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THE MONOPHYLY AND THE CLASSIFICATION OF THE TERRESTRIAL ISOPODS (CRUSTACEA, ISOPODA, ONISCIDEA)

IONEL TABACARU^{1*}, ANDREI GIURGINCA¹

Abstract. In accordance with our previous opinions (Tabacaru & Danielopol, 1996, 1999; Tabacaru & Giurginca, 2014, 2019), we argue again the monophyly of Oniscidea one of the well-defined suborders of the Order Isopoda. The monophyly of Oniscidea was maintained by numerous authors but the polyphyly of this group is recently claimed by molecular analysis papers. Also, in our opinion, the first dichotomy within the suborder Oniscidea is represented by the separation between two infraorders: Tylomorpha and Ligiamorpha. From the common ancestor of the existing Oniscidea detached the lineage Tylomorpha that retained clearly distinct coxal plates but differentiated by many autapomorphies (we note the simplification of the copulatory apparatus: the disappearance of the genital apophyses, the reduction of pereopode 1) and remained a restricted group. The ancestor of the lineage Ligiamorpha, which was close to the common ancestor of Oniscidea, continued to evolve following the second important dichotomy separating Diplocheta (present day Ligiidae) from Orthogonopoda (Microcheta + Synocheta + Crinocheta). The ancestor of the monophylum Orthogonopoda, characterized by the refining and diversification of the copulatory apparatus, evolved by a third important dichotomy: the sister-group Microcheta + Synocheta, closer to Diplocheta, and Crinocheta which represents the most evolved and diversified group of Oniscidea and which truly conquered the terrestrial environment.

Key words: Isopoda, Oniscidea, phylogeny, classification.

1. INTRODUCTION

In a previous note (TABACARU & GIURGINCA, 2019), we presented the definition and the taxonomic position of the family Trichoniscidae Sars, 1899, and also the superior taxa in which, in our opinion, this family is included: Order Isopoda Latreille 1817, Suborder Oniscidea Latreille 1802, Infraorder Ligiamorpha Vandel 1943, Supra-section Orthogonopoda Tabacaru & Danielopol, 1996, Section Synocheta Legrand 1846. In the following, our intention is to analyze the classification of the representatives of the family Trichoniscidae. Meanwhile the paper *Genetic evidence against monophyly of Oniscidea implies a need to revise scenarios for the origin of terrestrial isopods* by DIMITRIOU *et al.* (2019) was

published and reading this paper led us to re-examine and argue again our conception regarding the monophyly and the classification of the suborder Oniscidea. We have to point out that, unlike previous papers of molecular phylogeny on terrestrial Isopoda, within the aforementioned paper, the authors take into consideration for the first-time representatives from all the five groups of Oniscidea regarded as monophyletic: Ligiidae, Tylidae, Mesoniscidae, Synocheta and Crinocheta.

The classification we will argue for in the following is based initially on 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 results have been presented (oral presentation, 30.VIII.1994) at the round table “Phylogenetic systematic in biospeology” taking place within the XI International Symposium of Biospeology, Firenze-Montegufoni Castle (Italy). The memoire was accepted after peer-review and presented at 27.XI.1995 by the regretted member of the French Science Academy LUCIEN LAUBIER and published in Comptes rendus de l’Academie (TABACARU & DANIELOPOL, 1996 a).

2. THE PROBLEM OF THE MONOPHYLY OF THE TERRESTRIAL ISOPODS

Albert Vandel, one of the best experts on terrestrial isopods, sustained a polyphyletic origin for the Oniscidea. In the end (VANDEL, 1965), he argued for the existence of three independent lineages within Oniscidea, originating from distinct groups of marine isopods, lineages he named: Tylian, Ligian and Trichoniscian Series. Subsequently, Vandel’s theory was refuted and several authors argued for the monophyly of Oniscidea (SCHMALFUSS, 1974, 1989; WÄGELE, 1989; BRUSCA & WILSON, 1991; ERHARDT, 1995 A, 1996, 1997, 1998). We have maintained (TABACARU & DANIELOPOL, 1996A, 1996B; TABACARU, 2002; TABACARU & GIURGINCA, 2019) that the Tylidae have no affinities with the suborder Valvifera and, through the study of the species *Cantabroniscus primitivusi* Vandel, 1965 we underlined that the aquatic way of life of some species of Trichoniscidae does not argue for an independent origin of the Synocheta.

In our opinion, the main synapomorphies of the suborder Oniscidea are: the presence of water-conducting system; reduction of the antenule (first antenne) to 1–3 articles; mandible without palpus; maxillule (maxila II) reduced to a unitary piece; maxillipede endite without retinacles; endopodite of pleopode 2 male completely changed in a copulatory stylus. All these characters are present at all Oniscidea including those that have conserved ancestral characters (Tylidae, Ligiidae).

The hypothesis of the polyphyletic origin of the Oniscidea was reconsidered following molecular analyses. But now, the problem is represented by the family Ligiidae Brandt, 1833, respectively the section Diplocheta Vandel, 1957.

The family Ligiidae Brandt, 1833 contains three subfamilies: Ligiinae Brandt, 1833 with the genus *Ligia* Fabricius, 1798 (35 species), Ligidioidinae Borutzky,

1950 with the genus *Ligioides* Wahrberg, 1922 (1 species) and Ligidiinae Borutzky, 1950 with the genera *Ligidium* Brandt, 1833 (46 species), *Typhloligidium* Verhoeff, 1918 (3 species) and *Caucasoligidium* Borutzky, 1950 (1 species) (WAHRBERG, 1922; BORUTZKY, 1950; SCHMALFUSS, 2004; GONGALSKY & TAITI, 2014).

The section Diplocheta is clearly different from the other four sections of the suborder Oniscidea by several plesiomorphies: two distinct genital apophyses; the presence of the occipitalis fossa marking the limit of the maxillipedal segment; antenna with a rudimentary exopodite (squama). The Diplocheta present the apomorphies of the suborder Oniscidea but there are no evident autoapomorphies for them. For the Diplocheta, we have considered as characteristic the presence of a sexual differentiation of the pereopode 1 male marked by a bunch of pennaceous macrochetae on the exopodite and the endopodite (TABACARU & DANIELOPOL, 1996 A, B). But some species do not present this character and we cannot know if it is an apomorphy. SCHMALFUSS (1979) records these macrochete while defining the genus *Ligidium*. ERHARDT (1997, 1998) mentions several characters he regards as synapomorphies of the family Ligiidae.

Studying the papers presenting molecular analyses, we note that sometimes the results are not consistent and obviously contradict the morphological data.

MICHEL-SALZAT & BOUCHON (2000) regard the monophyletic section Synocheta as the sister-group of the section Crinocheta but specify that they did not taking into consideration the section Microcheta. But, in their dendrograms, *Ligidium hypnorum* is the sister-group of *Eurydice affinis*, while *Ligia oceanica* as the sister-group of *Tylos europaeus* seem close to Valvifera and Spheromatidea. As such, *Ligidium* seems close to the Cirolanidae (Cymotoidea) while *Ligia* and *Tylos* close to other two suborders, Valvivera and Spheromatidea.

MATTERN & SCHELEGEL (2003) regard the Ligiidae as the sister-group of Synocheta + Crinocheta which seems normal since neither the Tylidae, nor the Mesoniscidae are included in the analysis.

In a dendrogram of MATTERN (2003), *Ligia oceanica* + *Ligia italica* are regarded as sister-group with *Ligidium hypnorum* + *Ligidium germanicum* which are the sister-group of Synocheta + Crinocheta. Therefore, Diplocheta is not monophyletic as *Ligidium* is closer to Synocheta and Crinocheta than to *Ligia*.

JAVIDKAR & AL. (2014) presents a dendrogram showing that Diplocheta is a sister-group of Synocheta which is a sister-group of Crinocheta. Also, they did not examine neither the Tylidae nor the Mesoniscidae in their analysis.

According to LINS & AL. (2017), *Ligidium hypnorum* is the sister-group of the ensemble *Ligia italica* + *Ligia oceanica* which is the sister-group with *Tylos europaeus* + *Helleria brevicornis*. As a consequence, *Ligia* seems closer to *Tylos* and *Helleria* than to *Ligidium*.

In a dendrogram presented by HUA & AL. (2019) *Ligia oceanica* is the sister-group of *Limnoria quadripunctata* + *Gyge ovalis*. So, *Ligia* is close to Limnoriidea and Cymothoidea (Bopyridae).

DIMITROU & AL. (2019) present a dendrogram showing that *Ligia italica* + *Ligia* sp. are the sister-group of *Idotea chelipes* + *Sphaeroma serratum* while *Ligidium* (and the closely related genera *Typhloligidium* and *Tauroligidium*) are the sister-group of all the other Oniscidea. Synocheta and Crinocheta are regarded as monophyletic and sister-groups. In conclusion, Oniscidea is considered as a monophyletic group only by excluding *Ligia*. Consequently, the Diplocheta, respectively the family Ligiidae, are considered as a polyphyletic group: the genus *Ligidium* and the closely related genera form the basal clade of Oniscidea while the genus *Ligia* is grouped separately in a distinct clade, related to the marine isopods from the suborders Valvifera and Sphaeromatidea. As such, the family Ligiidae is established – so the subfamily Ligiinae Borutzky, 1950 is elevated to the rank of family.

ZHANG & AL. (2020) sequenced the complete mitochondrial genome of *Ligia exotica* (Roux, 1828) and *Mongoloniscus sinensis* (Dollfus, 1901) and conclude that Oniscidea is a polyphyletic group because *Ligia* is closely related with the marine isopods (Valvifera + Cymothoidea + Sphaeromatidea). As a consequence, they elevate the taxonomic rank of the family Ligiidae to that of suborder Ligiidea, so a parallel rank with Oniscidea.

Thus, a contradiction arises: ZHANG & AL. (2020) elevate the family Ligiidae to the rank of suborder and as a consequence the Section Diplocheta disappears from the suborder Oniscidea while DIMITROU & AL. remove *Ligia* from Oniscidea but the Diplocheta remains valid with the family Ligiidae.

Besides, in our opinion, the establishment of a new suborder within the order Isopoda, would have required an analysis within the entire order and establishing a differential diagnosis.

As we have specified, all Diplocheta (including *Ligia*) present the synapomorphies of the suborder Oniscidea and it is hard to believe they are all homoplastic characters.

We believe the assertion of the distinguished isopodologist SCHMALFUSS (2004) is still valid: namely the molecular studies regarding the phylogenetic relationships of Oniscidea have results that “contradict all other evidence and are partly very peculiar”. Schmalfluss sustains his affirmation with the example of *Eurydice* (Flabellifera) is regarded as close to *Ligidium*. Also “peculiar”, in our opinion, is considering *Caucasonethes* as the sister-group of *Calconiscellus* (DIMITROU & AL. (2019)). As the genera *Caucasonethes*, *Calconiscellus* and *Tauronethes* are taken into consideration, we can underline that *Caucasonethes* is clearly morphologically different from *Calconiscellus* and very close, perhaps even synonymous with *Tauronethes*.

We find it difficult to understand how specialists with an extensive experience in the study of the diversity of Oniscidea, consider that the phylogeny of Isopoda will be solved by “un’analisi filogenetica certa su basi molecolari” (TAITI, 2017, p. 84).

Assuming that the results of the molecular analyses record exact, comparable and correctly interpreted characters, we are still questioning why is it not considered that, just as in the case of the morphological characters, there exists the possibility of homoplasy?

Besides we fully share the opinion of Hennig, the founder of the consistently phylogenetic systematics: “Das phylogenetische System ist eine Aufgabe, deren endgültige Lösung in letztlich ebenso unerreichbarer Ferne liegt wie die Gesamtaufgabe jeder anderer Wissenschaft” (HENNIG, 1982, p. 35).

3. THE PROBLEM OF THE SISTER-GROUP OF ONISCIDEA

Within the order Isopoda, the Oniscidea is one of the suborders with the highest number of species. But its special significance resides not in the great number of species (over 3700) but in the fact that it is the sole crustacean group which conquered the terrestrial environment. Oniscidea is a very ancient group that appeared probably in Late Paleozoic (Permo-Carboniferous) and spread over the entire globe (BROLY & AL., 2013; SFENTHOURAKIS & TAITI, 2015; TAITI, 2017).

Isopoda Latreille, 1817, regarded as order or superorder (WATLING, 1983, 1999; WATLING & AL, 2000) represents one of the most numerous and highly diversified orders included in Class Malacostraca, Latreille, 1806, Subclass Eumalacostraca Grobben, 1892. Many authors include the Order Isopoda in the Superorder Peracarida Calman, 1904 on the basis of the presence of *lacinia mobilis* on the mandibles and of the brood pouch. But other authors do not accept Peracarida as a monophyletic taxa, arguing that the *lacinia mobilis* represents a larval character kept in the adults, which also exists in other groups and that the oostegites are not homologous (WATLING, 1981, 1983; MAYRAT & SAINT LAURENT, 1996).

On the basis of numerous characters, the Order Isopoda is, generally, considered, a monophyletic group but there are very divergent opinions about the sister-group of Isopoda (see TABACARU & DANIELOPOL, 2011, 2012). As such, Isopoda was regarded by different authors as the sister-group of Amphipoda, Tanaidacea, Cumacea or with Brachycarida (Cumacea + Tanaidacea + Spelaeogryphacea + Thermosbaenacea) as a superorder.

In their papers on the phylogeny of Malacostraca, TABACARU & DANIELOPOL (2011, 2012) argue that Amphipoda does not represent the sister-group of Isopoda. The cladistic analysis supports the ensemble Spelaeogryphacea + (Cumacea + Tanaidacea) as the sister-group of Isopoda (Fig. 1).

The position of the Order Isopoda within the Class Malacostraca and the division in suborders is still a much debated problem (WILSON, 2008, 2009; POORE & BRUCE, 2012). BOWMAN & ABELE (1999) included 9 suborders in the Order Isopoda: Gnathiidea, Anthuridea, Microcerberidea, Flabellifera, Asellota, Valvifera, Phreatoicidea, Epicaridea and Oniscidea. But, firstly, Flabellifera Sars, 1882 was regarded as a polyphyletic group. Even RACOVITZA (1912) said: “Le groupe des Flabellifera ne me semble pas naturel et il y a toutes sortes de bonnes raisons pour ne pas l’admettre”. WÄGELE (1989) replaced it with the suborders Spheromatidea and Cymothoida (including Gnathiidea, Anthuridea and Epicaridea).

Following the study of BRAND & POORE (2003), currently, 11 suborders are included within Isopoda: Aselloidea Latreille 1802, Oniscidea Latreille, 1802,

Valvifera G.O. Sars, 1883, Phreatoicidea Stebbing, 1893, Microcerberoidea Lang, 1961, Calabozoidea Van Lieshout, 1983, Spheromatidea Wägele, 1989, Cymotoidea Wägele, 1989, Limnoriidea Brandt and Poore, 2002, Phoratomidea Brandt and Poore, 2003, Tainisopidea Brandt and Poore, 2003.

It was asserted (MICHEL-SALZAT & BOUCHON, 2000, TAITI, 2017, DIMITRIOU & AL., 2019) that TABACARU & DANIELOPOL (1996) regard Valvifera as the sister-group of Oniscidea. In fact, in the mentioned paper it is stated (TABACARU & DANIELOPOL, 1996, p. 74): “The apomorphies 3,4,5, which the Valvifera share with all terrestrial isopods, do not represent, in our opinion, a proof of a close relation as they are characters also found in other suborders; they only show that Valvifera and the terrestrial isopods are closer to each other than they are in relation to Asellota”. The aim of the mentioned paper was the phylogeny of the terrestrial isopods and used the suborders Asellota and Valvifera as out-groups in the cladistic analysis.

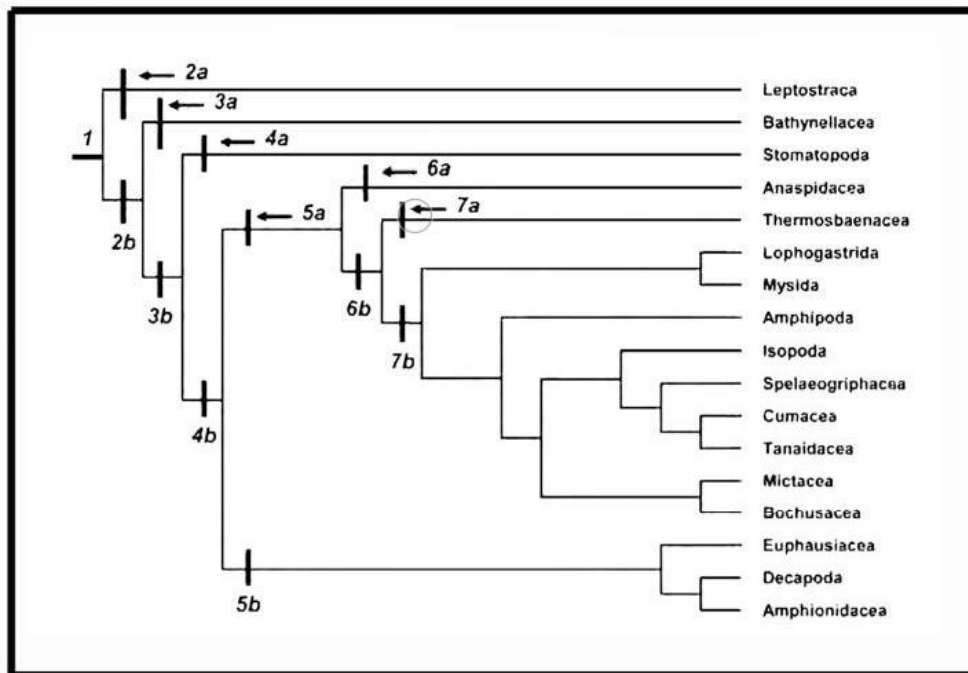


Fig. 1. Cladogram depicting the phylogenetic relationships of the major taxonomic groups of the Class Malacostraca, as proposed by Tabacaru and Danielopol (from TABACARU & DANIELOPOL 2012). Numbers refer to the following taxa: 1 – Class Malacostraca Latreille, 1802; 2a – Subclass Phylocarida Packard, 1879; 2b – Subclass Eumalacostraca Grobben, 1892; 3a – Infraclass Podophallocarida Serban, 1970; 3b – Infraclass Cephalothoracarida Tabacaru & Danielopol, 2012; 4a – Cohort Hoplocarida Calman, 1904; 4b – Cohort Caridoida Hessler, 1983; 5a – Subcohort Syneocarida Tabacaru & Danielopol, 2012; 5b – Subcohort Eucarida Calman, 1904; 6a – Infracohort Syn-carida Packard, 1885; 6b – Infracohort Neocarida Ax, 1999; 7a – Superorder Pancarida Siewing, 1958; 7b – Superorder Peracarida Calman, 1904.

The cladistic analysis of the order Isopoda (TABACARU & DANIELOPOL, 1999) included 12 suborders and concluded that the suborder Calabozoidea is the sister-group of the suborder Oniscidea.

Initially, the suborder Calabozoidea was established (VAN LIESHOUT, 1983) for the species *Calabozoa pellucida* Van Lieshout, 1983, discovered in Venezuela in wells and the hyporheic. After a comparison with the suborders Flabellifera, Valvifera, Asellota and Oniscidea, Van Lieshout endorsed a closer relationship between Calabozoidea and Asellota. As we have pointed out (TABACARU & GIURGINCA, 2019), Van Lieshout wrongly asserted that in *Calabozoa* the pleonites 1 and 2 are reduced to sternal part. Analyzing individuals of *Calabozoa pellucida* we have noted that the tergal part of the respective pleonites exists, but it is not visible being covered by pereonite 7. However, as other authors did not have the opportunity to study the species *Calabozoa pellucida*, the error persists in subsequent diagnoses of the suborder Calabozoidea (BRUSCA & WILSON, 1991, character 86; MESSANA & AL., 2002; PREVOČNIK & AL., 2012).

In his ample study on the phylogeny of Isopoda, WÄGELE (1989) considers Calabozoidea as the sister-group of Asellota. He clearly separates this sister-group from the ensemble Oniscidea, Valvifera, Anthuridea, Sphaeromatidea and Cymothoidea based on two reasons. In the first place, Wägele sustains that Calabozoidea, like Phreatoicidea and Asellota, have ring-like coxae (p. 13, 232–233). Secondly, he maintains that in Calabozoidea, the anterior filters of the stomach are straight, without lateral curves, and so belong to a plesiomorphic type.

Of contrary, BRUSCA & WILSON (1991) in their phylogenetic analysis, regard the suborder Calabozoidea as either a primitive oniscidean, adapted to an aquatic life, either as the sister-group of the suborder Oniscidea.

The detailed study of the species *Calabozoa pellucida*, showed that the anterior filters do not belong to a plesiomorphic type, as in Asellota (TABACARU & PLATVOET, 1997). Regarding the coxae, we have showed (TABACARU & DANIELOPOL, 1999, p. 167–168) that in *Calabozoa* there are no ring-like coxae but it is not possible to know if the coxae have become coxal plates and are completely fused with the former edge of the pereopodes or if they disappeared by reduction and merging with the sternites. RACOVITZA (1923) has shown that the involution of the coxa is a general phenomenon in isopoda but it can take place in different ways. Also, we showed that *Calabozoa* does not present the essential autapomorphies of Oniscidea: as such, the hypothesis of an oniscidean adapted to an aquatic life is untenable.

The cladistic analysis of Isopoda (TABACARU & DANIELOPOL, 1999) showed that Calabozoidea is the sister-group of Oniscidea (Fig. 2). This sister-group relationship is argued by the conformation of the pleon with 5 free pleonites, the first two pleonites are more reduced, and also by the fact that the pleopode 2 endopodite evolves entirely into a copulatory organ. Also, we can note the mandible without a palpus and the maxillipedal endite without retinacles in both suborders.

Currently, two families are included within the suborder Calabozoidea: the family Calabozoidae Van Lieshout, 1983 with two species, respectively *Calabozoa pellucida* Van Lieshout, 1983 and *Pongycarcinia xiphidiourus* Messana, Baratti and Benvenuti, 2002, discovered in a cave from Brasil; the family Brasileirinidae Prevočnik, Ferreira & Sket, 2012 with the species *Brasileirinho cavaticus* Prevočnik, Ferreira & Sket, 2012, also discovered in a cave from Brasil.

Subsequent studies (MESSANA & AL., 2002, PREVOČNIK & AL., 2012) confirmed our conclusions regarding the importance of the morphology of the pleon.

We have to mention that Calabozoidea does not present the ancestral characters of the basal Oniscidea. As we have shown, Calabozoidea does not present coxal plates like the ones existing at the Tylidae. Also, Calabozoidea does not have fossa occipitalis, squama on the antenna and does not have two genital apophyses as in the Ligiidae. In Calabozoidea, there is a sole genital apophysis as in the evolved Oniscidea. Within Isopoda, the fusion of the maxillipedal segment is rarely visible dorsally (*Onchotelson*, *Bathynomus*, *Sphaeromides*) while the squama, a rudiment of the antennal exopodite, was recorded only in some Asellota (Stenasellidae, Stenetroidae, Janiroidea (RACOVITZA, 1912, 1950; ROMAN & DALENS, 1999). Concerning the genital apophyses, it is well known that in Isopoda, the basal position is on the medial edge of the pereopode 7 coxae and, during a parallel evolution, they migrate on the caudal edge of pereonite 7 and draw near the medial line up to their merging as it is the case, for instance, in Crinocheta, Synocheta and, among Valvifera, the Arcturidae (WILSON, 1991).

If Calabozoidea is really the sister-group of Oniscidea, so they share a common ancestor, we note that Calabozoidea have retained some characters of that ancestor (antennula with 5 articles, maxilla II with 3 endites) while other characters evolved similarly with the derived Oniscidea (a single genital apophysis, the conformation of the pleopode 2 endopodite).

From our point of view, the origin and the sister-group of Oniscidea represents a problem still under study.

4. THE POSITION OF THE FAMILY TYLIDAE

The family Tylidae Milne-Edwards, 1840 comprise the genus *Tylos* Audouin, 1826 with 20 species and the genus *Helleria* Ebner, 1868 (syn. *Sypastus* Budde-Lund, 1879) with a single species *Helleria brevicornis* Ebner, 1868. Some authors sought to include these genera in different families. Thereby, VERHOEFF (1938) regards them as two separate families: Tylidae and Sypastidae. VANDEL (1960), in his volume *Isopodes terrestres* from the series *Faune de France*, considers the two genera in different subfamilies, Tylinae and Hellerinae, both included within the family Tylidae.

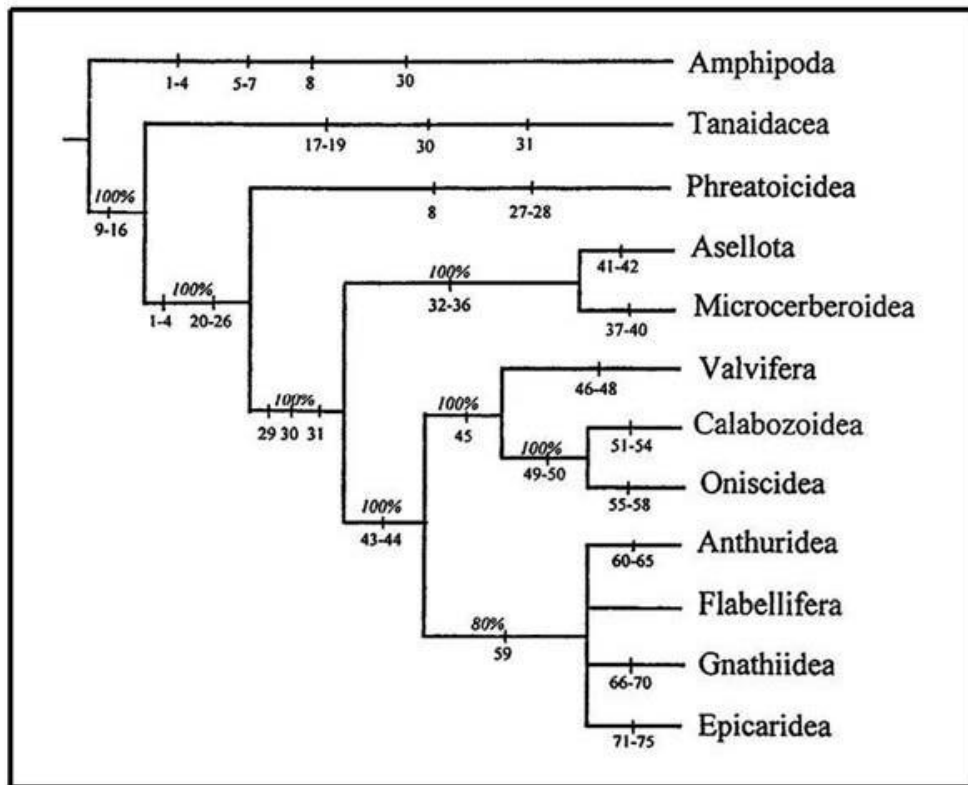


Fig. 2. Cladogram depicting the phylogenetic relationships of the major groups of the order Isopoda, using the 50 % Majority Rule algorithm on a matrix of 75 morphologic characters. The numbers on the cladogram belong to the morphologic traits in the matrix; additionally are displayed the percentage of contribution for each morphologic trait to the proposed cladistic solution (from TABACARU & DANIELOPOL 1999).

Regarding the place of the Tyliidae in the classification of Oniscidea, VANDEL (1943) maintains they are close to the suborder Valvifera, and especially to the Idoteidae and argues for the existence of two distinct phyletic lineages: Tylian Series or Tylomorpha and Ligian Series or Ligiamorpha.

GRUNER (1965) viewed Tyloidea and Ligioidea as apart within the suborder Oniscidea or, completely separating the Tyliidae, as the suborder Tyloidea and the suborder Oniscidea (GRUNER, 1969). KUSSAKIN (1982) also regards Tyloidea as a suborder apart.

In subsequent classifications, BOWMAN & ABELE (1982), HOLDICH & AL. (1984), BRUSCA & WILSON, 1991, WARBURG, 1993, TABACARU & DANIELOPOL, 1996, ROMAN & DALENS, 1999, agreed to consider two infraorders within the suborder Oniscidea: Tylomorpha Vandel, 1943 and Ligiamorpha Vandel, 1943.

In 1981, Vandel stated the two genera *Tylos* and *Helleria* belong to the suborder Valvifera.

WÄGELE (1989) endorses the monophyly of Oniscidea and considers that the origin of the Tylidae is not within the Valvifera. But, in his opinion, the family Tylidae is the sister-group of the family Mesoniscidae and this group, in its turn, is the sister-group of the family Ligiidae, forming the group Diplocheta. We note, however, that Diplocheta Vandel, 1957 was established for Oniscidea with two genital apophyses while the Tylidae have no genital apophysis.

SCHMALFUSS (1974, 1989) argued through numerous characters for the inclusion of the Tylidae within the Oniscidea and not within Valvifera. However, Schmalfuss includes the Tylidae within the Crinocheta and close to the Actaecidae. But he specifies this is a working hypothesis and that the problem remains open for subsequent studies. Starting from the analysis of this hypothesis, ERHARD (1995A) demonstrated that the Tylidae do not belong to the Crinocheta and the similarities between *Tylos* and *Actaecia* are convergences due to the conglobation mechanism. Also, according to Erhard, the sister-group relationship between the Mesoniscidae and the Tylidae - the hypothesis sustained by Wägele – has no valid basis.

Through a detailed analysis of the characters of the monophyletic groups belonging to the Oniscidea, ERHARD (1997) distinguishes within the Oniscidea, three basal groups, respectively Ligiidae, Tylidae and the monophyletic group Mesoniscidae + Synocheta + Crinocheta for which TABACARU & DANIELOPOL (1996A) gave the name Orthogonopoda. ERHARD (1996, 1997) considers the Tylidae as the sister-group of the Orthogonopoda, forming the group he subsequently named Holoverticata (ERHARD, 1998).

It was asserted (DIMITROU & ALL., 2019) that TABACARU & DANIELOPOL (1996A) support the hypothesis of a closer relationship between the Tylidae and the aquatic ancestor than the rest of the Oniscidea and that this hypothesis is based on a single morphologic character (coxal plates clearly distinct from the tergites).

First, we have to point out that Tabacaru & Danielopol did not state in any paper that the Tylidae are the closest to the aquatic ancestor. Of contrary, TABACARU & DANIELOPOL (1996, p. 75) clearly maintain: “*The Diplocheta (Ligiidae) are the most primitive among the Ligiamorpha; it can even be said that this section represents the most primitive type of the terrestrial isopods*”. Further on, at the conclusions, TABACARU & DANIELOPOL (1996, p. 78) state: “*Diplocheta (Ligiidae), the most primitive of the Ligiamorpha, display many plesiomorphic traits; they must be very close to the common ancestor of the lineage and, in the same time, the ancestor of all Oniscidea*”.

Of course, the presence of clearly distinct coxal plates on the pereionites 2–7 in Tylomorpha, represents a significant plesiomorphic trait and, as a consequence, we regard its disappearance as a synapomorphic trait of all the other Oniscidea, respectively the Ligiamorpha. In Ligiamorpha, the coxal plates are completely fused with the tergites or, at most, their joining is marked by a fusion line.

It must be specified the Tylidae are remarkable by many autapomorphic traits pointed out by EBNER, 1868; VERHOEFF, 1949; VANDEL, 1960; MEAD, 1963, 1965; SCHMALFUSS & FERRARA, 1978; HOESE, 1983; LEWIS, 1991; SCHMALFUSS & VERGARA, 2000.

The apomorphic traits are: male genital apophysis absent; rudimentary pleopode I (endopodite missing at both sexes, the exopodite present only at the males of *T. spinulatus* and *T. chilensis*). These two reductive characters imply a decrease in the specific diversity.

In the same time, there are numerous autapomorphic traits in the Tylidae linked to the transition to a terrestrial environment: pleopode-exopodites ventrally with lungs; conglobation ability (within the Oniscidea, this character appears convergent at the Buddelundiellidae and some Crinocheta); antennule reduced to 1 article; uropod-protopodite plate-like and laterally inserted on the pleotelson and ventrally folded forming opercula closing an anal region; uropod-exopodite completely reduced; brood pouch prolonged by an internal sack.

In our opinion, all these remarkable traits point to an isolated position of the Tylidae and an early separation from the Ligiamorpha series. As we see it, two distinct lineages evolved from the ancestor of the Oniscidea: 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.

5. THE ORIGIN AND THE MONOPHYLY OF THE ORTHOGONOPODA GROUP

SCHMALFUSS (1989) grouped for the first time Mesoniscidae + Synocheta + Crinocheta based on the derived character diminution and retraction of uropod-endopodite. In the same time, he suggested the name Section Microcheta for the family Mesoniscidae.

For the group Synocheta + Microcheta + Crinocheta, in opposition with Diplocheta (Ligiidae), TABACARU (1994, p. 51) based on the cladistics analysis obtained in collaboration with Danielopol, pointed the following common characters:

- disparition of the fossa occipitalis;
- disparition of the squama, the rudimentary exopodite of the antenna;
- reduction of the number of ommatidia;
- genital apophyses joined (Microcheta) or even fused in a single apophys (Synocheta și Crinocheta);
- endopodite of pleopode 2 male perpendicularly articulated on the basipodite without forming an angle between the first and the second article;
- uropodal endopodite with a tendency to reduce and retract and inserting on the medial side of the protopodite, more proximally than the exopodite (SCHMALFUSS, 1989).

In the cladistics analysis made by TABACARU & DANIELOPOL (1996A) the last three characters are regarded as the autapomorphies defining the group Microcheta + Synocheta + Crinocheta for which the name Orthogonopoda is

proposed. The essential character of this group is the autapomorphy regarding the conformation of the endopodite of pleopode 2 male in the evolution of the copulatory apparatus. According to the cladistics analysis presented by TABACARU & DANIELOPOL (1996 A & B) Orthogonopoda represents the evolved sister-group of Diplocheta.

ERHARD (1995A) illustrated the linear conformation of the endopodite of pleopode 2 male and showed the importance of this character as a synapomorphy of the group Mesoniscidae, Synocheta and Crinocheta. In his papers ERHARD (1995B, 1996, 1997, 1998) argues for the monophyly of Orthogonopoda but in his opinion the Tylidae represent the sister-group of this monophylum. As such, he endorses the hypothesis of the monophyly of all non-Ligiidae Oniscidea.

In our opinion, the differences between the Tylidae and Orthogonopoda are too great to be able to assume they come from a common ancestor. The sole characters common for the Tylidae and Orthogonopoda are the disparition of the fossa occipitalis (a rudiment of the maxillipedal segment) and the disparition of the squama (a rudiment of the exopodite). We note, however, that this means the disparition of two ancestral characters and we see their disparition at the Tylidae and Orthogonopoda not as a synapomorphy but it resulted in a convergent way.

According to the hypothesis we support, the Diplocheta and Orthogonopoda originate in a common ancestor close to the common ancestor of all Oniscidea while the Tylomorpha, following an early split, drifted far from this common ancestor. The common ancestor of the Oniscidea had, as the majority of the marine Isopoda, two genital apophyses as it is still the case at Diplocheta (Ligiidae) while at Tylomorpha (Tylidae) the genital apophyses disappeared completely and the ejaculatory ducts open by two distinct, distanced apertures.

6. THE POSITION OF THE FAMILY MESONISCIDAE

As we have previously pointed out (TABACARU & GIURGINCA, 2003, 2019), before the revision made by GRUNER & TABACARU (1963), two genera, respectively the genus *Mesoniscus* Carl, 1906 (syn. *Titanethes* pro. part., *Schioedtia* Budde-Lund, 1906 nom. preocc.) with 5 species and the genus *Nematoniscus* Verhoeff, 1930 with 3 species, were included in the family Mesoniscidae. After studying the holotypes and a very rich material, including specimens from the *locus typicus* caves, GRUNER & TABACARU (1963) established a sole genus, *Mesoniscus*, with two species *Mesoniscus alpicola* (Heller, 1858) (syn. *Titanethes alpicola* Heller, 1858, *M. cavicolus* Carl, 1906, *M. calcivagus* Verhoeff, 1914, *M. subteraneus* Verhoeff, 1914) and *Mesoniscus graniger* (Frivaldsky, 1865) (syn. *Titanethes graniger* Frivaldsky, 1865, *Trichoniscus penjanus* Verhoeff, 1901, *Nematoniscus prenjanus* Verhoeff, 1901, *N. triangulifer* Verhoeff, 19030, *N. illyricus* Verhoeff, 1933, *Mesoniscus histrianorum* Arcangeli, 1939, *Mesoniscus alpicola vulgaris* Chappuis, 1944, *M. alpicola meridionalis* Chappuis, 1944).

Initially, the family Mesoniscidae Verhoeff, 1908 was established by K.W. Verhoeff as a subfamily of the family Trichoniscidae for the genus *Mesoniscus* Carl, 1906. VERHOEFF (1908, p. 196) included within the family Trichoniscidae four subfamilies: 1. Subfam. Trichoniscinae (*Trichoniscus*, *Trichoniscoides*, *Androniscus*); 2. Subfam. Mesoniscinae (*Mesoniscus*); 3. Subfam. Haplophthalminae (*Haplophthalmus*); 4. Subfam. Cyphoniscellinae (*Cyphoniscellus*, *Pleurocyphoniscus*, *Leucocyphoniscus*). Subsequently, Verhoeff (1914) maintained that *Mesoniscus* is closely related with the Trichoniscidae.

In the same time, RACOVITZA (1908) includes the genus *Schioedtia* Budde-Lund, besides the genus *Trichoniscus*, in the section Trichonisci, subfamily Trichoniscinae but asserting the genus is insufficiently known in order to pinpoint its position.

It is easy to explain why initially the genus *Mesoniscus* was included within the Trichoniscidae as the body conformation and the structure of the buccal apparatus are similar. As VANDEL (1960) has emphasized, it was RACOVITZA (1907, 1908) who clearly pointed out the importance of the first two pairs of male pleopodes in the systematics of the terrestrial isopods.

In 1930, Verhoeff elevates the subfamily to the rank of family and in the classification of the terrestrial isopods (VERHOEFF, 1938) he includes the family Mesoniscidae, together with the family Ligiidae, in the group named *Protophora archaica*.

A. VANDEL (1943, 1945, 1952), just like Verhoeff, groups the Mesoniscidae together with the Ligiidae but replaces the name of *Protophora archaica* with *Protoniscoidea*. In 1957, VANDEL suggests the name *Diplocheta* for the oniscids with two distinct genital apophyses (Ligiidae). Although in the same paper, Vandel argues for an intermediary position of the Mesoniscidae between the Ligiidae and the Trichoniscidae, he includes the Mesoniscidae together with the Ligiidae, within the *Diplocheta* (VANDEL, 1960). Following the classification of Vandel, other authors include the Mesoniscidae beside the Ligiidae within *Diplocheta* Vandel, 1957, a group regarded as a Cohors (GRUNER, 1965; STROUHAL, 1968) or as a Section (BOWMAN & ABELE, 1982; HOLDICH ET AL., 1984; MARTIN & DAVIS, 2001).

Wägele (1989), however, maintains that *Diplocheta* Vandel, 1957 contains the family Ligiidae Leach, 1814 but also the family Mesoniscidae Verhoeff, 1908 with the family Tylidae Milne-Edwards, 1840. He asserts that the Tylidae and the Mesoniscidae have reduced genital papillae and the first pair of pleopodes shortened in comparison with the second pair of pleopodes. We have to point out that the Tylidae have no genital papillae and the first pair of pleopodes at the Mesoniscidae are not reduced. The differential characters between the Tylidae and the Mesoniscidae are so obvious, we cannot see any link between the disappearance of the genital apophyses in the Tylidae and the reduction in length of the genital apophyses in the Mesoniscidae. In our opinion, they are two characters evolved independently and they can be regarded as autapomorphies of the two groups.

In his classification, SCHMALFUSS (1989) considers the Mesoniscidae closer to the group Synocheta and Crinocheta than to the Diplocheta. He suggests including the Mesoniscidae in a separate section with the name Microcheta. Subsequent studies, confirmed this hypothesis and argued for the existence of the monophylum Orthogonopoda (Microcheta + Synocheta + Crinocheta). We have pointed out in the previous paper (TABACARU & GIURGINCA, 2019) the autapomorphies supporting the inclusion of the genus *Mesoniscus* in a separate family and a Section apart, namely Microcheta Schmalfluss, 1989.

As Orthogonopoda is well supported, the question is whether within it, Microcheta and Synocheta form a sister-group or if Synocheta and Crinocheta are a sister-group. WÄGELE (1989), SCHMALFUSS (1989), ERHARD (1995, 1996, 1997) and SCHMIDT (2008) regard Synocheta + Crinocheta as sister-groups. For this group, ERHARD (1998) reintroduces the name Eunisicoidea Vandel, 1943.

Vandel introduced the name Eunisicoidea for Synocheta + Crinocheta in opposition with the name Protonisicoidea for the Ligiidae + Mesoniscidae. But from Vandel's dendrograms (VANDEL, 1943, 1945, 1957) it is obvious that those names have not been conceived for monophyletic groups, as we conceive today a monophyletic group.

As we have pointed out (TABACARU & GIURGINCA, 2019), VANDEL (1957), in a paper on the traits and the origins of the different types of genital apophyses within the isopoda, argues that the genus *Mesoniscus* has an intermediary position between the Ligiidae and the Trichoniscidae. He underlines that Carl himself (CARL, 1906), defining the genus *Mesoniscus*, asserted this genus is closer to *Ligidium* by certain characters and closer to the Trichoniscidae by other characters. In Vandel's opinion, if *Mesoniscus* is probably not the ancestor of the Trichoniscidae, it provides an excellent image of it. Vandel maintains that the genital apophysis of the Trichoniscidae derived from *Mesoniscus* and has no relation with the genital apophysis from the superior Onisicoidea (Crinocheta). In his opinion, the genital apophysis from Crinocheta represents a slightly modified structure in comparison with the twin genital apophysis of the Ligiidae, a fact obvious at the Halophilosciinae.

In his study on the genus *Mesoniscus*, ERHARD (1997, p. 5) says: "The unpaired genital papilla from *Mesoniscus* seems completely merged from a ventral point of view, however, dorsally, there is a separation line, proving its origin from two initially paired papillae". Erhard concludes that this state can be regarded as a preliminary stage of the completely fused papilla from the Synocheta and Crinocheta. As such, it is clear that Erhard also, regards the structure of the genital apophysis from *Mesoniscus* as an intermediary between the conformation with two genital apophyses as present at the Ligiidae and the conformation from Synocheta and Crinocheta. The unitary conformation of the genital apophysis of *Mesoniscus* is clearly illustrated by Erhard in the photograph Abb. 3. pag. 7. Doesn't this also argue for the hypothesis that the sister group of Orthogonopoda are the Diplocheta and not the Tylidae who have no genital apophyses at all?

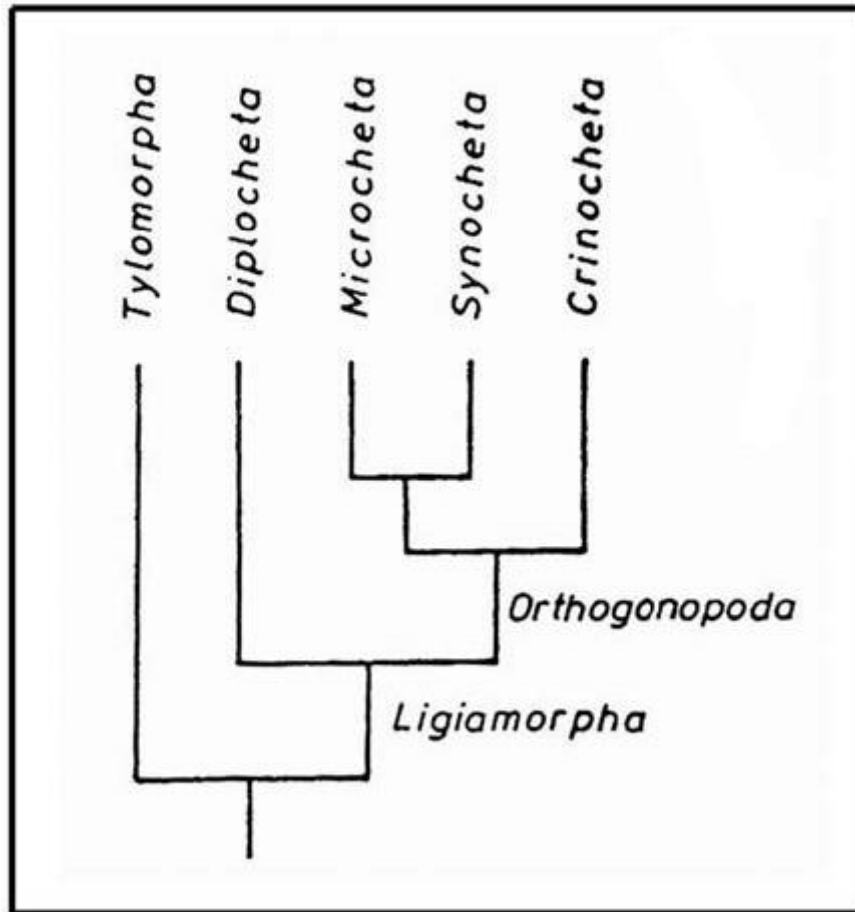


Fig. 3. Cladogram depicting the phylogeny of the Suborder Oniscidea as proposed by Tabacaru and Danielopol (from TABACARU & DANIELOPOL 1996).

We have argued (TABACARU & DANIELOPOL, 1996a, b; TABACARU & GIURGINCA, 2001, 2014) the sister-group relationship between the Mesoniscidae and the Synocheta based on numerous characters (Fig. 3). In the first place, we have to point that the Microcheta + Synocheta group retains the plesiomorphic characters that disappear in Crinocheta: mandibles with pars molaris; inner endite of the maxillula with three penicilla; dorsal side of the epipodites of pleopode 1 with scale belonging to the water-conducting system; stomach with superomedianum. As we have argued (TABACARU & GIURGINCA, 2019), the Microcheta + Synocheta sister-group presents the synapomorphies: a sole spermatophore resulting from the joining of two spermatophores (Microcheta) or from the fusion of the two vasa deferentia (Synocheta); visual apparatus reduced at most to three ommatidia; the claw of the pereopods is simple and unpaired, without a secondary claw.

In addition, at *Mesoniscus*, as at the basal forms of the Trichoniscidae from the tribe Typhlotricholigioidini (*Brakenridgia*, *Cantabroniscus*), the first pair of pleopodes have no sexual modifications. Also, *Mesoniscus*, as all Synocheta, presents an open water-conducting system of the “typ *Ligia*” (HOESE, 1982) featuring parallel, longitudinal rows of scales on the caudal side of pereopode 6 (excepting the basipodite) and on the rostral face of pereopode 7 (at least on the basipodite).

The Crinocheta are highly different from the Microcheta + Synocheta group by numerous autapomorphies clearly underlined by SCHMIDT (2002, 2008).

7. CONCLUSIONS

1. The family Ligiidae, both *Ligia* and *Ligidium* (including the closely related genera), present the morphological characters supporting the monophyly of the suborder Oniscidea and, in our opinion, it is highly unlikely that all those characters are convergences; a separation of the genus *Ligia* or of the entire family Ligiidae into a different suborder is unsupported by morphological characters.

2. The family Tylidae present remarkable autapomorphies clearly dividing them from all other Oniscidea, as a consequence it is difficult to assume that the monophylum Orthogonopoda evolved from a common ancestor with the Tylidae; it is more likely the Orthogonopoda originated from a more basal ancestor shared with the present-day Ligiidae.

3. Microcheta (Mesoniscidae) presents the autapomorphies of the monophylum Orthogonopoda but it represents the most basal group within this monophylum and form the sister-group of Synocheta, while Crinocheta diverge by many characters from all the other Oniscidea.

4. Two lineages evolved from the common ancestor of all Oniscidea: Tylomorpha represented by the present-day family Tylidae (distinguished by the disappearance of the genital apophyses and distanced genital openings) and Ligiamorpha represented by the family Ligiidae, which is close to the common ancestor (with two genital apophyses) and the monophylum Orthogonopoda (which evolved toward the merging of the two genital apophyses).

Acknowledgments: The authors are grateful to Prof. Dr. D.L. Danielopol (Karl-Franzens Universität, Nawi Graz Geocenter, Austria) for his suggestions in revising the paper.

Our study has been undertaken within the framework of Program I, project 1 of the “Emile Racovitza” Institute of Speleology of the Romanian Academy.

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