ON THE STRUCTURE OF THE STOMACH AT *MESONISCUS* (ISOPODA, ONISCIDEA, MICROCHETA). THE CONSTITUTIVE ELEMENTS OF THE STOMACH AT ISOPODA

IONEL TABACARU, ANDREI GIURGINCA

Sur les relations phylogénétiques ainsi que sur la position systématique des Mesoniscidae (Microcheta, Oniscidea) ont été argumentées des opinions très différentes. En vue de contribuer à l'élucidation du problème, après une succincte analyse des principaux éléments constitutifs de l'estomac des Isopodes, on donne une description de l'estomac chez les espèces du genre *Mesoniscus*.

1. INTRODUCTION

Considering their morphological structures and their varied way of life, the Isopoda represent one of the most complexe and diversified orders of the Malacostraca. They inhabit seas and oceans, from the abyssal zone to the seashore and brackish, surface and subterranean freshwaters, as well as the terrestrial environments from wet areas to arid, desertical ones.

The terrestrial Isopoda, respectively the suborder Oniscidea, are remarkable through the high number of representatives (approx. 400 genera and 4000 species) and being the sole group of Crustaceans which really conquered the terrestrial domain from sandy seashores to altitudes of 4700 m (Vandel, 1943, 1960; Gruner, 1995/1996; Schmalfuss,1983; Wägele, 1989; Tabacaru & Danielopol, 1996a, 1996b, 1999; Roman & Dalens,1999).

Contrary to the opinion sustained especially by Vandel (since 1943 to the end of his life) that terrestrial Isopods represent a heterogenous ensemble formed by phyletic lines with different origins, more recent researches (Schmalfuss, 1989; Wägele, 1989; Tabacaru & Danielopol, 1996a, 1996b, Tabacaru, 2002) proved the monophyly of this order.

The stomach of the Malacostraca has a very complexe constitution and numerous authors emphasized the importance of its study from a phylogenetic and systematic point of view (Vandel, 1943; Siewing, 1956; Mathes, 1956; V.V. Radu, 1959, 1961; Flasarova, 1967; Tomescu, 1974; Scheloske, 1976a; V.Gh. Radu, 1983; Wägele, 1989; Tabacaru et Danielopol, 1996b; Tabacaru & Platvoet, 2000). We should specify that studying the stomach of the crustaceans has numerous difficulties. First of all, there is the inherent and objective difficulty of investigating and understanding the structure of a very complicated, tubular internal

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organ with numerous superposed elements. Usually, in describing a species, this organ is not described or figured so in the vast majority of the species (whole groups, we may say) the constitution of the stomach is unknown. Hence the difficulty of any interpretation of the phylogenetic evolution of this organ. In addition, the comparative studies encounter difficulties in the homologation of diverse pieces. Often, descriptions given by different authors are incomplete as they include only transversal sections of the stomach. As Haffer (1965) pointed out: "Die Verwendung von Totalpräparaten der Chitinintima von Kaumägen malakostraker Krebse gestattet einen direkten Vergleich dieser komplizierten Gebilde. Sie machen bessser als Schnittpräparate augenfällig, wie weitgehend in den verschiedenen Mägen die gleichen Stücke vertreten sind. Ihre im gemeinsamen Verband gleichbleibende Einordnung – bei unterschiedlicher Form und Ausprägung in den einzelnen Gruppen – ermöglicht die Identifizierung und Homologisierung."

Another difficulty comes from the utilization of different names for the same structures of the stomach.

2. THE GENUS *MESONISCUS* AND ITS SYSTEMATIC POSITION

A revision of the family Mesoniscidae (Gruner and Tabacaru, 1963), based on the study of a very rich material including the types of the species described by Verhoeff, arrives at the conclusion that the family includes a sole genus, *Mesoniscus* Carl, 1906 with two species: *Mesoniscus alpicola* (Heller, 1858) and *Mesoniscus graniger* (Frivaldsky, 1865). This conclusion is the result of finding that the three species described as belonging to a separate genus, *Nematoniscus* Verhoeff, 1930 (*N. prenjanus* Verh., 1901, *N. triangulifer* Verh., 1930 and *N. illyricus* Verh., 1933), the species *M. histrianorum* Arcangeli, 1939 and the subspecies *M. alpicola vulgaris* Chappuis, 1944 and *M. alpicola meridionalis* Chappuis, 1944 are as a matter of fact synonymous with *M. graniger* while the species *M. cavicolus* Carl, 1906, *M. calcivagus* Verhoeff, 1914 and *M. subterraneus* Verhoeff, 1914 are synonymous with *M. alpicola.*

The isolated position of the genus *Mesoniscus* in a separate family, and consequently the validity of the family Mesoniscidae Verhoeff, 1908, is unanimously recognised but the phylogenetical and systematical position of this family within the framework of the suborder Oniscidea is still a much debated problem.

Thus, in the classification of the terrestrial Isopods proposed by Verhoeff (1938), the family Mesoniscidae is included beside the family Ligiidae in the group *Protophora arhaica.* In 1943, Vandel replaces this name with *Protoniscoidea* and in 1957 with that of *Diplocheta*, the representatives included here being characterized by the presence of two genital apophyses in opposition with *Synocheta* Legrand, 1946 and *Crinocheta* Legrand, 1946 which present a sole genital apophysis. We notice that Vandel (1945, 1957) considered *Mesoniscus* as

an intermediary type between the Ligiidae (Diplocheta) and the Trichoniscidae (Synocheta) taking into account the fact that in *Mesoniscus* the two genital apophyses are reduced and convergent in such a way that the spermatophores are joined, forming a unique one.

Both the term *Protoniscoidea* Vandel, 1943 and that of *Diplochaeta* Vandel, 1947, as they result from the phylogenetical patterns given by Vandel (1943, 1945, 1957), are not monophyletic taxa, according to modern phylogenetic systematics (as Hennig sees it) but a step characterized by a certain constitution in the evolution of the genital apophysis.

Ulteriorly, Vandel, in his last papers (1965, 1967), as a result of the discovery of the remarkable aquatic Trichoniscid *Cantabroniscus primitivus* (which he regarded as «the most primitive and oldest of the known Oniscoids»), considered the Mesoniscidae as a side line originating in the Ligiidae while the Trichoniscidae (in general the Synocheta) as an independent line originating directly from the marine Isopods. Some authors share this hypothesis that the aquatic way of life is the primitive way of life of some species belonging to the superfamily Trichoniscidea that implies a direct origin in an aquatic ancestor but numerous arguments contradict this hypothesis (Tabacaru, 1993; Tabacaru, 2002; Tabacaru and Danielopol, 1996a).

In his ample study on the evolution and phylogeny of Isopods, Wägele (1989) considered the suborder Oniscidea as divided into three sections, respectively Diplocheta, Synocheta and Crinocheta, but in the section Diplocheta he includes, beside the Ligiidae and Mesoniscidae, the family Tylidae considered by Vandel as an apart lineage, the "série tylienne".

At the same time, Schmalfuss (1989) suggests a quite different classification in which only the family Ligiidae is kept within the section Diplocheta but the family Mesoniscidae is considered in an apart section Microcheta, more closely related with the group Synocheta + Crinocheta than with the family Ligiidae.

The existence of a monophylum Microcheta + Synocheta + Crinocheta is argumented through numerous synapomorphies by Erhard (1995a, 1995b, 1996, 1998) and by Tabacaru and Danielopol (1996a, 1996b). For this monophylum, the name *Orthogonopoda* Tabacaru et Danielopol, 1996 was proposed.

At present, there are different opinions concerning the phylogenetical and systematical position of the taxa Microcheta (Mesoniscidae) within the monophylum Orthogonopoda. Thus, the opinion of Schmalfuss (1989) and Erhard (1995a, 1995b, 1996, 1998) is that Microcheta forms the sister-group of the ensemble Synocheta + Crinocheta. In the manner of Wägele (1989), Schmalfuss and Erhard regard Synocheta and Crinocheta as a monophylum for which Erhard (1998) re-establishes the name Euniscoidea Vandel, 1943, initially instituted in opposition to Protoniscoidea (Ligiidae + Mesoniscidae). On the contrary, Tabacaru and Danielopol (1996a, 1996b) argue a phylogenetic scheme in which the section Microcheta and

section Synocheta form a monophylum (the group Monospermophora) in his turn a sister-group of the section Crinocheta (the group Dispermophora).

Tabacaru and Danielopol (1996), on the one hand, and Erhard (1998), on the other hand, based on different cladograms regarding the evolution of suborder Oniscoidea, propose two different classifications (Table 1 and Table 2).

Table 1

The classification proposed by Tabacaru and Danielopol (1996b)

Suborder **Oniscidea** Latreille, 1929
Infraorder **Tylomorpha** Vandel, 1943
Family Tylidae
Infraorder **Ligiamorpha** Vandel, 1943
Suprasection **Diplocheta** Vandel, 1957
Family Ligiidae
Suprasection **Orthogonopoda** Tabacaru and Danielopol, 1996
«Group **Monospermophora**»
Section **Microcheta** Schmalfuss, 1989
Family Mesoniscidae
Section **Synocheta** Legrand, 1946
6 families
«Group **Dispermophora** »
26 families

Table 2

The classification proposed by Erhard (1998)

Suborder **Oniscidea** Latreille, 1829
Diplocheta Vandel, 1957
Family Ligiidae Brandt, 1833
Holoverticata Erhard, 1998
Tylida Erhard, 1998
Family Tylidae Milne- Edwards, 1840
Orthogonopoda Tabacaru & Danielopol, 1996
Microcheta Schmalfuss, 1989
Family Mesoniscidae Verhoeff, 1908
Euoniscoida Vandel, 1943
Synocheta Legrand, 1946
5 families
Crinocheta Legrand, 1946
26 families

As Erhard (1996) stated, we consider that this contradictory phylogenetic debate should lead to searching for more significative morphological characters. To identify this kind of characters we proposed a more accurate re-examination of the stomach at *Mesoniscus* as the sole description (Radu Varvara, 1950) is not enough for the precise understanding of the structure and for the comparison with the structure of the stomach in other groups of Oniscoidea.

3. THE STOMACH AT ISOPODA – CONSTITUTIVE ELEMENTS

At the anterior extremity, the oesophagus is dorsally delimited by the upper lip (labium, epistom), ventrally by the inferior lip (labium, hypostom, hypopharynx, paragnathes) and laterally by the mandibles. In Oniscids the oesophagus is narrow while the stomach appears as a sudden dilatation. We specify this because among the aquatic Isopods there are groups, like the Cirolanids, with a very wide oesophagus. In Anthurids the oesophagus is very long while the stomach is situated in the first or the second pereional segment and not in the cephalothorax as in the majority of Isopods.

The passage from the oesophagus to the stomach is bordered by chitinous thickenings. At Isopoda, there are always two slightly caudally prolonged lateral prominences; often, these prominences are equipped with hairs. Vandel (1943) named these formations "protubérances marginales" after Ide (1892); initially, Flasarova (1967, 1968) uses also the term "protubérances marginales" but afterwards (1969) she introduces the Latin term "Tubercula marginales". At the passage from the oesophagus to the stomach there might exist, more or less pronounced, a dorsal and a ventral prominence. Hassal (1977) adopts after Nicholls (1931) the term ampulla and distinguishes at the junction between the oesophagus and the proventriculus, four ampullae: "anterior median ampulla" (arising from the dorsal wall), two "antero-lateral ampullae" and a "ventral ampulla". We consider the use of the term ampulla for these formations can lead to confusions as this term is used by the same authors (Nicholls, 1931; Kensley, 1974; Hassal, 1977; Hames & Hopkin, 1989) for features from the inner part of the stomach. We find the terms proposed by Scheloske (1976 a): Valvula dorsalis oesophagi, Valvulae lateralis oesophagi, Valvula ventralis oesophagi, more appropriate.

The majority of authors divide the Isopod stomach into two parts: an anterior part, Cardia or the cardiac region containing a triturating apparatus, and a posterior part, Pylorus or the pyloric region containing a filter apparatus (Barnard, 1924; Vandel, 1943; V. V. Radu, 1950; Tuzet, Manier & Ormières, 1959; Flasarova, 1967, 1968, 1969, 1972; Tomescu, 1974; V.Gh. Radu, 1983; Roman & Dalens, 1999; Kobusch, 1999). Inspired by the vertebrate anatomy, the terms Cardia and Pylorus were introduced in 1834 by Milne-Edwards in studying the Decapods stomach and, little by little, were used in describing the stomach in other Malacostraca. In his study "Ist die Unterteilung des Magens der Malacostraca in "Cardia" und "Pylorus", berechtig?" Scheloske (1976 b) argues amply that this division does not agree with a morphological reality nor with a physiological one. If there is some transversal strangling in some Decapods, which might suggest a division of the stomach into two parts, there is no such strangling in Amphipods, Isopods and other Malacostraceans. We notice that Haffer (1965, p. 191) distinguishes two types of stomach: "Dekapodentyp" with a clear distinction between cardia and pylor and "Isopodentyp"

with no separation between cardia and pylor and with an elongated shape. As Huxley pointed out in 1879, Scheloske shows at the same time that the term Cardia is not proper here as the region named "cardiac region" is farther away from the heart than the "pyloric region".

If we consider the stomach of *Mesoniscus*, we cannot distinguish any transversal division of the stomach between a cardiac and a pyloric region. But, especially on the dorsal side, a transversal division line between the free anterior part of the stomach and the posterior part (respectively the caudal lamellae, placed in the gut), can be observed. On the stomach side, the insertion of the lamellae is enforced by a strongly chitinized rod, which marks even more obviously the division between the anterior and the posterior parts.

In our studies, we adopt partially the nomenclature proposed by Scheloske (1976a) and we distinguish in the constitution of the Isopods stomach the following essential elements:

Lateralia – term adopted by Vandel (1943) from Nauk (1880) and Schoninchen (1899), and used by the majority of the authors (Radu, V.V., 1950; Tuzet, Manier, Ormière, 1959; Flasarova, 1967, 1968, 1969, 1972; Licar, 1970; Licar and Sket, 1971; Scheloske, 1976a; Storch, 1987; Storch, Dreyer, Mummert, Böckeler, 1987; Storch and Strus, 1989; Wägele, 1981, 1989, 1992; Brecko, Licar, Rode, 1991; Strus, Drobne, Licar, 1995; Kobusch, 1999; Tabacaru & Platvoet, 2000; Storch, Strus, Brand, 2002). Only some English speaking authors (Tiwari and Ram, 1972; Kensley, 1974; Hasssal, 1977; Hames & Hopkin, 1989) adopted the term "lateral ampullae" used by Nicholls in 1931. Lateralia are two deep lateral invaginations, respectively two hemispheric or oval shaped prominences inside the anterior part of the stomach. The lateralia leave between them a free median gap dorsally covered by the superomedianum or, if this does not exist, by the dorsal wall of the stomach. They present numerous hairs and sometimes teeth. In aquatic Isopods, there are usually more rows of strong teeth which might be split into several spikes at their end. In terrestrial Isopods, only one tooth remains in Diplocheta and Microcheta while in the other sections the teeth disappear completely. Lateralia are missing at Anthuridea and are weakly developed at some Flabellifera (Cirolanidae). In Oniscidea there are always well developed lateralia. In the section Crinocheta, they are very elongated and have on the ventral side in the caudal half one dentated plate; this was noticed for the first time by V. V. Radu (1959) which named it "superior triturating plate" and then by Hassal (1977) who used the same name. Storch (1987) called it "dorsal masticatory area".

Superomedianum – Strangely, Kobusch (1999, p. 144) states that: "None of the authors who described isopod foregut anatomy, mentioned a superomedianum for the Isopoda". The term superomedianum is used by Vandel (1943) after Nauk (1880) and accepted by numerous authors (Radu, V.V., 1950; Tuzet, Manier,

Ormière, 1959; Flasarova, 1968, 1972; Tomescu, 1974; Scheloske, 1976a; Radu, V. Gh., 1983; Storch and Strus, 1989; Kobusch, 1999; Tabacaru & Platvoet, 2000). Tiwari and Ram (1972) used the name "dorsal ampulla". Kensley (1974) used the term introduced by Nicholls (1931): "median-anterior ampulla" or "medio-dorsal ampulla". Superomedianum represents an anterior median prominence situated on the ventral side of the dorsal wall of the stomach above the lateralia. Wägele (1989, 1992) used for this formation the name "valvula dorsalis oesophagi" – following Wägele. We also used this term (Tabacaru, 1994; Tabacaru & Danielopol, 1996a, 1996b). The superomedianum is indeed a continuation of the dorsal wall of the oesophagus but considering this is about a chitinous formation developed on the surface of the dorsal wall of the stomach, sometimes far away from the oesophagus, we think it is better to use the term "superomedianum" and to keep the term "valvula dorsalis oesophagi" for a small membranous prominence situated dorsally, right at the passage from the oesophagus into the stomach. The superomedianum has, usually, the shape of an elongated apically rounded tongue with parallel sides and its median region may be either widened or, on the contrary, narrowed, as is the case at *Mesoniscus*. The superomedianum is always covered with many hairs. Unlike the Tanaidacea and other Peracarida, we did not find any hooks on the superomedianum at any species of Isopoda. There is a particular aspect in the Sphaeromatidae (Flabellifera): a narrow, oval lobe prolongs the superomedianum. The superomedianum is missing in Asellota, Anthuridea, at some Flabellifera (Cirolanidae, Serolidae, Aegidae) and among the Oniscidea it is missing in Crinocheta.

Superolateralia – term used by Scheloske in 1976 and afterwards by Wägele (1989, 1992), Storch, 1987a; Storch and Strus, 1989, Kobusch, 1999; Tabacaru & Platvoet, 2000. Vandel (1943) and after him Tuzet, Manier, Ormières (1959) used the name "lamelle annulaire". This name is not actually erroneous but it was used previously for another formation of the stomach. Flasarova (1967, 1969), Licar (1970), Licar and Sket (1971), Licar, Blejec, Urbanc-Burcic (1979) used the name " plica lateralis". The superolateralia forms two symmetrical folds which begin dorsally, above the lateralia, in their caudal part. Then they descend in a latero-caudal direction and go on the ventral part in a medio-caudal direction reaching a strogly chitinized point under the inferolateralia where the median edge of the ventral lamellae is inserted. In the Asellidae, the superolateralia descend caudally, getting closer to the ventral part but without curving in the median direction. In many species, the superolateralia end on the lateral side of the stomach, missing from the postero-ventral part. The edge of the superolateralia may have hairs or long fringes (*Mesoniscus*). The superolateralia are missing completely at the Anthuridae, at some Flabellifera (Cirolanidae) and among the Oniscidea at the Crinocheta.

Clatri setarum anteriores – term introduced by Scheloske (1976a) and used later on by Wägele (1981, 1989, 1999), Kobusch (1999) and by Tabacaru & Platvoet (2000). Vandel (1943) used the name "plaque broyeuse (plaque triturante cardiaque)"; Flasarova (1967, 1968, 1969, 1972) used the German term "Reibplatte" or "cardiacalen Reibplatten"; Kensley (1974) and Hasal (1977) used the term " bristle plate" while Licar (1976) and Licar and Sket (1971) used the term "scraping plates". The term "primary filter" is also used by: Licar, 1980; Storch, 1987a; Storch and Strus, 1989; Hames and Hopkin, 1989; Wägele, 1992; Kobusch, 1999, Storch, Strus and Brandt (2002). We think as more appropriate the term anterior filter or rough filter. The terms rough filter and fine filter were used by Coleman (1991) at Amphipoda and by Watling (1999) at Peracarida. The clatri setarum anteriores represent two plates made up of a row of parallel setae which may be longer or shorter, denser or rarer in different species. Each of these setal rows covers a filtratory groove. The two setal plates may be set differently: a) the bands form together a U, or O, or a V with the setae directed toward the median line (Phreatoicidea, Asellota); b) the setae bands have the caudal end curved toward the sides of the stomach making up two divergent arches (some Flabellifera, Valvifera, Ligiidae and Tylos); c) the setae bands form together an overturned V with the setae directed medio-caudally (Crinocheta); d) the setae bands form together a very wide opened, overturned V, making up a transversal, nearly straight band with the setae directed posteriorly (Synochaeta, Calabozoidea). The change in the shape of the two filtrating bands implies a move of the groove from the posterior end of the filtrating bands to their anterior end. Laterally and caudally of the clatri setarum anteriores is a field with long hairs and sometimes with tubercles. In Crinocheta, this field becames what V. V. Radu (1959) and Hassal (1977) described as "inferior triturating plate" and Storch (1987) as "ventral masticatory area".

Anteromedianum – term used by Vandel (1943) after Nauk (1880) and, later, by other authors (Flasarova, 1967, 1968, 1969; Licar, 1970, 1980; Licar & Sket, 1971; Hassal, 1977; Licar, Blejec, Urbanc & Bercic, 1979; Brecko, Licar & Rode, 1991; Storch, 1987; Storch and Strus, 1989; Tabacaru & Platvoet, 2000). Scheloske (1976 a) considered the term anteromedianum, introduced by Vandel, as equivocal and replaced it with inferomedianum anterius and introduces the name inferomedianum posterius for what the majority of authors named inferomedianum. Wägele (1981, 1989, 1992) and Kobusch (1999) adopted this terminology. Considering that the name anteromedianum is not erroneous, it is used and it cannot lead to confusions, we favour it to that of inferomedianum anterius. Anteromedianum represents a median formation between clatri setarum anteriores; it is shaped like a prominence or only like a narrow band equipped with hairs. Sometimes, the clatri setarum anteriores are so near that anteromedianum is barely visible as is the case of *Mesoniscus* and *Calabozoa*.

Inferomedianum – term used by Vandel (1943) after Rehorst (1914) which introduced it as Infero-Medianum. Ulteriorly, the term was used by the majority of authors (Radu, V. V., 1950, 1959; Tuzet, Manier, Ornieres, 1959; Flasarova, 1967, 1968, 1969; Licar, 1970, 1980; Licar & Sket, 1971; Licar, Blejec, Urbanc & Bercic, 1979; Brecko, Licar & Rode, 1991; Storch, Dreyer, Mummert and Böckeler, 1987; Storch and Strus, 1989; Storch, Strus, Brandt, 2002). Tiwari and Ram (1972) used the name "central valve". Kensley (1974) used the name "filter apparatus". Inferomedianum represents an elongated, rhomboidal, ventro-median element, comprising the posterior filtratory grooves, covered by two plates of dense setae (clatri setarum posteriores). The anterior part of the inferomedianum may be prolonged by an apodema, rarely by two apodemae. Posteriorly, the inferomedianum ends in a, sometimes elongated, tip (capuchon, zipfel, caudal tip).

Inferolateralia – term used by Vandel (1943) after Schonichen (1899), who introduced it as "Infero-Laterale" and used later by other authors (Tuzet, Manier, Ornieres, 1959; Flasarova, 1967, 1968; Storch, 1987; Storch, Dreyer, Mummert and Böckeler, 1987; Storch and Strus, 1989; Storch, Strus, Brandt, 2002). However, Kensley (1974) used the name "postero-ventral ampulla". Scheloske (1976 a) named this differentiation Inferolaterale posterius in opposition with what he named Inferolaterale anterius (regions found in *Asellus* on both sides of the inferomedianum anterius, namely anteromedianum). Wägele (1989, 1992) adopted this terminology.

Inferolateralia represent pieces situated on both sides of the Inferomedianum. As Wägele (1989, 1992) showed, the two anterior filter grooves join in a common area situated in a medio-caudal position toward the anteromedianum. But in this area, sometimes prolonged in a unique, median groove, they separate again into two grooves on both sides of the inferomedianum, namely between the inferomedianum and the two inferolateralia. Inferolateralia have different forms according to the species. Toward the interior of the stomach, they are cushion-shaped with numerous hairs and end caudally in a rounded or a pointed tip. Inferolateralia are often framed by a triangular or semicircular sclerite. Ventrally, toward the exterior of the stomach, the inferolateralia form a collar folding anteriorly and on the sides of the inferomedianum.

Clatri setarum posteriores – term introduced by Scheloske (1976a) and used ulteriorly by Wägele (1989, 1992) and by Tabacaru & Platvoet, 2000. Vandel (1943) used the term "appareil filtrant pilorique". Tiwari and Ram (1972) used the name "inner filter in filter 2". Numerous authors use the name "secondary filter" (Licar, Blejec & Urbanc-Bercic, 1979; Storch, 1987; Hames and Hopkin, 1989; Storch and Strus, 1989; Brecko, Licar & Rode, 1991; Kobusch, 1999). We think as more appropriate the term posterior filter or fine filter. Clatri setarum posteriores represent two bands of very dense, parallel setae covering the posterior filtratory

grooves found inside the inferomedianum. These bands diverge toward the posterior, shaping together an overturned, rarely wide-opened V and each of them ending with an orifice, opening in the postero-ventral valvule.

Lamella dorsalis – name introduced by Flasarova (1967, 1968, 1969, 1972) and used by the majority of authors (Licar, 1970, 1980; Licar & Sket, 1971; Scheloske, 1976a; Storch, 1987; Wägele, 1989, 1992; Brecko, Licar, Rode, 1991; Tabacaru & Platvoet, 2000). Vandel (1943) used the name "lame recouvrante" after Ide, 1892 and Tuzet, Manier, Ormières, 1959, used the same name. Tiwari and Ram (1972) used the name "postero-dorsal lamella". Kensley (1974) and Hames and Hopkin (1989) used the name "dorsal lamella". Lamella dorsalis represent one of the most characteristic elements for the different groups of Isopods. Its posterior edge may be concave or convex and may be prolonged in a pointed tip. Lamella dorsalis is rarely formed by two lobes, as Wägele has shown in his generalized scheme (1992), but only in some aquatic Isopods. In Crinocheta the lamella dorsalis is distinctive: it is short and less rectangular and inserted very anteriorly.

Lamellae ventrales – name introduced under its Latin form by Flasarova (1967, 1968, 1969) and used ulteriorly by the majority of authors (Licar, 1970, 1980; Licar & Sket, 1971; Scheloske, 1976a; Wägele, 1989, 1992; Brecko, Licar & Rode, 1991; Tabacaru & Platvoet, 2000). Vandel (1943) introduces the French term " lames ventrales". Tiwari and Ram (1972) and Kensley (1974) used the term "postero-ventral lamella", while Hames and Hopkin (1989) used the term "ventral ampulla". Unlike the lamella dorsalis, we did not find a lamella ventralis shaped like a whole piece as described by Wägele (1989) in *Aega antarctica* in any Isopod investigated by us – but we have found two long lamellae overlapping medially or leaving a narrow gap between them. Their median edges are more chitinized and proceed from a strongly chitinized point placed on both sides of the inferomedianum. Lamellae ventrales are rounded apically or are prolonged in a pointed tip. On their sides, in the anterior part, they continue with the Lamina dorsalis posterior.

Lamina dorsalis posterior – name introduced by Scheloske (1976a) and used ulteriorly by Wägele (1989). Flasarova used the name "lamella annularis" (1967, 1968, 1969); following Flasarova, we also used this term (Tabacaru & Platvoet, 2000). But as Scheloske argued, since the name lamella annularis was established for a circular, non-chitinized lamella, we think rather to use the term proposed by Scheloske for the extension of the ventral lamellae over the dorsal lamella. Lamina dorsalis posterior is a very thin, membraneous strip surrounding the stomach over the lamella dorsalis.

Apodemes – especially on the external-ventral side of the stomach, there are chitinized extensions. Usually, there is a well-developed pair of antero-lateral

apodemae on the ventral side and, in some Isopods, also on the ventral side, there is a median apodema representing an anterior extension of the inferomedianum. We have found well-developed antero-lateral apodemae on the dorsal side only at *Calabozoa* (Tabacaru & Platvoet, 2000).

4. THE DESCRIPTION OF THE STOMACH AT *MESONISCUS* (MICROCHETA)

The genus *Mesoniscus* Carl, 1906, the sole representative of the family Mesoniscidae Verhoeff, 1908 and of the section Microcheta Schmalfuss, 1989, comprises two species with the following spreading (Strouhal, 1947; 1951; Gruner et Tabacaru, 1963; Tabacaru, 1969): 1. *Mesoniscus alpicola* (Heller, 1858) – widespread in the Oriental Calcareous Alps and namely in the Southern Calcareous Alps (Lombardian Alps) and especially in the Northern Calcareous Alps of Austria (between Innsbruk, Vienna and Graz); 2. *Mesoniscus graniger* (Frivaldsky, 1865) – widespread from the Northern Carpathians (Eastern Slovakia), all along the Carpathian chain, the Bihor Mountains, Banat Mountains and to the Julian and Dinaric Alps.

In her study, Varvara Radu (1950) maintained that she investigated the stomach of the species *Mesoniscus alpicolus* from Peştera de la Călăţea (peştera = cave), the Aleşd region. We examined material from this cave and we have specified in the revision of the family Mesoniscidae (Gruner & Tabcaru, 1963) that it is about the species *Mesoniscus graniger*.

MATERIAL AND METHOD

For the present study, we investigated stomach material of *Mesoniscus graniger* coming from numerous caves collected by the authors or given by colleagues from the Speleological Institute "E. Racovitza". The description of the stomach at *Mesoniscus* is based especially upon the material from two stations: 1) the station examined by V.V. Radu, respectively Peştera Potriva (Ponorul Văii Mnierei, Peştera Călăţea, Peştera de la Pusta Călăţea, Peşteroaia), the Pădurea Craiului Mountains; 2) Peştera Măgura (Peştera de la Măgura Bihorului), the Bihor Mountains.

For the comparison with *Mesoniscus alpicola*, we used material from Austria from the following stations: 1) Lurhöhle Peggau-Semriach, Steiermark (material offered by the regretted Prof. Dr. H. Strouhal in 1962 for the revision of the Mesoniscidae); 2) Falkensteinhöhle, Semmering, leg. J. Vornatscher (material lent from Naturhistorisches Museum Wien, through the amability of Dr. V. Stagl; 3) NÖ Grabenweggraben, approx. 3 km west of the Pottenstein monastery, leg. Dr. J. Gruber.

The dissections needed to separate the stomach were made either by removing the dorsal part of the cephalothorax in order to examine the substomacal skeleton or

by removing the oral appendages. After the separation, the stomach (usually with the oesophagus, labrum and the hypopharynx) was kept several minutes in a warm solution of KOH or several hours in a cold solution of KOH; then the stomach was washed and cleaned in distilled water and trasferred gradually in glycerol. Also, we used stomachs untreated in KOH, coming from freshly collected exemplaries in 95° alcohol and then kept several hours in distilled water. To understand more accurately certain structures, staining with pyrogallol was used. They were mounted in gelatined glycerol between two slides so they may be examined in immersion on both sides. For a more precise understanding of the conformation of the inner pieces, we also examined opened and exposed stomach. The drawings were made under a microscope with an Olympus camera lucida.

THE DESCRIPTION OF THE STOMACH

Varvara Radu (1950) stated that at *Mesoniscus* the stomach has a conformation generally coresponding with that of the stomach at the Trichoniscidae. We have to specify that in *Mesoniscus* the stomach is narrower and more elongated, slightly flattened dorso-ventrally looking nearly circular in cross-section.

The caudal lamellae are relatively long, the posterior part of the stomach found in the gut being equal in length with the free anterior part.

At the passing from the oesophagus to the stomach there are well-developed and hair-equipped valvulae lateralis oesophagi. There is a rounded, weakly marked dorsal oesophagian valvula at the base of the superomedianum; a ventral oesophagian valvula is visible a bit more caudally.

On the dorsal part of the stomach (Fig. 1) the superomedianum and the superolateralia are obvious. In the anterior dorsal part, a triangle is conspicuous: its base is represented by the anterior edge of the stomach; it has slightly convexe sides. In the middle of this triangle, on the inner face of the stomach's dorsal wall, the superomedianum is differentiated, which has the shape of an elongated tongue slightly strangled in its middle region. The superomedianum is rounded or slightly ogival in its apical part. Both the edges and the surface of the posterior half of the superomedianum have dense hairs. In the middle of the widened caudal part of the superomedianum, the dorsal wall of the stomach presents on his external face a small tubercle.

Lateralia (Fig. 3, A) are nearly spherical and covered with numberous hairs. They leave between them a narrow space so the hairs touch each other. V. Radu gave a detailed description of these hairs and remarked, on the ventral face, the presence, in an incipient form, of a dented strip which in Crinocheta became what V. Radu (1959) named "placa triturantă superioară". But V. Radu did not remark the existence on the inner, anterior part of the lateralia of an apically crested tooth also signaled by Flasarova (1968) that we have always found in both species of *Mesoniscus*.

Superolateralia (Fig. 3, C) are inserted in the caudal part of the dorsal side of the lateralia. Superolateralia are remarkable by the presence on its edge of a row of strong and long fringes with serrated tips. The fringed edge of the superolateralia descends in a latero-caudal direction, then it continues on the ventral side in a medio-caudal direction and it ends, at *Mesoniscus*, on both sides of the inferomedianum in two chitinous points where the median edges of the two ventral lamellae are inserted.

On the ventral side of the stomach in *Mesoniscus* (Fig. 2), at the anterior extremity, we notice two angular apodemae with the tip pointed caudally. In profile, these apodemae are mushroom-shaped.

Long, thin and caudally oriented spines make up the clatri setarum anteriores; the spines are parallel and slightly curved, with the convexity toward the median line. The spines length decreases from the median toward the lateral ones. Being very close to each other, the two strips of clatri setarum anteriores form a wide, nearly straight and transversal band.

A strictly speaking anteromedianum (Fig. 3, B), edged by the filter grooves, does not exist here. We find only a narrow band caught between the clatri setarum anteriores and equipped with fine hairs at the posterior end.

Inferomedianum (Fig. 3, D) is rhomboidal-shaped. Inside the inferomedianum are situated the two filter grooves covered by clatri setarum posteriores (made up by very fine and very dense, parallel spines). Hairs cover the posterior half of the inferomedianum.

Medially, on the ventral side, above the two posterior filter grooves, there are two, chitinous rods, terminally widened like knobs. From these knobs begins the valvula postero-ventralis; in *Mesoniscus*, the valvula postero-ventralis is narrow and much extended toward the posterior side.

On both sides of the inferomedianum there are the triangular shaped inferolateralia with a pointed posterior tip. They present numerous hairs. Ventrally, in their anterior part, the inferolateralia are very rolled up taking together the aspect of a big funnel.

The insertion of the posterior lamellae is strengthened on the sides by two strongly chitinized rods. The lamella dorsalis is recurved on its sides toward the ventral side and its edges are intensely chitinized. Medially, the dorsal lamella is convexely elongated. The two lamellae ventrales surpass slightly the length of the dorsal lamella. Their median edge is more intensely chitinized and is equipped with hairs. On the external sides, the ventral lamellae continue with the lamina dorsalis posterior, only in their anterior part.

Comparing the constitution of the stomach in *Mesoniscus graniger* with that of *Mesoniscus alpicola*, we notice an obvious difference regarding the posterior filtering apparatus: the two clatri setarum posteriores are shorter and more caudally divergent in *Mesoniscus alpicola* and their setae are thicker. In *Mesoniscus alpicola* there are approximately 20 setae while in *Mesoniscus graniger* there are over 60 setae.

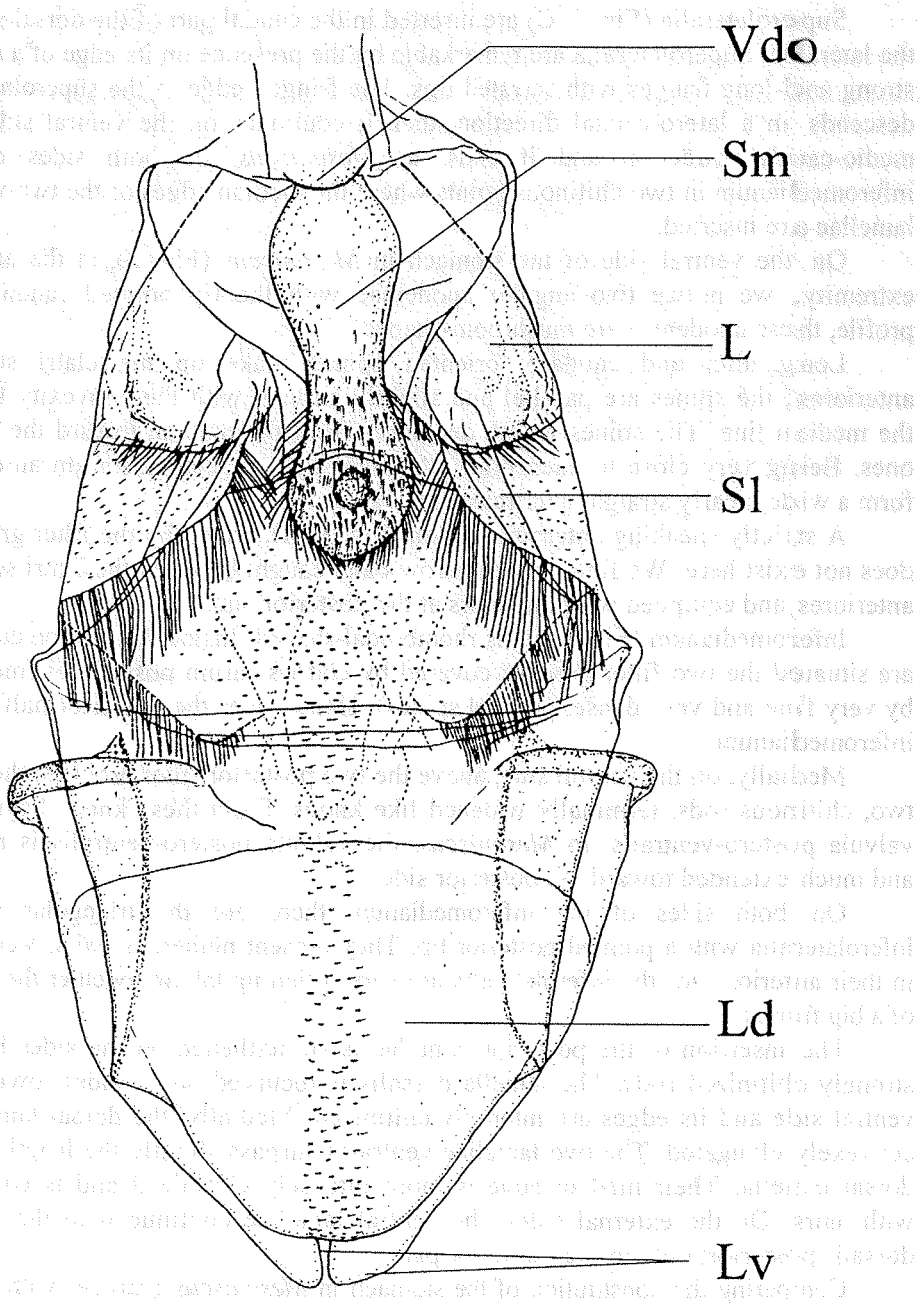

Fig. 1 – *Mesoniscus graniger*, stomach, dorsal view: Vdo – valvula dorsalis oesophagi; L – Lateralia; Sm – Superomedianum; Sl – Superolateralia; Ld – Lamella dorsalis; Lv – Lamellae ventralis.

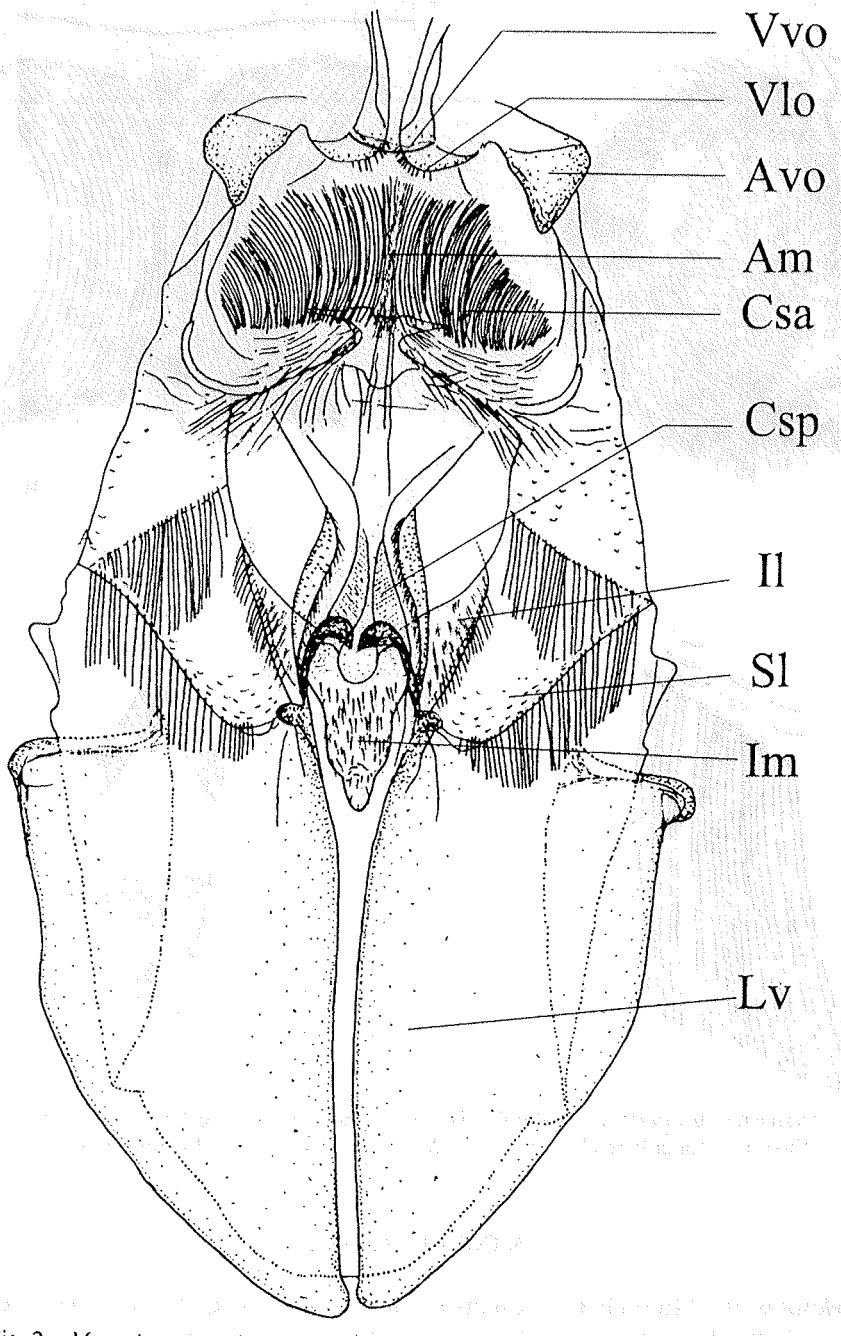

Fig. 2 – *Mesoniscus graniger*, stomach, ventral view: Vvo – Valvula ventralis oesophagi; Vlo – Valvula lateralis oesophagi; Ava – Antero-ventral apodema; Am – Anteromedianum; Csa – Clatri setarum anteriores; Csp – Clatri setarum posteriores; Il – Inferolateralia; Sl – Superolateralia; Im – inferomedianum; Lv – Lamellae ventrales.

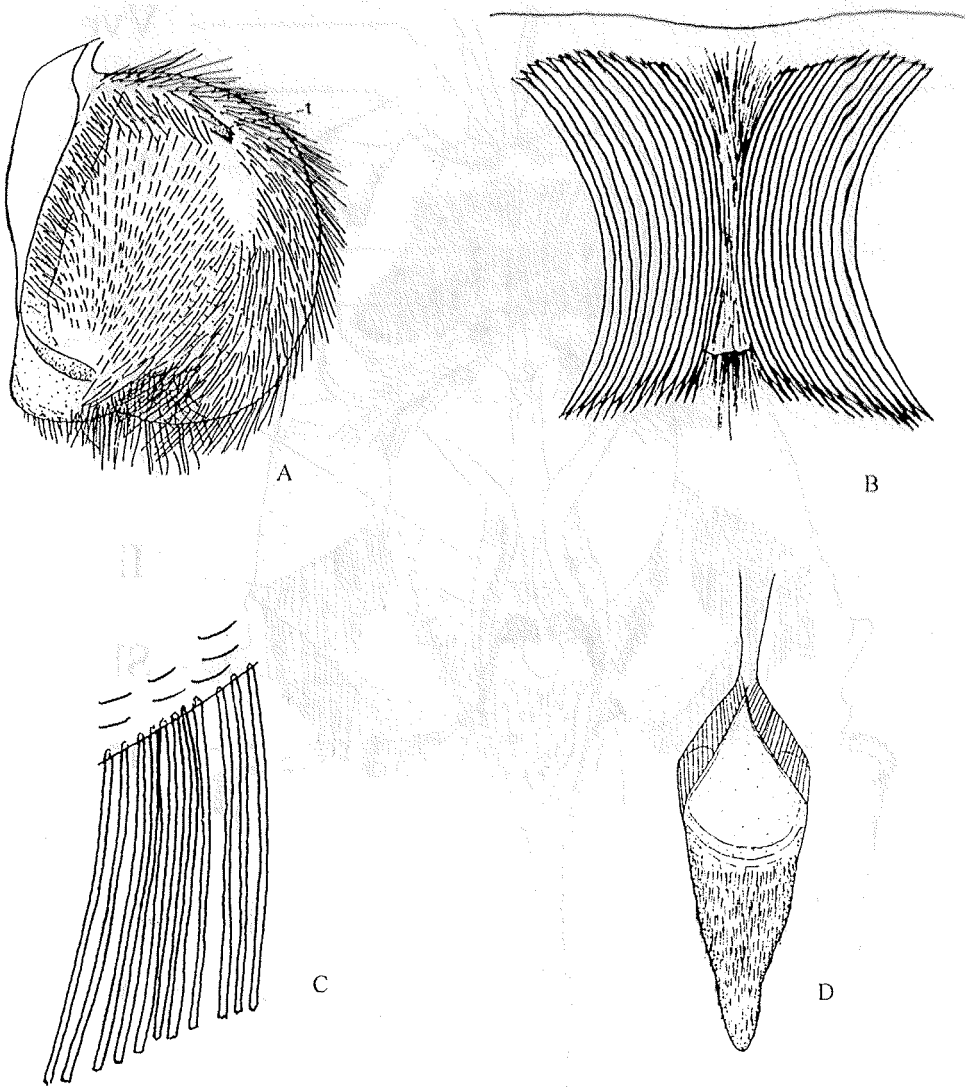

Fig. 3 – *Mesoniscus graniger*: A – Lateralia; B – Anteromedianum between the setae of the anterior filter; C – Superolateralia, fragment; *Mesoniscus alpicola*: D – Inferomedianum.

5. CONCLUSIONS

Mesoniscus (Microcheta) presents a primitive kind of stomach, all the essential structures of the Isopod stomach being found here; the sole reductive specialisation concerns the anteromedianum which, caught between the very close to each other clatri setarum anteriores, is represented only by a very narrow band. The most

characteristic features for *Mesoniscus*, as V.V. Radu also pointed out, are the strong and fringed edge of the superolateralia and the long superomedianum and narrowed in the middle.

In any case, the stomach of Microcheta does not represent an intermediary stade between that of the Trichoniscidae (Synocheta) and that of the superior Oniscids (Crinocheta), as V.V. Radu (1951) stated. The strong development of the superomedianum and of the superolateralia as well as the presence of a tooth on the lateralia draws near the stomach of Microcheta to that of some aquatic Isopods (Spheromatidae, Idoteidae) and that of the Diplocheta; the conformation of the anterior filtering apparatus shaped like a wide, nearly straight, transversal band, as well as the conformation of the dorsal lamella elongated medially, draw near the the stomach of Microcheta to that of the Synocheta.

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"Emil Racovitza" Institute of Speleology
Str. Frumoasă nr. 11, sect. 1, Bucharest 010985
Romania

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