

# THE CLASSIFICATION OF MALACOSTRACA – A RESPONSE TO SCHRAM & KOENEMANN (2021)

**IONEL TABACARU**<sup>(1)</sup>, ANDREI GIURGINCA<sup>(1)</sup>

*Abstract.* The classification of Malacostraca as presented by Schram & Koenemann (2021) is compared with the classification argued by Tabacaru & Danielopol (2011, 2012) and a new framework of the Malacostraca phylogeny and systematics is emphasized.

*Key words:* Crustacea, Malacostraca, revised systematics.

## 1. INTRODUCTION

In their volume “*Evolution and Phylogeny of Pancrustacea. A story of scientific method*”, published in 2021, SCHRAM & KOENEMANN, proposed a new classification of Malacostraca.

However, in 2011 and 2012, TABACARU & DANIELOPOL argued and supported a different classification, which, in our opinion has a stronger support in the characters of the taxa.

## 2. THE CLASSIFICATION OF MALACOSTRACA – METHOD

The phylogenetic analysis provided by TABACARU & DANIELOPOL (2011, 2012) is not a phenetic analysis but a phylogenetic in the sense and the conception of HENNIG (1950, 1965, 1982).

Only characters in a binary state (0–1) were used by TABACARU & DANIELOPOL (2011, 2012) as this coding has several advantages over the character coding represented by multiple character states as VAUPEL KLEIN (2009) has argued. With this aim, 68 morphological characters were cladistically treated using the parsimony programme *Paup* (Phylogenetic Analysis Using Parsimony) version 4.10 developed by SWOFFORD (1998); the complete list of the characters is detailed in TABACARU & DANIELOPOL (2011, 2012).

### 3. CLASSIFICATION OF MALACOSTRACA: DIFFERENCES AND REASONS

The classification SCHRAM & KOENEMANN (2021) proposed:

Subclass **Malacostraca** Latreille, 1806

Infraclass **Phyllocarida** Packard, 1879

Order **Leptostraca** Claus, 1880

Infraclass **Eumalacostraca** Grobben, 1892

Cohort **Caridoida** Hessler, 1983

Superorder **Podophalocarida** Serban, 1970

Order **Bathynellacea** Chappuis, 1915

Superorder **Syncarida** Packard, 1885

Order **Anaspidacea** Calman, 1904

Superorder **Peracarida** Calman, 1904

Order **Lophogastrida** Sars, 1870

Order **Mysida** Boas, 1883

Order **Stygomysida** Tchindonova, 1981

Order **Mictacea** Bowman, Garner, Ilife & Sanders, 1985

Order **Spelaeogriphacea** Gordon, 1957

Order **Cumacea** Kröyer, 1846

Order **Tanaidacea** Hansen, 1895

Order **Thermosbaenacea** Monod, 1927

Order **Amphipoda** Latreille, 1816

Order **Ingolfiella** Lowry and Myers, 2013

Order **Isopoda** Latreille, 1817

Superorder **Eucarida** Calman, 1904

Order **Euphausiacea** Dana, 1852

Order **Decapoda** Latreille, 1802

Cohort Hoplocarida Calman, 1904

Order **Stomatopoda** Latreille, 1817

The classification TABACARU & DANIELOPOL (2012) argued (see Fig. 1):

Class **Malacostraca** Latreille, 1802

Subclass **Phyllocarida** Packard, 1879

Order **Leptostraca** Claus, 1880

Subclass **Eumalacostraca** Grobben, 1892

Infraclass **Podophalocarida** Serban, 1970

Order **Bathynellacea** Chappuis, 1915

Infraclass **Cephalothoracarida** nov. infraclass

Cohort **Hoplocarida** Calman, 1904

Order **Stomatopoda** Latreille, 1817

Cohort **Caridoida** Hessler, 1983

Subcohort **Synneocarida** nov. sous-cohorte

Infracohort **Syncarida** Packard, 1885

Order **Anaspidacea** Calman, 1904

Infracohort **Neocarida** Ax, 1999

Superorder **Perancarida** Siewing, 1958

- Order **Thermosbaenacea** Monod, 1927  
 Superorder **Peracarida** Calman, 1904  
 Order **Mysida** Haworth, 1825  
 Order **Lophogastrida** G.O. Sars, 1870  
 Order **Amphipoda** Latreille, 1816  
 Order **Isopoda** Latreille, 1817  
 Order **Tanaidacea** Dana, 1849  
 Order **Cumacea** Krøyer, 1846  
 Order **Spelaeogriphacea** Gordon, 1957  
 Order **Mictacea** Bowman, Garner, Hessler, Iliffe & Sanders, 1985  
 Order **Bochusacea** Gutu & Iliffe, 1998  
 Sous-cohorte **Eucarida** Calman, 1904  
 Order **Euphausiacea** Dana, 1852  
 Order **Decapoda** Latreille, 1803  
 Order **Amphionidacea** Williamson, 1973

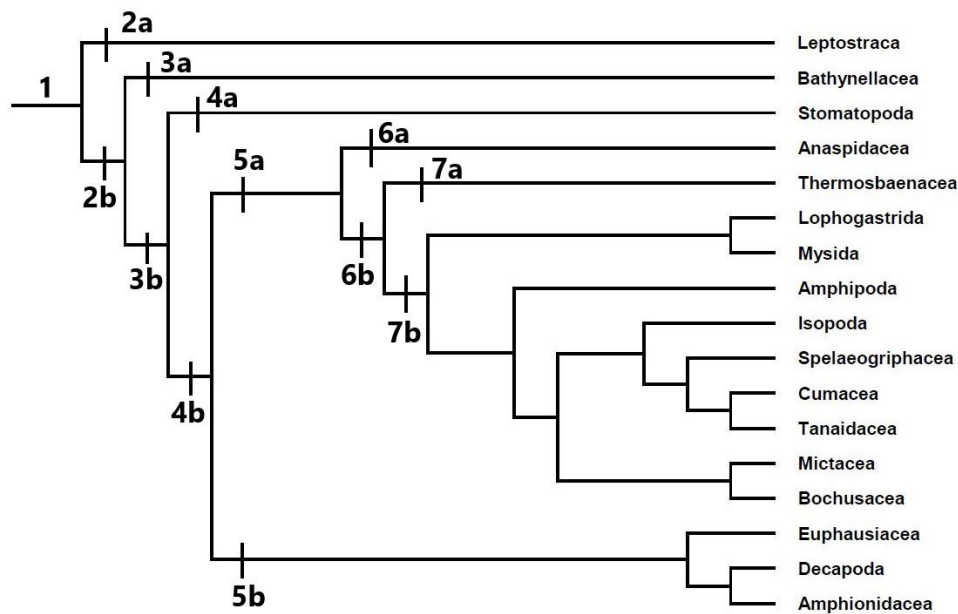


Fig. 1. Main taxonomic units of the Malacostraca, based on a matrix of 68 morphological characters cladistically treated with the parsimony programme *Paup* version 4.10 (the complete list of characters and the matrix is detailed in TABACARU & DANIELOPOL, 2011 & 2012: 1-Class Malacostraca Latreille, 1802; 2a-Subclass Phyllocarida Packard, 1879; 2b-Subclass Eumalacostraca Grobben, 1892; 3a-Infraclass Podophalocarida Serban, 1970; 3b-Infraclass Cephalothoracarida Tabacaru & Danielopol, 2012; 4a-Chohort Hoplocarida Calman, 1904; 4b-Cohorte Caridoida Hessler, 1983; 5a-Subcohort Synneocarida Tabacaru & Danielopol, 2012; 5b-Subcohort Eucarida Calman, 1904; 6a-Infracohort Syncarida Packard, 1885; 6b-Infracohort Neocarida Ax, 1999; 7a-Superorder Pancarida Siewing, 1958; 7b-Superorder Peracarida Calman, 1904 (after TABACARU & DANIELOPOL, 2012).

Differences:

1. SCHRAM & KOENEMANN (2021) considered Malacostraca as Subclass and, as a consequence, Phyllocarida and Eumalacostraca rank as Infraclass.

TABACARU & DANIELOPOL (2011, 2012) considered Malacostraca as Class while Phyllocarida and Eumalacostraca as Subclasses.

As a class, Malacostraca are well defined by two autapomorphies: tagmosis (cephalon with 5-6 somites, one pair of antennules, one pair of antennae, 3 pairs of mouthparts, pereon with 8 somites with thoracopods, pleon with 7 somites bearing except for the 7<sup>th</sup>, pleopods) and the constant position of the gonopores: thoracomeres 6 for the female, and thoracomeres 8 for the male (TABACARU & DANIELOPOL, 2011, 2012).

The monophyly of Malacostraca is confirmed by other studies based on several common morphological characters shared throughout the group and by molecular studies endorsing it.

According to RICHTER & SCHOLTZ (2001) five independent characters support the monophyly of the Malacostraca: (1) constant number of segments, namely eight thoracomeres and seven pleomeres (*as per* CALMAN, 1909); (2) defined position of the genital openings in the sixth thoracomere in females, in the eighth thoracomere in males (in the malacostracan ground pattern, the genital openings are on the coxae in both sexes *as per* CALMAN, 1909); (3) differentiation of the posterior part of the foregut to a proventriculus with oesophagus, stomach chamber and funnel region; (4) major part of the post naupliar germ band derived from a ring of exactly 19 ectoteloblasts (*as per* DOHLE, 1909); (5) biramous first antenna.

A study published by GRAMS *et al.* (2025), based on 207 characters for 35 terminal taxa across all recognized orders and using a multimethod framework including different degrees of implied weighting and one of the first applications of methods recently developed in TNT (with the *xlinks*-command), also considered the monophyly of Malacostraca as strongly supported by its unique body-plan, namely the same two autapomorphies used by TABACARU & DANIELOPOL (2011, 2012): eight-segmented thorax plus six-segmented pleon (seven only in Leptostraca), with gonopores on thoracomere eight in males and thoracomere six in females (GRAMS *et al.*, 2025).

Two molecular studies also support the monophyly of Malacostraca: HASSANIN (2006) based on six mitochondrial protein-coding genes (*atp6* and *8*, *cox1-3*, and *nad2*) and BERNOT *et al.* (2023), a phylogenomic analysis, based on total RNA and examining 149 transcriptomes and 16 genome assemblies.

TABACARU & DANIELOPOL (2011, 2012) regarded the Class Malacostraca as dichotomically divided into two Subclasses: Phyllocarida and Eumalacostraca, as, in their opinion, Hoplocarida present the essential synapomorphies of Eumalacostraca (especially the disappearance of 7<sup>th</sup> pleomere, the stenopodous thoracopods and the transformation of the 6<sup>th</sup> pleopods into uropods), have to be

included in Eumalacostraca (TABACARU & DANIELOPOL, 2012). This opinion contradicts SCHRAM (1978, 1981), MCLAUGHLIN, (1980), BOWMAN & ABELE (1982), DAHL (1983), MARTIN & DAVIS (2001) and FOREST (2004) who consider a distinct origin for Hoplocarida from the Eumalacostraca and see Class Malacostraca as divided into three Subclasses, namely Phyllocarida, Hoplocarida and Eumalacostraca.

2. SCHRAM & KOENEMANN (2021) included Podophallocarida within Cohort Caridoida Hessler, 1983; the cohort containing, according to their opinion, four Superorders: Podophallocarida, Syncarida, Peracarida and Eucarida.

TABACARU & DANIELOPOL (2011, 2012) considered Podophallocarida as an Infraclass separated from the other Eumalacostraca and as a sister-group of the Infraclass Cephalothoracarida nov. infraclass (TABACARU & DANIELOPOL, 2012).

Following TABACARU & DANIELOPOL (2012) the Superorder Syncarida Packard, 1885 with the Orders Bathynellacea Chappuis, 1915 and Anaspidacea Calman, 1904 is not a monophylum. The absence of the cephalothorax and the maxillipeds, the absence of the petasma, the presence of furcal rami and the transformation of the 8<sup>th</sup> thoracopod into a penis, TABACARU & DANIELOPOL (2012) endorse the opinion of SERBAN (1972) which regarded Bathynellacea Chappuis, 1915 as a distinct taxon, Podophallocarida Şerban, 1970 with the rank of Infraclass.

The Podophallocarida Serban, 1970 are defined by eight free thoracomeres (no cephalothorax), first thoracopod not modified into a maxilliped, thoracopod 8 reduced and transformed into a penis, pleon with 5 pleonites, 6<sup>th</sup> pleonite fused with the telson (pleotelson), reduced pleopods without exopodites, pleopods 3–5 absents, two furcal rami and development with free larval stages (SERBAN, 1970, 1972; TABACARU & DANIELOPOL, 2012).

As the sister-group of the Podophallocarida, the authors propose the name Cephalothoracarida nov. infraclass, defined by the following characters: first thoracomeres fused with the cephalon forming a cephalothorax, the first thoracopod always modified into the maxillipeds and the absence of the furcal rami (TABACARU & DANIELOPOL, 2012). As a consequence, Anaspidacea Calman, 1904 remain the sole order of the Superorder Syncarida Packard, 1885.

The basal position of Bathynellacea with respect to all other Eumalacostraca, the position argued by TABACARU & DANIELOPOL (2011), is in agreement with SCHRAM & HOFF (1998), POORE (2005), WILLS *et al.* (2009), JENNER *et al.* (2009) and the position endorsed by COINEAU & CAMACHO (2013) in the Grassé Treaty of Zoology.

In fact, CAMACHO *et al.* (2002) provided the first molecular evidence (16S rDNA) which confirmed the basal position of Bathynellacea as a sister-group to the other eumalacostracans and, as a consequence the paraphyly of Syncarida. This conclusion, of Bathynellacea sorting separately from Anaspidacea, is supported also by the more comprehensive molecular phylogenies of JENNER *et al.*

(2009), using four nuclear ribosomal and mitochondrial loci (18S rRNA, 28S rRNA, 16S rRNA and Cytochrome C oxidase subunit I, but the trees produced by JENNER *et al.* (2009) group Bathynellacea with Amphipoda, a position we do not support.

To sum up, all these morphological and molecular analyses agree that Syncarida are not a monophyletic group and, as a result, support the opinion of SERBAN (1972) who created the taxon Podophallocarida for Bathynellacea, separating them from Syncarida.

3. SCHRAM & KOENEMANN (2021) did not separate Thermosbaenacea from the rest of the Peracarida, so, in their classification the Peracarida are no longer defined by the ventral brood pouch and oostegites. As a consequence, they no longer consider neither Pancarida Siewing, 1948, neither Neocarida Ax, 1999.

TABACARU & DANIELOPOL (2011) recognized the isolation of the Thermosbaenacea within Pancarida and recognized the Infracohort Neocarida Ax, 1999 (Pancarida + Peracarida) and proposed Subcohort Synneocarida (Syncarida + Neocarida) as the sister-group of the Subcohort Eucarida (TABACARU & DANIELOPOL, 2012).

The absence of the oostegites and the incubation in a dorsal marsupium under the carapace support the clear separation of a Superorder Pancarida for the Thermosbaenacea TABACARU & DANIELOPOL (2011, 2012).

Taking into account the absence of the carapace and direct development (without free larval stages), TABACARU & DANIELOPOL (2012) rejected a close relation between Anaspidae and Eucarida as seen by SIEWING (1956, 1959), SCHRAM (1984) and WATLING (1999). Following the cladogram of TABACARU & DANIELOPOL (2011, Syncarida is the sister-group of the Neocarida and proposed for this group the name Synneocarida nov. Subcohort (Tabacaru & Danielopol, 2012) containing the Infracohorts Syncarida Packard, 1885 (with a sole order, Anaspidae) and Neocarida Ax, 1999 (containing Superorder Pancarida Siewing, 1958 with the order Thermosbaenacea Monod, 1927 and Superorder Peracarida Calman, 1904 with the orders Mysida Haworth, 1825; Lophogastrida G.O. Sars, 1870; Amphipoda Latreille, 1816; Isopoda Latreille, 1817; Tanaidacea Dana, 1849; Cumacea Krøyer, 1846; Spelaeogriphacea Gordon, 1957; Mictacea Bowman, Garner, Hessler, Iliffe & Sanders, 1985; Bochsacea Gutu & Iliffe, 1998; Euphausiacea Dana, 1852; Decapoda Latreille, 1803 and Amphionidacea Williamson, 1973).

As TABACARU & DANIELOPOL (2011, 2012) clearly point out, the taxon Neocarida Ax, 199 was establish to unite the sister-groups Pancarida and Peracarida. The Superorder Pancarida was established by SIEWING (1958) for the Thermosbaenacea and was accepted by many authors (KAESTENER, 1959; CROME & GRUNER, 1969; BOWMAN & ABELE, 1982; PIRES, 1987; BOUTIN, 1996; KOBUSCH, 1999; AX, 1999; RICHTER & SCHOLTZ, 2001).

The taxon Neocarida is justified for TABACARU & DANIELOPOL (2011, 2012), as Pancarida and Peracarida are undoubtedly sister-groups, defined by the presence of *lacinia mobilis* on the left mandible: the value of this character for phylogeny was considered doubtful by HESSLER & WATLING (1999) but other authors (e.g. RICHTER *et al.*, 2002) considered this structure as special for Peracarida (including Thermosbaenacea).

4. Both SCHRAM & KOENEMANN (2021) and TABACARU & DANIELOPOL (2011, 2012) considered 17 orders but SCHRAM & KOENEMANN (2021) do not recognize neither the Bochusacea, nor Amphionidacea but they do recognize the orders Stygomysida Tchindonova, 1981 and Ingolfielida Lowry and Myers, 2013.

Of contrary, TABACARU & DANIELOPOL (2011, 2012) recognized the orders Bochusacea Guțu & Iliffe, 1998, Stygomysida Tchindonova, 1981 and Amphionidacea, Williamson, 1973 but regarded Ingolfielida as a suborder.

According to TABACARU & DANIELOPOL (2011, 2012) the order Bochusacea Guțu & Iliffe, 1998 has to be considered as valid following the study of JAUME *et al.*, (2006) and represents the sister-group of Mictacea.

The Bochusacea are indisputably defined as a valid order by the following characters: paragnaths with a long filiform processus, setose oostegites situated on the postero-medial edge of the coxa, cephalothorax formed by the fusion of the cephalon and the first thoracic somite (except for *Thetispelecaris* where the cephalon fuses with two thoracic somites), carapace reduced to a cephalic shield, extended on the post-mandibular site and with lateral lobes, pereion with 6–7 somites, pleon formed by 5 somites and a pleotelson (6<sup>th</sup> pleomere fused with the telson), left mandible with *lacinia mobilis* at adults, maxillula with 2 endites and without palpus, maxilliped without epipodites, direct development with *manca* stadium (GUȚU, 2001; JAUME, BOXHALL & BAMBER, 2008; TABACARU & DANIELOPOL, 2011, 2012).

Similarly, the order Amphionidacea Williamson, 1973 was considered as valid by TABACARU & DANIELOPOL (2011, 2012) due to its particular characters: very elongated female first pleopode forming a brooding pouch with the carapace, cephalothorax formed by the fusion of the cephalon with all thoracomeres, laterally compressed carapace covering the cephalon and the thorax, stalked compound eyes, antennule with accessory flagellum, biramous antenna with scaphocerite exopodite, reduced mandible without palpus, biramous maxillipeds, distinct telson, not fused with the 6<sup>th</sup> pleomere, biramous uropods forming a fan with the telson and metamorphic development with free larval stages (see also WILLIAMSON, 1973). Despite these very peculiar characters, molecular comparisons moved the species into the Order Decapoda Latreille, 1803, Infraorder Caridea Dana, 1852, namely it belongs to the family Pandalidae Haworth, 1825, but it does not seem to be associated with any of the previously recognized pandalid genera, while it indeed has an inter-oceanic distribution (DE GRAVE *et al.*, 2015; WANG *et al.*, 2021).

5. SCHRAM & KOENEMANN (2021) seem to incline toward by uncovering Amphipoda Latreille, 1816 and Isopoda Latreille, 1817 as sister-groups within the order Edriophthalma Leach, 1815. But as they say: “We should not hesitate to reject the Edriophthalma hypothesis should molecule sequence data with both mitochondrial and nuclear protein-coding genes applied to the widest taxon sampling of peracaridans indicate we should do so” (SCHRAM & KOENEMANN, 2021, p. 474).

Here, TABACARU & DANIELOPOL (2011, 2012) clearly rejected the opinion which sees Amphipoda and Isopoda as suborders within the Order Edriophthalma Leach, 1815 or Order Acaridea Schram, 1981 and also rejected a sister-group relation between these two orders as maintained by many authors (SCHRAM, 1981, 1984, 1986; WAGNER, 1994; WILLS, 1997; SCHRAM & HOF, 1998; LANGE & SCHRAM, 1999; POORE, 2005; JENNER *et al.*, 2009; WILLS *et al.*, 2009).

According to TABACARU & DANIELOPOL (2011, 2012) the characters supporting this opinion are the resultant of parallel evolutions (sessile eyes, pereopodes without exopodites) or plesiomorphies (the absence of the carapace). Of contrary, the authors strongly underlined the differential characters differentiating these orders, the most phylogenetically significant being for Amphipoda: pleon divided into metasoma (or pleosoma) formed by three segments bearing the pleopods and urosoma formed by three segments bearing the uropods, beginning with pereopode 2 (gnathopod 2) up to pereopode 4, sometimes up to pereopode 5, there are respiratory epipodites with a medial position; for Isopoda: biramous, lamellate pleopods with respiratory function, thoracopods 2–8 without epipodites and biphasic molting.

Recently, BERNOT *et al.* (2023), in a phylogenomic analysis, based on total RNA and examining 149 transcriptomes and 16 genome assemblies, reached the same conclusion: they reject the sister-group relation between Amphipoda and Isopoda clearly stating that all their analyses (both ML, partitioned maximum likelihood, abd CAT-GTR) recovered Amphipoda as the sister to the other peracarids, namely as the sister-group of Mysida. Also, as BERNOT *et al.* (2023) showed Isopoda is grouped by all their analyses as sister to Cumacea, while TABACARU & DANIELOPOL (2011, 2012) support a sister-group relation between Isopoda and a group made by Spelaeogriphaceae+Cumacea+Tanaidacea.

#### 4. CONCLUSIONS

It is important to emphasize the significance of the classification of Malacostraca as argued by TABACARU & DANIELOPOL (2011, 2012):

(1) Phyllocarida (Order Leptostraca) represents a basal group of Malacostraca, which diverged early from its sister-group the Eumalacostraca; this latter group constitutes the major stock of Malacostraca (TABACARU & DANIELOPOL, 2011, 2012).

The authors consider, in accordance with the widely held opinion of carcinologists, Phyllocarida (Order Leptostraca) display essential synapomorphies with Malacostraca (tagmosis 5+7+8+telson, fixation of the gonopore on the 6<sup>th</sup> female thoracic-segment and on the 8<sup>th</sup> male-thoracic segment) and as a consequence, Phyllocarida belongs to the Class Malacostraca.

(2) TABACARU & DANIELOPOL (2011, 2012) regard the Class Malacostraca as dichotomously divided into Subclasses Phyllocarida and Eumalacostraca. This is due to the fact that Hoplocarida shares essential synapomorphies with the Eumalacostraca: loss of 7<sup>th</sup> somite of the pleon, stenopodous thoracic endopodite and pleopods of the 6<sup>th</sup> pleonal somite differentiated as uropods.

(3) Hoplocarida is a collateral stem diverging very early from Eumalacostraca: it presents a mosaic of basal and derived (original) morphological characters; the sister-group of Hoplocarida is Anaspidae+Neocarida+Eucarida, representing a major component of Eumalacostraca and which could be assimilated with the taxon Caridoida, but excluding Bathynellacea (TABACARU & DANIELOPOL, 2011, 2012).

(4) According to TABACARU & DANIELOPOL (2011, 2012) the Superorder Syncarida Packard, 1885 (including the orders Bathynellacea Chappuis, 1915 and Anaspidae Calman, 1904) does not represent a monophylum. They accept the view of SERBAN (1972), that Bathynellacea represents a separate taxon called Podophallocarida (SERBAN, 1970), based especially on the absence of a cephalothorax and maxillipeds, the lack of petasma, the telson with furcal rami and the 8<sup>th</sup> thoracopod transformed into a penis.

For the sister group of the Podophallocarida TABACARU & DANIELOPOL (2012) propose a new Infraclass, Cephalothoracarida (nov.). This latter taxon is defined by the first thoracomere fused to the cephalon and forming the cephalothorax, the 1<sup>st</sup> thoracopod differentiated as maxilliped and the telson without furca. Therefore, Anaspidae remains the solely order within the Superorder Syncarida and considered as the most basal branch of the Caridoida s.str.

In their cladogram (considering the lack of a carapace and the direct development without free larval stages), Syncarida represents the sister-group of the Neocarida and propose for them the name Synneocarida (TABACARU & DANIELOPOL, 2012); it is in their phylogenetic classification a new Subcohort within which two Infracohorts, the Syncarida Packard, 1885 and the Neocarida Ax, 1999 are distinguished.

(5) Thermosbaenacea is a well-defined lineage, taxonomically ranked as Superorder Pancarida, the sister-group of the Peracarida. As a result, the Neocarida (Pancarida+Peracarida) represents the sister-group of Syncarida (Anaspidae) and the grouping Syncarida+Neocarida forms the sister-group of Eucarida (TABACARU & DANIELOPOL, 2011, 2012).

(6) Amphipoda and Isopoda do not represent sister-groups: Amphipoda is a more basal group with affinities with a group of lineages united in the taxon Mancoida; both taxa are sister-groups.

TABACARU & DANIELOPOL (2011, 2012) considered the similarities between Amphipoda and Isopoda are the result of parallel evolution of several morphological characters like the sessile compound eyes, the absence of exopodites on all thoracopods or the presence of plesiomorphic characters like the absence of a carapace. Of contrary, TABACARU & DANIELOPOL (2011, 2012) emphasize the characters clearly differentiating the two orders: for the Amphipoda, the pleon divided into two separate functional units, the metasoma or pleosoma (pleomere 1, 2, 3) with three pairs of pleopods and the urosoma (pleomere 4, 5, 6) with three pairs of pleopods modified as uropods, medial epipodites gills on pereopodes and for the Isopoda: five pairs of pleopods with respiratory function and pereopodes without epipodites.

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<sup>1</sup>“Emile Racovitza” Institute of Speleology  
13 Septembrie No 13, 13059711, Bucharest  
E-mail: sankao2@yahoo.com