximally of inner lobe

In the groundpattern of the Oniscidea, the **maxilliped** (fig. 6) is bearing a palp - the endopodite of this appendage - which is composed of five partially fused articles, defined by the medial setal tufts, which are placed distally on the edges of the former articles [**Mp2-1**]. In the Crinochaeta, the number of articles is reduced, the palp is composed of three articles [**Mp2-2** to **Mp2-4**]. The proximal article remains unfused, it normally bears two spines which can be subequal in length [**Mp5-1**] as in *Halophiloscia*; in most cases the medial one is more prominent [**Mp5-2**]. In several species, the smaller lateral spine is totally reduced. The setal tufts are simplified in the different taxa and, thus, can be used for the reconstruction of phylogeny: in the basal taxa like *Quintanoscia* Leistikow, 2000, the setal tufts are very prominent, bearing more than 30 sensilla [**Mp2-2**]. These tufts are smaller in *Ischioscia* (fig. 6B) or *Mirtana*, though comprising more than 20 sensilla [**Mp2-3**]. The setal tufts may be even smaller, composed of even fewer setae [**Mp2-4**] as in *Andenoniscus* (fig.6D). Moreover, the smaller species have the proximal tuft reduced [**Mp2-5**]. Most of the South American genera with philosciid facies have the medial setal tuft on a slender stalk (fig. 6D), a medially directed protrusion of the second article [**Mp2-6**]. This character is shared with the Scleropactidae and is a common derived character of those taxa.

In *Deto* (fig. 6A) and several other taxa the endite is long, densely covered with setae and with a prominent penicil on the rostral surface [**Mp3-1**]. The length of both the endite and penicil and the setation are reduced in some taxa [**Mp3-2**], the more derived character state is a bare endite without penicil but with two prominent caudal teeth [**Mp3-3**]. In *Philoscia* (fig. 6C) and the

Porcellionidae, the endite is free of setation, but its distal margin is transverse, bearing some small points [**Mp3-5**], *Benthana* lacks these points [**Mp3-4**]. The basipodite is covered with tricorn-like setae caudally and may bear a latero-proximal groove, the sulcus lateralis [**Mp4-2**]; this groove is lacking in *Ligia* and *Deto* [**Mp4-1**]. In *Ligia* and the basal Crinocheta, the basipodite is rather weak [**Mp1-1**], whereas it is much more prominent in the more derived Oniscoidea [**Mp1-2** and **Mp1-3**]: it is rectangular in shape and almost as long as the maxillula, the palp is comparatively smaller.

Mp1-1	Basipodite only slightly broader than apical region with endite and palp (plesiomorphic)
Mp1-2	Basipodite much broader than apical region
Mp1-3	Similar to Mp-2, but latero-distal edge bearing fine hair-like setae

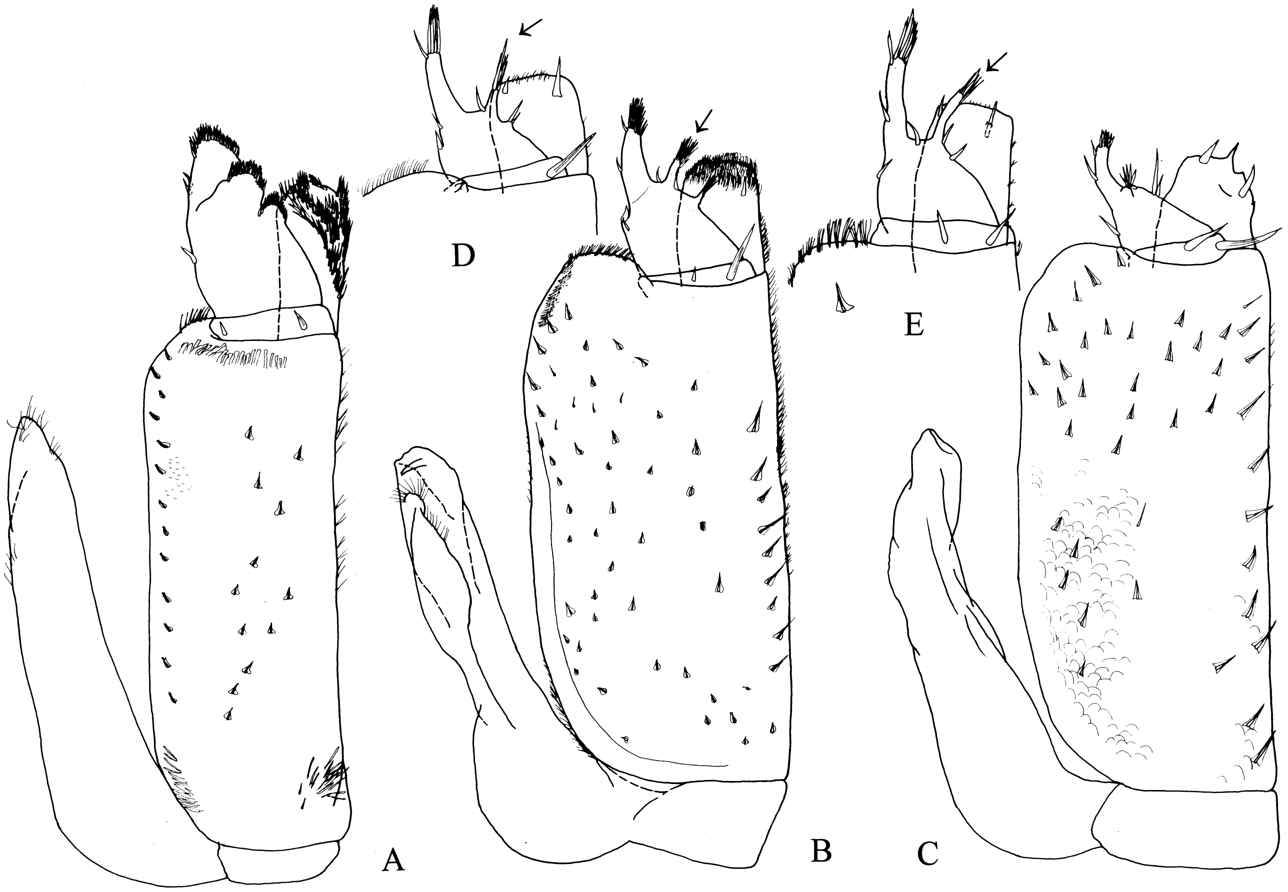

Fig. 6. Aspects of the morphology of the maxilliped in the Crinocheta, arrows indicating [Mp2-6].
A: *Deto echinata* Guérin, 1836 [Mp1-1/Mp2-2/Mp3-1]; B: *Ischioscia guamae* Leistikow, 2001 [Mp1-3/Mp2-3/Mp3-2]; C: *Philoscia muscorum* (Scopoli, 1793) [Mp1-2/Mp2-4/Mp3-4]; D: *Androdeloscia formosa* (Mulaik, 1960) [Mp2-4/Mp3-3]; E: *Caraiboscia christiani* Leistikow, 2001 [Mp2-5/Mp3-3]

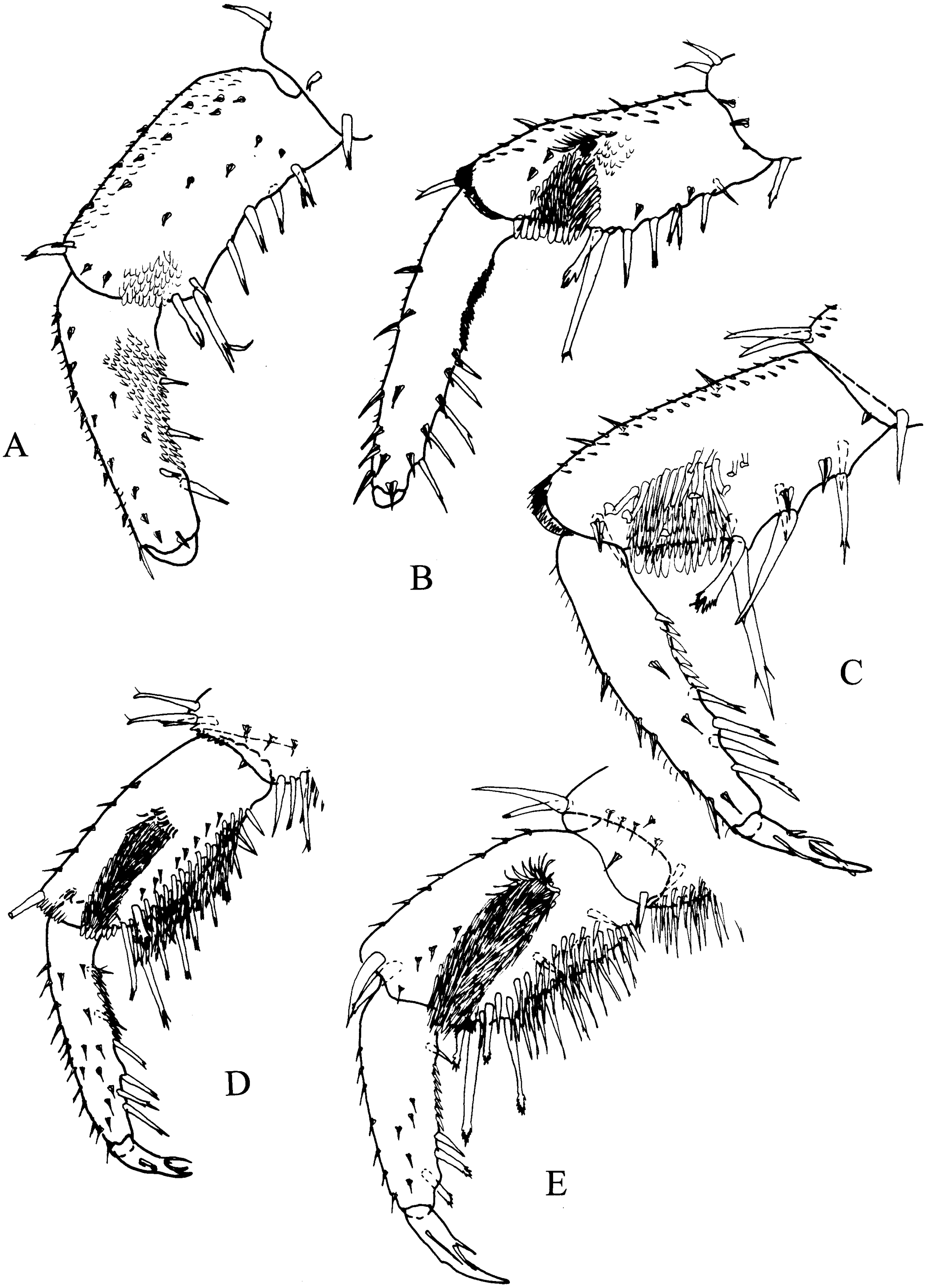

Fig. 7. Some examples of the structure of the pereopod 1 carpus and propus in the Crinocheta. A*: Deto echinata* Guérin, 1836; B: *Benthana taeniata* Araújo and Buckup, 1994; C: *Androdeloscia formosa* (Mulaik, 1960); D: *Philoscia muscorum* (Scopoli, 1793); E: *Plataoniscus borellii* (Dollfus, 1897)

Mp2-1	Palp with five articles, all but proximal one with prominent setal tufts of more than 30 setae (plesiomorphic)
Mp2-2	Palp with three articles, all but proximal one with prominent setal tufts of more than 30 setae
Mp2-3	Palp with three articles, distal setal tufts bearing 20-30 setae, inner tuft smaller
Mp2-4	Like Mp2-3, distal tuft of about 15 setae, medial and proximal tuft of a long and a short seta
Mp2-5	Proximal setal tuft reduced
Mp2-6	Medial setal tuft on a slender stalk

Mp3-1	Endite apically setose, very slender, with long penicil (plesiomorphic)
Mp3-2	Endite apically setose, much shorter, with knob-like penicil
Mp3-3	Endite rectangular, without setae and knob-like penicil
Mp3-4	Endite apically transverse, without setae and knob-like penicil
Mp3-5	Like Mp3-4, but with two latero-distal points

Mp4-1	Basipodite without sulcus lateralis (plesiomorphic)
Mp4-2	Basipodite with sulcus lateralis

Mp5-1	Setae of proximal article of palp subequal in length (plesiomorphic)
Mp5-2	Medial seta of proximal article of palp much longer than lateral one

In most taxa the seven pairs of **pereopods** are slender, enabling the animals to escape from danger by running fast. In most species, at least the pereopods 6 and 7 can be seen in dorsal view. Only in a few species, which have prominent neopleurae on the pleonites 3 to 5, the pereopods are covered by the neopleurae. As in all Crinocheta, the propus of pereopod 1 and also the carpus bear devices for antenna-grooming, and cleaning of the mouthparts (fig. 7). These devices were described by Verhoeff (1908b). The antenna-grooming brush of the carpus is composed of a furrow on the rostral surface of the carpus, which is equipped with elongate cuticular scales. The distal scales may be broader and combed on their distal part of the antenna-grooming brush ("Grannenkämmchen" of Verhoeff) [**PE10-2**]. The groove may be arranged in a longitudinal [**PE3-1**] or transverse [**PE3-2**] position. The latter character state is present in members of the Oniscoidea sensu Schmalfuss (1989) and similarly in the outgroup – e.g in several "Scyphacidae" like in *Deto echinata* (fig. 7A), and thus most probably reflecting the plesiomorphic character state. The distal part of the antenna-grooming brush may be broadened and then bears a set of fringed scales [**PE10-2**]. In the taxa with a transverse antenna-grooming brush, the representatives which are basal with respect to several characters, e.g. *Alloniscus*, have no latero-distal tuft of setae on the carpus [**PE1-1**]; this tuft is missing in *Pseudophiloscia* with a subquadrangular carpus [**PE5-3**] as well. But it is present in e.g. *Ischioscia* or *Benthana* [**PE1-2**].

The medial margin of propus to merus bears several sensory spines, long cuticular structures which contain a sensillum, that is uncovered in the subapically region in the basal taxa [**PE8-1**]. The sensillum may be enclosed by a cuticular cover [**PE8-2**], as in *Philsocia*; this certainly reflects the apomorphic chatacter state. This type of spine is similar to the spines of marine Isopoda (J.W. Wägele, pers. comm.) and are described in detail by Brandt (1988). In *Alloniscus* and also in *Philoscia* and the Porcellionidae, the medial margin of the carpus 1 bears many sensory spines which do not represent a distinct pattern [**PE4-1**]. The genera related to *Ischioscia* and *Prosekia* (fig. 7C) have two to four medial sensory spines which are increasing in length towards the distal margin of the carpus 1 [**PE4-2**]. In *Pseudophiloscia*, the sensory spines are located on small humps along the medial margin, forming three longitudinal rows [**PE4-3**].

At least one of the sensory spines differs considerably from the others: the cuticle is flattened on its apex and forms a double-fringed serrate [**PE7-1**] or hand-like [**PE7-2**] structure. This particular sensory spine is located proximally of the carpal antenna-grooming device and was called "Schutzstachel" by Verhoeff (1908b). Since its protective function is not evidenced, the term "ornamental sensory spine" will be used in the following; it should be used in a more descriptive way. Such a type of double-fringed sensory spine can be found in marine Isopoda and in *Ligia* and *Deto* as well, thus being a plesiomorphy for the Oniscoidea. The ornamental sensory spine is lost in the Balloniscidae [**PE7-3**].

In the males of several taxa, specialized devices for clinging to the female during copulation have evolved. Most taxa of philosciid facies bear more or less expanded setal fields on the rostral surface of the pereopod 1 carpus [**PE2-2**], whereas in the bulk of Oniscoidea the medial margin is flattened and the number of sensory spines is multiplied [**PE2-1**]. Since the most basal representatives of Oniscoidea (the species of *Alloniscus*) have such fields of sensory spines, it is considered the plesiomorphic character state in this work. Some genera like *Andenoniscus* do

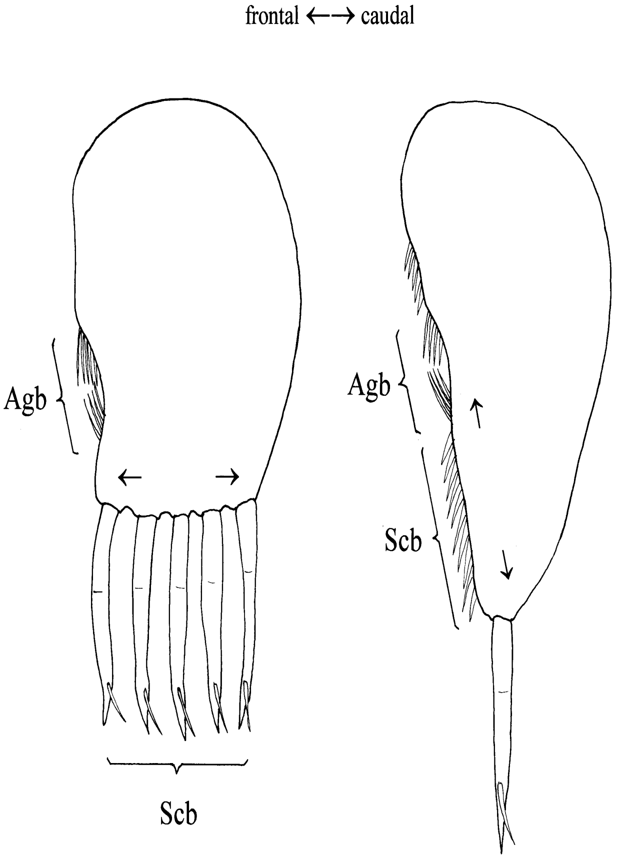

Fig. 8. Schematic cross sections of male pereopod 1 carpus showing position of the convergently evolved setose clinging brush (Scb) and the homologous antenna-grooming brush (Agb). Arrows mark the allometric changes of the carpus. Left: *Alloniscus* Dana, 1853, right: *Halophiloscia* Verhoeff, 1908

not bear any clinging devices [**PE2-3**]. The rostral setal brushes may be located on medially directed lobes in *Ischioscia* [**PE6-4**], in the Halophilosciidae, even the propus is flattened and enlarged [**PE6-2**]. A schematic cross section for the two types of clinging brushes is shown in fig. 8. The South American taxa with philosciid facies bearing such setal fields are characterized by a distinct arrangement of the medial sensory spines of the carpus, which may be evident only in the female in cases where the pereopod 1 is sexually dimorphic [**PE4-2**], in *Benthana*, *Plataoniscus* (fig. 7E) and other genera with brushes composed of sensory spines, the carpus 1 is more cylindrical in shape [**PE5-1**].

Furthermore, the merus and ischium of the pereopods 5 to 7 may be involved in sexual differentiation, a common character is the number of sensory spines on the lateral margin of the ischium 7; in the basal taxa, there are no more than four sensory spines [**PE9-1**], in *Philoscia*, the Balloniscidae and Porcellionidae, their number is much higher [**PE9-2**].

PE1-1	Pereopods without those setal tufts (plesiomorphic)
PE1-2	Pereopods with setal tufts on latero-distal edge of carpus and merus
PE2-1	Pereopods with brushes of sensory spines on carpus and merus (plesiomorphic)
PE2-2	Pereopods with brushes of cuticular scales on carpus and merus
PE2-3	Pereopods without setal brushes
PE3-1	Antenna-grooming brush longitudinal (plesiomorphic)
PE3-2	Antenna-grooming brush transverse, with hyaline scales distally at about one third of breadth of carpus
PE3-3	Similar to PE3-2, but broader, about one half of the breadth of the carpus
PE4-1	Sensory spines of carpus 1 arranged without distinct pattern (plesiomorphic)
PE4-2	Sensory spines of carpus 1 arranged in two rows of three (two to four) spines decreasing in length from distal to proximal, rostrally a parallel row of tricorn-like setae
PE4-3	Sensory spines of carpus arranged in three parallel rows of about four spines standing on humps
PE5-1	Pereopod 1 carpus cylindrical (plesiomorphic)
PE5-2	Pereopod 1 carpus rhomboidal
PE5-3	Pereopod 1 carpus subquadrangular
PE6-1	Male pereopods without enlargements (plesiomorphic)
PE6-2	Male pereopod 1 carpus and propus enlarged
PE6-3	Male pereopods 1 to 4 propus enlarged
PE6-4	Male pereopod 1 carpus with medial circular enlargement
PE7-1	Ornamental sensory spine apically with serrate double-fringe (plesiomorphic)
PE7-2	Ornamental sensory spine apically hand-like
PE7-3	Ornamental sensory spine reduced
PE8-1	Sensory spines with free sensillum (plesiomorphic)
PE8-2	Sensory spines with covered sensillum
PE8-3	Similar to PE8-2, but spines apically three-tipped

PE9-1	Male pereopod 7 ischium with laterally two to four sensory spines (plesiomorphic)
PE9-2	Male pereopod 7 ischium with laterally more than four sensory spines

PE10-1	Narrow distal end of antenna-grooming brush without fringed scales (plesiomorphic)
PE10-2	Broad distal end of antenna-grooming brush with fringed scales
PE10-3	Similar to PE10-1, but fringed scales present

Particular interest is focussed on the **dactylus** (fig. 9) of the pereopods. In all taxa, there is an inner claw, which may be short [**Da1-1**] or almost as long as the outer claw [**Da1-2**]. It is probably not homologous with the inner claw of the Ligiidae and Tylidae. Since the genus *Olibrinus* Budde-Lund, 1913 has no inner claw, the inner claw of the other Crinocheta may be a derived sensory spine. An interungual seta, which may be of sensory function, is present in all taxa, in most taxa it is slender, straight [**Da2-1**] or sinuous [**Da2-2**]; in the Halophilosciidae (fig. 9D), it is more prominent, with a particularly differentiated apical region [**Da2-3**]. The dactylar seta ("organ dactylien" of e.g. Vandel 1960) is a derived sensory organ with a plumose apex [**Da3-1**] in the basal genera like *Ischioscia* (fig. 9B), spatuliform [**Da3-2**] in *Ischioscia zebricolor* Leistikow, 1999, knob-like (fig. 9C/D) in *Philoscia* [**Da3-3**], or simple [**Da3-4**] in most higher taxa (fig. 9F) like *Balloniscus*, and e.g. Porcellionidae. The plumose type of dactylar seta is certainly plesiomorphic for the groundpattern of Oniscoidea, and it is even present in the Scyphacidae. In contrast to Vandel's (1943) statements, it is never totally reduced but shortened and of simpler structure in many species.

Da1-1	*Dactylus* with short inner claw (plesiomorphic)
Da1-2	*Dactylus* with long inner claw

Da2-1	Interungual seta straight (plesiomorphic)
Da2-2	Interungual seta sinuous
Da2-3	Interungual seta prominent

Da3-1	Dactylar seta apically plumose (plesiomorphic)
Da3-2	Dactylar seta apically spatuliform
Da3-3	Dactylar seta apically knob-like
Da3-4	Dactylar seta simple

The basal article of the pereopods, the **coxa** is broadened and fused with the tergites of the pereonites in most isopods except the basal ones (Asellota, Phreatoicidea). These coxal plates may be delimited from the tergites by a sulcus in ovigerous females, most probably for making this fusion more flexible due to the development of a marsupium in thoracic segments 3 to 5. Similar to the tergites, the tegument of the coxal

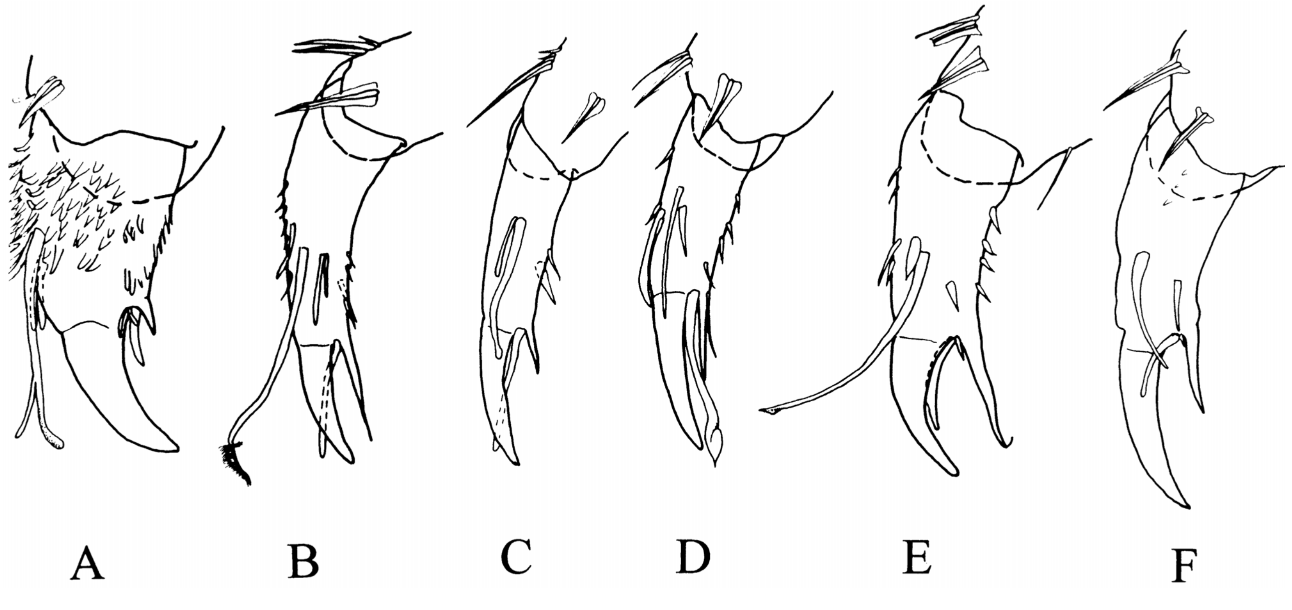

Fig. 9. The different shape of the pereopod dactylus in the Crinocheta.
A: *Deto echinata* Guérin, 1836 [Da1-1/Da2-1/Da3-1, modified]; B: *Ischioscia pariae* Leistikow, 2001 [Da1-2/Da2-1/Da3-1]; C: *Androdeloscia formosa* (Mulaik, 1960) [Da1-2/Da2-1/Da3-4]; D: *Littorophiloscia insularis* (Castro and Souza, 1986) [Da1-2/Da2-3/Da3-4]; E: *Philoscia muscorum* (Scopoli, 1793) [Da1-2/Da2-2/Da3-1]; F: *Plataoniscus borellii* (Dollfus, 1897) [Da1-2/Da2-2/Da3-4]

plates may be granulate or smooth and is covered with tricorn-like setae. Furthermore, the lateral margin is delimited by a faint sulcus marginalis [**Cx4-1**], which is reduced [**Cx4-2**] particularly in taxa with narrow coxal plates. The area between the sulcus marginalis and the lateral margin of the coxal plate may bear gland pores [**Cx1-2**], although in most taxa examined they were not present [**Cx1-1**]. Only one taxon of the examined genera has clearly defined glandular fields which can also be found in other taxa of Oniscidea (Porcellionidae, Trachelipodidae and other families) [**Cx1-3**].

Among the tricorn-like setae of the coxal plates, one or two can differ remarkably in structure and size, the noduli laterales ("Seitenknötchen" of Verhoeff 1907) [**Cx2-2**]. There are no ultrastructural investigations on these receptors and the homology of these structures has not been proved yet. Deviated dorsal receptors were found in some Synocheta by Schmidt (1999). According to the present systematics, the basalmost genus of the Oniscoidea sensu Schmalfuss is *Alloniscus* Dana, 1852, which lacks the noduli as well as outgroup taxa of the Oniscidea [**Cx2-1**]. Noduli laterales do not belong to the groundpattern of Oniscoidea. The question whether the noduli laterales are primarily lacking in several "philosciids"-like *Ischioscia*, or whether they are reduced remains still open debate. Possibly, there was a selective pressure to differentiate one or two of the dorsal receptors to fulfil a particular task which is still unknown. The different position of the noduli in many taxa may be an argument for treating the noduli laterales of different taxa as convergent structures. But more research is needed to clarify this question. In the Halophilosciidae, all noduli are inserted at the same distance from the lateral margin [**Cx3-1**]. Most taxa have the *nodulus* IV inserted more distantly from the lateral margin, the subsequent ones abruptly [**Cx3-3**]or gradually [**Cx3-4**] nearer to the margin. In *Burmoniscus* Collinge, 1914 and several Indopacific genera, the *nodulus* II also is more distantly inserted [**Cx3-5**]. The genus *Pseudophiloscia* with aequidistant noduli, bears two per coxal plate [**Cx3-2**].

Cx1-1	Coxal plates without gland pores (plesiomorphic)
Cx1-2	Coxal plates with scattered gland pores
Cx1-3	Coxal plates with gland pore fields

Cx2-1	Coxal plates without nodulus lateralis (plesiomorphic)
Cx2-2	Coxal plates with nodulus lateralis
Cx2-3	Similar to Cx2-1, but some variation in shape of tricorn-like setae

Cx3-1	All noduli laterales at same distance from medial margin (plesiomorphic)
Cx3-2	Coxal plates with two noduli laterales
Cx3-3	Nodulus lateralis IV extraordinarily shifted dorsally, distal ones abruptly nearer to margin
Cx3-4	Nodulus lateralis IV extraordinarily shifted dorsally, distal ones gradually nearer to margin
Cx3-5	Nodulus lateralis II and IV extraordinarily shifted dorsally
Cx3-6	Noduli laterales extraordinarily long

Cx4-1	Sulcus marginalis present (plesiomorphic)
Cx4-2	Sulcus marginalis reduced

The **pleopods** are at first glance rather similar in all species examined. The rami are plate-like, inserting on a broad sympodite. The endopodite is covered by a thin cuticle and has osmoregulatory function, the exopodite bears a lateral row of sensory spines, the medial margin is covered by pectinate scales. The endopodites of pleopods 3 to 5 are similar in both sexes, *Ligia* has subrectangular endopodites [**PL9-1**], most taxa examined in this study have bilobate exopodites [**PL9-2**] and in two taxa of northern South America, the females have the endopodite 3 distally drawn out at its medial point [**PL9-3**]. The exopodite 1 is rounded in several taxa of Oniscoidea [**PL3-2**]. The basal species of Oniscoidea have a pointed exopodite which is the plesiomorphic character state [**PL3-1**]. In the males, the pleopod 1 exopodite may have various shapes, being elongate in *Oniscophiloscia* [**PL3-6**], drop-shaped in *Caraiboscia* [**PL3-5**] or bearing a lateral incision [**PL3-3**]. Such an incision is present in *Benthana* or *Ischioscia*, these taxa acquired this character most probably independently, because the basal representatives of both taxa do not bear such an incision.

The exopodites bear a lateral row of sensory spines [**PL8-1**], which derived from the plumose setae in *Ligia*. In *Plataoniscus* Vandel. 1963 and *Roraimoscia* Leistikow, 2000, there are two rows of spines [**PL8-1**]. Since both taxa belong to different monophyletic groups, evidenced from several derived characters, the double row must have evolved independently.

On the caudal surface of pleopod 5 exopodite, a transverse or sinuous row of pectinate scales is present in almost all taxa examined [**PL7-2**], forming a creel to protect the pleoventral cavity (Hoese 1981). The taxa of the *Ischioscia*-group (pl. 62, PL5) have three rows of pectinate scales [**PL7-3**]. The basal Crinocheta like *Deto* do not bear such a creel [**PL7-1**].

The male pleopod 1 and 2 endopodites are transformed to copulatory organs which interact with the genital papilla. Thus, several interlocking structures have evolved, as recently demonstrated by Erhard (1997) and first described by Legrand (1946). The endopodite 1 has a caudal furrow, its medial margin bears a row of small spines [**PL4-2**], which may be reduced in several taxa [**PL4-1**]. The pointed shape of the endopodite is deviated several times and may be specifically complex in some neotropic "philosciids". The elongate endopodite 2 can reach a length of more than twice the length of the exopodite [**PL5-2**]. This faint structure is then retained by the pleopod 5 exopodite, which is medio-proximally protruding and may show a caudal furrow for holding the endopodite 2 [**PL6-3**]. Such a "guide slot" certainly evolved several times convergently in taxa with extremely prolonged pleopod 2 endopodites. For *Porcellio dilatatus* Koch, 1846, Legrand (1946) described the structure in detail. He also stated that this guide slot which he called "gouttière marginale" is present in several Synocheta, all higher Crinocheta, but is lacking in the Scyphacidae primarily, and in the Trachelipodidae and *Hemilepistus* Auduoin, 1825 due to the short pleopodite 2 endopodite. Verhoeff (1920) misinterpreted this guide slot as part of a water conducting system. He referred to the rim - the "Innenrandlängsrinne" - as a structure to divert a surplus of water from the pleoventral area.

Pleopodal lungs [**PL1-1**] are evolved several times in the Oniscoidea; among the taxa of philosciid facies, only few have pleopodal lungs [**PL1-2**]. The members Balloniscidae (pl. 150, E/F) both bear semi-covered [**PL2-1**] and covered lungs [**PL2-2**], semi-covered lungs are present in *Atlantoscia rubromarginata* Araújo and Leistikow, 1999, too.

PL1-1 Pleopods without respiratory areas on exopodites (plesiomorphic)
PL1-2 Pleopods with repsiratory areas on exopodite 1

PL2-1 Pleopods with semi-covered lungs on exopodites 1 to 5, bearing transverse clasps (plesiomorphic)
PL2-2 Pleopods with monospiracular covered lungs on exopodites 1 to 5

PL3-1 Male pleopod 1 exopodite pointed (plesiomorphic)
PL3-2 Male pleopod 1 exopodite rounded
PL3-3 Like PL3-1, but with lateral incision
PL3-4 Male pleopod 1 exopodite almost subquadrangular
PL3-5 Male pleopod 1 exopodite drop-shaped
PL3-6 Male pleopod 1 exopodite elongately pointed

PL4-1 Male pleopod 1 endopodite without caudomedial row of spines (plesiomorphic)
PL4-2 Male pleopod 1 endopodite with caudomedial row of spines
PL4-3 Similar to 1, but apex with hyaline cuticular lamellae

PL5-1 Male pleopod 2 endopodite slightly longer than exopodite (plesiomorphic)
PL5-2 Male pleopod 2 endopodite flagelliform
PL5-3 Similar to PL5-1, but apex club-like
PL5-4 Similar to PL5-1, but saw-like structure on half-length

PL6-1 Male pleopod 5 exopodite rhomboid (plesiomorphic)
PL6-2 Male pleopod 5 exopodite with straight medial margin
PL6-3 Similar to PL6-2, but with a guide slot caudally
PL6-4 Similar to PL6-2, but distally extremely drawn out

PL7-1 Pleopod 5 exopodite with scattered pectinate scales caudally (plesiomorphic)
PL7-2 Pleopod 5 exopodite with sinuous transverse row of pectinate scales
PL7-3 Pleopod 5 exopodite with three sinuous transverse rows of pectinate scales

PL8-1 Pleopod exopodites with one lateral row of sensory spines (plesiomorphic)
PL8-2 Pleopod exopodites with two lateral rows of sensory spines

PL9-1 Female pleopod 3 exopodite subrectangular (plesiomorphic)
PL9-2 Female pleopod 3 exopodite bilobate
PL9-3 Female pleopod 3 exopodite medially extremely drawn out

The shape of the **uropod** is uniform within the examined taxa, most have rather short endo- and exopodites which are inserted on a subtriangular, laterally grooved protopodite. The insertion may be at the same level [**UR2-1**], as in some species of *Benthana*; or the endopodite is inserted more proximally than the exopodite as in the bulk of taxa [**UR1-2**]. The insertion at the same level is found in *Ligia*, thus it is thought to represent the plesiomorphic character state; similarly, the protopodites surpassing the pleotelson caudally [**UR3-1**] are found in *Ligia* and are referred to as plesiomorphic in the Oniscoidea. In few taxa, the length of the rami is sexually dimorphic [**UR2-2**], this occurs in some species of *Benthana* and *Porcellio.* The dimorphism must have evolved convergently, since the two taxa are only distantly related.

UR1-1	Insertion of rami at the same level (plesiomorphic)
UR1-2	Insertion of endopodite proximally of exopodite

UR2-1	Length of rami similar in both sexes (plesiomorphic)
UR2-2	Length of rami sexually dimorphic

UR3-1	Protpodites surpassing apex of pleotelson caudally (plesiomorphic)
UR3-2	Protopodites shorter than pleotelson

All the species examined but *Ligia baudiniana* Milne Edwards, 1840 belong to the Crinocheta. This term was established by Legrand (1946) in order toreplace the taxon name Embolophora of Verhoeff (1938). Thus, all these species are characterized as having two vasa deferentia within the genital papilla. Within the Oniscoidea, the **genital papilla** bears a strongly sclerotized ventral shield [**Ge1-2**] (Erhard 1997), surpassed by the orifices of the two separate vasa deferentia. In the basal Crinocheta (pl. 136, Gen), the ventral shield is less sclerotized [**Ge1-1**]. These orifices are located on cuticular lobe, which was called "spatule terminale" by Legrand (1946) for *Porcellio dilatatus* Brandt, 1833. Within this work, the term "terminal spatula" will be used. The terminal spatula is rounded [**Ge2-1**] in *Alloniscus* and *Philoscia*, or truncate [**Ge2-2**] in *Ischioscia.* In the genus *Halophiloscia* Verhoeff, 1908, the ventral shield is very short and the orifices are located on a bilobate terminal spatula [**Ge2-4**]. Within this family, the vasa deferentia are much prolonged and are bent twice between the testes and the genital papilla [**Ge3-2**]. In all other taxa, the vasa deferentia are straight [**Ge3-1**], the proximal part slender [**Ge4-1**], but in *Formicascia* where it is inflated [**Ge4-2**].

Ge1-1	Genital papilla without sclerotized ventral shield (plesiomorphic)
Ge1-2	Genital papilla with sclerotized ventral shield

Ge2-1	Terminal spatula rounded, surpassing ventral shield (plesiomorphic)
Ge2-2	Terminal spatula truncate, surpassing ventral shield
Ge2-3	Terminal spatula truncate, as long as ventral shield
Ge2-4	Terminal spatula longer than ventral shield, bifurcate

Ge3-1	Vas deferens straight (plesiomorphic)
Ge3-2	Vas deferens bent two times

Ge4-1	Proximal part of vas deferens narrow (plesiomorphic)
Ge4-2	Proximal part of vas deferens bulbous

4.2 Generic Account

4.2.1 The South American Genera

In the following, for each genus the data on their distribution, status and type species are presented. The autapomorphies for the described taxa are subsequently listed. The genera are ordered in the sequence of their phylogenetic position proposed in chapter 5, where a phylogenetic interpretation of the characters and a hypothetical evolutionary scenario is given. Some distinct taxa and adelphotaxon relationships of several genera are indicated by their apomorphies. They are included in the generic account mainly to make the phylogenetic discussion clearer.

In the following, for each genus the data on their distribution, status and type species are presented. The autapomorphies for the described taxa are subsequently listed. The genera are ordered in the sequence of their phylogenetic position proposed in chapter 5, where a phylogenetic interpretation of the characters and a hypothetical evolutionary scenario is given. Some distinct taxa and adelphotaxon relationships of several genera are indicated by their apomorphies. They are included in the generic account mainly to make the phylogenetic discussion clearer.

Although this work deals with the phylogeny of the family "Philosciidae", some additional family names are included, viz. Halophilosciidae and Balloniscidae. These taxa are included in the analysis because historically they were treated as members of the genus *Philoscia* Latreille, 1804, separated at the beginning of this century by Budde-Lund (1908) and Verhoeff (1908) in new genera. Their phylogenetic status is not resolved until now and, therefore, it shall be elucidated in this work. The taxonomic units called families are artifacts of the traditional systematics and do not represent a hierachic category which is present in nature. The units should be avoided in the phylogenetic systematics.

The codes used to describe character states in the remarks to the taxa are identical with those in chapter 4.1; the symbol ■ indicates that a character is apomorphic, whereas the symbol ☐ is used for the plesiomorphic character state.

Adelphotaxa *Quintanoscia* Leistikow, 2000 and *Oxalaniscus* Leistikow, 2000

These two genera from Mexico are quite basal with respect to several characters: They bear a subrectangular maxilla, the maxillipedal palp is equipped with very prominent setal tufts and the penicil of the endite is still prominent. Nonetheless, they are united in an adelphotaxon relationship due to the following synapomorphies:
■ Cephalothorax with linea frontalis reduced [Ct1-3] ☐ linea frontalis present [Ct1-5]
■ Molar penicil composed of three branches [Md2-3] ☐ molar penicil composed of about ten branches [Md2-1]
■ Lateral endite of maxillula with 4and6 teeth, one of inner set absent or at least vestigial [Ml1-6] ☐ no tooth reduced in size [Ml1-1]
■ Maxillular teeth simple [Ml1-5] ☐ inner set of teeth cleft [Ml1-4]

In the outgroup, the mandibles bear molar penicils of about ten almost free branches, and the maxillular teeth of the inner set are pectinate or cleft. Therefore, the character states in both genera mentioned above are interpreted as being derived.

Genus *Quintanoscia* Leistikow, 2000

Type species: *Philoscia contoyensis* Mulaik, 1960 (by monotypy)
Number of nominal species: 1
Distribution: Only known from southeastern Mexico on the Yucatán Peninsula
Remarks: The genus was established for the Mexican species *Philoscia contoyensis* Mulaik, 1960 because of its unique character set (Leistikow 2000b). As indicated above, it is close to *Oxalaniscus* Leistikow, 2000, but differs in some characters in the cephalothorax, which are commonly accepted to be of importance on the generic level. The genus *Quintanoscia* is close to the groundpattern of the Oniscoidea, the shape of the maxilliped is similar to *Deto* Guérin and *Alloniscus* Dana, 1852. The pereopod 1 is equipped with a longitudinal carpal brush and the medial margin is bearing several bifid sensory spines. The autapomorphies of the genus are:
■ Reduction of the lateral lobes [Ctt1-6] ☐ lateral lobes present [Ctf1-3]
■ Cephalothorax broadened ☐ vertex not broader than height of cephalothorax

The coxal plates bear several tricorn-like setae. One of those setae bears a distinctly longer sensillum, which is twice as long as the basal cuticular plaque. This structure can be interpreted as a nodulus lateralis.

Genus *Oxalaniscus* Leistikow, 2000

Type species: *Philoscia ctenoscoides* Mulaik, 1960 (by monotypy)
Number of nominal species: 1
Distribution: Southern Mexico
Remarks: The genus *Oxalaniscus* belongs to the most basal species of the taxon Oniscoidea. It seems closely related to *Quintanoscia*. The putative synapomorphies are given above. The following characters are the autapomorphies of this genus:
■ Slender stalk of maxillula in a more lateral position [M12-3] ☐ slender stalk medially, surrounded by group of lateral teeth[M12-1]

In all other taxa with a slender stalk on the maxillula, it is in a medial position on the apical region, surrounded by the medial teeth of the outer group.

The Balloniscidae Vandel, 1963

Remarks: In his work on the Oniscidea of Venezuela, Vandel (1952) stressed the taxonomic value of the presence of five pairs of pleopodal lungs in the genus *Balloniscus* Budde-Lund, 1908 and placed this genus in the sub-family Porcellionidae quinquetracheatae (=Trachelipodidae Strouhal, 1953). In a subsequent paper, the genus was devided into the genera *Balloniscus* and *Plataoniscus* Vandel, 1963 to accommodate the differences in lung structure and morphology of the cephalothorax. Both genera were placed in an own family Balloniscidae of uncertain relationships.

Adelphotaxa *Balloniscus* Budde-Lund, 1908 and *Plataoniscus* [Vandel, 1963] gen. n.

Among the South American genera with three-articulate antennal flagellum, the two lung-bearing genera *Balloniscus* Budde-Lund, 1908 and *Plataoniscus* gen. n. from the southern temperate regions of the continent are united in a monophylum by a single character:

■ reduction of the ornamental sensory spine in the male [PE7-3] ☐ ornamental sensory spine present in both sexes [PE7-1]

This character is a reductive character and in consequence the hypothesis of an adelphotaxon relationship can not be falsified. It is desirable to find additional positive characters to support this sister group relationship. Another character, the presence of sencory spines on the medial margin of the male pleopod 1 is a symplesiomorphy, as a similar disposition can be observed in various palearctic genera from several families, e.g. *Philoscia* Latreille, 1804, *Protracheoniscus* Verhoeff, 1917 or *Acaeroplastes* Verhoeff, 1917. One has to focus on the putative common ancestor of all these genera. For the moment no ancestor for a group consisting exlusively of the genera with sencory spines on the medial margin of the male pleopod 1 can be reconstructed due to differences in the morphology of lungs, the shape of the cephalothorax among others. For the time being, the apomorphic character given above is used as indication for a close relationship of *Balloniscus* and *Plataoniscus*.

Genus *Balloniscus* Budde-Lund, 1885

Type species: *Philoscia sellowii* Brandt, 1833
Number of nominal species: 6, all from the New World (the records of *B. nigricans* (Budde-Lund, 1885) and *B. brevicornis* (Budde-Lund, 1885) from Mississippi/USA are unsubstantial and may be wrong)
Distribution: Southeastern Brazil and adjacent Argentina
Remarks: Among the genera described herein, *Balloniscus* is recognized by several autapomorphies:
■ Presence of semi-covered pleopodal lungs in all five pairs of pleopods, respiratory area formed by longitudinal foldings connected by transverse clasps [PL2-1] ☐ lungs lacking the transverse clasps [PL1-2]
■ Male pleopod 1 exopodite subquadrangular to rounded [PL3-4] ☐ pleopod 1 exopodite pointed [PL3-1]

Particularly the characteristic lung structure supports the monophyly of this genus.
The pereopods, which are stout with no setal tufts on the latero-distal edge of carpus and merus differ remarkably from the other genera, but since similarly shaped pereopods are known from several other genera, the systematic value is still unknown. Another autapomorphy is the lack of an ornamental sensory spine in the male pereopod 1 carpus, which is present in the female and similar to those of e.g. *Atlantoscia* Ferrara and Taiti, 1981. The genus was re-examined by Araújo and Leistikow (1999).

Genus *Plataoniscus* gen. n.

Diagnosis: Cephalothorax with linea frontalis and faint linea supra-antennalis, lateral lobes present, compound eyes composed of more than 20 ommatidia. Antennula not described, antenna with three-articulate flagellum bearing short apical organ.
Mandibles undescribed, maxillula with 4+5 slender teeth on lateral endite, maxillula with lateral lobe two times broader than medial one, maxilliped without knob-like penicil on endite.
Pereopods rather stout with longitudinal antenna-grooming brush on carpus 1, ornamental sensory spine double-fringed serrate, dactylar seta simple. Pleopods with exopodites bearing more than 20 sensory spines laterally, in apical region a second row more centrally, covered lungs in all pleopods, lungs 1 to 2 monospiracular, lungs 3 to 5 multispiracular, spiracular area covered with pectinate scales and a derivative of those scales, forming a triangular lobe. Uropod with protopodite subtriangular, laterally grooved, insertion of endopodite proximal to exopodite.
Type species: Vandel (1963) included in his new genus *Plataoniscus* two species of *Balloniscus*, namely *P. borelli* (Dollfus, 1897) and *P. griseus* (Dollfus, 1897) without designating a type species. Thus, the genus name is not available according to § 13a ICZN. To make the name *Plataoniscus* available to science, *P. borellii* is designated the type species of the genus herein.
Number of nominal species: 2, all reported from austral South America
Distribution: Temperate eastern South America

***Plataoniscus borellii* (Dollfus, 1897)** (figures 10-12)
Synonym: *Alloniscus borellii* Dollfus, 1897
Balloniscus borellii (Dollfus, 1897): Arcangeli (1958)
Material: Microscopic slides of an adult female (VC 4941) and male (VC 4942) and a juvenile male (VC 4940) of the Vandel collection, now courtesy of MNHN, Paris.
Colour: A figure of the habitus in dorsal view is given in Vandel (1963: 84, fig.12).
Cephalothorax: Differing from *Balloniscus* in the presence of a linea frontalis and a very faint linea supra-antennalis (Vandel 1963), slight lateral lobes, compound eyes described for *P. argentinus* as comprising about 20 ommatidia (Dollfus 1894) and for *P. borellii* a comparable size was mentioned (Dollfus 1897).

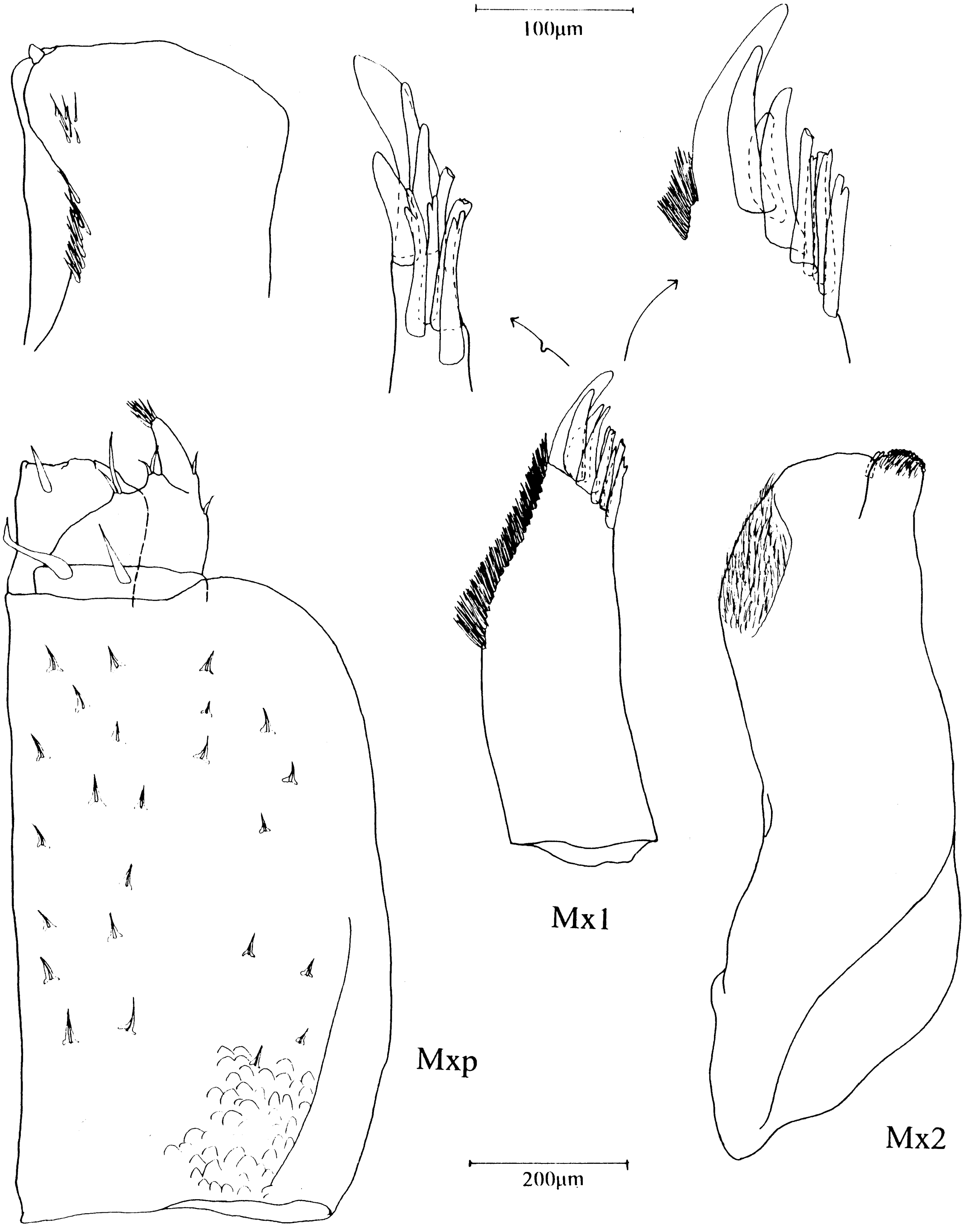

Fig. 10. *Plataoniscus borellii* (Dollfus, 1897), male (microscopic slides)
Mxp maxilliped, with detail of endite in rostral view; Mx1 lateral maxillular endite, with detail of apical lateral endite in caudal and lateral view; Mx2 maxilla

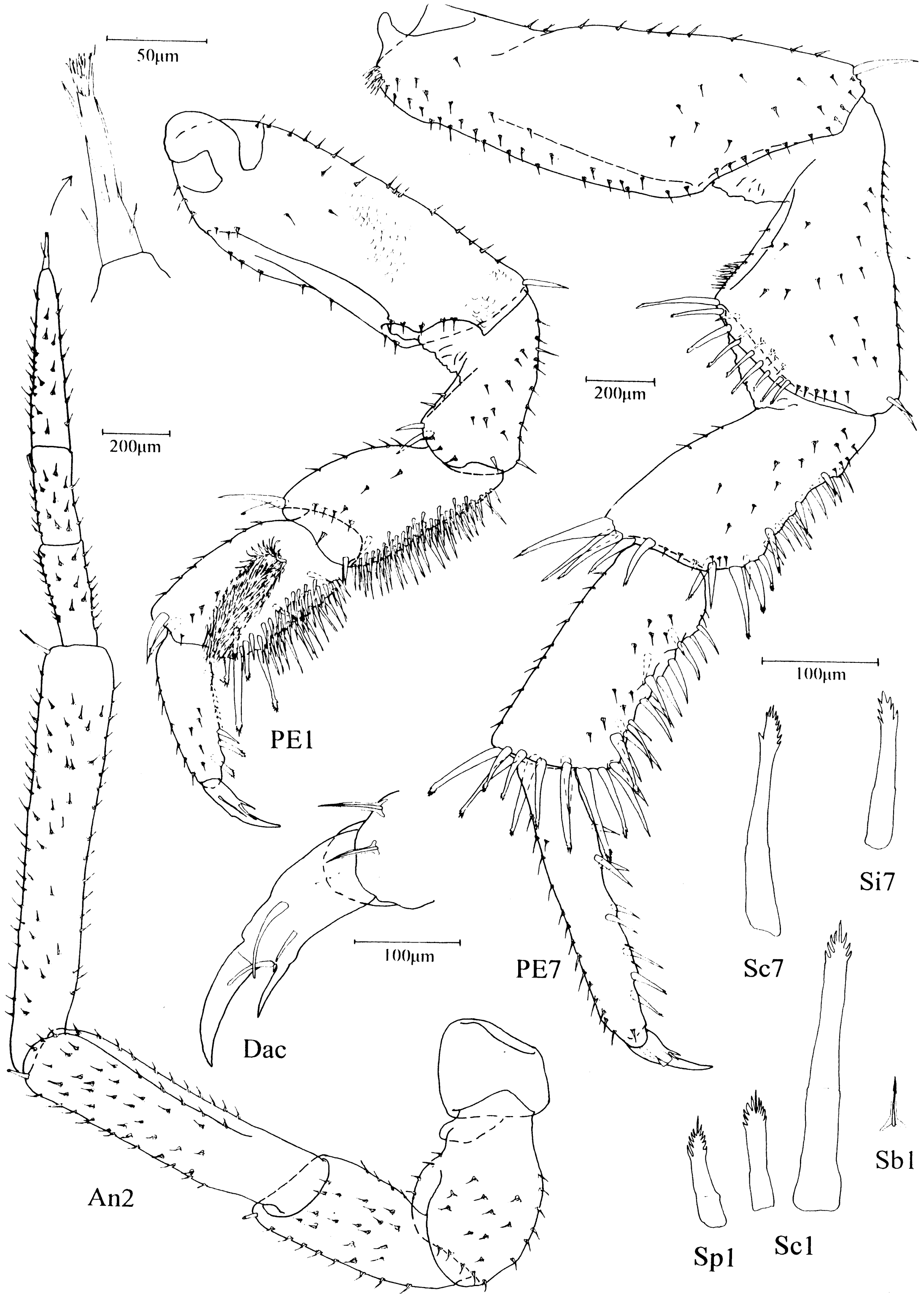

Fig. 11. *Plataoniscus borellii* (Dollfus, 1897), male (microscopic slides)
An2 antenna, with detail of apical organ; Dac dactylus of pereopod 1 in rostral view; PE1/7 pereopods 1 (rostrally) and 7 (caudally); Sb1 tricorn of basis 1; Sc1 sensory spines of carpal brush; Sc7 distal sensory spine of capus 7; Si7 lateral sensory spine of ischium 7; Sp1 distalmost sensory spine of propus 1

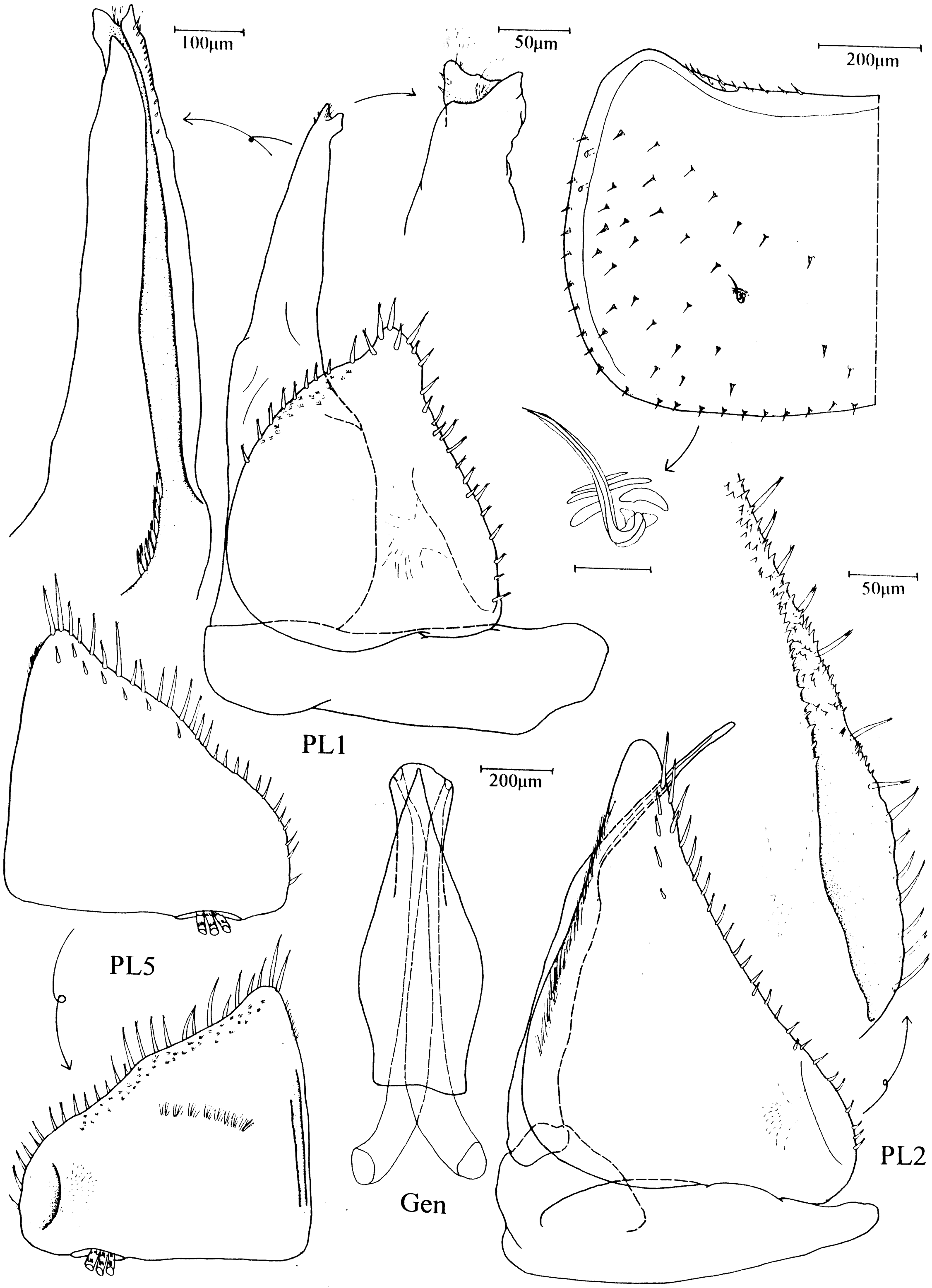

Fig. 12. *Plataoniscus borellii* (Dollfus, 1897), male (microscopic slides)
Cx4 coxal plate IV with detail of nodulus lateralis; Gen genital papilla; PL1 pleopod 1 in caudal view with details of endopodite in caudal and rostral view; PL2 pleopod 2 in rostral view, with detail of spiracular area in caudal view; PL5 pleopod 5 exopodite in caudal and rostral view

Pereon: Smooth tegument covered with tricorns, coxal plates with sulcus marginalis, nodulus lateralis and few gland pores (fig. 12, Cx4).

Pleon: Only slightly narrower than pereon, covered with tricorns, pleotelson acute.

Appendages:

Antennula: Not known in detail.

Antenna: Rather slender with article 5 four times longer than basal article, flagellum composed of three articles, distal article the longest, bearing short apical organ with long free sensilla (fig. 11, An2).

Mandible: Not known in detail.

Maxillula: Lateral endite with 4+5 slender teeth, the inner set cleft, no additional stalk or supapical spine discernible (, Mx1).

Maxilla: Lateral lobe two times broader than medial, bearing faint setation laterally, medial endite apically setose with several rows of cusps (fig. 10, Mx2).

Maxilliped: Basipodite stout with short sulcus lateralis, covered with tricorns, latero-proximally scaly, endite without setation, small smooth knob apically on rostral surface, palp three-articulate with distal setal tuft, two proximal pairs of a long and short seta on medial article, proximal article with two spines (fig. 10, Mxp).

Pereopods: Rather stout, covered with tricorns, no latero-distal setal tuft on carpus (fig. 11, PE1/7), antenna-grooming brush of carpus 1 longitudinal, most distal sensory spines with ornamental apex, medial sensory spines simple or bifid, dactylus with long inner claw and a cuticular scale in pereopod 7 (fig. 11, PE7), dactylar seta simple.

Sexual differentiation: Males with setal brushes on medial margin of pereopod 1 to 3, setal brush composed of sensory spines, ischium of pereopod 7 with medial margin slightly concave, distal margin of caudal side bearing about eight sensory spines.

Pleopods: Pleopod exopodites missing in examined material, exopodites with more than 20 sensory spines laterally, in apical region a second row more centrally (fig. 12, PL1-5), respiratory devices in all five pairs of pleopods: covered lungs with a single spiraculum in pleopod 1 and 2, pleopod 3 to 5 with main spiraculum and additional openings more proximally, perispiracular area with cuticle concentrically wrinkled, the periphery bearing several distinct cuticular scales (fig. 12, PL2).

Sexual differentiation: Male pleopod 1 exopodite circular with obtuse distal apex, sensory spines on lateral and medio-distal margin, endopodite slender, two times longer than exopodite, apex with three lobes, two delimiting spermatic channels, one on rostral side, two apical tufts of fine hairs, medio-caudal row of spines present (fig. 12, PL1). Pleopod 2 exopodite elongate with sinuous lateral margin, endopodite slightly longer, apex pointed (fig. 12, PL2). Pleopod 5 exopodite with medial furrow on caudal surface (fig. 12, PL5).

Uropod: Similar to *Balloniscus*.

Genital papilla: Ventral shield pyriform, orifices laterally of apex of ventral shield, terminal spatulae rounded (fig. 12, Gen).

<u>Remarks:</u> Arcangeli (1958) stressed the separate state of the genus *Balloniscus*, in which he placed *Plataoniscus borellii*, from the Porcellionidae, which have according to an earlier work of Arcangeli (1954) only two flagellar articles. The three-articulate flagellum is a plesiomorphic character found in all the species of philosciid facies which can not be used to define the relationship to other genera. This argument is also valid for the definition of the genus and the family Balloniscidae by Vandel (1963). The presence of a linea frontalis is a plesiomorphy and thus uninformative for differentiating the genus from *Balloniscus*. The following characters are autapomorphies of the genus:

■ Pleopod 1 to 5 exopodites with covered lungs, monospiracular in pleopods 1 and 2, multispiracular in pleopods 3 to 5 [PL2-2] ☐ lungs semi-covered [PL1-2]

■ Perispiracular area with triangular or three-tipped cuticular scales as derivatives of pectinate scales ☐ perispiracular area with simple pectinate scales

■ Pleopod exopodites with second, more centrally located row of sensory spines in apical region [PL8-2] ☐ only one row of lateral sensory spines present [PL-8-1]

■ Male pleopod 5 exopodite with furrow on medial margin of caudal surface [PL6-3] ☐ no such furrow [PL6-2]

Most of these characters are related to the respiratory organs. The pleopodal lungs are quite characteristic in having both mono- and multispiracular orifices.

Genus *Pulmoniscus* gen. n.

<u>Diagnosis:</u> Cephalothorax without lateral lobes and linea frontalis, linea supra-antennalis present, compound eyes consisting of 14 ommatidia in three rows. Antennula three-articulate with coniform distal joint, antennae with three-articulate flagellum bearing short apical organ.

Mandibles with molar penicil composed of about ten branches, maxillula with 4+5 teeth on lateral endite, inner set cleft, lateral lobe of maxilla two times broader than medial one, maxillipedal endite without knob-like penicil.

Pereopods stout, carpus 1 with brush of sensory spines medially, antenna-grooming brush longitudinal, dactylar seta simple, coxal plates with nodulus lateralis and sulcus marginalis. Pleopods with rhomboidal exopodites bearing covered lungs, perispiracular area concentrically wrinkled, endopodites subrectangular. Uropod protopodite subtriangular with lateral groove, endite inserting proximally of exopodite. Genital papilla with truncate terminal spatula.

Type species: *Balloniscus insularuminfraventum* Vandel, 1952 (by monotypy)

Number of nominal species: Only type species is known.

Distribution: Only known from Windward Islands.

***Pulmoniscus insularuminfraventum* (Vandel, 1952) comb. n.** (fig. 13-15)

Material: Microscopic slides of a male VC 3771.1-7 (designated holotype herein) and a female VC 3772 (paratype), Gran Roque (Windward Islands), Cerros orientales, leg. 2.IX.1950, G. Marcuzzi

Colour: Vandel (1952) gave the following description: "...sur un fond jaunâtre se détache un dessin de coulour brun composé d'une ligne médiane, et de deux lignes latérales qui n'atteignent pas le bord des pleurépimères, ce dernier restant clair. Entre les trois lignes foncées, apparaissent les zones de linéoles. Le pleon presente une coloration foncée. Le basis des péréiopodes est taché de brun; les autres articles sont recouvertes d'un réseau assez lâche de chromatophores."

Cephalothorax: A faint linea supra-antennalis is present, no linea frontalis and lateral lobes, compound eyes composed of about 14 ommatidia in three rows.

Pereon: Tegument smooth, covered with few tricorn-like setae, coxal plate with sulcus marginalis and nodulus lateralis, all at almost the same distance from the lateral margin.

Pleon: Slightly retracted from pereon, neopleurae of pleonites 3 to 5 distinct, pleotelson with sinuous lateral margins, slightly pointed, covered with tricorn-like setae, fringe of tricorns caudally.

Appendages:

Antennula: Three-articulate, medial article shortest, distal one coniform, bearing pairs of aesthetascs in stepped position (fig. 13, An1).

Antenna: Rather slender, peduncle similar to *Plataoniscus borellii*, flagellum three-articulate with articles subequal in length, apical organ much shorter than terminal article, bearing long free sensilla (fig. 14, An2).

Mandible: *Pars intermedia* with two penicils on right and one on left side, bearing few coniform setae, molar penicil prominent, composed of about ten branches, additional penicil present (fig. 13, Mxl/r).

Maxillula: Medial endite with two penicils, lateral endite apically bearing 4+5 teeth, inner set cleft, two prominent inner teeth with apex crown-shaped, composed of three tips, slender stalk present (fig. 13, Mx1).

Maxilla: Lateral lobe two times broader than medial one, only sparsely setose, medial lobe with about ten cusps apically (fig. 13, Mx2).

Maxilliped: Basipodite rectangular covered with tricorns, short sulcus lateralis, palp composed of three articles, apically with setal tuft, proximally two pairs of long and short seta, proximal article bearing two setae of subequal length. Endite with few setae, no knob-like penicil rostrally (fig. 13, Mxp).

Pereopods: Slender, densely covered with tricorns (fig. 14, PE1/7), carpus 1 with longitudinal antenna-grooming brush, small antenna-grooming brush on propus 1, dactylus with long inner claw and simple dactylar seta (fig. 14, Dac).

Sexual differentiation: Male pereopods with medial margin of carpus and merus bearing denser brushes of sensory spines, standing in three to four rows.

Pleopods: Pleopod endopodites subrectangular, distal margin slightly convex, exopodites rhomboid with about seven sensory spines laterally (fig. 15, PL1-5), covered lungs in all five pairs, spiracle opening proximally of half-length of lateral margin, perispiracular area covered with concentric cuticular wrinkles, latero-proximal edge of caudal side with slight ledge (fig. 15, PL5).

Sexual differentiation: Pleopod 1 exopodite medially rounded, laterally straight, endopodite two times longer, pointed, bearing a subapical lobe on lateral margin, some spines apically (fig. 15, PL1). Pleopod 2 exopodite more pointed than other, endopodite slender, almost two times longer than exopodite (fig. 15, PL2). Pleopod 5 exopodite with straight medial margin, bearing a caudal ledge (fig. 15, PL5).

Uropod: As in generic diagnosis.

Genital papilla: Apically truncate, ventral shield pyriform, not surpassed by orifices (fig. 15, Gen).

Remarks: The closest relative of this new genus most probably is not *Balloniscus* since it differs remarkably in the shape of the cephalothorax and the structure of the pleopodal lungs. The latter character is similar to *Agnara* Budde-Lund, 1908. The autapomorphies of *Pulmoniscus* gen. n. are:

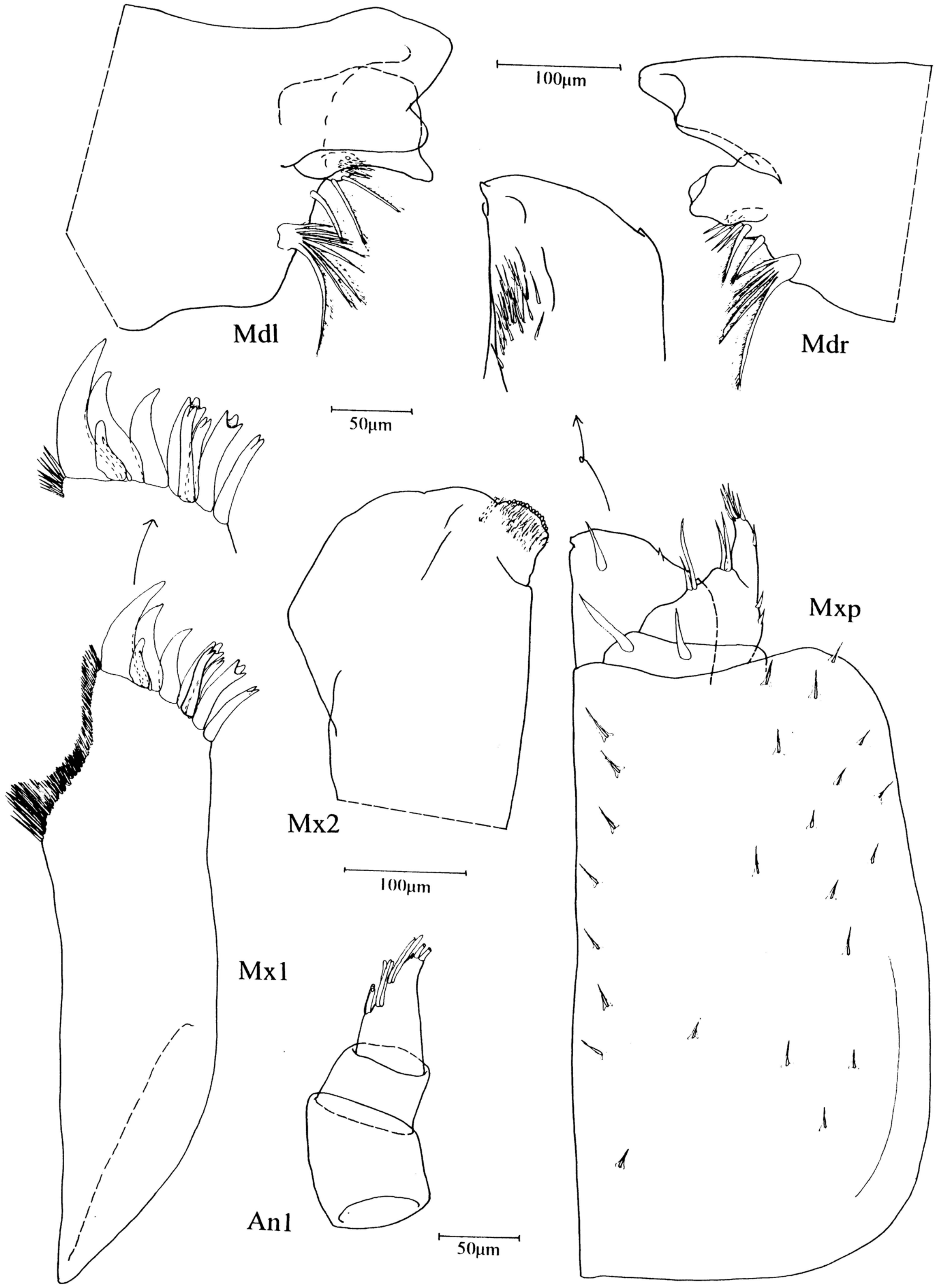

Fig. 13. *Pulmoniscus insularuminfraventum* (Vandel, 1952), male (microscopic slides)
An1 antennula; Mdl/r left and right mandible; Mxp maxilliped, with detail of endite in rostral view; Mx1 maxillula, with details of apical lateral endite in rostral view; Mx2 maxilla

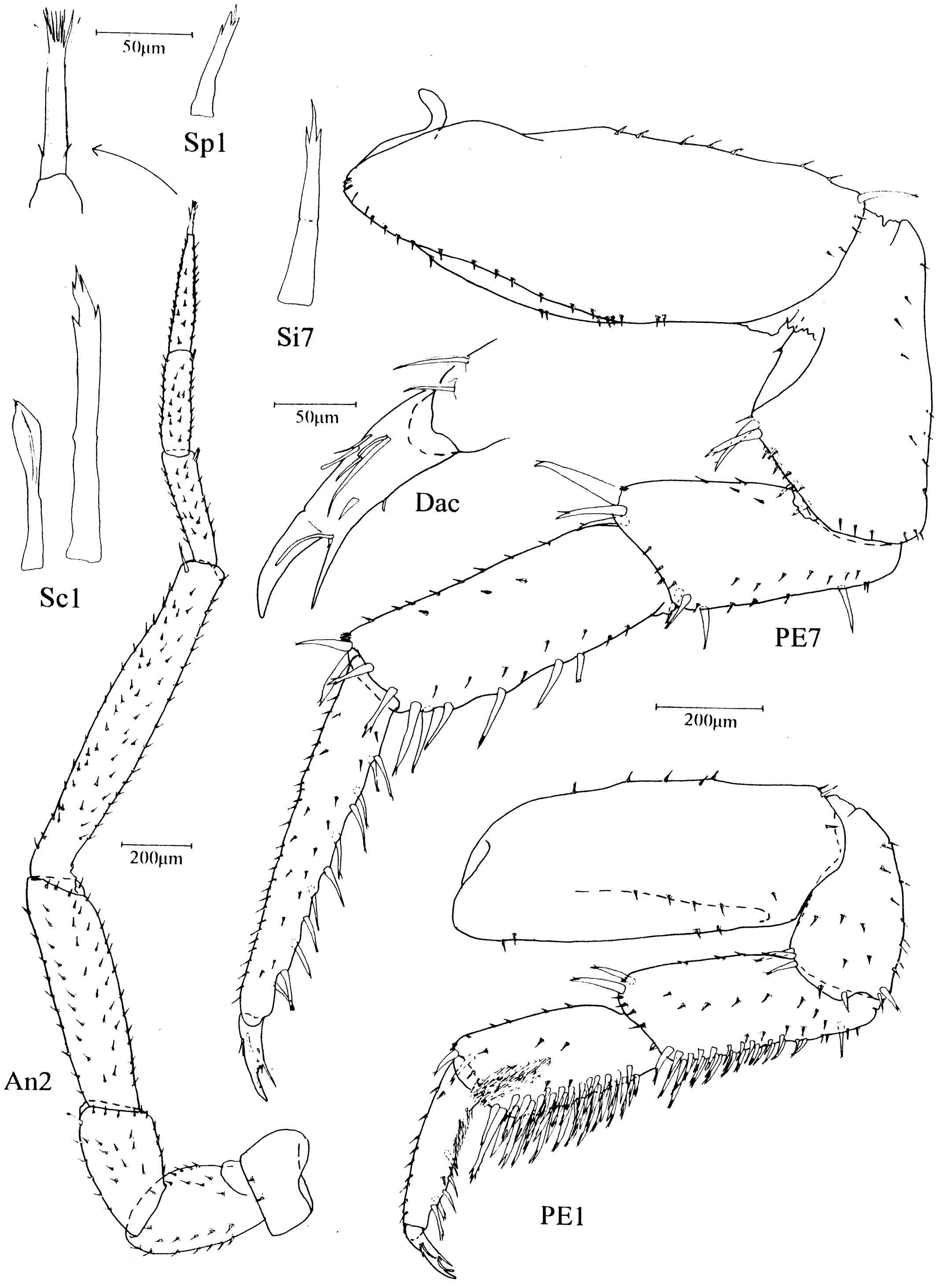

Fig. 14. *Pulmoniscus insularuminfraventum* (Vandel, 1952), male (microscopic slides)
An2 antenna, with detail of apical organ; Dac dactylus of pereopod 1 in rostral view; PE1/7 pereopods 1 (rostrally) and 7 (caudally); Sc1 sensory spines of carpal brush; Si7 lateral sensory spine of ischium 7; Sp1 distalmost sensory spine of propus 1

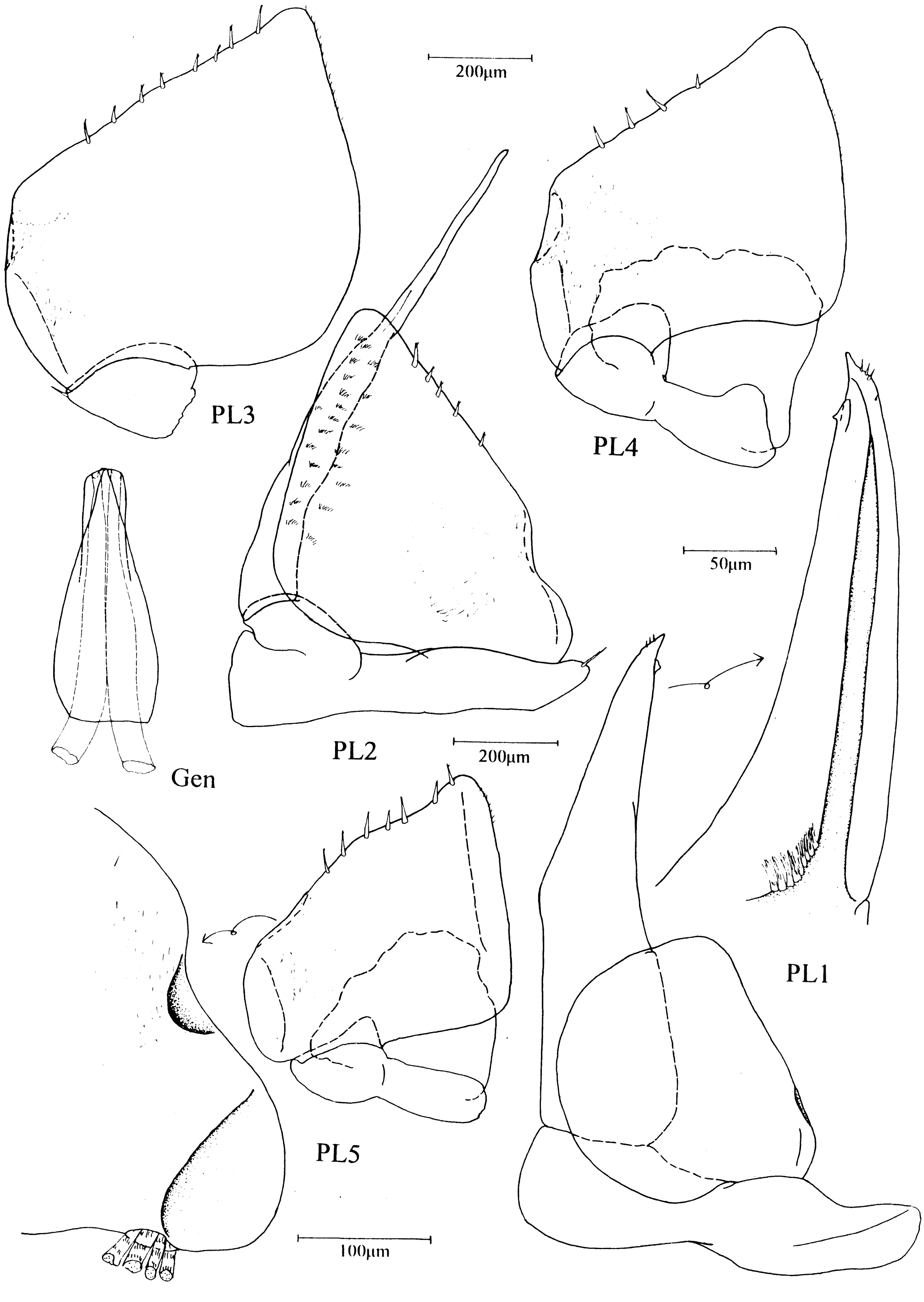

Fig. 15. *Pulmoniscus insularuminfraventum* (Vandel, 1952), male (microscopic slides)
Gen genital papilla; PLf female pereopod 1 in rostral view; PL1-5 pleopods 1 to 5 in rostral view, with detail of endopodite 1 and perispiracular area of exopodite 5 in caudal view

■ Cephalothorax without lateral lobes [Ct1-6] ☐ lateral lobes present [Ct1-3]

■ Lateral endite of maxillula with particular teeth, bearing a crown-shaped 3-tipped apex [Ml1-7] ☐ maxillular teeth cleft [Ml1-4]

■ Covered lungs in all five pairs of pleopod exopodites [PL2-2] ☐ semi-covered lungs [PL1-2]

■ Spiraculum opening distally at more than one third of lateral length ☐ no definite spiraculum

In contrast to the statements of Vandel (1952), the pleopod exopodites all bear covered lungs, and not only pleopod 1 and 2. The cuticle of the perspiracular area of these pleopods is slightly wrinkled in concentric lines. At 400x magnification, this wrinkling can be observed on pleopod 3 to 5, too. The spiracle is difficult to trace, it is located on half-length between the latero-proximal insertion of the exopodite and the most proximal sensory spine of the lateral margin.

The male of *Pulmoniscus insularuminfraventum* (Vandel, 1952) has pleopods quite similar to the species of the genus *Agnara* Budde-Lund, 1908. On the other hand, the genera differ in the shape of the cephalothorax, the tegument, which is smooth in *Pulmoniscus* but granulate in *Agnara*, and the number of flagellar articles with only two in *Agnara*. So this enigmatic species should be treated as a valid taxon.

Genus *Benthana* Budde-Lund, 1908

Synonym: *Benthanoscia* Lemos de Castro, 1958
Type species: *Philoscia picta* Brandt, 1833
Number of nominal species: 15, all from the New World
Distribution: Eastern tropical and subtropical South America, the genus *Benthanoides* is found in Andean temperate South America.
Remarks: The shape of the maxillular teeth is often used for defining this genus (Gruner 1955, Lemos de Castro 1958b), although some other Oniscoidea of philosciid facies with serrate teeth are known: *Ctenoscia* Verhoeff, 1928 from southern Europe, *Benthanops* Barnard, 1932 from South Africa, *Benthanoides* Lemos de Castro, 1958, *Benthanoscia* Lemos de Castro, 1958, both from southern South America and *Alboscia* Schultz, 1995 from Paraguay. Ctenate teeth are equally known from the members of Ligiidae Brandt and Ratzeburg, 1831. Thus, this may be the plesiomorphic character state for the Crinocheta of philosciid facies, as is the additional stalk, which is also found in Ligiidae and Scleropactidae Verhoeff, 1938. In *Benthana*, the maxillular teeth are arranged in a quite different manner than in the other genera examined herein. The apex of the lateral endite is broader. Therefore, the teeth are standing in a semicircle laterally, similar to *Ligia* Fabricius, 1798, representing the position found in the groundpattern of Oniscidea. This character can not be used to define the adelphotaxon of *Benthana* nor the close relationship of the forms bearing ctenate teeth.

The generic independence of *Benthana* and *Benthanoides* has to be doubted, it seems as if the species of *Benthanoides* are simply the more basal species which lack the characteristic dentiform protrusion of the pleopod 1 exopodite. This character was used by Lemos de Castro (1958b) for separation of *Benthana pauper* Jackson, 1928 in the genus *Benthanoides*. For a formal synonymization of the two genera, a detailed phylogenetic study of all the species hitherto known has to be undertaken. It is likely that the genus *Benthanoides* represents the basal representatives of the genus *Benthana* in its original extent (*Benthana* s.l.), with the autapomorphies of *Benthana* s.str.:

■ Cordiform shape of pleopod 1 exopodite with a lateral dentiform protrusion [PL3-3] ☐ exopodite pointed without protrusion [PL3-2]

■ Ornamental sensory spine of carpus 1 with hand-like apex, slightly merged with cuticular stalk [7-2] ☐ ornamental sensory spine with serrate double-fringe [PE7-1]

The second character is at first sight similar to that seen in *Ischioscia* Verhoeff, 1928, but details indicate that the similarity is a convergency: In *Ischioscia* and its allies, the stalk is clearly separated from the hand-like apex, whereas it is intervening in the present genus. It thus is postulated to have evolved independently.

More information on the phylogeny and a description of the hitherto unknown male of *B. convexa* Lemos de Castro, 1958 were given in Araújo and Leistikow (1999), the status of *Benthanoscia* Lemos de Castro, 1958 was discussed in Leistikow and Araújo (2000b).

Genus *Atlantoscia* Ferrara and Taiti, 1981

Synonym: *Ocelloscia* Schultz and Johnson, 1984
Type species: *Atlantoscia alceui* Ferrara and Taiti, 1981 (syn of. *Philoscia floridana* van Name, 1940), by monotypy
Number of nominal species: 2, one restricted to coastal Brazil (Sergipe)
Distribution: Coastal areas of the western Atlantic from Florida to Uruguay
Remarks: *Atlantoscia* is quite basal with respect to most of the neotropical Oniscidea of philosciid facies, characterized by the less derived shape of the antennula, the structure of the apical organ of the antenna

and the short noduli laterales. The structure of the cephalothorax is quite similar to that in the genera *Erophiloscia* Vandel, 1972, *Androdeloscia* Leistikow, 1999 or *Xiphoniscus* Vandel, 1968. The shape of the antennula and the presence of lateral lobes on the cephalothorax are plesiomorphies within the Oniscoidea. The apomorphic characters of this genus are:

■ Sensory spines of carpus and merus with up to five subapical tips, sensillum laterally ☐ sensory spines with up to two subapical tips, sensillum apically

■ Reduction of the tip on the medial endite of the maxillula [Mm1-3] ☐ medial endite with apical tip [Mm1-2]

■ Lateral lobe of the maxilla apically truncate ☐ lateral lobe apically rounded

These apomorphies have to be evaluated with respect to the closest relative of the genus *Atlantoscia*, the genus *Benthana*, with which it shares the shape of the maxilliped. They are mainly confined to the mouthparts and may be susceptible to convergence. At least the first character, the shape of the sensory spines is quite unique among the philosciids and supports monophyly of the genus.

The *Halophiloscia*-group: Halophilosciidae Kesselyák, 1931

Remarks: Taiti and Ferrara (1986a) in their revision of the genus *Littorophiloscia* Hatch, 1947 stressed the similarity of the male pereopods 1 and the interungual seta.

The following synapomorphies for *Halophiloscia* Verhoeff, 1928 and *Littorophiloscia* can be given:

■ Male with pereopod 1 carpus enlarged and propus inflated, both bearing prominent brushes composed of cuticular scales [PE6-2] ☐ male pereopod carpus and propus cylindrical, no setal fields [PE6-1]

■ Interungual seta strong, apically spatuliform [Da2-3] ☐ interungual seta simple, similar to inner claw in strength [Da2-1]

■ Vasa deferentia run from the genital papilla in pereonite 7 rostrally and bend two times caudally and again rostrally [Ge3-2] ☐ vasa deferentia running from genital papilla to pereonite 4, straight [Ge3-1]

The other character mentioned by Taiti and Ferrara (1986a), the shape of the maxillipedal palp, is a symplesiomorphy as stated below. It is similar to the groundpattern of Oniscoidea and can be found in *Alloniscus* Budde-Lund, 1908 and *Quintanoscia* Leistikow, 2000 as well.

The separation of the genera *Halophiloscia* Verhoeff, 1908 and *Stenophiloscia* Verhoeff, 1908 in a (sub)-family of their own was proposed by Kesselyák (1931). He gave reasons for this separation concerning the particular structure of the vasa deferentia which are prolonged and bent two times along their course. This character is present in the species of the genus *Littorophiloscia* as well (present study). They therefore, too, belong to this monophylum. The vasa deferentia differ slightly in size: they are more voluminous and slightly shorter than in *Halophiloscia*, but they are bent two times.

Genus *Halophiloscia* Verhoeff, 1908

Type species: *Halophiloscia couchi* (Kinahan, 1875)
Number of nominal species: 17, only one reported from the Neotropics
Distribution: Mediterranean, coast of eastern Atlantic, southern Caribbean
Remarks: The genus *Halophiloscia* Verhoeff, 1908 was instituted to comprise a couple of species of philosciid facies which are characterized by the setal fringes on the maxillipedal palp (Verhoeff 1908a). The presence of a bifurcate genital papilla and prominent vasa deferentia was observed by Kesselyák (1930). As mentioned in Taiti and Ferrara (1986a), the bifurcate genital papilla may be just the terminal stage of an evolutionary line from with intermediate stages in the genus *Littorophiloscia.* At the moment, with some restriction, the only autapomorphy of the genus is:

■ Vasa deferentia run from the genital papilla in pereonite 7 to pereonite 3 (part C), then bend backwards to pereonite 6 (part B) and run rostrally to segment 4 (part A), where the testes are located ☐ vasa deferentia run from the genital papilla in pereonite 7 rostrally and bend caudally and again rostrally, but not as far

Since the only species examined in detail are *Halophiloscia couchi* (Kinahan, 1875) and *Stenophioscia glarearum* Verhoeff, 1908, it is difficult to judge the value of the length ratios of the parts of the vasa deferentia for generic separation. In *S. glarearum*, the part B is turning rostrally in pereonite 5.

Furthermore, the number of noduli laterales or similar receptors on the coxal plate varies within the genus, e.g. several noduli-like receptors in *H. couchi* (Kinahan, 1875) but only one nodulus lateralis per coxal plate in *H. hirsuta* Verhoeff, 1928 (S. Taiti, pers. comm.). This family is in need of revision on a worldwide scale.

Genus *Littorophiloscia* Hatch, 1947

Diagnosis: Cephalothorax with linea supra-antennalis, slight lamina frontalis and lateral lobes, linea frontalis lacking, compound eyes composed of about 15 ommatidia. Antennula three-articulate, slender, antenna long with three-articulate flagellum, apical organ longer than distal article.

Mandible with molar penicil consisting of about ten free branches, maxillula with lateral endite bearing 4 and 6 teeth, inner set with five teeth cleft, slender stalk present, maxilla with both lobes subequal in breadth, maxilliped with endite setose, bearing prominent penicil rostrally, palp three-articulate, with three prominent setal tufts.

Pereopods slender, ornamental sensory spine of carpus 1 with serrate double-fringe, dactylus with interungual seta long, more conspicuous than dactylar seta, inner claw short, coxal plates without gland pores, sulcus marginalis and nodulus lateralis present, all noduli inserted at same distance from lateral margin. Male pereopod 1 propus and carpus inflated, bearing more or less prominent setal brushes.

Pleopods without respiratory areas, exopodites with about five sensory spines laterally, endopodites bilobate. Uropod with protopodite laterally grooved, endopodite inserting more proximally than exopodite. Genital papilla with short ventral shield, orifices on small to conspicuously elongate protrusions of the terminal spatula.

Type species: *Philoscia richardsonae* Holmes and Gay, 1904

Number of nominal species: 23, four reported from the Neotropics

Distribution: Interestingly, the genera *Halophiloscia* and *Littorophiloscia* vicariate each other. As stated above, the genus *Halophiloscia* is distributed in the Mediterranean area and on the Atlantic coasts of Europe. On the other hand, *Littorophiloscia* is found in the temperate Pacific, the western Atlantic coasts and the subtropical to tropical regions of the world.

Remarks: The genus was instituted by Hatch (1947) for the eastern pacific *L. richardsonae*. Lemos de Castro (1968) gave a synopsis of the genus and presented a generic definition without indicating the apomorphies of the genus. A close relationship of *Littorophiloscia*, *Halophiloscia*, and *Alloniscus* Dana, 1853 was postulated based on the similarities of the maxillipedal palp and the presence of a dactylar seta in the three genera. As stated above, the former character is a symplesiomorphy, and this is true for the latter character. Moreover, dactylar setae are present in most of the Crinocheta. Another character was interpreted erroneously as an ancestral state: the bifurcate genital papilla of *Halophiloscia* was thought to be intermediate between the two separate genital papillae of *Ligia* (plesiomorphic state) and the fused papilla of Crinocheta. Recent investigations of Erhard (1997), Schmidt (unpubl.) and own observations showed the secondary separation of the orifices in *Halophiloscia* within a highly derived genital papilla with heavily sclerotised ventral shield and interlocking mechanisms to pleopod 1 endopodite. Thus, the genital papillae of the species of *Littorophiloscia* represent the plesiomorphic character state in comparison with *Halophiloscia*.

The genus has been revised by Taiti and Ferrara (1986a) in detail and a new synonymy was established. They gave a diagnosis for recognition of this circumtropically distributed genus. A close relationship of both *Halophiloscia* and *Littorophiloscia* was postulated, the synapomorphies are the shape of the male pereopods 1 - particularly the inflated propus and carpus with prominent setal brushes - and a prominent interungual seta erroneously called the "dactylar organ". The other character mentioned - the palp with the more or less rounded, thick setal tufts - resemble the character state found in *Deto echinata* Guérin, 1836 which is close to the groundpattern of the Oniscidea realized in *Ligia* Fabricius, 1798. The maxillipedal palp is intermediate between the groundpattern of Crinocheta and the more derived forms of the "Philosciidae" with their three pointed setal tufts as in *Ischioscia* Verhoeff, 1928. Thus, it is a symplesiomorphy for the Halophilosciidae and *Deto*.

Since the most conspicuous characters of the genus - the shape of the male pereopod and the interungual seta - are also found in *Halophiloscia*, there are no autapomorphies known for *Littorophiloscia*. It is probable, that the genus *Littorophiloscia* just comprises the more basal representatives of the phylogenetic line of which the species of *Halophilosica* are the most derived, particularly since the morphology of the genital papilla of the members of *Littorophiloscia* shows all transitional stages from an *Ischioscia*-type, which will be described below (cf. chapter 5.2), and the bifurcate *Halophiloscia*-type (Taiti and Ferrara 1986a). A formal synonymization of the two genera requires the reexamination of the nominal species of the *Halophiloscia*-group.

Genus *Pentoniscus* Richardson, 1913

Type species: *Pentoniscus pruinosus* Richardson, 1913 (by monotypy and original designation)

Number of nominal species: 5 (4 from the Neotropics, two species are nomina dubia)

Distribution: Northern South America, Central America, Lesser Antilles; China

Remarks: *Pentoniscus* was originally considered to have a five-articulate antennal flagellum and therefore obtained its generic name. Schultz (1968) re-examined the material of Richardson and found the antennal to be flagellum three-articulate as in other Oniscidea of philosciid facies. Thus, he reduced *Pentoniscus* to a synonym of *Philoscia* without correct evaluation of the other characters of the genus. Obviously, the two genera differ in quite a lot of characters, i.e. the presence of a linea supra-antennalis, long apical organ of antenna, medial lobe of maxilla broader than lateral lobe, two setal tufts on palp of maxilliped, coxal plates without noduli laterales and gland pores, dactylus with short inner claw and plumose dactylar seta, lack of respiratory areas on pleopods in *Pentoniscus* whereas *Philoscia* shows the following charcters: lack of linea supra-antennalis, short antennal apical cone, lateral lobe of maxilla broader than medial lobe, medial setal tuft of palp reduced to two setae, coxal plates bearing gland pores and noduli laterales, dactylus with long inner claw and dactylar seta with knob-like apex, respiratory areas on pleopods 1 to 5.

Most of the the above mentioned characters are known from other South American genera of "Philosciidae", too. Autapomorphies of the genus *Pentoniscus* are:

■ Pleopod 5 exopodite triangular [PL6-2] ☐ pleopod 5 rhomboid in shape [PL6-1]

■ Quadrangular scales on male pereopod 2 and 3 merus [modified PE2-2] ☐ no scales of this shape present [typical PE2-2]

■ Molar penicil simple [Md2-4] ☐ molar penicil composed of about ten branches [Md2-1]

Since a simple molar penicil of the mandible occurs in several monophyla of crinochete Oniscidea, it is a character of little weight. It evolved most probably independently from other genera, thus representing an autapomorphy of the genus.

Genus *Yaerikima* Leistikow, 2000

Type species: *Philoscia kartaboana* van Name, 1936 (by monotypy)

Number of nominal species: Only known from type species

Distribution: Northeastern South America

Remarks: Like many other species of South American Oniscidea, the genus *Yaerikima* lacks conspicuous noduli laterales on its coxal plates. Among the many characters of this genus, three are autapomorphies:

■ Coxal plates with subrectangular margins, sulcus lateralis reduced ☐ coxal plates at least anteriorly rounded, sulcus marginalis present

■ Cephalothorax with two sinuous ridges on profrons ☐ profrons without ridges

■ Clypeus at its base as narrow as at its distal part [Ct4-2] ☐ clypeus basally two times broader than distally [Ct4-1]

Yaerikima kartaboana is quite similar to *Formicascia inquilina* but the structure of the cephalothorax differs remarkably in both species: *Y. kartaboana* has a more convex vertex and a lamina frontalis, the clypeus is narrow even at its base. In *F. inquilina* the vertex is more flattened and the basally broad clypeus is medially ridged. The shape of the coxal plates and the pleotelson differs, as does the shape of the female pleopod 3 exopodite.

The relations of *Y. kartaboana* to other species of philosciid facies in South America are difficult to establish, as most of the genera known from this region bear only slight differences from the groundpattern. There are some characters which might support a common ancestry of *Yaerikima* Leistikow, 2000 with the *Prosekia*-group, although the similarities are possibly due to convergence. This might be the case in the flagelliform endopodite of the male pleopod 2, the shape of the antennula. The divergent sets of aesthetasc resemble the character state in the genera close to *Prosekia*. But they are united in one tuft, no apical pair is separated. The pleopod 5 exopodite with its straight and proximally prolonged medial margin is similar to *Pentoniscus* Richardson, 1913, recently redescribed by Leistikow (1998b). This might be a common derived character of both taxa, but further research is necessary.

The *Roraimoscia* genus-group

To this monophylum belong the genera described in the following paragraphs: *Formicascia* Leistikow, 2000, *Roraimoscia* Leistikow, 2000, *Portoricoscia* Leistikow, 1999, *Parischioscia* Lemos de Castro, 1967 and the new taxon Ischiosciini (compare fig. 19 D). They all share the following character:

■ Profrons level with no depressions for holding the antennae, lateral lobes and linea frontalis reduced [Ct1-4] ☐ both lateral lobes and linea frontalis present, profrons with two slight depressions [Ct1-5]

The shape of the cephalothorax is different to that which is known as the "type chaetophiloscien" of Vandel (1952), although the presence of a linea supra-antennalis and the lack of a linea frontalis are shared with this type. It differs from those described by Jackson (1928) in the straight profrons without any depressions for holding the antennae, which is found even in the above mentioned "type chaetophiloscien", which may be considered to be the most primitive type within the Oniscoidea (H. Schmalfuss, pers. comm.) only differing in the lack of a linea frontalis. There are not few genera showing a level profrons. *Ischioscia* differs in the protruding compound eyes, and *Cubanophiloscia* Vandel, 1973 in the presence of noduli laterales on the coxal plates. This monopyhletic group is including the "*Ischioscia*"-group, which has a level profrons, too. Since the most derived genera of this taxon, *Ischioscia* and *Tropiscia*, have a linea frontalis, it must have been reduced several times within this monophylum.

Adelphotaxa *Formicascia* Leistikow, 2000 and *Roraimoscia* Leistikow, 2000

The two species *Formicascia inquilina* (van Name, 1936) and *Roraimoscia roraimae* (van Name, 1936) are very different in size. Nonetheless, they bear two characters which are synapomorphies of these sister species:

■ Medial part of female pleopod 3 exopodite elongate, surpassing the exopodite [PL3-3] ☐ pleopod exopodite more or less subrectangular [PL3-2]

■ Pleotelson with lateral margin bearing two concavities [Ha4-6] ☐ pleotelson with straight lateral margin [Ha4-2]

These characters are not found in any other species examined. Particularly the long pleopod 3 endopodite of the female is a unique character which supports monophyly of this group. On the other hand, the shape of the compound eyes, the pereopods, the coxal plates and the genital papilla are too different to lump them in a single genus.

Genus *Formicascia* Leistikow, 2000

Type species: *Philoscia inquilina* van Name, 1936 (by monotypy)
Number of nominal species: Only known from type species
Distribution: Northeastern South America
Remarks: *Formicascia inquilina* (van Name, 1936) is another small species of which the affinities remained uncertain until now. The genus is characterized by the shape of the cephalothorax with two slight depressions on the profrons as in *Chaetophiloscia* Verhoeff, 1908, but not only the frontal line, also the lateral lobes are missing.
The two following characters are autapomorphies of this genus, whereas the shape and setation of the mouthparts are plesiomorphic:

■ coxal plates without sulcus marginalis, distal edges broadly rounded ☐ sulcus marginalis present, distal edges only slightly rounded

■ genital papilla short, with the vasa deferentia proximal of the ventral shield much inflated [Ge4-2] ☐ vasa deferentia not inflated [Ge4-1]

The second character resembles the genus *Halophiloscia* Verhoeff, 1908, but the inflated part is close to the basis of the genital papilla, more bulbous and not as cylindrical as in *Halophiloscia*. The shape of the pleopod 1 exopodite of the male is a plesiomorphic character. It is similar to *Yaerikima* Leistikow, 2000, *Burmoniscus* Collinge, 1914 and *Atlantoscia* Ferrara and Taiti, 1981. From the latter two genera *Formicascia* Leistikow, 2000 differs in at least the shape of the cephalothorax, the structure of the apical organ of the antenna, the antenna-grooming brush of the pereopod 1 and several other characters.

Genus *Roraimoscia* Leistikow, 2000

Type species: *Philoscia roraimae* van Name, 1936 (by monotypy)
Number of nominal species: Only known from type species
Distribution: Northeastern South America
Remarks: This single species of the genus is - like the preceding ones - only known from the type series collected in the twenties of this century. *Roraimoscia roraimae* is quite different from all "philosciids" hitherto known, so it is separated in a genus on its own. The autapomorphies of the genus and of the type species, at the moment the only species known are:

■ Waxy plates covering the groove of the basis of the pereopods ☐ basis smooth

■ Very prominent sensory spine on the medial margin of the ischium ☐ sensory spines of the ischium much shorter

■ Two rows of sensory spines on the lateral margin of the pleopod exopodites [PL8-2] ☐ only one row of lateral sensory spines[PL8-1]

■ Male genital papilla with pectinate scales [Ge1-3] ☐ pectinate scales lacking [Ge1-2]

The coxal plates are covered with tricorn-like setae of different shapes, one being especially slender. This might be a nodulus lateralis, but to get more evidence, new material for ultrastructural investigations has to be collected.
R. roraimae bears several characters which are plesiomorphic, especially the setation of the mouthparts is shared with many basal genera of philosciid facies.

Genus *Portoricoscia* Leistikow, 1999

Type species: *Philoscia richmondi* Richardson, 1901 (by monotypy)
Number of nominal species: Only known from type species
Distribution: Confined to the Greater Antilles
Remarks: The only Crinocheta of philosciid facies known from Puerto Rico. It is a basal representative of Crinocheta since it shows in many features the plesiomorphic character state in comparison with higher Crinocheta, i.e. rich setation of palp and endite of maxilliped, dactylar seta apically plumose, inner claw of dactylus short. But there are several characters which are autapomorphic for this taxon:

■ Cephalothorax in frontal view much higher than broad [modified Ct1-4] ☐ cephalothorax at least as broad as high or broader than high [typical Ct1-4, Ct2-1]

■ Antennae very slender, apical organ extraordinarily long ☐ apical organ maximally half as long as flagellum

■ Longest sensory spines of propus and carpus 2 to 7 with sensillum much surpassing apex of cuticular sheath [modified PE8-1] ☐ sensillum only slightly surpassing cuticular sheath [typical PE8-1]

■ Male merus 1 to 5 with medial brushes of proximally directed cuticular scales [modified PE2-2] ☐ medial brushes lacking or different [PE2-2]

Concerning the pereopods, the carpus 1 of the male is almost cylindrical with parallel margins and there are no macroscopically visible differences in both sexes. Probably the meral brushes of proximally directed cuticular scales are a male adaptation to mounting during the precopula. The apomorphic shape of the sensory spines might be easily overlooked. The long free sensillum gives the spine a drawn out appearance; interestingly, the tricorn-like setae of the basis are long and slender. In contrast, the dactylar seta represents the plesiomorphical character state, the plumose area is even more prominent than in *Ischioscia*, it resembles that of *Scleropactes* Budde-Lund, 1885 (cf. Leistikow 1997a). All the characters given above are different to those found in *Philoscia* Latreille, 1804, to which it was ascribed by Richardson (1901). Since there is no other genus of philosciid facies showing this combination of characters, this species is best treated as belonging to a monotypic genus. For the time being, it is almost impossible to say if the closest relatives of *Portoricoscia richmondi* belong to the Caribbean fauna or are found on the adjacent regions of the South American continent, because of the lack of detailed descriptions of other Caribbean Oniscidea of philosciid facies.

Portoricoscia belongs to a basal group of crinochete Oniscidea due to the lack of noduli laterales and gland pores on the coxal plates and the slender pleon with caudally rounded pleotelson. In a monophyletic group within the Crinocheta, constituted by the autapomorphy of distinct noduli laterales, the dactylar seta is much derived, i. e. the plumose apex reduced.

From the Venezuelan *Roraimoscia roraimae* (van Name, 1936), it differs in the shape of the pleotelson, the dactylar seta, the endopodites of the pleopods 3 and 4 and by the molar penicil. Together with *Formicascia inquilina* (van Name, 1936), *Portoricoscia richmondi* is a close relative of this continental species, with respect to the molar penicil, which is composed of seven basally fused branches, it is more derived than *Formicascia* and *Roraimoscia*. *Portoricoscia* is most probably the sister species of the taxon described in the following paragraph.

Adelphotaxa *Parischioscia* Lemos de Castro, 1967 and *Ischioscia*-group

The monotypic genus *Parischioscia* Lemos de Castro, 1967 is the sister taxon of the most important subtaxon of the *Roraimoscia* genus-group, the *Ischioscia*-group. The adelphotaxon relationship of the two taxa is supported by two synapomorphies:

■ First article of the antennula with slightly shield-like lobe [A1-4] ☐ distal margin of first antennular article without lobe [A1-1]

■ Ornamental sensory spine with hand-like apex [PE7-2] ☐ apex with serrate double-fringe [PE7-1]

The second character is susceptible to convergence, a similar sensory spine can be found in many taxa, e.g. Benthana, although there are faint differences as described in the remarks to the latter genus. The small distal lobe of the first antennular article is much more evident in the *Ischioscia*-group, *Parischioscia* representing the plesiomorphic character state in comparison with its adelphotaxon (pl. 81, An1). The presence of such a sinuosity is not recorded from any other taxon of Oniscoidea. It strongly supports the monophyly of this taxon.

Genus *Parischioscia* Lemos de Castro, 1967

Type species: *Parischioscia omissa* (van Name, 1936) (by monotypy)
Distribution: Amazon basin, Guyana
Number of nominal species: Only known from type species

Remarks: This species was originally described by van Name (1936) on specimens collected at several sites at Guayana, e.g. Kartabo, Kamakusa, Mouth of Meama River. Further records are from Brazil (Lemos de Castro 1967). The largest specimens were about 11 mm, so the male paratype which could be examined is rather small. Nonetheless, it is a mature specimen since there are spermatids within the ductus ejaculatorii of the genital papilla.

The autapomorphic characters of this genus are:

■ Male pereopods 1 to 5 with transverse groove on carpus proximally bordered by hyaline cuticular fringe ☐ no transverse groove on pereopods 1 to 5

■ Cephalothorax laterally slightly expanded due to prominent compound eyes [Ct2-2] ☐ cephalothorax not laterally protruding [Ct2-1]

In a contribution to the Oniscidea of the Amazon region, Lemos de Castro (1967) erected for *Philoscia omissa* the monotypic genus *Parischioscia* mainly because of the great laterally protruding compound eyes and postulated a close relationship to *Ischioscia*. Since the pereopods 1 to 3 have no plate-like carpus with prominent setal fields, *Parischioscia* should be considered more primitive in this character. The close relationship between *Ischioscia* and *Parischioscia* is doubtful, because no convincing synapomorphies can be found: *Parischioscia* has no ventral pit on the pleotelson, the shape of the antennula is different.

Three characters may indicate a close relationship, i.e. the morphology of the cephalothorax with the distinct shape of the eyes, the distally prolonged proximal article of the antennula and the ornamental sensory spine of carpus 1 with its hand-like apex. The latter character can be found in several other genera and, therefore, must be considered to be a synapomorphy of a wider group. On the other hand, the morphology of the pleotelson represents a plesiomorphic character state: its shape is triangular and the semicircular ventral depression, an autapomorphic character of the Ischiosciini, is absent. And also a second character, which is apomorphic for the Ischiosciini, is missing in *Parischioscia*: the shield-like basal article of the antennula. Thus, other species might be better candidates to be the sistergroup of *Ischioscia*. For example *Tropiscia flagellata* Vandel, 1968, shares some apomorphic characters with *Ischioscia* as shown in the next paragraphs.

The *Ischioscia*-group: taxon Ischiosciini tax. n.

The taxon Ischiosciini is composed of several genera from northern South and Central America. The definition is different to the "groupe ischioscien" of Vandel (1952) for which no autapomorphies are known. The following genera should be considered members of this group: *Ecuadoroniscus* Vandel, 1968, *Oreades* Vandel, 1968, *Tropiscia* Vandel, 1968, *Ischioscia* Verhoeff, 1928 and *Mirtana* Leistikow, 1997. The autapomorphies of Ischiosciini are:

■ Antennula with proximal article bearing a shield-like protrusion distally [A1-3] ☐ antennula with distal margin of proximal article straight [A1-1]

■ Pleotelson with ventral semicircular pit apically [Ha4-5] ☐ distal part of pleotelson with transverse furrow [Ha4-3]

The shape of the mouthparts is quite similar to the groundpattern of the Oniscoidea. The setal tufts of the maxillipedal palp are prominent, composed of up to 15 setae, the endite bears a knob-like penicil and is densely covered with setae; the mandibles bear a molar penicil of about ten separate branches.

Genus *Ecuadoroniscus* Vandel, 1968

Diagnosis: Cephalothorax with lineae frontalis and supra-antennalis, no distinct lamina frontalis, compound eyes composed of about seven ommatidia, pereon with smooth tegument, pleon narrower than pereon, neopleurae on pleonites 3 to 5 present.

Antennula with shield-like protrusion of proximal article, antenna with three-articulate flagellum bearing long apical organ.

Mandibles with molar penicil composed of several branches, lateral endite of maxillula with 4 and 6 teeth, five of inner set cleft, maxilla with medial lobe broader than lateral, maxillipedal palp with tufts of setae, endite with knob-like penicil.

Pereopods with short inner claw on dactylus, dactylar seta apically plumose, ornamental sensory spine of carpus 1 with hand-like apex, antenna-grooming brush of carpus 1 transverse, coxal plates without gland pores and noduli laterales. Pleopods without respiratory areas, exopodites rhomboid. Uropod with protopodite subtriangular, laterally grooved, endopodite inserting proximally of exopodite.

Type species: *Ecuadoroniscus orientalis* Vandel, 1968 (by monotypy and original designation)

Number of nominal species: Only known from single female

Distribution: Ecuador

Remarks: This genus has to be treated as a nomen dubium and thus also is mentioned in the chapter 4.2.2. It is described herein for phylogenetic reasons: *Ecuadoroniscus orientalis* is a species only known a single female. Hence a recognition of the species in collections or the wild is almost impossible due to the lack of males, the species can not be defined in an unambiguous way and should be treated as a nomen dubium. The type locality is not precise, and the ascription of males found in the vicinity of Puyo to *E. orientalis* might be mere arbitrariness: for example, about ten species of *Androdeloscia* were found in the Peruvian province Huanuco, Distr. Puerto Inca, Rio Yuyapichis, Biological station "Panguana" 9°37'S 74°56'W, altitude 250m (Leistikow 1999c). All females are similar and it is difficult to determine a female of *Androdeloscia* in absence of males. That would mean that there is no type species for definition of the genus which has to be rejected as a vaild taxon, too.

Nonetheless, the genus could be defined by several characters and it is done so in the following for convenience of getting a better understanding of the phylogeny of the Ischiosciini.

The shape of the maxillula, prominent neopleurae, hand-like ornamental seta on pereopod 1 carpus and pleotelson with semicircular pit ventrally, all these characters link this form with *Ischioscia*, *Tropiscia*, *Mirtana*, and *Oreades*. Vandel (1968) described the presence of noduli laterales only on coxal plates I and II, which would be an autapomorphy of this form as could be evidenced from the few material. But the reexamination of the type material did not reveal the presence of any nodulus lateralis on the mentioned coxal plates. Possibly, the following character is an autapomorphy of *Ecuadoroniscus:*

■ Faint double-traced linea frontalis □ linea frontalis a single line

In contrast to Vandel (1968), it has to be stressed that no synapomorphy could be found to postulate a close relationship between *Ecuadoroniscus* and *Andenoniscus*. The lateral endite of *Ecuadoroniscus* bears 4 and 6 teeth, five cleft, and a triangular lobe whereas *Andenoniscus* has 4 and 4 teeth, three cleft. The shape of the pereopods, the strucutre of the ornamental sensory spines on carpus 1 and of the dactylar seta are different in these genera. Vandel (1968) overestimated the overall appearance of both genera, which both have a rather unspecialised habitus.

***Ecuadoroniscus orientalis* Vandel, 1968** (figs 16-17)
Material: microscopic slides of female (body length 4mm): Ecuador, Oriente, Puyo, tropical rain forest at 600 m alt., leg. IV.1965, N. Leleup, VC 5230.1-9

Colour: After Vandel (1968) "coloration claire, violacée. Région médiane des péréionites couverte de linéoles blanchâtres. Une tache blanche allongé forme la limite du tergite et du pleurépimère. Pleurépimères entièrement colorés. Pléon entièrement coloré, sauf une fine ligne blanche qui souligne le bord postérieur des pléonites."

Cephalothorax: Linea frontalis and linea supraantennalis faint, lamina frontalis lacking, no lateral lobes, vertex rounded, smooth, compound eyes composed of seven ommatidia.

Pereon: Tegument smooth, sparsely covered with tricorn-like setae, coxal plates without gland pores, no noduli laterales, only some long tricorn-like setae on coxal plate I and II, coxal plates V to VII distally pointed.

Pleon: Retracted from pereon but neopleurae of pleonites 3 to 5 prominent. Pleotelson with lateral margins concave, apex rounded, ventrally with semicircular pit, dorsally sparsely covered with tricorn-like setae.

Appendages:

Antennula: Three-articulate with distal article coniform, apically bearing five aesthetascs, proximal article with shield-like extension (fig. 17, An1).

Antenna: Flagellum three-articulate, distal article as long as proximal, as is the apical organ, second article of half the length, flagellum as long as peduncular article 5, both peduncle and flagellum covered with slender tricorn-like setae (fig. 16, An2).

Mandible: Only left mandible preserved but damaged, after Vandel (1968) molar penicil dichotomic.

Maxillula: Medial endite with two slender penicils, distally slightly pointed, lateral endite with 4 and 6 teeth, five of inner set cleft, rostrally beneath stout simple tooth with triangular lobe, setal fringe looking serrate, with sets of about five seta increasing in length proximally, then followed by the shortest seta of following set (fig. 17, Mx1).

Maxilla: Lateral lobe less broad than medial, bearing pectinate scales, medial lobe covered with trichiform setae, bearing about ten cusps medio-distally (fig. 17, Mx2).

Maxilliped: Basipodite with sulcus lateralis, palp three-articulate, distal one terminated by prominent setal tuft, medial article with setal tuft and two isolated setae medially and two setae latero-distally, proximal joint with two setae, endite rostrally with small setal tuft and knob-like penicil, caudally bearing two teeth and pectinate scales (fig. 17, Mxp).

Pereopods: Only pereopod 1 could be examined (fig. 16, PE1), rather slender, merus with translucent dentation medio-distally, carpus with rostral antenna-grooming brush slightly extending medio-proximally, ornamental sensory spine with hand-like apex (fig. 16, Sc1), dactylus with very short inner claw and long interungual seta, dactylar seta with plumose apex.

Pleopods: Could not be examined.

Uropod: Protopodite with lateral groove bearing some trichiform setae, endopodite inserting proximally of exopodite.

Genital papilla: Unknown due to lack of male specimens.

Genus *Oreades* Vandel, 1968

Diagnosis: Cephalothorax slightly broadened, linea supra-antennalis and lamina frontalis present, linea frontalis reduced, no lateral lobes. Compound eyes consisting of 14 ommatidia arranged in four rows. Pleon with prominent neopleurae, continuing the outline of pereon.

Antennula with distal article pointed, bearing several aesthetascs, mandible with simple molar penicil, lateral endite of maxillula with 4 and 6 teeth, five of inner set cleft, maxillipedal palp with three setal tufts, endite bearing knob-like penicil.

Pereopods with prominent coxal plates, lacking noduli laterales. Pleopods and uropod lost.

Type species: *Oreades lativentris* Vandel, 1968 (by monotypy and original designation)

Number of nominal species: Only known from a single female.

Distribution: Confined to Ecuador.

Remarks: Unfortunately, the antennae, maxillae, pereopods, pleopods and uropods are missing in the single known specimen. Since the specimen is a female and due to the incompleteness of the preserved material, the genus *Oreades* is merely a *nomen dubium* similar to *Ecuadoroniscus*. It is described here with respect to the phylogeny of the South American Oniscidea of philosciid facies.

As an autapomorphy of the genus one character can be mentioned:

■ Mandible with simple molar penicil [Md2-4] □ molar penicil composed of about seven branches [Md2-2]

There may be more and better characters of this kind in this form, but they remain unknown due to the loss of the rest of the material, i.e. the pereopods and pleopods of this species.

***Oreades lativentris* Vandel, 1968** (fig. 18)

Material: microscopic slides of female (body length 4 mm): Ecuador, Oriente, tropical forest at Puyo, alt. 800 m a.s.l., humus, leg. IV.1965, N. and J. Leleup, VC 5237.1-7

Colour: Vandel (1968) wrote: "Violacée. Le vertex et la partie médiane sont couverts de linéoles blanches, correspondant aux insertions musculaires. Les pleurépimères sont entièrement colorés. Le pléon est entièrement pigmenté à l'exception des deux premiers segments qui presentent, dans la région antérieure, une zone dépigmentée."

Cephalothorax: Linea frontalis and lamina frontalis lacking, faint linea supra-antennalis present, compound eyes composed of about 14 ommatidia arranged in four rows.

Pereon: Tegument smooth, only few tricorn-like setae, coxal plates with sulcus marginalis, lacking gland pores and noduli laterales (fig. 18, Cx3).

Pleon: Neopleurae of pleonite 3 to 5 continuing body outline of pereon, pleotelson with concave lateral margins and semicircular pit ventrally.

Appendages:

Antennula: Three-articulate with distal article pointed, bearing some aesthetascs apically, single aesthetasc more proximally (fig. 18, An1).

Antenna: Lacking in the only specimen.

Mandible: Only left mandible preserved, molar penicil simple, slender, pars intermedia bearing few coniform setae and two penicils, additional plumose seta more proximally (fig. 18, Mdl).

Maxillula: Only left lateral endite preserved, apically with 4+6 teeth, five of inner set deeply cleft, pointed triangular lobe rostrally, lateral fringe of trichiform

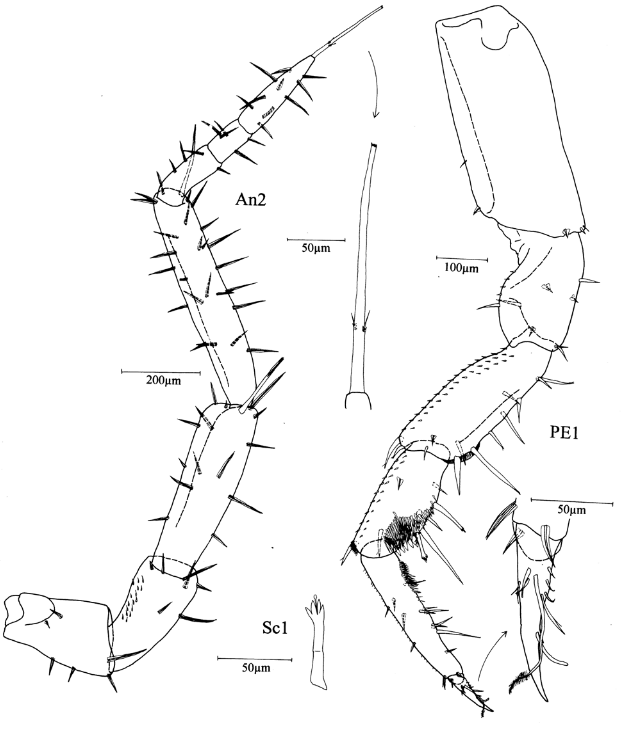

Fig. 16. *Ecuadoroniscus orientalis* Vandel, 1968, female 4mm
An2 antenna, with detail of apical organ; PE1 pereopod 1 in rostral view, with detail of dactylus; Sc1 ornamental sensory spine of carpus 1

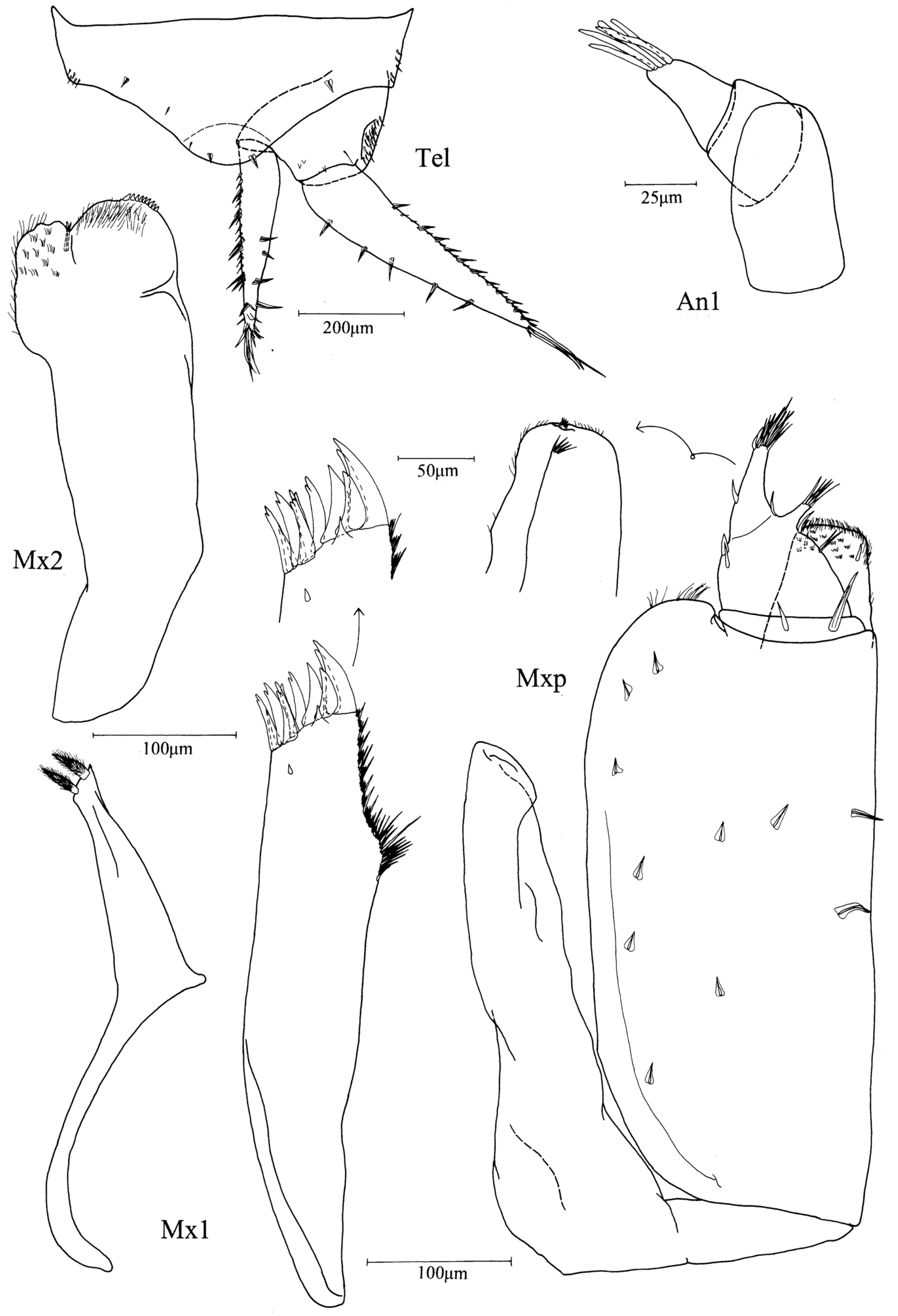

Fig. 17. *Ecuadoroniscus orientalis* Vandel, 1968, female 4mm
An1 antennula; Mxp maxilliped, with detail of endite in rostral view; Mx1 maxillula, with detail of apical lateral endite in rostral view; Mx2 maxilla; Tel pleotelson and uropod in situ

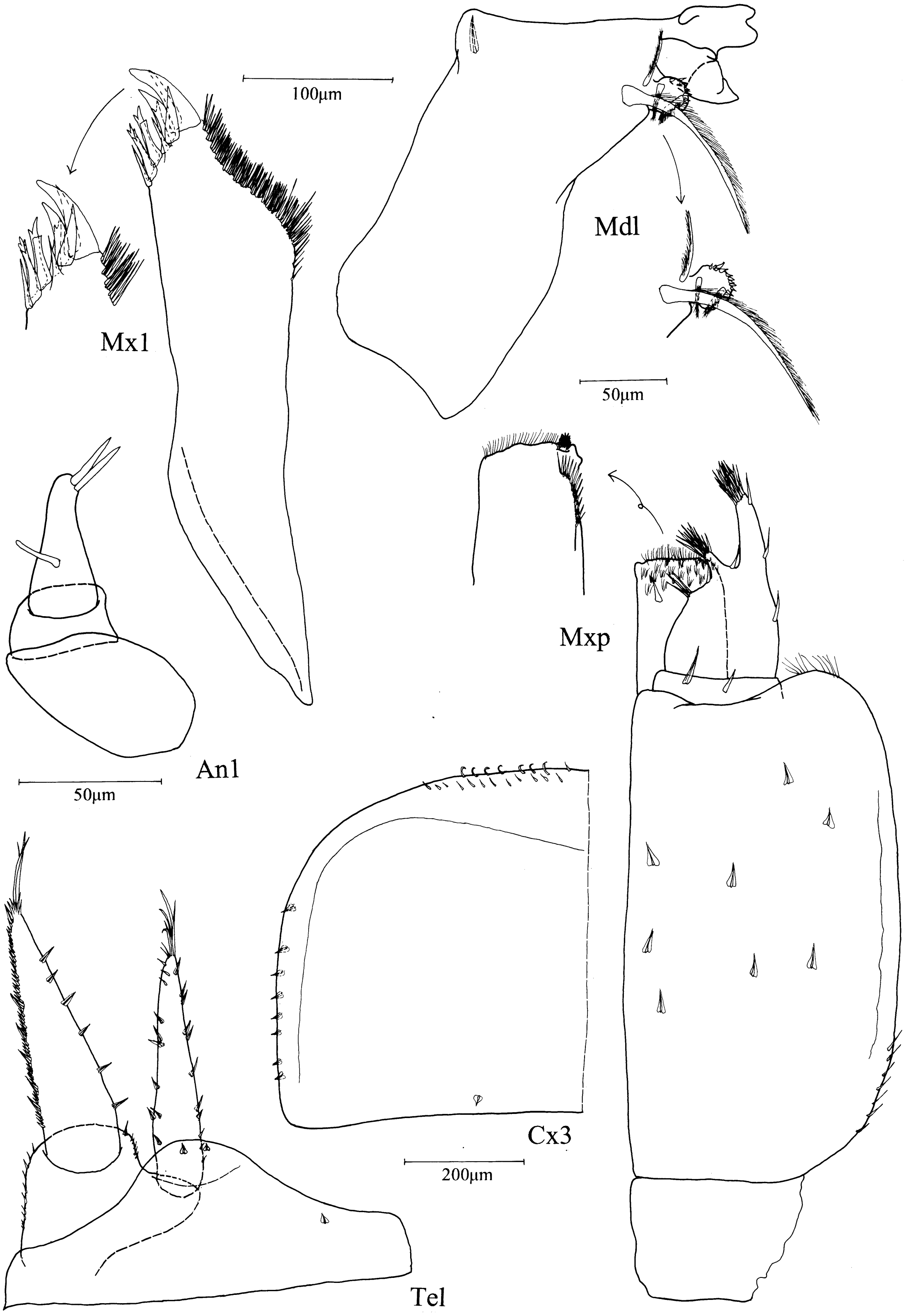

Fig. 18. *Oreades lativentris* Vandel, 1968, female
An1 antenna; Cx3 coxal plate III; Mdl left mandible with detail of pars intermedia; Mxp maxilliped, with detail of endite in rostral view; Mx1 lateral endite of maxillula with detail of apex in rostral view; Tel pleotelson and uropod in situ

setae with uneven insertion area (fig. 18, Mx1).
Maxilla: Both maxillae lost.
Maxilliped: Basipodite with short sulcus lateralis, palp with three setal tufts medially, proximal one composed of three to four setae, proximal article bearing two setae, endite rostrally with knob-like penicil, caudally with pectinate scales and slender tooth (fig. 18, Mxp).
Pereopods, pleopods and uropod lacking.
Genital papilla: The only representative was a female specimen.
Remarks: *Oreades lativentris* is another Oniscidea with long, caudally directed coxal plates V to VII and pleonal neopleurae continuous with the pereonal body outline as in *Mirtana costaricensis* Leistikow, 1997 or *Oniscophiloscia mirifica* Wahrberg, 1922. These species lack any pleopodal lungs and, therefore, do not seem to have closer links to the european genus *Oniscus* Linné, 1758. Vandel (1968) placed *Oreades* near *Ischioscia* in a "groupe ischioscien" mainly due to the laterally protruding compound eyes and the lack of a linea frontalis. The latter argument is worthless since there are members of *Ischioscia* still bearing a linea frontalis. They were formerly placed in *Proischioscia* Vandel, 1968, but it has been demonstrated that this character is present in the groundpattern of *Ischioscia* as well, and there are species intermediate between *Proischioscia* and *Ischioscia* (Schmalfuss 1980). As a consequence *Proischioscia* is a junior synonym of *Ischioscia*. Since there exist only some microscopic slides of the single specimen with all pereopods and pleopods lacking, it is rather difficult to find the relatives of *Oreades*. There is little evidence that *Oreades lativentris* could be treated as member of the "groupe ischioscien" in the sense of comprising species bearing a translucent triangular lobe on the rostral surface of the lateral endite of the maxillula. This triangular lobe is rather elongate in *Oreades*, thus separating the genus from all the other genera bearing this lobe. Whether the lack of noduli laterales is a synapomorphy or not is difficult to evaluate, most probably it is an autapomorphy of Ischiosciini or a taxon of even wider limits.

Adelphotaxa *Tropiscia* Vandel, 1968 and *Ischioscia* Verhoeff, 1928

The two genera were discussed in several contributions (Schmalfuss 1980, Leistikow, 1997, 1999d, 2000a, 2001e, f). Their distribution is in Ecuador (*Tropiscia* Vandel, 1968) and northwestern South America (*Ischioscia* Verhoeff, 1928). For the genus *Ischioscia*, a phylogeny is proposed in Leistikow (in press).

Genus *Mirtana* Leistikow, 1997

Type species: *Mirtana costaricensis* Leistikow, 1997 (by monotypy and original designation)
Number of nominal species: Only known by type species.
Distribution: Endemic to Costa Rica.
Remarks: The genus is somewhat enigmatic due to its body outline, which resembles the higher Crinocheta. The three-articulate antennal flagellum, the setation of maxillipedal endite and palp and the lack of respiratory areas are plesiomorphies which are common in some taxa of philosciid facies, too. Due to their status these characters lack a phylogenetic value. The pereopods and the pleopods, especially the shape of the copulatory organs of the latter, reflect affinities to *Ischioscia*. The morphology of the male pleopod 1 resembles in quite all details those known from members of *Ischioscia*, especially the proximally bent accessory process at the apex of the endopodite. This character and the shape of the distomedial sensory spine with its hand-like apex do not occur in any other known genus and justify the treatment of *Mirtana* and *Ischioscia* as close relatives, although their habitus is totally different.
The autapomorphies of *Mirtana* Leistikow, 1997 are:
■ Cephalothorax with rather two "swellings" instead of lateral lobes [Ct2-3] □ cephalothorax with level profrons [Ct2-2]
■ Pleon continuing the pereon by means of large neopleura [Ha2-2] □ pleon with small neopleurae [Ha2-1]
■ Pereonites covered with granulae [Ha1-2] □ pereonites smooth [Ha1-1]

Different to species of the family Oniscidae, which have large neopleurae on their pleonites and three-articulate antennal flagellum, the cephalothorax of *Mirtana* shows no lateral lobes formed by the linea frontalis and the antenna bears a long apical organ. The linea frontalis is medially interrupted, thus producing only two slight protrusions superficially resembling the profrons of *Yaerikima kartaboana* (van Name, 1936). The presence of large neopleurae is in convergence to other Oniscidea, the apomorphic shape of the antennula links *Mirtana* with the Ischiosciini.
For a detailed discussion and the description of the type species see Leistikow (1997b).

The *Prosekia*-group: Prosekiini tax.n.

Diagnosis: This monophyletic taxon is besides the Ischiosciini the largest group of South American philosciids. This group experienced a radiation which is much more impressive than that of the Ischiosciini. Especially conspicuous is the highly diverse and complex differentiation of the male pleopods. The monophyly of this group is supported by the autapomorphies listed below:

■ Antennula with the medial aesthetascs gathered in a tuft, directed more or less medio-distally, not attached to article 3 [Ae1-3] □ antennula with aesthetascs paired in a medial line [Ae1-1]

■ Transverse fold between aesthetasc tuft and distal pair of aesthetascs □ distal article coniform

■ Male pleopod 1 with hyaline lamellae near apex [PL4-3] □ no such lamellae on pleopod 1 exopodite [PL4-2]

In contrast to Vandel's statement (1952), no flagelliform noduli laterales could be observed in *Prosekia rutilans* (Vandel, 1952). The noduli are slightly longer than the tricorn-like setae but not considerably different to those of the genus *Chaetophiloscia* Verhoeff, 1908 in which the species was originally included. In *Metaprosekia* Leistikow, 2000, the noduli are not much longer than in *Chaetophiloscia*, too. Long Noduli laterales are confined to the more derived taxa of the Prosekiini. If flagelliform noduli were present in the groundpattern of the Prosekiini, an independent reduction of the length of the noduli in *Prosekia* and *Metaprosekia* has to be postulated. There is no evidence for such a reduction of the size, therefore, flagelliform noduli laterales are considered not to be a character of the groundpattern of this group.

Genus *Prosekia* Leistikow, 2000

Type species: *Chaetophiloscia rutilans* Vandel, 1952 - designated in Leistikow (2000d), by monotypy
Number of nominal species: Only know from type species.
Distribution: Confined to Venezuela.
Remarks: According to the § 13a ICZN, the genus name was unavailable since no type species was chosen. After the redescription of the genus (Leistikow 2000d). and a re-examination of all the members ascribed to *Prosekia* (see below and Leistikow 1999c), the genus now is monotypic with a Venezuela species. The autapomorphies of *Prosekia* are:

■ Cephalothorax with faint linea frontalis, medially interrupted [modified Ct1-5] □ linea frontalis continuous [Ct1-5]

■ Male pleopod 2 endopodite with club-like apex [PL5-3] □ pleopod 2 endopodite pointed [PL5-1]

■ Colour pattern: reddish brown with 3 lines of light patches □ colour more purplish brown, prominent patches solely on the coxal plates

Prosekia rutilans is recognized by the colour pattern of reddish brown with some darker patches, not found in any other species belonging to the Prosekiini. The faint medially interrupted linea frontalis is similarly found only in this species, in the outgroup of Prosekiini, the linea frontalis is continuous. The club-like apex of the male pleopod 2 endopodite is resembling those of several species of *Ischioscia,* but because it does not belong to the groundpattern of *Ischioscia* and the two taxa differ in the shape of the antennula, the more parsimonous explanation is the convergent acquisition of such a shape of the endopodite. Moreover, the structure of the endopodite is not identical in both taxa.

Genus *Metaprosekia* Leistikow, 2000

Type species: *Metaprosekia nodilinearis* Leistikow, 2000 (by monotypy)
Number of nominal species: 1
Distribution: The type series was collected in Venezuela .
Remarks: This new species is included in a separate genus due to the intermediate character set with similarities to *Prosekia*, *Androdeloscia*, and *Andenoniscus.* It is part of the monophyletic Prosekiini, sharing the characteristic shape of the antennula. The shape of the pleopod 1 exopodite resembles the one of *Prosekia*, a symplesiomorphy; its size and the flagelliform noduli laterales are synapomorphies with the remaining genera of the Prosekiini. Some characteristic features are only found in *Metaprosekia* Leistikow, 2000 and thus are the autapomorphies of the genus:

■ Eyes composed of three individualised ommatidia, surrounded by pigments [Ey-5] □ eyes with about eight ommatidia with lenses distally fused [Ey-4]

■ Noduli laterales all at same distance from lateral margin of coxal plates [Cx3-1] □ noduli*s lateralis* on coxal plate IV inserted more dorsally [Cx3-3]

The former character is linked with the size reduction of the entire group, but is here extremely marked. All the other genera have about eight ommatidia, the lenses are fused distally, this structure is missing in *Metaprosekia*, the ommatidia are individualized.

Genus *Andenoniscus* Verhoeff, 1941

Type species: *Andenoniscus silvaticus* Verhoeff, 1941
Number of species: 2 [4, if the *nomina dubia A. tropicalis* and *A. narcissi* are included, but see Leistikow (1998a)], both from the Neotropics
Distribution: Apparently disjunct distribution in Panama and northern Peru; species might have a wider distribution than presently known.

Remarks: *Andenoniscus* Verhoeff, 1941 is a genus of rather small species inhabiting mainly the cordilleras of South America. The recent re-examination (Leistikow 1998a) of the available material accomplished the generic diagnosis of *Andenoniscus*. It is quite similar to other small South American crinochete Oniscidea, particularly to *Erophiloscia* Vandel, 1972 in general appearance, and in the shape of the mouthparts.

Different to Verhoeff's (1941) diagnosis, the lateral endite of the maxillula is composed of 4 and 4 teeth with the inner set cleft, he may have taken the 8th tooth for a small additional tip of one of the other teeth, since he wrote that only one of the seven teeth is equipped with a small additional tip. Although there are several characters in common with the above mentioned genera, the species of *Andenoniscus* are united by the following synapomorphies:

■ Linea supra-antennalis reduced [Ct1-2] ☐ linea supra-antennalis present[Ct1-5]

■ Lateral lobes ventrally drawn out ☐ lateral lobes not reaching ventrally of antennal sockets

Particularly the shape of the lateral lobes represent a good character for the identification of the genus. This type of lateral lobes is not found in any other genus of the Prosekiini. The reduction of the linea supra-antennalis also is restricted to *Andenoniscus*, but as it is a reductive character, its weight is small, if there are no positive characters supporting monophyly of the genus.

Genus *Xiphoniscus* Vandel, 1968

Type species: *Xiphoniscus mirabilis* Vandel, 1968 (by monotypy and original designation)
Number of nominal species: 1
Distribution: Only known from Ecuador.

Remarks: The adult male of *Xiphoniscus mirabilis* is easily identified by its prolonged coxal plates II, a character which is unique among the Oniscidea. Apart from this, the genus is closely related to *Andenoniscus* Verhoeff, 1941, *Prosekia* and *Erophiloscia* Vandel, 1972, which can be concluded from the shape of the cephalothorax with itsslight lateral lobes and the stout male pleopod 1 endopodites, which are structurally similar in *Xiphoniscus*, *Andenoniscus* and *Prosekia*: the basis is stout and the apex denticulate. There are two characters which represent the autapomorphies of the genus:

■ Coxal plates II drawn out caudally in the male [Ha5-4] ☐ coxal plate II caudally rounded [Ha5-1]

■ Molar penicil composed of a strong branch and three shorter branches ☐ molar penicil composed of about five branches

The first character is a very striking autapomorphy of *Xiphoniscus* as it is found in no other taxon described up to now. The morphology of the mandible represents a more derived character state compared to the mandible of the above mentioned genera since it has a reduced and modified number of branches. In *Andenoniscus*, *Prosekia* and *Erophiloscia* Vandel, 1972 the molar penicil is composed of up to ten branches. All these genera are members of the presumably monophyletic "groupe chaetophiloscien" as postulated by Vandel (1968) with an excentric nodulus lateralis on coxal plate IV.

Adelphotaxa *Erophiloscia* Vandel, 1972 and *Androdeloscia* Leistikow, 1999

The two genera comprise the bulk of species of the Prosekiini, the differentiation of the male pleopod 1 endopodite reaching within this group its highest level of differentiation. Both genera share the following synapomorphic characters:

■ Lack of a proximal setal tuft on the maxillipedal palp [Mp2-5] ☐ palp with three setal tufts[Mp2-4]

■ Maxillipedal endite without setation [Mp3-3] ☐ endite covered with fine setae [Mp3-2]

■ Male pleopod 5 distally pointed, with straight medial margin somewhat prolonged proximally [PL6-2] ☐ pleopod 5 rhomboid in shape, without distal point [PL6-1]

Hence the former two characters are reductive, they are of minor weight for the evaluation of the hypothesis of a sister group relationship. On the other hand the latter character is a rather complex one, which supports the monophyly of *Erophiloscia* and *Androdeloscia*. The presence of a straight medial margin has to be seen in the light of its function for holding the flagelliform pleopod 2 endopodite. So it may be argued that there is a selective pressure in the evolution of a holding structure in pleopod 5. As can be seen in other taxa, e.g. in *Pentoniscus* or *Benthana taeniata*, a straight margin evolved convergently. Therefore, it is important to stress the similarity of the shape in the pleopods of *Erophiloscia* and *Androdeloscia*: the lateral margin is convex, bearing two sensory spines, and a single row of pectinate scales is present on the caudal side. Since both genera are closely related within the *Prosekia*-goup as will be shown in chapter 5, the explanation of a single event for the evolution of a straight medial margin is conform to the principle of parsimony.

Genus *Erophiloscia* Vandel, 1972

Type species: *Erophiloscia longistyla* Vandel, 1972 (by original designation)
Number of species: 4 [6, if the nomina dubia *E. tropicalis* and *E.narcissi* are included, but see Leistikow (1998a)], all from the Neoptropics
Distribution: Eastern parts of Ecuador and Peru.
Remarks: This remarkable genus is distinguished from other South American members of the Prosekiini, which have a apomorphic morphology of the antennula as discussed above, by the shape of the male pleopods, especially the drawn out pleopod 5 exopodites and the extraordinarily long pleopod 2 endopodites already noted by Vandel (1972).
For the time being, the following character is recognized as the autapomorphy of the genus:
■ Male pleopod 5 with extremely drawn out medio-distal point [PL6-4] ☐ pleopod 5 with moderate distal point [PL6-2]

The pleopod 5 exopodite bears no guide slot for the pleopod 2 exopodite as it can be found in *Androdeloscia*. The endopodite 2 is held simply by the medial margin of the exopodite 5.

Genus *Androdeloscia* Leistikow, 1999

Type species: *Androdeloscia hamigera* (Vandel, 1952)
Number of nominal species: 20, all from the Neotropics
Distribution: Northwestern South America and Central America north to Mexico.
Remarks: The new genus is of vast distribution in northern South America. It is also well represented in Central America north to southern Mexico. A new species is presented from Guatemala and a further species is reported from Mexico, which was described as *Philoscia formosa* Mulaik, 1960 with incomplete diagnosis (Mulaik 1960).
As stated above, *Androdeloscia* is the sister group of *Erophiloscia*. It is discriminated by the following autapomorphy:
■ Male pleopod 5 exopodite with medio-caudal groove delimited by pectinate scales [PL6-3] ☐ some pectinate scales along medial margin, no medio-distal groove present [PL6-2]

This character is found in a similar manner in several taxa of Crinocheta, for example in the Porcellionidae, but this is due to convergence since it is not found in any of the closer relatives of *Androdeloscia* and there are no synapomorphies shared by the Porcellionidae and the new taxon. A detailed analysis of this groove, the "Innenrandlängsrinne" of Verhoeff (1920), may show some differences in the fine structure: In the Porcellionidae, the margins of this groove is extended in a hylaine cuticular lobe (Legrand 1946, Hoese 1981), which is lacking in *Androdeloscia*.

Genus *Burmoniscus* Collinge, 1914

A diagnosis of *Burmoniscus* was given in Taiti and Ferrara (1986b).
Type species: *Burmoniscus moulmeinus* Collinge, 1914 (syn. of *Philoscia coeca* Budde-Lund, 1895)
Number of nominal species: 58, two are reported from the Neotropics, both most pobably introduced from West Africa and Southeast Asia
Distribution: Southeast Asia, East Africa, West Africa (?), some species circumtropically carried off by human activity.
Remarks: The genus *Burmoniscus* Collinge, 1914 has been revised and newly defined by Taiti and Ferrara (1986b). It is a heterogeneous group which probably is paraphyletic, comprising blind and unpigmented species and species which are superficially similar to several members of *Ischioscia*, e.g. *Burmoniscus davisi* Taiti and Manicastri, 1988. In fact, no autapomorphies of the genus are described until now. The characteristic position of the nodulus lateralis on coxal plate II is shared with e.g. A*nchiphiloscia* Stebbing, 1908 (Ferrara and Taiti, 1986), from which it differs in the presence of gland pores and a sulcus marginalis, characters which are with certainty plesiomorphies of *Burmoniscus*.
The genus is of oriental distribution where it occurs with more than 30 species. The first records from South America, *B. meussii* (Holthuis, 1949) was reported from Brazil by Araújo et al. (1996). New records for this species are from Venezuela. For the first time, records of the rather unknown species *Burmoniscus kohleri* (Schmalfuss and Ferrara, 1978) are presented from Guatemala by Leistikow (2000b).

Adelphotaxa *Caraiboscia* Vandel, 1968 and *Colombophiloscia* Leistikow, 2001

The two genera are adelphotaxa since they share the following apomorphic characters:
■ Modified tricorn-like setae on the dorsum: leaflet scales, "Blättchenschuppe" of Schmalfuss (1977) [Ha3-2] ☐ tricorn-like seate with simple cuticular scale [Ha3-1]
■ Compound eyes reduced to four ommatidia [Ey-5] ☐ compound eyes consisting of about ten ommatidia [Ey-4]

■ Antennula with a single row of erected aesthetascs [Ae1-4] ☐ antennula with aesthetascs paired in medial line [Ae1-1]
■ Lateral endite bearing mostly simple teeth [Ml1-5] ☐ teeth of inner set cleft [Ml1-4]

The two genera were discussed to some extent in Leistikow (2001d). Their adelphotaxon relationship appears to be well-reasoned.

Genus *Caraiboscia* Vandel, 1968

<u>Type species:</u> *Caraiboscia microphthalma* Vandel, 1968 (by monotypy and original designation)
<u>Number of species:</u> 2, both from the Neotropics
<u>Distribution:</u> Northern South America from Guyana to Ecuador.
<u>Remarks:</u> The genus *Caraiboscia* is a pigmentless taxon with reduced compound eyes and lives "un mode de vie humicole ou endogé" (Vandel 1968). The generic diagnosis comprises a set of plesiomorphies. Apomorphies of *Caraiboscia* are:
■ Drop-like shape of the male pleopod 1 exopodite [PL3-5] ☐ pleopod 1 expodite subtriangular [PL3-1]
■ Small bulbs at the apex of pleopod 1 endopodite ☐ apex of pleopod 1 endopodites smooth
■ Saw-like structure on male pleopod 2 endopodite [PL5-4] ☐ pleopod 2 endopodite smooth [PL5-1]
■ Linea supra-antennalis reduced [Ct1-2] ☐ linea supra-antennalis present [Ct1-5]
■ Profrons with two prominent depressions ☐ depressions on profrons shallow
■ Lateral endite with 4+5 teeth, only one cleft [Ml1-5; Ml1-6] ☐ lateral endite with 4 and 6 teeth, five of inner set cleft [M11-4]

The leaflet tricorns are slightly derived in *Caraiboscia* compared to *Colombophiloscia*. The leaf-like cuticle is fused with the supporting scale of the tricorn itself and the setae are bent anteriorly.
Very particular characters of *Caraiboscia* are the shape of the male pleopod 1 exopodite and the saw-like structure on the male pleopod 2 endopodite. These are complex characters which support the monophyly of the genus whereas the reduction of the linea supra-antennalis itself is rather susceptible to convergence. This latter character has to be seen with the differentiation of the cephalothorax, with respect to the modification of the profrons and its depressions.
In contrast to the statement of Vandel (1968), the noduli laterales are clearly discernible and are all inserted at the same distance to the lateral margin of the coxal plates.
After cautious re-examination of *Phalloniscus langi* (van Name, 1936) and *Phalloniscus pearsei* (van Name, 1936) the genus might be enlarged by these species from Guyana. Some material collected on Trinidad at Navet Dam Lake by the H.J. Just, deposited in the Zoological Muesum of Copenhagen, belong to this genus, too. The only male is too damaged to allow specific recognition.

Genus *Colombophiloscia* Leistikow, 2001

<u>Type species:</u> *Colombophiloscia alticola* Vandel, 1968 (designated by Leistikow, 2001d)
<u>Number of nominal species:</u> 4, all from the Neotropics
<u>Distribution:</u> Northern tropical Andes.
<u>Remarks:</u> Leistikow and Wägele (1999) pointed out the possible case of homonymy of *Colombophiloscia* Vandel, 1968 and *Colombophiloscia* Vandel, 1981. For the Cuban species, *C. romanorum* Vandel, 1981, probably a new genus has to be established after examiation of the type material.
The genus as defined herein is characterized by these autapomorphies:
■ Linea frontalis substituted by row of tricorn-like setae [modified Ct1-3] ☐ linea fontalis present [Ct1-5]
■ Molar penicil a simple seta [Md2-4] ☐ molar penicil composed of about five branches [Md2-3]
■ Gland pores reduced [Cx1-1] ☐ gland pores on all coxal plates [Cx1-2]

The first character is found in all species ascribed to this genus, whereas in *Caraiboscia*, the cephalothorax is even more modified. It is possible that the reduction of the linea frontalis is a synapomorphy of both genera, the presence of tricorn-like setae arranged in a row is typical only for *Colombophiloscia*. For the second character, a reduction of the molar penicil in *Colombophiloscia*, a convergency to character states found in other taxa like *Burmoniscus* or *Pentoniscus* is postulated, since there are no characters supporting an adelphotaxon relationship with one of these taxa. The adelphotaxon of *Colombophiloscia* excluding *C. romanorum* Vandel, 1981, the genus *Caraiboscia,* bears a compound molar penicil as postulated for the groundpattern of the Crinocheta, thus the reduction has occurred in *Colombophiloscia* solely.

Adelphotaxa *Pseudophiloscia* Budde-Lund, 1904 and *Araucoscia* Verhoeff, 1939

These two genera are closely related or might even be considered synonymous. This question can not be resolved since the material of *Pseudophiloscia angusta* (Dana, 1852) has been lost when the ship carrying the

Dana collections sunk in the last century. For the two genera these synapomorphies can be postulated:

■ Two rows of noduli laterales per side [Cx3-2] ☐ only one row of noduli laterales per side [Cx3-1]

■ Coxal plates very narrow [Ha5-2] ☐ coxal plates of normal breadth [Ha5-1]

■ Coxal plates without sulcus marginalis [Cx4-2] ☐ coxal plates with sulcus marginalis [Cx4-1]

■ Lateral endite of maxillula with about ten simple teeth not fitting the 4+6-pattern [M11-8] ☐ maxillula with 4+6 teeth, five of inner set cleft [M11-4]

The differences in the shape of the pereopods and pleopods in the male may be of significance at species level. As stated in an earlier work (Leistikow 1998c), good evidence for the synonymy of both genera can only be given if a sister-species-relationship of *Araucoscia chilenica* Verhoeff, 1939 with one of the species of *Pseudophiloscia* found in Chile is shown. In particular, it is difficult to do so since no material of *P. angusta* is available, which might be the sister species of one of the two species *P. inflexa* Budde-Lund, 1904 and *A. chilenica.*

Genus *Pseudophiloscia* Budde-Lund, 1904

Type species: *Pseudophiloscia inflexa* Budde-Lund, 1904

Number of species: 2, both from Chile

Distribution: Temperate trans-andean Chile.

Remarks: After nine decades of confusion with regard to the status and synonymy of *Paraphiloscia* Stebbing, 1900 and *Pseudophiloscia*, Leistikow (1998c) proposed to retain the genus name *Pseudophiloscia* for the South American species *P. inflexa* and *P. angusta* (Dana, 1852) exclusively. It was postulated that this genus is not related to the species of *Pseudophiloscia* from the Old World, which are now in *Paraphiloscia* Stebbing, 1900. In a footnote of a paper of the late Budde-Lund (1912), Stebbing reduced *Pseudophiloscia* to a synonym of *Paraphiloscia*. This synonymysation was followed by Jackson (1927), but Nunomura (1986) ignored the synonymization in a paper on "Philosciidae" from Japan and contributed to the confusion about these two genera.

Genus *Araucoscia* Verhoeff, 1939

Type species: *Araucoscia chilenica* Verhoeff, 1939 (by monotypy and original designation)

Number of nominal species: 1

Distribution: Temperate trans-andean Chile.

Remarks: The monotypic genus *Araucoscia* from Chile is one of the enigmatic genera from southern South America. It was found on Calbuco Island at 41°46'30"S and 73°8'W.

The genus is characterized by the peculiar lateral endite of the maxillula:

■ Lateral endite with seven simple teeth apically, described as 6+1 [2+1+1+1+1] by Verhoeff (1939) [M11-6] ☐ lateral endite with ten simple teeth [M11-8]

The lateral endite is superficially similar to the one of the Melanesian genus *Oroscia* Verhoeff, 1926, which shows a 4+4 pattern instead of the 1+6 pattern of *Araucoscia*. Interestingly, *Oroscia squamuligera* Verhoeff, 1926 bears a similar ornamental sensory spine on carpus 1 and the longer sensory spines of the medial margin of carpus and merus are raising from a prominent hump. Other genera from the Australasian region also have a most lateral tooth of the maxillula of huge dimensions, i.e. *Adeloscia dawsoni* Vandel, 1977 (North Island of New Zealand), *Leucophiloscia endogaea* Vandel, 1973 (Papua-New Guinea) and certain species of *Papuaphiloscia* Vandel, 1970 like *Papuaphiloscia rennelli* Vandel, 1973 (Solomon Islands). They all differ from *Araucoscia chilenica* in having the molar penicil simple and - save *Leucophiloscia endogaea* - bearing a knob-like penicil on the endite of the maxilliped. A comprehensive discussion of the genus was published in Leistikow (1998a).

Genus *Oniscophiloscia* Wahrberg, 1922

Diagnosis: Cephalothorax with medial and lateral lobes, linea frontalis and linea supra-antennalis both interrupted. Mandible with prominent compound molar penicil, lateral endite of maxillula with 4+7 simple teeth, maxilla with sparse setation, endite of maxilliped without knob-like seta and setation, bearing four teeth, palp with proximal setal tuft composed of long and short seta.

Pereopods stout, bearing three rows of sensory spines medially, coxal plates with sulcus marginalis, gland pore fields and noduli laterales, all inserted near lateral margin.

Pleopods without respiratory areas, exopodites pointed, endopodites small. Uropod protopodite laterally grooved, endopodite inserting proximally of exopodite.

Type species: *Philoscia (Oniscophiloscia) mirifica* Wahrberg, 1922 (by monotypy and original designation)

Number of nominal species: 3, restricted to Juan Fernández and adjacent coast of Chile

Distribution: Juan Fernández Islands and temperate trans-andean Chile (?).

Remarks: Morphologically spoken, this genus is an isolated representative of the Crinocheta. It is similar to the genera *Pseudophiloscia* and *Araucoscia* with respect to the shape of the pereopods and the dentation of the lateral maxillular endite, which bears solely simple teeth. For recognition of this genus, the autapomorphic characters are relevant:

■ Cephalothorax with T-shaped medial lobe on postfrons dorsally limited by linea frontalis [Ct2-4] ☐ no such medial lobe [Ct2-1]

■ Male pleopod 1 exopodite elongate, much longer than broad [PL3-6] ☐ male pleopod 1 subtriangular, not longer than broad [PL3-1]

■ Male pleopod 1 endopodite apically bulbous with cuticular granules ☐ pleopod 1 endopodite pointed, smooth

As in *Mirtana costaricensis*, the members of *Oniscophiloscia* have an oval outline of the body due to prominent neopleurae. This character is a convergent adaptation to a life style different to most genera of philosciid facies: the animals do not try to escape, they try to hide attached to the ground. The structure of the cephalothorax and the male pleopod are unique among the crinochete Oniscidea, thus they have to be treated as the autapomorphies of *Oniscophiloscia*. Wahrberg (1922) stressed the similarity of the apical organ of *Philoscia* Latreille, 1804. This type of apical organ is most probably a symplesiomorphy of the two genera. A better indication of the origin of this group may be found in the shape of the tricorns which are similar to those of *Porcellionides* Miers, 1877 (Wahrberg 1922). The lack of a phylogenetic analysis in Wahrberg (1922) was lamented by Strouhal (1960), but was not supplemented by this author. He placed *Oniscophiloscia* in the Oniscidae (Strouhal 1960), but gave no synapomorphies which support the close link to *Oniscus* Linné, 1758. Thus, this classification lacks a phylogenetic foundation.

4.2.2 Nomina dubia

The remaining nominal species are for the time being nomina dubia since they were described based only on female specimens which often do not have species-specific characters. It was common use to describe new species based on solely females in the first decades of this century. Pearse (1915) described some species of *Philoscia* from Colombia, and Paulian de Felice (1944) contributed to the Oniscidea fauna of the Guyanas, both giving descriptions of some interesting species of "philosciids" for which unfortunately male specimens are not available:

Andenoniscus narcissi Vandel, 1968 (syn. *Erophiloscia n.*)
Andenoniscus tropicalis Vandel, 1968 (syn. *Erophiloscia t.*)
Ecuadoroniscus orientalis Vandel, 1968
Ischioscia debilis (Budde-Lund, 1893)
Ischioscia nitida (Miers, 1877)
Oreades lativentris Vandel, 1968
Pentoniscus exilis van Name, 1925
Philoscia colimensis Mulaik, 1960
Philoscia diminuta Budde-Lund, 1893
Philoscia gracilior Paulian de Felice, 1944
Philoscia geayi Paulian de Felice, 1944
Philoscia moneaguensis van Name, 1936
Philoscia seriepunctata Budde-Lund, 1893

For the following species a correct specific or generic diagnosis can not be given due to the loss of intact males or the refusion of the permission to examine them in detail by the museum where the type is stored. Therefore, the species are not available to scientific work:

Chaetophiloscia frontalis Lemos de Castro, 1967
Chaetophiloscia walkeri (Pearse, 1915)
Philoscia demerarae van Name, 1925

As stated above, *Ecuadoroniscus orientalis* and *Oreades lativentris* are nomina dubia due to the lack of a male in the type material. Nonetheless, the genera were dealt with in the generic account due to their importance for the understanding of the phylogeny of the Ischiosciini. For *Chatophilosica frontalis* one can deduce a close relationship to one of the genera of the Prosekiini, particularly the antennula is similar to the members of this group. The male type material is lost, so a correct identification is not possible. Since Lemos de Castro (1967) did not give any description of the male pleopods, the species name remains dubious. In the case of *Philoscia demerarae*, there are males in the AMNH collections but due to the loan policies it was impossible to re-examine the material. The original description (van Name 1925) is too poor to recognize this species in the field. So it is decided to leave it as a nomen dubium.

4.2.3 Genera used as Outgroups

Besides *Ligia baudiniana* Milne Edwards, 1840, *Scleropactes talamancensis* Leistikow, 1997 and *Reductoniscus tuberculatus* Leistikow, 1997 which were recently dealt with (Ferrara and Taiti 1990; Leistikow 1997a and 1997c), three further taxa are used for comparison to the South American taxa ("Philosciidae":

Philoscia, *Adeloscia*) and for outgroup comparison (Detonidae Budde-Lund, 1904: *Deto*).

4.3 Key to the Genera of "Philosciidae" of the New World

1 Noduli laterales absent or weakly differentiated from tricorn-like setae 2
- Noduli laterales prominent, sensillum much longer than in tricorn-like setae 17

2 Maxilla with lobes of subequal breadth, maxillipedal palp with setal tufts composed of more than 30 setae, basis not much broader than both palp and endite put together 3
- Maxilla with lobes not subequal in breadth, maxillipedal palp with tufts of less than 20 setae, basis broader than both palp and endite put together 4

3 Cephalothorax without lateral lobes, nodulus lateralis tricorn-like, slightly longer sensillum distinguishing it from tricorn-like setae *Quintanoscia*
- Small lateral lobes present, no noduli-shaped tricorn-like setae on coxal plates *Oxalaniscus*

4 Cephalothorax with prominent compound eyes consisting of at least 20 ommatidia in four rows 5
- Cephalothorax with compound eyes consisting of a maximum of 15 ommatidia randomly arranged 9

5 Compound eyes laterally protruding, cephalothorax in frontal view T-shaped 6
- Cephalothorax different 8

6 Pereopod 1 with enlarged carpus, prominent setal fields *Ischioscia*
- Pereopods without prominent setal fields 7

7 Pereopods 2 to 5 with transverse setal fringe medially *Parischioscia*
- Tricorns of coxal plates flagelliform, pleopod 1 exopodite with small protrusion laterally *Tropiscia*

8 Tegument smooth and shiny, small neopleurae *Roraimoscia*
- Tegument with granules, prominent neopleurae *Mirtana*

9 Pleonites 3 to 5 with broad neopleurae, continuing pereon *Oreades*
- Pleonites with small neopleurae, not continuing pereon outline 10

10 Compound eyes of more than 5 ommatidia, dorsally well-pigmented 12
- Compound eyes absent or less than 5 ommatidia, pigmentation reduced 11

11 Pleopod 5 exopodite triangular with straight margins *Pentoniscus vargasae*
- Pleopod 5 of different shape *Colombophiloscia*

12 Linea frontalis present 13
- Linea frontalis absent 14

13 Linea frontalis medially interrupted, both halfs arched *Pentoniscus*
- Linea frontalis straight, very faint *Ecuadoroniscus*

14 Cephalothorax laterally broadened, pereonites zebra-patterned *Ischioscia zebricolor*
- Cephalothorax not broadened, pereonites light-spotted 15

15 Coxal plates latero-caudally rounded *Formicascia*
- Cephalothorax with two slight ridges on postfrons *Yaerikima*

16 Two rows of noduli laterales on each side 17
- One row of noduli laterales on each side 18

17 Lateral endite of maxillula with seven teeth *Araucoscia*
- Lateral endite of maxillula with ten teeth *Pseudophiloscia*

18 One of the noduli laterales more dorsally inserted than others 28
- All noduli laterales at same distance from lateral margin of coxal plates 19

19 Pleonites 3 to 5 with broad neopleurae, continuing pereon 24
- Pleonites with small neopleurae, not continuing pereon outline 20

20 Apical organ shorter than distal flagellar article, free sensilla of same length 22
- Apical organ longer than distal flagellar article, free sensilla short 21

21 Pigmentless with scale-shaped, frontally directed tricorns on pereonite *Caraiboscia*
- Pigmented, noduli laterales flagelliform *Metaprosekia*

22 Lateral endite of maxilla with cleft teeth, pereopod 1 propus inflated 23
- Lateral endite of maxilla with ctenate teeth *Benthana*

23 Slender with long pereopods, genital papilla apically with deep cleft *Halophiloscia*
- More stout with star-shaped chromatophores dorsally, genital papilla with slight cleft *Littorophiloscia*

24 Lungs on pleopods 1 to 5 25

- No pleopodal lungs but uncovered "respiratory areas" 27

25 Cephalothorax without lateral lobes, small: <6mm *Pulmoniscus*
- Lateral lobes present, large: > 10 mm 26

26 Linea frontalis present, covered pleopodal lungs *Plataoniscus*
- Linea frontalis reduced, semi-covered lungs *Balloniscus*

27 Lateral endite of maxillula with ctenate teeth, no gland pore fields *Benthana longicaudata*
- Maxillula with simple teeth, coxal plates with distinct gland pore fields *Oniscophiloscia*

28 Apical organ with long free sensilla, shorter than distal flagellar article 29
- Apical organ longer than distal article, free sensilla short 30

29 Respiratory areas or lungs present, mandible molar penicil dichotomic *Atlantoscia*
- No respiratory areas, molar penicil simple *Burmoniscus*

30 Both linea frontalis and linea supra-antennalis present 34
- Either linea frontalis or linea supra-antennalis reduced 31

31 Linea supra-antennalis reduced *Andenoniscus*
- Linea frontalis reduced 32

32 Pleopod 5 exopodite triangular and pointed 33
- Pleopod of different shape, coxal plate II drawn out caudally *Xiphoniscus*

33 Pleopod 5 exopodite with guide slot on medial margin *Androdeloscia*
- Pleopod 5 exopodite extraordinarily drawn out *Erophiloscia*

34 Compound eyes with more than 20 ommatidia arranged in 4 rows, pleopod 1 endopodite apically rounded *Prosekia*
- Compound eyes with seven to eight ommatidia, pleopod 1 endopodite flagelliform *Erophiloscia (waegelei, longistyla)*

5 Phylogeny of South American "Philosciidae"

In this chapter, the phylogeny of the South American genera of philosciid facies is reconstructed by means of the Hennigian methodology. A cladistic analysis is performed with the PAUP software, and both topologies are compared. Some preliminary remarks seem advisable: For comparison of characters, it is necessary to make sure that the structures dealt with are truly homologous, in the Crinocheta, specialized dorsal receptors are commonly called noduli laterales, but until now, no investigations on the ultrastructure of these receptors were published. The homologization is done merely by the differences in general appearance between the noduli and the tricorns.

Another problem is the case of pleopodal lungs in the Crinocheta, they are homologies since they are respiratory devices of the pleopod exopodite, but a thorough examination of the structure of lungs reveal that they evolved independently from simple respiratory areas. This problem is discussed in chapter 5.1 with respect to lung evolution in South American taxa of philosciid facies.

Additionally, difficulties in determining the polarity of characters should be mentioned. As in the case of the shape of the apical organ or the shape of pereopod 1, often two main character states can be discerned, which are not present in the outgroups. These problems of homologization were discussed by Hennig (1961) and recently by Patterson (1982), who pointed out the risk of defining paraphyla by means of homologous structures which are, phylogenetically spoken, symplesiomorphies.

5.1 Evolution of Lung Structures

A detailed analysis of the lung morphology was performed by Hoese (1982 and 1983). His excellent work led to some misinterpretations of the observed structures, and a simple morphological row was constructed and found its way even in treatises on zoology (e.g. Gruner 1993). Further research revealed the fact that the lungs, which until then on the basis of available data were supposed to have evolved only once in the Oniscoidea and then been modified in the course of further evolution must have evolved several times, starting with folded lateral areas of the exopodites and forming respiratory organs of different complexity, the most specialized being covered lungs, which have contact to the surrounding air solely by a spiracle. For example, this morphological row can be traced in the Eubelidae (Ferrara *et al.* 1990). Furthermore, the thorough examination of the genus *Aphiloscia* Budde-Lund, 1908 ended in the discovery of a convergent evolution of covered lungs within this genus (Ferrara et al. 1994). This contrasts with the opinion that within the family "Philosciidae" lungs never occur [cf. Vandel's (1962) definition of the family]. For this study, the respiratory organs of the genera *Balloniscus*, *Benthana* and *Atlantoscia* were examined and a convergent evolution of partially to totally covered lungs in the Balloniscidae and *Atlantoscia rubromarginata* (Araújo and Leistikow, 1999) has to be postulated.

The complexity of respiratory areas is very different in the four species examined in this work, they reflect a morphological transition from simple unfolded uncovered lungs to semicovered lungs with anastomising lung tubules. This morphological transition does not represent a phylogenetic transition, as can be seen by comparing the position of the taxa in the phylogram proposed in this study (chapter 5.2).These lung structures were described by Leistikow and Araújo (2000).

It has to be stressed that in contrast to the statements of Warburg et al. (1997), in *Androdeloscia tarumae* (Lemos de Castro, 1984) no pleopodal lungs are present. These small animals seem to breathe via the ventral cuticle of the exopods as most taxa of philosciid facies. This analysis of lung structures in South American Oniscidea of philosciid facies should demonstrate the necessity of thorough examinations of characters to avoid misinterpretations concerning the phylogeny.

5.2 Phylogenetic reconstruction

In contrast to the opinion of Vandel (1968, 1973a and b), the family "Philosciidae" has to be regarded as being paraphyletic. He postulated a "regressive evolution" of many characters like the reduction of neopleurae, simplification of the structure of the mouthparts, reduction of eyes and cephalic lobes. He misinterpreted the polarity of these character states. There are no autapomorphies for the family "Philosciidae". Moreover, as will be shown in the following paragraphs, the European genus *Philoscia* is not related to the remainder of the "Philosciidae", it is closely related to *Oniscus* Linné, 1758. The cladogram for the examined taxa is given in fig. 19, the main autapomorphies are indicated at the dichotomies and explained in the text.

The basalmost representatives of the Oniscoidea found in South America are the Central American species *Oxalaniscus ctenoscoides* and *Quintanoscia contoyensis*. In the former, there are no noduli laterales whereas in *Quintanoscia contoyensis* small tricorn-like setae are present which resemble the noduli laterales. The pereopod 1 carpus bears a brush of sensory spines medially and a longitudinally directed antenna-grooming brush [PE2-1, PE3-2]. The mouthparts, especially the maxillae and maxillipeds, have plesiomorphic character states [M2-1, Mp2-2, Mp3-1]. The mandible has a molar penicil composed of few branches [Md2-3], a derived character. These character states resemble those found in *Alloniscus*, another genus of Oniscoidea lacking noduli laterales. In *Alloniscus*, the maxillula bears five teeth in the outer set of the lateral endite, the plesiomorphic character state. In *Oxalaniscus* and *Quintanoscia*, there are only four prominent teeth [Ml1-5] present. The genera *Oxalaniscus* and *Quintanoscia* are adelphotaxa due to the apomorphic shape of the molar penicil, they are more derived in the shape of the maxillula than *Alloniscus*. The synapomorphies of *Oxalaniscus* and *Quintanoscia* are discussed in chapter 4.2.1. The tricorn-like setae of the three taxa are of the same structure: the sensillum is only loosely connected with the cuticular scales. This character is another argument for treating *Oxalaniscus* and *Quintanoscia* as basal. The derived character state is a sensillum joined with the cuticular scale which is found in the monophylum described below.

The remaining taxa of Oniscoidea belong to a taxon with noduli laterales. As can be concluded from the name of the taxon, the presence of noduli laterales is the autapomorphy of this monophylum [Cx2-2]. Two characters are important: For the groundpattern of the taxon bearing noduli laterales, a cylindric carpus of pereopod 1 with a longitudinal antenna-grooming brush has to be postulated. These characters are present in *Alloniscus* and less conspicuous in both *Oxalaniscus* and *Quintanoscia*. They can be found in a similarly developed way in *Philoscia*, in species of Oniscidae, Porcellionidae and Agnaridae, among others. In most of the philosciids found in South America, the antenna-grooming brush has a more transverse position. The medial margin of the carpus is flattened in the male bearing a dense cover of sensory spines which form a spiny brush. This brush plays an important role during courtship because it allows the male to mount on the "slippery" cuticle of the female. These brushes can be found on the pereopods 1 to 7 of several Armadillidiidae with very smooth dorsal cuticle. The other character, the apical organ, is composed of a tuft of sensilla wrapped in a cuticular sheath with two free sensilla. Both the central body and the free sensilla are of subequal length.

In the stem line leading to the sister taxon of most of the higher Oniscoidea, the new taxon 0, which is composed of the new taxon A and its adelphotaxon, comprising the genera *Adeloscia*, *Araucoscia* and *Pseudophiloscia*, two new characters evolved:

■ Antenna-grooming brush in transverse position [PE3-2] □ antenna-grooming brush in longitudinal position [PE3-1]

■ Reduction of number of sensory spines on the medial margin of carpus 1 □ dense cover of sensory spines on medial margin

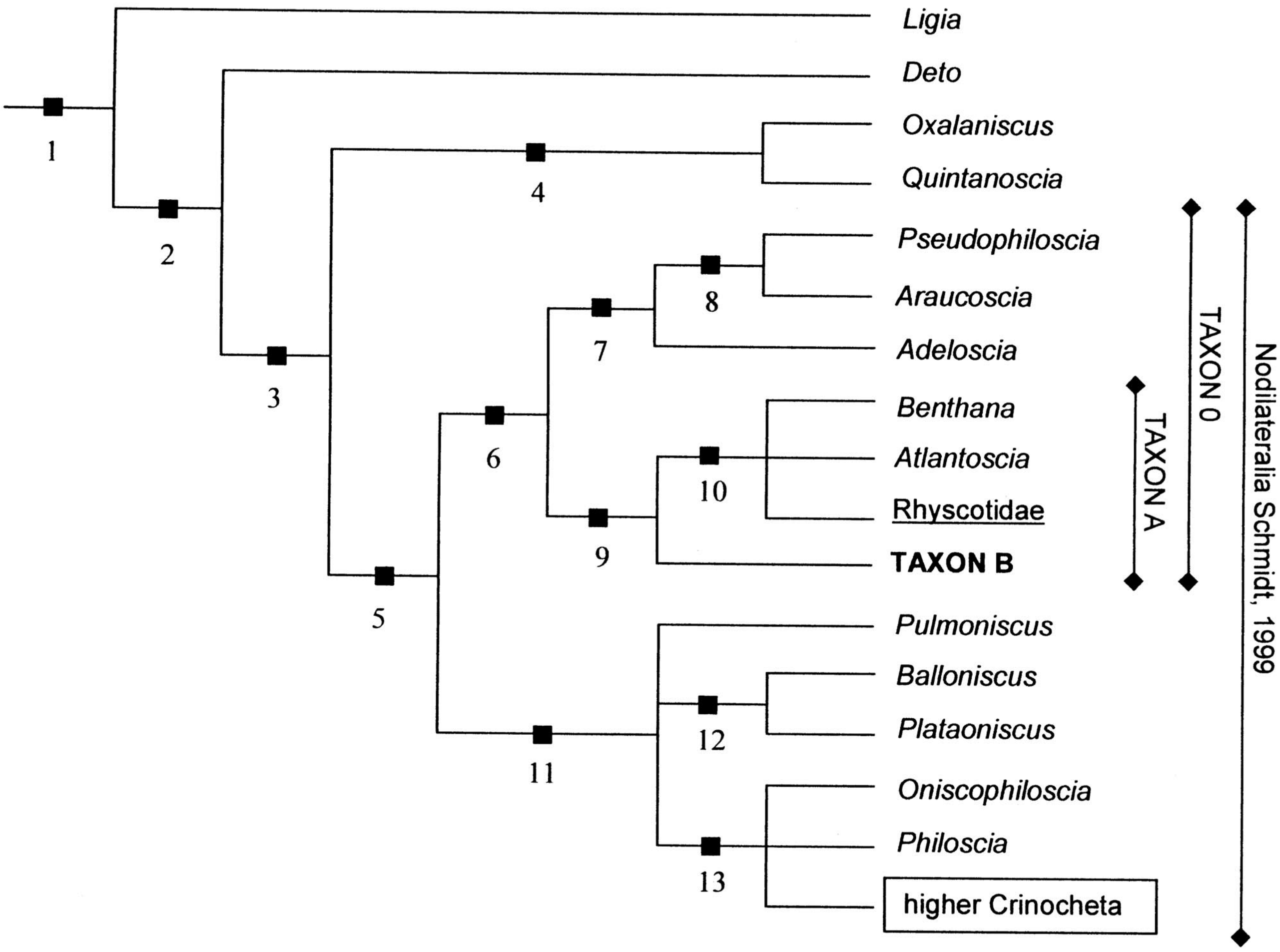

Fig. 19 A. Phylogeny of the South American "Philosciidae":
The dendrogram is reconstructed by brain work using the Hennigian principles, the phylogeny of the new taxon B is shown in fig. 19 B
Derived character states of the taxa are:

1 Reduction of palp of mandible; Antennula composed of three articles
2 Molar penicil replacing pars molaris [Md1-2]; lateral endite of maxillula bearing two penicils [Mm1-2]; Male pleopod 1 endopodite with furrow for styliform pleopod 2 endopodite; Pleopod endopodites with muscles M49, 74, 84, 92 (Erhard 1997); Female marsupium with cotyledones (Wägele 1989)
3 Ventral shield of genital papilla sclerotized [Ge1-2]; Antennal flagellum three-articulate [A2-3]; apical organ with cuticular sheath [Ao1-2]
4 Cephalothorax with linea frontalis reduced [Ct1-3]; molar penicil composed of 3 branches [Md2-3], lateral endite of maxillula with 4+6 teeth, one of inner set absent or at least vestigial [Ml1-6], maxillular teeth simple [Ml1-5]
5 Coxal plates with noduli laterales, specialized tricorn-like setae [Cx2-2]
6 Antenna-grooming brush transverse [PE3-2], reduction of number of sensory spines
7 Sensory spines arranged in three rows of four spines [PE4-3], inserted on small humps, carpus subquadrangular [PE4-3]; lateralmost tooth of lateral maxillular endite huge [Ml1-8]
8 Two rows of noduli laterales per side [Cx3-2] , coxal plates very narrow [Ha5-2], coxal plates without sulcus marginalis [Cx4-2]
9 Hyaline fringe of fused scales rostro-distally on carpus [PE3-2], laterodistal edge of carpus and merus with setal tufts [PE1-2]; terminal spatula of genital papilla truncate [Ge2-2]
10 Maxillipedal endite without setation, distal margin transverse [Mp3-4]
11 Tricorns with broadened basis, giving it the shape of an inverted ‘Y’ [Ha3-3], more than 5 sensory spines on the lateral edge of the male ischium 7 [PE9-2]
12 Reduction of the ornamental sensory spine on male pereopod 1 carpus [PE7-3]
13 Pleotelson with triangular distal part [Ha4-5]

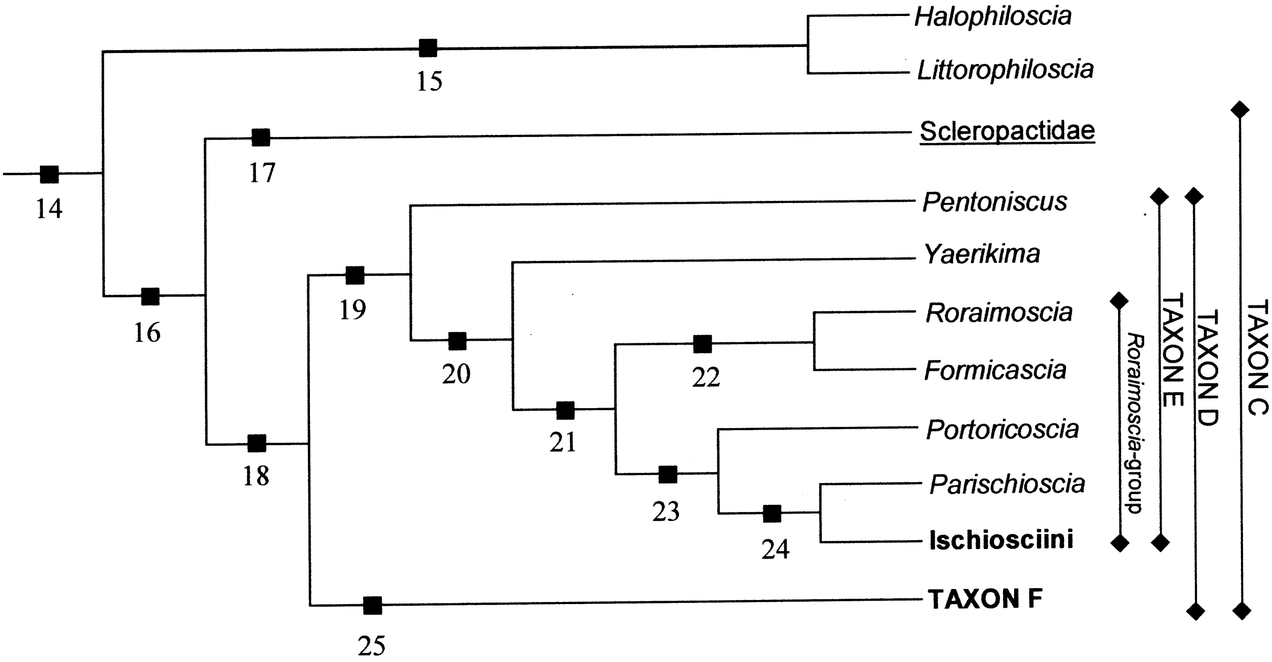

Fig. 19 B. Phylogeny of the new taxon B:
The dendrogram is reconstructed by brain work using the Hennigian principles, the phylogeny of the new taxon F in fig. 19C, of the new taxon Ischiosciini is shown in fig. 19D.
Derived character states of the taxa are:
14 Carpal brushes formed by cuticular scales [PE2-2]; rostral surface of at least the male carpus 1 flattened, sometimes medially enlarged [PE6-4]
15 Vasa deferentia run from the genital papilla in pereonite 7 to pereonite 3 (part C), then bend backwards to pereonite 6 (part B) and run rostrally to segment 4 (part A), where the testes are located [Ge3-2]
16 Apical organ of antenna at least as long as distal flagellar article, free sensilla short [Ao2-3]; medial setal tuft of maxillipedal palp located on a stalk-like protrusion of the medial article [Mp2-6]
17 Prominent neopleurae, oval body outline, pereonites very convex
18 Antenna-grooming brush distally broadened and deepened, terminated by a set of fringed scales [PE10-2]
19 Pleopod 5 exopodite with caudal creel composed of three sinuous rows of pectinate scales [PL7-3]
20 Cephalothorax without lateral lobes [Ct1-6]
21 Profrons level with no depressions for holding the antennae, lateral lobes and linea frontalis reduced [Ct1-4]
22 Medial part of female pleopod 3 exopodite elongate, surpassing the exopodite [PL3-3]; pleotelson with lateral margin bearing two concavities
23 Molar penicil partially fused and consisting of maximally 7 branches [Md2-2]
24 First article of the antennula with slight shield-like lobe [A1-4]; ornamental sensory spine with hand-like apex [PE7-2]
25 Medial margin of pereopod 1 carpus with angle between part of antenna-grooming brush and part of sensory spines [PE3-3]; two rows of three sensory spines and one row of three tricorn-like seta along medial margin of carpus 1 [PE4-2]

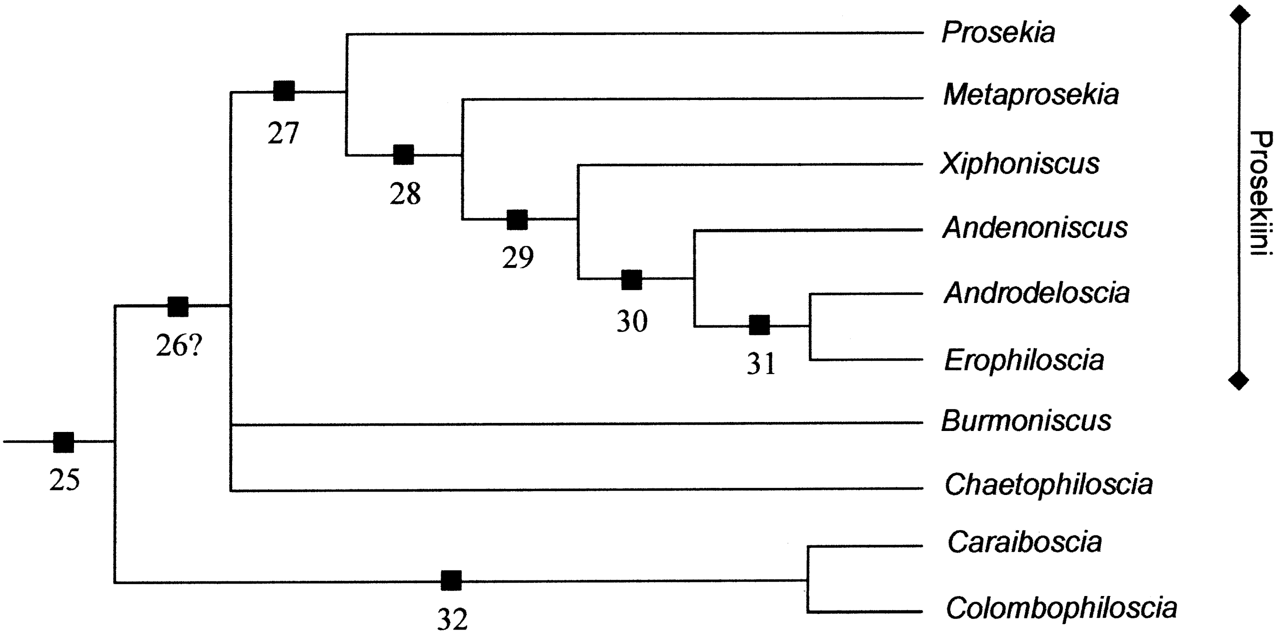

Fig. 19 C. Phylogeny of the of the new taxon F:
The dendrogram is reconstructed by brain work using the Hennigian principles
Derived character states of the taxa are:
25 Medial margin of pereopod 1 carpus with angle between part of antenna-grooming brush and part of sensory spines [PE3-3]; two rows of three sensory spines and one row of three tricorn-like seta along medial margin of carpus 1 [PE4-2]
26 Nodulus lateralis of coxal plate IV inserted more distantly from lateral margin [Cx3-3]
27 Antennula with the medial aesthetascs gathered in a tuft, directed more or less medio-distally, not attached to article 3 [Ae1-3], transverse fold between aesthetasc tuft and distal pair of aesthetascs; male pleopod 1 with hyaline lamellae near apex [PL4-3]
28 Body length less than 6 mm, cuticle soft; eyes consisting of up to ten ommatidia not arranged in distinct rows [Ey-4]
29 Noduli laterales extremely long [Cx3-6]; male pleopod exopodites rounded [PL3-2]
30 Male pleopod 2 endopodite flagelliform [PL5-2]
31 Reduction of a proximal setal tuft on the maxillipedal palp [Mp2-5], maxillipedal endite without setation [Mp3-3]; male pleopod 5 distally pointed, with straight medial margin somewhat prolonged proximally [PL6-2]
32 Modified tricorn-like setae on the pereonites: leaflet scales (Schmalfuss 1977) [Ha3-2]; compound eyes reduced to 4 ommatidia [Ey-5]; antennula with a single row of erected aesthetascs [Ae1-4]; lateral endite of maxillula bearing mostly simple teeth [Ml1-5]

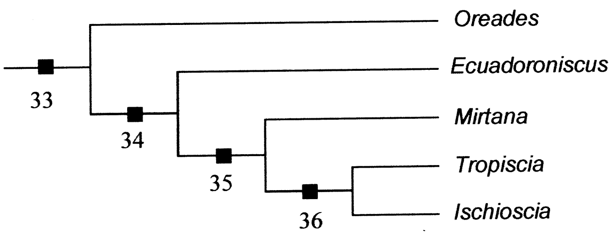

Fig. 19 D. Phylogeny of the new taxon Ischiosciini:
The dendrogram is reconstructed by brain work using the Hennigian principles
Derived character states of the taxa are:
33 Antennula with proximal article bearing a shield-like protrusion distally [A1-3]; pleotelson with ventral semicircular pit apically [Ha4-5]
34 Maxilla with sclerotized cuticular clasp proximally of the medial lobe [M2-4]
35 Cephalothorax laterally extended [Ct2-2]; male pleopod 1 exopodite with slight incision [partially PL3-3]
36 Cephalothorax with flattened vertex and compound eyes laterally protruding, appearing T-shaped in frontal view [Ct2-5]; male pleopod 1 exopodite with bulbous lateral protrusion [partially PL3-3]

These characters are autapomorphies for the taxon 0, the shift of the antenna-grooming brush in a more transverse position is most probably linked with a change in the antenna-grooming process: the planes, in which the articles of pereopod 1 move, must be slightly different to those where the brush is longitudinal. This would only be possible if there is a change in the insertion of musculature and the position of the articles in relation to each other. In fact, the carpus 1 is distorted against the merus in many taxa. Hence, this character is of great complexity and therefore unlikely to evolve several times.

The genera *Adeloscia*, *Araucoscia* and *Pseudophiloscia* are characterized by the following autapomorphies:

■ Sensory spines on carpus 1 arranged in three rows of four spines increasing in length from proximal to distal margin [PE4-3] ☐ sensory spines not arranged this way, not inserted on humps

■ Carpal 1 subquadrangular, almost as broad as long [PE5-3] ☐ carpus cylindrical [PE5-1]

■ Maxillular teeth are all simple and the lateralmost one is very prominent [Ml1-8] ☐ maxilla with 4+6 teeth, inner set ctenate [Ml1-3]

The unique shape of the carpus with the invariably placed sensory spines is supposed to be a good character to evidence the monophyly of the taxon. Similarly, the structure of the maxillula with the prominent lateral tooth and the set of up to nine much smaller and simple teeth is not found in any other taxon of Oniscoidea. The shape of the maxillipedal palp resembles the one of Benthana, but the reduction of the setation must have happened in convergence to this taxon.

In the new taxon A, comprising the taxa *Benthana*, *Atlantoscia*, the Rhyscotidae and the new taxon B, the modified structure of the carpus 1 and of the genital papilla are autapomorphies:

■ Hyaline fringe of fused cuticular scales on the rostro-distal margin of the carpus present [PE3-2]☐ no such fringe present

■ Latero-distal edge of carpus and merus with setal tuft [PE1-2] ☐ no setal tuft on carpus and merus [PE1-1]

■ Terminal spatula of genital papilla truncate [Ge2-2] ☐ terminal spatula rounded [Ge2-1]

The characters concerning the carpus are not found in any other taxon of Oniscoidea, some hair-like setae on the latero-distal edge of the carpus 1 can be found in *Detonella* Lohmander, 1927. Since a setal tuft is not present in the basal Oniscoidea and in the adelphotaxon of taxon A, it is considered a new acquisition of taxon A. The genital papilla is equipped with a strongly sclerotised ventral shield in the groundpattern of Oniscoidea as described by Erhard (1997). In taxon A, terminal spatula is truncate, and as long as or slightly shorter than the ventral shield, the orifices located laterally. The plesiomorphic character state is a terminal spatula longer than the ventral shield, apically rounded. The type of genital papilla with rounded, long terminal spatula is found in *Alloniscus* and most taxa of Oniscoidea. Hence, it must be present in its groundpattern (Erhard 1998), whereas the truncate terminal papilla is a derived character of taxon A.

The genera *Atlantoscia* and *Benthana* are basal representatives of the taxon A; together with the Rhyscotidae, they form the *Benthana*-group. The taxon is characterized by a slender pereopod 1 carpus with transverse antenna-grooming brush; a medial brush of sensory spines is present in several species of *Benthana*. It is lacking in *Atlantoscia* and Rhyscotidae, which bear a set of three to four sensory spines of decreasing length from distally to proximally, as some species of *Benthana*, which are not sexually differentiated in the male pereopods. The Rhyscotidae have the plesiomorphic structure of the ctenate maxillular teeth in common with *Benthana*. The *Benthana*-group is characterized by the following autapomorphy:

■ Maxillipedal endite without setation, distal margin transverse [Mp3-4] ☐ endite covered with hair-like setae, distal margin straight [Mp3-2]

The shape of the maxilliped is superficially similar to the maxilliped of the Porcellionidae and related taxa. In contrast to the latter, the endite is distally transverse and lacks the two points, which are present in the endite of the Porcellionidae and *Philoscia.* The reduction of the setation and the loss of the knob-like penicil are interpreted as convergent evolution in this work.

The habitus with the long uropods, the sympodite of which surpasses the pleotelson, reflects the basal position of these genera within the taxon A. Ctenate maxillular teeth are also found within the South American taxon *Alboscia* Schultz, 1995. No material of *Alboscia* was available for the present study, so nothing can be said about the relationships of this interesting taxon. Possibly, the genus is related to the Prosekiini in which case the ctenate teeth are a new acquisition of *Alboscia* and would not be the same character state as in *Benthana*. The drawings of the pereopod 1 presented by Araújo (1999) indicates that the genus might not belong to the taxon A, because the setal pattern is quite different to the one found in taxon A. For a statement founded on more facts, new material is necessary. A close relationship of *Benthana* and *Benthanops* Barnard, 1932 was postulated by several authors (H. Schmalfuss, pers. comm., Taiti and Ferrara 1980). However, there is no good evidence for such a relationship but the similar shape of the maxillipedal palp which is similar in both genera.

The sister taxon of the *Benthana*-group is the new taxon B to which the Halophilosciidae, the Scleropactidae and the new taxon C belong. The taxon B is characterized by two autapomorphies:

■ Carpal brushes formed by cuticular scales [PE2-2] ☐ carpal brushes formed by sensory spines [PE2-1]

■ Rostral surface of at least the male carpus 1 is flattened, sometimes medially enlarged [PE6-4] ☐ carpus 1 cylindrical [PE6-1]

The medial margin of the carpus is pointed and not broad as in the outgroup. The carpal brushes are important structures for the male to cling on the female during the precopula. The specific shape of the carpal brushes and the complexity of this character make a single evolution of such a structure highly probable. Hence the character is a good autapomorphy of the new taxon B.

Within the taxon B, the Halophilosciidae branch off. Many details of the mouthparts have a plesiomorphic character state in comparison with its sister taxon, the new taxon C (Scleropactidae and new taxon D). The shape of the maxilla is similar to the basal Oniscoidea *Alloniscus* and *Quintanoscia*, both lobes are subequal in breadth and only slightly rounded distally. The maxillipedal palp is prominent compared with the basipodite; it is equipped with prominent setal tufts, which are present in the Ligiidae and may belong to the groundpattern of Oniscidea. In *Halophiloscia couchii*, the maxillula bears an outer set of five teeth, whereas in *Littorophiloscia insularis* only four teeth are present. The autapomorphies of the Halophilosciidae were described above in the taxonomic section [PE6-2, Ge3-2].

Most of the South American philosciids belong to a monophyletic group which is called the taxon C in this study. An important character is the apical organ, a sensory device which was examined in detail by several authors [Mead et al. (1976) for *Porcellionides*, Seelinger (1977) for *Hemilepistus*, Alexander (1977) for *Ligia*]. Hoese (1989) gave some information on the structure of the apical organ of the Oniscoidea, which is divided into a basal and an apical part. The two parts are connected by an articulation which has disappeared in *Hemilepistus*. The phylogenetic evidence from this organ is still ignored, although Schmalfuss (1989) mentioned the apical organ as a synapomorphy of the taxa of Oniscoidea. In a recent survey, Schmalfuss (1998b) pointed out that the antenna*e* are the most important sensory organs; the apical organ and the aesthetascs are receptors for mechanical and chemical stimuli.

The primitive shape of the apical organ is still open to debate (cf. Schmidt 1999). No data are available if there was a short apical organ or an elongate one with short free sensilla laterally. All the basal representatives of Oniscoidea, which show several plesiomorphic characters in the mouthparts have a short apical organ with long free sensillae inserted laterally. These taxa are *Alloniscus* Dana, 1852; *Oxalaniscus* Leistikow, 2000; *Quintanoscia* Leistikow, 2000, *Hawaiioscia*, Schultz, 1973 (Taiti and Howarth 1997); some *Littorophiloscia* Hatch, 1947 and *Halophiloscia* Verhoeff, 1926 bearing a subrectangular maxilla with subequally broad lobes, a small maxillipedal basipodite and setal tufts of more than 30 setae on the maxillipedal palp, and *Benthana* Budde-Lund, 1908 and *Rhyscotus* Budde-Lund, 1904 with ctenate teeth of the maxillula. The evolution of this type of apical organ out of the short tuft of sensilla present in Detonidae appears to be simple: The cuticular sheath of the central body (Mead et al. 1976) may have been formed by fusion of cuticles of the neighboring sensilla. The apical organ underwent two allometric transformations: while the central body achieved the length of the distal flagellar article or even half the length of the flagellum [Ao2-2], the free sensilla were considerably shortened. The distribution of the short apical organ in most of the crinochete taxa makes it likely that the long apical organ is the more derived character. Provided these evolutionary scenario is correct, a monophyletic group can be established which comprises the Scleropactidae and most of the genera of "Philosciidae". Whether or not the Halophilosiidae have to be included depends on the character state present in the groundpattern of this taxon. In *Halophiloscia couchii* and *Littorophiloscia insularis*, the apical organ is similar to the one of *Benthana*. In *L. denticulata*, a considerably longer apical organ is present. This question can only be resolved by a re-examination of all the members of the family.

The autapomorphies of the new taxon C are:

■ Apical organ of antenna at least as long as distal flagellar article, free sensilla short [Ao2-3] ☐ apical organ much shorter than distal flagellar article, free sensilla as long as apical organ [Ao2-1]

■ Medial setal tuft of maxillipedal palp located on a stalk-like protrusion of the medial article [Mp2-6] ☐ medial setal tuft inserting directly on the body of the medial article [Mp2-3]

The stalked medial setal tuft of the maxillipedal palp [Mp2-6] is found exclusively in taxon C. Whether this character is due to a specific way of nutritition of taxon C and then may be a functional necessity is not known, because data on the live history of the members of taxon C are not available. In the basal members of taxon C, the maxillipedal endite is setose, the plesiomorphic character state within the Oniscoidea. In the more derived taxa, like the Prosekiini, the endite is free from setation in most species [Mp3-3]. With respect to their habitus, the Scleropactidae are the more derived taxon. Their ability of conglobation evolved convergently to the Eubelidae, Armadillidiidae and Armadillidae among others; but it is not a character of the groundpattern of this family since the basal genus *Colomboscia* Vandel, 1972 is non-conglobating (Taiti et al. 1995).

The South American taxa of philosciid facies, which are united in the new taxon D, comprise the *Roraimoscia* genus-group and its relatives, the adelphotaxa *Caraiboscia* and *Colombophiloscia* and the Prosekiini. Taxon D, the adelphotaxon of the Scleropactidae, is characterized an autapomorphy concerning the pereopod 1 carpus:

■ Antenna-grooming brush distally broadened and deepened, terminated by a set of fringed scales [PE10-2] ☐ antenna-grooming brush without fringed scales, subequal in breadth in proximal and distal part [PE10-1]

The derived character state of the antenna-grooming brush is a prerequisite for further modification of the carpus in taxon D. The broadened distal part is unique among the Oniscoidea, as are the fringe of specialized scales. These scales may have evolved from the broad scales of the antenna-grooming brush. The basal split in the South American members of the taxon D is into a new taxon E, comprising the genera *Pentoniscus*, *Yaerikima*, and the *Roraimoscia* genus-group, and a new taxon F, to which belong the genera *Caraiboscia*, *Colombophiloscia* and the Prosekiini. Possibly, several paleotropic genera and the genus *Chaetophiloscia* Verhoeff, 1908 belong to taxon F, but the data on their morphology are too scarce to establish this relation with more certainty. In the taxon E, the maxilliped presents the plesiomorphic character state with setose endite and setal tufts of about 15 to 20 setae on the palp. The following autapomorphic character was found:

■ Pleopod 5 exopodite with caudal creel composed of three sinuous rows of pectinate scales [PL7-3] ☐ creel composed of a single transverse row of pectinate scales [PL7-2]

The genus *Pentoniscus* is the basalmost representative of taxon E, its autapomorphies are discussed in Leistikow (1998b) and in chapter 4.2. It is excluded from the remainder of taxon E, because it does not share the synapomorphy of the genus *Yaerikima* and the *Roraimoscia* genus-group:

■ Cephalothorax without lateral lobes [Ct1-6] ☐ cephalothorax with lateral lobes [Ct1-5]

The autapomorphies of the *Roraimoscia* genus-group were given in chapter 4.2, as are those of the adelphotaxa *Formicascia* and *Roraimoscia*. The taxon *Formicascia* and *Roraimoscia* is the sister group of the remainder of the *Roraimoscia* genus-group, a subtaxon *Portoricoscia* and [*Parischioscia* and Ischiosciini] wich are united by the synapomorphic shape of the mandible:

■ Molar penicil partially fused and consisting of maximally seven branches [Md2-2] ☐ molar penicil composed of about ten individualized branches [Md2-1]

The sister group relationship *Parischioscia* and Ischiosciini and the autapomorphies of the Ischiosciini itself are presented in chapter 4.2. Within taxon E, the high number of monotypic genera is conspicuous: *Formicascia*, *Parischioscia*, *Portoricoscia*, and *Roraimoscia* are solely known by the type species. This is most probably a collection artifact, because our knowledge on the Oniscidean fauna of the Guyanan Shield and the Antilles is scarce. Particularly the adelphotaxa *Formicascia* and *Roraimoscia* differ remarkably in characters do not show much variation in species commonly united in genera.

Within the Ischiosciini, all genera but *Oreades* have a synapomorphic construction of the maxilla:

■ Maxilla with sclerotized cuticular clasp proximally of the medial lobe [M2-4] ☐ maxilla without a sclerotized clasp [M2-2]

In the overall morphology, *Ecuadoroniscus* is the most primitive form of this group, especially the cephalothorax is similar to the outgroup taxa of the Ischiosciini, e.g. the genus *Roraimoscia*. The remaining taxa of the Ischiosciini, i.e. *Mirtana*, *Tropiscia* and *Ischioscia* show the following synapomorphy:

■ Cephalothorax laterally extended [Ct2-2] ☐ cephalothorax not laterally extended [Ct2-1]

■ Male pleopod 1 exopodite with incision [PL3-3] ☐ male pleopod 1 exopodite triangular [PL3-1]

This extension is only slight in *Mirtana*, and more prominent in *Tropiscia* and *Ischioscia*. The second character is more conspicuous in *Mirtana* than in *Tropiscia*. Some caution with the second character is advisable, because both *Oreades* and *Ecuadoroniscus* are only known by females. So evidence for the shape of the male pleopod 1 exopodite in the groundpattern of the Ischiosciini is not available, the presumable character state is derived from the relations found in *Parischioscia*. The adelphotaxon relationship of *Tropiscia* and *Ischioscia* was established in Leistikow (2001e).

An exhaustive discussion of the phylogeny of the species of *Ischioscia* is presented in Leistikow (in press).

Besides the South American genera, taxon F comprises several genera of the Old World, e.g. *Chaetophiloscia* and *Burmoniscus*. In taxon F, the pereopod 1 is further derived: the carpus is shorter in these taxa, the antenna-grooming brush is broader, its distal end with the "Grannenhärchen" of Verhoeff (1908b) takes up almost one third to a half of the length of the carpus. The medial margin forms a conspicuous angle. The number of sensory spines is constant: A row of medial spines accompanied by submedial rows on the rostral and caudal carpus surface. The number of spines in each row is in most cases three, with some taxa bearing two to four spines:

■ Medial margin of pereopod 1 carpus with angle between part of antenna-grooming brush and part of sensory spines [PE3-3] □ medial margin of carpus 1 straight [PE3-2]

■ Two rows of three sensory spines and one row of three tricorn-like seta along medial margin of carpus 1 [PE4-2] □ number of sensory spines and tricorn-like setae variable

These characters are good autapomorphies of taxon F; the superficial simplification of the structure of the pereopod 1 carpus is in fact the establishment of a constant pattern with three prominent sensory spines, which increase in length from the proximal to distal spine. The three-spine pattern is found almost invariably in all the members of taxon F. *Burmoniscus kohleri* is an example of species which bear only a two-spine pattern.

Within taxon F, the small endogeous genera *Caraiboscia* and *Colombophiloscia* are adelphotaxa, their synapomorphies were given in the generic account. They are related to the next taxon. It is possible that there are further members of this taxon. The excentric position of the nodulus lateralis of coxal plate IV is likely to be an autapomorphy of the "groupe chaetophiloscien" postulated by Vandel (1973a). Most of this subtaxon of taxon F have a simple dactylar seta which possibly is another autapomorphy of a subtaxon; the new South American taxon Prosekiini is part of it. Whether they are the next relatives of the Prosekiini can only be concluded after re-examination of the paleotropic genera of taxon F.

The genera belonging to the Prosekiini, i.e. *Prosekia*, *Metaprosekia*, *Xiphoniscus*, *Andenoniscus*, *Androdeloscia* and *Erophiloscia*, are characterized by apomorphic characters mentioned in chapter 4.2. The genus *Prosekia* is the basalmost member of the Prosekiini. It is characterized by several plesiomorphic features like a linea frontalis and compound eyes consisting of about 22 ommatidia arranged in four rows and an overall size of about 10 mm, being about twice as long as the remaining taxa of this group. All the other genera are united by their synapomorphic body outline:

■ Body length less than 6 mm, cuticle soft [Ha6-1r] □ body length more than 10 mm, cuticle strong [Ha6-2]

■ Eyes consisting of up to ten ommatidia not arranged in distinct rows [Ey-4] □ compound eyes bearing more than 20 ommatidia arranged in four rows [Ey-2]

The size reduction and the reduction of the number of ommatidia depend on each other. With respect to the eyes, it is of more importance that the ommatidia are not arranged in rows. If these reductive characters would be due to convergent evolution, the reduction of the number of ommatidia would not necessarily lead to the loss of an arrangement of the ommatidia in rows. *Ischioscia zebricolor* is of comparable body length but has eyes consisting of ommatidia arranged in this way. Together with the reduction of body length, the cuticle in the following taxa is much softer, it must contain less calcium carbonate than in *Prosekia*.

The genus *Metaprosekia* lacks the autapomorphies of the group containing *Xiphoniscus*, *Andenoniscus*, *Androdeloscia* and *Erophiloscia*:

■ Noduli laterales extremely long [Cx3-6] □ noduli laterales only slightly longer than tricorn-like setae [Cx3-3]

■ Male pleopod exopodites rounded [PL3-2] □ male pleopod exopodites pointed [PL3-1]

The next character is found in the remaining taxa of the Prosekiini but in *Xiphoniscus.* It is the derived character state in this group:

■ Male pleopod 2 endopodite flagelliform [PL5-2] □ male endopodite 2 only slightly surpassing exopodite [PL5-1]

In the taxa *Erophiloscia* and *Androdeloscia* co-evolution between the slender pleopod 2 endopodite and the male pleopod 5 exopodite took place. These characters, which are discussed in chapter 4.2 support an adelphotaxon relationship of the two genera. Legrand (1946) found this structure in several Crinocheta, but he stated that it was not evolved in the Oniscidae inférieures, *Halophiloscia couchii* has a simple fold for retaining the endopodite 2. From the phylogeny proposed in htis study, a retention structure has co-evolved with a flagelliform endopodite 2, as stated above. In the basal genera of Prosekiini (*Prosekia*, *Metaprosekia*) such a structure is missing due to its short endopodite. The evolution within the genus *Androdeloscia* are treated in an additional publication (Leistikow 1999c).

Within the genus *Erophiloscia*, the reduction of the row of spines on the male pleopod 1 endopodite is a synapomorphy of all the species except *E. waegelei* Leistikow, 2001. This species and *E. longistyla* Vandel, 1972 are similar in the overall structure of this endopodite with lamellae on the distal part, a plesiomorphous character found in the groundpattern of the Prosekiini. The Peruvian *E. recurvata* Leistikow, 2000 and *E. acanthifera* Leistikow, 2000 are sister species due to the reduction of the linea frontalis, the lamellae and the specific shape of the distal sensory spine of the propus, which is similar to species of *Androdeloscia* but must have been acquired independently.

The sister taxon of the taxon 0 is the remainder of the Oniscoidea, the taxon 5 of Schmidt (1999). The Balloniscidae are probably a paraphyletic group. The Caribbean species *Pulmoniscus insularuminfraventum* may not belong to this taxon. The sole morphological character used for the inclusion in the Balloniscidae, five pairs of pleopodal lungs, is not convincing, since such respiratory structures have evolved convergently in several taxa as explained in Leistkow and Araújo (2000a) and is summarized in chapter 5.1. The habitat of *P. insularuminfraventum* is in hot desert climate (Bwh of the Köppen system). A selection pressure for more efficient respiratory devices has to be postulated: the lack of moisture in the air led to a deposit of waxes into the cuticle to reduce the risk of desiccation. The deposit of waxes reduces the perviousness for gasses. For a sufficient supply with oxygene, effective respiratory organs must have evolved. For the genera *Balloniscus* and *Plataoniscus* no synapomorphies other than the reduction of the ornamental sensory spine can be given, since the lung structure is supposed to be quite different in both taxa (Vandel 1963). Due to the lack of material, only the lungs of *Balloniscus* could be examined in detail, those of *Plataoniscus* are likely to be derived from this type of lungs. Nonetheless, both taxa belong to the same taxon as *Philoscia* and the higher Crinocheta with "real" tricorns:

■ Tricorns with broadened basis, giving it the shape of an inverted 'Y' [Ha3-3] □ tricorn-like setae without the Y-shape [Ha3-2]

■ More than 5 sensory spines on the lateral edge of the male ischium 7 [PE9-2] □ about four sensory spines on ischium 7 [PE9-1]

This taxon including the higher lung-bearing Crinocheta, is characterized by the high number of sensory spines on the lateral edge of ischium 7 in the male, another autapomorphy. In most of the genera, the male pleopod 1 bears sensory spines on both the medial and the lateral margins of the pleopod 1, another possible autapomorphy.

The genus *Pulmoniscus* has pleopods which resemble those of *Agnara* Budde-Lund, 1908: The position of the lungs, the structure of the cuticle of the perispiracular area and the outline of the pleopod exopodites are similar. If *Pulmoniscus* belonged to to a monophyletic group with the Agnaridae, the mandible would be simplified: it lacks the multiple intermediate penicils which are present in Agnaridae. Moreover, the antennal flagellum of *Pulmoniscus* is three-articulate, whereas the Agnaridae have a two-articulate flagellum. In the case of a close relationship of *Pulmoniscus* and the Agnaridae, the similarity in the mandible of the Agnaridae and the Porcellionidae, Cylisticidae and Porcellionidae, the multiplication of the intermedial penicils, and the two-articulate flagellum must be convergencies. For the moment, the phylogenetic relationships of *Pulmoniscus* remain obscure.

The genus *Oniscophiloscia*, too, is part of this monophyletic group characterized by the presence of Y-shaped tricorns [Ha3-3], but similar to *Balloniscus*, the pleotelson is different from the pleotelson with triangular distal part found in *Philoscia*, the Oniscidae, Trachelipodidae and Porcellionidae, among others. Anyway, the ascription of *Oniscophiloscia* to the Oniscidae (Strouhal 1960) is not justified by any character. It is more likely an early descendant of the unnamed taxon 6 of Schmidt (1999), which is quite isolated within this taxon.

Finally, the discussion of the phylogeny of South American Crinocheta of philosciid facies again has to focus on the noduli laterales. These "philosciids" belong to the recently established by Schmidt (1999). Thus, noduli laterales should be present in all the taxa dealt with. Interestingly, in some of the Scleropactidae and in the *Roraimoscia* genus-group, such receptors have not been found. Since they are present in the basal genera of the Halophilosciidae and in both *Atlantoscia* and *Benthana*, they must have been reduced in these taxa. Within the Scleropactidae, one of the tricorn-like dorsal receptors differentiated to a "nodulus lateralis". These noduli differ in their position from those known from other taxa. No ultrastructural work has been done on these noduli, so the question is still unanswered if these receptors were all homologous or if they evolved several times. The noduli laterales of the Prosekiini differ remarkably in size from those found in *Benthana* or the Porcellionidae, and they must not necessarily be homologues if there was a selective pressure to evolve specialized dorsal receptors. To clarify this question, more ultrastructural research on the dorsal receptors is necessary. Some first results were given by Holdich (1984) and Schmalfuss (1978). Noduli laterales are supposed to have evolved as an autapomorphy of the Oniscoidea apart from *Alloniscus* and *Oxalaniscus*. They therefore must have been reduced in the genera of the *Roraimoscia* genus-group and possibly in part of the Scleropactidae.

6 Biogeographic Section

6.1 Geological and Geographical Background

South America is part of the former supercontinent Gondwana. Until the late Triassic, Gondwana comprised Australia, Antarctica, Africa, India and South America. Beginning at about 200 mio. years ago in the Mozambique basin off East Africa (Mukasa and Dalziel 1996), continental drift caused the split of Gondwana into the continents of our days (fig. 20A). The largest fragment was the South America-Africa land mass which stayed unfragmented until the early Cretaceous (fig. 20B). With the spread of the Atlantic Ocean, the separation of Africa and South America began. The oldest sea floor in the southern Atlantic is about 130 mio. years old, it was formed in the Valangian stage of the Jurassic (Tarling 1980). Other authors date the split off to 150 mio. years in the south and due to the relative rotation of Africa around an Euler pole in Western Africa in the region of the Niger delta, to 110 to 95 mio. years in the north (Pindell and Dewey 1982, Pitman et al. 1993). In the late Cretaceous, both continents were separated by at least 200 km distance (fig. 20C). The shallow water might not have effectively inhibited a faunal exchange, but the young ocean was a great barrier for smaller organisms. An effective barrier is postulated for a period of the last 100 mio. years (Pielou 1979) although there was a long-lasting stepping stone route between northeastern Brazil and eastern West Africa due to the position of the Euler pole in West Africa: presumably a swampy area with small islets was filling the gap between the two continental crusts (Briggs 1987). For a period from 100 to 84 mio. years B.P. the pole of relative rotation shifted to a position in the central Atlantic (Pitman et al. 1993), with persisting anticlockwise relative rotation of Africa.

While South America and Africa have been separated for at least 80 mio. years, the connection of South America and Antarctica existed for a much longer time (fig. 20D). Although there is evidence for rocks in the Weddell Sea as old as 160 mio. years (Musaka and Dalziel 1996), the opening of the Drake passage began 35 mio. years ago, and the present position was reached 10 mio. years ago. For a period of about 7 mio. years, a faunal exchange was possible, whereas nowadays Antarctica is covered with ice and no terrestrial isopods are known from it or from the surrounding islands. Before the opening of the Drake passage, the western part of Antarctica consisted of several small fragments which were connected to New Zealand. A modern reconstruction of Gondwanaland and the key role of the Scotia Arc was presented by de Wit (1977) and Dalziel (1982), recent evidence support these findings (Acosta and Uchupi 1996).

In present times, South America and North America are connected via the Central American land bridge, but this is, on a geological scale, a relatively recent land mass. Such a connection existed in the Permo-Triassic, with the Yucatan peninsula placed in a central position in what nowadays is the Gulf of Mexico, whereas nuclear Central America, referred to as the Chortis block, was located where nowadays the bay of Guadalquivir in Ecuador is (Pindell and Dewey 1982). After the separation of Laurasia, of which North America was a part, from Gondwana by the ingressing Tethys 180 mio. years ago (basal Jurassic), there was no direct connection between the two continents for a long time (Rage 1995). Then, during the early Jurassic, South America drifted towards the eastern margin of North America. The spreading zone of the Caribbean plate led to a new separation of both continental blocks from the mid-Jurassic onwards to the Pliocene (Pitman et al. 1993). It caused the development of an island arch in the positon of Central America, which then drifted eastward, thus forming the Antillean arch. From the time of the ingression of the Caribbean plate from the Pacific eastwards at about 135 mio. years B.P., the Yucatán peninsula formed a part of the North American plate while being separated from South America (Pitman et al. 1993). This island arch arrived at its present position in a period from 80 to 65 mio. years ago (Pindell and Dewey 1982). It was replaced by volcanic islands which raised until a land bridge was formed about 3 mio. years ago (fig. 20E). Therefore, a faunal exchange took place for a rather short period. A stepping stone route may be postulated for the last 6 mio. years via the small islets of the volcanic arch now forming the peaks of the Central American cordillera (Pielou 1979). The uplift of the northern Andes in the last few mio. years due to the subduction of the southern margin of the Caribbean plate under the South American plate (Kellogg and Bonini 1982) may have canalized the faunal exchange. An overview of the continental drift on a more global scale is given by Norton and Sclater (1979) and Cocks (1981).

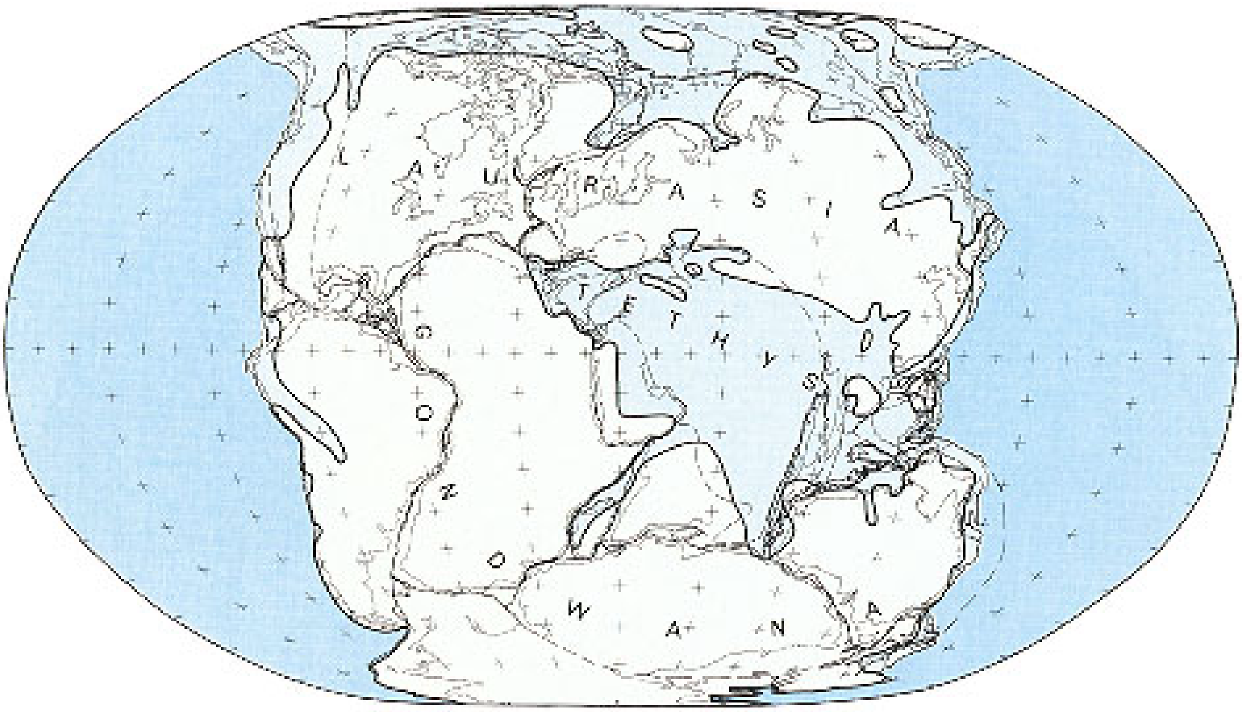

Fig. 20 A. The face of the earth in the Triassic (240-200 million years ago)
White: land masses, Light Blue: epicontinental water, Blue: ocean; after Cox (1981)

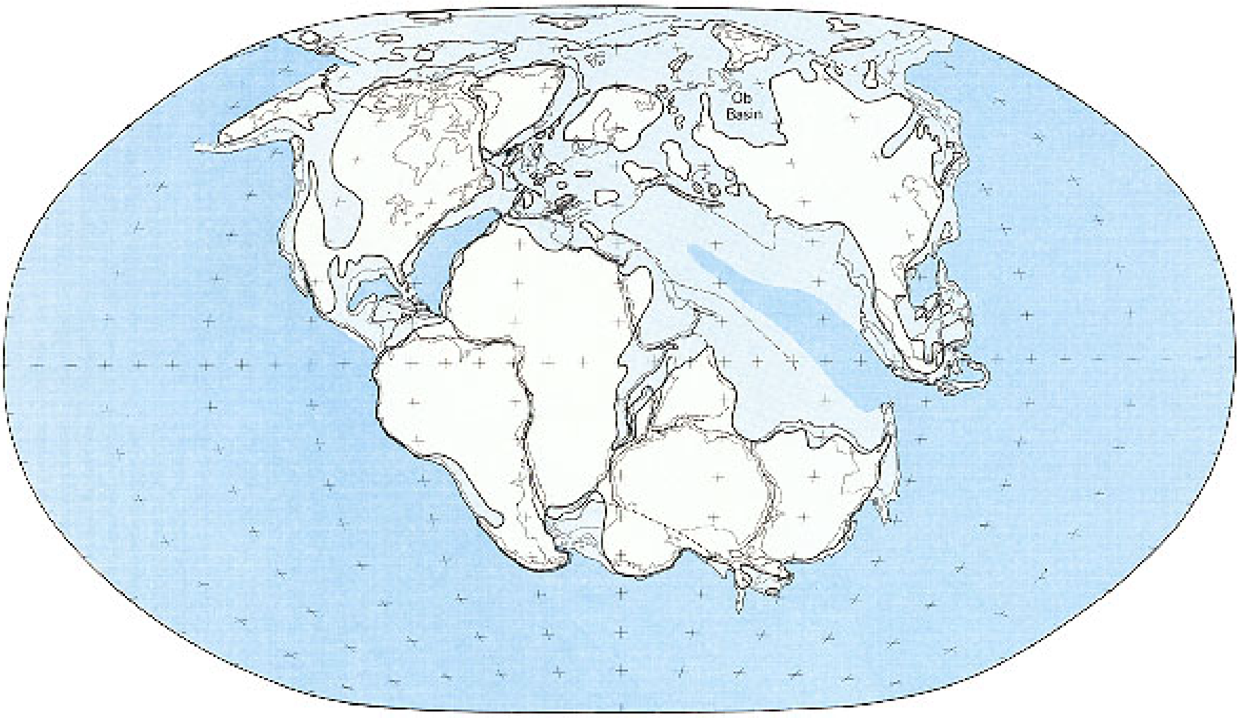

FIG. 20 B. The face of the earth in the upper Jurassic (Kimmeridgean stage: 145 million years ago)
White: land masses, Light Blue: epicontinental water, Blue: ocean; after Cox (1981)

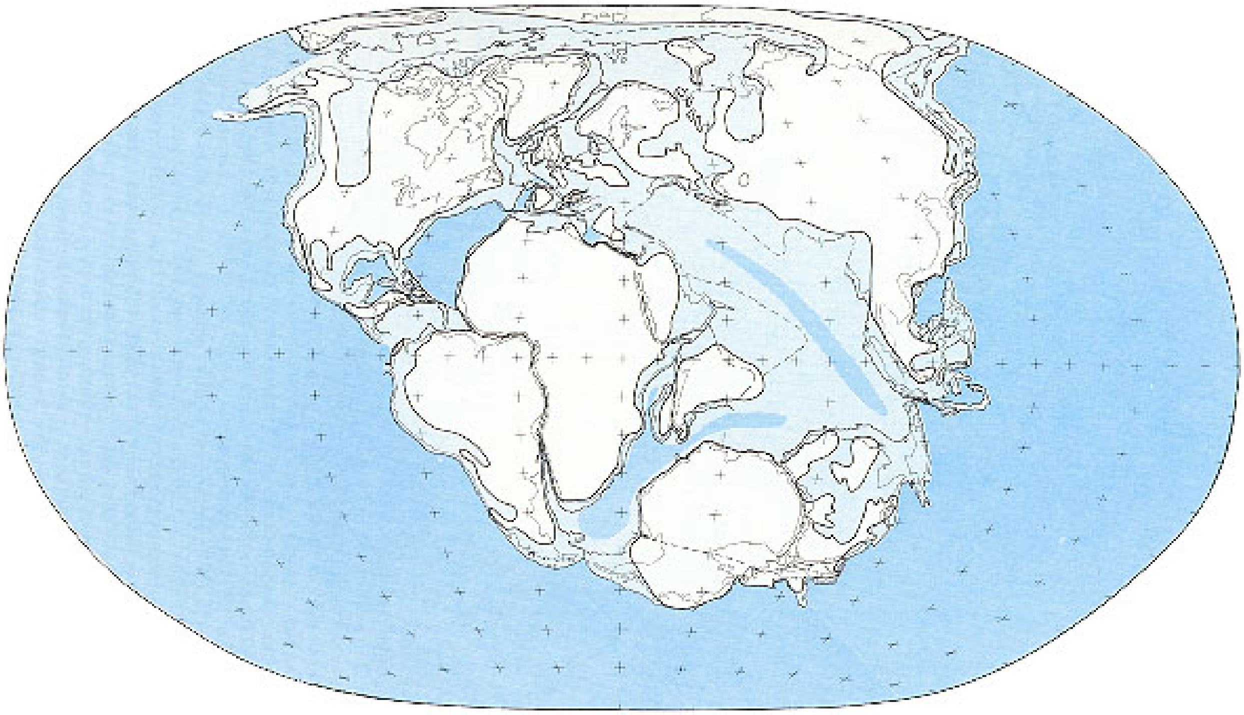

Fig. 20 C. The face of the earth in the lower Cretaceous (Hautevivian stage: 125 million years ago)
White: land masses, Light Blue: epicontinental water, Blue: ocean; after Cox (1981)

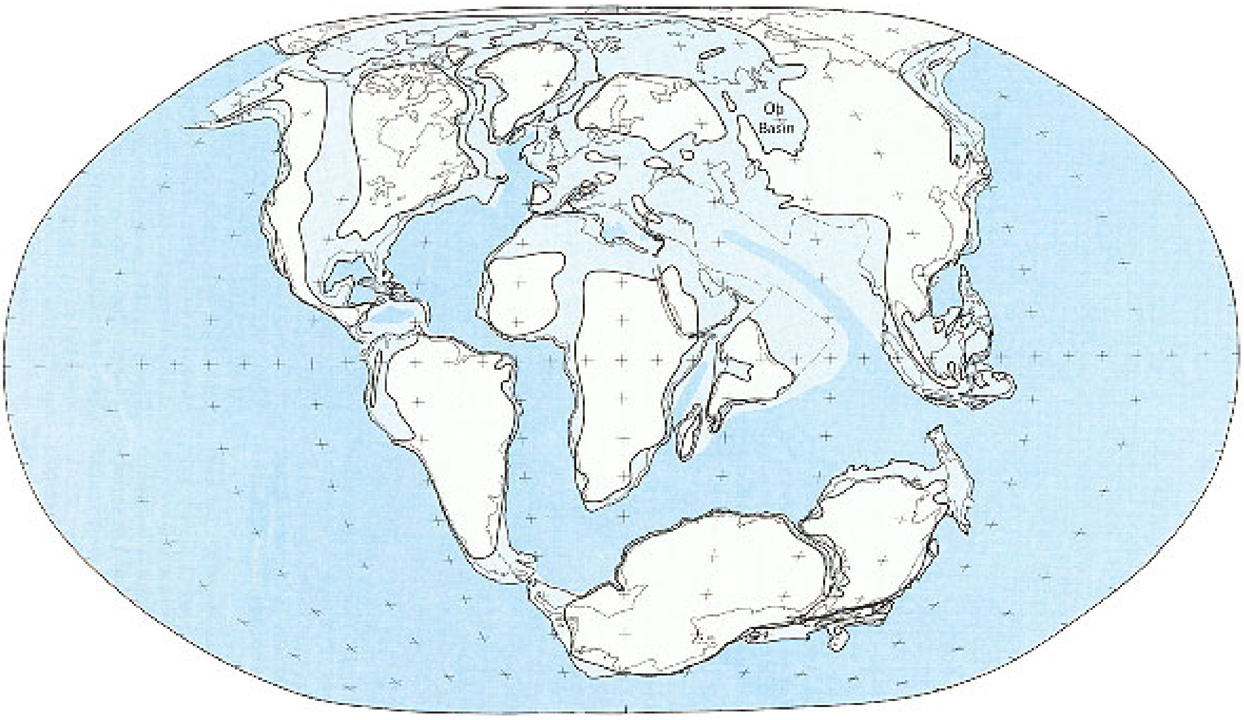

Fig. 20 D. The face of the earth in the upper Cretaceous (Senonian stage: 90-80 million years ago):
White: land masses, Light Blue: epicontinental water, Blue: ocean; after Cox (1981)

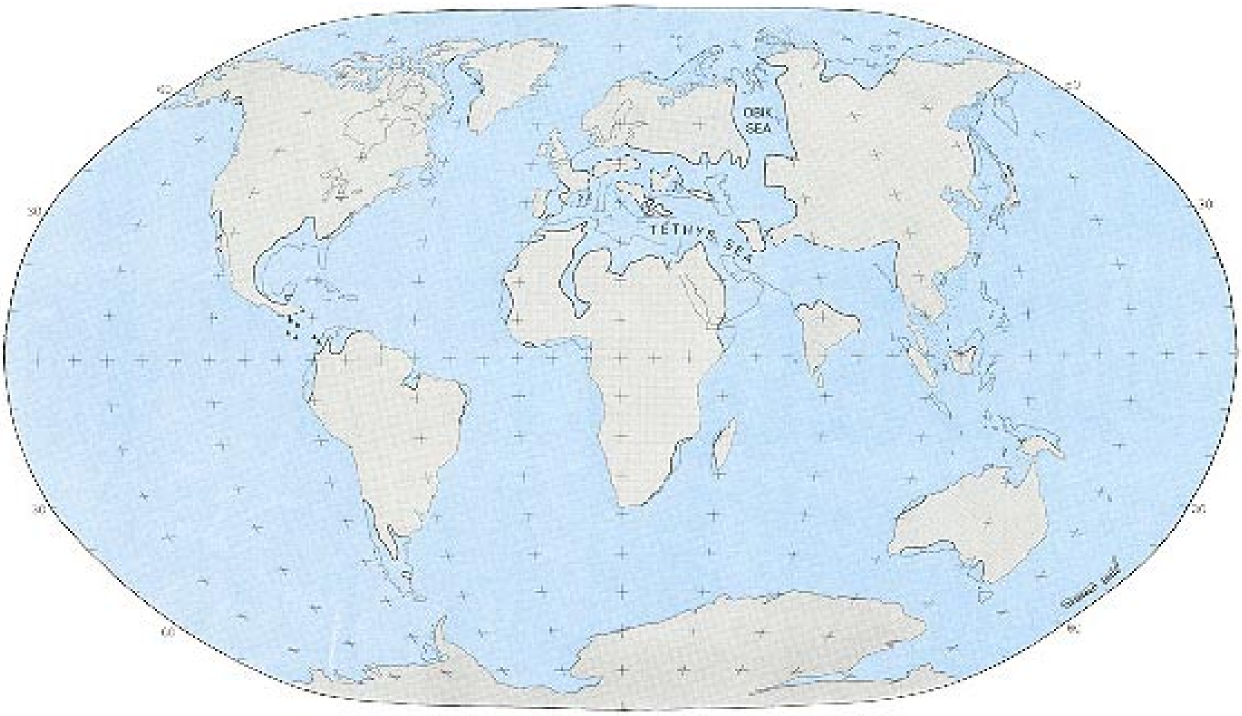

Fig. 20 E. The face of the earth in the Eocene (45 million years ago):
White: land masses, Light Blue: epicontinental water, Blue: ocean; after Cox (1981)

Today South America spreads from about 12°N to 45°S and has the longest north-south extension of all modern continents. It is quite clear that this situation leads to interesting climatic conditions, the southern areas are dominated by warm-temperate climates (Cfa, Csa and Cw of the Köppen system) north to the Tropic of Capricorn and in the higher mountain ranges of the Andes just crossing the equator. Dry climates of the BWh type are found in coastal Venezuela, BWk and BSk are confined to most parts of Argentina and the Atacama desert at the western slopes of the Andes.

The remainder of the continent is dominated by tropical climates of the Af and the Aw type. The climatic situation has changed remarkably since the ice-ages. Van der Hammen (1982) reported of about 20 glacial cycles. During the glacials, the Andean forest for example was found at an altitude of max. 2000 m whereas nowadays its upper limit is at 3200 to 3500 m (van der Hammen 1974). Since the climate in the pleniglacial of the last ice-age at about 30.000 to 10.000 B.P. was much drier (although it is difficult to say to what extent), the ecological zones were not only lowered, they were also vertically compressed due to the increase of the temperature gradient: The temperature was about 3 to 6°C lower than today in the higher Andes, for the lowlands a temperature 2 to 3°C lower than today can be calculated (Schubert 1988, van der Hammen 1974). Similar to parts of Africa, the lowlands were therefore covered with savanna vegetation or thorny forest due to the lower precipitation (van der Hammen 1974, Absy 1982). Tropical rain forests were restricted to moister areas. There is palynological evidence for higher precipitation in the Falcón/Maracaibo area of Venezuela and the Windward Islands (Schubert 1988). On the other hand, it is difficult to trace the forest refuges postulated by Haffer (1969) or Vanzolini (1973). For example, the lake Valencia area was too dry to support rain forest (Schubert 1988). For a new interpretation of the vegetational type in these glacial refuges cf. Colinveaux (1998).

The quarternary history of South America is important for the understanding of the present day biogeography in the Neotropics. The pleistocene glacial cycles had an effect on the vegetation of this area. The tropical rain forest may have been restricted to smaller separated areas in which allopatric speciation was postulated for many taxa (Haffer 1974, Whitmore and Prance 1987). The biogeographic patterns of South American Oniscidea of philosciid facies are compared with these historical data.

6.2 General Aspects

The South American Crinocheta of philosciid facies are quite abundant in most habitats where they were searched for. The voluminous collections gathered in Peru, Venezuela and Central America stress the importance of this group for the Neotropical biota. Within this chapter, an attempt is made to trace the biogeographic patterns which can be deduced from the literature and new data. This analysis incorporates quite an amount of uncertainty because the areas covered by sampling are rather small. Whitmore and Prance (1987) warned their readers not to draw conclusions on the biogeography of a taxon by using insufficient samples. The risk of producing artifacts is great. Moreover, there is some debate on the interpretation of biogeographical data with respect to the origin of a taxon. There are two competing modi of interpreting these data: in a phylogenetic approach, the centre of origin is defined as the distributional area where the basalmost representative of the taxon occurs (Brundin 1966); a more general approach interprets the area where a taxon has its highest diversity as its centre of origin (Darlington 1957). For both approaches there are pro and contra arguments. And ironically enough, some arguments are valid for both approaches. E.g. extinction may obscure both the "real" abundance and diversity of subtaxa within a given taxon and the location where the most primitive form was found. Cracraft (1973: 497) dealt with the distribution of the avian taxon Cathartidae, the so-called "New World vultures". The recent taxa are all confined to the New World – as indicated by their vernacular name. Ironically, both the most diverse fossil fauna and also the basalmost known fossil is from the early Eocene deposits in Germany. No concrete ideas exist about the dynamics of historical population biology. Basal representatives of a taxon may be forced against the margin of their range by more derived taxa or diversification may be high in an area far away from the "origin" of a taxon. So, one can not give a general hypothesis regarding the information content of distributional patterns of a distinct taxon until a foosil record would give new evidence.

Generally, South America is believed to be ambivalent in its fauna, with a dramatic split into a northern part, the Neotropis and a temperate to boreal southern part which belongs to the Australis also covering temperate Africa and Australia (Fittkau 1969, Crisci et al. 1991, Morrone 1992). The Australis reaches north beyond the equator in the higher Andes in the zones of Puna and Paramo vegetation as evidenced by the weevil faunas of Peru (Morrone 1994).

The high diversity of many taxa is of special interest. Haffer (1969) correlated species diversity and endemism with paleogeographic data and hence laid the cornerstone for applying the refuge theory on tropical ecosystems. The refuge theory explains diversity on a subordinate taxonomic level, whereas for higher taxonomic levels, vicariance theories taking continental drift in consideration are more appropriate (Haffer 1982). Evolution rates in the Neotropics seem rather high and e. g. in the vertebrate taxa, most species may be younger than 1.8 to 2 mio. years (Haffer 1979). Hence, for the species and subspecies level the 'refuge theory' as explained by Haffer in several publications (1969, 1974, 1990) seems to give an appropriate explanation for the patterns observed. The refuge theory does not exclude vicariance models, "refuge biogeography is but a recent chapter of vicariance biogeography on a sub-continental scale" (Whitmore and Prance 1987: 188).

But it is not only changes in precipitation postulated by the refuge theory (Haffer 1969) that caused a drastic change in vegetation. The fluctuations of the sea level are of importance, too. Inundation cylces, for example, caused the submergence of vast parts of central Amazonia three times in the last 100.000 years; this may be a cause for the separation of the Caribbean Amazonian and southern Amazonian region (Erwin and Adis 1982). The changing course of river beds and fluctuating water levels over millions of years contributed to the diversity of the Neotropis. For taxa with low vagility and even for some vertebrate taxa of Central Amazonia like forest birds (Haffer 1974) and primates (Hershkovitz 1977) Erwin and Adis (1982) postulated a strong influence of microbarriers like climatic differences or small rivers. Sometimes, even more motile taxa seem to be incapable of overcoming water bodies, e.g. 21 bird species of tropical Australia failed to cross the Torres Strait from Cape York peninsula to New Guinea despite the presence of stepping stones (Garnett 1991). Moreover, in South America, areas of endemism evidenced by bird distribution are greatly congruent to those obtained from data on butterfly distribution (Cracraft 1985). Hence, there are no general constraints to a direct comparison of distributional patterns of birds and terrestrial isopods in spite of differences in motility.

Biogeographic analyses were performed for many of the taxa mentioned above. For South America, a synopsis of the biogeography of the well-studied tree flora, the avifauna and the distributional patterns of several Lepidoptera revealed areas of high species diversity and endemism (Whitmore and Prance 1987). Several other authors found similar patterns, e.g.

Spassky et al. (1971) described five regions for *Drosophila paulistorum* semispecies: the Centroamerican, Orinocan, Amazonian, Interior, and Andean-Brazilian (coast) region.

Within the Neotropics, the easterns slopes of the Andes intervening into the wide Amazon lowland, which is lower than 500 m, are especially rich in species of terrestrial isopods of philosciid facies. These lowlands of the western part of Amazonia in eastern Ecuador and northeastern Peru do not only harbour a rich Oniscidean fauna, they are also among the most diverse regions in relation to birds (Haffer 1990), reptiles (Dixon 1979), amphibians (Duellman 1988), butterflies, mammals and plants (cf. Gentry 1988). Interestingly, high diversity is not evidenced for the Gastropoda, which are quite abundant in other parts of South America. Fittkau (1981) related this discrepancy to the lack of calcium in the soils and to the nutrient cycles which give place for many destruents (like Oniscidea) but only little for phytophagous animals (like Gastropoda).

The climatic history of Central America seems to be similar to that of Colombia, thus cylces of harsher climates during the ice ages (cooler/drier) may have led to the retraction of the tropical rain forests, e.g in the Petén Itza and Izabal lake region of Guatemala (Toledo 1982). The spread of rain forest persisted until recently as can be evidenced from xeric floral elements within the tropical rain forests (Prance 1982). Nowadays the tropical forests spread northwards to the 22nd parallel. It is characterized by a low rate of endemism and species diversity (Toledo 1982).

In a summary of the distribution of Andean Arthropoda, Morrone (1992) published a map detailing the biogeographic subregions of South America.

In this work, the main focus is directed to the diverse Oniscidean fauna of the Neotropis, however some considerations on the distributional patterns found in southern South America and their consequences for the relationships to other continents are discussed. Some of the findings on the biogeography of South American Oniscidea of philosciid facies coincide with those made in various taxa of both plants and animals from the Neotropics and are discussed below, starting in the north in Central America and going south to the temperate climate of Argentina. The most interesting fact is, that the phylogeny is reflected by the biogeography of the taxa: while the temperate South America is devoid of members of the taxon B, members of Balloniscidae and *Benthana* are exclusively found in this region. Conversely, the tropical taxon B is widespread in the Neotropis. The distributional patterns of e.g. Prosekiini and Ischiosciini coincide with the subregion concept of Morrone (1992), with some interesting details given below.

6.3 Tropical Central America and Caribbean

Within the neotropical fauna, there is a gradient from south to north in Central America. A similar pattern is seen in frogs: the anuran genera of the *Leptodactylus*-complex has a northern distributional limit in Texas. Along the Central American land bridge, the number of species decreases nordwards. The highest number of species is found in the Amazon basin (Heyer and Maxson 1982). This coincides with observations made on butterflies of the taxa Heliconiini and Ithominae, which occur with many species in South America, whereas the Central American fauna is impoverished (Whitmore and Prance 1987). The Central American isthmus is a filter for the dispersal of taxa of South American origin. For isopods, the total absence of autochthonous species of Crinocheta from North America supports the assumption that these Oniscidea radiated in South America. In contrast to this, the Gastropoda, which may be an older taxon, were present in both the northern part of South America and North America before the separation of the two continents in the oligocene or miocene (Scott 1997).

Central America shall now be examined from the north to the south, with a final look to the Antilles:

The presence in Mexico of two endemic genera of Crinocheta, *Oxalaniscus* and *Quintanoscia*, confirm the separate status of the Yucatán peninsula in both geologic (Pindell and Dewey 1982, Pitman *et al.* 1993) and biogeographic (Toledo 1982) respects. The corresponding species were originally described as members of the genus *Philoscia.* However, their systematic position within the Oniscoidea is much more basal. They actually belong to the same taxon as *Philoscia* (with longitudinal antenna-grooming brush), but in the morphology of the mouthparts they show the same plesiomorphies as the genus *Alloniscus*, which represents the same evolutionary level. Only one species of *Alloniscus* was described from the New World, *Alloniscus thalassophilus* Rioja, 1963 (Rioja 1963), whose taxonomic relationships within the genus are uncertain. *A. thalassophilus* is like all the members of its genus of Indo-Pacific distribution. The distributional areas of the two genera from Yucatán and *Alloniscus* exclude each other. A member of the mainly South American genus has reached the Mexican-Guatemalan border, *Androdeloscia formosa* (Mulaik, 1960). In Guatemala, only few more species of Oniscidea of philosciid facies were found, belonging to the species-rich genera *Ischioscia* and *Androdeloscia.* They occur in low densities.

Interestingly, both species of *Androdeloscia*, *A. formosa* and *A. valdezi* Leistikow, 2000 belong to different subtaxa within the genus. A possible explanation may be found in the distant position of nuclear Central America and Yucatán in Triassic times (Pindell and Dewey 1982). The presence of a member of the group bearing three hooks on the merus 7 (i.e. *A. formosa*) and of the hookless group (i.e. *A. valdezi*) in Guatemala was due to the colonization by an ancestor of the hook-bearing group of Proto-Yucatán from Venezuela. An ancestor of the hookless group must have colonized the "Protoguatemalan" portion (Chortis block) from the Ecuadorian region in the Triassic before a northward drift of the Chortis block led to a separation from South America. Alternatively, Central America might have been colonized twice after the Isthmus of Panama was formed.

From the data available in the literature (Brian 1929, Schultz 1977b and 1984), the genus *Troglophiloscia* Brian, 1929 is restricted to Yucatán peninsula and the adjacent areas, i. e. in recent times Belize and Cuba. This genus may be close to *Colombophiloscia* from northern South America. A faunistic link between the Greater Antilles and nuclear Central America was also found for several poeciliid fishes in the Caribbean, which occur only in fresh water (Rauschenberger 1988).

For Costa Rica, besides the genera *Androdeloscia*, *Ischioscia* and *Mirtana*, records of *Pentoniscus* and "*Chaetophiloscia*" were reported (Arcangeli 1930; Richardson 1913; van Name 1936). Especially in the genus *Ischioscia*, many species occur in the southern part of the Central American land bridge: seven species were described in recent times(Leistikow 1997a and 1999d). Southern Central America must have been colonized by representatives of the taxon Ischiosciini at least twice: a first colonization gave rise to *Mirtana costaricensis*, subsequently, members of *Ischioscia* colonized the land bridge. The very distinct species of the genus *Ischioscia* present in Panama, *I. zebricolor*, suggesting a correlation of the Central American faunas and those of trans-andean Amazonia even found in Scopiones (Lourenço 1984). A further colonization of Central America must have taken place from Venezuela, the core area of the *martinae-variegata* subtaxon. It are members of this subtaxon, which probably reached the rain forest of northern Guatemala. A resolution of this question will be possible when the males of these forms will be found (cf. Chapter 4.2).

The Greater Antilles have shifted from a more westerly to their present day position since the late Cretaceaous to early Tertiary (Briggs 1987, Pindell and Dewey 1982, Pitman et al. 1993), so the ancestor of *Portoricoscia* may have colonized Puerto Rico via the Northern Andes than from the Guianas via island hopping. Therefore, the northwestern parts of South America could be a source for the closest relatives of *Portoricoscia*; possibly *Roraimoscia* is one of the closer allies. While *Portoricoscia* is the only taxon of philosciid facies known from Puerto Rico, the carstic regions of Cuba harbour many taxa of philosciids (Vandel 1973c, 1981). This discrepancy may be more than a collecting artifact, because the moist forests of the Greater Antilles seem to be less diverse than the drier areas, an unusual pattern observed by Gentry (1992). The Greater Antilles are biogeographically connected to the Central American lowlands, and to northern South America (Liebherr 1988), but there are some relationships in the scorpion fauna of Hispaniola and the northeastern Brazil (Lourenço 1997b). The island of Dominica in the Lesser Antilles harbours its own distinct species of the genus *Ischioscia*, *I. mineri*. It belongs to the *martinae-variegata*-group the distributional centre of which is in northern South America. For several arthropod taxa of the Lesser Antilles, a closer link to the South American mainland than to the Greater Antilles was postulated by Liebherr (1988). For stingless bees of the taxon Meliponini, a similar pattern was observed (Roubik et al. 1997).

6.4 Neotropical South America

The two major monophyla of South American philosciids, the Prosekiini and the Ischiosciini, are both found in the Amazonian-Caribbean subregions, where several genera occur. Interestingly, the basal representatives of both groups live in different subregions. The basal genera *Prosekia* and *Metaprosekia* are found in the coastal cordilleras of Venezuela and the Cordillera Oriental, whereas the more derived *Erophiloscia*, *Androdeloscia* and *Andenoniscus* occur in the Cordilleras of Colombia, Ecuador and Peru (fig. 22). Species of the former genus live at elevations from 250 m to 2500 m in both lowland and montane forest. Species of the latter genus were collected in Peru and Panama. Most probably they occur in the intermediate areas, too. As similar case in the Colombian and Ecuadorian scorpion fauna, where strong affinities between these regions and the Amazon area and a displacement of some faunal elements to Venezuela were observed. Furthermore, a high endemicity of more than 60 per cent was registered (Lourenço 1995 and 1997a). This may be parallel to the case of *Erophiloscia* with its distinct species in Colombia and Peru. The disjunct distribution of *Andenoniscus* may be a sampling artifact since particularly the higher elevations are still unexplored. In contrast to the taxon Prosekiini, the genera of the taxon Ischiosciini found in the foothills of the Andes from Peru to Colombia are the more basal ones (*Oreades* and *Ecuadoroniscus*, fig. 21). As in the Ischiosciini, the most primitive representatives of the Lepidopteran taxa Heliconiini and Ithomiinae are distributed in the Andean region of the Neotropis, which is postulated to be a centre of diversification of these groups (Whitmore & Prance 1987: 81). Caution is needed when searching for the origin of a taxon, because the centres of high biodiversity do not have to coincide with the centres of diversification (Lourenço & Blanc 1994) The split into the genera *Tropiscia* and *Ischioscia* lead to a high diversification of this monophylum. Besides the eastern Brazilian genus *Benthana* and the mainly Andean-Amazonian genus *Androdeloscia*; *Ischioscia* is the largest genus of Oniscidea of philosciid facies known from the Neotropis. Most of the species are known from the Caribbean Amazonas region, as discussed below. This is quite interesting, since this relations are contrary to those of *Androdeloscia*, which is most

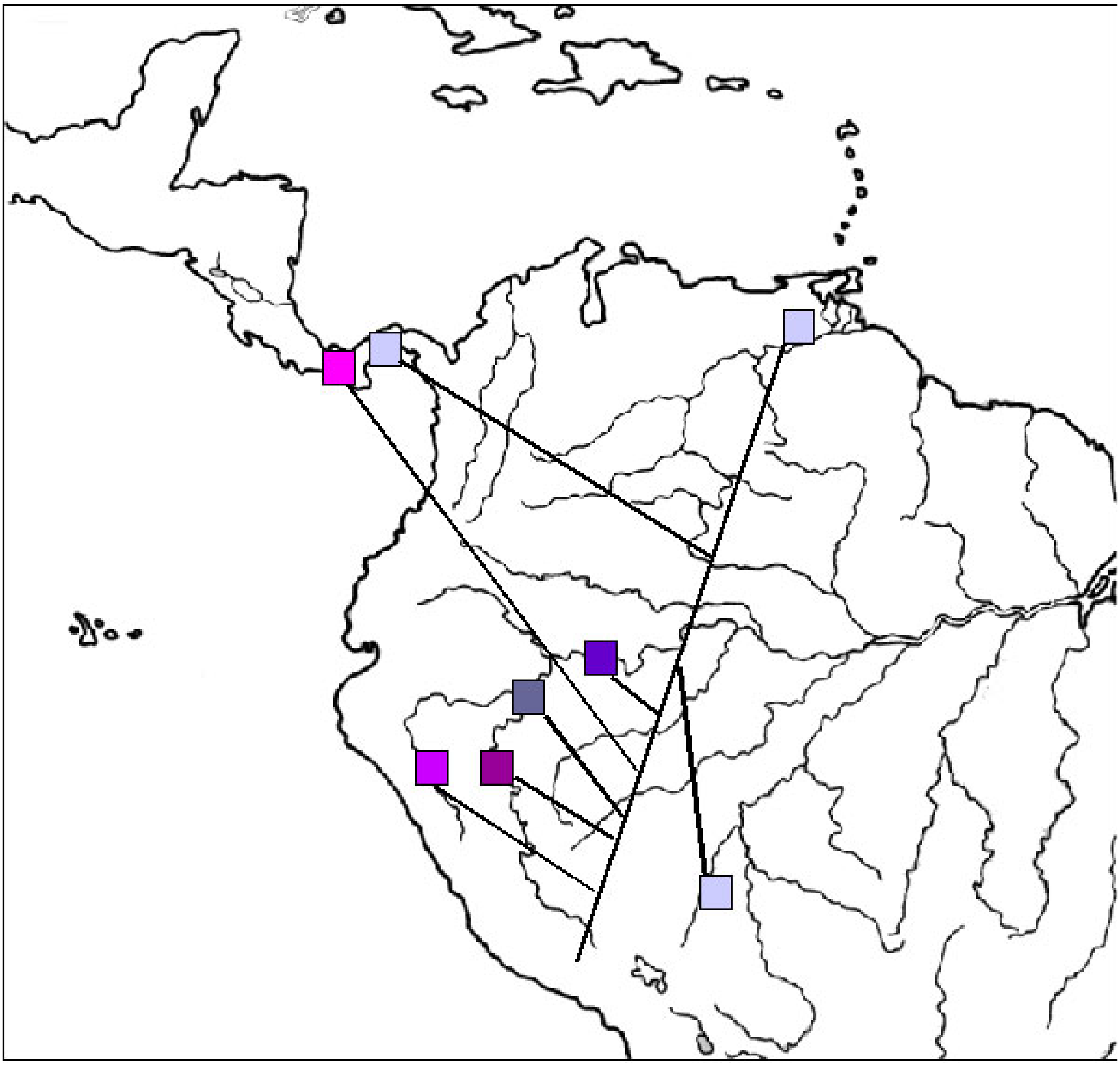

Fig. 21. Projection of the dendrogram of the Ischiosciini on the map of South America: Each square colour represents a genus

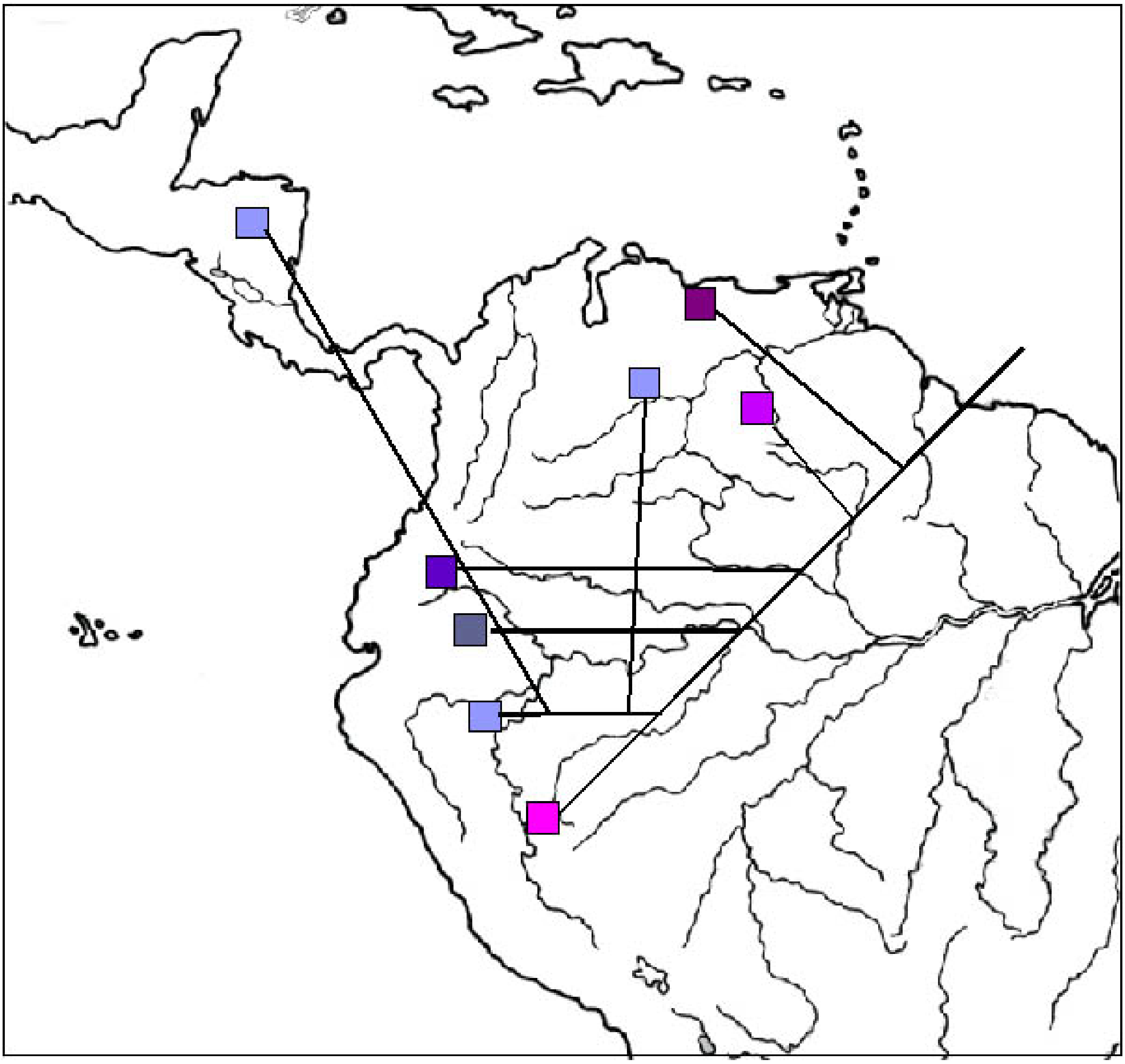

Fig. 22. Projection of the dendrogram of the Prosekiini on the map of South America: Each square colour represents a genus

diverse in the Andean-Amazonian region. Together with the former genus, *Ischioscia* is the only genus of Oniscidea of philosciid facies known to occur both in South and Central America north to the northern limits of the tropical rain forests.

6.4.1 Andean Amazonas Subregion

A north-south distributional pattern along the Andes can be found in several taxa, among the Crinocheta e.g. *Androdeloscia* or *Ischioscia*. In several cases, differentiation is still at an infraspecific level. For example, the *Leptodactylus pentadactylus* frogs from Panama differ in their immunological data based on serum albumine from the conspecific populations of Peru (Heyer & Maxson 1982). As the Oniscidea have a shorter reproductive circle, speciation may occur faster than in Vertebrates. At least the number of generations in a given period is higher.

With regards to the genera *Erophiloscia* and *Androdeloscia*, the high number of species in the Peruvian Huanuco area is interesting, though possibly reflecting a sampling artifact due to systematic collection. Further collecting in South America may reveal other areas which have such a diverse fauna of Oniscidea. The many sympatric species in the Huanuco area must prefer different microhabitats to avoid concurrence. A case of microhabitat differences was observed for two savanicolous species of *Tityus* scorpions from Brazil (Lourenço 1994a). Haffer (1990) reported a high avian species density in the foothills of the eastern Andes in the western Amazon area and correlated this fact to the higher nutritient content of the soils compared to the Central Amazon basin (Fittkau 1982). Furthermore, in this region the lowland and montane faunas come into contact. On the other hand, the Peruvian Amazon area was postulated to be a pleistocene refuge (Prance 1982). Gentry (1993) reported a high diversity of several plant taxa in this region with a high amount of endemism. Genera are large and exceptionally speciose. Furthermore, a particular exceedingly dynamic speciation process was postulated for this region, similar to the founder effects leading to the high diversity of Hawaiian *Drosophila* (an "open-ended phenomenon": Gentry 1989). On a supraspecific level, this statement may be supported by the occurrence of four closely related genera in the Andean region, i.e. *Xiphoniscus*, *Andenoniscus*, *Erophiloscia*, and *Androdeloscia*. Lourenço (1994b) encountered a highly diverse scorpion fauna in these regions with a rate of endemism of over 70 per cent. The probably best studied taxon Aves is highly diverse in this region and many endemics occur, their ranges being restricted by intrageneric competition or topological and ecological barriers (Terborgh and Winter 1982).

In the Andean-Amazonian region, the species of *Ischioscia* are highly diverse in the morphology of the male pleopods and the male pereopods 7, although the species *I. longicaudata*; *I. stenocarpa*, and *I. hanagarthi* have a similar setation on the pereopod 7 merus; these species are closely related to *I. zebricolor* from southern Central America, as discussed in chapter 6.3. The subandean and amazonian species are close to each other because of their simple molar penicil and the spatuliform dactylar seta (chapter 5.4). This reflects a biogeographical relation of the Napó Centre in eastern Colombia with central Amazonia (Whitmore and Prance 1987), especially with the parts north of the Amazon river (Cardoso da Silva and Oren 1996).

Several genera have an interesting cis- and trans-Andean distribution. Moreover, the genera *Androdeloscia* and *Caraiboscia* are also found in the lowlands of the Caribbean subregion. *Androdeloscia* is found even on the Galapagos Islands. *Caraiboscia* is distributed throughout the Caribbean region and on Guadeloupe. In Venezuela, it was collected in considerable numbers, and it is also present on the nearby island of Trinidad. Some species of *Phalloniscus* from northern South America are likely to belong to this genus. The pseudoscorpion genus *Pseudochthonius* is distributed in Central and South America, on Galapagos and in the Caribbean (Liebherr 1988). The distribution on such a remote archipelago like the Galapagos Islands which are of volcanic origin must be due to hydrochorous drift. Since the Hawaiian archipelago harbours a rich fauna of Crinocheta of philosciid facies partially belonging to widespread genera (Taiti & Howarth 1996 and 1997), the colonization of these islands, which likewise are close to South America, by taxa inhabiting this continent is not surprising. Similarly to other taxa, the faunal elements are closely related to the fauna of northern South America (Vandel 1968). The closest relative of *Caraiboscia*, the genus *Colombophiloscia*, is known to have a similar distribution in the Andes of Ecuador and Venezuela and on the Galapagos islands. For the genera *Androdeloscia* and *Colombophiloscia*, the same vicariance events are posulated for the continental distributions, whereas they may have arrived on Galapagos independently.

6.4.2 Caribbean Amazonas Subregion

The Caribbean Amazonas region north to the drier areas of Venezuela is another important centre of several taxa of terrestrial isopods of philosciid facies. In constrast to the Andean-Amazonian region, the Caribbean and partially the Central American representatives of *Ischioscia* are closely related to each other, and therefore form the *martinae-variegata* group within the genus *Ischioscia.* The ancestor of this subtaxon must have reached the Venezuelan area along the raising Andes. The uplift of e.g. the Sierra de Santa Marta and adjacent areas of the northern Andes runs along a northwest-southeast direction persisting until today (Kellogg and Bonini 1982). This mountain range may have canalized the colonization of Venezuela from Colombia and vice versa by the members of the genus *Ischioscia*: In northwestern South America, the mountain ranges run in a northeast-southwestern direction, the Paramó region of the summits displays an adverse climate for the colonization by tropical fauna elements, the isopods would fail in crossing these barriers. Dispersion must take place following the valleys with tropical climates. In Venezuela, several species of *Ischioscia* can be found which are restricted to small areas as the coastal region near Caracas (*I. colorata*, Venezuelan Montane Centre), the eastern slope of the Andes (*I. hirsuta*, *I. guamae*, Meridan Montane Centre) or on the Península de Paria (*I. pariae*, Parian Centre); these distributional patterns coincide with the postulated pleistocene forest refuges which were evidenced from various biogeographical studies (Cracraft 1985, Prance 1982). Some bird taxa are endemic to the Caracas and Paria cordilleras (Whitmore and Prance 1987: 145). Interestingly, these restricted-range species partially occur sympatrically with *I. variegata* which is found in almost all the areas where distinct regional species were collected. These regional species are found in locations with a high rate of endemism. *I. variegata* might be an expansive species which colonized many regions of Venezuela relatively recently. It lives synantropically in many areas (Leistikow 2001f). The phenomenon of one widespread species which lives in sympatry or parapatry with restricted-range species is well-kown in many taxa as diverse as marine Peracarida (C.O. Coleman, pers. comm.), birds (several monographs on neotropical bird taxa) or plants: the genus *Tecoma* of the family Bignoniaceae, for example, is composed of one widespread species which can be found from the southern U.S.A. to Argentina, two widespread South African species and a set of about ten species endemic to certain Andean ridges (Gentry 1992). Nonetheless, some of the records of *I. variegata* from northern South America and Central America have to be reconsidered (Richardson 1914, Arcangeli 1930). With respect to the records from the Caribbean islands, a different species might be involved.

Some elements of the Guyanan and southern Venezuelan fauna may be derived from the evolutionary line leading to the last common ancestor of the Ischiosciini, i.e. *Pentoniscus*, *Formicascia* and *Roraimoscia*. They may also be close to the fauna of the Caribbean islands. The avifauna of the Pantepuí region is related both to the Venezuelan cordilleras and the Andes (50 per cent of species) and to lowland Amazonia (30 per cent) (Whitmore and Prance 1987).

6.5 Temperate South America

For the nontropical areas of South America which form a part of the Australis, two different distributional patterns are observed: On the one hand, there are the transandean genera *Pseudophiloscia*, *Araucoscia* and *Oniscophiloscia*, on the other hand, the Balloniscidae, *Atlantoscia* and *Benthana* are found in Brazil and northern Argentina.

Firstly, the affinities of the Chilean taxa are discussed. Both *Pseudophiloscia* and *Araucoscia* if they are at all separable, have their closest relatives in the western Pacific fauna, possibly in the genera *Adeloscia* or *Paraphiloscia*, which have a similarly built maxillula, as discussed above (chapter 4.2). Of course, some divergent evolution occurred since New Zealand and New Caledonia were separated from other land masses at the beginning of the Tertiary, and even the fligtless Insect faunas of New Caledonia and New Zealand are quite different (Darlington 1965). Some of the faunal elements of New Zealand and Chile might be closer related to each other than those of New Zealand and New Caledonia (cf. Verhoeff 1926). Some strong affinities of the Chilean fauna to the New Zealand faunas is supported by the findings of Simonsen (1992) for the polydesmidean milliped family Dalodesmidae from Chile and Australia. Woodbourne and Zinsmeister (1984) discussed the fossils of Marsupialia from southern South America and Antarctica in relation to the Australian fauna. The situation of New Zealand in paleogeography is still to debate. De Wit (1977) and Dalziel (1982) postulated an isolation of the islands and of New Caledonia along a common geosyncline in the late Mesozoic, whereas Kamp (1980) postulated that these islands were the eastern border of a lost continent Pacifica. At least there was an ancient connection between these regions and southern South America, so an amphipacific relation of the genera *Pseudophiloscia* and *Paraphiloscia* is supported by paleogeography. Vandel (1973a) discussed some amphipacific distribution but focussed on the distantly related *Palaioscia* and *Proischioscia* (a junior synonym of *Ischioscia*), thus his statements may be erroneous. The oniscidean fauna of Australia and Oceania have strong affinities to the Oriental fauna (Vandel 1973a and b) but some relationships with South America still prevail. These relations are similar to the Herpetofauna of the two areas (Tyler 1979).

The eastern Brazilian shield and the coastal forests of Brazil are quite distinct from those of the remaining Neotropis, although there is some similarity in the composition of the respective faunas (Whitmore and Prance 1987). Lourenço (1994a) postulated a faunal rupture in this area and a dispersion pathway along a north-south axis. The genera found in this region are *Atlantoscia*, *Benthana*, and the Balloniscidae, first described as belonging to the genus *Philoscia* and then transferred to a separate subgenus (Budde-Lund 1908). These three taxa are quite different in their distributional patterns. One species of *Atlantoscia* is present along the western Atlantic coast from Florida in the north to Uruguay in the south, possibly dispersed by hydrochorous or anthropogenous mechanisms, the other is found in the coastal forests of the Brazilian state of Sergipe. The family Balloniscidae in its present concept may be paraphyletic, with the genus *Pulmoniscus* belonging to a different taxon. Its distribution on one of the Windward Islands north of Venezuela in the Caribbean is biogeographic evidence for the paraphyly of Balloniscidae, with the remaining species found in southeastern and southern Brazil and Argentina.

Lastly, the genera *Benthana* and *Benthanoides* are true austral faunal elements, which penetrated the Neotropis at its southeastern edge. The apparently disjunct distribution of *Benthana* and *Benthanoscia* in southern South America - if not a collecting artifact - may have been caused by the lowering of the vegetational zones during the glacials. The common ancestor of this stock may have occurred in the intervening areas but is now extint due to the drier climate in the cerrado areas of Brazil, where no representatives of *Benthana* have been found. Such a disjunct distribution has been found for several taxa (Simpson 1973). Bigarella and de Andrade-Lima (1982) reported of a disjunct distribution of the *Araucaria*-forests in the Andes and Brazil. They found a colonization of Brazil by Andean genera in the Oligocene with the pre-Andes as a ressource for this colonization. This would coincide with a phylogenetic scenario of *Benthanoides* being the less derived and *Benthana* the more derived taxon. *Benthana*/*Benthanoides* is thought to be the sole strong link of the South American and African fauna with *Benthanops* from South Africa the closest recent relative (H. Schmalfuss, pers.comm.). Similarly, despite considerable coincidence the herpetofauna of South America and Africa are distinct as regards the vicariance of the two continents (Laurent 1979).

6.6 Littoral and introduced taxa

The members of the Halophilosciidae are truly litoral species, and are found almost world-wide. Vandel (1946) gave a short overview of the distribution of the hitherto known species. The interpretation of their phylogeny and thus the interpretation of the biogeography is misleading. It is not the European species of the genus *Halophiloscia* but the species which in recent systematics were placed in *Littorophiloscia* which are the more basal ones with respect to several characters. The genus *Littorophiloscia* is of circumtropical distribution and can also be found on the temperate coasts of the North Pacific and the northwestern Atlantic. The Halophilosciidae may be of circum-Tethyian distribution dating back to the Mesozoic. The separation of Laurasia and Gondwana took place between the early to the late Jurassic (Rage 1995). The ancestor of the Halophilosciidae or of some distinct subtaxa of this monophylum must have existed since the early stages of the separation of Pangaea. This concurs with the basal Oniscidea of the families Ligiidae and Tylidae. Representatives of the paraphyletic taxon *Littorophiloscia* are now found in most of the area. The forms found in the Mediterranean and the Eastern Atlantic differentiated to the *Halophiloscia*-stock, which is defined by the bifurcate genital papilla. Since the phylogeny within the family is not resolved, giving more details on the biogeography on a global scale would be speculative. Even the monophyly of the genus *Halophiloscia* is doubted in recent times (S. Taiti, pers. comm.). In the Americas, one widespread species is found on tropical beaches of the Indopacific and the Western Atlantic (*Littorophiloscia tropicalis*). The other species is not known but from the Andamanes and the new record in Guatemala may be due to anthropogenous causes (*Littorophiloscia denticulata*). Within the litoral Oniscidea, only one other species, *Ligia exotica* Roux, 1835, is distributed circumtropically. As can be seen from the distributional centre of the genus in the Mediterranean, the Caribbean records of *Halophiloscia couchi* are due to anthropogenous displacement.

Finally, those species of Oniscidea of philosciid facies introduced to South America shall be briefly mentioned. Two groups can be recognised: one is the littoral family Halophilosciidae, the other is the genus *Burmoniscus*. These species differ in their ecological requirements: *Littorophiloscia denticulata* and *Halophiloscia couchi* live at the shore and thus may gain new habitats quickly when escaping in the vicinity of harbours. The two *Burmoniscus* species, i.e. *B. meeusei* and *B. kohleri*, are synanthropic and were found in disturbed habitats and cultivations. These species have to be displaced to adequate habitats where they can establish themselves. Ideally, these habitats should have a low density of other Oniscidea. *B. kohleri* was collected in Guatemala in areas where no autochthonous species of Oniscidea was found; and particularly *B. meeusei* seems to be of broad ecological capacity as it has adapted to a life in greenhouses where it was first encountered (Holthuis, 1949).

6.7 Faunal exchange between North and South America

From the data available, it seems as if the Crinocheta of philosciid facies have failed to establish in North America. The northernmost records of neotropical taxa are from Southern Mexico and Guatemala (Mulaik 1960, present study). Probably, the harsh climatic changes in Mexico, with tropical climates in the south and desert climates in the north is an effective barrier for the dispersion of taxa with philosciid facies. In most cases, these taxa do not bear pleopodal lungs, a prerequisite for a successful colonization of dry habitats, where an effective reduction of water loss is necessary. Since in this morphotype respiration takes place via the entire cuticle of the pleopod exopodites, water loss is essentially high. A reduction of water loss would coincide with a reduction of gas exchange. In desert species of the genera *Hemilepistus* Budde-Lund, 1885 or *Periscyphis* Gerstäcker, 1873 effective lungs are present (*cf.* Ferrara et al. 1997) which allow reduction of water loss via the cuticle of the pleopods by deposition of waxes. Studies of other desert areas (e.g. Barnard 1941, Ferrara and Taiti 1985, Taiti and Ferrara 1986) failed to find this morphotype. In contrast to the distribution of Crinocheta with philosciid facies, some species of the genus *Venezillo* Verhoeff, 1928 (Armadillidae) which is adopted to xeric environments, are found in Mexico (Rioja 1951, 1954 and 1955) and southern USA (Arcangeli 1932, Mulaik and Mulaik 1942). Interestingly, many species are confined to caves with a more humid climate.

The only area in North America, where autochthonous species with philosciid facies are found, is the Peninisula of Florida. *Floridoscia fusca* Schultz and Johnson, 1984 lives close to the shore. It may be related to the Crinocheta with philosciid facies from Cuba. The largest island of the Greater Antilles is rich in such taxa (Vandel 1973c and 1981), and probably some shore-living species may have reached Florida. *Atlantoscia floridana* is found along the subtropical and tropical coasts of the western Atlantic. Its occurrence in Florida may be due to human activity because in this area it is mainly synantropically distributed (Schultz and Johnson 1984). On the other hand, its natural habitat is also close to the shore and hydrochorous drift might have led to its vast distribution.

It is the genus *Littorophiloscia* which is found in both North and South America. The North American species are quite distinct and exclusively found on this continent. Their relationships to the tropical species *L. insularis* is difficult to establish due to the lack of a reliable analysis of the phlyogeny of the Halophilosciidae. Similar to other littoral taxa like the genera *Ligia* and *Tylos* Audouin, 1826, *Littophiloscia* is circumtropically distributed and there is no particular evidece for a close relationship of *L. insularis* and the North American species *L. culebrae*, *L. richardsonae*, and *L. vittata*.

7 Summary

The analysis of South American Crinocheta of philosciid facies revealed the fact, that the family "Philosciidae" and the genus *Philoscia* are paraphyla in which species are united mainly due to a similar habitus as indicated by Wägele (1989). All the representatives of "Philosciidae" are species of the ecomorphological runner type described by Schmalfuss (1984b): small coxal plates, narrow pleon and long pereopods. This habitus is similar to the basalmost Oniscidea, the representatives of the family Ligiidae and it is the plesiomorphic character state. For several neotropical species of "*Philoscia*", new genera had to be established to accommodate their unique character sets differing considerably from all the known genera: *Androdeloscia*, *Formicascia*, O*xalaniscus*, *Portoricoscia*, *Pulmoniscus*, *Quintanoscia*, *Roraimoscia* and *Yaerikima.* For the genera *Colombophiloscia*, *Plataoniscus* and *Prosekia*, a type species was chosen; 32 new species were identified and subsequently described in the course of this study (cf. publications of Leistikow 1997-1999).

The relationships of the taxa examined were resolved by the phylogenetic analysis: Two taxa from Mexico, O*xalaniscus* and *Quintanoscia* do not belong to the taxon bearing noduli laterales due to the primary lack of these noduli laterales, whereas these sensilla are the autapomorphy of all noduli-bearing taxa. The genera *Araucoscia* and *Pseudophiloscia* are related to the genus *Adeloscia* from New Zealand with which they share the apomorphic structure of pereopod 1 carpus. The monophyly of Balloniscidae, comprising *Balloniscus* and *Plataoniscus* is still open to debate. The autapomorphic character found for Balloniscidae is a reductive character which can not be evaluated to falsify the hypothesis of monophyly. It could be demonstrated that the Balloniscidae are distinct from the other South American taxa of philosciid facies and belong to the unnamed taxon 6 of Schmidt (1999) due to the presence of Y-shaped tricorns. In *Oniscophiloscia*, such tricorns also are observed, it is an aberrant member of taxon 6 due to severa autapomorphies. Its relationships within taxon 6 are unresolved. The genus *Philoscia*, namegiving for the family, is particularly close to *Oniscus* and its European relatives. The structure of the pleopodal lungs is similar in *Philoscia* and *Oniscus*, a synapomorphy of these taxa (Schmalfus 1990 and present study). As a consequence, if the family Oniscidae should not be paraphyletic, *Philoscia* has be included in this family. This would render the taxon name "Philosciidae" superfluous. In recognition of the far-reaching nomenclatural changes of the suppression of the term "Philosciidae", it should only be done after a re-examination of all the taxa ascribed to "Philosciidae" and the establishment of new taxa for the Crinocheta of philosciid facies not included in this study.

Most of the South American members of the family "Philosciidae" are separated in a monophyletic taxon A, which also comprises the families Rhyscotidae, Scleropactidae and Halophilosciidae. The Rhyscotidae are shown to be closely related to *Atlantoscia* and *Benthana* due to the shape of the maxillipedal endite, the Scleropactidae are the adelphotaxon the new taxon D, both have an apumorphic structure of the antenna-grooming brush. Taxon D comprises all the South American genera but the beforementioned. Most probably, several tropical taxa of philosciid facies have to be included in taxon D when re-examined in detail. At least *Burmoniscus kohleri*, a species native to Cameroon, and the mediterranean genus *Chaetophiloscia* have to be included in taxon D. The genera *Pentoniscus*, *Yaerikima*, *Formicascia*, *Roraimoscia*, *Portoricoscia*, *Parischioscia* and the new taxon Ischiosciini form a monophylum with similarly shaped creel on the pleopod 5 exopodite; the taxon Ischiosciini is characterized by the apomorphic shape of the antennula, the maxillula and the pleotelson, it comprises the genera *Ecuadoroniscus*, *Oreades*, *Mirtana*, *Tropiscia* and *Ischioscia*. In a subtaxon of taxon D with simple dactylar seta, the new taxon Prosekiini is exclusively neotropical. It is characterized by the apomorphic shape of the maxillula; *Prosekia*, *Metaprosekia*, *Xiphoniscus*, *Andenoniscus*, *Androdeloscia* and *Erophiloscia* are members of the Prosekiini.

The distribution of the taxa examined is essentially Gondwanian, the closest relatives of the Chilean genera *Araucoscia* and *Pseudophiloscia* are occur in New Zealand and New Caledonia, those of *Benthana* are found on bothsides of the Atlantic in Africa and South America. The taxa Prosekiini and Ischiosciini are essential neotropical. They occur in the Amazon basin and the adjacent tropical areas of the Andes and in Venezuela. The evaluation of the distributional patterns recognises areas of endemism which were found by examination of the distributions of representatives of various taxa.

Until now, only few taxa are known from Central America. *Androdeloscia* of the Prosekiini and *Ischioscia* of the Ischiosciini have their northernmost distributional limits in Guatemala and southeastern Mexico. The northern boundary coincides with the northern limits of tropical rain forests. Possibly, ecolocigal factors prevent them from expanding their ranges northwards. Both *Androdeloscia* and *Ischioscia* do not bear pleopodal lungs. Such lungs are postulated to be a prerequisite to colonize the dry parts of central and northern Mexico and southern USA. Effective internal respiratory organs could replace respiration via the pleopodal cuticle with the compromise of high water loss. Reduction of water loss is thought to be essential for a successful colonization of Mexican deserts.

Few taxa were introduced to South America by human activity: two species of *Burmoniscus* from the Paleotropis were encountered in Brazil, Venezuela and Guatemala in degraded habitats, two species of Halophilosciidae may be brought to South America by ship and then spread along the coasts where they occur in natural habitats.

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