

CONTRIBUTIONS TO THE STUDY OF THE TRICHONISCIDAE (ISOPODA, ONISCIDEA). I. DEFINITION AND TAXONOMIC POSITION

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Abstract. In this first note, we present the taxonomic position and the differential diagnosis of the family Trichoniscidae. In our opinion from the common ancestor of Oniscidea two lineages evolved: a lineage evolved toward the complete disappearance of the genital apophyses leaving only two separated male genital openings (Infraorder Tylomorpha) while the other lineage evolved toward merging the two genital apophyses up to the fusion of the ejaculatory ducts and a single genital opening (Infraorder Ligiamorpha). Within Ligiamorpha, the family Trichoniscidae is included in Suprasection Orthogonopoda, Section Synocheta. We argue for the sister group relationship of Section Synocheta with Microcheta (Mesoniscidae) and not with Crinocheta, the most evolved group among the terrestrial Isopods.

Key words: Isopoda, Oniscidea, Orthogonopoda, Synocheta, Trichoniscidae, taxonomic position, definition.

1. INTRODUCTION

EMIL RACOVITZA, the founder, one hundred years ago, of the Institute of Speleology bearing his name, is a renowned explorer of the Antarctic fauna and father of Biospeleology but also a forerunner of the phylogenetic systematics.

EMIL RACOVITZA pointed since 1910 how to study the characters of the species: «It is necessary to study the taxonomic characters of the group from the point of view of their history and their phylogenetic significance to reach an exact understanding of their classification... It is necessary to study the particular history of each character». He stated very clearly the aim of the taxonomic research: «The main purpose of taxonomic studies, the sole interesting me anyway, is, in my opinion, the natural classification of the animals, that is a classification mirroring as exactly as possible the real kinship of the various animal lineages. Seen in this way, the taxonomy becomes one of the branches of general biology, as it provides the material for the study of the laws and the ways of evolution» (1912: p. 204). RACOVITZA remarked the important role of isolation in evolution and offered a precise definition of the

species concept (1912, p. 208): «For there to be a subdivision of lineages, so speciation, a certain isolation is essential but sufficient. The morphological differentiation is an obligatory continuation of isolation. A colony which is isolated, evolving from now on independent from others, is a new factor that is introduced into the history of the globe. These premises once admitted, the conclusion will be that the definition of the species as a taxonomic unit cannot be anything else but «An isolated colony of individuals sharing the same descent».

We can say RACOVITZA provided a new definition of Taxonomy based on phylogenetics: «This incursion in Taxonomy...gave me the conviction that there is no other possible Taxonomy but that based on phylogeny and geographical repartition, that it is impossible to correctly place a species within the classification of beings without knowing its origin in time and its extension in space. *Taxonomy cannot be anything but applied phylogeny*» (1926a, p. 42-43).

In his zoological researches, EMIL RACOVITZA was preoccupied especially by the study of the Isopoda, both aquatic (1904, 1910, 1912, 1950) and terrestrial ones (1907, 1908). His researches have been so thorough that even today it can be stated (SCHMIDT, 2008): “The description of the relative position of parts and appendages follows RACOVITZA (1923) ...”

The exceptional value of the isopodological studies of Emile Racovitza was emphasized many times by renowned isopodologists like RAGNAR WAHRBERG (1922-1924, pp. 24 & 65), ALCESTE ARCANGELI (1942, p.175-176), ALBERT VANDEL (1960, p. 10), HANS STROUHAL (1963, p.157), JEAN-PAUL HENRY (1976), JOHANN-WOLFGANG WÄGELE (1989, p. 1). In the volume terrestrial Isopods from the series Faune de France, the French scientist ALBERT VANDEL (1960, p. 10) said: “Ce sont les deux mémoires de E. G. Racovitza (1907, 1908) consacrés à l'étude des premières récoltes de *Biospeologica* qui ouvrent une ère nouvelle de l'isopodologie, en décrivant, pour la première fois, de façon précise, la structure des *Trichoniscidae*, et en soulignant l'importance systématique des deux premières paires de pléopodes mâles pour la distinction des genres et des espèces.”

Regarding the Trichoniscidae, we can state with certainty their systematic study owes to Racovitza the fundamental premises. At the centenary of Emile Racovitza birth, VANDEL (1970, p. 146) stated: “Ce n'est pas tant le nombre considérable d'espèces nouvelles qu'il a décrites au cours de sa carrière d'isopodologue qui représente la véritable valeur de son oeuvre, mais la clarté qu'il a portée dans la systématique de cet ordre de Crustacés. C'est le cas, en particulier, pour la famille des *Trichoniscidae*, dont on peut dire que la classification était inexistante avant les deux mémoires classiques qu'il a publiés en 1907 et en 1908”.

The Trichoniscidae represent one of the most numerous terrestrial Isopods family. Synthetizing the current data (SCHMALFUSS, 2003, 2004; SCHMIDT & LEISTIKOW, 2004; SFENTHOURAKIS & TAITI, 2015; KARAMAN & HORVATOVIČ, 2018, TAITI ET AL., 2018; BEDEK, GOTTSTEIN, TAITI, 2019; CIFUENTES, 2019), we consider 85 genera and 500 species as belonging to this family. We did not include the genera *Buddelundiella*, *Borutzkyella* and *Pseudobuddelundiella* since we consider

them as part of the family Buddelundiellidae; also, we did not include the genus *Cylindroniscus* as it found to belong to the family Styloniscidae (CAMPOS-FILHO *ET AL.*, 2017), *Utopioniscus* synonymous with *Alpioniscus* (TAITI *ET AL.*, 2018). But we consider as valid the genera *Stylohylea*, *Tachysoniscus*.

As we have already pointed out (TABACARU, 1994), the Trichoniscidae and, in general, the group they belong to, respectively Synocheta, inhabit especially humid biotopes and are frequently found in caves. Following MANICASTRI & ARGANO (1989), 80% of the cave-dwelling terrestrial Isopoda belong to the section Synocheta (74% Trichoniscidae, 2% Buddelundiellidae, 4% Styloniscidae). In Romania (TABACARU & GIURGINCA, 2013), 15 species of Oniscidea can be considered as strictly troglobitic, 12 of them belonging to the family Trichoniscidae.

However, we have to note that some specialists do not regard the Trichoniscidae as a monophyletic group. J.-W. WÄGELE (1989) writes the Trichoniscidae with quotation marks since he regards the family as “nicht-monophyletischen Sammelgruppen”, while SCHMALFUSS (2005) maintained about the family Trichoniscidae: “however, will certainly turn out to be paraphyletic and therefore will have to be split up in a number of separate families”. We do not share the opinion the Trichoniscidae are a paraphyletic group. As defined by W. HENNIG (1982), a paraphyletic group reunites elements with a common ancestor but does not include all the descendants of that ancestor. In the case of a paraphyletic group, the problem is to include all the descendants of the common ancestor in order to become a monophyletic group. The problem of splitting in a series of monophyletic groups comes up in the case of a polyphyletic group, so a group based on convergences and reuniting elements lacking a common ancestor. We do not think this is the case of the family Trichoniscidae.

In the classification we use here, the family Trichoniscidae Sars, 1899 belongs to: Order Isopoda Latreille, 1817, Suborder Oniscidea Latreille, 1802, Infraorder Ligiamorpha Vandel, 1943, Supersection Orthogonopoda Tabacaru & Danielopol, 1996, Section Synocheta Legrand, 1946.

2. ORDER ISOPODA-TAXONOMIC POSITION, SYSTEMATICS

Isopods represent one of the most numerous and diversified groups of the Class Malacostraca Latreille, 1806 (Subclass Eumalacostraca Grobben, 1892, Superorder Peracarida Calman, 1904). Usually, Isopoda is considered an order, rarely a suborder (SCHRAM, 1986) or a superorder (WATLING, 1999). The high diversity of this order is obvious both in its morphology and in its ecology. The majority of authors consider the Isopoda as a monophyletic group. However, ROMAN & DALENS (1999) in the chapter Isopoda from the Grassé *Traité de Zoologie*, consider the monophyly of Isopoda as debatable taking into account the original characters present in several suborders (Anthuridea, Gnathidea, Phreatoicidea).

In the present, we can say the monophyly of the Isopoda is unanimously accepted and was well demonstrated through numerous characters (see TABACARU

& DANIELOPOL, 2012). But the sister-group of the Isopoda, as WILSON (2009) has pointed out, is still a controversial proposition.

Numerous authors offered various opinions regarding the position of the Isopoda (TABACARU & DANIELOPOL, 2011 & 2012).

The relationship of the Isopoda with the other orders of the Peracarida represented a long debated problem. The question was if the Tanaidacea or the Amphipoda represent the closest group to the Isopoda. Firstly, the Tanaidacea have been grouped together with the Isopoda and, in 1895, HANSEN defined the Order Tanaidacea. SIEWING (1963) argued amply for a sister-group relationship between the Isopoda and the Tanaidacea. Other authors, among which Haeckel, Perrier, Hertwig, considered the Amphipoda as the closest group to the Isopoda. This hypothesis was argued especially by REIBISCH in *Kukental-Handbuch der Zoologie* (1926-1927).

Concerning the order Isopoda, the paper about the phylogeny of the Malacostraca, published by TABACARU & DANIELOPOL (2011, 2012) argues against a sister-group relationship between Amphipoda and Isopoda and, following a cladistics analysis, the authors argue for a sister-group relationship between Isopoda and the ensemble Spelaeogriphacea+(Cumacea+Tanaidacea).

As for the division of the order Isopoda, MARTIN & DAVIS (2001) in their synthesis paper *AN UPDATED CLASSIFICATION OF THE RECENT CRUSTACEA* consider the suborders: Phreatoicoidea Stebing, 1893, Anthuridea Monod, 1922, Microcerberoidea Lang, 1961, Flabelifera Sars, 1882, Asellota Latreille, 1802, Calabozoidea Van Lieshout, 1983, Valvifera Sars, 1882, Epicaridea Latreille, 1831 and Oniscidea Latreille, 1802. The classic treaties also include a suborder Gnathiidea Hansen, 1916, subsequently included by some authors within Flabelifera. But, we have to specify that the phylogeny and, so, implicitly, the classification of Isopoda is still under debate, especially based on cladistics analyses (SCHMALFUSS, 1989; WÄGELE, 1989; BRUSCA & WILSON, 1991; TABACARU & DANIELOPOL, 1999; BRANDT & POORE, 2003; WILSON, 2008, 2009; POORE & BRUCE, 2012). At present, the following suborders are considered: Phreatoicoidea, Asellota, Microcerberoidea, Calabozoida, Oniscidea, Spheromatidea Wägele, 1989, Cymothoidea Wägele, 1989, Limnoriida Brandt & Poore, 2002, Phoratopidea Brandt & Poore, 2003.

3. SUBORDER ONISCIDEA-MONOPHYLY, PROBLEMS ABOUT THE SUBORDERS' DIVISIONS

Within the order Isopoda, the suborder Oniscidea has a special importance due to the high number of species (over 3700 species, 500 genera belonging to 37 families-after SCHMALFUSS, 2003, 2004, SFENTHOURAKIS & TAITI, 2015) but also due to the fact it is the sole crustacean group that conquered the terrestrial environment starting from a marine ancestor. Oniscidea inhabit terrestrial environments from high-humidity ones to arid regions (TAITI, 2017). Fossil Oniscidea and biogeographic data argue for very old group with a pre-Pangean origin in the Late

Paleozoic most likely during the Carboniferous (BROLY *ET AL.*, 2013; BROLY *ET AL.*, 2015).

At present, the majority of authors regard Oniscidea as a monophyletic group including five monophyletic groups: Tylidae, Ligiidae, Mesoniscidae, Synocheta and Crinocheta. We have to note that ALBERT VANDEL, one of the great specialists in this group, maintained in many papers that Oniscidea is a polyphyletic group. From 1943, VANDEL considered the Tylidae as related with the suborder Valvifera while the other terrestrial Isopoda as originating in the suborder Flabelifera. The family Tylidae contains only two genera, respectively *Tylos* Latreille with 20 halophilic species (SCHMALFUSS & VERGARA, 2000), spread on sea shores and *Helleria* Ebner with a sole species, a Tyrrhenian relict living in forest humus. Starting from this idea, VANDEL considers two different phyletic lineages within the suborder Oniscidea, lineages named by him Tylian Series and Ligian Series. In 1981, VANDEL maintains that the Tylidae should be included in the Valvifera beside the Idoteidae. Subsequently, by describing an aquatic trichoniscid, *Cantabroniscus primitivus* Vandel, 1965, he reaches the conclusion the Trichoniscidae and the entire group they belong to, the Synocheta, represent a third phyletic lineage that evolved independently from the aquatic to the terrestrial environment.

Thus, after VANDEL, the terrestrial Isopods represent a polyphyletic group because the transit from an aquatic to a terrestrial lifestyle, took place through three independent, phyletic lineages with different origins: Tylian Series, Ligian Series and Trichoniscian Series.

Supporting the monophyly of the terrestrial Isopods, SCHMALFUSS (1974, 1989) argued that *Tylos* is obviously related with *Ligia*, respectively with Oniscidea and not with *Mesidotea*, respectively Valvifera. Also, TABACARU & DANIELOPOL (1996A, B, 1999) do not share (as erroneously stated by SCHMIDT, 2008, p. 202) the hypothesis sustained by Vandel of a diphyletic origin of the terrestrial Isopoda but, of contrary, argue for the monophyly of Oniscidea.

The conformation and position of the uropods is the most important character that led to considering a link between the Tylidae and the Valvifera. The uropods have a widened (plate-like) protopodite and are inserted laterally on the pleotelson and are ventrally folded. But a comparative study (TABACARU & DANIELOPOL, 1996A, B) between Tylidae species (*Tylos ponticus* Grebinsky and *Helleria brevicornis* Ebner) and species of *Idotea* (Valvifera) showed they are two independent apomorphies with different functions. In Valvifera, the pleotelson is long and shelters the pleopods while the uropods, also elongated, cover the pleopods forming a respiratory chamber; at the Tylidae, the pleotelson is short and shelters only the anal valves, also covered by the uropods, and, together with a transversal septum, divide the anal from the respiratory space.

The problem of an aquatic lifestyle in the section Synocheta was extensively analyzed leading to the conclusion (TABACARU & DANIELOPOL, 1996A, B, TABACARU, 1999) it represents a secondary reversal to the aquatic environment and not a proof

of an independent origin of the Synocheta. This conclusion was confirmed by subsequent studies (SCHMALFUSS, 2005; TAITI & XUE, 2012; SOUZA, FERREIRA, SENNA, 2015).

The monophyly of the suborder Oniscidea and especially its splitting were debated in numerous studies (SCHMALFUSS, 1974, 1989; WÄGELE, 1989; BRUSCA & WILSON, 1991; ERHARD, 1995A, B, 1996, 1997, 1998; TABACARU, 1994, 1999; TABACARU & DANIELOPOL, 1996A, B, 1999; SCHMIDT, 2008; BROLY, DEVILLE, MAILLET, 2013).

In our opinion, the most important characters arguing for the monophyly of the suborder Oniscidea are:

1. The presence of a scale system ensuring the circulation of a liquid on the surface of the body. This complex water-conducting system ensures the moisturizing of the tegument and has an important role in multiple functions: respiration, excretion, thermoregulation. It was discovered by VERHOEFF (1917) who presumed its importance for the shift towards a terrestrial life-style in Isopoda. The system was minutely studied by HOESE (1981, 1982) who distinguished two types of functioning: "Ligia-type" and "Porcellio-type". The Trichoniscidae present the first type, featuring parallel, longitudinal rows of scales on the caudal side of pereopode 6 (excepting the basipodite) and pereopode 7 (at least on the basipodite) absorbing water from the substrate by capillarity.

2. Reduction of the antennules to 1-3 articles. VANDEL (1943, 1960) considers this as the sole character of all the terrestrial Isopods.

3. Mandibles without palpus. This character is found also in the suborders Calabozoidea and Valvifera excepting a single species *Holognathus stewarti* (Filhol) but this is certainly a reversal of the subordinal synapomorphic state (POORE G.C.B, 2001, p. 218).

4. The maxillulae (maxilla II) reduced to a single bilobed piece. The majority of Isopoda, including Calabozoidea, have maxillae formed by three distinct endites.

5. The maxillipeds endite without retinacles. The majority of the aquatic Isopoda, the maxillipeds present retinacles.

6. Endopodite of pleopode 2 male completely changed in a copulatory stylus.

Regarding the relations between the suborder Oniscidea and the other suborders, respectively considering a sister group, the problem is still debated. SCHMALFUSS (1989) in a phylogenetic cladogram, first separates the suborder Asellota and then Oniscidea that becomes in this way a sister group with all the other suborders of Isopoda. WÄGELE (1989) separates firstly the suborder Phreatoicoidea and then considers a sister group Calabozoidea-Asellota while Oniscidea is regarded as a sister group with an ensemble of suborders Valvifera, Anthuridea, Spheromatidea, Cymothoidea. BRUSCA & WILSON (1991) consider Calabozoidea is either a primitive oniscidean or is the sister group of the Oniscidea. A detailed analysis of the species *Calabozoa pellucida* Van Lieshout led to the conclusion (TABACARU & PLATVOET, 2000;

TABACARU & DANIELOPOL, 1999) that Calabozoidea cannot be a sister group of Asellota and that the presence of five free pleonites (the first two being reduced) point to a close relationship with Oniscidea. The conclusion is confirmed by subsequent studies (MESSANA, BARATTI & BENVENUTI, 2002; PREVORČNIK, FERREIRA & SKET, 2012). The statement that in *Calabozoa* the pleonites 1 and 2 are reduced to sternal part (VAN LIESHOUT, 1983) is inexact; the tergal part of the respective pleonites is not visible being covered by pereonite 7.

As we have pointed out, we consider as erroneous the hypothesis sustained by VANDEL about the separate origin of the Tylidae from Valvifera but neither can we agree with the hypothesis of WÄGELE (1989) regarding the Tylidae as a sister group of the Mesoniscidae and, together, with Ligiidae, they form the section Diplocheta. The main character of Diplocheta is the presence of two very close genital apophyses but at the Tylidae the genital apophyses are completely missing and each ductus is opening directly by distant openings. Also, we cannot agree with the hypothesis of SCHMALFUSS (1989) following which the Tylidae are included in the section Crinocheta. We have to note the family Tylidae present none of the important apomorphies that define the Crinocheta.

The Tylidae are the sole group of Oniscidea that keep an important plesiomorphic character namely coxal plates distinct from the tergite. Also, the Tylidae present remarkable autapomorphies clearly separating it from all other groups of Oniscidea demonstrating their early split from the common ancestor of all terrestrial Isopods. Among the most remarkable autapomorphies of the family Tylidae are: male genital papillae absent; rudimentary pleopode 1 at both sexes (endopodite missing at both sexes, the exopodite present only at males of *T. spinulosus* and *T. chilensis* after SCHMALFUSS & VERGARA, 2000); 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; frontal process strongly developed; antennule becomes rudimentary.

Taking into account all these facts, in our opinion (TABACARU & DANIELOPOL, 1996A, B; TABACARU & GIURGINCA, 2014) the monophyletic suborder Oniscidea contains two evolutive lineages, so sister groups with a common origin, and we maintain the division into two infraorders as named by VANDEL: Tylomorpha and Ligiomorpha. The same division is also used by other authors (BOWMAN & ABELE, 1982; HOLDICH *ET AL.*, 1984; BRUSCA & WILSON, 1991; ROMAN & DALENS, 1999; MARTIN & JUHAULT, 1999; GREEN, LEW-TON, POORE in POORE, 2002; NOEL & SECHET, 2007; PÉREZ-SCHULTHEISS, 2009; MARTIN, HOEG, OLESEN, 2014).

SCHMALFUSS (1989), WÄGELE (1989) and ERHARD (1995) do not recognize this division and include the Tylidae either in Crinocheta, in Diplocheta or regard them as a basal group within the series Tylidae+Mesoniscidae+Synocheta + Crinocheta.

4. INFRAORDER LIGIAMORPHA – SUPRASECTION ORTHOGONOPODA

As we have shown, the phyletic series Ligiamorpha is characterized by the fusion of the coxal plates to their respective tergites, sometimes with an obvious fusion line. This character clearly differentiates Ligiamorpha from Tylomorpha which presents distinct coxal plates, articulated to the tergites. In the same time, we note in Ligiamorpha two close genital papillae or even fused while in Tylomorpha there are no genital papillae and there are distant genital ductus openings.

From the Ligiamorpha phyletic lineage, including all Oniscidea except the Tylidae, the most plesiomorphic group, respectively the closest to the common ancestor of Oniscidea, is Diplocheta (the family Ligiidae). This is argued by the plesiomorphic characters of the family that subsequently disappear at all the other groups: the presence of fossa occipitalis marking the fusion line of the maxillipedal segment with the cephalon; antenna with a rudimentary exopodite (squama); the presence of two distinct genital apophyses.

At present, the section Diplocheta includes only the family Ligiidae Leach. This family contains two widespread genera and genera with only one or two species and a restricted spreading: *Ligia* Fabricius (35 species), *Ligidium* Brandt (45 species), *Ligidioides* Wahrberg (1 species), *Typhloligidium* Verhoeff (2 species), *Tauroligidium* Borutzky (1 species), *Caucasoligidium* Borutzky (1 species). *Ligia*, with halophilic species inhabiting sea-shores, represents a transition between ancestral marine forms and completely terrestrial forms and can be considered the prototypal terrestrial isopod (CAREFOOT & TAYLOR, 1995).

WÄGELE (1989) also includes in the section Diplocheta, the family Mesoniscidae but as a sister group with the family Tylidae, while the sister group Mesoniscidae-Tylidae, in his turn, is sister group with the family Ligiidae. But SCHMALFUSS (1989) argues for the first time for a close connection between the Mesoniscidae, Synocheta and Crinocheta. In the same time, he uses for the Mesoniscidae the name Microcheta.

The group Microcheta+Synocheta+Crinocheta, for which the name Suprasection Orthogonopoda Tabacaru & Danielopol, 1996 was introduced, is well defined by numerous synapomorphies (TABACARU, 1994; ERHARD, 1995A, B, 1996, 1997, 1998; TABACARU & DANIELOPOL, 1996 A, B, 1999; TABACARU & GIURGINCA, 2003B; SCHMIDT, 2008; TABACARU & GIURGINCA, 2014). In our opinion, the most important characters are:

1. Endeopodite of pleopode 2 male perpendicularly articulated on the basipodite without forming an angle between the first and the second article.
2. Genital apophyses joined and fused ventrally (Microcheta) or even fused in a single apophysis (Synocheta, Crinocheta).
3. Disparition of the fossa occipitalis. This represents a rudiment of the fusion line of the maxillipedal segment with the cephalon, existing only in Diplocheta.
4. Disparition of the squama, the rudimentary exopodite of the antenna. Squama is present at Diplocheta.
5. Uropodes endopodite inserted on the medial side of the protopodite, more proximally than the exopodite.

After SCHMALFUSS (1989), ERHARD (1996, 1997, 1998) and SCHMIDT (2008) within the monophylum Orthogonopoda, the section Synocheta is the sister group of Crinocheta. For the sister group Synocheta+Crinocheta they use the name Eunoscoidea Vandel, 1943.

We have to note that VANDEL (1957) regards the Mesoniscidae as an intermediary group between the Ligiidae and the Trichoniscidae. Also, according to VANDEL, if the Mesoniscidae are probably not exactly the ancestor of the Trichoniscidae, at least it provides an excellent image of this ancestor. The structure of the genital apophysis of the Trichoniscidae with the vasa deferentia completely fused cannot represent, noted VANDEL, the ultimate level of the genital apophyses fusion (as it is found in Crinocheta) as Synocheta is group more basal than Crinocheta. Since at *Mesoniscus*, as VERHOEFF has pointed out, there is a single spermatophore, VANDEL considers this condition close to the genital apophysis of Synocheta. According to Vandel the genital apophysis of Synocheta is a new formation with no connection with the genital apophysis of Crinocheta and, in conclusion, he sees a *fundamental dichotomy* in the evolution of Oniscidea that *very early* divided Synocheta from Crinocheta.

As we have shown (TABACARU & DANIELOPOL, 1996A, B; TABACARU & GIURGINCA, 2014), within the monophylum Orthogonopoda, the sections Microcheta and Synocheta form a sister group, representing in turn the plesiomorphic sister group of the Crinocheta. Firstly, we have to specify that the sister group Microcheta-Synocheta maintains a series of characters, here plesiomorphic, found at the Tylidae and the Ligiidae but missing in Crinocheta: mandibles with pars molaris; inner endite of the maxillula with three penicilla; stomach with superomedianum; dorsal side of the epipodites of pleopode 1 with scales belonging to the water conducting system.

For the group Microcheta+Synocheta, the name Monospermophora was used (TABACARU & DANIELOPOL, 1996B) and we define it by the following characters:

1. There is a single spermatophore resulting either through the joining of the two spermatophores (Microcheta) or through the fusion of the two vasa deferentia in a single ductus (Synocheta). ERHARD (1996) states the single genital papilla of *Mesoniscus* is ventrally completely fused but dorsally it presents a division proving its origin from initially paired genital papillae. Also, ERHARD points the different causes underlying the single spermatophore: at the Mesoniscidae, the joining of the initially two spermatophores is due to the very short genital papillae with very close gonopores while at Synocheta the single spermatophore results from the fusion of the ejaculatory ducts at least in the distal half of the genital papilla. In our opinion, the main difference is the fact that at Crinocheta the two spermatophores are conducted separately by each of the two endopodites, something inexistent when there is a single spermatophore.

2. Visual apparatus reduced at most to three ommatidia. The Mesoniscidae lack a visual apparatus, while at the Synocheta with a visual apparatus, it is formed either by three ommatidia or by a single, big ommatidia. We have to point out that the visual apparatus of the Tylidae, Ligiidae and Crinocheta is made up by numerous ommatidia (sometimes on the order of hundreds).

3. The claw of the pereopodes is simple, without a secondary claw. SCHMIDT (2008) suggests the inner claw as present in Ligiidae and Tylidae was lost in the stemline of Orthogonopoda and that the inner claw present in most Crinocheta is a new structure. But this hypothesis has no support.

Within the Microcheta-Synocheta, the section Microcheta, respectively the family Mesoniscidae Verhoeff, represents the plesiomorphic group. Following a revision of the family (GRUNER & TABACARU, 1963) based on an extended material, including the types of the species described by Verhoeff, it was established the family contains a single genus, *Mesoniscus* Carl, 1906 with two species: *M. alpicola* (Heller, 1858) and *M. graniger* (Frivaldsky, 1865). The analysis of the material showed that *Nematoniscus* Verhoeff, 1930 is synonymous with the genus *Mesoniscus* Carl, 1906. Also, *M. cavicolus*, *M. calcivagus*, *M. subterraneus* are synonymous with *M. alpicola* while *Nematoniscus prenjanus*, *N. triangulifer*, *N. illyricus* and *Mesoniscus histrianorum* Arcangeli, 1939 are synonymous with *M. graniger*.

The section Microcheta, respectively the family Mesoniscidae, is well defined (GRUNER & TABACARU, 1963; TABACARU & DANIELOPOL, 1996; ERHARDT, 1996, 1998; TABACARU & GIURGINCA, 2003; GIURGINCA, 2005) by a series of apomorphies:

1. Distal article of the antennule reduced and included in the second article;
2. Visual apparatus completely missing;
3. Genital apophyses short and ventrally united while the genital openings and the spermatophores joined;
4. Pleopodes 4 and 5 with trilobed endopodites, with one lobe directed over the protopodite;
5. Stomach with long and narrow superomedianum, surpassing the lateralia while superolateralia presents a fringe of long hairs.

Mesoniscus alpicola has a disjunctive spreading in the Alps, respectively in a restricted limestone region from the Southern-Central Alps and a larger region in the Northern Calcareous Alps; *Mesoniscus graniger* is spread along the entire Carpathian chain, beginning from the Northern Carpathians, the Romanian Carpathians, South-Danube Carpathians and in the Dinarids and the Julian Alps (GIURGINCA, 2003, 2005, 2009).

The section Crinocheta represents the most diversified group of the Oniscidea, including 80% of all the described species of Oniscidea (SCHMIDT, 2008). Concomitantly, Crinocheta comprises the species best adapted to terrestrial life and is defined by numerous apomorphies. SCHMIDT (2008) sums 21 apomorphies arguing for the monophyly of the group but also a clear difference from the other groups of Oniscidea. In the first place, in opposition with the sister group Microcheta-Synocheta, we note the presence of some plesiomorphic characters existing at the Tylidae and the Ligiidae: visual apparatus with a high number of ommatidia and the pereopodes claw is doubled by a robust spine. Among the apomorphies, we note:

1. Mandible without pars molaris;
2. Inner endite of maxillula with only two penicilla;
3. Endopodite of pleopode 1 male with a spermatic channel;

4. Brood pouch with cotyledons;

5. Superomedianum absent while inferolateralia are limited by a strongly chitinized frame and divided into two areas by an oblique bar.

The study of the stomach at all sections of Oniscidea (TABACARU & GIURGINCA, 2003A, B) emphasized the very different structure of the stomach in Crinocheta, so different a comparison is very difficult to draw. We have noted only the most obvious characters of the stomach of the Crinocheta.

The section Crinocheta has a very wide spreading, including after the current data 29 families (SFENTHOURAKIS & TAITI, 2015).

5. SECTION SYNOCHETA – THE FAMILY TRICHONISCIDAE

The section Synocheta is well defined from the other sections of Oniscidea by the genital apophysis with the ejaculatory ducts fused at least in the distal part of the genital apophysis. As a result, there is a single genital opening and a single spermatophore.

In our opinion, two lineages evolved from the common ancestor of the Oniscidea: a lineage evolved toward the complete reduction of the genital apophyses leaving behind two distanced male genital openings while the other lineage evolved toward very close genital apophyses going up to a merging of the ejaculatory ducts and a single genital opening. But the Crinocheta are obviously the most evolved group of Oniscidea from the point of view of their diversification degree and their level of adaptation at the terrestrial life. In some Crinocheta the genital apophysis is forked in the distal part. This was regarded by KESSELYAK and VANDEL as a remainder of the primitive duality, while MACCAGNO and VERHOEFF as a secondary condition due to the coaptation at the endopodites of the first pleopode (VANDEL, 1962). In both cases, the clear difference of the section Crinocheta from the Monospermophora is obvious.

Section Synocheta contains 6 families: Trichoniscidae Sars, 1899 Buddelundiellidae Verhoeff, 1930, Styloniscidae Vandel, 1952, Schoebliidae Verhoeff, 1938, Titaniidae Verhoeff, 1938 and Turanoniscidae Borutzki, 1969.

ALBERT VANDEL (1952) grouped these families in two superfamilies: Superfamily Trichoniscoidea Sars, 1899 with the families Trichoniscidae, Buddelundiellidae and Superfamily Styloniscoidea Vandel, 1952 with the families Styloniscidae, Schoebliidae, Titaniidae, Turanoniscidae.

The two superfamilies (as Vandel has pointed) have a clearly different spreading (TABACARU, 1993). Superfamily Styloniscoidea has a predominant Gondwanan spreading while the Superfamily Trichoniscoidea is spread in the northern hemisphere.

Between the two superfamilies there is a difference in the structure of the muscles of the first pleopode. At Styloniscoidea the muscles of the first pleopode are extremely well developed. This aspect was noted by VANDEL in Styloniscidae and Titaniidae. ERHARDT (1997) verified this character at *Styloniscus magelanicus*

and we could verify this character at *Cordioniscus stebbingi*. But, as ERHARD (1993) has pointed, the other families included within Stytoniscoidea are insufficiently studied and as a result the division into the superfamilies is not clear.

Regarding the Buddelundiellidae, included in the same superfamily with the family Trichoniscidae, we have to note that in the present many authors consider it as synonymous with the family Trichoniscidae. We do not support with this opinion (TABACARU, 1993, TABACARU & GIURGINCA, 2014).

The family Buddelundiellidae contains three genera: *Buddelundiella* Verhoeff, 1930, *Pseudobuddelundiella* Borutzky, 1967 and *Borutzkiella* Tabacaru, 1993. Initially, the genus *Buchnerillo* Verhoeff, 1942 (with three species) was also included in this family. However, there is a consensus (TAITI & FERRARA, 1991, 1996; TABACARU, 1993; SCHMALFUSS, 2003; TAITI, MONTESANTO & VERGAS, 2018) that the characters of *Buchnerillo* do not allow its inclusion in the section Synocheta.

The genus *Pseudobuddelundiella* (with two species) and the genus *Borutzkiella* (with one species) are known from caves from the Caucasus. The genus *Buddelundiella* contains 12 species, one of them, respectively *B. cataractae* is an expansive and synanthropic species, with eyes and slightly pigmented found in numerous disjunctive stations from Europe (FLASAROVA, 1966, TABACARU, 1971, CARUSO & BRISOLESE, 1974, OLIVER, 1981). The other species are troglobitic or endogenous and have very narrow ranges within a restricted areal: South-Eastern France and North-Western Italy (Maritime Alps, Piedmont, Liguria, Tosco-Emilian o Apeninnes), only two species being found outside this areal: *B. sporadica* Schmalzfuss (recorded in a cave from Giura Island-Northern Sporades) and *B. serbani* Tabacaru collected in the endogenous from the south-west of the Southern Carpathians.

The synonymy between Buddelundiellidae and Trichoniscidae is based on the idea that *Buddelundiella* is close to the representatives of the subfamily Haplophthalminae within the framework of the Family Trichoniscidae (VANDEL, 1960, SCHMALFUSS, 1981). A thorough analysis of the species of *Buddelundiella* led us to the conviction that there is no close relation between this genus and the Haplophthalminae and there are differences between the Buddelundiellidae and the Trichoniscidae supporting their consideration as distinct families. This fact can also be seen from the detailed description of *Buddelundiella cataractae* Verhoeff, by MARIE FLASAROVA (1966). In the following, we present the most significant differential characters:

Buddelundiellidae

1. Endoantennal volvational ability;
2. Cephalon with linea frontalis and supraantennalis;
3. Linea supraantennalis medially extended toward clypeus with an edge (crista interantennalis);
4. Weakly developed antennal lobes but posterior to the antennal lobes, the linea frontalis continues on the edge of the cephalon with the lateral lobes;
5. Three ommatidia at the Buddelundiellidae species that present visual apparatus;

6. Primary, in the pereionites ornamentation there is a medial ridge of tubercles (we noted the presence of a medial ridge at *B. cataractae*, *B. voluta*, *B. insubrica*, *B. serbani*);

7. Exopodite of the first pleopode oval-shaped and very narrow in relation with the protopodite width;

8. Widened telson and flattened uropodes protopodites ensure the ability to roll into a ball, leaving outside only the endo- and exopodite of the uropodes.

Trichoniscidae

1. Non conglobation ability;

2. Cephalon without linea frontalis but presenting supraantennalis;

3. Linea supraantennalis is medially curved toward clypeus and there is no crista interantennalis;

4. Well developed antennal lobes but there are no lateral lobes;

5. The visual apparatus formed by a single, big ommatidia at all species of the Haplophthalminae presenting a visual apparatus;

6. At the Haplophthalminae, there is no medial ridge within the ornamentation of the pereionites; only exceptionally at the species *Sanfilippia concii* Brian there is a medial ridge resulting from the merging of the paramedian tubercles;

7. Usually, the exopodite of the first pleopode has a more or less triangular shape, surpassing by half the length of the protopodite;

8. Telson not widened and the uropodes protopodite not flattened.

Acknowledgments: Our study has been undertaken within the framework of Program 1 of the "Emile Racovitza" Institute of Speleology of the Romanian Academy. The translation in English of the quotations from Racovitza belongs to one of us (A.G.).

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