THE GENUS *KARAMANONISCUS* TABACARU, 2021 AND THE TRIBUS SPELAEONETHINI SCHMÖLZER, 1965 (ISOPODA, ONISCIDEA, TRICHONISCIDAE)

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Abstract. The synonymy of *Macedonethes* Buturović, 1955, described as a subgenus of *Alpioniscus* and subsequently considered by Tabacaru as a distinct genus, with *Alpioniscus* Racovitza, 1908 is argued, while *Macedonethes skopjensis* Buturović, 1955, considered as the type species of the genus, belongs to the genus *Alpioniscus*, as *Alpioniscus skopjensis* Buturović, 1955. Moreover, the authors argue that *Macedonethes* Buturović, 1955 sensu Ivo Karaman, 2003 (partim) = *Alpioniscus* Racovitza, 1908 while *Macedonethes castellonensis* (CRUZ & DALENS, 1989) = *Alpioniscus castellonensis* (CRUZ & DALENS, 1989). The validity of the genus *Karamanoniscus* Tabacaru, 2021, with the type species *Macedonethes stankoi* Karaman, 2023, is again endorsed based on differential characters in comparison with the other genera of the Trichoniscidae. The structure of the tribe Spelaeonethini Schmölzer, 1965 is analyzed.

Keywords: Isopoda, Oniscidea, Trichoniscidae, Spelaeonethini, Macedonethes, Alpioniscus, Karamanoniscus.

1. INTRODUCTION

The genus *Karamanoniscus* Tabacaru, 2021 was established within the framework of a study on the trichoniscids belonging to the tribe Spelaeonethini, for the species *Macedonethes stankoi* Karaman, 2003, collected "From a spring in the cave at the source of the Babuna River, slopes of Solunska glava peak, Jakupica Mt., south of Skopje, Macedonia" (IVO M. KARAMAN, 2003B, p. 3). But the differential diagnosis of the genus *Karamanoniscus* was not designed in relation with the genus *Macedonethes* but in relation with all the genera included in the family Trichoniscidae. This was due to the fact that, at present, the genus *Macedonethes* Buturović, 1955, cannot be considered as valid. This genus was described initially as a subgenus of *Alpioniscus* Racovitza, 1908 and subsequently elevated to generic rank (TABACARU, 1993, 1996) and then redefined as a genus with three species (KARAMAN, 2003). The characters shared by the three species included by Karaman in the genus exist also in species included at present in the genus *Alpioniscus* Racovitza, 1908.

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In 2022, Ivo M. Karaman and Mladen Horvatović described from a Serbian cave a new, amphibious species of the genus *Bureschia* Verhoeff, 1926, a genus known only by the species *Bureschia bulgarica* Verhoeff, 1926, recorded only from three caves from Bulgaria (BERON, 2020). In their paper, the authors (KARAMAN, HORVATOVIĆ, 2022, p. 156) stated: "Unfortunately, we cannot agree with this change because it reflects the different physical conditions of the environment for which the two stygobite species, *M. skopjensis* (nominal taxon) and *M. stankoi*, have adapted, and not a reflection of their phylogenetic distance".

As a result, the *World List of Marine, Freshwater and Terrestrial Crustaceans* published the following:

Isopoda name details

Karamanoniscus Tabacaru, 2021

Status: unaccepted > junior subjective synonym

Accepted name: *Macedonethes* Buturović, 1955

Source of synonymy: Karaman, I., Horvatović, M., 2022

Taxonomic edit history: Date 22.12.05, action created by Taiti Stefano.

The genus *Macedonethes* Buturović, 1955 is invalid, as one of us has argued (TABACARU, 2021, p. 30) showing that the three species reunited by I. KARAMAN (2003) in this genus do not present characters common to this grouping. The characters shared by the three species are found at species of *Alpioniscus* Racovitza, 1908. Here, we argue again for the following synonymies: *Macedonethes* Buturović, 1955 (sensu TABACARU, 1993, 1996) = *Alpioniscus* Racovitza, 1908; *Macedonethes* Buturović, 1955 (sensu KARAMAN, 2003, partim) = *Alpioniscus* Racovitza, 1908; *Macedonethes castellonensis* (Cruz & Dalens, 1989) = *Alpioniscus castellonensis* (Cruz & Dalens, 1989).

Also, we argue for the validity of the genus *Karamanoniscus* Tabacaru, 2021 and we analyze its position within the family Trichoniscidae. We point out that the erection of the new genus *Karamanoniscus* was not based on the difference concerning the number of penicilli on the mandibles between *M. skopjensis* and *M. stankoi*. On the contrary, as underlined (TABACARU, 2021, p. 28), the number of penicilli on the mandibles as well as the number of articles of the male pleopode 2 endopodite cannot be used as a differential between genera given the characters of the species described more recently (TAITI & ALL., 2018) in the genus *Alpioniscus*.

At present, *Alpioniscus* Racovitza, 1908 is the genus with the highest known number of species in the tribe Spelaeonethini (subfamily Trichoniscinae). However, the affiliation of the genus *Karamanoniscus* to the tribe Spelaeonethini is problematic given that the structure of the pleopode 1 male exopodite corresponds with the conformation of the exopodite at some representatives of the tribe Oritoniscini.

Herewith, we reconsider the definition and the componence of the tribe Spelaeonethini. Also, we argue for the necessity of redefining some genera included in this tribe and propose a new identification key in order to differentiate the genera.

2. *MACEDONETHES* BUTUROVIĆ, 1955 (sensu Tabacaru, 1993) = *ALPIONISCUS* RACOVITZA, 1908

In 1955, the zoologist Adem Buturović described a new trichoniscid, collected by the famous zoologist Stanko Luka Karaman from a spring on the shore of Treska River, near Skopje. Buturović included the species in the genus *Alpioniscus* Racovitza, 1908, a genus to which he attributed several other species: *A.* (*Alpioniscus*) *karamani* Buturović, 1954; *A.* (*Illyrionethes*) *vardarensis* Buturović, 1954; *A.* (*Alpioniscus*) *slatinensis* Buturović, 1955; *A.* (*Illyrionethes*) *trogirensis* Buturović, 1955. Taking into account the two subgenera considered by VANDEL (1946) within the genus *Alpioniscus*, respectively *Alpioniscus* s.str. and *Illyrionethes* Verhoeff, 1927, Buturović established for the new species a new subgenus, *Macedonethes*, naming the species *Alpioniscus* (*Macedonethes*) *skopjensis*.

From the diagnosis given for the subgenus *Macedonethes* as well as from the identification key established by Buturović for the subgenera of *Alpioniscus*, he defined the subgenus proposed by him, in relation with the other two known subgenera, by the following characters:

1. At the subgenus *Macedonethes*, the right mandible presents 2 penicilli while at the subgenera *Alpioniscus* and *Illyrionethes* the right mandible presents only 1 penicillum;

2. At the subgenus *Macedonethes*, the maxillipedal palpus presents 4 lobes while at the subgenera *Alpioniscus* and *Illyrionethes* the internal edge of the palpus has no lobes or, at most, 3 lobes;

3. At the subgenus *Macedonethes*, male pleopode 2 exopodite presents a convex distal edge while at *Alpioniscus* and *Illyrionethes*, the distal edge is concave or almost straight.

4. At the subgenus *Macedonethes*, the articulations of the uropodal exopodite and endopodite are at the same level, while at *Alpioniscus* and *Illytionethes*, the articulations are more distanced longitudinally.

Taking into account the differential characters presented by Buturović and the descriptions of the species included at that moment in the genus *Alpioniscus*, Tabacaru, in two successive papers (TABACARU, 1993, 1996) considered the subgenus *Macedonethes* as a distinct genus. The characters endorsing the definition of a distinct genus were: male pleopode 2 endopodite triarticulated, male pleopode 2 exopodite presents a convex external edge; right mandible with 2 penicilli between *pars incisiva* and *pars molaris*; uropodal exopodite and endopodite inserted at the same level.

In the identification key of the genera of the tribe Spelaeonethini presented in the two papers, the author considered the genera *Alpioniscus* Racovitza, 1908, *Aegonethes* Frankenberger, 1938 and *Macedonethes* Buturović, 1955, as defined by the triarticulated male pleopode 2 endopodite. Although RACOVITZA (1908, p. 371) wrote "Endopodite II biarticulé" in the description of the subgenus *Alpioniscus*, subsequently it was considered that the male pleopode 2 endopodite is triarticulated. VERHOEFF (1932) maintained that the male pleopode 2 endopodite is triarticulated at the genera *Illyrionethes* Verhoeff, 1927 and *Bureschia* Verhoeff, 1927 while at the genera *Titanethes* Schiödte, 1849, *Spelaeonethes* Verhoeff, 1932 and *Caucasonethes* Verhoeff, 1932, the endopodite becomes biarticulated by

the reduction of the short, basal article. *Illyrionethes*, in the opinion of KESELYAK (1930) is synonymous with *Alpioniscus* but VANDEL (1960) regarded *Illyrionethes* as a subgenus. As a consequence, the pleopode 2 male endopodite was considered as triarticulated at *Alpioniscus* (STROUHAL, 1939; BUTUROVIĆ, 1954, 1955; VANDEL, 1960; SCHMÖLZER, 1965; POTOČNIK, 1983; CRUZ & DALENS, 1989; TAITI & ARGANO, 2009; BEDEK & TAITI, 2011; BEDEK & HORVATOVIĆ, 2017). In the volume *Isopoda* from *Faune de France*, VANDEL (1960) specified that the male pleopode 2 endopodite is triarticulated as a result of the differentiation of a short basal article in connection with the basis. However, at present, as maintained by KARAMAN (2003), this basal article is considered as a part of the propodus and, as such, the male pleopode 2 endopodite is biarticulated at all genera.

In 1996, 27 species were known within the genus *Alpioniscus* Racovitza, 1908, while, at present, 41 species are included in this genus. It is a well-known fact that description of new species leads frequently to the emendation of the genus in which they were included, so to the completion or to changes of the diagnosis of the respective genus. Sometimes, the description of new species leads to more important changes, respectively to the splitting of a genus in more genera or, on the contrary, to the combination of genera by synonymy. Considering the species subsequently included in the genus *Alpioniscus*, we find that the species described by Buturović fits, as it was initially described, in the genus *Alpioniscus*.

All the characters regarded by BUTUROVIĆ (1955) and TABACARU (1993, 1996) as characteristic for the genus *Macedonethes* are found at more recently described species of *Alpioniscus* as follows.

At the majority of the species of the genus *Alpioniscus*, the right mandible presents between the *pars incisiva* and *pars molaris*, a sole penicillum but, at present, there are species at which the right mandible presents 2 penicilli: *Alpioniscus kuehni* (Schmalfuss, 2005), *A. stochi* Taiti & Argano, 2018. The presence of lobes on the maxillipedal palpus cannot represent a differential character as there are clear differences at the species from the same genus. Male pleopode 2 exopodite with a convex external edge is a character found at some species of *Alpioniscus*: *A. kuehni* (Schmalfuss, 2005), *A. stochi* Taiti & Argano, 2018, *A. sideralis* Taiti & Argano, 2018. The uropod with the exopodite and the endopodite inserted at the same level is also present at the species *Alpioniscus kuehni* (Schmalfuss, 2005), *A. stochi* Taiti & Argano, 2018.

In conclusion, *Macedonethes* Buturović, 1955 sensu Tabacaru 1993, 1996 is obviously synonymous with *Alpioniscus* Racovitza, 1908 while the species considered as the type of the genus *Macedonethes*, should be regarded as it was initially described as a species of the genus *Alpioniscus* Racovitza, 1908.

3. *MACEDONETHES* BUTUROVIĆ, 1955 (sensu IVO KARAMAN, 2003, partim) = *ALPIONISCUS* RACOVITZA, 1908

In 2003, IVO M. KARAMAN described a remarkable new trichoniscid species, an aquatic species adapted to life in flowing water, collected from a spring in the cave at the source of the Babuna River (Macedonia, Jalupka Mt., south of Skopje).

He included the new species within the genus *Macedonethes* Buturović, 1955 and named it *Macedonethes stankoi* as it was dedicated to the famed carcinologist Stanko Karaman, founder of the Natural History Museum in Skopje. Ivo Karaman provided a new diagnosis for the genus *Macedonethes* including in this genus, besides the type species of the genus, respectively *Macedonethes skopjensis* Buturović, 1955, the new species *Macedonethes stankoi*, but also a species described from Spain under the name *Spelaeonethes castellonensis* Cruz & Dalens, 1989.

KARAMAN (2003B, P. 2) provided for the genus *Macedonethes* Buturović, 1955, containing the three above mentioned species, the following diagnosis:

"**Diagnosis**. Troglobite blind animals. Maxilliped strongly dilated in its distolateral part, palp on medial edge with pronounced lobes bearing setae; exopods and endopod of uropod subequal, articulated at the same level; endopod of male pleopod 2 with abruptly narrowed tip, basal article 2.5-3 times as long as wide at its base, antennulae with two aesthetascs (if the third article is not totally reduced); male merus 7 with protrusion at its base ventrally".

From the differential characters specified by Buturović for the genus *Macedonethes* and listed here, we note that in the diagnosis of Ivo Karaman was retained only character 4, respectively "Exopod and endopod of uropods articulated on the same level". In fact, the other differential characters mentioned by Buturović are not found at all three species reunited under the name *Macedonethes*. For instance, the right mandible presents between *pars incisiva* and *pars molaris* 2 penicilli at *S. castellonensis* as is the case at *A. (M.) skopjensis* but only one penicillum at *M. stankoi*; exopodite of pleopode 2 male at *S. castellonensis* does not present a distally convex external edge; endopodite of pleopode 2 at *S. castellonensis* presents, as CRUZ & DALENS (1989, P. 92) specified, two subequal articles, while at *A. (M.) skopjensis* and *M. stankoi* the end article of male endopodite 2 is shorter than the preceding article.

In the diagnosis of the genus *Macedonethes*, apart from the character regarding the uropods, Karaman gave, in the first place, a special importance to the maxillipeds structure. He regards this character as most conservative from a phyletic point of view.

In our opinion, based on the study of the maxilliped within the family Trichoniscidae, the maxilliped structure can be characteristic for species but it cannot distinguish a genus as it presents very different aspects at the species of the same genus.

Analyzing the maxilliped structure at *Alpioniscus*, a high diversity in the conformation of this organ can be noted at the different species of this genus. For instance, the maxilliped basis can present the external edge enlarged in the middle or distally enlarged with an angular (*A. kuehni*, *A. stochi*) or rounded (*A. sideralis* and the species considered as *Macedonethes*) distal lobe; palpus broad, obscuring the endite or narrow and bent in the medial direction (*A. kuehni*, *A. stochi*, *A. sideralis*) and can present more or less pronounced lobes on the median edge lobes or only tufts of setae; endite can be narrow triangular with apical penicillum or widely quadrangular with a penicillum in the apical medial corner.

The maxilliped presents different aspects in other genera according to the species as seen, for instance, at the genus *Brackenridgia* (LEWIS, 2004, FIG.3; TABACARU, GIURGINCA, SÂRBU, 2023).

In conclusion, we consider the distolateral dilatation of the basis and the presence of pronounced lobes on the palpus as representing relatively similar aspects at the three species reunited by Karaman in the genus *Macedonethes* but which can be found also at species belonging to *Alpioniscus*. In our opinion, the maxilliped structure, highly variable within a genus, cannot represent an important phyletic character able to define a particular genus.

The second character considered by Karaman as important for the definition of *Macedonethes*, and namely "exopod and endopod of uropod subequal, articulated on the same level", it was recorded by BUTUROVIĆ (1955) and used by TABACARU (1993, 1996) but, at present, it cannot be used to define a particular genus. This character cannot be found only at the three species considered in the genus *Macedonethes* as it was also recorded at species assigned to the genus *Alpioniscus* respectively at *Alpioniscus kuehni* (Schmalfuss, 2005), *A. stochi* Taiti & Argano, 2018.

In the original description of *Utopioniscus kuehni* it is textually stated: "Uropods: exopodite and endopodite inserting at the same level" (Fig. 2) (SCHMALFUSS, 2005, P. 14) while in the description of the species *Alpioniscus stochi* it is stated about the uropod: "endopod slightly shorter than exopods, exopods and endopod inserted at the same level" (TAITI & ALL., 2018, P. 252). This fact is perfectly visible in the figures provided for these species (SCHMALFUSS, 2005, P. 3, FIG. 2; TAITI & ALL., 2018, P. 245, FIG. 9E, P. 249, FIG. 12F).

We have to underline that all characters mentioned by Karaman in the diagnosis of the genus *Macedonethes* are found at species of *Alpioniscus*. The sole character which does not correspond with the genus *Alpioniscus* is the antennule ("if the third article is not totally reduced") and this clearly refers only to the newly described species *Macedonethes stankoi*. But in this diagnosis are not mentioned other remarkable characters of the species *Macedonethes stankoi*.

As it is well-known, the taxonomy of the Trichoniscidae is based on the male sexual differentiations, respectively the specific characters of pereiopode VII, the genital apophysis and pleopodes 1 and 2. The generic diagnosis given by Karaman for *Macedonethes* contains characters of pereiopode VII and pleopode 2 endopodite also found at the genus *Alpioniscus*.

A comparison between the figures given for the male pleopodes 1 and 2 at *Alpioniscus* (*Macedonethes*) *skopjensis* (BUTUROVIĆ,1955, P. 149, FIG.9, FIG. 10), at *Spelaeonethes castellonensis* (CRUZ & DALENS, 1989, P. 92, FIG. 1A and B) and at *Macedonethes stankoi* (KARAMAN, 2003, p. 12, FIG. 6A and B) shows clearly that *Macedonethes stankoi* is decidedly different from the other two species and, in any case, is not close to the species *Alpioniscus boldorii*, as mentioned by KARAMAN et HORVATOVIĆ (2022, P. 156).

In conclusion, the genus *Macedonethes* (sensu Karaman, 2003) cannot be a valid genus as the type species *Alpioniscus* (*Macedonethes*) *skopjensis* Buturović,1955 as well as the species *Spelaeonethes castellonensis* Cruz et Dalens, 1989 belong to the genus *Alpioniscus*.

4. *MACEDONETHES CASTELLONENSIS* (CRUZ ET DALENS, 1989) = *ALPIONISCUS CASTELLONENSIS* (CRUZ ET DALENS, 1989)

In 1989, in a study on the terrestrial isopods from the Iberian Peninsula, the isopodologists ANTONIO CRUZ SUAREZ and HENRI DALENS published the description of several new cavernicolous species from Eastern Spain. Their study contained the description of 7 new, depigmented and blind species: 6 species are included in the family Trichoniscidae and one belongs to the family Philoscidae. The first species described comes from the Cueva del Toro, town Alcudia de Veo, in the province Castillón, Community of Valencia and was attributed to the genus *Spelaeonethes* Verhoeff, 1932 and named *Spelaeonethes castellonensis*. The same paper contains the description of a new species attributed to the genus *Alpioniscus* Racovitza, 1908 and named *Alpioniscus escolai*.

Clearly, CRUZ & DALENS (1989) considered the distinction between the genera *Spelaeonethes* and *Alpioniscus* based on the then recognized differential characters, respectively *Spelaeonethes* distinguished by the biarticulated male 2 pleopode endopodite and by the right mandible with two penicilli in addition to molar penicilli at both mandibles, while *Alpioniscus* by the triarticulated male 2 pleopode endopodite, the right mandible with a sole penicillum and lacking molar penicilli (VANDEL, 1960; SCHMÖLZER, 1965; CRUZ, 1989). As we have argued, these characters cannot be used to distinguish the two genera. Currently, it is thought that in all genera the male 2 pleopode endopodite is biarticulated while the right mandible with two penicilli along with molar penicilli is also found at more recently described species of *Alpioniscus*.

An analysis of the tribe Spelaeonethini (TABACARU, 1996), after evaluating the species attributed to the genus *Spelaeonethes* and taking into account the revision and the definition of this genus (TAITI & FERARA, 1996), reached the conclusion that the species *Spelaeonethes castellonensis* Cruz et Dalens, 1989 is clearly apart from the other species of the genus due to the presence of a protuberance on the meros of the male pereiopode VII and the conformation of the male 2 pleopode endopodite. At the species named *S. castellonensis* the male 2 pleopode endopodite has two sub-equal articles and the distal article is tapering while at the species included in the genus *Spelaeonethes* the male 2 pleopode endopodite has a robust distal article which is much longer than the basal article. We have to add that at the species of *Spelaeonethes*, the male 1 pleopode endopodite is short and conical while at *S. castellonensis*, the male 1 pleopode endopodite is narrow and elongated similar to that of the species included in the genus *Alpioniscus*.

IVO KARAMAN (2003A AND B) also maintained that *Spelaeonethes castellonensis* is clearly different from the species of the genus *Spelaeonethes*.

At the same time, in his opinion, the published descriptions and illustrations argue for a close relationship between *S. castellonensis* and *Macedonethes skopjensis* Buturović, 1955, the type species of the genus *Macedonethes*. As a result, Karaman considered *S. castellonensis* as belonging to the genus *Macedonethes* and proposed the new combination *Macedonethes castellonensis* (Cruz et Dalens).

But analyzing the description and the illustrations given by BUTUROVIĆ (1955) for *Alpioniscus* (*Macedonethes*) *skopjensis* and those of CRUZ & DALENS (1989) for *Spelaeonethes castellonensis*, it is obvious that both species fit within the genus *Alpioniscus* Racovitza, 1908 due to their characters. We note there are similarities and differences between the two species that fall within the limits of the differences existing between the species of *Alpioniscus*. The similarities are: antennule with only two aesthetascs (as in the species *Alpioniscus kuehni* and *A. stochi*), right mandible with two penicilli, maxilliped with distolaterally enlarged basis, uropod exopodite and endopodite inserted at the same level; as we have pointed out, all are characters existing at some species of *Alpioniscus*.

Following the published descriptions, the two species present clear differences in the conformation of the male 1 and 2 pleopode. At *Alpioniscus* (*Macedonethes*) *skopjensis*, pleopode 1 exopodite has a very convex internal edge and a widely rounded tip; pleopode 2 exopodite with a convex external edge, as Buturović underlined, and also a widely rounded tip while the proximal article of the endopodite is clearly longer than the distal article. At *Spelaeonethes castellonensis*, pleopode 1 exopodite has a straight internal edge and the tip is narrow; pleopode 2 exopodite has a straight external edge and a pointed tip while the two articles of the endopodite are sub-equal in length.

If the definition of the subgenera *Alpioniscus* s. str. and *Illyrionethes* (TABACARU, 1996) corresponds to a phyletic reality, then we can assert that the Spanish species *A. castellonensis* and *A. escolai* belong to the subgenus *Alpioniscus* s. str. while the species from Macedonia, *A. skopjensis* belongs to the subgenus *Illyrionethes*. We note that CRUZ & DALENS (1989) considered the species described by them, *A. escolai*, as belonging to the subgenus *Illyrionethes*, a fact leading to the conclusion that the species needs to be revised (TABACARU, 1993; HORVATOVIĆ, 2014, P. 77; BEDEK, 2019, P. 8; BEDEK ET ALL., 2019, P. 9). But if we analyze the illustration given by CRUZ & DALENS (1989, P. 93, FIG. 3B) for the male 2 pleopode, the contradiction becomes explainable.

Currently, the male 2 pleopode endopodite of *Alpioniscus*, as in all genera of the Spelaeonethini, is considered as biarticulated; also, at the subgenus *Alpioniscus* s. str. the two articles are sub-equal or the proximal article is shorter than the distal one while at the subgenus *Illyrionethes* Verhoeff, the proximal article is clearly longer than the distal article. When CRUZ & DALENS (1989) described the species *A. escolai*, all authors considered the male 2 pleopode endopodite as triarticulated because a more developed medial part of the protopodite was regarded as the first article; currently, this part of the protopodite is no longer considered as a distinct article (KARAMAN, 2003, P. 2). In the description and the illustrations for the species *A. escolai*, it is maintained that male 2 pleopode endopodite is

triarticulated, but as a first article is considered not a part of the protopodite but what is currently regarded as the proximal article.

But for the third article, CRUZ & DALENS (1989) considered a short and narrow part of the distal article ("Artejo distal corto y muy afilado"-distal article short and very pointed/narrow). If we consider as biarticulated the male 2 pleopode endopodite at the species *A. escolai*, then the proximal article is obviously shorter than the distal article and, of course, shorter than the exopodite.

As a conclusion, we note that the characters of the species described as *Spelaeonethes castellonensis* CRUZ & DALENS, 1989, correspond to the characters of the genus *Alpioniscus* as currently defined (TAITI & ALL., 2018; BEDEK, 2019). As a consequence, we consider *Spelaeonethes castellonensis* CRUZ et DALENS, 1989 = *Macedonethes castellonensis* (Cruz & Dalens, 1989) = *Alpioniscus castellonensis* (Cruz & Dalens, 1989).

5. *KARAMANONISCUS* TABACARU, 2021

In agreement with the opinion of IVO KARAMAN (2003, P. 2), we note the descriptions and the drawings for the species *Alpioniscus* (*Macedonethes*) *skopjensis* Buturović, 1955 and *Spelaeonethes castellonensis* CRUZ & DALENS, 1989 prove the close relationship between these species. But, as we have argued, according to their characters, both species should be included in the genus *Alpioniscus* Racovitza, 1908, as this genus is defined at present (TAITI ET AL., 2018; BEDEK, 2019). But, as we emphasized, if we consider the two subgenera as valid, respectively *Alpioniscus* s. str. and *Illyrionethes* Verhoeff, 1927, considering the differences of the male 2 pleopode endopodite, the species *Alpioniscus skopjensis* is included in the subgenus *Illyrionethes* while the species *Alpioniscus castellonensis* in the subgenus *Alpioniscus* s. str. Concerning the new species described by IVO KARAMAN (2003A, 2003B) and included along these two species in the genus *Macedonethes* Buturović, 1955, we noted its clear differences and we suggested for it the new genus *Karamanoniscus* Tabacaru, 2021.

The new genus is based, first and foremost, on the conformation of the male 1 and 2 pleopodes, which clearly differ from the conformation of the respective pleopodes at the other two species regarded by Karaman as belonging to the genus *Macedonethes*, and not on the number of penicilli on the right mandible. In our opinion, shared by most isopodologists, in the systematics of the Trichoniscidae, the most important characters in defining taxa are the male sexual characters, respectively pereiopode VII and pleopodes 1 and 2. As VANDEL (1960, P. 10) pointed out, it is the merit of EMILE RACOVITZA (1907, 1908) to argue the significance of the first two pairs of male pleopodes in the systematics of Oniscidea.

Concerning the species *M. skopjensis* and *M. stankoi*, KARAMAN (2003, P. 3) stated: "Superficially, differences between the two most closely related *Macedonethes* species are on the generic level, if we use the same criteria for differentiating genera throughout the family (Tabacaru, 1993)". In the opinion of

Karaman, it is the character analysis that led him to the conclusion these differences represent morphological adaptations that help the species live successfully in running water or plesiomorphic characters (developed epimera on pleonites 3-5). After KARAMAN (2003B) and KARAMAN & HORVATOVIĆ (2022) the three species reunited in the genus *Macedonethes* present similarities in the characteristics of the maxillipeds and uropods. But, as we have showed, these characters, similar at the three species, are not particular for them so they do not represent synapomorphies and, as such, cannot define a genus. The conformation of the maxillipeds, in general, characteristic at the species level, presents within genera a great diversity and cannot represent a character able to define a particular genus. Regarding the conformation of uropods, we have showed that it is not characteristic for *Macedonethes* as it is also found at species of *Alpioniscus*. Besides, even at the new species *Bureschia serbica* Karaman & Horvatović, 2022, the uropods are described (see p. 152) as identical with those of *Macedonethes stankoi*: "Uropod. Basis dilated posteriorly; exopodite and endopodite subequal in length, conical, inserted at the same level and with a tuft of several short setae at apex". How then can this character be an autapomorphy of the genus *Macedonethes* if it is exactly the same at species from other genera?

We repeat here the diagnosis of the genus *Karamanoniscus* based on the description and the diagnosis of the Species *Macedonethes stankoi* given by KARAMAN (2003A, 2003B) underlining the characters we consider as significant for the definition of the new genus, respectively the differential characters in relation with the genera of the Trichoniscinae.

Diagnosis

Large species (up to 15.7 mm in length; 12.7 mm in males) with rather convex body.

Blind; cephalon hypognathous.

Sternum of male 5 pereionite with unique "clasping" structures; sternum of female 5 pereionite with a pair of elongate, nipple-like structures.

Epimera of pleonites 3-5 well developed.

Antennule article 3 and aesthetascs reduced to varying degree (from slightly developed with two aesthetascs to almost completely reduced).

Right mandible with one penicillum, left mandible with three penicilli. Maxilliped strongly dilated in its distolateral part.

Pereiopodes 1-4 subchelate, i.e. with elongate carpus opposed to propodus and dactylus. No water-conducting structures on pereiopodes 6 and 7. Pereiopode 7 ischium with strongly dilated distal part; meros with a triangular posteriorly recurved protrusion at the base of the sternal margin.

Genital papilla with a dorsally directed tip.

Male 1 pleopode (according the drawing provided by KARAMAN, 2003B, FIG. 6A): oval exopodite with strongly convex edges and lateral-distally a prominent, digitiform lobe (Fig. 1).

Male 2 pleopode (according the drawing provided by KARAMAN, 2003B, FIG. 6B, D, E): biarticulated endopodite with proximal article slightly longer than

the distal article; distal article laterally oriented but medial-ventrally recurved at the tip and terminally forked (Fig. 3).

Uropod with subequal exopodite and endopodite, articulated at the same level.

Type species: *Macedonethes stankoi* Karaman, 2003.

Discussion: As we can note from the diagnosis of the genus *Karamanoniscus*, the type species presents many autapomorphies clearly distinguishing it from the other two species included by Karaman in the genus *Macedonethes* as well as the species included in other genera of the Trichoniscidae. But KARAMAN & HORVATOVIĆ (2022, P. 156) regard the differences between *M. skopjensis* and *M. stankoi* as reflecting the adaptation to different conditions of the two stygobitic species and not their phylogenetic divergence. But we cannot note any synapomorphy particular to the two species arguing for a sister-group relationship and which can represent an autapomorphy of the genus *Macedonethes*.

In the following, we will analyze again the most significant differential characters justifying the inclusion of *M. stankoi* Karaman, 2003 in a separate genus and, as a consequence, the establishment of the genus *Karamanoniscus*.

1.Epimera of pleonites 3-5 well developed

This character represents a clear difference in relation with the other two species reunited in the genus *Macedonethes*. At the species regarded as type species of the genus *Macedonethes*, respectively *Alpioniscus* (*Macedonethes*) *skopjensis*, the pleon, as described by BUTUROVIĆ, 1955, is long and narrow. In the genus *Alpioniscus*, which includes both *A. skopjensis* and *A. castellonensis*, all the 41 species known until now present a pleon clearly narrower than the pereion. JANA BEDEK (2019, P. 9) specifies in the genus description: "Pleon epimera are reduced, as in all Trichoniscinae species; subsequently, pleon is narrower than pereion (Taiti et al 2018; Strouhal 1939a; Frankenberger 1939)".

Within the Trichoniscidae (leaving aside the taxa with a problematic position, respectively *Thaumatoniscellus* and *Mladenoniscus*), beginning with VERHOEFF and RACOVITZA, the isopodologists distinguished two subfamilies: Trichoniscinae and Haplophthalminae. To differentiate the two subfamilies, VANDEL (1960, P. 137 and 354) considers as essential the size of the pleonal epimerae: at the Trichoniscinae, the 3-5 epimerae (néopleuron) are small, narrow, delineating a wide hiatus separating the pereion from the pleon, while at the Haplophthalminae the 3-5 epimerae are well-developed continuing the external shape of the pereional epimerae, so there is no hiatus separating the pereion from the pleon.

Analyzing from an eco-morphological point of view the general body conformation of the terrestrial Isopods, HELMUT SCHMALFUSS (1984) included the representatives of the subfamily Trichoniscinae in the Runner type with a pleon clearly narrower than the pereion while the representatives of the subfamily Haplophthalminae are included in the Creeper type with well-developed pleonal epimerae continuing the external edge of the pereion. The Clinger and Roller types (volvational forms) also have the pleonal margin continuing the pereion margin.

Except for *Karamanoniscus stankoi*, in the subfamily Trichoniscinae, only at *Bulgaronethes haplophthalmoides* Vandel, 1967 the pleon is only slightly narrower than the pereion due to the well-developed pleonal epimerae. VANDEL (1967, P. 341) includes the genus *Bulgaronethes* in the subfamily Trichoniscinae, Second Division, Legion II (at present tribe Spelaeonethini).

In the volume *Isopodes Terrestres* from the series *Faune de France* (64, 1960, P. 354), VANDEL considered the apparition of the pleonal epimerae (néopleuron) as an evolutive phenomenon and, as at some genera (*Cyphoniscellus*, *Vardaroniscus*, *Bulgaroniscus*) the 3 pleonite has relatively short epimerae, thought the pleonal epimerae developed in a postero-anterior direction. Subsequently, VANDEL (1967, p. 349), in an undernote, contradicted himself, maintaining that the ancestors of the subfamilies Trichoniscinae and Haplophthalminae would have had, like the ancestors of family Ligiidae, a pleon continuing the pereion without any gap.

While describing the amphibious species *Balearonethes sesrodesanus*, regarded by him as the most basal representative of the subfamily Haplophthalminae, HENRI DALENS (1977, P. 300) maintained the development of the pleonal epimerae represents an evolutive character preceding, at the Haplophthalminae, the tergal ornamentation. On the contrary, KARAMAN (2019, P. 102) regarded as plesiomorphic the development of the pleonal epimerae at the Haplophthalminae but also at the species *M. stankoi*. As he maintained (KARAMAN, 2003B, P. 3): "Developed epimera on pleonites 3-5 together with the arched body shape are considered as plesiomorphic characters. The rationale for this opinion will be presented in another paper".

The notions of plesiomorphic and apomorphic character have been introduced by the well-known German zoologist WILLI HENNIG and, as he pointed out, the analysis presupposes to establish the homology (excluding the possibility of a homoplasy) as well as establishing the sense of the character's evolution (polarity). But HENNIG (1982, p. 93) specified that plesiomorphic and apomorphic are relative notions. As clearly explained by PETER AX (1988), a plesiomorphic character is a character inherited from an ancestor anterior to the direct ancestor of the considered taxa. Plesiomorphic and apomorphic are not intrinsic traits of the characters as they depend on the taxonomic framework considered. Synapomorphies of supraspecific sister-groups (Adelphotaxa) are the autapomorphies of the hypothetical, direct ancestor and represent autapomorphies for the higher ranking taxa which includes them but are plesiomorphies for lower ranking taxa. As at the Ligidiinae (Diplocheta, Ligiidae), at Mesoniscidae (Microcheta-the basal sister-group of the Section Synocheta) and at Trichoniscinae, beginning with the most basal tribe, respectively the Typhlotricholigioidini, as well as the majority of the representatives of the family Styloniscidae (excepting the Notoniscinae and Iuiuniscinae), the pleon is narrower than the pereion, the development of the epimerae seems less likely to be a character inherited from an ancestor. In our opinion this character is a convergence with the traits of a reversion. As we have argued previously (TABACARU, 1999, P. 118), when a

character appears at an isolated taxon within a group where that characters does not exist, the character represents an apomorphy of the respective taxa even if in ensemble the character appears like a convergence. We note that BEDEK & TAITI (2009, P. 64), in the case of the species *Struhaloniscellus biokovoensis*, considered that "the small epimera of pleonites 3-5 may also be an apomorphic trait as a secondary reduction due to the small size". Similarly, the apparition of developed epimerae at *Karamanoniscus stankoi* with the subfamily Trichoniscinae, characterized by a narrow pleon, represents, in our opinion, an apomorphy.

2.Sternum of pereionite 5 with unique "clasping" structures

At the new species *Macedonethes stankoi*, Karaman noted on sternite 5 a structure unknown in other species of Trichoniscidae so it can be considered as an autapomorphy of this species and, probably, of the genus *Karamanoniscus*. IVO KARAMAN (2003B, P. 3) presents this structure in this way: "Sternum of pereionite 5 with two transverse, lateral protuberances which are rolled posteriorly into two «clasps». Medial margins of these «clasps» are curved towards the body surface. Posterior to these structures the 5th sternum is depressed. The «clasps» are strongly chitinized and probably serve to arrest the nipple-like structures of the female 5th pereionite sternum during copulation. This probably happens in the way that the «nipple» of the female sits in the male «clasp» from its lateral to medial end. This fixation of the «nipple» on the female 5th sternite enables precise transfer of spermatozoids to the genital opening of the female under running-water conditions".

3.Article 3 of antennule and aesthetascs reduced to varying degree

The drawings provided for the antennule of *M. stankoi* (2003B, FIGS. 2C and 8D) clearly show the very reduced third article. In the description of the species, KARAMAN specifies: "Antennula with elongate basal article; second article narrowing toward the tip, third article reduced, with reduced aesthetascs. The degree of reduction of the third article and aesthetascs shows some variability in the specimens examined, from an almost normally developed third segment (with 2 thin aesthetascs) to almost total reduction. In most of the Paratypes the degree of antennula reduction is similar to that of the holotype".

Within the order Isopoda, the reduction of the antennule to at most three articles is regarded as an autapomorphy of the suborder Oniscidea (VANDEL, 1960; TABACARU & DANIELOPOL, 1996A, 1996B, 1999). But SCHMALFUSS has showed the importance of this appendage: the terminal article, sometimes seen as a vestige of the flagellum, bears aesthetascs, hygroreceptive or perhaps chemoreceptive sensorial organs.

At some Oniscidea, the number of articles is reduced to two articles or even only one article. At the genera *Tylos* and *Helleria* (Infraorder Tylomorpha) the antennule is reduced to one article; at Ligiidae (Infraorder Ligiamorpha, Section Diplocheta) there are three articles but the third article is strongly reduced; at *Mesoniscus* (Mesoniscidae, Section Microcheta), the third article is reduced to a

sclerite contained within the second article (GRUNER & TABACARU, 1966, FIGS. 3A-F). In the Section Crinocheta, the antennule presents, at most genera, three articles but there are genera at which the third article is reduced as it is the case at *Detonella* and *Actaecia* or even completely reduced as at *Armadilloniscus* and *Spelaeoniscus* (SCHMIDT, 2002, FIG. 5).

However, we know no representative of the Section Synocheta with the third article of the antennule as reduced as described at *Karamanoniscus stankoi*. As we have previously noted (TABACARU, 2021; TABACARU, GIURGINCA, SARBU, 2023), especially at species with an amphibious or aquatic way of life, this article is very elongated, for instance at *Typhlotricholigioides aquaticus* Rioja, 1952, *Cantabroniscus primitivus* Vandel, 1965, *Alpioniscus kuehni* (Schmalfuss, 2005).

4.Pereiopodes 1-4 subchelate

The species of Trichoniscidae with an amphibious or aquatic way of life sometimes lack the groove of scales on the pereiopodes 6 and 7 for the water conducting system but we know no species from this family with subchelate pereiopodes. The description and the drawings provided by KARAMAN (2003, FIG. 4A, B, C, D) clearly show the subchelate pereiopodes 1-4 with the dactylus and propodus opposable to the carpus. Only in the family Styloniscidae, in the genus *Troglonisсus* Taiti et Xue, 2012 (syn. *Sinoniscus* Schultz, 1995), known from China, the species *T. clarkei* Taiti et Xue, 2012, with an aquatic way of life, have been described pereiopodes 1-4 subchelate with enlarged carpus.

5.Conformation of pleopode 1 exopodite (Figs. 1 and 2)

For the systematic study of the family Trichoniscidae the male pleopode 1 has a special significance, as ALBERT VANDEL (1960, P. 138) underlined. Analyzing the male pleopode 1 drawn by KARAMAN (2003B, FIG. 6A) for the species *M. stankoi*, we note the endopodite has the same conformation as at the other two species attributed to the genus *Macedonethes*, as well as, at the species of the genus *Alpioniscus*, but the exopodite has a clearly different conformation from that known at these species.

BUTUROVIĆ (1955, FIG. 9) stated that the male 1 pleopode at *Alpioniscus* (*Macedonethes*) *skopjensis* has a triangular exopodite with strongly rounded tip and a concave external side. CRUZ & DALENS (1989, FIG. 1A), at the species named by them *Spelaeonethes castellonensis*, stated that the male 1 pleopode exopodite is sub-triangular with an almost straight internal side while the external side is concave.

At the genus *Alpioniscus*, the male 1 pleopode exopodite is described as follows: “male pleopod 1 with triangular exopod” (BEDEK & TAITI, 2011). But within the genus *Alpioniscus*, with numerous species, there are small variations as pointed out by BEDEK (2019, P. 10): “Basically, it is triangular with more or less concave outer and/or inner margin, differing in the shape of the ending point, relative length, and width”.

The male 1 pleopode exopodite at the species described by KARAMAN as *Macedonethes stankoi* doesn't have a triangular shape. Karaman did not mention the male 1 pleopode exopodite in the diagnosis of the species *M. stankoi* and did not compare this appendage with that of the other two species included by him in the genus *Macedonethes*. In the description of *M. stankoi*, he stated: "exopods strongly arched, dilated mediodistally, distally with elongate, protruding tip, lateral margin ring-shaped".

KARAMAN & HORVATOVIĆ, (2023, P. 156) stated: "As for the structure of male pleopods in three species of *Macedonethes*, they are basically of the *Alpioniscus* s. str. type, the group of species close to *A. boldorii*". This statement can be valid only for the species *M. skopjensis* and *M. castellonensis,* but it is invalid in the case of the species described as *Macedonethes stankoi*. At this species, the male 1 pleopode exopodite has an oval shape with a lateral-extern digitiform lobe; the internal edge is very convex while the external side is also convex but distally hollowed delimitating the digitiform lobe.

The conformation of the male 1 pleopode exopodite at *Karamanoniscus stankoi* is close to the conformation of this appendage at some species from the tribe Oritoniscini like *Catalauniscus puddui* Argano, 1973 or even *Bureschia serbica* Karaman & Horvatović, 2022.

6.Conformation of pleopode 2 endopodite (Figs. 3 and 4)

At some genera from the subfamily Trichoniscinae, the male 2 pleopode endopodite, an appendage differentiated for mating, represents the most important character for the definition of the respective genus. This is the case at the genera *Troglonethes*, *Rhodopioniscus*, *Mexiconiscus*, *Nippononethes*.

Analyzing the drawings of KARAMAN (2003b, Fig. 6b, d, e) of the male 2 pleopode endopodite of *M. stankoi*, it is clear the appendage has a different conformation in comparison with that of the other two species attributed to the genus *Macedonethes* and the conformation described at the species of *Alpioniscus*. The characteristic medial-ventral curvature of the distal part of the male 2 pleopode endopodite of *Karamanoniscus stankoi* cannot be found in none of the above mentioned species.

As at any genus described as monotypic, its diagnosis cannot be based on the synapomorphies of sister-species but on remarkable autapomorphies which define the genus in relation with other genera from the same family. We cannot exclude the possibility that future investigations might lead to the discovery of other species from the respective genus as it was the case at several genera, described initially as monospecific, such as the genera *Kithironiscus*, *Thaumatoniscellus*, *Biharoniscus*, *Strouhaloniscellus*.

6. TRIBE *SPELAEONETHINI* SCHMÖLZER, 1965

Following several attempts to group the genera of the subfamily Trichoniscinae, VANDEL (1953A) suggested the classification he subsequently

maintained in the volume *Faune de France* (1960, p. 137–140). In 1953, he reunited the genera of the Trichoniscinae in three tribes, but, in 1960, he no longer used the term Tribe but Division as he reserved the term Tribe for taxa higher than super-family, but this does not correspond to the Code of Nomenclature.

The classification of Vandel is exclusively based on the conformation of the first two male pleopod pairs. He grouped the genera in three tribes corresponding to three stages in the development of the endopodite of the first pair of pleopodes. The first tribe presents an unisegmented endopodite and always without a terminal rod; the second tribe presents the endopodite of the first pleopod with a terminal rod, more or less ciliated or a rigid portion; the third tribe has a clearly biarticulated endopodite of the first pleopod, more or less cylindrical in shape, modified into a paracopulatory organ. The second tribe, containing most of the genera, is divided in Vandel's classification in 5 Legions.

K. SCHMÖLZER (1965) in the volume *Ordnung Isopoda* from the series *Bestimmungsbücher zur Bodenfauna Europas* assumed the classification of the Trichoniscinae proposed by Vandel as follows: Tribe Protrichoniscini (First Division), Tribe Spelaeonethini (Second Division, Legions I-IV), Tribe Trichoniscoidini (Legion V), Tribe Trichoniscini (Third Division). Subsequently, TABACARU (1993) proposed Tribe Androniscini for Legion III and Tribe Oritoniscini for Legion IV. Thus, the Tribe Spelaeonethini is restricted to Legion I and II. As a consequence, the tribe is defined by the endopodite of the male first pleopod presenting a ciliated or rigid rod while the exopodite the male first pleopod has a triangular shape ends apically with either a narrow or a widely rounded angle or rarely, it is lobed or divided terminally (*Hyloniscus* and some species of *Alpioniscus*). From the genera of the subfamily Trichoniscinae, based on these characters, we include in the tribe Spelaeonethini the following genera: *Titanethes* Schiödte, 1894, *Alpioniscus* Racovitza, 1908, *Hyloniscus* Verhoeff, 1908, *Cyphonethes* Verhoeff, 1926, *Tachysoniscus* Verhoeff, 1930, *Spelaeonethes* Verhoeff, 1932, *Protonethes* Absolon & Strouhal, 1932, *Aegonethes* Frankenberger, 1938, *Libanothes* Vandel, 1955, *Mexiconiscus* Schultz, 1964, *Bulgaronethes* Vandel, 1967, *Hondoniscus* Vandel, 1968, *Troglonethes* Cruz, 1991, *Nippononethes* Tabacaru, 1996, *Karamanoniscus* Tabacaru, 2022.

Taking into account the last analysis (TABACARU, 1996) of the tribe Spelaeonethini and the current references, we note a series of significant changes.

Foremost, we note the description of 14 new species within the genus *Alpioniscus* so the number of species increased from 27 to 41. Then, within the genus *Troglonethes*, known in 1996 with a sole species, 3 new species have been described raising the number of species to 4. Also, a new species was attributed to the genus *Hondoniscus*, so there are within this genus 4 species. In the 1996 analysis of the tribe Spelaeonethini, 3 species were included in the genus *Titanethes* Schiödte, 1849 (*T. albus*, *T. biseriatus*, *T. dahli*) while the subgenus *Cyphonethes* Verhoeff, 1926, elevated to the genus rank, included only one species, *C. herzegovinensis* Verhoeff, 1900. More recently, KARAMAN & HORVATOVIĆ (2018) published a revision of the genera *Cyphonethes* and

Titanethes proposing important modifications. Firstly, we note that *Titanethes* is regarded as monotypic including only the species *T. albus* (C. L. Koch, 1941). The species named *T. biseriatus* (Verhoeff, 1900) is moved to the genus *Cyphonethes* while *Titanethes dahli* Verhoeff, 1926 is regarded as a junior synonym of *Titanethes albus* (C. L. Koch, 1941). Within the genus *Cyphonethes*, a new species, *C. tajanus* is described and as such the genus is considered as including three species: *Cyphonethes herzegovinensis* Verhoeff, 1900, *C. biseriatus* (Verhoeff, 1900) and *C. tajanus* Karaman & Horvatović, 2018. The genus *Microtitanethes* Plakic, 1977, with the sole species *M. licodrensis* Plakic, 1977 is considered as synonymous with the genus *Cyphonethes*, respectively the species *M. licodrensis* as synonymous with the species *C. biseriatus*. Also, a new genus, *Cetinjella* with a new species *C. monasterii* is instituted.

Studies following the analysis of the tribe Spelaeonethini refuted two significant differential characters frequently used in identification keys for the genera. Thus, as we have noted, the endopodite of the male second pleopode is no longer considered as a difference between the genera as at some genera this appendage is bi-articulated while at other genera is triarticulated. There is at present an accord among the isopodologists not to consider the differentiation of the basipodite as an independent article. But we can point out that some papers describe the endopodite of pleopod 2 as biarticulated while in the figures it is clearly triarticulated. A second character which cannot be considered as a difference among the genera is the number of penicilli on the mandibles between the *pars incisiva* and *pars molaris*, as at some genera with numerous species, there are differences among the species.

On another side, we note at KARAMAN & HORVATOVIĆ (2018) the tendency to accord an exclusive significance to the conformation of the maxilliped. Taking into account the high diversity in the conformation of the maxilliped within genera with numerous species, we cannot share this opinion.

As we showed, within the tribe Spelaeonethini, the shape of the body, respectively the ratio between pereion and pleon, the genera *Bulgaronethes* and *Karamanoniscus* are characterized by well-developed pleonal epimerae (neopleuron). In our opinion, within the Section Synocheta, the developed pleonal epimerae do not represent a plesiomorphy but a reversion. We take into account that in Section Microcheta (*Mesoniscus*), the more basal sister group of Section Synocheta (TABACARU & GIURGINCA, 2019, 2020), the pleon is obviously narrower than the pereion. We also take into account that studies on fossil Oniscidea (BROLY & ALL., 2015; SANCHEZ-GARCIA & ALL., 2021) showed that the pleon is much narrower at Cretaceous Synocheta (*Autrigoniscus* and *Myanmariscus*). We also mention that HENNIG (1982, P. 116), in agreement with Remane, emphasized the possibility and the frequency of reversions. As we have pointed out, the pleonal epimerae of *Bulgaronethes* and *Karamanoniscus* are convergences looking like reversions. As such, they are autapomorphies useful to describe the respective taxa but with no value in establishing the phylogenetic relationships.

Based on our data, the visual apparatus is an important character for the definition of the genera of the Trichoniscidae. There are two types of visual apparatus at Trichoniscidae, namely either three small ommatidia or one big ommatidia. There is no genus within this family with both types of visual apparatus. Within the Spelaeonethini, at *Protonethes* and at *Hyloniscus* there is a sole big ommatidia while at *Tachysoniscus* and *Nippononethes*, there are three small ommatidia. But the majority of the species of the Spelaeonethini are troglobionts completely depigmented and without a visual apparatus.

SCHMÖLZER (1965) considered *Spelaeonethes* Verhoeff, 1932 as the type genus when he established the tribe Spelaeonethini. But the definition of this tribe also raised several problems. Also, within the tribe Spelaeonethini, two genera containing a high number of species, sometimes with very diverse characters raise problems regarding their definition. It is the case of the genus *Alpioniscus* Racovitza, 1908 and the genus *Hyloniscus* Verhoeff, 1908. The genera *Troglonethes* and *Hondoniscus* are also not clearly defined.

Genus *Spelaeonethes* Verhoeff, 1932

Verhoeff established the genus *Spelaeonethes* for the species *S. nodulosus* discovered by Karl Strasser in a cave in Northern Italy (Oliero, Brenta Valley). This species becomes automatically the type species of the genus and, as we have pointed before, the genus type cannot be changed with *S. medius* as VANDEL (1973) proposed. At present, four species are included within this genus: *S. nodulosus* Verhoeff, 1932, *S. medius* (Carl, 1908) (syn. *S. occidentalis* Vandel, 1972), *S. mancinii* (Brian, 1913) and *S. brixensis* Brian, 1938 (syn. *S. briani* Arcangeli, 1938).

While establishing the genus *Spelaeonethes*, Verhoeff considered it as close to the genus *Titanethes* but he separated these two genera from the genus *Illyrionethes* (at present a subgenus of *Alpioniscus*) and from *Caucasonethes* considering the endopodite of pleopod 2 as biarticulated at the first two genera and triarticulated at the latter two. VANDEL (1953, 1960) considered the genus *Spelaeonethes* as close to the genus *Protonethes* and *Alpioniscus* differing according to Vandel from the first genus by the number of penicilli on the mandibles and from the second by the biarticulated endopodite 2 instead of triarticulated. Both characters, as we have showed, are no longer usable to differentiate the genera. As the genus *Spelaeonethes* is not well defined, a series of species have been included in this genus before being moved to other genera. This is the case of the species *Libanonethes novus* (Arcangeli, 1953), *Nesiotoniscus dianae* (Vandel, 1953), *N. affinis* (Argano & Manicastri, 1990), *N. grafitti* (Argano & Manicastri, 1990), *N. ferrarai* (Argano & Manicastri, 1990) and the species discussed by us here, namely *Alpioniscus castellonensis* (Cruz & Dalens, 1990).

There are several attempts (VANDEL, 1953, 1960, 1972; PAOLETTI, 1980) to define the genus *Spelaeonethes*, but the most precise diagnosis is that of TAITI & FERRARA (1996). Based on this diagnosis, the description of the four species included in this genus and a comparison with the other genera of the tribe

Spelaeonethini, we can note for the genus *Spelaeonethes* the following differential characters for the male: pereiopode VII without a hook on the meros (sexual differentiations on pereiopode VII exist only at the species *S. medius*); triangular first pleopod exopodite with an apical rod while the endopodite has a conical proximal article, much shorter than the exopodite, but with a long apical rod; pleopod 2 endopodite with the distal article longer than the proximal article (approximately 2.5 times longer), robust and ending in a short, stiletto-like processus at the tip.

Genus *Hyloniscus* Verhoeff, 1908

VERHOEFF (1908) established the genus *Hyloniscus* for four species: *H. vividus* (C.L. Koch, 1841), *H. marginalis* (Verhoeff, 1901), *H. narentanus* Verhoeff, 1908 and *H. mariae* Verhoeff, 1908. *H. vividus* was established as the type species of the genus but considering the synonymy with *Itea riparia* (C.L. KOCH, 1838), the type species of the genus is named *Hyloniscus riparius* (C.L. KOCH, 1838). It the sole expansive and widespread species of the genus.

In the analysis of the tribe Spelaeonethini (TABACARU, 1996), 27 species of *Hyloniscus* have been included and, since then, one more species was described, *Hyloniscus zorae* Karaman & Cemerlic, 1999 but it was considered as synonymous with *Hyloniscus beckeri* Herold, 1939 (SCHMALFUSS, 2003).

Concerning the importance of the different characters in the definition of this genus, we have to point out that Vandel had sustained in time some contradictory opinions. In 1953, while he established the classification of the Trichoniscinae genera, Vandel isolated the genus *Hyloniscus* in a legion apart based on the differentiation of the male 2 pleopod endopodite, namely robust and ending like a funnel. He argued for the same opinion in the volume included in the series *Faune de France* (1960, P. 139). Subsequently, VANDEL (1965) described a remarkable new species, collected by P. Beron and B. Antonov in a cave from Bulgaria, which he included in the genus *Hyloniscus*. This species, named by him *H. flammula*, is the sole troglobitic, depigmented and blind species of the genus. As *H. flammula* the male 2 pleopode endopodite is pointed at the tip, unlike the other species of this genus, Vandel considered the genus *Hyloniscus* as defined by the hook on the male pereiopode VII meros and the elongated and apically lobed male 1 pleopod exopodite. In 1968, probably in order to endorse a certain biogeographic hypothesis, VANDEL included in the genus *Hyloniscus* a new, troglobitic species discovered in Japan, although it had many difference with the species of this genus. Vandel considered in the case of this species only the thickened pleopod 2 endopodite. In 1970, VANDEL, attempting to argue that *Mexiconiscus* is included in the first tribe and is not close to the genus *Hyloniscus*, said: "En effet, le caractère le plus remarquable du genre *Hyloniscus* reside dans la complexité de structure de l'exopodite du premiere pleopode male, alors que cet appendice ne présente aucune differenciation particulière chez *Mexiconiscus*" (Indeed, the most remarkable character of the genus *Hyloniscus* resides in the structural complexity of the male first pleopod, while this appendage lacks any particular differentiations at *Mexiconiscus*).

We have argued (TABACARU, GIURGINCA, SÂRBU, 2023) that *Mexiconiscus* is not included in the tribe Typhlotricholigioidini but within the tribe Spelaeonethini as the male first pleopod endopodite is provided with a rod. Regarding the genus *Hyloniscus*, considering that subsequently three new species without a robust pleopod 2 endopodite have been described, we agree with Vandel: the most significant character of the genus is the structure of the male first pleopod exopodite.

Genus *Alpioniscus* Racovitza, 1908

RACOVITZA (1908, P. 370) established the genus *Alpioniscus* for the species *Trichoniscus dispersus* Racovitza, 1907. In his study, Racovitza established and provided detailed diagnoses for a series of subgenera, within the genus *Trichoniscus*, which, subsequently, have been considered genera: *Oritoniscus*, *Phymatoniscus*, *Scotoniscus*, *Nesiotoniscus* and *Alpioniscus*. But the species *Trichoniscus* (*Alpioniscus*) d*ispersus* Racovitza, 1907 was regarded as synonymous with *Alpioniscus feneriensis* (Parona, 1880), initially describes as *Titanethes feneriensis* Parona, 1889, which is therefore the type species of the genus.

Alpioniscus is a genus distributed in the Mediterranean region from Spain to the Balkanic Peninsula.

In the 1996 analysis, 27 species were included in the genus *Alpioniscus*, respectively 12 in the subgenus *Alpioniscus s. str*. and 15 in the subgenus *Illyrionethes* Verhoeff, 1927. Since then, 14 more species have been described: *A.* (*I.*) *kuehni* (Schmalfuss, 2005), *A.* (*I.*) *thanit* Taiti & Argano, 2009, *A. beroni* Andreev, 2013, *A. gueorguevi* Andreev, 2013, *A.* (*I.*) *iapodicus* Bedek, Horvatović & Karaman, 2017, *A.* (*I.*) *stochi* Taiti & Argano, 2018, *A.* (*I.*) *sideralis* Taiti & Argano, 2018, *A.* (*I.*) *onnisi* Taiti & Argano, 2018, *A.* (*I.*) *hirci* Bedek & Taiti, 2019, *A.* (*I.*) *velebiticus* Bedek & Taiti, 2019, *A.* (*I.*) *lossini* Bedek, Gottstein &Taiti, 2019, *A.* (*I.*) *drazinai* Bedek, Gottstein & Taiti, 2019, *A.* (*I.*) *mandalinae* Bedek, Gottstein & Taiti, 2019, *A* (*I.*) *busljetai* Bedek, Gottstein & Taiti, 2019. To these, should be added the two species which we include here in the genus *Alpioniscus*, respectively *Alpioniscus* (*Illyrionethes*) *skopjensis* Buturović, 1955 and *Alpioniscus* (*Alpioniscus*) *castellonensis* (Cruz & Dalens, 1989), so, in total, there are 43 species included in the genus *Alpioniscus*.

Although there are recent, detailed diagnoses (BEDEK & TAITI, 2011, BEDEK, 2019), considering the species diversity, it is difficult to pinpoint the synapomorphic characters able to define the genus. Depending on the length ratio of the articles of the male 2 pleopod endopodite, two subgenera can be distinguished: *Alpioniscus* s. str. with the proximal article shorter or equal in length with the distal article; *Illyrionethes* Verhoeff, 1927 with the proximal article longer than the distal article.

Also, as we have pointed out (TABACARU, 2021), there are groups of species. Thus, *A. henroti* Vandel, 1964, *A. epigani* Vandel, 1959, *A. matsakisi* Andreev, 1984 and *A. giurensis* Schmalfuss, 1981 are characterized by the elongated and with an apical differentiation on the male 1 pleopod exopodite. From the species of *Alpioniscus* from Sardinia (TAITI & ALL., 2018), another group of species:

A. kuehni (Schmalfuss, 2005), *A. stochi* Taiti & Argano, 2018 and *A. sideralis* Taiti & Argano, 2018, is characterized by the conformation of the maxilliped endite.

Genus *Troglonethes* Cruz, 1989

CRUZ (1989) established the genus *Troglonethes* Cruz, 1989 for the troglobitic species collected in a cave from Spain (Valencia), namely *T. aurouxi* Cruz, 1989. Other three troglobitic species, also found in the Iberian Peninsula, have been included in this genus: *T. olissipoensis* Reboleira & Taiti, 2015 and *T. arrabidaensis* Reboleira & Taiti, 2015 from caves in Portugal, while the species *T. fonsocalvoi* Cifuentes & Prieto, 2021 was collected in numerous caves from Spain (Bizkaia, Burgos, Cantabria) (REBOLEIRA & all., 2015, CIFUENTES & PRIETO, 2021). CIFUENTES & PRIETO (2021) maintained that *Troglonethes* can be separated from the other three genera (*Spelaeonethes*, *Alpioniscus*, *Libanonethes*) from the Second Legion (VANDEL, 1960), found in the caves of the Iberian Peninsula, using the identification key of CRUZ (1989). But in the key provided by CRUZ, the genus *Troglonethes* is differentiated by the number of articles of the male 2 pleopod endopodite and by the number of penicilli from the right mandible. As we have showed, both characters are not usable to define the genera.

Analyzing the descriptions of the four species attributed to the genus *Troglonethes*, we note that the species differ between them especially by the conformation of the distal article of the male 2 pleopod endopodite, but we cannot see any synapomorphic characters that might clearly define the genus. The genus *Troglonethes* is close to the genus *Alpioniscus* and they present the male 2 pleopod endopodite distal article much shorter than the proximal article and, in the distal portion, with an outwards curve.

Genus *Hondoniscus* Vandel, 1968

VANDEL (1968) established the genus *Hondoniscus* for the troglobitic species discovered in a cave in Japan (Iwate Prefecture) *H. kitakamiensis* Vandel, 1968. Subsequently, two more species found in Japan have been attributed to this genus: NOBURU NUNOMURA (1990) described a new, troglobitic species *H. mogamiensis* Nunomura, 1990 (from Yamagata Prefecture), and NUNOMURA & KOMATSU (2018) described the species *H. ureirensis* Nunomura & Komatsu, 2018, from the underground of the mountainside of Mount Ureira (Iwate Prefecture).

The two troglobitic species are described as depigmented and eye-less but for the species *H. ureirensis*, the authors maintained: “eyes present, each with 7-8 ommatidia, but each not distinctly and strictly discerned”. This is a bizarre statement since there is no mention of a Synocheta with more than three ommatidia. NUNOMURA (1983), KOMATSU & NUNOMURA (2019), NUNOMURA & all. (2021) provided a redescription of the species *H. kitakamiensis* completing the short description made by Vandel. However, analyzing the description and the illustration provided for the three species, we could not find any synapomorphic character which might define the genus *Hondoniscus* and, as a consequence, we do not include the genus *Hondoniscus* in our identification key. Besides, a comparison

of the figures given by the authors for the male 1 and 2 pleopodes at the three species does not argue for their inclusion in the same genus. The male 1 and 2 pleopod exopodite at *H. mogamiense* seem to be very different from the same appendage at the other two species.

Genus *Libanonethes* Vandel, 1955

Within the identification keys of the genera included in the tribe Spelaeonethini (TABACARU, 1993, 1996), the genus *Libanonethes* Vandel, 1955 was considered only through the type species as the second species of this genus presents remarkable morphological differences and we could not be sure about its appartenance within this genus.

The genus *Libanonethes* was established by Vandel for a species discovered by Coiffait and Anavy in three caves from Liban, situated close to Beirut and named *L. probosciferus* Vandel, 1955. It is a troglobitic species with remarkable sexual characters in males at the pereiopode VII, pleopod 1 endopodite and the pleopod 2 exopodite. The second species was attributed to this genus only based on the similarity of the pleopod 1 endopodite and namely the fusiform and densely ciliated rod of the endopodite. This second species was described from Spain (las Minas de Canal, Espluga, prov. Lerida) under the name *Trichoniscus* (*Trichoniscus*) *novus* Arcangeli, 1935. It was redescribed by VANDEL (1953) on material from the type locality and other caves from Spain and included within the genus *Spelaeonethes*. Subsequently, VANDEL (1972) completed the description of the species and placed it within the genus *Libanonethes*. We note that the species *L. probosciferus* was also collected in Greece (Kasos Island) while the species *Libanonethes novus* was recorded in many caves from Northeastern Spain.

In the following identification key, we consider both species in the genus *Libanonethes* but mentioning only the character regarding the pleopode 1 male endopodite.

Identification key for the genera of the Tribe Spelaeonethini

1 (2) Pleopod 1 male exopodite has an oval shape with a lateral-extern digitiform lobe; pleopod 2 male endopodite with a distal article laterally oriented but medial-ventral recurved at the tip; pereiopodes 1-4 subchelate.....***Karamanoniscus*** Tabacaru, 2021.

Monotypic genus; troglobitic species, depigmented and without ocelli, collected from a spring located in the cave at the source of the Babuna River (Macedonia) (KARAMAN, 2003).

2 (1) Pleopod 1 male exopodite triangular; pleopod 2 male endopodite not medial-ventral recurved; no subchelate pereiopodes…….3

3 (4) Cephalon, pereion and pleonite 3 with tergal protuberances; pereiopode 7 male with a long digitiform lamella at the distal part of the ischium……..…. ***Bulgaronethes*** Vandel, 1967.

Monotypic genus; troglobitic species, depigmented and without ocelli, found in two caves from Bulgaria (BERON, 2020).

4 (3) Body without tergal protuberances, at most with granulations; pereiopode 7 male ischium without a digitiform lamella……..5

5 (8) Ocular apparatus formed by a big ommatidia (except for *Hyloniscus flammula*)……...6

6 (7) Pleopod 1 male exopodite apically differentiated in a lobe; pereiopode male 7 meros with a prominence or a hook……... ***Hyloniscus*** Verhoeff, 1908

Genus containing 26 species with pigmented tegument and one big ocellus, except for *H. flammula*, the sole troglobitic species, depigmented and without ocelli, found in Bulgaria. The genus is distributed in Central Europa, Carpathian regions, Italy, Balkanic Peninsula; only *H. riparius* is an expansive species that reached North America.

7 (6) Pleopod 1 male exopodite apically rounded without any differentiation; pereiopode male 7 meros without any prominence or a hook……..***Protonethes*** Absolon et Strouhal, 1932.

Monotypic genus. The species is yellowish-white with a big ocellus; found in Montenegro.

8 (5) Ocular apparatus made by three small ocelli or absent ……. 9

9 (10) Pleopod 2 male endopodite robust and ending in a pedunculated vesicle……...***Nippononethes*** Tabacaru, 1996.

The genus contains 6 species found in Japan, only one, *H. kuramotoi* Nunomura, presents 3 small ocelli, the other species are blind and depigmented.

10 (9) Pleopod 2 male endopodite without an apical pedunculated vesicle……..11

11 (12) Three pigmented ocelli; apically, the genital apophysis presents a tip bordered by two lobes……..***Tachysoniscus*** Verhoeff, 1930.

Monotypic genus. Species known from North Italy, Austria, Slovenia, Croatia, Bosnia and Hercegovina.

12 (11) Ocular apparatus completely absent; the genital apophysis is simple, narrowed toward the tip ……..…...13

13 (14) Pleopod 1 male endopodite with a widened, fusiform, densely ciliated rod…….***Libanonethes*** Vandel, 1955.

Two troglobitic species, one known from Lebanon and Greece (Kasos Island), the other from North-Eastern Spain.

14 (13) Pleopod 1 male endopodite never shaped like a fusiform rod, but is simple and thin, or like a rigid rod, ……..…....15

15 (24) Pleopod 1 male endopodite with a thin, flagellum-like, more or less ciliated rod……..……16

16 (17) Pleopod 2 male exopodite oval and very small, much shorter than the basal article of the endopodite; pleopod 2 male endopodite robust until the tip……...***Mexiconiscus*** Schultz, 1964.

Monotypic genus; troglobitic species found in several caves from Mexico, in the south of the San Luis Potosi province.

17 (16) Pleopod 2 male exopodite never reduced so much; pleopod 2 male endopodite is narrow or at least narrowed at the tip…….……...18

18 (19) Pleopod 1 male exopodite apically curved toward the external side like a horn and presenting a subapical tooth.....***Aegonethes*** Frankenberger, 1938.

Two troglobitic species, recorded in caves from Croatia (Dubrovnik and the Korcula, Vis and Mljet islands) and from Italy (Gargano).

19 (18) Pleopod 1 male exopodite triangular with / without an apical rod but never curved like a horn…….…….20

20 (21) Pleopode 1 male endopodite triangular, short and wide at the base; pleopode 2 male endopodite as robust as the basal article but much longer ending in a short, stiletto-like processus at the tip…….***Spelaeonethes*** Verhoeff, 1930.

The genus includes 4 troglobitic species, known from Italy, Southern France and Northern Spain.

21 (20) Pleopode 1 male endopodite is narrow and as long as the exopodite; pleopode 2 male endopodite ends without a short, stiletto-like processus……..22

22 (23) Pleopode 2 male endopodite with the distal article much shorter than the proximal article (less than half), apically very different according to each species, but always curved toward the external side……***Troglonethes*** Cruz, 1991.

The genus contains four troglobitic species, two known from one cave each from Portugal, one species from a cave in Eastern Spain and one from many caves in Northern Spain.

23 (22) Pleopode 2 male endopodite with the distal article longer or equal in length with the proximal article (sg. *Alpioniscus* s. str.) or much shorter than the proximal article (sg. *Illyrionethes*), but the tip is not curved like a hook toward the external side……..***Alpioniscus*** Racovitza, 1906.

The genus includes 43 species, most of them troglobitic, some are stygobitic (*A. kuehni*, *A. stochi*, *A. sideralis*) and one was found in the endogeous (*A. thanit*). It is distributed in the Mediterranean region from North-Eastern Spain to Eastern Greece (TAITI & ALL., 2018; BEDEK, 2019).

24 (15) Pleopode 1 male endopodite distinctly biarticulated, the distal article being a rigid rod and not a flagellum-like rod……..……..25

25 (26) Pleopode 1 male endopodite with the distal article shorter than the basal article; pleopode 2 male endopodite distal article robust with a sharp tip……..***Titanethes*** Schiödte, 1849.

Considering the latest revision of the genus (KARAMAN & HORVATOVIĆ, 2018), *Titanethes* contains a single large sized, troglobitic, depigmented and blind species, distributed in caves from North-Eastern Italy, Slovenia, Croatia.

26 (25) Pleopode 1 male endopodite with the distal article longer than the basal article; pleopode 2 male endopodite with a very long and apically narrowed distal article.....27

27 (28) Maxilla 1 endopodite with very short penicilli; pereiopodes with notably elongated, fused dactylus and unguis almost the same length as propodus…….***Cetinjella*** Karaman & Horvatović, 2018.

Monotypic genus. Troglobitic, depigmented and blind species, discovered in a cave from Cetinje, Montenegro.

28 (27) Maxilla 1 endopodite with normally developed penicilli; dactylus and unguis visibly shorter than propodus and not unusually long…..***Cyphonethes*** Verhoeff, 1926.

Following the latest taxonomic revision (KARAMAN & HORVATOVIĆ, 2018), the genus includes three troglobitic species distributed in Serbia, Bosnia and Hercegovina, Macedonia, Montenegro.

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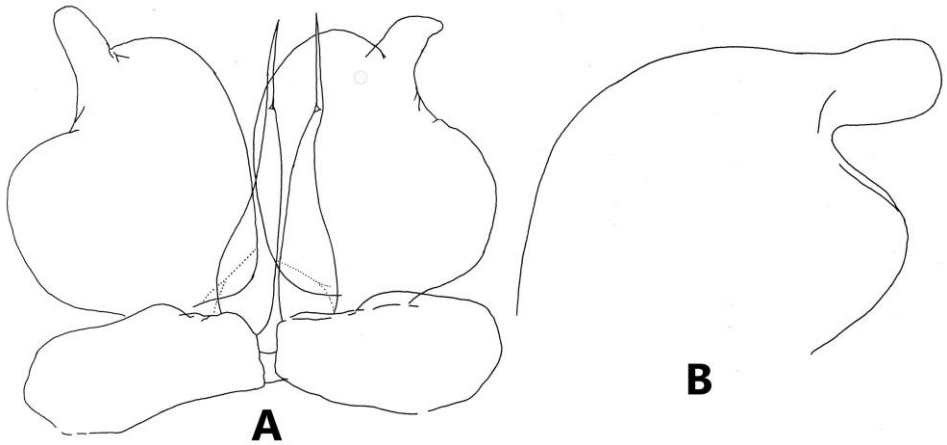

Fig. 1. Karamanoniscus stankoi (= Macedonethes stankoi): A. Pleopod 1 male (after KARAMAN, 2003); B. *Catalauniscus pudui*: Pleopod 1 male (after ARGANO, 1973).

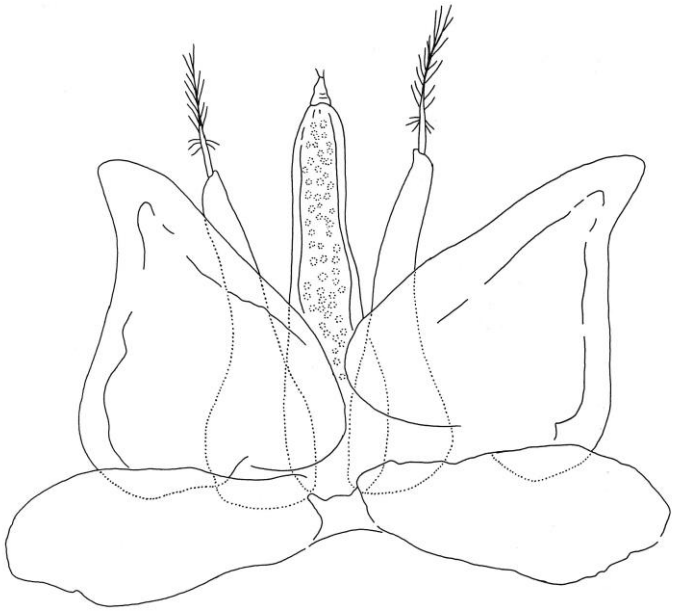

Fig. 2. Alpioniscus castellonensis (= Macedonethes castellonensis, *Spelaeonethes castellonensis*): Pleopod 1 male (after CRUZ & DALENS, 1989).

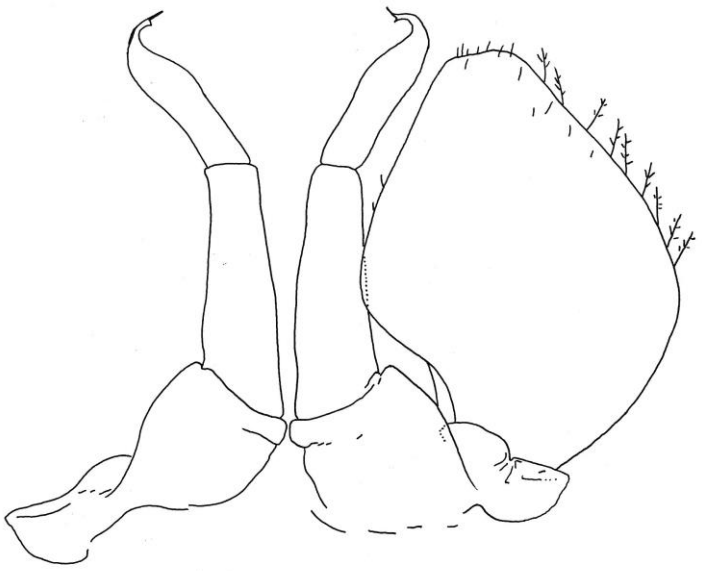

Fig. 3. Karamanoniscus stankoi (= Macedonethes stankoi): A. Pleopod 2 male (after KARAMAN, 2003).

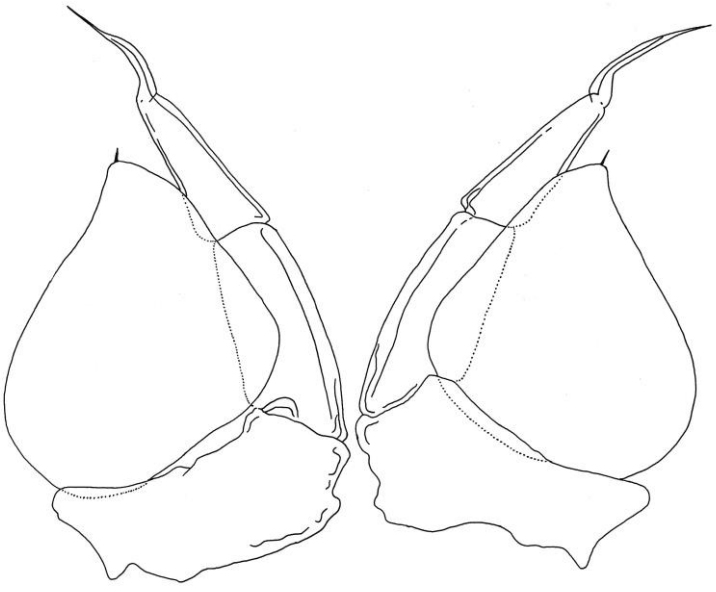

Fig. 4. Alpioniscus castellonensis (= Macedonethes castellonensis, Spelaeonethes castellonensis): Pleopod 2 male (after CRUZ & DALENS, 1989).