

CONTRIBUTIONS TO THE STUDY OF THE TRICHONISCIDAE (ISOPODA, ONISCIDEA). II. ANALYSIS OF THE MORPHOLOGICAL CHARACTERS

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Abstract. Following an introductory presentation of the problems raised by the examination of the morphological characters according to the phylogenetic systematics, a detailed analysis of the morphological characters of the family Trichoniscidae within the context of the characters of the representatives of the suborder Oniscidea, is achieved, based on the author's personal data and an examination of the literature. Starting from this analysis we argue once more the author's conclusions concerning controversial issues: the monophyly of the terrestrial isopods; the dichotomy of the suborder Oniscidea; the dichotomy of the infraorder Ligiamorpha; the dichotomy of the monophylum Orthogonopoda.

Key words: Isopoda, Oniscidea, Ligiamorpha, Orthogonopoda, Synocheta, Trichoniscidae, differential characters.

1. INTRODUCTION

According to recent data, the suborder of terrestrial Isopoda (Oniscidea) includes more than 4000 species belonging to over 500 genera and 38 or 39 families (LOPEZ-OROZCO *et al.*, 2024). Among the Oniscidea, the family Trichoniscidae has one of the highest number of species, only the families Armadillidae and Philoscidae having more species (SFENTHOURAKIS & TAITI, 2015).

According to TAITI (2017), over 300 species of terrestrial isopods are strictly troglobitic and many species can be considered as troglophilous. 16 families of terrestrial isopods contain troglobitic and stygobitic species, but the majority belong to the families Trichoniscidae and Styloniscidae.

Considering the high number of species belonging to the family Trichoniscidae found in caves, within the "Emil Racoviță" Institute of Speleology, we attached a special importance to this family. In the first part of this paper (TABACARU & GIURGINCA, 2019), we analyzed the definition and the taxonomic position of the family Trichoniscidae. In the present paper, we intend to examine the morphological characters of this family of terrestrial isopods and the possibility to use them in classification according to the principles of the phylogenetic systematics.

The idea that classification should mirror evolution was born and developed along with the realization that the living world is the result of evolution. Clearly, the classification of present day organisms cannot be superimposed over the phylogenetic tree as it represents a transversal section through the course of evolution. But it can represent encaptically, the succession of the lineages origin and development by a hierarchic description of taxa.

The principles of the consistently phylogenetic systematics or cladistics, as it was named subsequently, were conceived by the German zoologist Willi Hennig and argued and developed by his supporters. According to this method, the classification should strictly reflect the relatedness between the species. As HENNIG (1957, 1982) showed, a general similarity cannot prove a relationship between the species. As Hennig argued, in order to pinpoint the kinship relations, a detailed analysis of the characters within the investigated sample, in comparison with the characters of the most closely related group (*sister group*), is necessary. In order to know the direction of the transformation of characters (*polarity*), the comparison should be also done with more distantly related groups (*out-groups*) and following the series of morphological changes of the characters (the so called *morphoclines*). The analysis of the characters should lead to the separation of the *homologous* characters (structural similarities inherited from a common ancestor) from *homoplasies*, as the characters not inherited and evolved independently in different groups, are defined. In the same time, Hennig argued for the necessity to distinguish the basal, inherited, un-modified characters, named by him *plesiomorphies*, from the derived, evolved characters, named *apomorphies*. Only the shared presence of derived characters inherited from a direct common ancestor (*synapomorphies*) can argue for a close relationship between the taxa. The sister groups, those sharing synapomorphies, form along with their direct ancestor a *monophylum*. Taxa forming a monophylum are more closely related among them than with any other taxa outside the monophylum. This conception implies that any taxa should be *monophyletic* sensu Hennig, namely it should have a common ancestor and it should include all descendants of that ancestor. MAYR (1982, 1986) thinks that Hennig modified the definition of the monophyletic notion which envisaged only a common ancestor and uses for the sense given by Hennig the term *holophyletic* conceived by Ashlock. If a group does not have a common ancestor it is considered as *polyphyletic*, while a group which has a common ancestor but does not include all its descendants is regarded by Hennig as *paraphyletic*. Using only homoplastic characters leads to polyphyletic groups, while using only plesiomorphic characters leads to paraphyletic groups. As a consequence, the degree of phylogenetic relationship depends on the proximity of the common ascendance. Species are defined by the latest evolved characters while gradually higher rank taxa (genus, family, order...) are defined by progressively earlier characters.

We wish to underline again that EMILE RACOVITZA (1908, 1910, 1912) maintained long before the idea of classification reflecting as exactly as possible

the real relationship between various lineages and in order to achieve this, a detailed analysis of the characters from the point of view of their history and phylogenetic significance.

In the contemporary cladistics methodology (WILEY, 1991; DARLU & TASSY, 1993; LECOINTRE, 2009), based on character analysis leads firstly to the hypothetical establishment of the structural or primary homologies and the direction of the transformation of characters (polarity). After forming the matrix of characters and applying the parsimony method, the most probable phylogenetic tree is obtained and, also, the hypothetical primary homologies are verified, accepting those becoming lineage or secondary homologies and rejecting the homology hypotheses (as homoplasies) which do not agree with the resulting phylogenetic tree.

We intend to analyze the morphological characters of the species of Trichoniscidae according to the principles of the phylogenetic systematics within the context of the suborder Oniscidea. Our intention is to emphasize the significance of the different characters as criteria for the classification of taxa.

2. REQUIREMENTS AND PROBLEMS CONCERNING THE CHARACTER ANALYSIS

Clearly, the detailed comparative study of the characters implies some requirements. Beginning with a good knowledge of the studied group, the character analysis should compare only adults or individuals in the same developmental stage. The use in taxonomy of characters considered as differential but resulting from the comparison of individuals in different developmental stages leads certainly to errors. As an example, it was argued (GRUNER & TABACARU, 1963) that the genus *Nematoniscus* Verhoeff, 1930, with three species, *N. prenjanus* (Verhoeff, 1901), *N. triangulifer* Verhoeff, 1930 and *N. illyricus* Verhoeff, 1933, was established only by comparing different developmental stages of the species *Mesoniscus graniger*.

As many individuals as possible should be analyzed and, if it is the case, individuals from the same species but from different populations in order to establish the range of the characters' variability, respectively the stability of the characters used to define species and subspecies.

The sex of the animals should be taken into account in order to compare only individuals of the same sex and to consider the sexual differential characters. In the case of the Trichoniscidae, the majority of the characters defining species and higher taxa represent male differential characters. Establishing taxa based only on female specimens leads to errors and names that cannot define taxa. As we have shown (TABACARU, GIURGINCA & SARBU, 2022), the genus *Oregoniscus* Hatch, 1947, established for a species at which only the female was described, is, in fact, a *nomen dubium*. The description of the female, probably a trichoniscid, under the name *Trichoniscus nearcticus* Arcangeli, 1932, does not indicate any character

allowing the identification of a species and, even less, the identification of a separate genus.

Analyzing a sample of Oniscidea based on a detailed comparison following the principles of the phylogenetic systematics, we can differentiate a series of character categories:

- characters common to all the specimens from the investigated sample, which can be supposed to belong to the same species, and are not found outside that particular species, nor in the most closely related species (sister species). These are the so called *autapomorphies* of the species. From a taxonomic point of view, they are important in the identification and definition of the species but they cannot tell us anything about the relationships of the species.

- characters common to all the specimens from the investigated sample but shared with the sister species (named *adelphotaxa* by AX, 1988) but are not found outside the sister species. We can assume this group of species shares an ancestor common only to them and we can reunite them in a monophyletic taxon, respectively a genus (or subgenus, or a group of species). These characters are *synapomorphies* of the sister species and define as autapomorphies the genus containing those species.

- basal characters, inherited unchanged from an ancestor anterior to the direct, common ancestor of the sister species and which exist also outside the monophyletic group of the sister species. These are the so called *plesiomorphies*. A group of species based only on such characters is a paraphyletic group as it does not reunite all the taxa with that character. But such characters can be inherent to higher level taxa where they evolved successively as autapomorphies. In the case of genera, if they are inherent to a group of genera, they represent the synapomorphies of those genera. At the level of their apparition, they characterized as autapomorphies the direct common ancestor of these genera so the family that contains these genera.

- similar characters but which are not inherited from a common ancestor but evolved independently several times in different groups of species. These characters represent *convergences*. Of course, here we refer to the species level, but convergence is also present at higher taxa. When convergence appears in closely related lineages, assuming a higher initial potential for the evolution of the respective similar characters, the character is considered a *parallelism*.

- characters which disappeared during the evolution of the respective phyletic lineage and have re-appeared at the analyzed taxon (*reversals*). A frequent case of reversal is, for example, the disappearance of a character developed during the evolution of the group so a reversal to the initial state, namely the absence of the respective character.

- individual characters which differ on an individual basis being the expression of the variability within the species. Also, there may be population level differences but which are not affect the unity of the species. During the course of evolution, these characters might become common, inherent for a species, but at the individual or population level, they do not have a taxonomic significance.

Within the family Trichoniscidae, there are sometimes individual variations, for instance concerning the body size, the number of aesthetascs on antennule or the number of articles of the antennal flagellum.

According to the phylogenetic systematics, a valid taxon is defined by at least one autapomorphy. An autapomorphy can be represented by the apparition, the changes or even the disappearance of a character. As an example, within the Oniscidea, the reduction of the antennule to at most three articles and the disappearance of the mandibular palpus represent autapomorphies. For the infraorder Tylomorpha, we consider the complete reduction of the genital apophyses as the essential autapomorphy. The Suprasection Orthogonopoda is defined, among other characters, by the reduction of the occipital fossa and the antennal squama. The section Crinocheta, the most advanced section of the terrestrial isopods, is defined among other characters by the reduction of the pars molaris from the mandibles, a character existing at all the other sections.

According to the principles of the phylogenetic systematics, a species has to be compared with the most closely related species, namely the one or more sister species, in order to note the autapomorphies defining the respective species and the synapomorphies defining the genus to which those species belong. However, in the taxonomic research, we consider, initially automatically through experience in the study of the respective group, the plesiomorphic characters, which evolving as autapomorphies, defined successively the higher-ranking taxa to which the species belongs. Without considering these characters, the general similarity might lead to the error of searching for the sister group within another taxon than the one to which the examined sample really belongs. There are many examples in this case. Of course, the analysis of the essential autapomorphy of the Synocheta, namely the fusion of the ejaculatory ducts, is sometimes difficult to notice, but in some cases we have to consider the absence at the respective genera of some plesiomorphic characters which are always present at Synocheta. As we have pointed out in the definition of the family Trichoniscidae, this was the cause for the mistaken inclusion of the genera *Buchnerillo*, *Cylindroniscus*, *Castellanethes*. At the genera *Buchnerillo* and *Castellanethes*, the absence of the molar process and of the penicilli of the inner endite of the maxilla were not taken into account, but these are plesiomorphic characters which are always present at the Trichoniscidae. In the case of the genus *Castellanethes*, the muscles of the first male pleopod also have not been considered.

In some situations, the differential characters are so remarkable we have to follow the characters of the higher taxa to step-by-step find the closest taxa. In the case of establishing a genus of a single species, the autapomorphies of the respective species are so significant we have to search for the sister group, or the sister groups, at the genus level or even at higher level taxa. As an example, the discovery of the species *Calabozoa pellucida* led to the definition of a new genus, a new family and even a new suborder, the Calabozoidea. Many genera have been described initially on the basis of a single species, such as *Kithironiscus*,

Biharoniscus, *Thaumatonicellus* but in these cases the subsequent finding of new species established the validity of the genus. In other cases, the discovery of new species might rise the problem of re-defining the respective genus.

The convergences, the parallelisms and the reversions, respectively characters newly evolved but which are not inherited from an ancestor but are similarities evolved independently (homoplasies), so in opposition with the homologies, and unlike synapomorphies, cannot indicate a phyletic relationship. A relatively frequent, remarkable convergence, is the conglobation, the characteristic defense mechanism by rolling into a sphere. This mechanism, which involves many morphological changes, evolved independently in numerous crustacean groups. As it did not exist at the basal Oniscidea (Ligiidae) we cannot regard it as exiting at the groups ancestor but that it evolved convergently at Tylomorpha, at Buddelundiellidae among the Synocheta and some groups from the section Crinocheta.

We have to admit: the recognition of the homoplastic characters, especially in the case of parallelisms, is difficult or even impossible based on the primary homology and becomes evident only after establishing a cladogram and noting the characters lack of concordance.

As we have argued previously (TABACARU, 2002; TABACARU & GIURGINCA, 2023) when a homoplastic character appears at an isolated taxon, within a group characterized by the absence of the respective character, that character has to be regarded as an autapomorphy of the respective taxon.

In the cladistics methodology, the characters used to reconstruct the phylogenetic tree are considered to have the same weight meaning characters do not have a special taxonomic importance. As such, the methodology does not take into account a different importance of the characters in defining the rank of the taxa. Willi Hennig specifies: "...ebenso wichtige Feststellung besagt, das es keine Merkmale gibt die ihrem Wesen nach als Merkmale einer bestimmten Kategorienstufe (Artmerkmale, Gattungsmerkmale etc.) zu bewerten wären" (HENNIG, 1982, p. 215). But we think that experience in several groups might show there is a parallelism, respectively a certain regularity in the diversification succession of some characters on different lineages, so that the differences of one character seem to define the taxa of a certain rank. But as it is obvious, this different consideration of the characters' weight is not based on a subjective evaluation but it results *a posteriori* from the ranking of the taxa based on synapomorphies.

In order to reconstitute the phylogeny of a group, the aim is to find the highest number of congruent characters. From a practical point of view, characters do not evolve synchronous so in the same taxa the characters may be at different stages of their evolution. This process, called mosaic evolution, or heterobathmy (term adopted by Hennig), is frequent and represents of course an impediment in the reconstitution of the groups history but is essential for the dissociation of the characters within the phylogenetic systematics. The parsimony method aims for the solution with the least number of homoplasies and the highest congruence of characters.

Applying the cladistics methodology on the family Trichoniscidae would face great difficulties for several reasons. Firstly, we have to admit that the representatives of this family have, in general, very few autapomorphic and synapomorphic characters. Then, as VANDEL (1960, p. 90) underlined, the characters which are very diversified and varied in a group of species (and as such have a special taxonomic interest), in another group of species are structurally monotonous. Thus, in the case of the subfamily Trichoniscinae, the diversification is conveyed by the different structures of the male sexual characters while in the subfamily Haplophthalminae, the diversification is conveyed by the very varied tergal ornamentation.

A major difficulty resides in the existence of numerous incomplete descriptions of species which cannot be used for proper comparisons. In this regard, we can note two different methods. RACOVITZA (1907) recommended descriptions as complete as possible: “for a species description to be useful in all situations, it has to be complete and accompanied by images representing at least the main characters”. Of contrary, VANDEL (1960, p. 91) maintained that “long diagnoses have the inconvenience to drown the truly differential characters within a lot of details with no value”. Unfortunately, using this method the descriptions provided by VANDEL (1977) for species belonging to the genus *Amerigoniscus* present only the apex of the male pleopode 1 exopodite which does not differ very much depending on the angle from which it was viewed. As a conclusion, we think it is necessary to achieve descriptions as complete as possible but accompanied by differential diagnoses.

3. ANALYSIS OF THE DIFFERENTIAL CHARACTERS

In his study on the eco-morphological strategies of the terrestrial isopods, SCHMALFUSS (1984) defines the different types of habitus in Oniscidea as follows: runner, clinger, roller, spin form, creeper and non-conformist.

We can assume the runner represents the plesiomorphic habitus as it is present at the Ligiidae. At the Trichoniscidae, we find both the runner and the creeper type of habitus. Within the Section Synocheta, only the family Buddelundiellidae present the roller habitus, implying a conglobating ability.

Concerning the habitus of the Trichoniscidae, we have analyzed in previous papers several aspects which, from a phylogenetic point of view, are still problematic. As we have argued (TABACARU & GIURGINCA, 2023) we cannot specify if the plesiomorphic condition is represented by the epimera of the pleonites 3–5 forming a continuous line with the margin of the pereion, or that with the epimera of pleonites 3–5 narrowed so shaping pleon clearly narrower than the pereion. Also, another problem we have pointed out (TABACARU, 2021) is if, within the Trichoniscidae family, the tergal ornamentation represents the basal aspect or if the basal aspect is represented by the morphology of the male pleopodes.

As we have argued in the present paper, when one character appears at one genus or at one species from a group lacking that character, it can be regarded as an apomorphy.

Ocular apparatus. At basal Oniscidea, the ocular apparatus presents a high number of ommatidia. At Ligiidae, after VANDEL (1960), at *Ligia oceanica*, there are approximately 500 ommatidia, at *Ligia italica*, 700–800 ommatidia and at the Ligidiidae, respectively at *Ligidium hypnorum*, 120 ommatidia. For the Tylidae, he mentions at *Tylos*, 40 ommatidia and at *Helleria*, 20 ommatidia.

At Crinocheta, as shown by SCHMIDT (2002), the number of ommatidia varies greatly: approximately 80 ommatidia at *Actaecia* and *Scyphax*, at the majority of species no more than 30, but at some species, like *Triceratosphaera*, only 3 ommatidia. There are, however, numerous endogeous or cavernicolous species, where the ocular apparatus is completely depigmented or absent.

At Microcheta (*Mesoniscus*) the ocular apparatus is absent.

Concerning Synocheta, VANDEL (1952, p. 93) specifies that the ocular apparatus is characterized by 3 ommatidia but it may be reduced at one ommatidia or can disappear completely. As we pointed out, *Trichoniscus inferus* Verhoeff, 1908 is erroneously mentioned with 2 ommatidia, as this species has 3 ommatidia as all eyed species of *Trichoniscus* (TABACARU & GIURGINCA, 2013).

In the cladistics analysis of the terrestrial isopods (TABACARU & DANIELOPOL, 1996A, 1996B) we regarded as a synapomorphy of the group Microcheta-Synocheta the reduction of the ommatidia at maximum 3. As the eyed species of the Styloniscidae and those from the most basal tribe of the Trichoniscinae, respectively the Typhlotricholigioidini, present 3 ommatidia, we consider this as the plesiomorphic state of the Synocheta.

Regarding the number of ommatidia at the genera comprised within the Trichoniscidae, there are three cases (TABACARU, 1993, 1996):

– 3 ommatidia at the genera: *Psachonethes* Borutzky, 1969, *Chasmatoniscus* Strouhal, 1971, *Tachysoniscus* Verhoeff, 1930.

– a sole ommatidia at the genera: *Protonethes* Absolon et Strouhal, 1932, *Hyloniscus* Verhoeff, 1908 (excepting *H. flammula* Vandel, 1965 which is completely blind), *Miktoniscus* Kesselyak, 1930, and the eyed genera from the subfamily Haplophthalminae.

– without an ocular apparatus: *Typhlotricholigiodes* Rioja, 1953, *Brackenridgia* Ulrich, 1902, *Cantabroniscus* Vandel, 1965, *Finaloniscus* Brian, 1951, *Caucasonethes* Verhoeff, 1932, *Alpioniscus* Racovitza, 1908, *Spelaeonethes* Verhoeff, 1932, *Titanethes* Schiödt, 1849, *Cyphonethes* Verhoeff, 1926, *Aegonethes* Frankenberger, 1938, *Mexiconiscus* Schultz, 1964, *Libanonethes* Vandel, 1955, *Trogloniscus* Cruz, 1991, *Cetinjella* Karaman et Horvatović, 2018, *Karamanoniscus* Tabacaru, 2021, *Bureschia* Verhoeff, 1926, *Biharoniscus* Tabacaru, 1963.

As we pointed out (TABACARU, 1996), we have never found in the same genus species with 3 ommatidia and species with 1 ommatidia. As such, the

presence of 3 ommatidia or 1 ommatidia is a well-defined character at the genus level. But there are numerous genera including both species with an ocular apparatus and blind species:

– genera comprising species with 3 ommatidia and also blind species: *Trichoniscus* Brandt, 1833, *Escualdoniscus* Sechet et Noel, 2015, *Nippononethes* Tabacaru, 1996.

– genera comprising species with 1 ommatidia and also blind species: *Trichoniscoides* Sars, 1899, *Androniscus* Verhoeff, 1908, *Oritoniscus* Racovitza, 1908, the subfamily Haplophthalminae.

Antennule. As BOXSHALL *et al.* (2010) argued, the crustacean antennules are not homologous with the bi-ramous post-antennal appendages so there is no need to use the terms exopodite and endopodite not even in cases where there are one or two accessory flagella.

Within the order Isopoda, the reduction of the antennule to at most three articles is considered as an autapomorphy of the suborder Oniscidea (VANDEL, 1960; TABACARU & DANIELOPOL, 1996A, 1996B, 1999).

At some Oniscidea, the number of articles is reduced to 2 articles or even a sole article. At the genera *Tylos* and *Helleria* (Infraorder Tyломorpha), the antennule is reduced to a sole article; at Ligiidae (Infraorder Ligiamorpha, Section Diplocheta) there are 3 articles but article 3 is strongly reduced; at *Mesoniscus* (Mesoniscidae, Section Microcheta), article 3 is reduced to a sclerite included in article 2 (GRUNER & TABACARU, 1963, Fig. 3 A–F). Within the Crinocheta, the antennule presents at most genera 3 articles but there are some genera at which the third article is reduced (*Detonella* and *Actaecia*) or even completely absent, as at *Armadilloniscus* and *Spelaeoniscus* (SCHMIDT, 2002, Fig. 5).

At the section Synocheta, the antennule presents 3 distinct articles. As we have noted (TABACARU, 2021; TABACARU, GIURGINCA, SARBU, 2023), especially at amphibious or aquatic species belonging to the Trichoniscidae, the third article is very elongated, as in *Typhlotricholigioides aquaticus* Rioja, 1952, *Cantabroniscus primitivus* Vandel, 1965, *Alpioniscus kuehni* (Schmalfuss, 2005). An exception within the Section Synocheta, is the species *Karamanoniscus stankoi* (Karaman, 2003), at which the antennule article 3 is reduced.

The terminal article of the antennule, considered sometimes as a vestige of the flagellum, has three aesthetascs whose shape and number differ from one species to another.

Antenna. As RACOVITZA (1925) has argued, the antenna is homologous with the bi-ramous segmented appendages. Initially, at Malacostraca, the antenna had a peduncle with three articles and two flagella. At Isopoda, the antenna presents a peduncle with 5 articles and a sole flagellum, respectively the endopodite. But at some species, on the third article there is a rudiment of the exopodite shaped as a small scale (squama). At Oniscidea, the squama is present only at the Ligiidae. Within the suborder Oniscidea, the flagellum presents a highly variable number of

articles. At Diplocheta (Ligiidae), the antennal flagellum has a high number of articles, between 9 and 38, but the number is brusquely reduced at Tylomorpha, respectively 3–4 articles at *Tylos* and only 2 articles at *Helleria*. At Microcheta (Mesoniscidae), the antennal flagellum has 7–8 articles. The majority of the Crinocheta, there are 2–3 articles but there are genera with 4 articles and genera with 7–18 articles (Olibrinidae).

Within the Trichoniscidae family, the number of antennal flagellum articles varies highly according to the species: between 2 and 30 articles. The number of antennal flagellum articles varies with the genus, but quite often there are differences within the species. A higher number of antennal flagellum articles is especially found at cavernicolous species. For instance, at *Alpioniscus kuehni* (Schmalfuss, 2005) there are 20 to 30 articles (SCHMALFUSS, 2005; TAITI *et al.*, 2018).

Mouthparts. In previous cladistics analyses (TABACARU & DANIELOPOL, 1996A & 1996B) and previous papers (TABACARU, 1994, 2002; TABACARU & GIURGINCA, 2019, 2020) we have specified the apomorphic characters of the mouthparts of the suborder Oniscidea.

In the first place, we note the disappearance of the mandibular palpus. We have also to note the disappearance of the mandibular palpus, probably convergently, at other suborders of the Isopoda, respectively at Calabozoa and Valvifera, with the exception of the genus *Holognathus*. Another important character is represented by the maxilla: at other Isopoda, it is trilobed, at Oniscidea it becomes a narrow blade, apically bilobed. Only a single species, *Ligioides intermedius* Wahrberg, 1922, presents a maxilla with a rudiment of a third median lobe. Also, as SCHMALFUSS (1989, Fig. 4) has showed, the morphology of the maxilliped at Oniscidea, differs much from the morphology found at other Isopoda by the disappearance of the retinaculum and the obvious reduction in size of the epipodites and the palpus.

Within the suborder Oniscidea, the mandibles always have *pars molaris*, except for the Crinocheta where it disappears. As such, we can regard this as an autapomorphy of the Crinocheta: mandibles without *pars molaris*. Another difference of the Crinocheta in comparison with all other Oniscidea: the inner endite of the maxillula (first maxilla) presents at all Oniscidea, except the Crinocheta, three penicilli. At Crinocheta, the majority of species present the inner endite with two penicilli and in some genera the penicilli are completely absent (Olibrinidae). There are very few genera of Crinocheta with more penicilli on the inner endite of the maxillula, as it is the case at some genera of Eubelidae.

Certainly, the different morphology of the mouthparts at Crinocheta in comparison with the other Oniscidea is related with a difference in food type and this difference is also reflected in the structure of the masticatory stomach. We specify that the structure of the stomach at Crinocheta is very different (TABACARU & GIURGINCA, 2001, Fig. 4; SCHMIDT, 2008, Fig. 16). As we have

argued (TABACARU & GIURGINCA, 2001, 2003A, B) there are differences in the conformation of the stomach between the Tylomorpha, Diplocheta, Microcheta, Synocheta (Fig. 1A, B), it is clear the morphology of the stomach at Crinocheta is very different from that of the other Oniscidea. Mainly, we note at Crinocheta the disappearance of the superomedianum, the strong development of the ventral apodemae and the median apodema and especially, the presence of a highly chitinized frame bordering the inferolateralia.

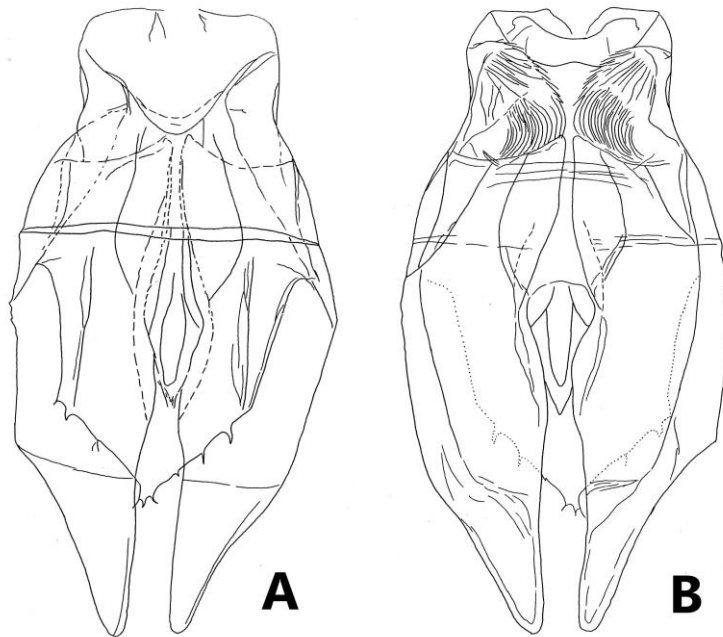


Figure 1. *Caucasonethes centralis*: A. Stomach, dorsal view; B. Stomach, ventral view.

Sexual differential characters. In the taxonomy of Isopoda, the male sexual characters are highly significant both at a superior taxonomic level and for the species identification. Generally, within the family Trichoniscidae, the main reference point of the present paper, without an analysis of the male sexual characters, the species cannot be identified.

The male sexual characters are: glandular-piliferous organs; pereopode I and especially pereopode VII; genital papillae; pleopode I and pleopode II.

The name of glandular-piliferous organs was established by VANDEL (1951) for glandular organs opening on evaporation surfaces provided with piliferous formations. Although a histological study of such an organ was carried out on the species *Trichoniscus alexandrae* Caruso, 1978 (LOMBARDO *et al.*, 2006) and *Cyphonethes herzegowinensis* (Verhoeff, 1900) (VITTORI & ŠTRUS, 2017) their exact function is still unknown. Vandel supposed they play a role similar with that of the odoriferous organs of the insects.

Within the Trichoniscidae, the glandular-piliferous organs present various positions: on the head (*Trichoniscus sulcatus* Verhoeff, 1917, *T. nicaensis* Legrand, 1953); on the antennae (*Trichoniscus biformatus* Racovitza, 1908, *Hyloniscus vividus* (C. Koch, 1841), *H. marginalis* Verhoeff, 1901, *H. mariae* Verhoeff, 1908, *H. adonis* Verhoeff, 1927, *H. inflatus* Verhoeff, 1927, *H. siculus* Mehely, 1929, *H. dalmaticus* Verhoeff, 1930, *H. refugiorum* Verhoeff, 1933, *H. travnicensis* Buturović, 1955); on the head and the first pereionite (*Trichoniscus circuliger* Verhoeff, 1931, *T. karawakianus* Verhoeff, 1939, *T. alexandrae* Caruso, 1978, *T. dancaui* Tabacaru, 1996); on the first pereionite (*Trichoniscus foveolatus* Vandel, 1951, *T. selenae* Giurginca, 2023, *Oritoniscus notabilis* Herold, 1944, *O. remyi* Dalens, 1964); on the first and the second pereionite (*Cyphonethes herzegowinensis* Verhoeff, 1900); on the pereionite III (*Trichoniscus vandeli* Tabacaru, 1996); on pereionite IV (*Trichoniscus racovitzae* Tabacaru, 1995, *T. tuberculatus* Tabacaru, 1996); on pereionite I and VII and on pleonites 1 and 2 (*Trichoniscus darwini* Vandel, 1938); on pereionite VII and pleonites 1 and 2 (*Trichoniscus korsakovi* Vandel, 1947); on pleonite 4 (*Titanethes albus* C. Koch, 1841, *Cyphonethes biseriatus* (Verhoeff, 1900)).

Rarely, species of Crinocheta also present glandular-piliferous organs.

We have to point out that glandular-piliferous organs represent important autapomorphies for the species identification but they do not show anything on the relationships between the species.

The most important aspect within the phylogenetic study of the suborder Oniscidea, is, in our opinion, the evolution of the genital papillae. Studies concerning the evolution of Isopoda (WÄGELE, 1989; BRUSCA & WILSON, 1991; WILSON, 1991; ERHARD, 1998B) showed that the plesiomorphic of the genital papillae is on the pereopode VII coxopodite and migrated convergently at different evolutive lineages until they merged medial-sternal in a single papilla.

At the suborder Oniscidea, the genital papillae are inserted on the membrane between the pereion and the pleon. Only Diplocheta has two genital papillae. At Tylomorpha, the genital papillae disappear completely and there are two separated genital openings. At Microcheta, the two genital papillae are short, ventrally fused and with the opening in close proximity. At Crinocheta and Synocheta, there is only one papilla but at Crinocheta the ejaculatory ducts are separated while they are fused at Synocheta.

At the Trichoniscidae, the genital papilla has an elongated, cone-like shape and differs from the genital papilla of the Styloniscidae which is subapically enlarged and with acute apical part. There are genera of Trichoniscidae which have a genital papilla shaped differently. For instance, at *Tachysoniscus* Verhoeff, 1908, it presents two terminal lateral lobes, at *Biharoniscus* Tabacaru, 1963, the genital papilla is enlarged in the distal half and ends in a M-shaped blade, while at *Thaumatoniscellus* Tabacaru, 1973, it ends in an anchor-like shape.

Between the genital papilla and the first two pairs of pleopodes there are various coaptations studied by LEGRAND (1946).

Concerning the pereopodes, we note in the first place the presence on pereopode VII of modifications leading to a prehensile pincer between the meros and the carpus. The evolution of this coaptation was studied by VANDEL (1950). It is present at the genera *Androniscus* Verhoeff, 1908, *Trichoniscus* Brandt, 1833, *Miktoniscus* Kesselyak, 1930 but also at the genera belonging to the subfamily Haplophthalminae Verhoeff, 1908. Another frequent differential character of the pereopode VII is the presence at the basis of the meros on the sternal side of a protuberance which can be shaped like a hook. This character is evident at the genera *Hyloniscus* Verhoeff, 1908, *Alpioniscus* Racovitza, 1908, *Aegonethes* Frankenberger, 1938.

The first pleopode is well differentiated and very diverse at Synocheta. The first pleopode separates the Trichoniscidae from the Styloniscidae: the muscles moving the endopodite are more developed at the Styloniscidae.

For the Trichoniscidae, VANDEL (1953, 1960) considered the first pleopode as very important, defining three stages in the evolution of the pleopodes as a base for their classification:

- unisegmented endopodite, small and ovoid or like an elongated blade but always without a terminal rod. Vandel named the group of genera with this character the *First Division*. We have recently studied (TABACARU & GIURGINCA & SARBU, 2022) these genera under the name Tribe Typhlotricholigioidini Rioja, 1953.

- endopodite ending with a stem or rarely with a rod. Vandel named the group of genera presenting this character as the *Second Division* and he grouped them in 5 *Legions*. Later on, for the genus *Androniscus* Verhoeff, 1908, the sole genus in *Legion III* distinguished by an endopodite with a paddle-like tip, the Tribe Androniscini Tabacaru, 1993 was erected; for the genera in *Legion IV* characterized by an exopodite extended by a lobe or divided by a lateral groove, the Tribe Oritoniscini Tabacaru, 1993; for the genera in *Legion V* characterized by an exopodite with 2–3 rods, the Tribe Trichoniscoidini Schmölzer, 1965 was erected; the genera from the first two legions for the Tribe Spelaeonethini Schmölzer, 1965 which was recently re-analyzed (TABACARU & GIURGINCA, 2024).

- biarticulated endopodite with a blade-like second article with a paracopulatory role distinguishing the group of genera named by Vandel as the *Third Division*, presently considered as Tribe Trichoniscini Sars, 1899. But a similar structure is found at the subfamily Haplophthalminae.

Pleopode 1 exopodite is foliaceous with a morphology varying from one genus to another, sometimes very complex as in the genera *Phymatoniscus* Racovitza, 1908 and *Thaumatonicellus* Tabacaru, 1973.

As in all Isopoda, pleopode 2 ensures the sperm transfer (WILSON, 1991). At Oniscidea, pleopode 2 presents a foliaceous exopodite and a narrow and elongated endopodite, which, according to Vandel, has a coupling function by apposition of

intromission. The endopodite is biarticulated and, in the plesiomorphic state, respectively at Tylomorpha and Diplocheta, the two articles form an angle between them, while at Orthogonopoda, the endopodite is straight, with a perpendicular insertion on the basipodite. The second article can be robust and apically differentiated according to the species.

4. DISCUSSION

As we have argued for in numerous papers concerning phylogenetic classification (TABACARU & DANIELOPOL, 1996A, 1996B, TABACARU, 1999, TABACARU & GIURGINCA, 2013, 2014, 2019, 2020), we have included the family Trichoniscidae in the Section Synocheta Legrand, 1946, Supersection Orthogonopoda Tabacaru et Danielopol, 1996, Infraorder Ligiamorpha Vandel, 1943, Order Isopoda Sars, 1817, Suborder Oniscidea Latreille, 1802.

Based on the character analysis, we will argue this classification focusing only on the contentious issues: 1. the monophyly of the suborder Oniscidea; 2. the dichotomy of the suborder Oniscidea; 3. the dichotomy of the infraorder Ligiamorpha; 4. the dichotomy of the monophylum Orthogonopoda.

4.1. THE MONOPHYLY OF THE SUBORDER ONISCIDEA

Within his study “*Phylogeny of Terrestrial Isopoda (Oniscidea): a review*”, CHRISTIAN SCHMIDT (2008) stated that the monophyly of Oniscidea is well established. He refers to the papers published by SCHMALFUSS (1974, 1989), WÄGELE (1989), BRUSCA & WILSON (1991), ERHARD (1995), TABACARU & DANIELOPOL (1996). To support the monophyly of Oniscidea, he presents 28 apomorphies.

We have to mention that ALBERT VANDEL, one of the most well-known specialists in the domain of the terrestrial isopods, considered the suborder Oniscidea as polyphyletic. Since 1943, he claimed the genera *Tylos* Audouin, 1892 and *Helleria* Ebner, 1868 are related to the marine suborder Valvifera while the other Oniscidea have their origin within the suborder Flabelifera. VANDEL (1960) considered the cephalic morphology and the uropodal disposition at *Tylos* and *Helleria* as very close to that found in Idoteidae, so clearly these two genera are connected to the Valvifera while the other Oniscidea have another origin. As a consequence, Vandel considered within Oniscidea two lineages with different origins which he named Tylian and Ligian series.

Later on, describing a remarkable trichoniscid, *Cantabroniscus primitivus* Vandel, 1965 with an exclusively aquatic life-style, VANDEL (1965, 1976) claimed this species is related to two other aquatic species, respectively *Typhlotricholigioides aquaticus* Rioja, 1953 and *Mexiconiscus laevis* (Rioja, 1956), both discovered in caves from Mexico. Influenced by these discoveries, Vandel infers paleogeographic and phylogenetic conclusions and maintained these Trichoniscidae have a basal

aquatic life-style. This led him to consider that the Trichoniscidae, and Synocheta in general, represent an independent lineage which colonized the terrestrial environment and, as a consequence, the suborder Oniscidea is heterogeneous being formed by three distinct lines: Tylian series, Trichoniscian series and the Ligian series.

Subsequent studies showed the connection of the Tylidae to the Valvifera, as envisaged by Vandel, as based on clearly convergent characters. SCHMALFUSS (1974, 1989) argued extensively for the inclusion of the Tylidae within the suborder Oniscidea and that they are not related to Valvifera.

Regarding the aquatic life-style of some species of Trichoniscidae, which led Vandel to consider Synocheta as a distinct phyletic lineage, it was demonstrated by many characters (TABACARU & DANIELOPOL, 1996A, p. 77; TABACARU, 1999) to represent a secondary reversal to an aquatic life-style and not a proof of the persistence of a distinct phyletic lineage. This fact was further supported by other authors (SCHMALFUSS, 2003; TAITI & XUE, 2012; SOUZA *et al.*, 2015; SFENTHOURAKIS & TAITI, 2015).

The hypothesis of the polyphyly of the suborder Oniscidea was reconsidered again by the studies based on molecular biology. The family Ligiidae, respectively the Section Diplocheta or just the genus *Ligia* were regarded a separated from the monophylum Oniscidea and close to other suborders of Isopoda or even as the distinct suborder Ligiidea (LINS *et al.*, 2017; DIMITRIU *et al.*, 2019; ZHANG *et al.*, 2020).

As suggested by these authors, there are two issues challenging the monophyly of Oniscidea: the reduction of the antennule, considered an apomorphy, might be in fact a homoplasy and that there are two different water-conducting systems described by HOESE (1981, 1982): *Ligia* type and *Porcellio* type. But, as we have already mentioned, within his revision, SCHMIDT (2008), the monophyly of Oniscidea is supported by 28 apomorphies. In our opinion (TABACARU & GIURGINCA, 2020) the main synapomorphies of the suborder Oniscidea are: the presence of water-conducting system; reduction of antennule (first antenna) to 1–3 articles; mandible without palpus; maxillula (maxilla II) reduced to a unitary piece; maxillipede endite without retinacles; endopodite of pleopode 2 male completely changed in a copulatory stylus. As the Diplocheta (including *Ligia*) have the synapomorphies of the suborder Oniscidea, it is difficult to assume all are homoplasies.

We present here the conclusions reached by different recent studies based on molecular analysis and there are evident contradictions at least as marked as in the case on the conclusions based on morphologic characters:

“The multiple analyses presented in our study challenge the notion of monophyly of Oniscidea. In the case of the mitogenome data set, although only

17 ingroup taxa were analyzed, strong support was found for *L. oceanica* being more closely related to non-oniscid taxa” (LINS *et al.*, OCTOBER 2017, p. 817).

“The constructed phylogenetic analyses show that Oniscidea is polyphyletic group, with *Ligia* being more closely related to marine isopods (Valvifera + Cymothoidea + Sphaeromatidea). Conclusions: we elevate the status of family Ligiidae to suborder Ligiidea which are with parallel rank with Oniscidea.” (ZHANG *et al.*, MAY 2020, p. 2).

“As regards the rogue taxa, whose position often vary among studies our analyses offer additional evidence that Ligiidae (here represented by *L. oceanica*) are the most primitive family in the Oniscidea suborder” (ZOU *et al.*, FEBRUARY 2020, p. 10).

“According to our mitogenome analysis result, *Ligia* appears to form a statistically well supported monophyletic group with Crinocheta, the more evolutionary recent Oniscidea lineage whose representatives exhibiting some of the most pioneer adaptations to terrestrial life. These results are also supported by a series of well described Oniscidea synapomorphies (SCHMALFUSS, 1989; SCHMIDT, 2008). Based on the same mitochondrial loci, running analyses under different evolutionary substitution models recently published works came up with different results (LINS *et al.*, 2017; ZOU *et al.*, 2020). In contrast with LINS *et al.* (2017) our results are in agreement with ZOU *et al.* (2020) findings whose analysis was conducted under a CAT-GTR model” (YANG *et al.*, April 2020, p. 6).

“Oniscidea is a polyphyletic suborder within the Order Isopoda (Superorder Peracarida, Subclass Eumalacostraca, Class Malacostraca, Subphylum Crustacea, Phylum Arthropoda, Kingdom Animalia) and contributes 50% of its species (LINS *et al.*, 2017)” (GUAN *et al.*, 2023, p. 144).

“The resulting phylogenetic analyses support monophyly of terrestrial isopods and suggest that conflicting relationships based on nuclear ribosomal sequences may be caused by long-branch attraction”. “In contrast to previous molecular phylogenies of Isopoda, this study finds compelling evidence for a monophyletic Oniscidea, as originally proposed by morphological analysis” (THOMAS THORPE, 2024, pp. 1 & 14).

The excerpts presented above show a clear contradiction between the papers separating *Ligia* from the other Oniscidea and the work of YANG *et al.* 2020, which considers *Ligia* as close to Crinocheta. Also, we have to point the contrast between the papers maintaining that Oniscidea is a polyphyletic group (LINS *et al.*, 2017; ZHANG *et al.*, 2020; GUAN *et al.*, 2023) and those accepting the monophyly of Oniscidea (ZOU *et al.*, 2020; YANG *et al.*, 2020; THORPE, 2024).

Of course, just as in the case of the hypotheses based on morphological characters, new studies and the fine tuning of the research methods, may lead in the case of molecular studies to different hypotheses. Moreover, just as is the case for morphological data, there might exist homoplasies within the molecular structures.

4.2. THE DICHOTOMY OF THE SUBORDER ONISCIDEA

The study of the morphological characters of the terrestrial Isopoda (Oniscidea) led, according to ERHARD (1997) to the recognition of five distinct, probably monophyletic, groups: Ligiidae Leach, 1814, Tylidae Dana, 1852, Mesoniscidae Verhoeff, 1908, Synocheta Legrand, 1946 and Crinocheta Legrand, 1946. However, these five distinct groups present the autapomorphies of the suborder Oniscidea so, as we have pointed out, the monophyly of the suborder is well supported. But the affinities between these groups are clearly different so they cannot have a direct common ancestor and it is evident they evolved successively. In the cladograms of the suborder Oniscidea, they are the terminal taxa.

Since his great study on the terrestrial Isopoda, VANDEL (1943) recognized the basal characters of the Ligiidae, a group for which he erected in 1957 the name Diplocheta. Also, he argued for the Mesoniscidae as having an intermediary position between the Ligiidae and the Synocheta. But he persisted (Vandel, 1960, 1981) to consider, erroneously as proved subsequently, the Tylidae as having a distinct origin from the suborder Valvifera.

In his study on the phylogenetic evolution of the suborders of Isopoda, SCHULZ (1979) presents, successively, on the same line: Tylidae, Diplocheta, Synocheta and Crinocheta.

In a previous paper (TABACARU & GIURGINCA, 2020), we have enumerated the various opinions concerning the position of the family Tylidae within the suborder Oniscidea (SCHMALFUSS, 1974, 1989; WÄGELE, 1989; ERHARDT, 1995A, 1996, 1997, 1998; TABACARU & DANIELOPOL, 1996A, 1996B). As the hypothesis regarding the phylogeny of the terrestrial Isopoda supported by us was misinterpreted (SCHMIDT, 2008; DIMITRIU *et al.*, 2019), we shall clarify several aspects here.

In the revision of the terrestrial Isopods phylogeny, SCHMIDT (2008, p. 202) claimed: “Ligiamorpha (Oniscidea excl. Tylidae). This goes back to VANDEL’s idea of a diphyletic origin of the terrestrial isopods, with the Tylidae more closely related to Valvifera. This hypothesis reappeared in the cladogram of TABACARU & DANIELOPOL (1996) but was supported by only 1 character.”

This claim is completely erroneous. Of contrary, in the mentioned paper, Tabacaru & Danielopol argue for the monophyly of Oniscidea and the Tylidae are not related to Valvifera. Even in the Abstract it is clearly stated: “*It is concluded that the Oniscidea is a monophyletic group. The Tylidae are not closely related to Valvifera*”.

The cladogram provided by Tabacaru & Danielopol is the result of a cladistics analysis obtained by the use of heuristic (the methods Wagner and Camin-Sokal) and exact algorithms (the method<branch and bound>Penny) existing in the software Phylip 3.5c and Paup 3.0.

The phylogenetic reconstruction followed the methodology of Hennig and two suborders, respectively Asellota and Valvifera, were used as out-groups in

order to establish the direction of the character modifications. These two suborders correspond to the exigencies of the cladistics method as they are two monophyletic groups clearly distinct from the studied group, namely the Oniscidea. The matrix was made up of 43 characters: 18 synapomorphies and 25 autapomorphies. The selection of the autapomorphies followed the principles of Hennig: within a dichotomy, a character regarded as an apomorphy at one group was considered as a plesiomorphy at the sister group. As such, the polarity of the characters resulted from the comparison with the sister group.

The cladistics analysis resulted in a sole tree with a first dichotomy in the clear division between the Tylidae and the ensemble of the other groups with the Diplocheta (Ligiidae) as the basal adelphotaxa. For the sister groups resulting from the first dichotomy, we suggested the names infraorder Tylomorpha and infraorder Ligiamorpha, used by FRANKENBERGER (1959, p. 63), SCHMÖLZER (1965), BOWMAN & ABELE (1982) in the treatise *The Biology of Crustacea* and also by HOLDICH, LINCOLN & ELLIS, 1984. The same names were used by BRUSCA & WILSON (1991), ROMAN & DALENS in *Grasse Traité de Zoologie* (1999), MARTIN & DAVIS (2001) and by numerous other authors as we have pointed out in a previous paper (TABACARU & GIURGINCA, 2019, p. 53).

We did not use the terms Tylomorpha and Ligiamorpha to support a diphyly but to convey the first dichotomy. As we have clearly stated, the common apomorphies of Valvifera and Oniscidea show that Valvifera is closer to Oniscidea than the Asellota, a statement unanimously accepted.

ERHARD (1996, p. 33) and SCHMIDT (2008, p. 202) objected that the sister group Ligiamorpha is supported by a single synapomorphy. But we have to remember that at the base of this group is the family Ligiidae, so the group recognized as the most plesiomorphic and, certainly, the closest to the common ancestor of the terrestrial Isopoda. But the distinct and mobile coxal plates are an important character for the Tylomorpha.

We have to note that the hypothesis proposed by ERHARD (1998) does not advance well defined characters for Holoverticata. Apparently, the most significant character is the synapomorphy: disappearance of the occipital fossa. But BRUSCA & WILSON (1991, p. 171) claim that the occipital fossa is a sporadically occurring character in many suborders and as such it is unsuitable for phylogenetic analysis. The other apomorphies mentioned by Erhard are debatable. For instance, B3: the absence of the sternal processus on the sternites 3–5. As ERHARD (1997, p. 12) himself specifies, this sternal processus exists only at *Ligia* but not at *Ligidium*, so its absence cannot be an autapomorphy. At the character B5, the number of digestive glands cannot be a synapomorphy. As ERHARD (1997, p. 56) shows there are 3 pairs digestive glands at *Ligia* but at *Ligidium* and *Tylos* there are 2 pairs and a rudiment, so there no difference can be mentioned between Diplocheta and Holoverticata regarding this character. Moreover, SCHMIDT (2008) no longer considers these characters to define Holoverticata.

ERHARD (1997, p. 63) does not regard as valid the apomorphy provided for Diplocheta by TABACARU & DANIELOPOL (1996, apomorphy 25), respectively the presence of a fascicle of macrochaeta on the males first pleopodes as they are absent in one species. But as this character is clear and has a precise physiological role, it seems more likely that this apomorphic character disappears in one species (as Erhard himself mentions). Instead, to support the monophyly of the Ligiidae group, Erhard uses characters that cannot be sustained. For instance, character A4 apomorphy: distal article of antenna 1 Ligiidae-specific reduced; plesiomorphy: article not reduced. This is about the article 3 of the antennule and ERHARD (1995, p. 106) himself shows that at the Tylidae, articles 3 and 2 are absent while at the Mesoniscidae and some Crinocheta genera, article 3 is reduced and even absent. Besides, from our own observations and bibliographic data, clearly show that the distal article of the antennule is completely different at *Ligia* in comparison with *Ligidium*. While at *Ligia*, the distal article of the antennule is very short, at *Ligidium*, this article is very narrow and has a distal-lateral insertion.

Within the demonstration of ERHARD (1998A) the first character indicating the monophyly of the Orthogonopoda and the opposition between Orthogonopoda and the sister group Tylidae, supports our hypothesis: Character D1 (ERHARD, 1998A, p. 307), C72 (SCHMIDT, 2008, p. 203) apomorphy: genital papillae partially fused; plesiomorphy: genital papillae separated.

But it is well known that genital papillae separated or even “fully separated”, as Schmidt writes, exist only at Diplocheta so the sister group of Orthogonopoda according to the hypothesis supported by us. The genital papillae do not exist at the Tylidae. At some genera of Crinocheta, the conformation of the genital papilla clearly shows it represents the partial fusion of the two genital papillae of the Ligiidae.

Concerning the Tylidae, we have presented in a previous paper (TABACARU & GIURGINCA, 2020), our studies and opinions on the two genera included in this family, respectively *Tylos* Audouin, 1826 and *Helleria* Ebner, 1868.

Both Erhard and Schmidt accept that the family Tylidae is defined by numerous apomorphic characters. SCHMIDT (2008, p. 202) maintains: “The Tylidae are a well defined monophyletic group with numerous apomorphic characters (Erhard, 1997)”. ERHARD (1998A, p. 305) sustains: “Therefore, the monophyly of Tylidae is unequivocal”. Also, SCHMALFUSS & VERGARA (2000), in a study on the genus *Tylos* Audouin, 1826 maintained that *Tylos* and the monospecific genus *Helleria* form a certainly monophyletic family and pointed out the many synapomorphic characters.

This clear difference between the Tylidae and the other Oniscidea is, in our opinion, explainable by an initial dichotomy of the ancestor of the suborder Oniscidea. For this reason, we have considered within the suborder Oniscidea, two different infraorders as the cladistics analysis cladogram clearly showed.

As the cladistics analysis emphasized (TABACARU & DANIELOPOL, 1996A, 1996B) and we have subsequently argued (TABACARU & GIURGINCA, 2014, 2019, 2020), the infraorders Tylomorpha and Ligiamorpha are clearly differentiated by important characters:

Infraorder Tylomorpha: Coxal plates clearly distinct from tergites; male genital papillae absent; rudimentary pleopode 1 at both sexes (endopodite missing at both sexes, the exopodite present only at males of *T. spinulosus* after ERHARD, 1996); exopodites of pleopodes 2–5 with respiratory organs with ventral stigma; uropod protopodite plate-like laterally inserted on the pleotelson and ventrally folded forming opercula closing an anal region by a transversal septum; brood pouch prolonged by an internal sack; antennule becomes rudimentary, having only one article.

Infraorder Ligiamorpha: Coxal plates fused to the tergites; male genital papillae (two or one) always present; pleopode 1 well developed, at least in the male; exopodites of pleopodes 2–5 without respiratory organs with ventral stigma; uropods not laterally inserted on the pleotelson and do not form an opercula closing an anal region; brood pouch without internal sack; antennule formed by two or, more frequently, by three articles.

In conclusion, as we have showed (TABACARU & GIURGINCA, 2020), in our opinion, all these remarkable traits point to an isolated position of the Tylidae and an early separation from the Ligiamorpha. As we see it, two distinct lineages evolved from the ancestor of the Oniscoidea: the Tylomorpha and the Ligiamorpha. Tylomorpha have remained a small group due to highly specialized autapomorphic traits and negative and restrictive apomorphies. Of contrary, the Ligiamorpha, beginning from a group close to the ancestor, underwent a highly diversifying evolution.

4.3. THE DICHOTOMY OF THE INFRAORDER LIGIAMORPHA

As mentioned above, we have used (TABACARU & GIURGINCA, 2014, 2019, 2020) the names infraorder Tylomorpha and infraorder Ligiamorpha, indicating Vandel 1943 as author, as used by BOWMAN & ABELE (1982), HOLDICH & LINCOLN & ELLIS (1984), MARTIN & DAVIS (2001) and, subsequently, by many other authors, considering that Art. 23. 2 maintains that the Principle of priority should be used to promote stability. But if we apply the Principle of priority of the author (Art. 50) at the level of sub-order, then we have to consider FRANKENBERGER the author of these names published in the volume Oniscoidea in Fauna ČSR (Praga, 1959, p. 62–63) where he specified: Tylomorpha (Série tylienne Vandel) and Ligiamorpha (Série ligienne Vandel). We also note that STROUHAL (1968, p. 304) used the name “Series Ligiamorpha Frankenberger, 1959”.

Hence, it is clear the name Ligiamorpha was introduced by Frankenberger in 1959 in the sense established by Vandel 1943 under the name Série ligienne and in

the same sense was used by other authors. Thus, in the classification of BOWMAN & ABELE (1982) the Infraorder Ligiamorpha Vandel, 1943 contains: Section Diplocheta Vandel, 1957, Section Synocheta Legrand, 1946 and Section Crinocheta Legrand, 1946. We note the inclusion in this classification of Section Diplocheta and the family Mesoniscidae following the classification given by VANDEL (1960). Although Vandel clearly sustained that he proposed the term Diplocheta for the Oniscidea with two distinct genital apophyses (Ligiidae) and argued for a close relationship of the Mesoniscidae with the Trichoniscidae, in his 1960 classification published in the volume *Isopodes terrestres* (Faune de France 64), he included the Mesoniscidae within the Diplocheta.

In 1989, SCHMALFUSS groups the family Mesoniscidae in a section apart, named by him Section Microcheta and argued a closer relationship of the Mesoniscidae with the Synocheta and Crinocheta than with the Ligiidae. SCHMALFUSS (1989, Fig. 10) showed that the derived character “diminution and retraction of uropod-endopodit” indicates the grouping of Mesoniscidae+Synocheta+Crinocheta and the sister-group relationship of this ensemble with the Ligiidae.

At the genus *Mesoniscus* (see GRUNER & TABACARU, 1963, Fig. 8E and F), the genital papillae are short and but not completely separated as in Diplocheta. ERHARD (1995A) sustained: “Die verküzte Genitalpapille männlicher Mesonisciden ist jedoch nur partiell unterteilt und kann deshalb als Rudiment einer phylogenetischen Vorstufe der vollkommen verschmolzen Genitalpapille des Synocheta und Crinocheta interpretiert werden”.

Later on (TABACARU, 1994; ERHARD, 1995A, 1995B), a new character was added supporting the grouping Microcheta+Synocheta+Crinocheta: endopodite of pleopode 2 male perpendicularly articulated on the basipodite without forming an angle between the first and the second article.

The monophylum Microcheta+Synocheta+Crinocheta was clearly supported in the cladistics analysis of Tabacaru & Danielopol and the name Orthogonopoda was proposed for it. This grouping was argued many times (TABACARU, 1994; ERHARD, 1995B, 1996, 1997, 1998; TABACARU & DANIELOPOL, 1996A, 1996B; SCHMIDT, 2008; TABACARU & GIURGINCA, 2019, 2020).

In his study on the classification of Oniscidea, ERHARD (1998, p. 305) maintained: “The Orthogonopoda also represent a well-defined group of undoubtedly monophyletic origin”. But Erhard suggested Tylida as the sister-group of the monophylum Orthogonopoda unlike the classification resulted from the cladistics analysis made by Tabacaru & Danielopol where Diplocheta is considered as the sister-group of the monophylum Orthogonopoda.

The genital papilla in Microcheta as well as in Crinocheta, show evident modifications from the two distinct genital papillae existing at a Diplocheta-type ancestor. It is difficult to maintain that the Tylidae, which completely lack genital papillae, might represent the plesiomorphic sister-group of the monophylum Orthogonopoda.

The cladistics analysis made by Tabacaru & Danielopol presented a phylogenetic tree where the Tylidae are isolated from the other Oniscidea due to the numerous apomorphies of this family and due to the fact that they are the sole group of terrestrial isopods retaining the coxal plates distinct from the tergites (plesiomorphy).

As we have maintained before, we regard the Tylidae as a distinct branch with an early separation from the common ancestor of all Oniscidea. That ancestor, as CAREFOOT & TAYLOR (1995) argued, surely must have been close to marine Isopoda with two genital papillae, but the Tylidae, which lack both the genital papillae and the first pleopode, have remained a branch restricted to two genera, while the other branch, beginning from less specialized forms (Diplocheta) could evolve further to highly diversified groups well-adapted to the terrestrial environment.

4.4. THE DICHOTOMY OF THE MONOPHYLUM ORTHOGONOPODA

In the classification made by ERHARD (1998), the monophylum Orthogonopoda Tabacaru & Danielopol, 1996 is divided in Microcheta Schmalzfuss, 1989 and Euniscoidea Vandel, 1943 (Synocheta Legrand, 1946+Crinocheta Legrand, 1946). Furthermore, ERHARD (1998, p. 309) asserted: “inside the Orthogonopoda, the taxon Synocheta is probably more closely related to the Crinocheta than to the Microcheta as proposed by Tabacaru and Danielopol (1996a, b)”.

In the first place, the name Euniscoidea Vandel, 1943 should not be used: if we analyze the phylogenetic tree given by VANDEL (1943, 1946) (Fig. 2), we can notice that Vandel regarded the Mesoniscoidea as the ancestor of the Trichoniscoidea and the names proposed by him, Protoniscoidea and Euniscoidea, do not represent a monophylum but a certain level of evolution, namely twin genital papillae and, respectively, a single genital papilla.

In our view, the sole character which might show a close relationship between Synocheta and Crinocheta is the presence of a single genital papilla. But the morphology of the genital papilla in Crinocheta still shows the fusion of two genital papillae by retaining two distinct ejaculatory ducts and two distinct openings. At some genera of Crinocheta, the fusion of two genital papillae is clear in the morphology of the papilla. At Synocheta, there is a single genital papilla but with the ducts fused inside the papilla and with a sole opening.

We agree with VANDEL (1957), who considered the morphological characters of the Synocheta as less derived than those of the Crinocheta: as a consequence, we cannot consider the genital papilla of the Synocheta as the final stage of fusion of the two genital papillae, only partially completed in Crinocheta. In conclusion, as Vandel argued, we also consider that the evolution of the genital papilla at Synocheta has no relationship with the evolution of the genital papilla at Crinocheta. Probably, this is a case of heterobathmy as the genital papilla evolved separately in a parallel way in Synocheta and Crinocheta. But, in comparison with Synocheta, in Crinocheta the general characters evolved faster than the genital papilla.

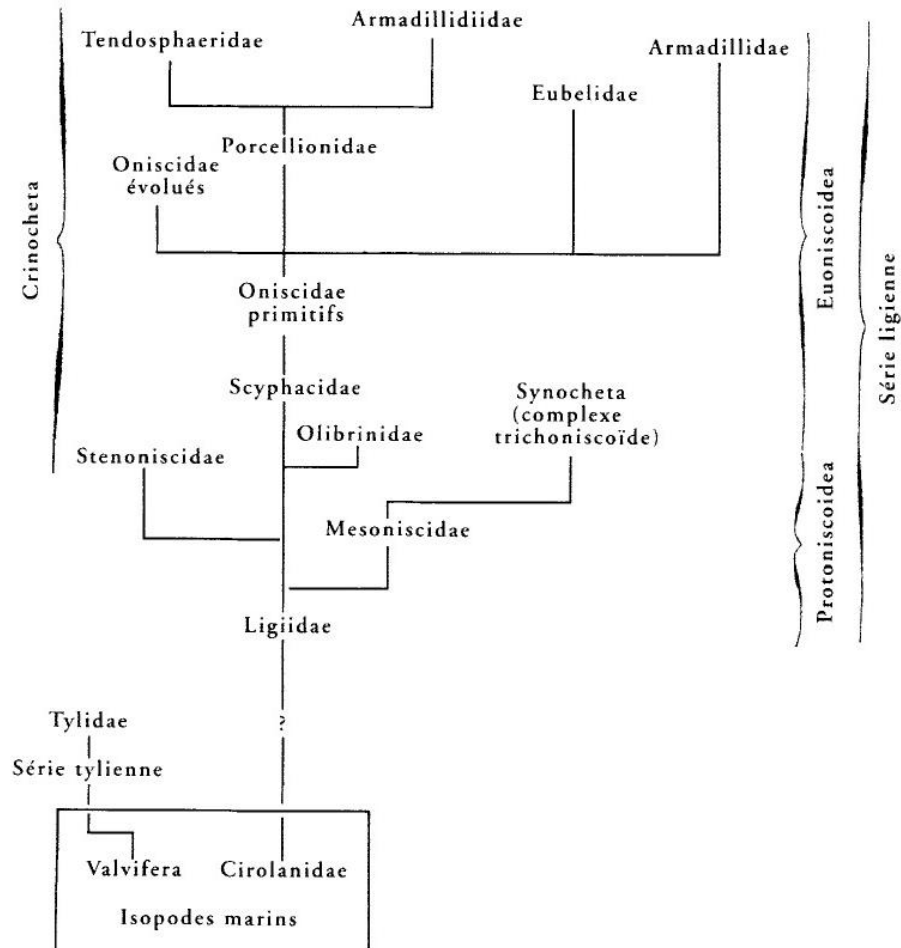


Figure 2. Classification of Oniscidea after Vandel, 1946.

In the same paper, Vandel regards the morphology of the genital papilla of *Mesoniscus*, with close openings and a fused spermatophores, as pointing to a close relationship with the *Synocheta*. The genus *Mesoniscus*, following Vandel, in agreement with the opinion of the author of the genus, represents, morphologically, an intermediary between the *Ligiidae* and the *Trichoniscidae*. As Vandel asserted: “S’il n’est probablement point l’ancêtre des *Trichoniscidae*, il nous en fournit du moins une excellente représentation”.

The cladistics analysis made by Tabacaru and Danielopol show a clear dichotomy of the monophylum *Orthogonopoda*: on one side, the sister-group *Microcheta*-

Synocheta and on the other side Crinocheta. The sister-group Microcheta-Synocheta retains some characters which we can regard as plesiomorphic, shared with Tylomorpha and Diplocheta and which disappear at Crinocheta, such as mandibles with *pars molaris* and the inner endite of maxillula with three penicilli. Clearly, the Crinocheta are the most diversified group and the best adapted to the terrestrial environment. In the cladogram, it is clearly distinct from the other Oniscidea. We can also note that in cladograms of ERHARD (1998) and SCHMIDT (2008), Crinocheta is defined by numerous apomorphies.

Our studies (GRUNER & TABACARU, 1963; TABACARU & GIURGINCA, 2003; GIURGINCA, 2009) concerning the genus *Mesoniscus* Carl, 1906, the sole representative of the family Mesoniscidae Verhoeff, 1908 and the Section Microcheta Schmalzfuss, 1989, pointed to the close relationship with the Trichoniscidae (Synocheta).

In two previous papers (TABACARU & GIURGINCA, 2019, 2020), we analyzed the dichotomy of the Orthogonopoda and the characters of the sister-group Microcheta-Synocheta.

ERHARD (1996, 1997) and SCHMIDT (2008) object that our sister-group Microcheta-Synocheta is based on only three doubtful synapomorphies. As we have showed in the case of the Section Diplocheta, this is about the plesiomorphic adelphotaxa which retains plesiomorphic characters; these characters disappear at Crinocheta, where they represent the apomorphy.

In the cladistics analysis, three synapomorphies were considered for the sister-group Microcheta+Synocheta: 1. a sole spermatophore resulting from the fusion of two spermatophores (Microcheta) or from the fusion of the two vasa deferentia (Synocheta); 2. the claw of the pereopodes is simple and unpaired, without a secondary claw; 3. visual apparatus reduced at most to three ommatidia. As we have pointed out (TABACARU & GIURGINCA, 2019), the presence of a sole or two distinct spermatophores implies a different way of mating. At Crinocheta, the two spermatophores are retrieved separately by each of the two endopodites. Concerning the second character, SCHMIDT (2002, 2008) hypothesized: "It is also possible that the inner claw as present in Ligiidae and Tylidae was lost in the stemline of the Orthogonopoda and that the inner claw present in most Crinocheta is a new structure". But the presence of a doubled by the existence of an inner claw at fossil Crinocheta from the Cretaceous (SANCHEZ-GARCIA *et al.*, 2021) does not support this hypothesis.

Within the Section Synocheta, the most representative families are: Trichoniscidae Sars, 1899, Styloniscidae Vandel, 1952 and Buddelundiellidae Verhoeff, 1930. As we have repeatedly argued (TABACARU, 1971, 1993, 2021; TABACARU & GIURGINCA, 2014, 2019), the Buddelundiellidae and the Trichoniscidae are two clearly distinct families and the Buddelundiellidae are not related with the Haplophthalminae. Recently, GARDINI & TAITI (2023) also considered the Buddelundiellidae as a distinct family based on the presence of the lateral noduli, a character supporting this conclusion.

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