State of the art of the free-living marine Monhysteridae (Nematoda)

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The family Monhysteridae is characterized by 17 valid genera, seven of which are known to be free-living, inhabiting marine sediments. In total, 70 valid marine species are ascribed to these seven genera. Overall, the family is characterized by a confused taxonomic history with a large list of synonyms and species inquirendae. *The taxonomic problem is not restricted to the old literature, but inconsistencies also appeared in recent studies. The aim of this study is to show the most important diagnostic characters to identify each genus and provide taxonomic tools for species identification. Dichotomous-keys and illustration-guides are attempted for the marine monhysterid species. For the family and each subfamily, tribe and marine genus a brief historical background, diagnosis and a list of valid species is provided. Hereby, we propose to transfer eight species of the genus* Thalassomonhystera *to the genus* Monhystrella.

INTRODUCTION

The family Monhysteridae is regarded as one of the most successful families within the free-living nematodes (Lorenzen, 1978). Members of this family inhabit marine and continental biotopes. Unfortunately, the two most recent studies covering this family (Andrássy, 2005; Coomans & Eyualem-Abebe, 2006) only considered the inland (limnic and terrestrial) species. The last study covering the whole family, including marine representatives, was carried out by Jacobs (1987a). Jacobs recognized 12 valid genera (*Eumonhystera* Andrássy, 1981, *Monhystera* Bastian, 1865, *Thalassomonhystera* Jacobs, 1987, *Diplolaimella* Allgén, 1929, *Diplolaimelloides* Meyl, 1954, *Monhystrium* Cobb, 1920, *Odontobius* Roussel de Vauzéme, 1834, *Tripylium* Cobb, 1920, *Gammarinema* Kinne & Gerlach, 1953, *Geomonhystera* Andrássy, 1981, *Monhystrella* Cobb, 1918 and *Sinanema* Andrássy, 1960) and two *genera inquirenda* (*Anguimonhystera* Andrássy, 1981 and *Sitadevinema* Khera, 1921). More recently, four additional genera have been described, *Cryonema* Tchesunov & Riemann, 1995, *Halomonhystera* Andrássy, 2006, *Tridentula* (Eyualem-Abebe & Coomans, 1995) Andrássy, 2007 and *Hieminema* Tchesunov & Portnova, 2005, and the genus *Anguimonhystera* was provisionally retained by Coomans & Eyualem-Abebe (2006). From these, 17 valid genera, seven are known to be free-living inhabiting thalassic, saline and brackish waters: *Cryonema* (Tchesunov & Riemann, 1995), *Halomonhystera* (Andrássy, 2006; Zekely et al., 2006; Derycke et al., 2007), *Thalassomonhystera* (Tchesunov & Miljutina, 2005; Zekely et al., 2006),

Monhystrella (Vanhove et al., 1999), *Hieminema* (Tchesunov & Portnova, 2005), *Diplolaimella* (Kito & Aryuthaka, 1998; Zhou, 2001; Da Rocha et al., 2006) and *Diplolaimelloides* (Alkemade et al., 1994; Moens et al., 1999; Moens & Vincx, 2000). These taxa are distinguished from each other by few diagnostic characters and the combination of several other morphological characters.

The marine monhysterid genera mainly occur in shallow marine areas and brackish waters. In the last two decades, however, the importance of this family in other marine environments such as anoxic regions (Jensen, 1986) and deep seas (Vanreusel et al., 2000; Van Gaever et al., 2006; Fonseca & Soltwedel, 2007) has become apparent. For instance, a nematode assemblage of the deep-sea sediment may be characterized by 50% of monhysterids (Vanreusel et al., 2000) with more than 10 species per 10 cm^2 of mud (Fonseca & Soltwedel, 2007). It is believed that the majority of marine monhysterid species belong to the genus *Thalassomonhystera* (Vopel & Thiel, 2001). However, ecologists who encountered individuals from the family Monhysteridae usually overlooked their taxonomic distinctness and reported only one group 'monhysterids' (Vanreusel et al., 2000; Muthumbi et al., 2004).

The identification of the group is considered difficult because, on the one hand, most of the taxonomic descriptions of marine species are based on few poorly described individuals and often published in less accessible scientific journals, while on the other hand, recent descriptions often do not include data on morphological variability and identification keys to genus or species level. Moreover, many species encountered during ecological studies are new to science. For example, Bussau (1993) recognized 14 *Thalassomonhystera* species coming from bathyal depths of which only one was previously described. Unfortunately, the low number of active taxonomists together with the lack of

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taxonomic identification tools and the large number of unde-scribed nematode species hampers ecological and evolution-ary assessments of the marine environment (Coomans, 2000).

Nevertheless, two attempts to assemble all data on descrip-tions and records of the monhysterid species were carried out. The first database compiling all aquatic species of the family Monhysteridae, known as the Bremerhaven-checklist, was pub-lished by Gerlach & Riemann (1973). The authors considered all taxonomic descriptions which resulted, more in particular for the family Monhysteridae, in a large number of synonyms. Several years later, a more comprehensive checklist on the family Monhysteridae regardless of the environment was pub-lished by Jacobs (1987a). This author presented a new classifi-cation for the Monhysteridae, followed by a checklist including a list of valid species, *species inquirendae*, and synonyms. In this checklist, Jacobs introduced one new subfamily Diplolaimellinae, three new tribes Thalassomonhysterini, Diplolaimellini and Geomonhysterini, and one new genus *Thalassomonhystera*. Jacobs (1987a) erected the genus *Thalassomonhystera* with the purpose of encompassing all marine species previously described within the genus *Monhystera*. His classification has been accepted and used later as reference by numerous authors (Bussau, 1993; Riemann, 1995; Eyualem-Abebe *et al.*, 2001; Andrássy, 2005, 2006; Coomans & Eyualem-Abebe, 2006). In the last two decades, several new species were added to this family. Although some of these recent studies stated clearly the taxonomic grounds for proposing new species, others did not and embroiled the taxo-nomic identity of the group as proposed by Jacobs (1987a). With the exception of Andrássy (2006) and Tchesunov & Riemann (1995), other recent studies including marine species did not provide taxonomic tools for species identification.

In the current study, we first present an adapted diagnosis of the family followed by an illustrated classification of the marine taxa. Then, we provide for each subfamily, tribe and marine genus a brief historical background, a diagnosis and a list of valid species. Based on the species lists, dichotomous keys to species level and illustration 'guides' are given to stimulate and facilitate future ecological and taxonomic studies of the family Monhysteridae.

BACKGROUND, DIAGNOSIS AND SPECIES LIST OF THE FREE-LIVING MARINE MONHYSTERIDAE

In the present study, the historical backgrounds of each taxo-nomic level are given. The diagnoses provided include poss-ible morphological variability of all valid species listed. The lists of species are based on the most recent checklists and/or generic reviews published together with recent descriptions. In the species lists, the type species is underlined and the marine/brackish species/genera are marked in bold. For each species, the sampling location of the original description is given in parentheses. Additional, dichotomous-keys to species level and illustrations from the anterior and posterior end of each species are added. The keys are solely based on the original descriptions. In all genera, males and females are needed to identify up to species level. Unfortunately, not all original illustrations could be reproduced here; some of them were printed too small and/or were of poor quality. All the illustrations presented in this study were also based

on the original description but did not intend to reproduce all the details from the original drawings.

SYSTEMATICS
Order MONHYSTERIDA Filipjev, 1929
Superfamily MONHYSTEROIDEA de Man, 1876
Family MONHYSTERIDAE de Man, 1876

According to Eyualem-Abebe & Coomans (2006), the Monhysteridae is the only family within the superfamily Monhysteroidea de Man, 1876. The Monhysteroidea are easily distinguishable from the other two superfamilies, Sphaerolaimoidea Filipjev, 1918 and Siphonolaimoidea Filipjev, 1918 by the type of cuticle, absence of sub-cephalic setae and the presence of a single gonad on the right side of the intestine (see diagnosis below).

Jacobs (1987a) divided the family Monhysteridae into two subfamilies based on the shape of the buccal cavity: (1) the Monhysterinae including species with a single V-shaped buccal cavity; and (2) the Diplolaimellinae possessing species with a double buccal cavity (features 2 and 4; Figure 1 and Table 1). He further divided the Monhysterinae into two tribes based on the presence of peri-oral plates and apex of the lips fused (Figure 2) for the tribe Monhysterini (features 9 and 38; Figure 1 and Table 1) and absence of such plates and separate lip tips (Figure 2) for the Thalassomonhysterini. The Monhysterini are represented by the genera *Tridentula*, *Eumonhystera*, *Anguimonhystera* and *Monhystera*. These four genera are restricted to freshwater and terrestrial environ-ments and will not be considered in this study. The tribe Thalassomonhysterini is monogeneric with *Thalassomonhystera* being restricted to marine and brackish water environments.

The sub-family Diplolaimellinae is also divided into two tribes, Diplolaimellini and Geomonhysterini, based on the shape of the second buccal chamber and post-cloacal sup-plements which both are largely developed in the first tribe (fea-tures 5 and 6; Figure 1 and Table 1). The Diplolaimellini consists of 5 genera, two of which are commonly found in marine environments (*Diplolaimella* and *Diplolaimelloides*). The main differences between these two genera are: long or short spicules, vagina sclerotized or not, presence or absence of a copulatory bursa and presence or absence of a caudal apophysis of guberna-culum (features 12–15; Figure 1 and Table 1). The tribe Geomonhysterini includes seven genera with the genera *Cryonema*, *Halomonhystera*, *Hieminema* and *Monhystrella* being mainly free-living marine. These four genera differ from each other by a combination of different characters (see features 25–27 versus 28–29 and features 32, 36, 38 43 and 44; Figure 1 and Table 1).

In total, seven of the 17 genera in the family Monhysteridae are known to be free-living mainly inhabiting marine and coastal sediments (*Cryonema, Diplolaimella, Diplolaimelloides, Halomonhystera, Hieminema, Monhystrella* and *Thalassomonhystera*). Three genera comprise species living in gill chambers of aquatic (*Gammarinema*) or inland (*Monhystrium* and *Tripylium*) crustaceans. The other 7 genera are known to inhabit inland water bodies (see Appendix 1 for species lists of the inland and commensal genera).

DIAGNOSIS

Aadapted after Jacobs (1987a), Lorenzen (1994), Andrássy (2005) and Coomans & Eyualem-Abebe (2006).
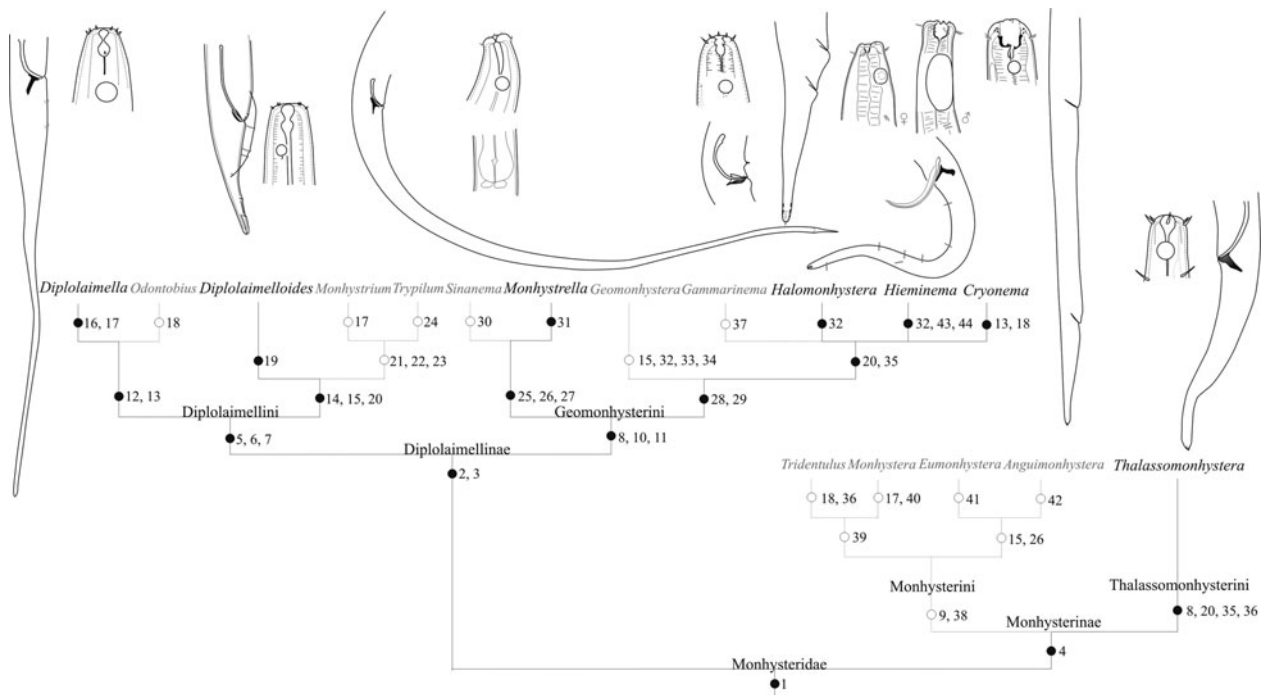
Fig. 1. Identification-key for the genera from the family Monhysteridae and schematic drawings for the free-living marine genera. Full lines and circles, and black names stand for the marine genera; dashed lines, open circles and grey names stand for the non-marine. List of characters is given in Table 1.

Monhysteroidea. Small, slender nematodes with body length usually less than 2.5 mm (except *Odontobius*, L > 3 mm); body cuticle finely striated and frequently smooth under light microscope. Anterior sensillae in two circles: anterior circle with six inner labial sensillae (usually papilliform), posterior circle with six outer labial sensillae and four cephalic (usually setiform) sensillae. Amphidial fovea circular or cryptospiral ventrally wound, varying in size (may be result of sexual dimorphism) and in position from the anterior end. Ocelli often present in shallow-water and inland species. Buccal cavity (excluding cheilostome) surrounded by pharyngeal tissue and of varying shape: either bipartite or single

Table 1. List of diagnostic characters used in Figure 1 to identify at genus level the family Monhysteridae.

|		
1. One outstretched gonad at right side of intestine	16. Small denticle at base of buccal cavity	31. Spinneret long
2. Subdivided buccal cavity (pharyngostom) in two parts	17. Ocelli present	32. Vulva close to the anus (V% ≥ 75)
3. Pharyngeal lumen sclerotized	18. Buccal cavity with three teeth	33. Somatic setae (length < 30% of the cbd)
4. Non-divided buccal cavity, V-shaped	19. Spicules long	34. Rectum well developed
5. Well developed second chamber of buccal cavity	20. Ventral gland well developed	35. Ventral gland opening at anterior neck region
6. Well developed postcloacal genital papillae	21. Two caudal glands	36. Inner labial sensillae papilliform
7. Apex of the lips partially fused (three lips) (Figure 2)	22. Metarhabdia forming three large hook-like teeth	37. Buccal cavity denticulate
8. Apex of the lips not fused (Figure 2)	23. Cardia-progaster cell complex	38. Peri-oral plates present
9. Apex of the lips fused (Figure 2)	24. Second chamber of the buccal cavity cylindrical	39. Tail tip swollen
10. Protrusion of the labial cuticle surrounding the inner labial sensilla	25. Small oral aperture, posterior buccal cavity part tube-like	40. Cristalloid bodies present
11. Well sclerotized cheilostome (except in *Monhystrella*), weakly or non-sclerotized second chamber	26. Tail long and filiform	41. Cheilostome weakly sclerotized and small
12. Spicules arcuate and robust	27. Pharynx with posterior bulbus	42. Gubernaculum slipper-shaped
13. Vagina sclerotized	28. Tail conoid	43. Strong sexual dimorphism in shape of amphidial fovea and buccal cavity
14. Copulatory bursa present	29. Spinneret with a hyaline plug-like structure	44. Two lateral setae posterior to the amphidial fovea
15. Gubernaculum without apophysis	30. Ovary reflexed	
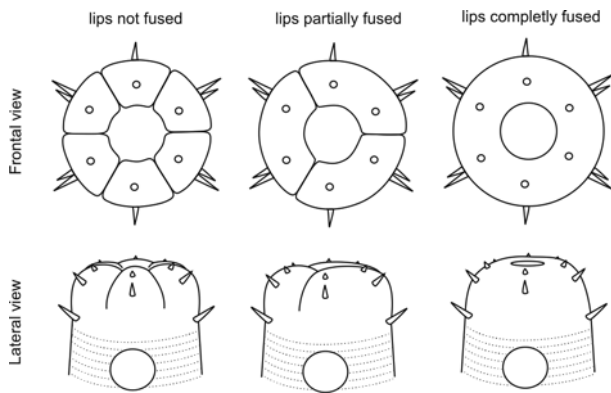
Fig. 2. Frontal and lateral views of the three types of lips within the family Monhysteridae.

V-shaped, cylindrical or minute; with or without denticles. Pharynx cylindrical, well muscularized, sometimes slightly swollen at its anterior end and in some genera (*Monhystrella, Sinanema* and partly in *Eumonhystera*) with more or less developed muscular posterior bulb. Cardia with conoid part lying between pharynx and intestine, and oblong valve-like, inner part protruding in intestinal lumen. Intestine with few cells (oligocytous) arranged in two rows; dorsal and ventral. Ventral gland often present in marine and freshwater species; secretory–excretory pore from just anterior to nerve ring to the labial region. Female reproductive system monodelphic, prodelphic, with the gonad always outstretched (except in *Sinanema* where the ovary is reflexed) on the right side of the intestine. Male monorchic, spicules generally simple, of varying length, 1–5 times the anal body diameter (abd). Gubernaculum of varying shape: thin without apophysis to robust with apophysis. Spermatozoan spherical. Tail conoid to elongate–conoid, similar in sexes with caudal glands opening through a single pore at the terminal spinneret; terminal setae absent.

Subfamily DIPLOLAIMELLINAE Jacobs, 1987

This subfamily was erected by Jacobs (1987a) mainly to accommodate all the genera with a subdivided (i.e. double) buccal cavity (feature 2; Figure 1 and Table 1) and originally included nine genera (*Diplolaimella, Odontobius, Diplolaimelloides, Monhystrium, Trypilium, Sinanema, Monhystrella, Gammarinema* and *Geomonhystera*). Since then, three genera have been added: *Halomonhystera Hieminema*, and *Cryonema*.

DIAGNOSIS

Adapted after Jacobs (1987a).

Monhysteridae. Buccal cavity complex; rhabdia separated, forming a second buccal chamber. Radii of pharyngeal lumen, short and sclerotized. Common spinneret chamber and/or duct elongated and/or sclerotized. Reproductive mode: bisexual or parthenogenetic. Two tribes.

Tribe DIPLOLAIMELLINI Jacobs, 1987

This tribe was introduced by Jacobs (1987a) with the intention of grouping the genera *Diplolaimella, Odontobius, Diplolaimelloides, Monhystrium* and *Trypilium* based mainly on the shape of the second chamber of the buccal cavity, the presence of fused lips and paired postcloacal genital papillae (features 5–7; Figure 1 and Table 1). *Diplolaimella* and *Odontobius* are distinguished from the other genera by the robust arcuate spicules, a sclerotized vulva and small denticles or teeth in the second chamber, (features 12, 13, 16 and 18; Figure 1 and Table 1). *Diplolaimelloides, Monhystrium* and *Trypilium* are grouped together by the presence of a copulatory bursa, gubernaculum without apophysis, a well developed ventral gland (features 14, 15 and 20; Figure 1 and Table 1) and absence of denticles (Figure 1).

DIAGNOSIS

Adapted after Jacobs (1987a).

Diplolaimellinae. Inner labial sensillae papilliform. Apex of lips almost completely fused; sometimes forming three lips. Second buccal chamber (buccal cavity) well sclerotized and well developed; shape of second buccal chamber similar for at least all the first and second juvenile stages. Males with well developed postcloacal genital papillae, gubernaculum apophyse present and caudal alae absent or caudal alae present and gubernaculum apophyse absent. Common spinneret chamber well developed. Reproductive mode: bisexual. Type genus *Diplolaimella* and four other genera (see classification).

Genus *Diplolaimella* Allgén, 1929

Allgén (1929) erected the genus *Diplolaimella* on the basis of a single female of *D. monhysteroides* and differentiated the new taxon from *Monhystera* mainly on the basis of the double buccal cavity (see also Allgén, 1934: p. 296). In the following year, Allgén (1930) described a single male of the same species. Later on, when more species were added to the genus *Diplolaimella*, two types of males were observed: (1) males with short spicules and without bursa; and (2) males with long spicules and a bursa. The latter group was transferred by Meyl (1954) into a new genus *Diplolaimelloides*, morphologically highly similar to *Diplolaimella* except for presence of a bursa in male versus absent and shape amphidial fovea cryptospiral versus circular in *Diplolaimella*. Chitwood & Murphy (1964) introduced a new subgenus *Diplolaimita* (type species *D. schneideri*) within *Diplolaimella* for males with short arcuate spicules and gubernaculum with apophysis and differentiated from the monotypic subgenus *Diplolaimella sensu stricto* (type species *D. monhysteroides*) with long spicules and gubernaculum not observed; thus the genus *Diplolaimelloides* was not accepted (p. 313). Timm (1967) deduced from the lengthy spicule and curved tail tip that the male specimen described by Allgén (1930) was actually a *Diplolaimelloides* species in which the thin bursa and thickening of the wall of the rectum were assumed overlooked. He synonymized *Diplolaimita* with *Diplolaimella*. Timm also remarked that Allgén's male specimen was rather similar in measurements and structure of the copulatory apparatus with *Diplolaimelloides delyi* Andrássy, 1958. Further, the posterior position of the vulva (V = 63.6%) in *Diplolaimella monhysteroides* female holotype is characteristic of *Diplolaimelloides* species but the thinner body confines it to *Diplolaimella*. Consequently, Timm (1967) considered *D. monhysteroides* a *species dubia* (i.e. a *species inquirenda* according to the *Code of Zoological Nomenclature*) although he still included *D. monhysteroides* in his key to the species of *Diplolaimella*. So far, *D. monhysteroides* was never reported again nor redescribed

more in detail. Jacobs (1987a) classified *D. monhysteroides sensu* Allgén (1930) as a new species *Diplolaimelloides longispicula* (based on a male) without further comment or additional data. Subsequent reviewers of the genus all have accepted *Diplolaimella monhysteroides* as type species (Gerlach & Riemann, 1973; Jacobs, 1987a; Coomans & Eyualem-Abebe, 2006). It would be preferable in the future to substantiate *Diplolaimella monhysteroides* either by redescribing the holotype (provided it still exists) or by designating a neotype. With the exception of *D. monhysteroides*, all species are illustrated in Figure 3.

DIAGNOSIS

Adapted after Coomans & Eyualem-Abebe (2006).

Diplolaimellini. Posterior labial and cephalic sensillae small setiform. Sub-median somatic setae less than 20% of long. Cheilostome inverted funnel- or cup-shaped, second chamber of stoma spherical, may be denticulate. Amphidial fovea circular, 1.5–3 times the head diameter (hd) from anterior end. Ocelli may be present. Ventral gland obscure, opening in anterior region. Spicules arcuate and robust (1.3–2.0 abd), gubernaculum and apophysis well developed, pre- and postcloacal papillae (or setae) usually present. Vagina may be sclerotized; vulva located at mid-body region. Tail elongated with an anterior conical portion and a posterior cylindrical portion ventrally curved.

SPECIES LIST

1. *D. allgeni* **Schneider, 1937** (Indonesia)
2. *D. chitwoodi* **Gerlach, 1957** (Brazil)
3. *D. dievengatensis* **Jacobs, Van de Velde, Geraert & Vranken, 1990** (brackish, The Netherlands)
4. *D. gerlachi* **Pastor de Ward, 1984** (Argentina)
5. *D. monhysteroides* **Allgén, 1929** (Baltic Sea)
6. *D. ocellata* (**Bütschli, 1874**) **Gerlach, 1957** (Kiel Bay, Baltic Sea)
7. *D. ophthalmophora* **Timm, 1952** (Chesapeak Bay, USA)
8. *D. punicea* **Timm, 1952** (Chesapeak Bay, USA)
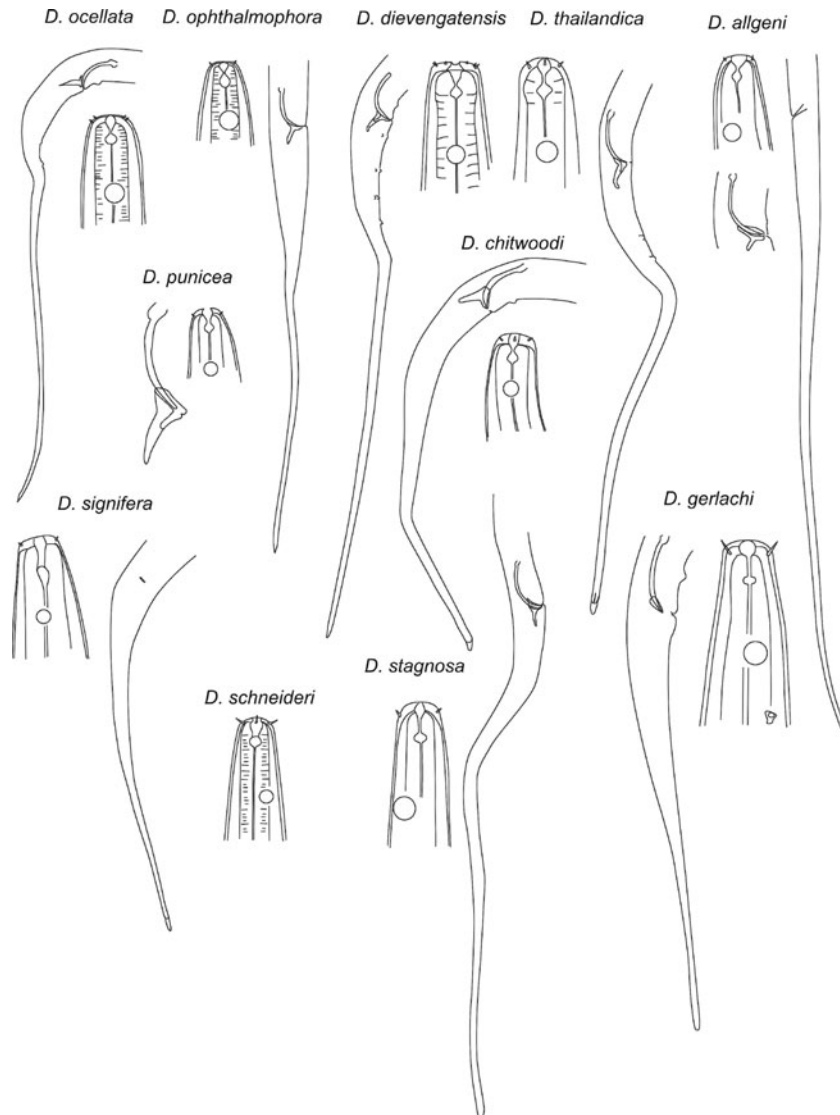9. *D. schneideri* **Timm, 1952** (Chesapeak Bay, USA)

Fig. 3. Illustration guide: *Diplolaimella*.

10. **D. signifera (Paramonov 1929) Gerlach & Riemann, 1973** (brackish, Black Sea)
11. **D. stagnosa Lorenzen, 1966** (brackish, North Sea)
12. **D. thailandica Kito & Aryuthaca, 1998** (shrimp pounds, Thailand)

IDENTIFICATION KEY FOR THE SPECIES OF THE GENUS *DIPLOLAIMELLA*

1. Ocelli absent 2
 – Ocelli present at the level of the first quarter of the pharynx ($<$25%) 4
 – Ocelli present at the level of one-third and half of the pharynx.. 5
2. Ratio a smaller than 35 .... *D. signifera*
 – Ratio a between 35 and 55...................... *D. allgeni*
 – Ratio a equal or larger than 59 3
3. Vulva located anteriorly to the mid-body ...... *D. stagnosa*
 – Vulva located at least at 64% of the total body length .... *D. monhysteroides*
4. Ratio c equal or larger than 15 .... *D. schneideri*
 – Ratio c equal or smaller than 12.............. *D. gerlachi*
5. Amphidial fovea between 1 and 1.4 head diameters from the anterior end .... *D. chitwoodi*
 – Amphidial fovea between 1.5 and 2 head diameters from the anterior end 6
6. Pre-cloacal supplements absent........................ 7
 – Pre-cloacal supplements present....................... 8
7. Size of the amphidial fovea equal or less than 25% of the corresponding body diameter........... *D. punicea*
 – Size of the amphidial fovea equal or larger than 35% of the corresponding body diameter .... *D. ophthalmophora*
8. Ratio c equal or larger than 17 .... *D. ocellata*
 – Ratio c between 14 and 15 .... *D. thailandica*
 – Ratio c smaller than 13 .... *D. dievengatensis*

Genus *Diplolaimelloides* Meyl, 1954

The genus was erected by Meyl (1954) to embrace all the species from the genus *Diplolaimella* with males and bursa with fine genital papillae. The most recent checklist published for the genus recognized nine valid species (Jacobs, 1987a), including a new species *D. longispicula* Jacobs, 1987 for *Diplolaimella monhysteroides* Allgén, 1929 *sensu* Allgén, 1930. Since, the original description of *D. longispicula* based on a single male is poor, i.e. no bursa nor genital papillae were described nor illustrated, we consider it as *species inquirenda*. Timm (1967) considered both *D. monhysteroides* Allgén, 1930 based on a female as well as *D. monhysteroides sensu* Allgén, 1930 based on a male as doubtful species. The nine species are illustrated in Figure 4.

DIAGNOSIS

Adapted after Coomans & Eyualem-Abebe (2006).

Diplolaimellini. Outer labial and cephalic sensillae small, setiform. Cheilostome sub-cylindrical, second chamber of buccal cavity often denticulate. Amphidial fovea cryptospiral, i.e. ventrally wound spiral with a broken or circular aspect, placed 1–2 hd from anterior end. Ventral gland mostly present, opening anterior to nerve ring (mid-pharynx). Ocelli usually present, varying in position from anterior end. Vulva located at mid-body region in long-tailed species, more posterior in shorter-tailed ones. Spicules slender, arcuate to almost straight, varying in length from 1.8 to 4.4 abd. Gubernaculum poorly sclerotized, without dorsal apophysis. Bursa encompassing the anterior portion of the tail and supported by several pairs of fine postcloacal papillae. Tail with posterior section cylindrical; length equal in sexes, but variable according to species. Reproductive mode: bisexual.

SPECIES LIST

1. **D. altherri Meyl, 1954** (brackish, North Sea)
2. **D. bruciei Hopper, 1970** (Lousiana, USA)
3. **D. deconincki (Gerlach, 1951) Meyl, 1954** (Kiel Bay, Germany)
4. **D. delyi Andrássy, 1958** (brackish, Egypt)
5. **D. islandicus (De Coninck, 1943) Meyl, 1954** (Iceland)
6. **D. meyli Timm, 1961** (Bay of Bengal, India)
7. **D. oschei Meyl, 1954** (brackish, Germany)
8. *D. palustris* Tsalolikhin, 1985 (Mongolia)

SPECIES *INQUIRENDA*

1. **D. longispicula Jacobs, 1987**
 Syn. *Diplolaimella monhysteroides* apud Allgén, 1930.

IDENTIFICATION KEY FOR THE SPECIES OF THE GENUS *DIPLOLAIMELLOIDES*

1. Ratio c equal or larger than 14.5 .... *D. oschei*
 – Ratio c between 7 and 14.............................. 2
 – Ratio c smaller than 6 5
2. Ratio c between 4.6 and 9.4 3
 – Ratio c equal or smaller than 4.5 4
3. Spicules length divided by the anal body diameter equal or larger than 4 .... *D. altherri*
 – Spicules length divided by the anal body diameter equal or smaller than 2.6................................. *D. delyi*
4. Ocelli present, ventral gland absent .... *D. palustris*
 – Ocelli absent, ventral gland present .... *D. deconincki*
5. Amphidial fovea placed less than one head diameter from the anterior end .... *D. bruciei*
 – Amphidial fovea placed further than one head diameter from the anterior end 6
6. Body length equal or shorter than 750 μm............... .... *D. islandicus*
 – Body length equal or longer than 800 μm ....*D. meyli*

Tribe GEOMONHYSTERINI Jacobs, 1987

This tribe was erected by Jacobs (1987a) with the intention of grouping four genera (*Sinanema, Monhystrella, Geomonhystera* and *Gammarinema*) according to their
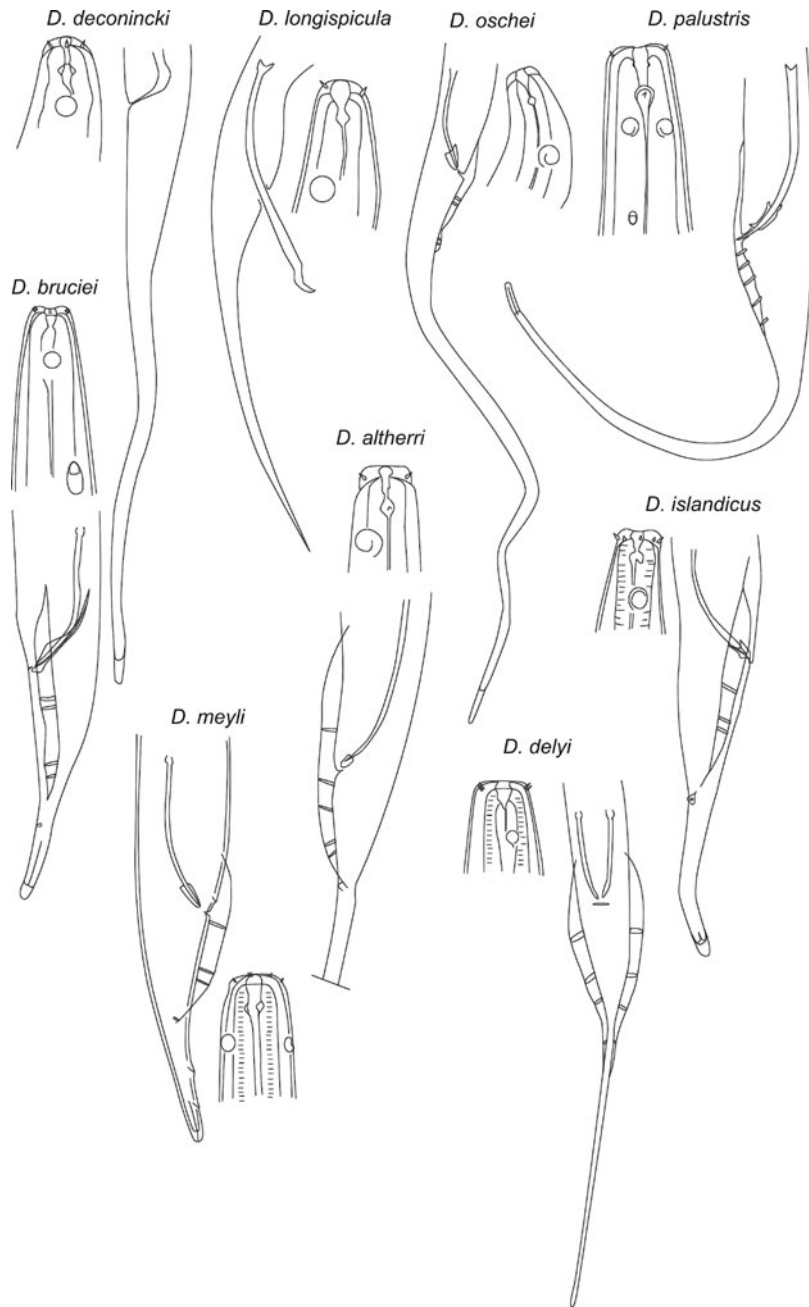
Fig. 4. Illustration guide: *Diplolaimelloides.*

bipartite buccal cavity, which is less developed compared to that in its sister tribe Diplolaimellini, their lip apices not fused, protrusion of the labial cuticle surrounding inner labial papillae and a prominent spinneret (features 8, 10 and 11; Figure 1 and Table 1). Later, three new genera have been described: *Cryonema* Tchesunov & Riemann, 1995, *Hieminema* Tchesunov & Portnova, 2005 and *Halomonhystera* Andrássy (2006). These three genera are closely related to *Gammarinema* by sharing a similar tail shape, a well developed ventral gland opening at the anteriormost neck region and a tube- or cap-like hyaline structure surrounding a common spinneret chamber (features 20, 28, 29, 30 and 35; Figure 1 and Table 1). The two remaining genera, *Sinanema* and *Monhystrella*, resemble each other by a small oral aperture, a tube-like buccal cavity, a pharynx with

posterior bulbus and a long filiform tail (features 25–27; Figure 1 and Table 1). At present, six genera are recognized within this tribe.

DIAGNOSIS

Adapted after Jacobs (1987a).

Diplolaimellinae. Inner labial sensillae surrounded by cylindrical protrusion of labial cuticle. Apex of lips not fused, sometimes forming valve-like structures closing the oral opening like a diaphragm. Cheilostome well sclerotized, but rest of buccal cavity only weakly developed or absent. Median zone of cuticle of tail tip expanded, forming a tube- or

cap-like structure that surrounds the common spinneret duct. Reproductive mode: bisexual or parthenogenetic.

Genus *Cryonema* Tchesunov & Riemann, 1995

This genus has been erected based on the material collected from drifting sea-ice of the Laptev Sea. According to their descriptions, this genus shares the features from the tribe Geomonyhsterini (features 8, 10 and 11; Figure 1 and Table 1), more precisely within the subgroup composed by the genera *Geomonhystera*, *Gammarinema* and *Halomonhystera* (features 28 and 29; Figure 1 and Table 1). With these last two genera, *Cryonema* shares the features 20 and 35 (Figure 1 and Table 1). The genus *Cryonema* is distinguished by the presence of three uniform teeth (feature 43) and the setiform inner labial sensillae (opposed to the feature 36). Tchesunov & Riemann (1995) also noticed the resemblance between *Cryonema* and *Odontobius*. Both genera have a sclerotized vagina and presence of three teeth on the base of the buccal cavity (features 13 and 18; Figure 1 and Table 1). The genus has only two species (Figure 5).

DIAGNOSIS

Aadapted after Tchesunov & Riemann (1995).

Geomonhysterini. Anterior end truncated. Anterior sensillae setiform arranged in two crowns in the 6 + 10 pattern. Inner labial sensillae shorter than outer and cephalic sensillae. Second crown formed by inflated outer labial setae and slender cephalic setae. Amphidial fovea cryptospiral, with a marked circular contour. Short somatic setae sparsely distributed in the sublateral body region. Buccal cavity strongly sclerotized, barrel- or cup-shaped, with three equal-sized teeth on its base. Pharynx cylindrical, muscular, slightly expanding to the posterior end. Ventral gland well developed opening at the anterior neck region, at level of the amphids. Males unknown.

SPECIES LIST

1. *C. crassum* Tchesunov & Riemann, 1995
2. *C. tenue* Tchesunov & Riemann, 1995

IDENTIFICATION KEY FOR THE SPECIES OF THE GENUS *CRYONEMA*

1. Buccal cavity (cheilostome) barrel-shaped; second chamber absent; amphidial fovea one head diameter from the anterior end .... *C. crassum*
2. Buccal cavity cup-shaped; second chamber small and conical; amphidial fovea more than one head diameter from the anterior end .... *C. tenue*

Genus *Halomonhystera* Andrássy, 2006

This genus has been recently erected by Andrássy (2006) to accommodate all the marine species previously described within the genus *Geomonhystera* as well as two new species. Since Andrássy (2006), only one species has been added (Zekely *et al.*, 2006). Currently, 11 species are recognized; all species are illustrated in Figure 6, except *H. antarctica* (Cobb, 1914) Andrássy, 2006 and *H. ambiguoides* (Bütschli, 1874) Andrássy, 2006.

DIAGNOSIS

Adapted after Andrássy (2006).

Geomonhysterini. Cuticle thin, smooth with few inconspicuous somatic setae (mostly papilliform). Labial region not set off. Outer labial and cephalic setae very short, never longer than 1/4 of labial width. Cheilostome sclerotized, cup- to funnel-shaped, rest of buccal cavity weakly developed. Amphidial fovea circular, located from 1–3 hd from anterior end. Pharynx nearly cylindrical and relatively short (b = 5–10). Ventral gland well developed with opening at level of first third of pharynx, occasionally close to the labial region. Gonads (testis and ovary) usually long almost reaching the ventral gland. Vulva far posteriorly at 76% to 92% of the body length from anterior; mostly close to anus. Spicules thin, arcuate with or without a marked capitulum and always longer than (1.2–2.5 times) abd. Gubernaculum short, enveloping distal section of spicules and usually possessing a caudal process or apophysis. One large ventromedian precloacal papilla and two or three pairs of smaller caudal papillae. Rectum short and thin. Tail conoid, length ranging from 2.5 to 7 abd, usually shorter in males than in females. Three caudal glands: two large and one more anterior smaller. Spinneret duct sclerotized, surrounded by a tube like structure.
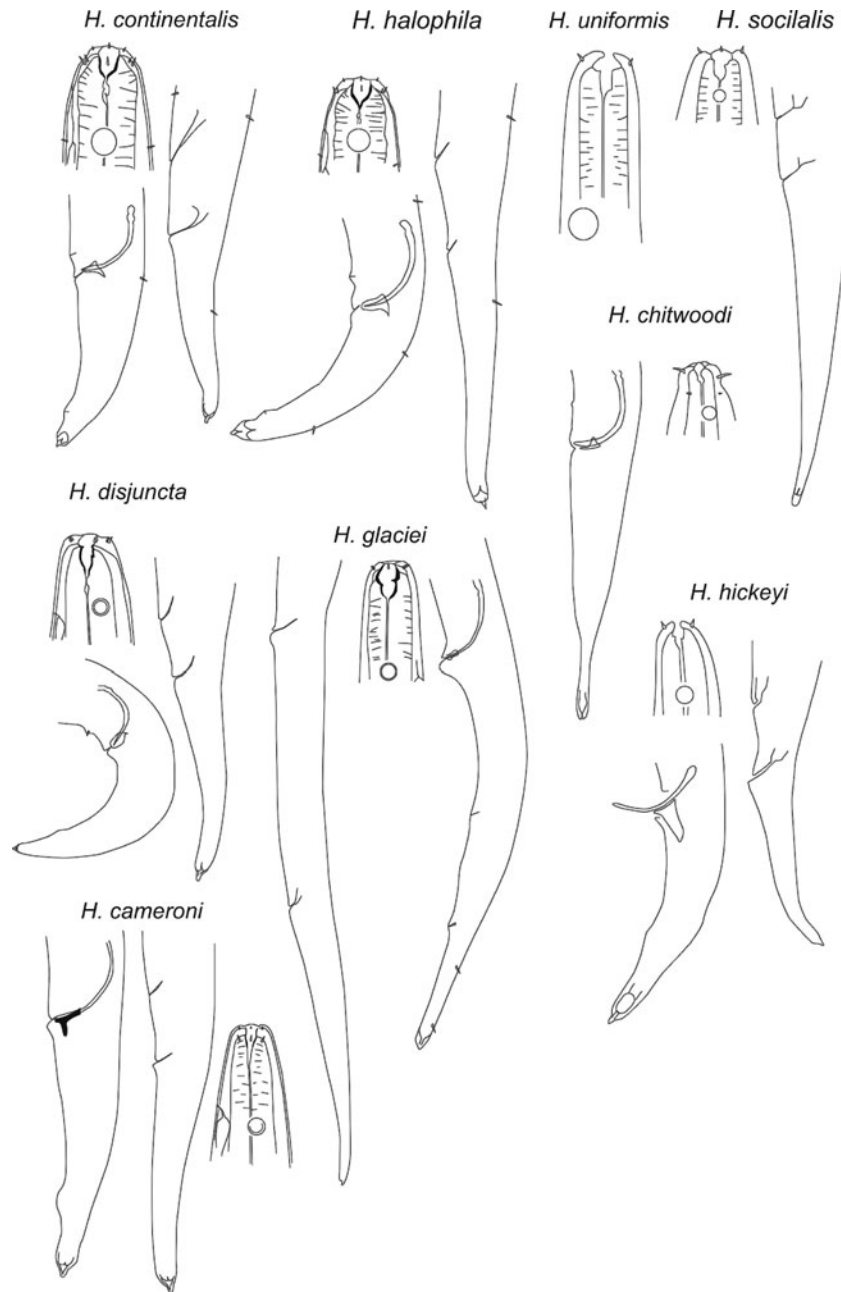

Fig. 5. Illustration guide: *Cryonema*.

Fig. 6. Illustration guide: *Halomonhystera.*

SPECIES LIST

1. ***H. ambiguoides* (Bütschli, 1874) Andrássy, 2006** (Kiel Bay, Baltic)
2. ***H. antarctica* (Cobb, 1914) Andrássy, 2006** (Antarctic Ocean)
3. ***H. cameroni* (Steiner, 1958) Andrássy, 2006** (Bay of Chaleur, commensal in crustaceans)
4. ***H. chitwoodi* (Steiner, 1958) Andrássy, 2006** (in *Sargassum*, Gulf of Mexico)
5. ***H. continentalis* Andrássy, 2006** (Antarctic, Ace Lake)
6. ***H. disjuncta* (Bastian, 1865) Andrássy, 2006** (cosmopolitan)
7. ***H. glaciei* (Blome & Riemann, 1999) Andrássy, 2006** (Antarctic Ocean)
8. ***H. halophila* Andrássy, 2006** (Antarctic, Highway Lake)
9. ***H. hyckeyi* Zekely, Sørensen & Bright, 2006** (Hydrothermal vents, East Pacific Rise)
10. ***H. socialis* (Bütschli, 1874) Andrássy, 2006** (North Sea)
11. ***H. uniformis* (Cobb, 1914) Andrássy, 2006** (Antarctic Ocean)

IDENTIFICATION KEY FOR THE SPECIES OF THE GENUS *HALOMONHYSTERA*

1. Body length equal or longer than 1900 μm 2
   – Body length longer than 800 μm and shorter than 1900 μm. 3
   – Body length longer than 600 μm and shorter than 800 μm. .... *H. hickeyi*

– Body length shorter than 600 μm 7
2. Ratio a equal or larger than 60 .... *H. glaciei*
– Ratio a equal or smaller than 50 .... *H. socialis*
3. Spicules length divided by the anal body diameter equal or larger 1.5 4
– Spicules length divided by the anal body diameter less than 1.5 5
4. Amphidial fovea placed equal or less than 1.2 head diameters from the anterior end .... *H. halophila*
– Amphidial fovea placed equal or further than 1.3 head diameters from the anterior end............. *H. antarctica*
5. Distance between the vulva and the anus equal to the tail length .... *H. chitwoodi*
– Distance between the vulva and the anus equal to 1.5 the anal body diameter .... *H. disjuncta*
– Distance between the vulva and the anus equal to the anal body diameter 6
6. Amphidial fovea placed equal or less than one head diameter from the anterior end .... *H. ambiguoides*
– Amphidial fovea placed equal or further than two head diameters from the anterior end............. *H. cameroni*
7. Ratio a equal or smaller than 24 .... *H. continentalis*
– Ratio a equal or larger than 38 .... *H. uniformis*

Genus *Hieminema* Tchesunov & Portnova, 2005

This monospecific genus was recently described by Tchesunov & Portnova (2005) from coastal ice-cores collected in the White Sea. According to Tchesunov & Portnova (2005), females and juveniles belonging to this genus were already found in ice-regions along the Arctic Canadian coast by Riemann & Sime-Ngando (1997). Within the tribe Geomonhysterini the genus *Hieminema* resembles *Halomonhystera* by having a conoid tail, papilliform inner labial sensillae and a well developed ventral gland opening at the anterior neck region (features 20, 28, 35; Figure 1 and Table 1). *Hieminema* differ from the other genera within the tribe by a combination of characters: (1) strong sexual dimorphism, where the male has a large buccal cavity and the amphidial fovea as large as the corresponding body diameter, while the female has a small buccal cavity and small amphidial fovea; (2) spinneret without a refractive plug-like structure; (3) the presence of two somatic setae just posterior to the amphids; and (4) buccal cavity weakly sclerotized. The type species of this genus is illustrated in Figure 7.

DIAGNOSIS

Aadapted after an English translation provided by A.V. Tchesunov based on Tchesunov & Portnova (2005).

Geomonhysterini. *Hieminema obliquorum* is characterized by long body length (>2 mm). Cuticle finely striated, with inconspicuous somatic setae. Six inner labial sensillae papilliform. Six outer labial and four cephalic sensillae setiform of equal length. Lips apices not fused. Cheilostome weakly sclerotized, cup- to funnel-shaped, larger in males than in the females. Three small teeth may be present at the base of the buccal cavity. Size and shape of the amphidial fovea dependent on the gender: females with a small and
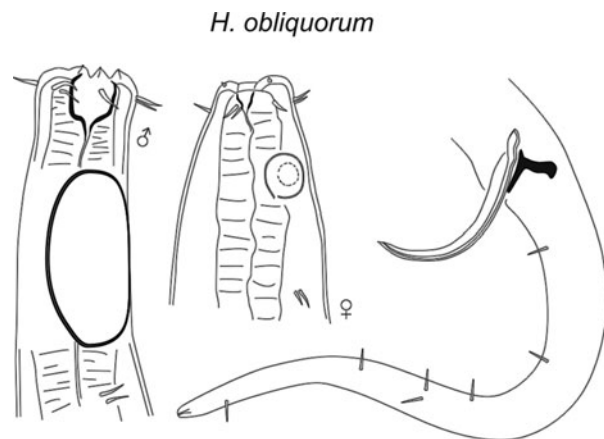

Fig. 7. Illustration *Hieminema obliquorum*.

circular aperture, males with a large and ovoid circular aperture. In both genders, they are located 1–1.5 hd from anterior end. Two small lateral setae posterior to the amphidial fovea. Pharynx nearly cylindrical and relatively short (b = 9.5–12.5). Pharyngeal region dorsally bent. Ventral gland well developed with the ampulla at level of the amphids, pore not seen. Gonads (testis and ovary) usually long almost reaching the ventral gland. Vulva not sclerotized, far posteriorly at 75.5 to 78.4% of the body length from anterior end. Spicules arcuate with a marked capitulum. Gubernaculum short, enveloping distal section of spicules and usually possessing a caudal process or apophysis. Rectum short and thin. Tail conoid, length ranging from 4.5 to 6.5 abd. Three caudal glands of equal size opening in a common duct. Spinneret as a hyaline cap with a thin axial canal weakly sclerotized.

SPECIES LIST

1. *H. obliquorum* Tchesunov & Portnova, 2005

Genus *Monhystrella* Cobb, 1918

The genus *Monhystrella* was introduced by Cobb (1918) with *M. plectoides* as type species and *Monhystera bulbifera* de Man, 1880 as second species. Jacobs (1987b) redefined the genus *Monhystrella* and provided a dichotomous-key to species level. He transferred three *Monhystera* species to the genus *Monhystrella* bringing the total number of valid species to 18. *Monhystrella elegantula* (Schuurmans & Stekhoven, 1935) Jacobs, 1987 and *Monhystrella bulbifera* (de Man, 1880) Cobb, 1918 were considered as *species inquirendae* due to the poor taxonomic descriptions. Although Jacobs (1987b) provided precise identification tools for all valid species, confusion appears when he published the Monhysteridae checklist (Jacobs, 1987a). In his checklist, *Monhystera trichura* Allgén, 1930 was also transferred to the genus *Monhystrella*. The transfer was consistent, since *M. trichura* has typical *Monhystrella* features: a cylindrical buccal cavity, a posterior bulbus, a long and filiform tail and a long tail tip. However, the measurements given by Allgén (1930) are within the range of the original description of *M. microphthalma* de Man, 1880, with the

exception of the larger ratio a (57.9 versus 35–40). It is important to note that the description made by Allgén was based on a single female. Therefore, as suggested before by Wieser (1956) and Schneider (1939), we considered *M. trichura* as synonym of *Monhystrella microphthalma*. Recently, Eyualem-Abebe & Coomans (1996) added six species to the genus, thereby raising the total number of species to 24.

According to the generic definition proposed by Jacobs (1987b), the seven new *Thalassomonhystera* species (*T. amabilis*, *T. gracilis*, *T. mortalis*, *T. peruensis*, *T. praetenuis*, *T. subtilis* and *T. tristis*) described by Bussau (1993) from the East Pacific deep sea, and one species *Thalassomonhystera oxycephalata* described by Tchesunov & Miljutina (2005) from the Arctic deep sea, should be classified in the genus *Monhystrella*. All these species do not present the typical diagnostic characters of the genus *Thalassomonhystera* (see

further) but instead share more similarities with the *Monhystrella* species such as, a minute oral aperture, amphidial fovea far posterior from the anterior end, a narrow pharynx slightly enlarged at the posterior end, absence of ventral gland, females with a short ovary, tail with a long cylindrical posterior portion and spinneret present (as deduced from Bussau's illustrations). The present transfers of these species do not change the diagnosis of *Monhystrella* nor *Thalassomonhystera*. In total we recognize 36 valid species of which only 13 appear in the marine environment. All the marine species are illustrated in Figure 8.

DIAGNOSIS

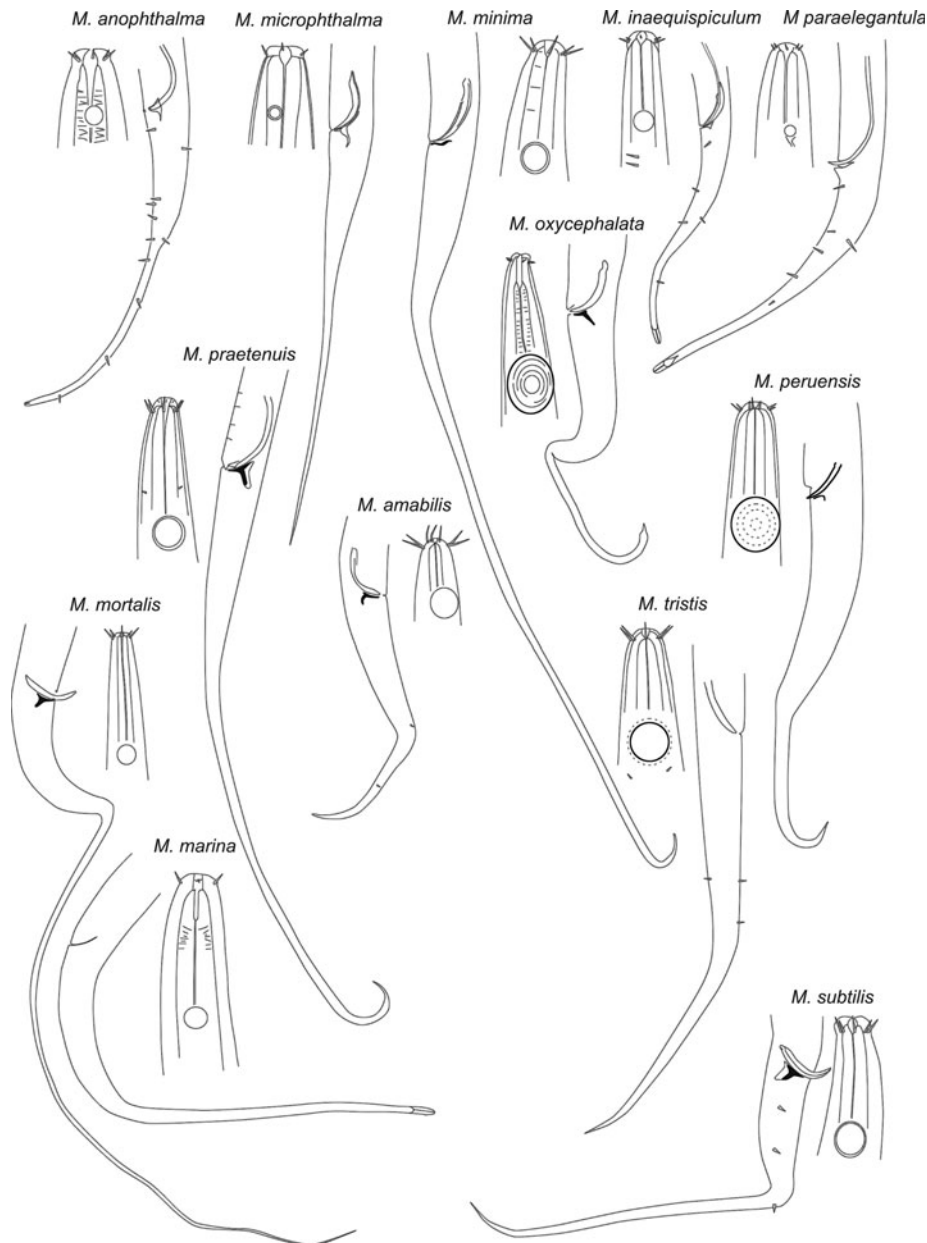Adapted after Jacobs (1987a, b) and Coomans & Eyualem-Abebe (2006).

Fig. 8. Illustration guide: *Monhystrella*.

Geomonhysterini. Short body length (<0.8 mm). Cuticle finely striated, often with small somatic setae. Six outer labial and four cephalic sensillae usually setiform. Labial region often set-off. Cheilostome usually small, rest of buccal cavity tubiform, funnel-shaped or conoid, often with well cuticularized walls. Dorsal denticle usually present, but difficult to observe in small species. Amphidial fovea circular or cryptospiral usually 1.5–2 or more hd from anterior end, rarely closer to anterior end (about 1 hd in *M. parvella*). Ocelli rarely present. Posterior part of the pharynx enlarged forming a single or double bulb without valves. Anterior part of intestine (progaster) globe-like. Ventral gland usually absent. Female reproductive system medium-sized to short with ovary comprising few oocytes; gravid females mostly with only one egg in uterus. Vulva near mid-body. Males rare or unknown in freshwater species (except in *M. macrura*) and more common in marine species. Spicules mostly arcuate and short (<2 abd) or less commonly unequal and large as in *M. inaequispiculum* Lorenzen, 1979. Tail with usually ventrally curved conical anterior portion and dorsally curved cylindrical filiform posterior part in fixed specimens. Spinneret a long and slender cone or cylinder.

SPECIES LIST

1. **M. amabilis (Bussau, 1993) comb. nov.** (deep sea, Pacific Ocean)
   Syn. *Thalassomonhystera amabilis* Bussau, 1993
2. **M. anophthalma (Lorenzen, 1969) Jacobs, 1987** (North Sea)
3. *M. arsiensis* Eyualem-Abebe & Coomans, 1996
4. *M. atteae* Eyualem-Abebe & Coomans, 1996
5. *M. ethiopica* Eyualem-Abebe & Coomans, 1996
6. *M. fukiensis* (Hoeppli & Chu, 1932) Jacobs, 1987
7. *M. gracilis* Khera, 1966
8. *M. hastata* Andrássy, 1968
9. *M. hoogewijsi* Eyualem-Abebe & Coomans, 1996
10. **M. inaequispiculum Lorenzen, 1979** (sand beach, Patagonia)
11. *M. iranica* Schiemer, 1965
12. *M. jacobsi* Eyualem-Abebe & Coomans, 1996
13. *M. kerryi* Khan, Hussain, Sultana & Tahssen, 2005
14. *M. lepidura* (Andrássy, 1963) Andrássy, 1968
    M. lepidura lepidura Andrássy, 1963
    M. lepidura chinensis Eyualem-Abebe, Liang & Coomans, 2001
    M. lepidura altherri (Juget, 1969) Jacobs, 1987
    M. lepidura seelyae Heyns & Coomans, 1989
15. *M. longistoma* (Khera, 1971) Andrássy, 1981
16. *M. macrura* (de Man, 1880) Andrássy, 1981
17. **M. marina Timm, 1964** (Bay of Bengal)
18. **M. microphthalma (de Man, 1880) Jacobs, 1987** (brackish, Netherlands)
    Syn. *Monhystera trichura* (Allgén, 1930) Jacobs, 1987
19. **M. minima (Bussau, 1993) comb. nov.** (deep sea, Pacific Ocean)
    Syn. *Thalassomonhystera gracilis* Bussau, 1993
20. *M. monachilensis* Picazo-Muñoz, 1988
21. **M. mortalis (Bussau, 1993) comb. nov.** (deep sea, Pacific Ocean)
    Syn. *Thalassomonhystera mortalis* Bussau, 1993

22. **M. oxycephalata (Tchesunov & Miljutina, 2005) comb. nov.** (deep sea, Arctic)
    Syn. *Thalassomonhystera oxycephalata* Tchesunov & Miljutina, 2005
23. *M. paramacrura* (Meyl, 1954) Andrássy, 1968
24. **M. parelegantula (De Coninck, 1943) Andrássy, 1981** (brackish, Iceland)
25. *M. parvella* (Filipjev, 1931) Jacobs, 1987
    M. parvella parvella (Filipjev, 1931) Jacobs, 1987
    M. parvella filiformis (Gerlach, 1951) Jacobs, 1987
26. **M. peruensis (Bussau, 1993) comb. nov.** (deep sea, Pacific Ocean)
    Syn. *Thalassomonhystera peruensis* Bussau, 1993
27. *M. plectoides* Cobb, 1918
28. *M. postvulvae* Khan & Araki, 2001
29. **M. praetenuis (Bussau, 1993) comb. nov.** (deep sea, Pacific Ocean)
    Syn. *Thalassomonhystera praetenuis* Bussau, 1993
30. *M. raphae* Ocaña, 1987
31. **M. subtilis (Bussau, 1993) comb. nov.** (deep sea, Pacific Ocean)
    Syn. *Thalassomonhystera subtilis* Bussau, 1993
32. *M. spiralis* (Wu & Hoeppli, 1929) Andrássy, 1981
33. *M. stewarti* (Khera, 1971) Andrássy, 1981
34. *M. thermophila* (Meyl, 1953) Andrássy, 1981
35. **M. tristis (Bussau, 1993) comb. nov.** (deep sea, Pacific Ocean)
    Syn. *Thalassomonhystera tristis* Bussau, 1993
36. *M. woitorum* Eyualem-Abebe & Coomans, 1996

SPECIES INQUIRENDAE

1. *M. elegantula* (Schuurmans Stekhoven, 1935) Jacobs, 1987
   Syn. *Monhystera elegantula* Schuurmans Stekhoven, 1935
2. *M. bulbifera sensu* de Man, 1880 *nec* Steiner, 1920; Jacobs, 1987

IDENTIFICATION KEY FOR THE MARINE SPECIES OF THE GENUS MONHYSTRELLA

1. Amphidial fovea placed less than 2 head diameters from the anterior end 2
– Amphidial fovea placed equal or further than 2 head diameters from the anterior end 4
2. Ratio c equal or smaller than 4.7; size of the amphidial fovea equal or smaller than 35% of the corresponding body diameter 3
– Ratio c equal or larger than 5.4; size of the amphidial fovea equal or larger than 60% of the corresponding body diameter .... *M. amabilis*
3. Ocelli present; apophysis weakly cuticularized .... *M. microphthalma*
– Ocelli absent; apophysis strongly cuticularized .... *M. anophthalma*
4. Size of the amphidial fovea equal or less than 50% of the corresponding body diameter 5
– Size of the amphidial fovea between 50% and 65% of the corresponding body diameter 8
– Size of the amphidial fovea equal or larger than 65% of the corresponding body diameter 10
5. Ratio c equal or smaller than 4.7; spicules symmetrical 6
– Ratio c equal or larger than 5.2; spicules asymmetrical. . . . .*M. inaequispiculum*

6. Double bulbus . . . . *M. marina*
– Single bulbus 7
7. Ratio c equal or smaller than 10 . . . . . *M. paraelegantula*
– Ratio c equal or larger than 16 . . . . *M. minima*
8. Ratio c equal or smaller than 10 . . . . *M. subtilis*
– Ratio c equal or larger than 14 9
9. Ratio a equal or larger than 50; pre-cloacal supplements present . . . . *M. praetenuis*
– Ratio a between 40 and 46; pre-cloacal supplements absent . . . . *M. mortalis*
10. Body length equal or longer than 785 μm . . . . . *M. tristis*
– Body length equal or shorter than 450 μm 11
11. Apophysis present . . . . *M. oxycephalata*
– Apophysis absent . . . . *M. peruensis*

Subfamily MONHYSTERINAE de Man, 1876

When reviewing the family, Jacobs (1987a) grouped the genera *Thalassomonhystera*, *Monhystera* and *Eumonhystera* based on the shape of the buccal cavity; i.e. a single chamber, V-shaped, weakly sclerotized (feature 4; Figure 1 and Table 1) and he considered *Anguimonhystera* as a *genus inquirenda*. However, Andrássy (2005) and Coomans & Eyualem-Abebe (2006) retained the genus as valid. Eyualem-Abebe & Coomans (1995) added the genus *Tridentulus* within this subfamily. Andrássy (2007) noted that the genus *Tridentulus* was already described under Reptilia, and suggested *Tridentula* as a new name. Presently, Monhysterinae is divided into two tribes, Thalassomonhysterini and Monhysterini, based on separated lips or fused lips apices (respectively features 8 and 9 in Figure 1 and Table 1) and absence or presence of peri-oral plates (feature 38; Figure 1 and Table 1).

DIAGNOSIS

Adapted after Jacobs (1987a).

Monhysteridae. Inner labial sensillae setiform or papilliform. Buccal cavity with a single V-shaped chamber, poorly sclerotized. Radii of pharyngeal lumen broad, long and only slightly sclerotized. Common spinneret chamber and duct not elongated or sclerotized. Reproductive mode: bisexual or parthenogenetic. Two tribes.

Tribe THALASSOMONHYSTERINI Jacobs, 1987

This tribe is monogeneric with *Thalassomonhystera* as type genus. Jacobs (1987a)'s intention was to separate this marine genus from the other inland genera (Monhysterini). The separation of this tribe was mainly based on the apex of the lips not fused, opening of the ventral gland at level of the first third of pharynx and occasionally in the labial region, papilliform inner labial sensillae and absence of peri-oral plates (features 8, 20, 35 and 36; Figure 1 and Table 1).

DIAGNOSIS

Adapted after Jacobs (1987a).

Monhysterinae. Labial sensillae papilliform. Apex of lips not fused. Buccal cavity wide and V-shaped without peri-oral plates. Ocelli mostly absent. Ventral gland usually well developed and opening at the anterior neck region. Crystalloides bodies absent. Tail tip not swollen with the exception in *T. gerlachii* (Meyl, 1954) Jacobs, 1987. Reproductive mode: bisexual.

Genus *Thalassomonhystera* Jacobs, 1987

When Jacobs (1987a) erected the genus *Thalassomonhystera* he included all the marine species (except those transferred to *Monhystrella*) previously belonging to the genus *Monhystera*. The new genus was mainly characterized by the presence of a large ventral gland with outlet in the anterior neck region. The division of the *Monhystera* species over two genera coincides with an environmental separation, *Thalassomonhystera* marine versus *Monhystera* inland. Consequently, authors started to identify the genus *Thalassomonhystera* based on its ecological occurrence rather than on the diagnostic set of characters proposed by Jacobs (1987a). For instance, in a recent taxonomic paper, Tchesunov & Miljutina (2005) considered all the marine '*Monhystera*' belonging either to the genus *Geomonhystera* (*G. disjuncta* related species) or to *Thalassomonhystera* (not related to *G. disjuncta*). There are two main problems when genera are separated based on such a statement: first it is well known that in the marine realm there are seven genera of the family Monhysteridae (as presented in this study) and second, most important, a genus cannot be defined because its members do not belong to the other known genera without indication of diagnostic features. Tchesunov & Miljutina (2005) proposed two new *Thalassomonhystera* species, *T. molloyensis* and *T. oxycephalata*. The first species resembles *T. bathyslandica* Riemann 1995, while the second belongs to the genus *Monhystrella*. *Thalassomonhystera oxycephalata* is characterized by a small oral opening and a sclerotized cylindrical buccal cavity instead of a V-shape as in *Thalassomonhystera*. Furthermore, the amphidial fovea is located five times the head diameter from the anterior end and such a far posterior position is unknown for *Thalassomonhystera* but has been more frequently observed in the genus *Monhystrella*. Finally, the tail in *T. oxycephalata* is divided into two equal parts, one conical anterior portion and a cylindrical posterior part with a well developed spinneret, two characters that are typical for the genus *Monhystrella*, while *Thalassomonhystera* has a conical tail tapering gradually towards the tip and the spinneret is very small and barely distinguishable.

In the same way, Bussau (1993) appeared to have overlooked some diagnostic characters of the genera *Thalassomonhystera* and *Monhystrella* as proposed by Jacobs (1987a, b) when describing 9 new species of *Thalassomonhystera*, 3 unnamed species and one known species. Seven of the new species belong to *Monhystrella* (see previously).

Recently, Eyualem-Abebe *et al.* (2001) described *T. traesti* Eyualem-Abebe, Liang & Coomans, 2001 from a river in China, expanding the occurrence of the genus to the freshwater environment. They stated that 'Although our species was found in fresh water and despite some differences (slightly longer than the longest species in the genus so far, more developed inner labial sensillae, ventral gland poorly developed), it better fits the generic diagnosis of *Thalassomonhystera* than that of any other genus so far established in the Monhysterinae de Man, 1876' (Eyualem-Abebe *et al.*, 2001).

However, the position of this species is rather uncertain. According to Jacobs (1987a), in order to belong to the genus *Thalassomonhystera*, a species should possess separated lip apices, no peri-oral plates, a well developed ventral gland opening at the anterior neck region and papilliform inner labial sensillae. Peri-oral plates and separated lips apices were not reported and discussed in their description. It could be argued that both characters were implicit in their description, since they are diagnostic characters to genus level. However, *T. traesti* has inner labial sensillae setiform and a poorly developed ventral gland with its opening at the mid-pharynx, which are common features of the subfamily Monhysterinae. Nevertheless, *T. traesti* does not completely agree with the other generic diagnoses of the subfamily Monhysterinae. The genera *Eumonhystera* and *Anguimonhystera* are characterized by a long filiform tail (feature 26; Figure 1 and Table 1), *Tridentula* by the presence of three teeth in the buccal cavity (feature 18; Figure 1 and Table 1) and *Monhystera* by the presence of crystalloid bodies and ocelli (features 17 and 40; Figure 1 and Table 1). Thus, in order to classify *T. traesti* in a genus, a revision considering all these genera should be conducted, followed by a redescription of the taxa. At the moment, *T. traesti* has an uncertain taxonomic position (*incertae sedis*).

Coomans & Eyualem-Abebe (2006) transferred *Monhystera amabilis* Gagarin, 2001 to the genus *Thalassomonhystera* without substantiating their decision. Since this species does not present the diagnostic characters of the genus *Thalassomonhystera* (well developed ventral gland, ventral pore in the anterior neck region, apex of the lips not fused and inner labial papillae), we do not recognize the relocation. At present, the genus *Thalassomonhystera* comprises most of the marine species described within the family Monhysteridae. After the erection of the genus by Jacobs (1987a), seven new species were added and at present, there are 25 valid species. With the exception of *T. uria* (Stewart, 1914) Jacobs, 1987, all the species, including *T. traesti incertae sedis*, are illustrated in Figure 9.

DIAGNOSIS

Adapted after Jacobs (1987a).

Thalassomonhysterini. Body medium-sized, submedian somatic setae less than 30% of cbd. Inner labial sensillae papilliform. Outer labial sensillae (usually setiform) and cephalic setae shorter than 1/3 of the head diameter. Buccal cavity undivided, funnel-shaped. Pharynx cylindrical with the posterior part slightly broader. Ocelli absent. Ventral gland well developed, opening in the anterior end (labial region). Spermatheca may be well developed. Spicules length varying between 1–2.2 abd; spicules vary from arcuate-shaped and well sclerotized to setaceous and slender. Gubernaculum either small and robust with a dorsal apophysis, or slender without apophysis. Tail elongate conical usually with the anterior part ventrally bent and the posterior dorsally bent. Tail of females shorter than V–a distance.

SPECIES LIST

1. **T. abnormis Bussau, 1993** (deep sea, Pacific)

2. **T. anoxybiota (Jensen, 1986) Jacobs, 1987** (brine seep, Gulf of Mexico)
3. **T. attenuata (Filipjev, 1922) Jacobs, 1987** (Black Sea)
4. **T. bathislandica Riemann, 1995** (deep sea, north-east Atlantic)
5. **T. cuspidospiculum (Allgén, 1932) Jacobs, 1987** (Campbell Island)
6. **T. denticulata (Timm, 1952) Jacobs, 1987** (Chesapeak Bay, USA)
7. **T. diplops (Cobb, 1894) Jacobs, 1987** (Australia)
8. **T. fisheri Zekely, Sørensen & Bright, 2006** (deep sea, East Pacific Rise)
9. **T. gerlachii (Meyl, 1954) Jacobs, 1987** (vulcanic sand beach, Ische Island)
10. **T. islandica (De Coninck, 1943) Jacobs, 1987** (brackish, Iceland)
11. **T. magallanica (Wieser, 1956) Jacobs, 1987** (littoral algae, Chile)
12. **T. molloyensis Tchesunov & Miljutina, 2005** (deep sea, Arctic)
13. **T. multisetosa (Meyl, 1955) Jacobs, 1987** (saltmarsh, North Sea)
14. **T. ocellidecorus (Hopper & Meyers, 1967) Jacobs, 1987** (Biscayne Bay, Florida)
15. **T. ovifera Bussau, 1993** (deep sea, Pacific)
16. **T. parasimplex (De Coninck, 1943) Jacobs, 1987** (brackish, Iceland)
17. **T. parva (Bastian, 1865) Jacobs, 1987** (tide pools, England)
18. **T. pusilla (Boucher & Helleouetes, 1977) Jacobs, 1987** (sublittoral, Atlantic-France)
19. **T. refringens (Bresslau & Schuurmans-Stekhoven, 1935) Jacobs, 1987** (North Sea)
20. **T. rotundicapitata (Filipjev, 1922) Jacobs, 1987** (Black Sea)
21. **T. siamensis Kito & Aryuthaka, 2001** (shrimp pounds, Thailand)
22. **T. tasmaniensis (Allgén, 1927) Jacobs, 1987** (Tasmania)
23. **T. uria (Stewart, 1914) Jacobs, 1987** (Bay of Bengal)
24. **T. vandoverae Zekely, Sørensen & Bright, 2006** (deep sea, Mid-Atlantic Ridge)
25. **T. venusta (Lorenzen, 1979) Jacobs, 1987** (sublittoral, North Sea)

SPECIES INQUIRENDAE

See Jacobs (1987a).

SPECIES INCERTAE SEDIS

1. *Thalassomonhystera traesti* (Eyualem-Abebe, Peng & Coomans, 2001)

SPECIES TRANSFERED TO THE GENUS *MONHYSTRELLA*

1. **M. amalbilis (Bussau, 1993) comb. nov.**
   Syn. *Thalassomonhystera amabilis* Bussau, 1993
2. **M. minima (Bussau, 1993) comb. nov.**
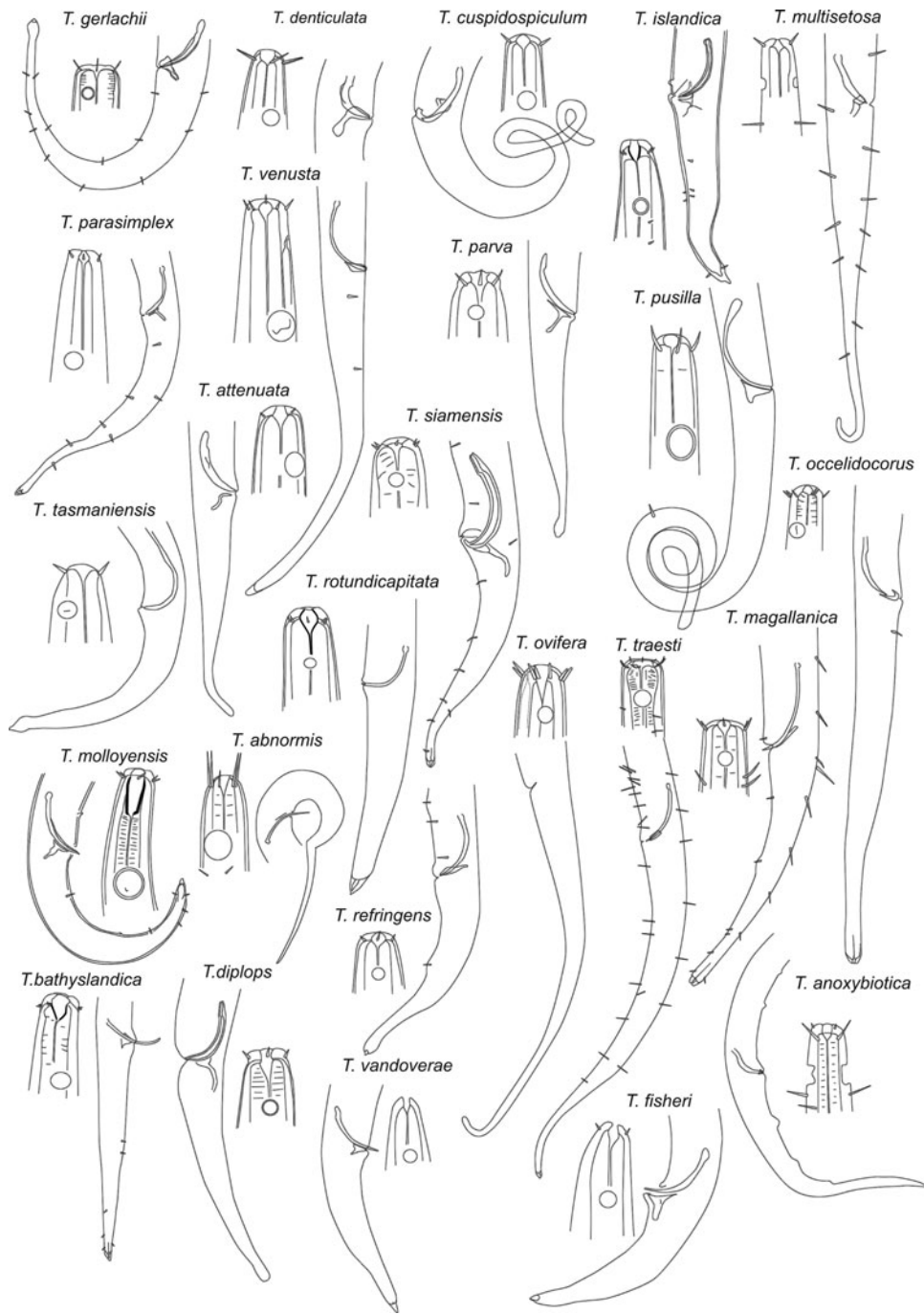   Syn. *Thalassomonhystera gracilis* Bussau, 1993

Fig. 9. Illustration guide: *Thalassomonhystera.*

3. ***M. mortalis*** (Bussau, 1993) comb. nov.
   Syn. *Thalassomonhystera mortalis* Bussau, 1993
4. ***M. oxycephalata*** (Tchesunov & Miljutina, 2005) comb. nov.
   Syn. *Thalassomonhystera oxycephalata* Tchesunov & Miljutina, 2005
5. ***M. peruensis*** (Bussau, 1993) comb. nov.
   Syn. *Thalassomonhystera peruensis* Bussau, 1993
6. ***M. praetenuis*** (Bussau, 1993) comb. nov.
   Syn. *Thalassomonhystera praetenuis* Bussau, 1993
7. ***M. subtilis*** (Bussau, 1993) comb. nov.
   Syn. *Thalassomonhystera subtilis* Bussau, 1993
8. ***M. tristis*** (Bussau, 1993) comb. nov.
   Syn. *Thalassomonhystera tristis* Bussau, 1993

IDENTIFICATION KEY FOR THE SPECIES OF THE GENUS *THALASSOMONHYSTERA*

Since this key is based on characters from both genders, *T. ovifera* was not included in it because it was described based solely in females; diagnostic data for this species are: $L = 730 - 1075$ μm, $a = 39.8 - 44$, $b = 5.5$, $c = 6 - 7.2$, $c' = 8.3 - 10$ and somatic setae absent. Although the classification of *T. traesti* is uncertain, we include it in the key.

1. Caudal apophysis present 2
– Caudal apophysis absent 9

2. Body length longer than 1000 μm; ratio a equal or larger than 50; ratio c equal or larger than 10 . . . . *T. denticulata*
 – Body length between 700 μm and 1000 μm 3
 – Body length shorter than 700 μm 4
3. Ratio a equal or larger than 50 . . . . *T. pusilla*
 – Ratio a between 28 and 45 . . . . *T. fisheri*
 – Ratio a equal or smaller than 25 . . . . *T. diplops*
4. Amphidial fovea located equal or less than one head diameter from the anterior end 5
 – Amphidial fovea located between 1.7 and 2.5 head diameters from the anterior end 8
 – Amphidial fovea located equal or further than 2.7 head diameters from the anterior end . . . . *T. molloyensis*
5. Ratio c equal or smaller than 6.1 6
 – Ratio c equal or larger than 6.5 7
6. Somatic setae absent . . . . *T. parva*
 – Somatic setae present . . . . *T. gerlachii*
7. Spicules length divided by the anal body diameter equal or shorter than one . . . . *T. attenuata*
 – Spicules length divided by the anal body diameter equal or larger than 1.8 . . . . *T. siamensis*
8. Body length equal or smaller than 470 μm . . . . *T. multisetosa*
 – Body length equal or larger than 570 μm . . . . *T. bathyslandica*
9. Ratio a equal or larger than 40 10
 – Ratio a smaller than 40 11
10. Ratio c equal or larger than 6 . . . . *T. anoxybiotica*
 – Ratio c equal or smaller than 5.6 . . . . *T. cuspidospiculum*
11. Body length equal or shorter than 550 μm 12
 – Body length equal or longer than 600 μm 17
12. Amphidial fovea located equal or further than 2.5 head diameters from the anterior end 13
 – Amphidial fovea located equal or less than 2 head diameters from the anterior end 14
13. Spicules length divided by the anal body diameter equal or longer than 1.8 . . . .*T.venusta*
 – Spicules length divided by the anal body diameter equal or shorter than 1.7 . . . . *T. parasimplex*
14. Ratio c equal or smaller than 7.5 15
 – Ratio c equal or larger than 8 16
15. Spicules length divided by the anal body diameter equal or longer than 1.8 . . . . *T. uria*
 – Spicules length divided by the anal body diameter equal or shorter than 1.7 . . . .*T. islandica*
16. Size of the amphidial fovea equal or smaller than 40% of the corresponding body diameter; cephalic setae 1.3 times longer than the head diameter . . . .*T. ocellidecorus*
 – Size of the amphidial fovea equal or larger than 60% of the corresponding body diameter; cephalic setae equal to the head diameter . . . . *T. abnormis*
17. Ratio c equal or longer than 8 18
 – Ratio c equal or smaller than 7.8 19
18. Body length equal or longer than 850 μm . . . . *T. rotundicapitata*
 – Body length equal or shorter than 760 μm . . . . *T. vandoverae*
19. Somatic setae present 20
 – Somatic setae absent 21
20. Ratio c equal or smaller than 6 . . . . *T. magallanica*
 – Ratio c between 8.5 and 9.3 . . . . *T. traesti*
21. Ratio c equal or smaller than 5.4 . . . . *T. refringens*

 – Ratio c between 5.5 and 6.2 . . . .*T. tasmaniensis*
 – Ratio c equal or larger than 6.7 . . . . *T. uria*

DISCUSSION

From the literature, it appears that all species descriptions within the Monhysteridae are based on the morphological species concept whereby species boundaries are defined on the basis of particular essential features. There is no proof of gene flow and morphological distinctiveness is considered as a surrogate to lineage independence. The hypothesis of a new species using the morphological species concept can more easily be tested compared to new species based on the phylogenetic species concept. So far no phylogenetic study has been carried out for the Monhysteridae below the family level. An attempt for a phylogenetic analysis was made by Jacobs in his PhD thesis but never published (Jacobs, 1988). The main difficulty to perform such analysis in this family is to determine the polarity of the characters; several features being probably convergent.

At present, the family Monhysteridae is composed of 17 genera with a total of 207 valid species (Table 2). Roughly, 58.5% of the species are described from the inland environment and 33.8% from the marine realm. On average, the inland and marine genera are species rich and characterized by a large morphological diversity (Table 2). Although the number of species descriptions within this family is large, only few studies provide complete illustrations, morphometric data and discuss relationships with other species of the genus. Most species descriptions are poor and even the most recent papers do not include data on variability within genus. However, we do realize that the diagnostic characters in such small nematodes are not always evident and are easily overlooked leading to a misclassification (Riemann, 1995). Therefore, instead of increasing our knowledge in the different groups, many problems have arisen (Coomans, 2002).

Wrong classification is particularly evident in the two most species rich marine Monhysteridae genera, *Thalassomonhystera* and *Monhystrella*. For the latter, the situation became clearer after the redefinition of the genus and redescription of a

Table 2. Number of valid species of each Monhysteridae genus at the different biotopes.

Genera	Marine	Inland	Commensal	Total
1. Monhystrella	13	23		36
2. Eumonhystera		35		35
3. Monhystera		30		30
4. Thalassomonhystera	25			25
5. Geomonhystera		18		18
6. Diplolaimella	12			12
7. Halomonhystera	10		1	11
8. Diplolaimelloides	7	1		8
9. Gammarinema			8	8
10. Tridentula		7		7
11. Monhystrium			5	5
12. Sinanema		4		4
13. Anguimonhystera		3		3
14. Cryonema	2			2
15. Hieminema	1			1
16. Odontobius			1	1
17. Tripylium		1		1
Total	70	121	16	207

species by Jacobs (1987b, c). Nevertheless, as shown in the present study, the diagnostic characters of the genus *Monhystrella* have been largely overlooked. For the genus *Thalassomonhystera*, the situation is somewhat more complicated because the characters that separate it from the tribe Monhysterini are sometimes difficult to recognize by light microscopy and were barely reported in the older literature. Consequently, there is a huge morphological variability, no well defined genus border nor clear differentiation from the other genera. Additional characters that help to identify the genus *Thalassomonhystera*, such as well developed ventral gland opening at the labial region and inner labial sensillae papilliform, are also present in the genera *Halomonhystera* and *Tridentula* respectively.

The lack of phylogenetic information and molecular data hampers the progress of systematics in the group as well as a straightforward identification method. In fact, as shown in the present study, the mostly used characters to separate monhysterids species throughout the different genera are the same (e.g. body length, size and position of the amphidial fovea, length of the tail, length of the spicules; see dichotomous-keys). In some way, this means that evolutionary processes are selecting the same characters in the different genera and therefore generating a large number of homoplasies (Hall, 2003). For instance, the transfer of the eight deep-sea species from the genus *Thalassomonhystera* to the genus *Monhystrella* proposed here did not disrupt the morphological unity of the latter genus, but increased the morphological range of two characters. As presented in the dichotomous-key, nearly all deep sea species have a larger amphidial fovea and a longer tail in relation to the anal body diameter (c ratio) than shallow-water species.

Morphological adaptation to live in the deep-sea is a common feature among other invertebrate taxa (Kaariainen & Bett, 2006 and references therein) and seems to be related to the low input of food (Thiel, 1975). Perhaps, having large sensorial organs, such as amphidial fovea, may increase their ability for foraging and mating recognition in such nutrient poor environment characterized by low population densities. The increase in tail length towards the deep is probably related to the very fine sediment type and the hemi-sessile life-strategy adopted by these organisms in this environment (Riemann, 1974). So far, without extra taxonomic information, it is still difficult to speculate whether the deep-sea species within the genus *Monhystrella* have a common ancestor and species with large amphidial fovea and long tails represent one monophyletic group, or whether they have different ancestors and therefore their body shape converged to similar morphotypes. Conjectures in favour of a monophyletic deep-sea group were already suggested within the family Draconematidae (*Bathychaetosoma* (Kito, 1983) Decraemer, Gourbault & Backeljau, 1997, *Cephalochaetosoma* Kito, 1983 and *Dinetia* Decraemer & Gourbault, 1997; Decraemer et al., 1997).

At this point, the classification of the Monhysteridae into subfamilies, tribes and genera is based on similarity/dissimilarity of diagnostic morphological features with the assumption that phenetic similarity underlay similarity of genotype. Now, if this classification is one that reflects natural grouping or phylogenetic relationships remains to be tested by other methods. Thus, to avoid further confusion in this family, new descriptions should also include user friendly identification-keys to species level and a more detailed differential diagnosis. Preferably they should also integrate different taxonomic methods (Fonseca et al., in press). There are numerous possibilities for identification tools used in nematology: dichotomous (Andrássy, 1981, 2006), polytomous (Decraemer & Gourbault, 2000; Lamberti et al., 2000), graphical polytomous (Fonseca et al., 2006a), pictorial (Platt, 1984; Decraemer et al., 1997; Tchesunov & Mokievsky, 2006), tabular (Fonseca et al., 2006b; Zhang & Zhang, 2006) and computer-assisted (Diederich et al., 2000). Recently, several authors have shown the importance of using statistics for species differentiation (Gozel et al., 2006; Derycke et al., 2008; Fonseca et al., in press). Independent of the method used, identification tools are especially necessary in order to transmit the taxonomic knowledge to non-taxonomists. Moreover, it guides researchers to identify and describe different taxa increasing our taxonomic knowledge in the group. Hopefully, in the near future, when molecular markers will become generally accessible and their use compulsory in taxonomic descriptions, identification-keys may also become phylogenetically informative.

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REFERENCES

For references up to 1972 see Gerlach & Riemann (1973).

Alkemade R., Wielemaker A., Herman P.M.J. and Hemminga M.A. (1994) Population dynamics of *Diplolaimelloides bruciei*, a nematode associated to the salt marsh plant *Spartina anglica*. *Marine Ecology Progress Series* 105, 277–284.

Andrássy I. (1981) Revision of the order Monhysterida (Nematoda) inhabiting soil and inland waters. *Opuscula Zoologica Instituti Zoosystematici Universitatis Budapestinensis* 17–18, 63–70.

Andrássy I. (2005) Free-living nematodes of Hungary, I (Nematoda Errantia). *Pedozoologica Hungarica* 3, 1–518.

Andrássy I. (2006) *Halomonhystera*, a new genus distinct from *Geomonhystera* Andrássy, 1981 (Nematoda: Monyhsteridae). *Meiofauna Marina* 15, 11–24.

Andrássy I. (2007) Free-living nematodes of Hungary, II (Nematoda Errantia). *Pedozoologica Hungarica* 4, 1–496.

Bussau C. (1993) *Taxonomische und ökologische Untersuchungen an Nematoden des Perus-Beckens.* PhD thesis, University of Kiel, Kiel, Germany.

Coomans A. (2000) Nematode systematics: past, present and future. *Nematology* 2, 3–7.

Coomans A. (2002) Present status and future of nematode systematics. *Nematology* 4, 573–582.

Coomans A. and Eyualem-Abebe (2006) Order Monhysterida. In Eyualem-Abebe, Traunspurger W. and Andrássy I. (eds) *Freshwater*

nematodes: ecology and taxonomy. Wallingford: CABI Publishing, pp. 574–603.

Da Rocha C.M.C., Venekey V., Bezerra T.N.C. and Souza J.R.B. (2006) Phytal marine nematode assemblages and their relation with the macrophytes structural complexity in a Brazilian tropical rocky beach. *Hydrobiologia* 553, 219–230.

Decraemer W., Gourbault N. and Backeljau T. (1997) Marine nematodes of the family Draconematidae (Nemata): a synthesis with phylogenetic relationships. *Hydrobiologia* 357, 185–202.

Decraemer W. and Gourbault N. (2000) New species of *Metepsilonema* (Nemata, Epsilonematidae) from the Channel and the Mediterranean Sea with a polytomous key for the identification of species of the genus. *Hydrobiologia* 429, 25–47.

Derycke S., Backeljau T., Vlaeminck C., Vierstraete A., Vanfleteren J., Vincx M. and Moens T. (2007) Spatiotemporal analysis of population genetic structure in *Geomonhystera disjuncta* (Nematoda, Monhysteridae) reveals high levels of molecular diversity. *Marine Biology* 151, 1799–1812.

Derycke S., Fonseca G., Vierstraete A., Vanfleteren J., Vincx M. and Moens T. (2008) Disentangling taxonomy within the *Rhabditis (Pellioditis) marina* (Nematoda, Rhabditidae) species complex using molecular and morphological tools. *Zoological Journal of the Linnean Society* 152, 1–15.

Diederich J., Fortuner R. and Milton J. (2000) Genisys and computer-assisted identification of nematodes. *Nematology* 2, 17–30.

Eyualem-Abebe and Coomans A. (1995) *Tridentulus*, a new genus of Monhysteridae (Nematoda) from Galápagos archipelago. *Bulletin de L'Institut Royal des Sciences Naturelles de Belgique* 65, 5–10.

Eyualem-Abebe and Coomans A. (1996) Aquatic nematodes from Ethiopia II: the genus *Monhystrella* Cobb, 1918 (Monhysteridae: Nematoda) with the description of six new species. *Hydrobiologia* 324, 53–77.

Eyualem-Abebe, Liang Y.P. and Coomans A. (2001) *Thalassomonhystera traesti* n.sp., *Eumonhystera andrássy* and three *Monhystrella* species (Monhysteridae: Nematoda) from Li River, China. *Hydrobiologia* 462, 185–197.

Fonseca G., Vanreusel A. and Decraemer W. (2006a) Taxonomy and biogeography of *Molgolaimus* Ditlevsen, 1921 (Nematoda: Chromadoria) with reference to the origins of deep sea nematodes. *Antarctic Science* 18, 23–50.

Fonseca G., Decraemer W. and Vanreusel A. (2006b) Taxonomy and species distribution of the genus *Manganonema* Bussau, 1993 (Nematoda: Monhysterida). *Cahiers de Biologie Marine* 47, 189–203.

Fonseca G., Derycke S. and Moens T. (2008) Integrative taxonomy in two cosmopolitan nematode species. *Biological Journal of the Linnean Society* 94, 737–753.

Fonseca G. and Soltwedel T. (2007) Deep-sea meiobenthic communities underneath the marginal ice zone off eastern Greenland. *Polar Biology* 30, 607–618.

Gerlach S.A. and Riemann F. (1973) The Bremerhaven checklist of aquatic nematodes. A catalogue of nematoda Adenophora excluding the Dorylaimida. *Veröffentlichungen des Intituts für Meeresforschung in Bremerhaven* supplement 4, 1–104.

Gozel U., Lamberti F., Duncan L., Agostinelli A., Rosso L., Nguyen K. and Adams B.J. (2006) Molecular and morphological consilience in the characterisation and delimitation of five nematode species from Florida belonging to the *Xiphinema americanum*-group. *Nematology* 8, 521–532.

Hall B.K. (2003) Descent with modification: the unity underlying homology and homoplasy as seen through an analysis of development and evolution. *Biological Reviews* 78, 409–433.

Jacobs L.J. (1987a) *A checklist of the Monhysteridae (Nematoda, Monhysterida)*. Johannesburg, South Africa: Rand Afrikaans University.

Jacobs L.J. (1987b) A redefinition of the genus *Monhystrella* Cobb (Nematoda, Monhysteridae) with keys to the species. *Zoologica Scripta* 16, 191–197.

Jacobs L.J. (1987c) Redescription of *Monhystrella parvella* (Filipjev) comb.n. (Nematoda, Monhysteridae). *Zoologica Scripta* 16, 117–127.

Jacobs L.J. (1988) *Monografische studie van de Monhysteridae de Man, 1876 (Nematoda)*. PhD thesis, University of Ghent, Ghent, Belgium.

Jensen P. (1986) The nematode fauna in the sulphide-rich brine seep and adjacent bottoms of East Flower Garden, NW Gulf of Mexico. II Monhysterida. *Zoologica Scripta* 13, 1–11.

Kaariainen J.I. and Bett B.J. (2006) Evidence of benthic body-size miniaturization in the deep-sea. *Journal of the Marine Biological Association of the United Kingdom* 86, 1339–1345.

Kito K. and Aryuthaka C. (1998) Free-living marine nematodes of shrimp culture ponds in Thailand. I. New species of the genera *Diplolaimella* and *Thalassomonhystera* (Monhysteridae) and *Theristus* (Xyalidae). *Hydrobiologia* 379, 123–133.

Lamberti F., Molinari S., Moens M. and Brown D.F.G. (2000) The *Xiphinema americanum* group. I. Putative species, their geographical occurrence and distribution, and regional polytomous identification keys for the group. *Russian Journal of Nematology* 8, 65–84.

Lorenzen S. (1978) The system of the Monhysteroidea (Neamtodes)—a new approach. *Zoologischer Jahrbücher zur Systematik* 105, 515–536.

Lorenzen S. (1994) *The phylogentic systematics of free-living nematodes*. London: The Royal Society.

Moens T. and Vincx M. (2000) Temperature and salinity constraints on the life cycle of two brackish-water nematode species. *Journal of Experimental Marine Biology and Ecology* 243, 115–135.

Moens T., Verbeeck L., de Maeyer A., Swings J. and Vincx M. (1999) Selective attraction of marine bacterivorous nematodes to their bacterial food. *Marine Ecology Progress Series* 176, 165–178.

Muthumbi A.W., Vanreusel A., Duineveld G., Soetaert K. and Vincx M. (2004) Nematode community structure along the continental slope off the Kenyan Coast, western Indian Ocean. *International Review of Hydrobiology* 89, 188–205.

Platt H.M. (1984) Pictorial taxonomic keys—their construction and use for the identification of freeliving marine nematodes. *Cahiers de Biologie Marine* 25, 83–91.

Riemann F. (1974) On hemisessile nematodes with flagelliform tails living in marine soft bottoms and micro-tubes found in deep sea sediments. *Mikrofauna des Meeresbondens* 40, 249–261.

Riemann F. (1995) The deep-sea nematode *Thalassomonhystera bathislandica* sp. nov. and microhabitats of nematodes in flocculent surface sediments. *Journal of the Marine Biological Association of the United Kingdom* 75, 715–724.

Riemann F. and Sime-Ngado T. (1997) Note on sea-ice nematodes (Monhysteroidea) from resolute passage, Canadian High Arctic. *Polar Biology* 18, 70–75.

Tchesunov A.V. and Miljutina M.A. (2005) Three new minute nematode species of the superfamily Monhysteroidea from Arctic Abyss. *Zootaxa* 1051, 19–32.

Tchesunov A.V. and Mokievsky V.O. (2005) A review of the genus *Amphimonhystera* Allgén, 1929 (Monhysterida: Xyalidae, marine freeliving nematodes) with description of three new species. *Zootaxa* 1052, 1–20.

Tchesunov A.V. and Portnova D.A. (2005) Free-living nematodes in seasonal coastal ice of the White Sea. Description of *Hieminema*

obliquorum gen. et. sp. n. (Nematoda, Monhysteroidea). *Zoologichesky Zhurnal* 84, 899–914.

Tchesunov A.V. and Riemann F. (1995) Arctic sea ice nematodes (Monhysteroidea), with descriptions of *Cryonema crassum* gen. n., sp. n. and *C. tenue* sp. n. *Nematologica* 41, 35–50.

Thiel H. (1975) The size structure of deep-sea benthos. *Internationale Revue der Gesamten Hydrobiologie* 60, 575–606.

Van Gaever S., Moodley L., de Beer D. and Vanreusel A. (2006) Meiobenthos at the Arctic Håkon Mosby Mud Volcano, with a parental-caring nematode thriving in sulphide-rich sediments. *Marine Ecology Progress Series* 321, 143–155.

Vanhove S., Arntz W. and Vincx M. (1999) Comparative study of the nematode communities on the southeastern Weddell Sea shelf and slope (Antarctica). *Marine Ecology Progress Series* 181, 237–256.

Vanreusel A., Clough L., Jacobsen K., Ambrose W., Jivaluk J., Ryheul V., Herman R. and Vincx M. (2000) Meiobenthos of the Central Arctic Ocean with special emphasis on the nematode community structure. *Deep-Sea Research* 147, 1855–1879.

Vopel K. and Thiel H. (2001) Abyssal nematode assemblages in physically disturbed and adjacent sites of the eastern equatorial Pacific. *Deep-Sea Research II* 48, 3795–3808.

Zekely J., Sørensen M.V. and Bright M. (2006) Three new nematode species (Monhysteridae) from deep-sea hydrothermal vents. *Meiofauna Marina* 15, 25–42.

Zhang Y. and Zhang Z.N. (2006) Two new species of the genus *Elzalia* (Nematoda: Monhysterida: Xyalidae) with description of three new species. *Journal of the Marine Biological Association of the United Kingdom* 86, 1047–1056.

and

Zhou H. (2001) Effects of leaf litter addition on meiofaunal colonization of azoic sediments in a subtropical mangrove in Hong Kong. *Journal of Experimental Marine Biology and Ecology* 256, 99–121.

APPENDIX 1

Checklist of the valid species of the inland and commensal genera belonging to the family Monhysteridae (after Andrássy, 1981; Jacobs, 1987a; Andrássy, 2005; Coomans & Eyualem-Abebe, 2006). Type species of each genus are underlined.

INLAND GENERA

Anguimonhystera Andrássy, 1981

1. *A. ampliceps* (Goffart, 1950) Andrássy, 1981
2. *A. stadleri* (Goffart, 1950) Andrássy, 1981
3. *A. tenuissima* (Goffart, 1950) Andrássy, 1981

Eumonhystera Andrássy, 1981

1. *E. alpina* (Filipjev, 1918) Andrássy, 1981
2. *E. altherri* Andrássy, 1981
3. *E. andrassy* (Biró, 1969) Andrássy, 1981
4. *E. ballesterosi* Picazo-Muñoz, 1988
5. *E. barbata* Andrássy, 1981
6. *E. borealis* Turpeenniemi, 1997
7. *E. dispar* (Bastian, 1865) Andrássy, 1981
8. *E. elegans* (Allgén, 1928) Jacobs, 1987
9. *E. filiformis* (Bastian, 1865) Andrássy, 1981
10. *E. geraerti* Eyualem-Abebe & Coomans, 1996
11. *E. gerlachi* (Meyl, 1954) Andrássy, 1981
12. *E. gracilior* (Johnston, 1938) Andrássy, 1981
13. *E. hungarica* Andrássy, 1981
14. *E. huruii* Yunliang, Eyualem-Abebe & Coomans, 2002
15. *E. kuzmini* Gagarin, 1997
16. *E. longicaudata* (Gerlach & Riemann, 1973) Andrássy, 1981
17. *E. maxima* Gagarin, 1996
18. *E. media* Hernández & Jordana, 1988
19. *E. minuta* (Filipjev, 1929) Jacobs, 1987
20. *E. mwerazii* (Meyl, 1957) Andrássy, 1981
21. *E. pannonica* Andrássy, 2002
22. *E. papuana* (Daday, 1899) Andrássy, 1981
23. *E. parasimilis* (Allgén, 1926) Andrássy, 1981
24. *E. patiens* Armendariz, Agudo & Hernandez, 1992
25. *E. pseudobulbosa* (Daday, 1896) Andrássy, 1981
26. *E. rustica* (Bütschli, 1873) Andrássy, 1981
27. *E. serena* Gagarin 1993
28. *E. sibirica* Gagarin, 2003
29. *E. similis* (Bütschli, 1873) Andrássy, 1981
30. *E. simplex* (de Man, 1880) Andrássy, 1981
31. *E. subfiliformis* (Cobb, 1918) Andrássy, 1981
32. *E. sudanenesis* Zeidan, Jacobs & Geraert, 1990
33. *E. tatrica* (Daday, 1896) Andrássy, 1981
34. *E. tuporis* Gagarin, 1991
35. *E. vulgaris* (de Man) Andrássy, 1981

Geomonhystera Andrássy, 1981

1. *G. aenariensis* (Meyl, 1953) Andrássy, 1981
2. *G. altaica* Gagarin, 2002
3. *G. antarticola* Andrássy, 1998
4. *G. auvillis* Saha, Lal & Singh, 2002
5. *G. breviseta* Brzeski, 1993
6. *G. dubia* Siddiqi & Shahina, 2004
7. *G. glandulata* Khan & Tahseen, 2006
8. *G. japonica* Khan & Araki, 2001
9. *G. karuni* Siddiqi & Shahina, 2004
10. *G. longicaudata* Gagarin, 2002
11. *G. media* Gagarin, 2002
12. *G. mexicana* Brzeski, 1993
13. *G. parvillosa* (Meyl, 1954) Andrássy, 1981
14. *G. pervaga* (Argo & Heyns, 1973) Andrássy, 1981
15. *G. steineri* (Micoletzky, 1922) Andrássy, 1981
16. *G. taurica* Tsalolikhin, 2007
17. *G. tripyloides* (Andrássy, 1968) Andrássy, 1981
18. *G. villosa* (Bütschli, 1873) Andrássy, 1981

Monhystera Bastian, 1865

1. *M. africana* Andrássy, 1964
2. *M. afromacramphis* Jacobs, 1987
3. *M. amabilis* Gagarin, 1997
4. *M. coomansi* Jacobs & Heyns, 1992
5. *M. deleyi* Eyualem-Abebe & Coomans, 1996
6. *M. euromacramphis* Jacobs, 1987
7. *M. fasciculate* Skwarra, 1921
8. *M. gabaza* Joubert & Heyns, 1980
9. *M. hamata* Gagarin & Vu Thanh, 2005
10. *M. lemani* Juget, 1969
11. *M. longicaudata* Bastian, 1865

12. *M. macramphis* Filipjev, 1929
13. *M. magnacephala* Joubert & Heyns, 1980
14. *M. nubiae* Eyualem-Abebe & Coomans, 1996
15. *M. paludicola* de Man, 1880
16. *M. paramacramphis* Meyil, 1954
17. *M. psammophila* Juget, 1969
18. *M. psilocephalus* (Onorato de Cillis, 1917) Meyl, 1960
19. *M. riemanni* Jacobs & Heyns (in Jacobs, 1987a)
20. *M. rivularis* Bastian, 1865
21. *M. robustospiculum* Jacobs & Heyns (in Jacobs, 1987a)
22. *M. shibrui* Eyualem-Abebe & Coomans, 1996
23. *M. somereni* Allgén, 1952
24. *M. stagnalis* Bastian, 1865
25. *M. taaiboschiensis* Joubert & Heyns, 1980
26. *M. tanae* Eyualem-Abebe & Coomans, 1996
27. *M. uncibrevispiculata* Lemzina, 1990
28. *M. uncigubernaculum* Zeidan, Jacobs & Geraert, 1990
29. *M. uncispiculata* Gagarin, 1979
30. *M. wangi* Wu & Hoeppli, 1929

Sinanema **Andrássy 1960**

1. *S. ginlingensis* (Hoeppli & Chu, 1932) Andrássy, 1960
2. *S. godeti* (Steiner 1920) Jacobs, 1987
3. *S. mongolicum* Tsalolikhin, 1985
4. *S. mysorensis* (Moorthy, 1938) Jacobs, 1987

Tridentula **(Eyualem-Abebe & Coomans, 1995) Andrássy, 2007**

1. *T. bidenticulata* (Gagarin, 1997) Andrássy, 2007
2. *T. brzeskii* (Gagarin & Gusakov, 2000) Andrássy, 2007
3. *T. floreana* (Eyualem-Abebe & Coomans, 1995) Andrássy, 2007
4. *T. fluviatilis* (Gagarin, 2004) Andrássy, 2007
5. *T. minor* (Gagarin, 2001) Andrássy, 2007

6. *T. obscura* (Gagarin, 2001) Andrássy, 2007
7. *T. palustris* (Gagarin & Holovachov, 2001) Andrássy, 2007

COMMENSAL GENERA

Gammarinema **Kinne & Gerlach, 1956**

1. *G. ampullocauda* (Paramonov, 1926) Lorenzen, 1986
2. *G. cambari* (Allgén, 1933) Osche, 1955
3. *G. cardisomae* Riemann, 1968
4. *G. gammari* Kinne & Gerlach, 1953
5. *G. ligiae* Gerlach, 1967
6. *G. mesidoteae* Belogurov, Kulikov & Russkikh, 1978
7. *G. paratelphusae* (Farrouqui, 1967) Sudhaus, 1974
8. *G. prilepskyi* Tchesunov & Pletnikova, 1986

Monhystrium **Cobb, 1920**

1. *M. brevis* Yoshimura, 1990
2. *M. inquilinus* Riemann, 1969
3. *M. transitans* Cobb, 1920
4. *M. tenuis* Yoshimura, 1990
5. *M. wilsoni* (Baylis, 1915) Cobb, 1920

Odontobius **Roussel del Vauzéme, 1834**

1. *O. ceti* Roussel del Vauzéme, 1834

Trypilium **Cobb, 1920**

1. *T. carcinicula* (Baylis, 1915) Cobb, 1920

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