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The state of the art of Chromadoridae (Nematoda, Chromadorida): a historical review, diagnoses and comments about valid and dubious genera and a list of valid species

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Abstract

Chromadoridae is a widespread family of mostly free-living marine nematodes. This systematic review provides for each genus: a historical background, an updated diagnosis and a list of species. Our review recognizes 37 valid genera, 395 valid species, 57 descriptions without enough morphological information for accurate identification (*species inquirenda*) and 10 species *incerta sedis*. We also recognize 21 species as *nomena nuda.* Additionally, polytomous keys were con-

structed for the subfamilies and for the genera of the three major subfamilies (Chromadorinae, Euchromadorinae and Hypodontolaiminae) using the most important diagnostic characters. A phylogenetic analysis based on rDNA sequences of species available in the GenBank was also conducted. Phylogenetic trees based on the 18S and 28S rDNA confirmed the classification into three subfamilies (Spilipherinae, Hypodontolaiminae and Chromadorinae), despite the absence of defined synapomorphies. Phylogenetic relationships at lower taxonomic level are problematic given the large number of sequences not identified to species level.

Key words: Marine nematodes, Chromadorinae, Euchromadorinae, Hypodontolaiminae, taxonomy, Phylogeny

Introduction

Nematodes are mostly small, ubiquitous and the most abundant metazoans on the planet. In terms of abundance, three-quarters, or more, of all animals on Earth are nematodes (Bongers & Ferris 1999). The group is mostly known for its parasitic species, but most species and individuals are free-living in soils and sediments, often numbering millions per m^2 (Heip *et al.* 1985). A total of 11,400 marine species have been described and a conservative estimation of more than 50,000 species yet to be described have been presented (Appeltans *et al.* 2012). One important issue, however, concerning nematode taxonomy, is that for most of the taxa taxonomic diagnoses and lists of valid species are not organized in systematics reviews (e.g. Fonseca & Decraemer, 2008; Venekey *et al*. 2014; Miljutin & Miljutina, 2016).

Chromadoridae Filipjev, 1917 is one of the largest families of nematodes, essentially marine but also occurring in freshwater habitats (Decraemer & Smol 2006). The family was systematically reviewed by Lorenzen (1994) and more recently by Tchesunov (2014), when 37 genera were recognized. In his review, Tchesunov (2014) presented for each genus the diagnosis, the number of valid species, indicated the type species, but did not provide a list of valid species.

The most recent list of valid species of Chromadoridae dates back to Gerlach & Riemann (1973). After that, numerous new species and genera have been described (*e.g.* Kito 1978a, b; Jensen 1985; Muthumbi & Vincx 1998a, b; Kito & Nakamura 2001; Vermeeren *et al.* 2004; Nguyen *et al.* 2012; Tchesunov 2015). The references of the new descriptions can be easily retrieved from taxonomic data banks, such as Nemys (Bezerra *et al*. 2018). Nevertheless, the information for Chromadoridae is not congruent and often not up-to date or incomplete in Nemys platform, hampering the progress in species identification, taxonomic descriptions and even phylogenetic analysis.

In order to guide future taxonomic and phylogenetic studies within this family and help with its identification, we provide the systematic review of each valid genus, followed by a generic diagnosis and a list of valid species. Additionally, three polytomous keys for genera from the three major subfamilies Chromadorinae Filipjev, 1917; Euchromadorinae Gerlach & Riemann, 1973 and Hypodontolaiminae De Coninck, 1965 are provided, as well as phylogenetic analysis considering rDNA sequences available in the GenBank.

Materials and methods

Taxonomic review. The work of Gerlach & Riemann (1973) was checked first to provide us with a list of genera and species synonyms, as well as sampling locations of original descriptions. For new records and taxonomical studies published afterwards we checked information available on Nemys (Bezerra *et al.* 2018) database. Additional searches were done using Google Scholar and Web of Science. All records were critically evaluated as they are often not up-to date or incomplete across the platforms.

The information in the section "comments about valid genera" is presented in the following order: how and when the genus was proposed, history of species including new descriptions and transfers from other genera, comments about reviews and species identification keys. References are indicated when decisions of synonymizations, new combinations and validity of genera and species were made in the past by other authors. Only new decisions about status of taxa, are explained. Finally, for each genus a diagnosis and a number of valid species are also presented. The occurrence of genera and species in freshwater and brackish water habitats was checked in Andrássy (2005), Decreamer & Smol (2006) and FADA database (Eisendle-Flöckner *et al*. 2018).

A list of valid species is presented for each valid genus in which the type species is underlined and for each

species the type locality from the original description is given in parentheses, as well as a list of synonyms. *Species inquirenda*, *nomena nuda* and *incerta sedis* are cited in separate lists following the valid species list. When necessary, names were adjusted to comply with the Latin grammar. Polytomous keys were constructed for the subfamilies and for the genera of the three major subfamilies (Chromadorinae, Euchromadorinae and Hypodontolaiminae) using the most important characters. It is important to emphasize that these keys do not consider phylogenetic relationships of genera, but they are useful tools to visualize the morphological differences between taxa. The characters represented by two or more numbers (e.g. cuticle of *Chromadorita* Filipjev, 1922) mean that two or more states were described among genera of a subfamily or among different species within the same genus.

Phylogenetic inference. The 18S and 28S rDNA sequences of species from the family Chromadoridae were retrieved from GenBank, except for the species from the subfamilies Euchromadorinae and Harpagonchinae Platonova & Potin, 1972, which do not have available sequences of the selected regions. The trees were rooted using sequences from the closely related family Cyatholaimidae Filipjev, 1918. The data was aligned with all multiple sequence algorithms available in T-Coffee package (Notredame *et al.* 2010) and the most appropriate nucleotide substitution model for the set of sequences was determined by maximum likelihood in Mega 6 (Tamura *et al.* 2013). Phylogenetic analyses were done using Bayesian Inference (maximum posterior probability, MPP) in Beast v1.8.4 (Drummond *et al.* 2012). The Yule Process was used as tree prior (Gernhard 2008). Other priors were maintained as default. Two Markov Chain Monte Carlo (MCMC) for each dataset were run for 10 million generations under the best-fit model for 18S (TN93 + G) and for 28S (GTR + G). Tracer v.1.6 (Rambaut *et al.* 2014) was used to assess convergence and 10% of the trees were removed as the burn-in in TreeAnnotator v1.8.1 (Drummond *et al.* 2012). The trees were visualized in FigTree v1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/).

Results and discussion

Historical background and general comments about Chromadoridae. Nematodes from the family Chromadoridae occur in nearly all types of marine environments and are frequently one of the most abundant nematode taxa. Lorenzen (1994) established the holophyly of Chromadoridae based on the following synapomorphies: there is always only a single anterior testis, the anterior ovary is always situated to the right of the intestine and the posterior ovary is always to the left of it. Other characteristics present in most genera are a typical ornamentation of the cuticle in each genus and the transverse oval shape of the amphids (which is not always easily detectable!).

Lorenzen (1994) recognized 5 sub-families (Chromadorinae, Euchromadorinae, Harpagonchinae, Hypodontolaiminae and Spilipherinae Filipjev, 1918) but was not able to establish apomorphies for them. Forty valid genera within this family were recognized (Lorenzen 1994): *Atrochromadora* Wieser, 1959; *Chromadora* Bastian, 1865; *Chromadorella* Filipjev, 1918; *Fusonema* Kreis, 1928; *Prochromadora* Filipjev, 1922; *Prochromadorella* Micoletzky, 1924; *Punctodora* Filipjev, 1929 and *Timmia* Hopper, 1961 in Chromadorinae; *Actinonema* Cobb, 1920; *Adeuchromadora* Boucher & De Bovée, 1971; *Austranema* Inglis, 1969; *Dicriconema* Steiner & Hoeppli, 1926; *Endeolophos* Boucher, 1976; *Euchromadora* de Man, 1886; *Graphonema* Cobb, 1898; *Nygmatonchus* Cobb, 1933; *Parapinnanema* Inglis, 1969; *Protochromadora* Inglis, 1969; *Rhips* Cobb, 1920; *Steineridora* Inglis, 1969 and *Trochamus* Boucher & De Bovée, 1971 in Euchromadorinae; *Harpagonchoides* Platonova & Potin, 1972 and *Harpagonchus* Platonova & Potin, 1972 in Harpagonchinae; *Chromadorissa* Filipjev, 1917; *Chromadorita*; *Deltanema* Kreis, 1929; *Denticulella* Cobb, 1933; *Dichromadora* Kreis, 1929; *Hypodontolaimus* de Man, 1886; *Innocuonema* Inglis, 1969; *Megodontolaimus* Timm, 1969; *Neochromadora* Micoletzky, 1924; *Panduripharynx* Timm, 1961; *Parachromadorita* Blome, 1974; *Ptycholaimellus* Cobb, 1920 and *Spilophorella* Filipjev, 1917 in Hypodontolaiminae; *Acantholaimus* Allgén, 1933; *Spiliphera* Bastian, 1865; *Trichromadorita* Timm, 1961 and *Tridentellia* Gerlach & Riemann, 1973 in Spilipherinae. *Dasylaimus* Cobb, 1933 and *Odontocrius* Steiner, 1918 were regarded as dubious genera (Lorenzen 1994), following the recommendations of Hope & Murphy (1972) and Inglis (1969), respectively. More recently Tchesunov (2014) recognized the same 5 subfamilies, but only 37 genera were considered valid. *Fusonema* in Chromadorinae, *Dicriconema* and *Nygmatonchus* in Euchromadorinae and *Trichromadorita* and *Tridentellia* in Spilipherinae were not included by Tchesunov (2014) and *Deltanema* was considered a dubious genus. On the other hand, contrary to Lorenzen

(1994), *Chromadorina* Filipjev, 1918 in Chromadorinae, *Crestanema* Pastor de Ward, 1985 in Euchromadorinae and *Karkinochromadora* Blome, 1982 in Hypodontolaiminae were regarded as valid genera by Tchesunov (2014).

According to Decraemer & Smol (2006), *Fusonema* has an unclear taxonomic position because it is based on a poor description of a single species. *Fusonema* was first classified in Chromadoridae and was moved later to Monoposthiidae Filipjev, 1934 due to its cuticular pattern (Hope & Murphy 1972). Lorenzen (1994) returned *Fusonema* to Chromadoridae suggesting that cuticle ornamentation as a differential character is not completely useful to differentiate the genus. Therefore, he argued that the transfer of *Fusonema* to Monoposthiidae based on cuticle pattern is incorrect. Tchesunov (2014) omitted *Fusonema* without any comment and here we consider it as a genus of Monoposthiidae following Hope & Murphy (1972).

Dicriconema was described based on a single female and the only species was considered *inquirendum* by Inglis (1969). Although Lorenzen (1994) considered it as valid genus, we considered it invalid based on Inglis (1969). *Nygmatonchus* was considered valid by Lorenzen (1994) but was omitted by Tchesunov (2014) without any comments. Here we consider *Nygmatonchus* valid since it has one valid described species. In the case of *Trichromadorita* and *Tridentellia*, these genera include poorly described two and one species, respectively. *Trichromadorita* has two decribed species (*T. marinus* Khan, 1991 and *T. mobilis* Timm, 1961) difficult to distinguish. Therefore, we consider *Trichromadorita* as dubious genus until new records and more detailed descriptions are available. As for *Tridentellia*, the only species description was based on a single female with poor details, consequently we consider it invalid. *Chromadorina* was described by Filipjev (1918), revised by Wieser (1954) and included in Gerlach & Riemann (1973), therefore, its absence in Lorenzen (1994) may be a mistake. *Crestanema* and *Karkinochromadora* were not included on Lorenzen (1994) (the English edition) since it is a direct translation of the German edition (Lorenzen, 1981) and both genera were described later by Pastor de Ward (1985) and Blome (1982), respectively.

Both Lorenzen (1994) and Tchesunov (2014) considered *Trichromadora* as invalid genus. Lorenzen (1994) probably followed the synonimization of this genus with *Prochromadorella* by Lorenzen (1971). This genus was reinstated by Muthumbi & Vincx (1998a) who provided a detailed re-description of the type species and transferred other two species to it. Tchesunov (2014) omitted *Trichromadora* without any comment, but we consider it valid based on the work of Muthumbi & Vincx (1998a). The monospecific genus *Portmacquaria* Blome, 2005 was first described as *Macquaria* by Blome (2002), but as the name was already preoccupied by a fish genus it was replaced (Blome 2005). Tchesunov (2014) omitted *Portmacquaria*, but its species is very well described, thus we consider it a valid genus.

Both Lorenzen (1994) and Tchesunov (2014) considered *Adeuchromadora*, *Austranema* and *Protochromadora* as valid genera, but all three genera were synonymized earlier: the single species within *Adeuchromadora* (*A. megamphida* Boucher & De Bovée, 1971) was synonymized with a species of *Actinonema* (*A. pachidermatum* Cobb, 1920) by Boucher (1976), *Austranema* was synonymized with *Parapinnanema* (Warwick & Coles 1975) and *Protochromadora* with *Graphonema* (Warwick & Coles 1975). Therefore, we consider these three genera as junior synonyms. *Dasylaimus* and *Odontocricus* were considered dubious genera by Lorenzen (1994) and they were not mentioned in Tchesunov (2014). Both genera are monospecific, the description of *Dasylaimus* is poor and is based on a single female, and *Odontocricus hupferi* was transferred to *Euchromadora* as *species inquirendum* (Coles 1965). For these reasons, both *Dasylaimus* and *Odontocrius* are considered here as invalid genera. Deltanema is considered a valid genus by Lorenzen (1994), but although Tchesunov (2014) included it in his review, he considered it dubious. Smol & Decraemer (2006) and Tchesunov (2014) argued that *Deltanema* has limited description and illustrations. We agree with them and also consider *Deltanema* as a dubious genus. The genera *Chromanema* Khera, 1975; *Algoanema* Heyns & Furstenberg, 1987; *Paradichromadora* Dashchenko, 1991 and *Euchromanema* Kulikov & Dashchenko, 1991 are not mentioned in both Lorenzen (1994) and Tchesunov (2014). These genera were described in publications with limited access. We consider them as dubious genera due to poor and/or questionable descriptions.

Considering all the situations explained above, the family Chromadoridae currently consists of 37 valid genera belonging to five subfamilies. The list of genera and species is given in the sections below. Furthermore, additional comments are presented about dubious and invalid genera of Chromadoridae in a separate section.

Diagnosis of Chromadoridae. (Modified from Tchesunov, 2014): Cuticlar ornamentation as punctuations which may be evenly distributed and of equal size (cuticle homogenous), or unevenly distributed, for example, enlarged in the lateral body regions or different along the body (cuticle heterogenous) or the ornamentation may be

made up of rods jointed in a "basket weave". Anterior sensilla arranged in two or three circles. Amphidial fovea a simple transverse slit, often inconspicuous, or ventrally wound spiral, located between the cephalic setae or posterior to them. Pharyngostoma with dorsal tooth usually larger than ventrosublateral ones; teeth hollow or solid; denticles may be present; three nearly equal solid teeth also occur in some genera. Male monorchic with anterior testis (synapomorphy); pre-cloacal supplements cup-shaped (never tubular), may be absent. Females with two antidromously reflexed ovaries, the anterior gonad to the right of the intestine, the posterior gonad to the left of the intestine (synapomorphy). Mostly marine.

Polytomous Identification Key for subfamilies of Chromadoridae. The polytomous key is based on eight characters to separate the five sub-families (Table 1). According to diagnosis, the morphology of the buccal cavity can be grouped into nine states, the shape of amphideal fovea and cuticle into five types, precloacal supplements into four states, the pharynx into three states and all the remaining characters in two distinct types. The most useful character to discriminate the five sub-families is the shape of the amphideal fovea; however, this character cannot always be easily detected.

TABLE 1. Polytomous key for subfamilies of Chromadoridae.

	Cuticle	Anterior sensilla pattern	Outer labial sensilla shape	Amphideal fovea shape	Amphideal fovea position	Buccal cavity	Pharynx	Supplements
Chromadorinae	1/2/3/4	2	2	1	1	1/2/3	2	2/3
Euchromadorinae	1/3/5	1/2	2	2	2	2/3/8/9	1/2	1
Harpagonchinae	2	2	1	5	-	7	1/2	1/2
Hypodontolaiminae	1/2/3/4	2	1/2	2/3	1/2	4/5/8/9	2/3	1/2
Spilipherinae	1/2/3/4	1	2	4	2	6	3	1/4

Character states:
Cuticle:
1. Homogenous ornamentation but with lateral differentiation;
2. Homogenous ornamentation without lateral differentiation;
3. Heterogenous ornamentation with lateral differentiation;
4. Heterogenous ornamentation but without lateral differentiation;
5. Lateral alae present.

Anterior sensilla pattern:
1. 2 circles;
2. 3 circles.

Outer labial sensilla shape:
1. Papilliform;
2. Setiform

Amphideal fovea shape:
1. Transverse, more or less slit-like;
2. Transverse oval;
3. Loop shaped;
4. Cryptospiral or single spiral;
5. Absent/Unknown.

Amphideal fovea position:
1. Between bases of cephalic setae;
2. Posterior to cephalic setae bases.

Buccal cavity:
1. Solid dorsal tooth about equal or larger than ventrosublateral teeth;
2. Single dorsal tooth, absence of ventrolateral teeth;
3. Large solid or hollow dorsal tooth and two small ventrosulateral teeth;

4. Hollow dorsal tooth with ventrosulateral teeth;
5. Hollow dorsal tooth without ventrosulateral teeth;
6. Three solid teeth more or less of equal size;
7. Three motile mandibles with solid hooks;
8. Denticles absent;
9. Denticles present.

Pharynx:
1. Cylindrical;
2. Single bulb;
3. Double bulb.

Supplements:
1. Absent;
2. Cup-shaped;
3. Tubular;
4. Setose.

Comments about valid genera of Chromadoridae

Subfamily Chromadorinae

Diagnosis (modified from Tchesunov, 2014): Cuticle homo- or heterogenous with or without lateral differentiation of larger dots. Anterior sensilla in three separate circles (6+6+4). Amphideal fovea oval loop or transverse slit-like, sometimes difficult to be observed under light microscope. Presence of three (sub)equal solid teeth (except for *Prochromadora* that present one single dorsal tooth and *Trichromadora* with three hollow teeth). Pharyngeal tissue not enlarged around the buccal cavity. Posterior pharyngeal bulb simple and well defined (except for *Prochromadorella* and *Trichromadora* with poorly developed bulb). Precloacal cup-shaped supplements usually present in males. Mostly marine but some genera have representatives in fresh- or brackish waters (see more details in each genus).

Genus *Atrochromadora* Wieser, 1959

This genus was proposed by Wieser (1959a) with the original description of *A. obscura* Wieser, 1959 and to accommodate other three species [*A. dissoluta* (Wieser, 1954), *A. parva* (de Man, 1893), *A. microlaima* (de Man, 1889)] previously placed in *Chromadoropsis* (described by Wieser 1954). The generic name *Chromadoropsis* was already preoccupied by *Chromadoropsis* Filipjev, 1918 and therefore it was necessary to propose a replacement name (Wieser 1959a). Additionally, another species similar to *A. parva* was described later, *A. denticullela* Wieser & Hopper, 1967, that differs from the type species by spacing of longitudinal rows at middle body level, length of spicules and spinneret and shape of the distal end of gubernaculum (Wieser & Hopper 1967). Although Tchesunov (2014) considered 12 valid species in this genus, we can only account for five.

Diagnosis (modified from Tchesunov 2014): Cuticle with homogeneous punctation pattern along the entire body and with rows of larger dots forming lateral differentiation. Amphideal fovea transversely oval, open loop-shaped. Buccal cavity usually with three solid teeth, dorsal tooth larger than ventrosublateral teeth. Males usually with cup-shaped precloacal supplements (*A. dissoluta*, *A. microlaima* and *A. obscura*) or supplements are absent (*A. denticulata* and *A. parva*). Marine.

Number of valid species: 5
Genus *Atrochromadora* Wieser, 1959
Syn. *Chromadoropsis* Wieser, 1954 nec Filipjev,1918
VALID SPECIES
1. *Atrochromadora denticulata* Wieser & Hopper, 1967 (Florida, USA)

2. *Atrochromadora dissoluta* (Wieser, 1954) Wieser, 1959 (Chile)
Syn. *Chromadoropsis dissoluta* Wieser, 1954
3. *Atrochromadora microlaima* (de Man, 1889) Wieser, 1959 (North Sea)
Syn. *Chromadora microlaima* de Man, 1889
Chromadorella microlaima (de Man, 1889) Wieser, 1951
Chromadorina microlaima (de Man, 1889) de Man, 1922
Chromadorina parva sensu Schuurmans Stekhoven & Adam, 1931
4. *Atrochromadora obscura* Wieser, 1959 (Washington, USA)
5. *Atrochromadora parva* (de Man, 1893) Wieser, 1959 (North Sea)
Syn. *Spiliphera parva* de Man, 1893
Chromadorina parva (de Man, 1893) Micoletzky, 1924
Chromadoropsis parva (de Man, 1893) Wieser, 1954
Spiliphera antarctica Cobb, 1914

Genus C*hromadora* Bastian, 1865

The genus *Chromadora* was proposed by Bastian (1865) who included the original description of *C. nudicapitata* Bastian, 1865 and *C. vulgaris* Bastian, 1865. The latter species was designated as type species of *Chromadora,* but it had to be replaced by the former because *C. vulgaris* had already been designated as the type species of *Euchromadora* (Filipjev 1918). Several species described later within this genus were considered junior synonyms of *C. nudicapitata*: *C. brevipapillata* sensu Schuurmans Stekhoven, 1942; *C. chlorophthalma* de Man, 1876; *C. crucifera* Wieser, 1954; *C. flamoniensis* Daday, 1901; *C. macrolaimoides* sensu Steiner (1921), *C. micropapillata* Schuurmans Stekhoven, 1942; *C. natans* Bastian, 1865; *C. quadrilinea* Filipjev, 1918; *C. quadrilineoides* Chitwood, 1951; *C. quarnerensis* Daday, 1901; *C. quinquepapillata* Micoletzky, 1922; *C. siciliana* Wieser, 1954; *C. tridenticulata* Platonova, 1971; *C. trilinea* Paramonov, 1927; and *C. trilineata* Gerlach & Meyl, 1957 (Gerlach & Riemann 1973).

Wieser (1954) reviewed the genus proposing some synonimizations, as well as a key separating the species in two main groups based on the number of teeth. *C. buesumensis* Kreis, 1924; *C. kreisi* Schuurmans Stekhoven & Adam, 1931 and *C. macrolaima* de Man, 1889 belong to the group formed by species bearing one dorsal tooth, while other nine species bear a buccal cavity armed with three teeth (*C. axi* Gerlach, 1951; *C. bipapillata* Micoletzky, 1922; *C. macrolaimoides* Steiner, 1915; *C. hentscheli* Micoletzky, 1922; *C. micropapillata*; *C. nudicapitata*; *C. quadrilinear*; *C. quadrilineoides* and *C. siciliana*). The latter three species present on Wieser's key, as well as *C. micropapillata* and *C. kreisi*, are no longer valid. *C. micropapillata*, *C. quadrilinea*, C. *quadrilineoides* and *C. siciliana* were synonymized with *C. nudicapitata* as mentioned before. *C. kreisi* is here considered a *species inquirendum* since its description is based only on females and such characters as amphids were not seen (Kreis, 1929 and Schuurmans Stekhoven & Adam, 1931). *C. antillensis* Allgén, 1947 and *C. brevipapillata* were considered synonyms of *C. macrolaimoides* based on tail shape and weak postcloacal supplements (Wieser 1954). Gerlach & Riemann (1973) considered *C. antillensis* as valid, although suggested the possibility of this species being a synonym of *C. brevipapillata*. Therefore, we prefer to consider *C. antillensis* as *species inquirendum*. In the case of *C. brevipapillata*, we consider this species as valid, since Gerlach & Riemann (1973) listed it as valid and Kito (1978a) described a subspecies from Japan: *Chromadora brevipapillata japonica*. *C. perlasi* Allgén, 1947 was first considered a synonym of *C. macrolaima* by Wieser (1954) and later it was considered a synonym of *C. macrolaimoides* based on the similar shape of pharynx, number of precloacal supplements and shape of the spicules (Wieser 1956). Gerlach & Riemann (1973) considered *C. perlasi* as valid but also suggested the possibility of synonymy. This species needs to be re-examined to define its correct taxonomic status, therefore here we consider it as *inquirendum C. heterostomata* and *C. undecipapilata* were described by Kito (1978b) and Wieser (1959a), respectively. Another key, which considers the number of teeth as the main diagnostic feature for species level, was provided by Kito (1978a), but it includes only five species found in Japan. Kito (1978a) also described *C. yamadai* and redescribed *C. macrolaimoides* and *C. nudicapitata* from specimens found in the Japanese coast. Timm (1978) transferred *C. serrata* (Cobb, 1914) from *Dichromadora*. The last species added to this genus, *C. lorenzeni*, was described by Jensen (1980) but later Blome (1982) transferred it to *Karkinochromadora*.

Diagnosis (modified from Tchesunov 2014): Cuticle with homogeneous punctation pattern along the body, with lateral differentiation of larger dots. Transverse slit-like amphideal fovea. Buccal cavity with three solid teeth, the dorsal tooth larger than ventrosublateral teeth. Ocelli may be present. Males usually with cup-shaped precloacal supplements. It is very similar to *Atrochromadora*, the main difference is the amphideal fovea shape which is more circular in the current genus; the variable number of teeth (one or three) is also another feature that can be easily used in the identification of *Chromadora* species. Marine.

Number of valid species: 12

Genus *Chromadora* Bastian, 1865

Syn. *Parachromadora* sensu Micoletzky 1914
Triodontolaimus sensu Micoletzky, 1913

VALID SPECIES

1. *Chromadora axi* Gerlach, 1951 (North Sea)
2. *Chromadora bipapillata* Micoletzky, 1922 (Red Sea)
Syn. *Chromadora nudicapitata bipapillata* Micoletzky, 1922
3. *Chromadora brevipapillata* Micoletzky, 1924 (Red Sea)
Syn. *Chromadora nudicapitata bipapilata* forma brevipapillata Micoletzky 1922
Chromadora paramacrolaimoides Allgén, 1947
4. *Chromadora buesumensis* Kreis, 1924 (North Sea)
5. *Chromadora hentscheli* Micoletzky, 1922 (Brazil)
Syn. *Chromadora nudicapitata hentscheli* Micoletzky, 1922
6. *Chromadora heterostomata* Kito, 1978 (Oshoro)
7. *Chromadora macrolaima* Allgén, 1929 (Skagerrak)
Syn. *Chromadorina macrolaima* Allgén, 1929
Chromadora macrolaima pigmentata Allgén, 1933
Chromadora macrolaima bergensis Allgén, 1932
8. *Chromadora macrolaimoides* Steiner, 1915 (Indonesia)
Syn. *Chromadorella macrolaimoides* Chitwood, 1951
9. *Chromadora nudicapitata* Bastian, 1865 (English Channel)
Syn. *Chromadora brevipapillata* sensu Schuurmans Stekhoven, 1942
Chromadora chlorophthalama de Man, 1876
Chromadora crucifera Wieser, 1954
Chromadora flamoniensis Daday, 1901
Chromadora macrolaimoides sensu Steiner, 1921
Chromadora micropapillata Schuurmans Stekhoven, 1942
Chromadora micropapillata crucifera Wieser, 1954
Chromadora natans Bastian, 1865
Chromadora quadrilinea Filipjev, 1918
Chromadora quadrilinea sensu Micoletzky, 1924
Chromadora quadrilinea sensu Chitwood, 1938
Chromadora quadrilineoides Chitwood, 1951
Chromadora quarnerensis Daday, 1901
Chromadora quinquepapillata Micoletzky, 1922
Chromadora siciliana Wieser, 1954
Chromadora tridenticulata Platonova, 1971
Chromadora trilinea Paramonov, 1927
Prochromadora longitubus Wieser, 1951
10. *Chromadora serrata* (Cobb, 1914) Timm, 1978 (Antarctica)
Syn. *Spilophora serrata* Cobb, 1914
Dichromadora serrata (Cobb, 1914) Wieser, 1954
11. *Chromadora undecimpapillata* Wieser, 1959 (Washington, USA)
12. *Chromadora yamadai* Kito, 1978 (Japan)

SPECIES INQUIRENDA
1. *Chromadora antillensis* (Allgén, 1947) Wieser, 1954 (Lesser Antilles)
2. *Chromadora balatonica* Daday, 1894 (Hungary)
3. *Chromadora caeca* Bastian, 1865 (English Channel)
4. *Chromadora cincta* Villot, 1875 (English Channel)
5. *Chromadora crassicauda* Allgén, 1957 (Labrador)
6. *Chromadora kingojacobseni* Allgén, 1954 (Greenland)
7. *Chromadora kreisi* Schuurmans Stekoven & Adam, 1931 (North Sea)
8. *Chromadora neoheterophya* Allgén, 1947 (Gulf of Panana)
9. *Chromadora palmensis* Pagenstecher, 1881 (Germany)
10. *Chromadora papillata* Bastian, 1865 (English Channel)
11. *Chromadora papuana* Daday, 1899 (New Guinea)
12. *Chromadora paracylindricauda* Allgén, 1959 (Falkland Isands)
13. *Chromadora pellucida* Allgén, 1959 (South Georgia)
14. *Chromadora perlasi* Allgén, 1947 (Gulf of Panama)
15. *Chromadora polaris* Cobb, 1914 (Antarctica)
16. *Chromadora sabelloides* Bastian, 1865 (English Channel)
17. *Chromadora wallini* Allgén, 1927 (Tasmania)

Genus *Chromadorella* Filipjev, 1918

This genus largely resembles *Chromadora* except for the heterogenous cuticular pattern in the former. This was the main character to propose *Chromadorella* when *C. mytilicola* Filipjev, 1918 was described and to accommodate four species previously described as *Chromadora* (*C. filiformis* Bastian, 1865; *C. sumatrana* Steiner, 1915; *C. sabangensis* Steiner, 1915 and *C. macrolaimoides*). Among these species only the type species remains currently accepted as valid. *C. sumatrana* and *C. sabangensis* were already postulated as possible *species inquirenda* by Filipjev (1918) and they were later transferred to *Prochromadorella* and *Graphonema,* respectively (Micoletzky 1924; Wieser 1954). *C. mytilicola* was considered as *species inquirendum* by Wieser & Hopper (1967), since only female specimens were known, and *C. macrolaimoides* was returned to *Chromadora* by Wieser (1954). Later, other two *Chromadora* species described by Micoletzky (1922) were also transferred to *Chromadorella*: *C. parapoecilostoma* Micoletzky, 1922 and *C. membranata* Micoletzky, 1922 (Gerlach & Riemann 1973). Wieser & Hopper (1967) described *C. trilix* and *C. vanmeterae* and provided a key for the genus including nine (*C. filiformis*; *C. circumflexa* Wieser, 1954; *C. parapoecilostoma*; *C. membranate*; *C. edmondsoni* Wieser, 1959; *C. galeata* Wieser, 1959; *C. parabolica* Wieser, 1954; *C. trilix* and *C. vanmeterae*) out of the 15 currently valid species. Species missing in this review were described later (*C. duopapillata* Platt, 1973; *C. problematica* Boucher, 1976 and *C. salicaensis* Boucher, 1976) or subsequently transferred to this genus from *Prochromadorella* (*C. cobbiana* Johnston, 1938). *C. macris* (Gerlach, 1956) was described as *Trichromadora*, and despite the fact that Lorenzen (1971) proposed to synonymise *Trichromadora* with *Prochromadorella*, *C. macris* was regarded as belonging to *Chromadorella* based on the presence of a continuous lateral differentiation in the cuticle. The species *Chromadorella paramucrodonta* mentioned in Pastor de Ward (1985) is a mistake. This species is currently known as *Prochromadorella paramucrodonta*.

Diagnosis (modified from Tchesunov 2014): Heterogeneous punctated cuticle along the body, with lateral longitudinal rows of large dots. Amphideal fovea transverse slit-like. Buccal cavity with three solid teeth of about equal size in most species. Posterior pharyngeal bulb not always distinct, but with plasmatic interruptions that may appear double in some species. Males with five to twelve (mostly five) cup-shaped precloacal supplements. Marine.

Number of valid species: 14
Genus *Chromadorella* Bastian, 1865
VALID SPECIES
1. *Chromadorella circumflexa* Wieser, 1954 (Chile)

2. *Chromadorella cobbiana* (Johnston, 1938) Blome & Schrage, 1985 (Australia)
Syn. *Chromadora cobbiana* Johnston, 1938
Chromadora dubia Cobb, 1930
Prochromadorella cobbiana (Johnston, 1938) Wieser, 1954
3. *Chromadorella duopapillata* Platt, 1973 (Northern Ireland)
4. *Chromadorella edmondsoni* Wieser, 1959 (Washington, USA)
5. *Chromadorella filiformis* (Bastian, 1865) Filipjev, 1918 (English Channel)
Syn. *Chromadora filiformis* Bastian, 1865
Chromadorella filiformoides Chitwood, 1951
Dichromadora tenuicauda Schuurmans Stekhoven, 1950
6. *Chromadorella galeata* Wieser, 1959 (Washington, USA)
7. *Chromadorella macris* (Gerlach, 1956) Lorenzen, 1972 (Brazil)
Syn. *Trichromadora macris* Gerlach, 1956
8. *Chromadorella membranata* (Micoletzky, 1922) Micoletzky, 1924 (Red Sea)
Syn. *Chromadora filiformis membranata* Micoletzky, 1922
9. *Chromadorella parabolica* Wieser, 1954 (Chile)
10. *Chromadorella parapoecilosoma* (Micoletzky, 1922) Wieser, 1951 (Red Sea, Mediterranean, Sea of Marmara)
Syn. *Chromadora parapoecilostoma* Micoletzky, 1922
Chromadorella ocellata Micoletzky, 1922
11. *Chromadorella problematica* Boucher, 1976 (Manche Occidentale)
12. *Chromadorella salicaliensis* Boucher, 1976 (Manche Occidentale)
13. *Chromadorella trilix* Wieser & Hopper, 1967 (Key Biscayne)
14. *Chromadorella vanmeterae* Wieser & Hopper, 1967 (Florida Bay)
SPECIES INQUIRENDA
1. *Chromadorella meridiana* (Cobb, 1914) Wieser, 1954 (Antartica)
2. *Chromadorella mytilicola* Filipjev, 1918 (Black Sea)

Genus *Chromadorina* Filipjev, 1918

This genus was proposed by Filipjev (1918) who designated *C. obtusa* Filipjev, 1918 as the type species; it was later revised by Wieser (1954). In the latter review, *Heterochromadora* Wieser, 1951 was synomized with *Chromadorina* and two species belonging to the former genus were transferred [*C. cervix* (Wieser, 1951) and *C. granulopigmentata* (Wieser, 1951)]. In the same review several other species were also transferred from *Spiliphera* [*C. rognoeensis* (Allgén, 1932)], *Chromadorita* [*C. longisetosa* (De Coninck & Schuurmans Stekhoven, 1933)], *Prochromadora* [*C. macropunctata* (Wieser, 1954)], *Prochromadorella* [*C. astacicola* (Schneider, 1932) and *C. ocellata* (Paramonov, 1929)] and *Chromadora* [*C. armata* (Allgén, 1933), *C. bergensis* (Allgén, 1932), *C. bioculata* (Schultze in Carus, 1857), *C. erythrophtalma* (Schneider, 1906), *C. germanica* (Bütschli, 1874), *C. pacifica* (Allgén, 1947), *C. parobtusa* (Allgén, 1947) and *C. viridis* (Linstow, 1876)]. However, *C. parobtusa* and *C. pacifica* were considered as synonyms of *C. laeta* (de Man, 1876), and *C. ocellata* was suggested to be a synonym of *C. bioculata. C. cylindricauda* (Allgén, 1928) was regarded as a dubious species by Wieser (1954) and here we consider it as *inquirendum* since its original description is poor and is based on a single female. A key based on male characters was also developed by Wieser (1954), but fourteen of the current valid species were described later (*C. bercziki* Andrássy, 1962; *C. demani* Inglis, 1962; *C. epidemos* Hopper & Meyers, 1967; *C. hiromii* Kito & Nakamura, 2001; *C. incurvata* Wieser, 1956; *C. inversa* Wieser, 1955; *C. longispiculum* Pastor de Ward, 1985; *C. majae* Wieser, 1968; *C. metulata* Aissa & Vitiello, 1977; *C. micoletzkyi* Inglis, 1962; *C. nuda* Wieser, 1954; *C. paradoxa* Timm, 1961; *C. salina* Belogurov, 1978 and *C. supralitoralis* Lorenzen, 1969). In the description of *C. demani*, Inglis (1962) argued concerning the validity of *C. laeta*, therefore a new name for *C. laeta* sensu Micoletzky, 1924 was proposed (therein called *C. micoletzkyi* Inglis, 1962) and *C. laeta* sensu Daday, 1901, *C. laeta* sensu de Man, 1876 and *C. laeta* sensu Wieser, 1954 were considered *species inquirenda* due to the poor description provided by all these authors. *C. pacifica* and *C. parobtusa* are not considered as valid species here as they were previously indicated as possible synonyms of *C. laeta* (Wieser 1954). Finally, the most recently

described species in this genus was *C. hiromii* by Kito & Nakamura (2001), but they pointed out to the similarity of this species to *C. inversa*, which was originally described by Wieser (1955) based on a single female from the Sea of Japan and subsequently re-described based on both genders from Mediterranean (Wieser 1956). For Kito & Nakamura (2001), there is an uncertainty concerning conspecific specimens from Mediterranean and Japan and they suggested that topotypic males of *C. inversa* should be compared to *C. hiromii.* Here, we consider both species (*C. inversa* and *C. hiromii*) as valid until further studies are done.

Diagnosis (modified from Tchesunov 2014): Homogeneous punctated cuticle with transverse rows of dots and without lateral differentiation. Amphideal fovea, when visible, transverse slit-like. Buccal cavity with three (sub)equal solid teeth. Ocelli may be present. Cup-shaped precloacal supplements usually present. Tail elongate-conoid with glands and well-developed spinneret. It is largely a marine genus (23 species) with only four limnetic species (*C. astacicola*, *C. bercziki*, *C. bioculata* and *C. viridis*). *C. erythrophthalma*, *C. germanica* and *C. laeta* live in marine habitats but occasionally can be found in island body waters.

Number of valid species: 27

Genus *Chromadorina* Filipjev, 1918

Syn. *Heterochromadora* Wieser, 1951

VALID SPECIES

1. *Chromadorina armata* (Allgén, 1933) Wieser, 1954 (Norway)

Syn. *Chromadora armata* Allgén, 1933

2. *Chromadorina astacicola* (Schneider, 1932) Wieser, 1954 (Germany)

Syn. *Phrochromadorella astacicola* Schneider, 1932

3. *Chromadorina bercziki* Andrássy, 1962 (Hungary)

4. *Chromadorina bergensis* (Allgén, 1932) Wieser, 1954 (Norway)

Syn. *Chromadora macrolaima bergensis* Allgén, 1932

5. *Chromadorina bioculata* (Schultze in Carus, 1857) Wieser, 1954 (?—no locality indicated)

Syn. *Chromadora bioculata* (Schultze in Carus, 1857) Bütschli 1873
Enoplus bidentatus Diesing, 1861
Prochromadorella bioculata (Schultze in Carus, 1857) Loof, 1961
Rhabditis bioculata Schultze in Carus, 1857
Spiliphera ophrydii Stefanski, 1914
Spiliphera paniewensis Stefanski, 1923

6. *Chromadorina cervix* (Wieser, 1951) Wieser, 1954 (English Channel)

Syn. *Heterochromadora cervix* Wieser, 1951

7. *Chromadorina demani* Inglis, 1962 (Mediterranean)

8. *Chromadorina epidemos* Hopper & Meyers, 1967 (Florida)

9. *Chromadorina erythrophthalma* (Schneider, 1906) Wieser, 1954 (Baltic)

Syn. *Chromadora erythrophthalma* Schneider, 1906
Heterochromadora erythrophthalma (Schneider, 1906) Gerlach, 1951
Prochromadora erythrophthalma (Schneider, 1906) Gerlach, 1951
Prochromadora orleji sensu Filipjev, 1930
Prochromadorella erythrophthalma (Schneider, 1906) Schütz & Kinne, 1955

10. *Chromadorina germanica* (Bütschli, 1874) Wieser, 1954 (Kiel Bay)

Syn. *Chromadora droebachiensis* Allgén, 1931
Chromadora germanica Bütschli, 1874
Chromadora minor Cobb, 1894
Chromadorina minor (Cobb, 1894) Wieser, 1954
Heterochromadora germanica (Bütschli, 1874) Wieser, 1951
Prochromadorella germanica (Bütschli, 1874) De Connick & Schuurmans Stekhoven, 1933

11. *Chromadorina granulopigmentata* (Wieser, 1951) Wieser, 1954 (English Channel)

Syn. *Heterochromadora granulopigmentata* Wieser, 1951

12. *Chromadorina hiromii* Kito & Nakamura, 2001 (Sea of Japan)

13. *Chromadorina incurvata* Wieser, 1956 (Mediterranean)

14. *Chromadorina inversa* Wieser, 1955 (Sea of Japan)
15. *Chromadorina longisetosa* (De Coninck & Schuurmans Stekhoven, 1933) Wieser, 1954 (North Sea)
Syn. *Chromadorita longisetosa* De Coninck & Schuurmans Stekhoven, 1933
16. *Chromadorina longispiculum* Pastor de Ward, 1985 (Deseado river, Argentina)
17. *Chromadorina macropunctata* (Wieser, 1954) Wieser, 1954 (Mediterranean)
Syn. *Prochromadora macropunctata* Wieser, 1954
18. *Chromadorina majae* Wieser, 1968 (Mediterranean)
19. *Chromadorina metulata* Aissa & Vitiello, 1977 (Tunisia)
20. *Chromadorina micoletzkyi* Inglis, 1962 (Red Sea)
Syn. *Chromadorina laeta* sensu Micoletzky, 1924
21. *Chromadorina nuda* Wieser, 1954 (Mediterranean)
22. *Chromadorina obtusa* Filipjev, 1918 (Black Sea)
23. *Chromadorina paradoxa* Timm, 1961 (Bay of Bengal)
24. *Chromadorina rognoeensis* (Allgén, 1932) Wieser, 1954 (Norway)
Syn. *Spiliphera rognoeensis* Allgén, 1932
25. *Chromadorina salina* Belogurov, 1978 (Shikton Island, Japan)
26. *Chromadorina supralitoralis* Lorenzen, 1969 (North Sea; Germany)
27. *Chromadorina viridis* (Linstow, 1876) Wieser, 1954 (Germany)
Syn. *Chromadora bathybia* Daday, 1894
Chromadora lehberti Schneider, 1906
Chromadora oerleyi sensu Ditlevsen, 1911
Chromadora oerleyi sensu Plotnikov, 1901
Chromadora viridis Linstow, 1876
Prochromadorella viridis (Linstow, 1876) Filipjev, 1930
SPECIES INQUIRENDA
1. *Chromadorina cylindricauda* (Allgén, 1928) Wieser, 1954 (Campbell Island)
2. *Chromadorina laeta* (de Man, 1876) Micoltezky, 1924 (Mediterranean)
3. *Chromadorina ocellata* (Paramonov, 1929) Wieser, 1954 (Black Sea)
4. *Chromadorina pacifica* (Allgén, 1947) Wieser, 1954 (Hawaii; Australia; Gulf of Panama)
5. *Chromadorina parobtusa* (Allgén, 1947) Wieser, 1954 (California, USA)

Genus *Prochromadora* Filipjev, 1922

This genus was established with *P. orleji* (de Man, 1880) as the type species (Filipjev, 1922) and it is unique within Chromadorinae in having homogenous cuticle without transversal rows of dots or lateral differentiation. Filipjev (1930) reviewed the genus and transferred three species from *Chromadora* to *Prochromadora*: *P. orleji, P. erythrophthalma* and *P. minor.* These latter two species were regarded as *Chromadorina* in the review of Wieser (1954), who also transferred *Chromadorita* and *Chromadora* species to *Prochromadora* [*P. magna* (Schulz, 1935) and *P. exigua* (Ditlevsen, 1928), respectively]. In this review, a key based on the length of nematodes was also proposed, in which *P. magna* is distinguished from the other species based on its relatively large body length (2-2.5mm). Tarjan *et al.* (1991) redescribed *P. orleji* and proposed a key for the nine species valid at that time. Based on this key, males of this genus can be easily separated in two groups based on the presence (*P. argentinensis* Pastor de Ward, 1984; *P. exigua*; *P. megodonta* Filipjev, 1922; *P. orleji*; *P. spiltzbergensis* Gerlach, 1965 and *P. trisupplementa* Murphy, 1963) and absence (*P. asupplementa* Hopper, 1961 and *P. bulbosa* Galtsova, 1976) of precloacal supplements. When precloacal supplements are present they can range from 3 to 20. *P. helenae* was the most recent species described in this genus by Tchesunov (2015) and it can be included in the group of species without precloacal supplements.

Diagnosis (modified from Tchesunov 2014): Homogeneous punctated cuticle without transversal rows of dots and without lateral differentiation. Amphideal fovea transverse slit-like, but not visible in several species. Single large dorsal tooth opposed by a ventrosublateral pit or at most by a small elevation of the buccal wall or small ventrosublateral teeth. Posterior pharyngeal bulb well developed. Precloacal supplements usually present in males. It is mainly marine genus, but *C. orleji* is also recorded in freshwater.

Number of valid species: 10

Genus *Prochromadora* Filipjev, 1922

VALID SPECIES

1. *Prochromadora argentinensis* Pastor de Ward, 1984 (Puerto Deseado, Argentina)
2. *Prochromadora asupplementa* Hopper, 1961 (Alabama, USA)
3. *Prochromadora bulbosa* Galtsova, 1976 (White Sea)
4. *Prochromadora exigua* (Ditlevsen, 1928) Wieser, 1954 (Greenland)
Syn. *Chromadora exigua* Ditlevsen, 1928
5. *Prochromadora helenae* Tchesunov, 2015 (Mid-Atlantic Ridge)
6. *Prochromadora magna* (Schulz, 1935) Wieser, 1954 (Mediterranean)
7. *Prochromadora megodonta* Filipjev, 1922 (Black Sea)
8. *Prochromadora orleji* (de Man, 1880) Filipjev, 1922 (North Sea)
Syn. *Chromadora orleji* de Man, 1880
9. *Prochromadora spitzbergensis* Gerlach, 1965 (Svalbard)
10. *Prochromadora trisupplementa* Murphy, 1963 (Oregon, USA)

Genus *Prochromadorella* Micoletzky, 1924

This is the most species rich genus within Chromadorinae. It was erected to accommodate some *Chromadora* species [*P. arabica* (Cobb, 1890), *P. mediterranea* (Micoletzky, 1922), *P. neapolitana* (de Man, 1876) and *P. sumatrana*] showing a dissimilar cuticular pattern along the body (*i. e.* heterogenous cuticle). *P. neapolitana* was designated as the type species. Wieser (1951) described *P. macroocellata* and transferred *P. norwegica* (Allgén, 1932) (misspelled as *P. norvegica*) and *P. paramucrodonta* (Allgén, 1929), both from *Chromadora* and *P. obtusidens* (Schuurmans Stekhoven & Adam, 1931) from *Chromadorita* to this genus. However, later Wieser (1954) indicated the doubtful position of *P. macroocellata* because the description was based on a female specimen. In his review, Wieser (1954) assumed that the taxonomic status of some species was dubious due to the insufficient descriptions (diagnoses and figures) of the buccal cavity, but nevertheless some species were transferred to this genus: *P. acridentata* (Schulz, 1932) previously described as *Chromadorella*; *P. affinis* (Allgén, 1930), *P. ambigua* (Ditlevsen, 1928), *P. cobbiana*, *P. conicaudata* (Allgén, 1927), *P. ditlevseni* (de Man, 1922) and *P. maculata* (Ditlevsen, 1918) (all described as *Chromadora*); *P. kryptospiculum* (Allgén, 1942) and *P. ungulidentata* (Allgén, 1932) (both described as *Spiliphera*); *P. antarctica* (Cobb, 1914) and *P. quinquepapillata* (Schuurmans Stekhoven, 1935) previously described as *Euchromadora* and *Neochromadora*, respectively. *P. sumatrana* and *P. affinis* must be considered as *species inquirenda* since only poorly described females are known up till now. Wieser (1954) suggested that *P. acridentata* is a dubious species that could be a synonym to *P. neapolitana* or *P. maculata* but we prefer to consider *P. acridentata* as *species inquirendum* because there is only a female described and based on this specimen it is not possible to determine its taxonomic position. *P. arabica* and *P. quinquepapilata* are also considered as *species inquirenda* following the suggestion of Micoletzky (1924) and Riemann (1966), respectively. Wieser (1954) also proposed a key based on the presence and absence of ocelli combined with the orientation of the dorsal tooth. *P. subterranea* and *P. tenuicaudata* were described by Gerlach (1953 and 1954, respectively) and they are absent in the key proposed by Wieser (1954), probably because these descriptions were published at the same time as the review. *P. micoletzkyi* Chitwood, 1951 was considered a synonym of *P. paramucrodonta* by Wieser (1954) but based on the shape of the gubernaculum the former species was distinguished from the latter by Hopper & Meyers (1967) and we agree here with its validity. After Wieser's review, eighteen species were described by several authors: *P. actuaria* Vitiello, 1971; *P. crassispicula* Galtsova, 1976; *P. calvus* Lemzina, 1982; *P. codiuma* Pastor de Ward, 1985; *P. daroae* Muthumbi & Vincx, 1998; *P. filiformis* Lemzina, 1982; *P. graciosa* Kulikov, Belogurova & Luzganova, 1990; *P. gracilis* Huang & Wang, 2011; *P. hexapapilata* Blome, 1985; *P. oculata* Kulikov, Belogurova & Luzganova, 1990; *P. papillata* Jensen, 1985; *P. parazygophora* Kulikov, Belogurova & Luzganova, 1990; *P. salpingifera* Blome, 1985; *P. septempapillata* Platt, 1973; *P. spinosa* Gerlach, 1957; *P. striatus* Lemzina, 1982; *P. triangularis* Wieser, 1959 and *P. zygophora* Blome, 1985. Among these species, *P. spinosa* was later transferred to *Endeolophos* (Holovachov *et al.* 2011) and *P.*

cobbiana to *Chromadorella* (Blome & Schrage, 1985). *P. attenuata* (Gerlach, 1952) was previously described as *Neochromadora attenuata* Gerlach, 1952 but transferred to *Prochromadorella* by Lorenzen (1971). Lorenzen (1971) also considered *Trichromadora* as a synonym of this genus, but Muthumbi & Vincx (1998a) reinstated the validity of *Trichromadora* (see below). These authors also redescribed *P. ditlevseni*.

Diagnosis (modified from Tchesunov 2014): Heterogeneous punctated cuticle along the body, lateral differentiation absent, but dots may be enlarged not forming longitudinal rows. Amphideal fovea oval to slit-like located between four cephalic setae. Pharyngeal bulb single or absent. Buccal cavity with three solid teeth of subequal size. Ocelli may be present. Males usually with cup-shaped precloacal supplements. Marine.

Number of valid species: 33

Genus *Prochromadorella* Micoletzky, 1924

VALID SPECIES

1. *Prochromadorella actuaria* Vitiello, 1971 (Mediterranean)
2. *Prochromadorella ambigua* (Ditlevsen, 1928) Wieser, 1954 (Greenland)
Syn. *Chromadora ambigua* Ditlevsen, 1928
3. *Prochromadorella antarctica* (Cobb, 1914) Wieser, 1954 (Antarctica)
Syn. *Chromadora mucrodonta antarctica* Allgén, 1929
Euchromadora antarctica Cobb, 1914
4. *Prochromadorella attenuata* (Gerlach, 1952) Lorenzen, 1971 (North Sea)
Syn. *Neochromadora attenuata* Gerlach, 1952
5. *Prochromadorella calvus* Lemzina, 1982 (Lake Issyk-Kul)
6. *Prochromadorella codiuma* Pastor de Ward, 1985 (Argentina)
7. *Prochromadorella conicaudata* (Allgén, 1927) (Tasmania)
Syn. *Chromadora conicaudata* Allgén, 1927
Euchromadora paramokurae Allgén, 1930
8. *Prochromadorella crassispicula* Galtsova, 1976 (White Sea)
9. *Prochromadorella daroae* Muthumbi & Vincx, 1998 (Indian Ocean)
10. *Prochromadorella ditlevseni* (de Man, 1922) Wieser, 1954 (North Sea)
Syn. *Chromadora ditlevseni* de Man, 1922
Chromadorita ditlevseni de Man, 1922
11. *Prochromadorella filiformis* Lemzina, 1982 (Lake Issyk-Kul)
12. *Prochromadorella gracilis* Huang & Wang, 2011 (Yellow Sea)
13. *Prochromadorella graciosa* Kulikov, Belogurova & Luzganova, 1990 (Sea of Japan)
14. *Prochromadorella hexapapillata* Blome, 1985 (Galapagos)
15. *Prochromadorella kryptospiculum* (Allgén, 1942) Wieser, 1954 (Mediterranean)
Syn. *Spiliphera kryptospiculum* Allgén, 1942
16. *Prochromadorella macroocelata* Wieser, 1951 (English Channel)
17. *Prochromadorella maculata* (Ditlevsen, 1918) Wieser, 1954 (Danish Belt Sea)
Syn. *Chromadora maculata* Ditlevsen, 1918
Spiliphera borealis Allgén, 1940
18. *Prochromadorella mediterranea* (Micoletzky, 1922) Micoletzky, 1924 (Red Sea; Mediterranean)
Syn. *Chromadora mediterranea* Micoletzky, 1922
Chromadorella pontica Filipjev, 1922
19. *Prochromadorella micoletzkyi* Chitwood, 1951 (Texas, USA)
Syn. *Prochromadorella chitwoodi* Timm, 1952
20. *Prochromadorella neapolitana* (de Man, 1876) Micoletzky, 1924 (Mediterranean)
Syn. *Chromadora neapolitana* de Man, 1876
Chromadora procera Micoletzky, 1922
21. *Prochromadorella obtusidens* (Schuurmans Stekhoven & Adam, 1931) Wieser, 1951 (North Sea)
Syn. *Chromadorita obtusidens* Schuurmans Stekhoven & Adam, 1931
22. *Prochromadorella oculata* Kulikov, Belogurova & Luzganova, 1990 (Sea of Japan)
23. *Prochromadorella papillata* Jensen, 1985 (Gulf of Mexico)

24. *Prochromadorella paramucrodonta* (Allgén, 1929) Wieser, 1951 (Macquarie Island)
Syn. *Chromadora paramucrodonta* Allgén, 1929
25. *Prochromadorella parazygophora* Kulikov, Belogurova & Luzganova, 1990 (Sea of Japan)
26. *Prochromadorella salpingifera* Blome, 1985 (Galapagos)
27. *Prochromadorella septempapillata* Platt, 1973 (Northern Island)
28. *Prochromadorella striatus* Lemzina, 1982 (Lake Issyk-Kul)
29. *Prochromadorella subterranea* Gerlach, 1953 (Mediterranean)
30. *Prochromadorella tenuicaudata* Gerlach, 1954 (Mediterranean)
31. *Prochromadorella triangularis* Wieser, 1959 (Washington, USA)
32. *Prochromadorella ungulidentata* (Allgén, 1932) Wieser, 1954 (Campbell Island)
Syn. *Euchromadora ungulidentata* (Allgén, 1932) Allgén, 1950
Spiliphera ungulidentata Allgén, 1932
33. *Prochromadorella zygophora* Blome, 1985 (Galapagos)
SPECIES INQUIRENDA
1. *Prochromadorella acridentata* (Schulz, 1932) Wieser, 1954 (Kiel Bay)
2. *Prochromadorella affinis* (Allgén, 1930) Wieser, 1954 (Fuegan Archipelago)
3. *Prochromadorella arabica* (Cobb, 1890) Micoletzky, 1924 (Gulf of Aden)
4. *Prochromadorella norwegica* (Allgén, 1932) Wieser, 1951 (Norway)
5. *Prochromadorella quinquepapillata* (Schuurmans Stekhoven, 1935) Wieser, 1954 (North Sea)
6. *Prochromadorella sumatrama* (Steiner, 1915) Micoletzky, 1924 (Indonesia)

Genus *Punctodora* Filipjev, 1929

This genus was established by Filipjev (1929) designating *P. ratzeburgensis* (Linstow, 1876), which was previously described as *Chromadora ratzeburgensis* Linstow, 1876, as the type species. Wieser (1954) later suggested that *Chromadora salinarum* Linstow, 1901 should be considered as *Punctodora salinarum* (Linstow, 1901) (misspelled as *P. salinarium*) and we agree with him. Schneider (1943) described *P. ohridiensis* and *Neochromadora trilineata*, but the latter was considered a synonym of the former considering the diagnostic feature of this species (three longitudinal rows of coarse punctuations) as an intraspecific variation in *P. ohridensis* (Gerlach & Meyl 1957). However, subsequently, Hopper (1963) reinstated the separate species status for *Neochromadora trilineata* from *Punctodora ohridiensis* and considered the former species as *incertae sedis* since there was not material available for further investigation. This author also described *P. exochopora*. The last species described in this genus was *P. dudichi* by Andrássy (1966).

Diagnosis (modified from Tchesunov 2014): Homogenous punctated cuticle with lateral dots, some bigger than the submedian dots. Amphideal fovea flattened, spiral and situated at the level of dorsal tooth. Stoma with well-developed dorsal tooth and two smaller ventrosublateral teeth visible at the anterior and posterior border of an indentation. Ocelli present. Secretory-excretory pore in head region. Well defined posterior pharyngeal bulb. Presence of one to 18 cup shaped precloacal supplements. This genus largely resembles *Prochromadora* by the cuticle pattern, but it differs by having large dots in the lateral view, but not forming a longitudinal row. All species are mainly freshwater although *P. salinarum* can occur in inland waters with salinity ranging from 4 to 21‰.

Number of valid species: 5
Genus *Punctodora* Filipjev, 1919
VALID SPECIES
1. *Punctodora dudichi* Andrássy, 1966 (Hungary)
2. *Punctodora exochopora* Hopper, 1963 (Canada)
3. *Punctodora ohridensis* Schneider, 1943 (Yugoslavia)
4. *Punctodora ratzeburgensis* (Linstow, 1876) Filipjev, 1929 (Germany)
Syn. *Chromadora bulbosa* Daday, 1894
Chromadora dubiosa Daday, 1903
Chromadora ratzeburgensis Linstow, 1876

5. *Punctodora salinarum* (Linstow, 1901) Wieser, 1954 (Germany)

Genus *Timmia* Hopper, 1961

The genus was erected in Chromadorinae to accommodate two species [(*T. bipapillata* (Chitwood, 1951) and *T. parva* (Timm, 1952)] which were previously described as *Parachromadora* by Timm (1952). The generic name *Parachromadora* was already preoccupied by *Parachromadora* Micoletzky, 1914 and for this reason it was necessary to propose a new genus name (Hopper 1961). *T. bipapillata* was firstly described as *Prochromadorella bipapillata* by Chitwood (1951), but this author also suggested that the species could belong to a different genus since its terminal bulb was very well developed. The last species added to this genus was *T. acuticauda* Galtsova, 1976. *Timmia* largely resembles *Chromadorina* except for the presence of tubular precloacal supplement, which was not described or even drawn for *T. bipapillata*, but detected later by Hopper (1961) when checking some *T. bipapillata* specimens.

Diagnosis (modified from Tchesunov 2014): Homogeneous cuticle with transverse rows of dots but without lateral differentiation. Amphideal fovea slit-like, when visible. Buccal cavity with three teeth of about equal size. Posterior single pharyngeal bub well developed. Presence of tubular curved precloacal supplements. Marine.

Number of valid species: 3
Genus *Timmia* Hopper, 1961
Syn. *Parachromadora* sensu Timm, 1952
VALID SPECIES
1. *Timmia acuticauda* Galtsova, 1976 (White Sea)
2. *Timmia bipapillata* (Chitwood, 1951) Hopper, 1961 (Texas, USA)
Syn. *Prochromadorella bipapillata* Chitwood, 1951
Parachromadora bipapillata (Chitwood, 1951) Timm, 1952
3. *Timmia parva* (Timm, 1952) Hopper, 1961 (Maryland, USA)
Syn. *Parachromadora parva* Timm, 1952

Genus *Trichromadora* Kreis, 1929

This genus was erected by Kreis (1929) with *T. longicaudata* as the type species. Later, *T. arimiensis* Gerlach, 1953, *T. macris* and *T. ophiocephala* Schuurmans Stekhoven, 1950 were described. Lorenzen (1972) synonymized this genus with *Prochromadorella* based on tail shape and presence of lateral differentiation in three rows on the anterior part of *T. longicaudata*. In the same work Lorenzen (1972) transferred *T. arimiensis* and *T. macris* to *Chromadorella* and *T. ophiocephala* was synonymized with *T. longicaudata.* However, Muthumbi & Vincx (1998a) reinstated the genus mainly based on the differences in cuticle pattern found between *Trichromadora* and *Prochromadorella*. The former genus bears a homogenous cuticle with lateral differentiation of three longitudinal rows of dots, while the latter has a heterogenous cuticle. These authors recognized *T. arimiensis*, *T. brachyura* (Schuurmans Stekhoven, 1950) (transferred from *Prochromadorella*) and *T. longicaudata* as valid species in the genus. Decraemer & Smol (2006) and Tchesunov (2014) agreed with the synonymization proposed by Lorenzen (1972), but since many genera within Chromadorinae are differentiated by the cuticular pattern, this differential feature seems to be robust enough to consider *Trichromadora* a valid genus. Therefore, based on the cuticle pattern, we consider *Trichromadora* a valid genus.

Diagnosis (modified from Muthumbi & Vincx 1998a): Homogeneous cuticle with a lateral differentiation of three longitudinal rows of thicker dots. Amphideal fovea slit-like. Buccal cavity with a large dorsal hollow tooth and ventrosublateral teeth not evident. Posterior pharyngeal bulb poorly developed. Five precloacal supplements cup-shaped. Marine.

Number of valid species: 3
Genus *Trichromadora* Kreis, 1929

VALID SPECIES

1. *Trichromadora arimiensis* Gerlach, 1953 (Mediterranean)

Syn. *Chromadorella arimiensis* (Gerlach, 1953) Lorenzen, 1972

2. *Trichromadora brachyura* (Schuurmans Stekhoven, 1950) Muthumbi & Vincx, 1998 (Mediterranean)

Syn. *Prochromadorella brachyura* Schuurmans Stekhoven, 1950

3. *Trichromadora longicaudata* Kreis, 1929 (English Channel)

Syn. *Prochromadorella longicauda* (Kreis, 1929) Lorenzen, 1972

Prochromadorella ophiocephala (Schuurmans Stekhoven, 1950) Lorenzen, 1972

Trichromadora ophiocephala Schuurmans Stekhoven, 1950

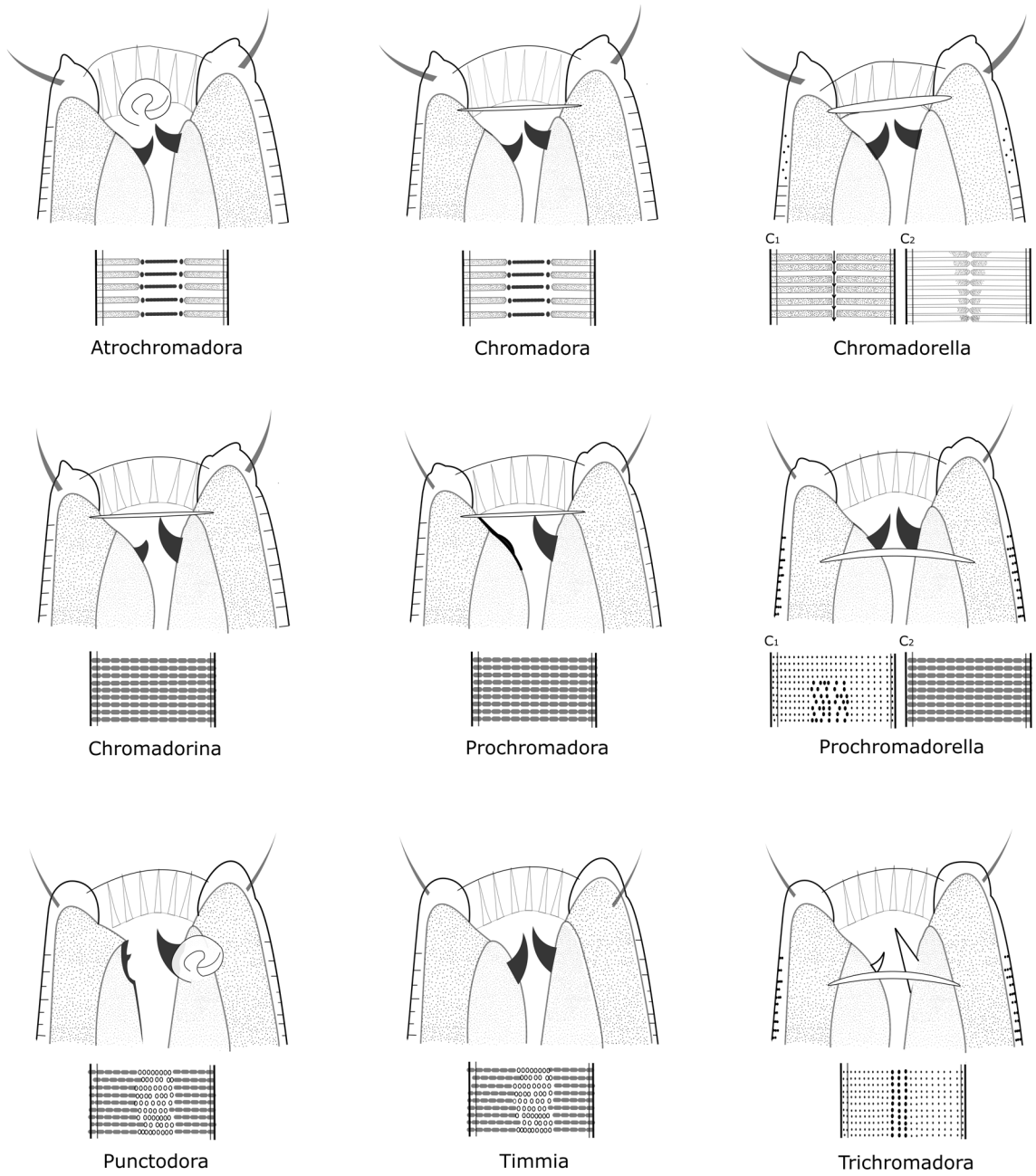

FIGURE 1. Schematic representation of Chromadorinae genera. The drawings aim to show head with buccal cavity and amphideal fovea, and cuticle ornamentation (general pattern or C1 at anterior body level and C2 at posterior body level). In all drawings the right side is the dorsal side of the nematode.

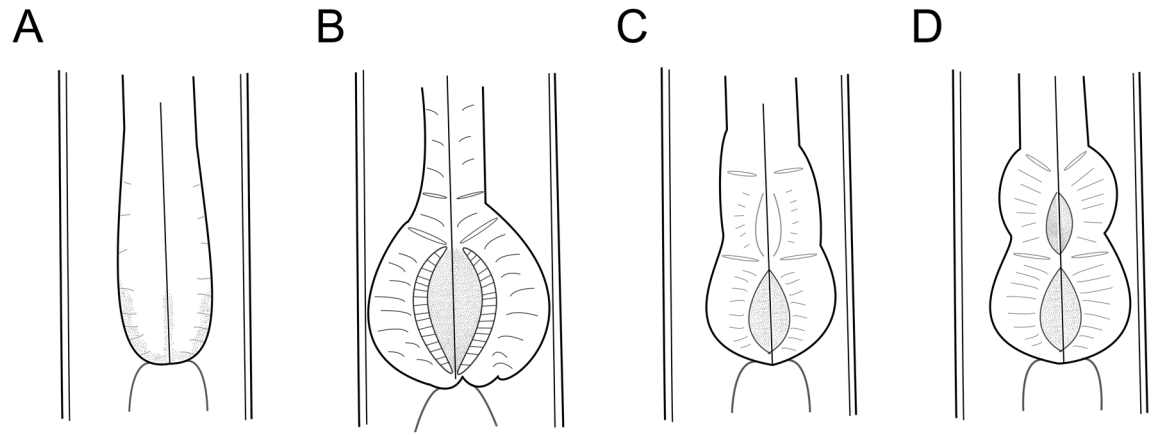

FIGURE 2. Schematic representation of the pharynx states. A: cylindrical. B: single pharyngeal bulb. C: single pharyngeal bulb, but plasmatic interruptions resemble a double bulb. D: double pharyngeal bulb.

Polytomous Identification Key for Chromadorinae

The polytomous key is based on six characters to separate nine genera of the sub-family Chromadorinae (Table 2, Figures 1 and 2). According to the descriptions, the cuticle can be separated into five states, the buccal cavity and pharynx (Figure 2) into four types, amphideal fovea into three states and all the remaining characters in two distinct levels. The cuticle pattern indicates five groups within subfamily Chromadorinae: group 1 formed by *Atrochromadora* and *Chromadora*, which can be distinguished by the amphideal fovea shape; group 2 and group 4 composed exclusively of *Chromadorella* (presence of latteral differentiation) and *Prochromadorella* (absence of lateral differentiation), respectively; group 3 composed of *Chromadorina* and *Prochromadora* and group 5 includes *Punctodora*, *Timmia* and *Trichromadora.* Genera belonging to groups 3 and 5 can be distinguished by teeth shape and/or size.

TABLE 2. Polytomous key of Chromadorinae.

	Cuticle	Amphideal fovea	Ocelli	Buccal cavity	Pharynx	Supplements
Atrochromadora	1	1	1	1/4	2	1/2
Chromadora	1	2/3	1/2	1/4	2/4	2
Chromadorella	2	2/3	2	1/2	2/3	2
Chromadorina	3	2/3	1/2	1/2	2	1/2
Prochromadora	3	2/3	1/2	4	2	1/2
Prochromadorella	4	1/2	1/2	1	1	1/2
Punctodora	5	1	2	1	2	2
Timmia	5	3	2	2	2	2
Trichromadora	1	2	1	3	1	2

Character states:
Cuticle:
1. Homogenous punctated ornamentation but with lateral differentiation;
2. Heterogenous punctated ornamentation with lateral differentiation;
3. Homogenous punctated ornamentation without lateral differentiation;
4. Heterogenous punctated ornamentation but without lateral differentiation;
5. Homogenous punctated ornamentation with enlarged dots along lateral body sectors but not forming rows.

Amphideal fovea:
1. Oval loop-shaped;

2. Transverse slit-like;
3. Not described/Unknown.

Ocelli:
1. Absent;
2. Present.

Buccal cavity:
1. Three solid subequal teeth;
2. Three solid equal teeth;
3. Three hollow subequal teeth;
4. One solid dorsal tooth and ventrosublateral teeth not evident.

Pharynx (Figure 2):
1. Cylindrical;
2. Single pharyngeal bulb;
3. Single pharyngeal bulb, but plasmatic interruptions resemble a double bulb;
4. Double pharyngeal bulb.

Supplements:
1. Absent;
2. Present.

Subfamily Euchromadorinae

Diagnosis (modified from Tchesunov, 2014): Cuticle with complex heterogenous ornamentation (except in *Endeolophos* with homogenous ornamentation). The six outer labial and four cephalic setiform sensilla may be arranged in a single circle (6+10) or two separate circles (6+6+4). Amphideal fovea transverse slit-like or oval (elliptical). Buccal cavity with large or small dorsal tooth, with or without denticles or smaller ventrosublateral teeth. Pharynx with or without defined terminal bulb. Gubernaculum usually with hammer- or L-shaped lateral pieces (wrongly indicated as telamon in some descriptions). Precloacal supplements absent in males, but a precloacal differentiation of body cuticle may be present. All genera in this subfamily are marine, with no records so far in freshwater.

Genus *Actinonema* Cobb, 1920

The genus *Actinonema* was proposed by Cobb (1920) with the description of *A. pachydermatum*. Wieser (1954) synonymized *Pareuchromadora* Schuurmans Stekhoven & Adam, 1931 with *Actinonema* transferring all species (*P. amphidiscatum* Schuurmans Stekhoven & Adam, 1931; *P. fragile* sensu Allgén, 1942; *P. longicaudatum* Chitwood, 1951 and *P. setifer* Schuurmans Stekhoven, 1943). Wieser (1954) also transferred *Spiliphera fragilis* described by Allgén (1929) to *Actinonema* and synonymized *P. amphidiscatum* with it. Furthermore, Wieser (1954) transferred *Euchromadora longicaudata* described by Steiner (1918) to *Actinonema* and synonymized the recently transferred *P. fragile* and *P. setifer* with it. In order to avoid homonymy of *P. longicaudatum* with *E. longicaudata*, Wieser (1954) renamed the first to *A. chitwoodi* but this species should be considered *species inquirendum* since the description was based only on a poorly described single female. Later *A. fragile*, mentioned as *Spiliphera fragilis*, was synonymized with *A. pachydermatum* by Lorenzen (1972). The species *A. fidatum*, *A. celtica* and *A. grafi* were described by Vitiello (1970), Boucher (1976) and Jensen (1991), respectively. Muthumbi & Vincx (1998b) described *A. paraceltica* and *A. smolae* and also discussed differences between *Actinonema* and the closely related genus *Rhips*. The authors state that two main characters are considered to distinguish *Actinonema* and *Rhips* in the majority of identification works: cuticle with solid cones in *Rhips* (absence of the same in *Actinonema*) and double-jointed spicules in *Rhips* (simple spicules in *Actinonema*). However, Muthumbi & Vincx (1998b) affirm that sometimes is difficult to assign the correct genus because males of *Rhips* can lose their spicules. Therefore, we agree with them that solution for a correct identification can come only at molecular level and in mixed populations

of *Actinonema* and *Rhips* the individuals should be treated as one single ecological unit. The last addition to *Actinonema* was by Shi *et al.* (2018), who described *A. falciforme* and also presented an identification key for the species in this genus.

Diagnosis (modified from Muthumbi & Vincx 1986b and Tchesunov 2014): Cuticle heterogenous with lateral differentiation as a ridge beginning at the end of the pharynx. Six outer labial and four cephalic setae arranged in one circle of ten setae. Amphideal fovea conspicuous, transversally oval with a double contour. Buccal cavity with one small dorsal tooth and two ventrosublateral teeth. Posterior pharyngeal bulb may be developed or not. Spicules simple and curved. Gubernaculum with L-shaped pieces.

Number of valid species: 8.
Genus *Actinonema* Cobb, 1920
Syn. *Adeuchromadora* Boucher & De Bovée, 1971
Pareuchromadora Schuurmans Stekhoven & Adam, 1931

VALID SPECIES
1. *Actinonema celtica* Boucher, 1976 (West Channel)
2. *Actinonema falciforme* Shi, Yu & Xu, 2018 (East China Sea)
3. *Actinonema fidatum* Vitiello, 1970 (Mediterranean)
4. *Actinonema grafi* Jensen, 1991 (Norwegian Sea)
5. *Actinonema longicaudatum* (Steiner, 1918) Wieser, 1954 (SW Africa)
Syn. *Actinonema setifer* (Schuurmans Stekhoven, 1943) Wieser, 1954
Euchromadora longicaudata Steiner, 1918
Pareuchromadora fragilis sensu Allgén, 1942
Pareuchromadora setifer Schuurmans Stekhoven, 1943
6. *Actinonema pachydermatum* Cobb, 1920 (Florida)
Syn. *Actinonema amphidiscatum* (Schuurmans Stekhoven & Adam, 1931) Wieser, 1954
Actinonema fragile (Allgén, 1929) Wieser, 1954
Adeuchromadora megamphida Boucher & De Bovée, 1971
Pareuchromadora amphidiscata Schuurmans Stekhoven & Adam, 1933
Spiliphera fragilis Allgén, 1929
7. *Actinonema paraceltica* Muthumbi & Vincx, 1998 (Indian Ocean)
8. *Actinonema smolae* Muthumbi & Vincx, 1998 (Indian Ocean)
SPECIES INQUIRENDUM
1. *Actinonema chitwoodi* Wieser, 1954 (Texas, USA)

Genus *Crestanema* Pastor de Ward, 1985

The monospecific genus *Crestanema* was described by Pastor de Ward (1985) from Argentina. *Crestanema* is closely related to *Nygmatonchus* and *Trochamus* but differs from the former by the absence of pre-cloacal modifications and from the latter in having a gubernaculum with telamon or lateral guiding piece.

Diagnosis (modified from Pastor de Ward 1985): Cuticle formed by rings with internal anterior and posterior processes, with alternate hooking. Wing type lateral differentiation nerve ring level onward. Six outer labial and four cephalic setae arranged in one circle. Amphideal fovea transversally oval, with slightly concave posterior margin. Buccal armature formed by one dorsal and two small ventrosublateral teeth. Spicules simple in structure. Gubernaculum with two central pieces and two lateral guiding pieces.

Number of valid species: 1.
Genus *Crestanema* Pastor de Ward, 1985
VALID SPECIES
1. *Crestanema patagonicum* Pastor de Ward, 1985 (Argentina)

Genus *Endeolophos* Boucher, 1976

The genus *Endeolophos* was erected by Boucher (1976) to accommodate three species originally described as *Nygmatonchus*: *E. fossiferus* (Wieser, 1954), *E. minutus* (Gerlach, 1967) and *E. spinosus* (Gerlach, 1957). Blome (1982) described *E. subterraneus* and more recently Holovachov *et al.* (2011) described a new species, *E. skeneae*, and also provided comparisons of diagnostic characters in different species and populations of the genus. According to these authors, species within this genus can be distinguished by body measurements and ratios, as well as shape of the spicule tip and presence and shape of gubernaculum apophysis.

Diagnosis (modified from Holovachov *et al.* 2011 and Tchesunov 2014): Cuticle with homogenous ornamentation along the body: each annule with very fine and numerous longitudinal ridges. Lateral differentiation in shape of a subcuticular discontinuity in cuticular pattern along the lateral sectors of the body. Six outer labial sensilla and four cephalic sensilla setiform arranged in a single circle. Amphideal fovea as a transversal slit. Buccal cavity with dorsal tooth and two tiny ventrosublateral teeth. No posterior pharyngeal bulb developed. Spicules well developed. Gubernaculum slightly arcuate, plate-like, with or without apophysis and telamons absent.

Number of valid species: 5.
Genus *Endeolophos* Boucher, 1976
VALID SPECIES
1. *Endeolophus fossiferus* (Wieser, 1954) Boucher, 1976 (Chile)
Syn. *Nygmatonchus fossiferus* Wieser, 1954
2. *Endeolophus minutus* (Gerlach, 1967) Boucher, 1976 (Red Sea)
Syn. *Nygmatonchus minutus* Gerlach, 1967
3. *Endeolophus skeneae* Holovachov, Bostrom, Reid, Warén & Schander, 2011 (North-east East Atlantic)
4. *Endeolophus spinosus* (Gerlach, 1957) Boucher, 1976 (Brazil)
Syn. *Neochromadora bicoronata* Wieser, 1959
Nygmatonchus bicoronatus (Wieser, 1959) Inglis, 1969
Nygmatonchus spinosus (Gerlach, 1957) Riemann & Rachor (1973)
Prochromadorella spinosa Gerlach, 1957
5. *Endeolophus subterraneus* Blome, 1982 (North Sea)

Genus *Euchromadora* de Man, 1886

The genus *Euchromadora* was erected by de Man (1886) to accommodate *Chromadora vulgaris* Bastian, 1865. During the last century, dozens of species were referred to *Euchromadora* and subsequently transferred or considered *species inquirenda* or *dubia* or *incerta sedis*. Wieser (1954) was the first to review the genus presenting also an identification key. Subsequently, Coles (1965) and Inglis (1969) also reviewed the genus comparing it to other related genera within Euchromadorinae. After these reviews seven species were considered valid and additional three species were described: *E. ezoensis*, *E. atypica* and *E. robusta* by Kito (1977), Blome (1985) and Kulikov *et al.* (1998), respectively.

Diagnosis (modified from Tchesunov 2014): Complex heterogeneous cuticle, structured with hexagonal or ovoid punctuations anteriorly and posteriorly, with slimmer markings restricted to the lateral surface over the middle of the body. Transversally elliptical amphideal fovea without surrounding cuticle fringe. Six outer labial sensilla and four cephalic sensilla setiform, arranged in separate circles. Buccal cavity with large dorsal tooth, ventrosublateral teeth and rows of denticles. No distinct pharyngeal bulb. Gubernaculum with prominent hammer or L-shaped lateral pieces.

Number of valid species: 10.
Genus *Euchromadora* de Man, 1886
VALID SPECIES
1. *Euchromadora atypica* Blome, 1985 (Galapagos)

2. *Euchromadora eileenae* Inglis, 1969 (Australia)
3. *Euchromadora ezoensis* Kito, 1977 (Japan Sea)
4. *Euchromadora gaulica* Inglis, 1962 (Mediterranean)
Syn. *Euchromadora chitwoodi* Coles, 1965
Euchromadora tridentata sensu Wieser, 1951
5. *Euchromadora meadi* Wieser & Hopper, 1967 (Florida)
6. *Euchromadora permutabilis* Wieser, 1954 (Chile)
7. *Euchromadora robusta* Kulikov, Dashchenko, Koloss & Yushin, 1998 (Japan Sea)
8. *Euchromadora striata* (Eberth, 1863) de Man, 1886 (Mediterranean)
Syn. *Euchromadora gaulica* sensu Inglis, 1962 (partim females)
Odontobius striatus Eberth, 1863
9. *Euchromadora tokiokai* Wieser, 1955 (Japan Sea)
10. *Euchromadora vulgaris* (Bastian, 1865) de Man, 1886 (North Sea)
Syn. *Chromadora vulgaris* Bastian, 1865
SPECIES INCERTA SEDIS
1. *Euchromadora arctica* Filipjev, 1946 (New Siberian Islans)
2. *Euchromadora denticulata* Cobb, 1914 (Antarctica)
3. *Euchromadora meridiana* Cobb, 1914 (Antarctica)
4. *Euchromadora strandi* Allgén, 1934 (Baltic)
SPECIES INQUIRENDA
1. *Euchromadora africana* Linstow, 1908 (South Africa)
2. *Euchromadora elegans* Allgén, 1947 (California, USA)
3. *Euchromadora eumeca* Steiner, 1918 (West Africa)
4. *Euchromadora hupferi* (Steiner, 1918) Coles, 1965 (West Africa)
5. *Euchromadora inflatispiculum* Schuurmans Stekhoven, 1943 (Mediterranean)
6. *Euchromadora kryptospiculoides* (Allgén, 1951) Coles, 1965 (California, USA)
7. *Euchromadora linstowi* Allgén, 1959 (Falkland)
8. *Euchromadora luederitzi* Steiner, 1918 (South Africa)
9. *Euchromadora mortenseni* (Allgén, 1947) Wieser, 1954 (Lesser Antilles)
Syn. *Spiliphera mortenseni* Allgén, 1947
10. *Euchromadora septentrionalis* Cobb, 1914 (Antarctica)
11. *Euchromadora stateni* Allgén, 1930 (Fuegian Archipelago)
12. *Euchromadora tridentata* Allgén, 1929 (Skagerrak)

Genus *Graphonema* Cobb, 1898

The genus *Graphonema* was erected by Cobb (1898) when the type species *G. vulgare* Cobb, 1898 was described from Australian samples. In the same work, *G. pachydermum* was mentioned, but never described, therefore it is considered a *nomen nudum*. Cobb (1935) and Johnston (1938) considered *Graphonema* a synonym of *Euchromadora* but later Wieser (1954) reinstated the genus and transferred *Chromadora sabangensis*, *Spilophora amokuroides* Allgén, 1927, *Spilophora norwegica* Allgén, 1932 and *Chromadora paraheterophya* Allgén, 1932 to it. Also, in Wieser (1954), *Chromadora spectabilis* Allgén, 1932 was synonymized with *G. vulgare* and both *Spilophora pusilla* Allgén, 1947 and *Chromadora suilla* Allgén, 1947 were synonymized with the recently transferred *Graphonema amokuroides*. Subsequently, Wieser (1959a) transferred other two species to *Graphonema*: *G. tentabunda*, a new combination for *Chromadora tentabunda* sensu de Man, 1890, and *G. chitwoodi*, a new combination for *Chromadorita tentabunda* sensu Chitwood, 1951. Also, in Wieser (1959a), two new species were described (*G. flaccida* and *G. clivosa*) and *Chromadorita crassa* Timm, 1952 was synonymized with the recently transferred *G. tentabunda*. In the same year, *Graphonema biseriale* is cited in Wieser (1959b) but this species was never described, consequently it is also considered *nomen nudum*. Inglis (1969) described *G. georgei* and reviewed the situation of many *Graphonema* species, resulting in the transfer of *G. amokuroides*, *G. clivosa*, *G. flaccida*, *G. norwegica*, *G. paraheterophyla* and *G. tentabunda* to *Innocuonema*. Also, Inglis (1969)

considered that *Spilophora amokurae* Ditlevsen, 1921, re-described as *Euchromadora amokurae* by Wieser (1954), is most probably a *Graphonema* species, and *Euchromadora arctica* is *incertae sedis* between *Euchromadora* and *Graphonema*. Inglis (1969) also stated that *G. sabangensis* should be considered as *species inquirendum* due to description based only on females, which according to him makes discussion difficult, and *C. spectabilis* (which was synonymized with *G. vulgare*) should be transferred to *Innocuonema*. Platonova (1971) and Kito (1981) described *G. achaeta* and *G. metuliferum*, respectively. Meanwhile, Warwick and Coles (1975) synonymized *Protochromadora* with *Graphonema* transferring all species [*P. scampae* (Coles, 1965); *P. mediterranea* (Allgén, 1942); *P. parafricana* (Gerlach, 1958)] and described *G. northumbriae*. According to Inglis (1969), *Graphonema* is easily recognized within Chromadoridae looking at the head: distinctly set-off as a swollen, almost globular form, and with very fine dot-like punctations in the cuticle of this region of the body. Inglis (1969) also comments that the cuticle of *Graphonema* becomes thicker over the region of the pharynx but always remains relatively thin and delicate in appearance when compared to *Euchromadora* and other close genera.

Diagnosis (modified from Tchesunov 2014): Complex cuticle heterogeneous, structured with hexagonal or ovoid punctuations anteriorly and posteriorly, with slimmer markings restricted to the lateral surface over the middle of the body. Six outer labial sensilla and four cephalic sensilla setiform, arranged in separate circles. Transversally elliptical amphideal fovea with cuticular fringe. Buccal cavity with large, seemingly hollow dorsal tooth, ventrosublateral teeth; rows of denticles absent. No distinct posterior pharyngeal bulb. Gubernaculum with prominent hammer or L-shaped lateral pieces.

Number of valid species: 9.
Genus *Graphonema* Cobb, 1898
Syn. *Protochromadora* Inglis, 1969
VALID SPECIES
1. *Graphonema achaeta* Platonova, 1971 (Japan Sea)
2. *Graphonema amokurae* (Ditlevsen, 1921) Inglis, 1969 (Auckland Islands)
Syn. *Euchromadora amokurae* (Ditlevsen, 1921) Wieser, 1954
Spiliphera amokurae Ditlevsen, 1921
3. *Graphonema georgei* Inglis, 1969 (Australia)
4. *Graphonema mediterranea* (Allgén, 1942) Warwick & Coles, 1975 (Mediterranean)
Syn. *Euchromadora mediterranea* Allgén, 1942
Protochromadora mediterranea (Allgén, 1942) Inglis, 1969
5. *Graphonema metuliferum* Kito, 1981 (Japan Sea)
6. *Graphonema northumbriae* Warwick & Coles, 1975 (Scilly Island)
7. *Graphonema parafricana* (Gerlach, 1958) Warwick & Coles, 1975 (Red Sea)
Syn. *Euchromadora parafricana* Gerlach, 1958
Protochromadora parafricana (Gerlach, 1958) Inglis, 1969
8. *Graphonema scampae* (Coles, 1965) Warwick & Coles (1975) (English Channel)
Syn. *Euchromadora scampae* Coles, 1965
Protochromadora scampae (Coles, 1965) Inglis, 1969
9. *Graphonema vulgare* Cobb, 1898 (Australia)
SPECIES INQUIRENDUM
1. *Graphonema sabangensis* (Steiner, 1915) Wieser, 1954 (Indonesia)
NOMENA NUDA
1. *Graphonema biseriale* Wieser, 1959 (Chesapeake Bay)
2. *Graphonema pachydermum* Cobb, 1898 (Australia)

Genus *Nygmatonchus* Cobb, 1933

The genus *Nygmatonchus* was established by Cobb (1933) when the type species *N. scriptus* was described. Later *N. fossiferus*, *N. alii* and *N. minutus* were described by Wieser (1954), Murphy (1965) and Gerlach (1967), respectively. Wieser (1954) also suggested the transfer of *Spiliphera edentata* Cobb, 1914 to *Nygmatonchus*. Inglis

(1969) reviewed *Nygmatonchus* and transferred *Neochromadora bicoronata* to it and *N. alii* to a new genus (*Austranema*). Inglis (1969) also commented about the doubtful status of *N. fossiferus*, *N. bicoronata* and *N. minutus*. Boucher and De Bovée (1971) transferred *N. fossiferus* when described the new genus *Trochamus*. Riemann & Rachor (1973) established the new combination *N. spinosus* [originally described by Gerlach (1957)] when transferred *Prochromadorella spinosa* to *Nygmatonchus* and synonymized *N. bicoronata* with it. Juario (1974) described *N. minimus*. Boucher (1976) created the genus *Endeolophos* and stated that *N. fossiferus*, *N. minutus* and *N. spinosus* should be transferred to it and *N. minimus* to *Trochamus*. Timm (1978) redescribed *N. edentata* (using its original name *Spilophora edentata*) based on new specimens and transferred this species to *Neochromadora*. Considering all changes within the genus, only the originally described type species *N. scriptus* remained in *Nygmatonchus*. The species was described nearly 100 years ago and is not well detailed but here we consider *Nygmatonchus* as valid due to distinctive characteristics compared to other genera in the family (cuticle pattern and only one small tooth in the buccal cavity).

Diagnosis (modified from Inglis 1969): Cuticle complex with basket-work markings anteriorly, elongate punctuations posteriorly on middle of body; distinct lateral differentiation. Six outer labial sensilla and four setiform cephalic setae arranged in a single circle. Amphideal fovea prominent with double contour. Buccal cavity with small hollow anteriorly directed dorsal tooth. Pharynx without definitive posterior bulb. Tail long and slim. Possible pre-cloacal modification on males and gubernaculum not L-shaped.

Number of valid species: 1.
Genus *Nygmatonchus* Cobb, 1933
VALID SPECIES
1. *Nygmatonchus scriptus* Cobb, 1933 (Massachusetts, USA)

Genus *Parapinannema* Inglis, 1969

The genus *Parapinannema* was established by Inglis (1969) together with *Austranema*, both in Euchromadorinae. Subsequently, Warwick & Coles (1975) synonymized the second with the first, described *P. harveyi* and recognized 6 valid species in *Parapinnanema*: *P. alii* (Murphy, 1965), *P. colesi* (Inglis, 1968), *P. harveyi*, *P. pectinatum* (Wieser & Hopper, 1967), *P. shirleyae* (Coles, 1965) and *P. wilsoni* Inglis, 1969. Belogurov *et al*. (1985) described *P. imbricatum* and Jensen (1985) described *P. mexicanum*. Gourbault & Vincx (1994) described *P. bableti*, *P. rhipsoides* and *P. ritae* and provided a comparative table with measurements of all *Parapinnanema* species. The authors commented that the presence of a double sphincter surrounding the uterine chamber seems to be related to the shape of the wide-open vagina as well as to the elongated vulva. Among marine nematodes this type of vulva is just known in *Parapinnanema*. Recently, Semprucci & Sørensen (2014) described a new species, *P. hawaiiensis*, and provided an identification key to the genus. These authors commented that the male copulatory apparatus is the most useful character to distinguish species in this genus.

Diagnosis (modified from Semprucci & Sørensen 2014 and Tchesunov 2014): Cuticle usually sculptured in minute hexagonal blocks that become more elongate in posterior part of the body; cuticle with punctuations dorsally and ventrally; cuticle very thick over pharyngeal region and battlement-like. Six outer labial sensilla and four cephalic setae arranged in a single circle. Transversally elliptical amphideal fovea with surrounding cuticular fringe. Buccal armament consists of larger dorsal tooth on the dorsal plate and three denticles plus a ventral tooth in each of the two ventrosublateral plates. No posterior pharyngeal bulb. In males ventral cuticle anterior to the cloaca forms a prominent modification. Tail long and slim.

Number of valid species: 12.
Genus *Parapinannema* Inglis, 1969
Syn. *Austranema* Inglis, 1969
VALID SPECIES
1. *Parapinannema alii* (Murphy, 1965) Warwick & Coles, 1975 (Chile)
Syn. *Austranema alii* (Murphy, 1965) Inglis, 1969
Nygmatonchus alii Murphy, 1965

2. *Parapinnanema bableti* Gourbault & Vincx, 1994 (Fangataufa Atoll)
3. *Parapinnanema colesi* (Inglis, 1968) Warwick & Coles, 1975 (New Caledonia)
Syn. *Austranema colesi* (Inglis, 1968) Inglis, 1969
Euchromadora colesi Inglis, 1968
4. *Parapinnanema harveyi* Warwick & Coles, 1975 (Scilly Island)
5. *Parapinnanema hawaiiensis* Semprucci & Sørensen, 2014 (Hawaii)
6. *Parapinnanema imbricata* Belogurov, Belogurova & Smolyanko, 1985 (Sea of Japan)
7. *Parapinnanema mexicanum* (Jensen, 1985) Gourbault & Vincx, 1994 (Gulf of Mexico)
Syn. *Austranema mexicanum* Jensen, 1985
8. *Parapinnanema pectinatum* (Wieser & Hopper, 1967) Warwick & Coles, 1975 (Florida, USA)
Syn. *Austranema pectinatum* (Wieser & Hopper, 1967) Inglis, 1969
Euchromadora pectinata Wieser & Hopper, 1967
9. *Parapinnanema rhipsoides* Gourbault & Vincx, 1994 (Guadeloupe)
10. *Parapinnanema ritae* Gourbault & Vincx, 1994 (Guadeloupe)
11. *Parapinnanema shirleyae* (Coles, 1965) Warwick & Coles, 1975 (South Africa)
Syn. *Austranema shirleyae* (Coles, 1965) Inglis, 1969
Euchromadora shirleyae Coles, 1965
12. *Parapinnanema wilsoni* Inglis, 1969 (Australia)

Genus *Portmacquaria* Blome, 2005

The monospecific genus *Portmacquaria* was described by Blome (2002) under the name *Macquaria* from a sandy beach of eastern Australia. Later it was renamed into *Portmacquaria* by Blome (2005) to avoid homonymy with a fish genus. *Portmacquaria* is characterized by a unique combination of Euchromadorinae characters: the dorsal tooth is obviously solid in its basal part and in the dorsal shoulder, and there are flanges on the lateral walls of oesophastome as well as ventral onchia. The cuticle in the anterior part of the pharynx is more thickened and has a conspicuous posterior bulb.

Diagnosis (modified from Blome 2002): Cuticle complex with lateral differentiation formed by two longitudinal rows of enlarged dots joined by transversal bars. Anterior sensilla in three separate circles, whereas the sensilla of the first circle are papilliform and the four setae of the third circle are longer than the ones of the second circle. Amphideal fovea as a transverse slit without market thickening of the margins. Solid dorsal tooth opposed by two small ventrosublateral teeth, all with flanges forming a cylindrical posterior part of buccal cavity. Pharynx with well-developed posterior bulb. Spicules weakly cuticularised and arcuated. Gubernaculum of irregular shape, and lateral pieces of indistinctly L-shaped form. Ventrally pre- and postvulvar cuticular thickenings in females. Tail conical with three indistinct caudal glands.

Number of valid species: 1.
Genus *Portmacquaria* Blome, 2005
Syn. *Macquaria* Blome, 2002
VALID SPECIES
1. *Portmacquaria chimaira* (Blome, 2002) Blome, 2005 (Australia)
Syn. *Macquaria chimaira* Blome, 2002

Genus *Rhips* Cobb, 1920

The genus *Rhips* was proposed by Cobb (1920) with the description of *R. ornata*. Timm (1961) described *R. longicauda* and Platt & Zhang (1982) described *R. paraornata*. They considered *R. longicauda* as a dubious species since its description was based on a poorly described single immature female. Subsequently, four species were added to the genus: *R. anoxybiotica* by Jensen (1985), *R. carenata* by Pastor de Ward (1985) and *R. galapagensis* and *R. gracilicauda*, both described by Blome (1985). Kulikov (1993) described *R. orientalis* and

presented an identification key to the genus but some species were missing. The last species (*R. reginae*) was added to this genus by Muthumbi & Vincx (1998b). According to Kulikov (1993), members of *Rhips* are characterized by the large transversally elongated amphideal fovea with thickened margins of the punch, articulate spicules with two arcuate parts and the gubernaculum with two L-shaped auxiliary pieces. Muthumbi & Vincx (1998b) discussed differences between *Rhips* and *Actinonema* and commented about the spicules loss in some males of *Rhips*—the fact that makes it difficult the distinction of these two genera.

Diagnosis (modified from Muthumbi & Vincx 1998b and Tchesunov 2014): Heterogeneous cuticle with lateral differentiation as a narrow ridge beginning at the end of the pharynx. Six outer labial sensilla and four cephalic setae arranged in a common circle. Amphideal fovea conspicuous transversally oval with a double contour. Buccal cavity with one small dorsal tooth and two ventrosublateral teeth. Pharynx gradually enlarged posteriorly. Spicules double-jointed. Gubernaculum with lateral pieces.

Number of valid species: 8.

Genus *Rhips* Cobb, 1920

VALID SPECIES

1. *Rhips anoxybiotica* Jensen, 1985 (Gulf of Mexico)
2. *Rhips carenata* Pastor de Ward, 1985 (Argentina)
3. *Rhips galapagensis* Blome, 1985 (Galapagos)
4. *Rhips gracilicauda* Blome, 1985 (Galapagos)
5. *Rhips orientalis* Kulikov, 1993 (Kuril Islands)
6. *Rhips ornata* Cobb, 1920 (Florida)
7. *Rhips paraornata* Platt & Zhang, 1982 (Scotland)
8. *Rhips reginae* Muthumbi & Vincx, 1985 (Indian Ocean)

SPECIES INQUIRENDUM

1. *Rhips longicauda* Timm, 1961 (Bay of Bengal)

Genus *Steineridora* Inglis, 1969

The genus *Steineridora* was established by Inglis (1969) to accommodate four species with a distinct posterior pharynx bulb, which were previously in *Euchromadora* [*S. archaica* (Steiner & Hoeppli, 1926) and *S. dubia* (Steiner, 1918)] or in *Spiliphera* [*S. adriatica* (Daday, 1901) and *S. loricata* (Steiner, 1916)]. According to Inglis (1969), the latter species should be considered *species inquirendum* due to its insufficient description. The last addition to the genus was made by Kito (1977) who described *S. borealis* from Japan.

Diagnosis (modified from Inglis 1969 and Tchesunov 2014): Cuticle complex with relatively stout, elongate punctuations anteriorly and posteriorly; no lateral differentiation. Anterior sensilla in three circles. Amphideal fovea elongated, transverse slit, not bounded by prominent fringe of cuticle. Massive squarish dorsal onchium and sickle-like prominent onchia laterally and ventrally. Posterior pharyngeal bulb present. No precloacal cuticular modification. Gubernaculum with prominent L-shaped lateral pieces. Tail relatively short and stout.

Number of valid species: 4.

Genus *Steineridora* Inglis, 1969

VALID SPECIES

1. *Steineridora adriatica* (Daday, 1901) Inglis, 1969 (Mediterranean)
Syn. *Euchromadora tyrrhenica* Brunetti, 1951
Spiliphera adriatica Daday, 1901
2. *Steineridora archaica* (Steiner & Hoeppli, 1926) Inglis, 1969 (Japan)
Syn. *Euchromadora archaica* Steiner & Hoopli, 1926
Euchromadora loricata sensu Wieser, 1954
3. *Steineridora borealis* Kito, 1977 (Japan)
4. *Steineridora loricata* (Steiner, 1916) Inglis, 1969 (Barents Sea)
Syn. *Spiliphera loricata* Steiner, 1916

SPECIES INQUIRENDUM
1. *Steineridora dubia* (Steiner, 1918) Inglis, 1969 (SW Africa)

Genus *Trochamus* Boucher & De Bovée, 1971

The genus *Trochamus* was created by Boucher & De Bovée (1971) with the description of *T. carinatus*. These authors also transferred *Nygmatonchus fossiferus* to *Trochamus*, but later this species was transferred to *Endeolophos* by Boucher (1976). This author also described *T. complexus* and synonymized *Nygmatonchus minimus* with *T. carinatus*. Blome (1985) described *T. prosoporus* and the last additions to *Trochamus* were *T. bulbosa* and *T. polki*, both described by Muthumbi & Vincx (1998a), who also presented redescriptions of *T. complexus* and *T. prosoporus*. According to Muthumbi & Vincx (1998a) *Trochamus* can be distinguished from *Nygmatonchus* by the amphids (faint slit-like in the first and large conspicuous in the second), lack of cuticular differentiation at pre- and post-anal regions and simple copulatory apparatus (without telamons). Also, according to Muthumbi & Vincx (1998a), *Trochamus* differs from *Endeolophos* by having a heterogenous cuticle with complex lateral alae. *T. falciformis* is considered *nomen nudum* since it was described in a PhD thesis (Tingting 2014).

Diagnosis (modified from Tchesunov 2014): Cuticle heterogenous, with a crest-like lateral differentiation. Six outer labial and four cephalic setae arranged in one circle. Amphideal fovea as poorly visible transversal slit. Buccal cavity armed with one dorsal tooth and two small ventrosublateral teeth. Gubernaculum without lateral pieces.

Number of valid species: 5.
Genus *Trochamus* Boucher & De Bovée, 1971
VALID SPECIES
1. *Trochamus bulbosa* Muthumbi & Vincx, 1998 (Indian Ocean)
2. *Trochamus carinatus* Boucher & De Bovée, 1971 (Mediterranean)
Syn. *Nygmatonchus minimus* Juario, 1974
3. *Trochamus complexus* Boucher, 1976 (West Channel)
4. *Trochamus polki* Muthumbi & Vincx, 1998 (Indian Ocean)
5. *Trochamus prosoporus* Blome, 1985 (Galapagos)
NOMEN NUDUM
1. *Trochamus falciformis* Tingting, 2014 (China)

Polytomous Identification Key for Euchromadorinae

The polytomous key of this subfamily is based on six characters to separate 11 genera of the sub-family Euchromadorinae (Table 3, Figure 3). The combination of cuticle, anterior sensilla pattern, amphidial fovea, buccal cavity, pharyngeal bulb and gubernaculum are the most useful characters to distinguish genera within the sub-family Euchromadorinae.

The buccal cavity having one dorsal tooth and two ventrosublateral teeth and the absence of a distinct pharyngeal posterior bulb seems to be the most consistent characteristics within the subfamily Euchromadorinae. For the former character, only *Euchromadora*, *Graphonema*, *Nygmatonchus* and *Parapinnanema* are those presenting different buccal armature. As for the latter character, a distinct posterior bulb is observed only in *Portmacquaria* and *Steineridora* and some species of *Actinonema* and *Trochamus*. Considering anterior sensilla pattern, both 6+10 and 6+6+4 are present in Euchromadorinae, although the former is the pattern in the majority of the genera within the subfamily. The latter pattern can be found only in *Euchromadora*, *Graphonema*, *Portmacquaria* and *Steineridora*. The cuticle is the most variable character within subfamily Euchromadorinae, with very distinct and exclusive patterns in most genera, consequently this might be a useful character to distinguish the genera. *Euchromadora* and *Graphonema* are very similar, can be differentiated only by the amphideal fovea and the buccal cavity (Table 3). This observation is consistent with many changes and new combinations of species between these two genera. The gubernaculum is mostly well developed within

Euchromadorinae, presenting prominent lateral pieces in most genera, but this character should be used with caution as descriptions of shapes are variable within species and genera, indicating distinct interpretations through publications.

TABLE 3. Polytomous key of Euchromadorinae.

	Cuticle	Anterior sensilla pattern	Amphideal fovea	Buccal cavity	Pharyngeal posterior bulb	Gubernaculum
Actinonema	1	1	1	1	1/2	1
Crestanema	3	1	2	1	2	2
Endeolophos	2	1	3	1	2	1/3
Euchromadora	4	2	4	2	2	1
Graphonema	4	2	5	3	2	1
Nygmatonchus	5	1	1	4	2	3
Parapinannema	4	1	5	5	2	2
Portmacquaria	6	2	3	1	1	4
Rhips	1	1	1	1	2	1
Steineridora	7	2	3	1	1	1
Trochamus	8	1	3	1	1/2	3

Character states:
Cuticle:
1. Heterogeneous punctated ornamentation with lateral differentiation as a ridge;
2. Homogeneous punctated ornamentation but with lateral differentiation as a ridge;
3. Rings with internal anterior and posterior processes, with alternate hooking;
4. Heterogenous ornamentation structured with hexagonal or ovoid punctuations;
5. Ornamentation with basket-work markings anteriorly and elongate punctuations posteriorly;
6. Ornamentation with lateral differentiation presenting two longitudinal rows of enlarged dots joined by transversal bars;
7. Ornamentation with relatively stout, elongate punctuations anteriorly and posteriorly but without lateral differentiation;
8. Heterogenous ornamentation with a crest-like lateral differentiation.

Anterior sensilla pattern:
1. 6+10;
2. 6+6+4.

Amphideal fovea:
1. Transversally oval with a double contour;
2. Transversally oval with slightly concave posterior margin;
3. Transversal slit without marked thickening of the margins;
4. Transversally elliptical without surrounding cuticular fringe;
5. Transversally elliptical with surrounding cuticular fringe.

Buccal cavity:
1. One small dorsal tooth and two ventrosublateral teeth/denticles;
2. One large dorsal tooth and presence of ventrosublateral teeth and rows of denticle;
3. One large dorsal tooth and presence of ventrosublateral teeth;
4. Only one small dorsal tooth;
5. One large dorsal tooth, presence of three denticles and two ventrosublateral teeth.

Pharyngeal posterior bulb:
1. Present;
2. Absent.

Gubernaculum:

1. Hammer or L-shaped lateral pieces;
2. Two central pieces and two lateral pieces;
3. Without L-shaped lateral pieces;
4. Irregular shape, and lateral pieces of indistinctly L-shaped form.

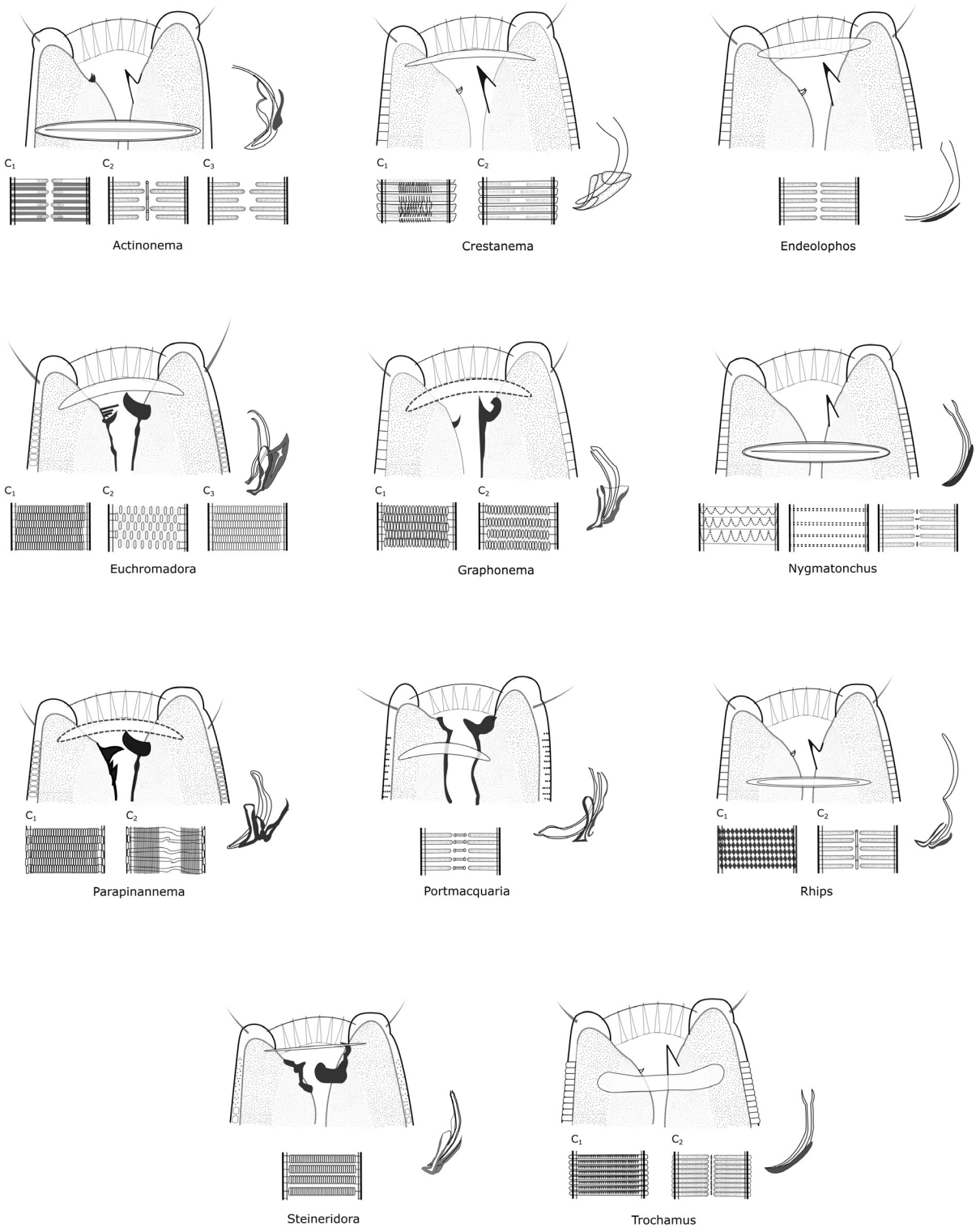

FIGURE 3. Schematic representation of Euchromadorinae genera. The drawings aim to show head with buccal cavity and amphideal fovea, cuticle ornamentation (general pattern or C1 to C3: variation from anterior to posterior region of the body) and copulatory apparatus. In all drawings the right side is the dorsal side of the nematode.

Subfamily Harpagonchinae

Diagnosis (modified from Decraemer & Smol 2006 and Tchesunov, 2014): Cuticle with homogenous ornamentation without lateral differentiation. Anterior sensilla in three separate circles with the four cephalic sensilla setiform. Buccal cavity with three movable triangular-shaped mandibles with anterior solid hooks. Pharynx enlarged anteriorly around the mandibular apparatus and posteriorly widened with or without terminal bulb. Males with precloacal supplements present (cup-shaped) or absent. The genera of this sub-family are either considered ectoparasites (Decraemer & Smol 2006) or ectosymbionts (Tchesunov 2014) of polychaetes in marine environments.

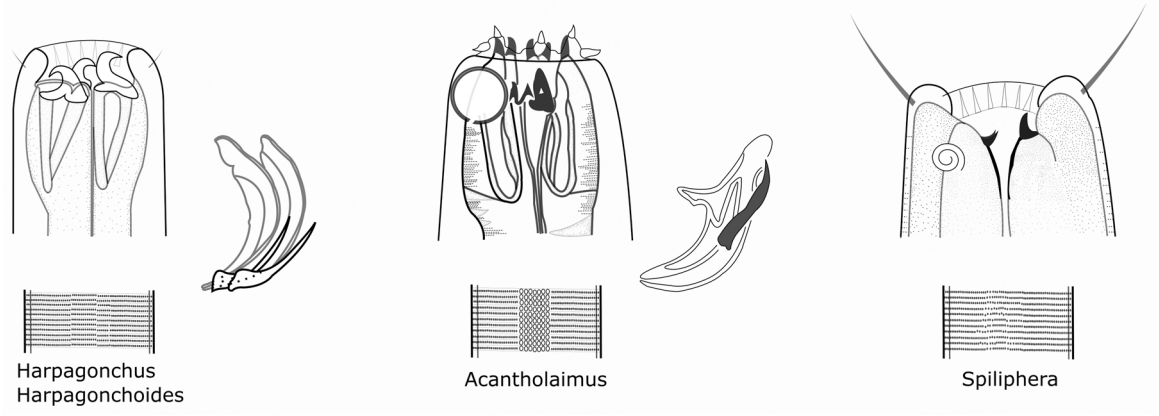

FIGURE 4. Schematic representation of Harpagonchinae and Spilipherinae genera. The drawings aim to show head with buccal cavity and amphideal fovea and cuticle ornamentation (general pattern). For *Harpagonchus*, *Harpagonchoides* and *Acantholaimus* the copulatory apparatus is also presented. In all drawings the right side is the dorsal side of the nematode.

Genus *Harpagonchoides*, Platonova & Potin, 1972

The genus *Harpagonchoides* (Figure 4) was established by Platonova & Potin (1972), who described *H. crassus* and initially established the family Harpagonchidae within Chromadorida. Lorenzen (1994) re-examined type specimens and lowered the rank of Harpagonchidae to the level of subfamily within Chromadoridae, particularly based on a single testis of males. All nematodes of this genus were collected from subantarctic and antarctic polychaete worms, between parapodia of *Hemipodus digitifera* Knox, 1960 (Glyceridae).

Diagnosis (modified from Decraemer & Smol 2006 and Tchesunov 2014): Cuticle homogenous without lateral differentiation. Amphideal fovea unknown. Buccal cavity armed with three motile mandibles with hooks. Pharynx posteriorly terminated with a bulb. No preclocal supplementary organs.

Number of valid species: 1.
Genus *Harpagonchoides*, Platonova & Potin, 1972
VALID SPECIES
1. *Harpagonchoides crassus* Platonova & Potin, 1972 (Antarctica)

Genus *Harpagonchus*, Platonova & Potin, 1972

The genus *Harpagonchus* (Figure 4) was established by Platonova & Potin (1972) when *H. averincevi* and *H. simillis* were described. All species of this genus were collected from the sub Antarctic and Antarctic polychaete worms of the species *Aglaophamus macroura* (Schmarda, 1861) (Nephtydae).

Diagnosis (modified from Decraener & Smol 2006 and Tchesunov 2014): Cuticle homogenous without lateral differentiation. Amphideal fovea unknown. Buccal cavity armed with three motile mandibles with hooks. Pharynx posteriorly widened but not forming a true terminal bulb. Cup-shaped midventral precloacal supplementary organs present in males.

Number of valid species: 2.
Genus *Harpagonchus*, Platonova & Potin, 1972
VALID SPECIES
1. *Harpagonchus averincevi* Platonova & Potin, 1972 (Antarctica)
2. *Harpagonchus similis* Platonova & Potin, 1972 (Antarctica)

Sub-family Hypodontolaiminae

Diagnosis (after Tchesunov, 2014): Cuticle homo- or heterogenous with or without the presence of lateral differentiation of larger dots. Six outer labial papillae and four cephalic setae in two separate circles (except in *Megodontolaimus coxbazari*). Amphidial fovea distinct or rather obscure, transverse flattened oval, generally located between the four cephalic setae. Stoma funnel shaped, armed with hollow teeth; the larger dorsal tooth maybe opposed by two smaller ventrosublateral teeth, denticles may be present; anterior part of pharynx often with prominent dorsal muscular swelling. Males with cup-like precloacal supplements, rarely absent. Mostly marine but some genera have representatives in freshwater or brackish water (see more detailed in each genus).

Genus *Chromadorissa* Filipjev, 1917

The genus *Chromadorissa*, originally considered as part of sub-family Chromadorinae, was established by Filipjev (1917) with the description of the type species *C. beklemishevi*. Filipjev (1917) also suggested that *Monhystera bulbosa* Grimm, 1876 should belong to *Chromadorissa*. Baylis & Daubney (1926) considered this genus, as well as several others, such as *Ptycholaimellus* and *Spilophorella*, as synonyms of *Chromadora*, but Kreis (1928) separated *Chromadorissa* from them. In that study, Kreis (1928) described *C. strandi,* but did not considered *C. bulbosa* as a valid species. Aminova & Galtsova (1978) considered *C. bulbosa* as valid and described *C. inaequibulba* but later Jensen & Nehring (1992) transferred this last species to *Ptycholaimellus*.

Diagnosis (modified from Tchesunov 2014): Cuticle punctuated with heterogeneous ornamentation and lateral differentiation of larger dots arranged in two longitudinal rows. Six outer labial papillae and four cephalic setae in separate circles. Amphideal fovea transverse slit-like and loop shaped. Buccal cavity with one large hollow dorsal tooth and smaller ventrosublateral teeth. Pharynx extending from the peribuccal region, swollen moderately and nearly symmetrically, to the bipartite posterior bulb. Males with five to six complex supplements. Marine.

Number of valid species: 3
Genus *Chromadorissa* Filipjev, 1917
VALID SPECIES
1. *Chromadorissa beklemishevi* Filipjev, 1917 (Caspian Sea)
2. *Chromadorissa bulbosa* (Grimm, 1876) Filipjev, 1917 (Caspian Sea)
Syn. *Monhystera bulbosa* Grimm, 1876
3. *Chromadorissa strandi* Kreis, 1928 (Mediterranean)

Genus *Chromadorita* Filipjev, 1922

The genus *Chromadorita* was established by Filipjev (1922) when the type species *C. demaniana* was described from males collected in Russia. Wieser (1954) synonymized *Odontonema* Filipjev, 1930 and *Allgeniela* Strand, 1934 with *Chromadorita.* In his key, Wieser (1954) transferred some species of *Chromadora*, *Chromadorina*, *Hypodontolaimus*, *Odontonema*, *Prochromadorella* and *Spilophora* to *Chromadorita* and described *Chromadorita leptopharynx*, ending up with 16 species at that time. *Chromadorita inornata* (Cobb, 1915) was not included in the key, but considered as dubious species. Its description was based in a single imature and badly preserved female in which characters such as amphids and cephalic setae could not be observed. Wieser (1954) also did not cite *Chromadorita brevisetosa* Gerlach, 1953; *Chromadorita obliqua* (Gerlach, 1953) and *Chromadorita*

schuurmansstekhoveni Timm, 1952. The species *C. chitwoodi* Wieser, 1954 is now accepted as *Innocuonema tentabunda* (de Man, 1890). Gerlach & Riemann (1973) cited 22 valid species. The species *C. norvegica* is now accepted as *Prochromadorella norwegica* based on its cuticular pattern (Wieser, 1954). Subsequently, fourteen new species were described [*C. nana* Lorenzen, 1973; *C. mucrocaudata* Boucher, 1976; *C. fennica* Jensen, 1979; *C. deseadensis* Pastor de Ward, 1984; *C. nephramphida* Blome, 1985; *C. pallida* Blome, 1985; *C. ceratoserolis* Lorenzen, 1986; *C. inaequispiculata* Dashchenko, 1989; *C. abyssalis* Bussau, 1993; *C. dimeris* Bussau, 1993; *C. pentameris* Bussau, 1993; *C. humila* (Baranova & Dashchenko, 1992); *C.mirabilis* Gagarin, 1993; *C. arctica* Gagarin, 1999; *C. longispiculata* Gagarin, 2012 and *C. pygmaea* Gagarin, 2012]. The last species, *C. regabi*, was described by Baldrighi *et al*. (2018), who also presented an identification key but did not include *C. arctica* and *C. humila*. This work considered *C. abyssalis*, *C. dimeris* and *C. pentameris*, described by Bussau (1993) in his PhD thesis, as valid but, despite their descriptions with good quality and widespread divulgence, they should be considered as *nomena nuda* following the International Code of Zoological Nomenclature. Dashchenko (1989) suggested the reinstation of *Allgeniella* and the species *C. humila* was described as *Allgeniella humila* by Baranova & Dashchenko (1992) but later descriptions of species in *Chromadorita* did not accept *Allgeniella* as valid. Furthermore, *C. heterophya* should be considered as *species inquirendum* due to its poor description (missing details of cuticle and dorsal tooth). Therefore, we recognize 33 valid species.

Considering the generic diagnoses, one of the characters of *Chromadorita* was the lack of lateral differentiation in the cuticle (Wieser, 1954; Pastor de Ward, 1984 and Lorenzen, 1986), but Platt & Warwick (1988) observed cuticle with lateral differentiation in *Chromadorita tenuis* (Schneider, 1906), suggesting that at least this species does not belong to *Chromadorita*. Moreover, Platt & Warwick (1988) pointed out the difficulty of distinguish some species of *Chromadorita* and *Innocuonema.* The authors presented these species (e.g. *I. tentabunda* and *C. nana*) as a complex of *Chromadorita*/*Innocuonema*, characterized by slightly elongated and angular cuticle punctations, the absence of precloacal supplements and a tail with a tip characteristically bent to the left and curved dorsally. We maintain *C. nana* in *Chromadorita* and *I. tentabunda* in *Innocuonema,* since the cuticle and the buccal cavity of *Chromadorita* and *Innocuonema* are different (Table 4). When comparing these characters in the polytomous key, *Chromadorita* is more similar to *Neochromadora* and *Ptycholaimellus* than to *Innocuonema*.

Diagnosis (modified from Tchesunov 2014): Cuticle with homogeneous ornamentation and slightly more pronounced punctuation at the level of lateral fields. Six small outer labial setae or papillae and four cephalic setae in separate circles. Two circles of labial setae are conspicuous in some species (e.g. *C. abnormis*, *C. abyssalis, C. ceratoserolis* and *C. pharetra*). Somatic setae may be present. Amphideal fovea transverse slit-like and loop shaped. Buccal cavity mostly with one dorsal and one or two ventrosublateral teeth, rarely one indistinct dorsal tooth only; sometimes tiny denticles may be present. Peribuccal pharyngeal tissue may be symmetrically swollen or with asymmetrical dorsal swelling anteriorly; posterior bulb single (absent in *C. ceratoserolis*). Males with or without precloacal supplements. It is a largely marine genus, but six species were recovered in brackish and freshwater habitats (*C. arctica*, *C. fennica*, *C. inornata*, *C. leuckarti*, *C. mirabilis* and *C. paetzoldi*).

Number of valid species: 33

Genus *Chromadorita* Filipjev, 1922

Syn. *Algeniella* Strand, 1934

Odontonema Filipjev, 1930

VALID SPECIES

1. *Chromadorita abnormis* (Kreis, 1928) Wieser, 1954 (Barents Sea)

Syn. *Chromadora abnormis* Kreis, 1928

2. *Chromadorita arctica* Gagarin, 1999 (Arctic Sea, Vaygach Island)

3. *Chromadorita brachypharynx* (Allgén, 1932) Wieser, 1959 (New Zealand, Campbell Island)

Syn. *Chromadora brachypharynx* Allgén 1932

4. *Chromadorita brevisetosa* Gerlach, 1953 (Italy)

5. *Chromadorita ceratoserolis* Lorenzen, 1986 (Antarctic Sea)

6. *Chromadorita demaniana* Filipjev, 1922 (Black Sea)

7. *Chromadorita deseadensis* Pastor de Ward, 1984 (Argentina)

8. *Chromadorita fennica* Jensen, 1979 (Archipelago of Finland, Vitsand and Storfjärden)

9. *Chromadorita gracilis* (Filipjev, 1922) Wieser, 1954 (Black Sea)

Syn.*Chromadorina gracilis* Filipjev, 1922
10. *Chromadorita guidoschneideri* (Filipjev, 1929) Wieser, 1954 (Baltic Sea)
Syn. *Odontonema guidoschneideri* Filipjev, 1929
Allgeniella guidoschneideri (Filipjev, 1929) Gerlach, 1951
11. *Chromadorita humila* (Baranova & Dashchenko, 1992) (Sea of Japan) new combination
Syn. *Allgeniella humila* Baranova & Dashchenko, 1992
12. *Chromadorita hyalocephala* (Steiner, 1916) Filipjev, 1922 (Barents Sea)
Syn. *Chromadora hyalocephala* Steiner, 1916
13. *Chromadorita inaequispiculata* Dashchenko, 1989 (Japan Sea)
14. *Chromadorita leptopharynx* Wieser, 1954 (Southern Chile, the Magallanes area)
15. *Chromadorita leuckarti* (de Man, 1876) Filipjev, 1929 (Netherlands)
Syn. *Chromadora leuckarti* de Man, 1876
Spiliphera impatiens Cobb, 1888
Chromadora tyroliensis Stefanski, 1916
Euchromadora viridis sensu Micoletzky, 1922
Chromadora viridis sensu Micoletzky, 1923
16. *Chromadorita longispiculata* Gagarin, 2012 (Vietnam, South China Sea)
17. *Chromadorita macrodonta* (Crites, 1961) Gerlach & Riemann, 1973 (USA, Piver's Island)
Syn. *Allgeniella macrodonta* Crites, 1961
18. *Chromadorita minima* (Kreis, 1929) Wieser, 1954 (France, Trebeurden)
Syn. *Spiliphera minima* Kreis, 1929
19. *Chromadorita minor* (Allgén, 1927) Wieser, 1954 (Tasmania, Brown River)
Syn. *Hypodontolaimus minor* Allgén, 1927
20. C*hromadorita mirabilis* Gagarin, 1993 (Sakhalin Island, Russia)
21. *Chromadorita mucrocaudata* Boucher, 1976 (France, Morlaix Bay)
22. *Chromadorita mucrodonta* (Steiner, 1916) Wieser, 1954 (Barents Sea)
Syn. *Chromadora mucrodonta* Steiner, 1916
Spilophorella mucrodonta (Steiner, 1916) Schuurmans-Stekhoven, 1935
Prochromadorella mucrodonta (Steiner, 1916) Chitwood, 1951
23. *Chromadorita nana* Lorenzen, 1973 (North Sea, Helgoland)
24. *Chromadorita nephramphida* Blome, 1985 (Ecuador, Archipelago of Galapagos)
25. *Chromadorita obliqua* (Gerlach, 1953) Wieser, 1954 (Mediterranean)
Syn*. Allgeniella obliqua* Gerlach, 1953
26. *Chromadorita pachydema* (Schneider, 1926) Wieser, 1954 (Gulf of Finland)
Syn. *Chromadora pachydema* Schneider, 1926
Odontonema pachydema (Schneider, 1926) Filipjev, 1930
Allgeniella pachydema (Schneider, 1926) Allgén, 1947
27. *Chromadorita paetzoldi* Meyl, 1960 (Germany, Hale)
Syn. *Chromadorita gracilis* Paetzold, 1958
Chromadorita paetzoldi Goodey, 1963
28. *Chromadorita pallida* Blome, 1985 (Ecuador, Archipelago of Galapagos)
29. *Chromadorita pharetra* Ott, 1972 (USA, North Carolina)
30. *Chromadorita pygmaea* Gagarin, 2012 (Vietnam, South China Sea)
31. *Chromadorita regabi* Baldrighi, Vanreusel, Zeppilli, Sandulli & Segonzac, 2018 (Gulf of Guinea)
32. *Chromadorita schuurmansstekhoveni* Timm, 1952 (USA, Chesapeake Beach)
33. *Chromadorita tenuis* (Schneider, 1906) Filipjev, 1922 (Sweden, Öresund)
Syn. *Chromadora tenuis* Schneider, 1906
Chromadorita leuckarti sensu Otto, 1936
SPECIES INQUIRENDA
1. *Chromadorita heterophya* (Steiner, 1916) Filipjev, 1922 (Barents Sea)
Syn. *Chromadora heterophya* Steiner, 1916
2. *Chromadorita inornata* (Cobb, 1915) Filipjev, 1930 (USA, Maple River and Bessey Creek)

Syn. *Chromadora inornata* Cobb, 1915
NOMENA NUDA
1. *Chromadorita abyssalis* Bussau, 1993 (SE Pacific, Peru Basin)
2. *Chromadorita dimeris* Bussau, 1993 (SE Pacific, Peru Basin)
3. *Chromadorita pentameris* Bussau, 1993 (SE Pacific, Peru Basin)

Genus *Denticulella* Cobb, 1933

The genus *Denticulella* was established by Cobb (1933) with the description of *D. pellucida* originally from the USA. It was first described as closely related to *Hypondontolaimus,* differing from it in having a smaller and more acute dorsal tooth and the presence of crenated pharyngeal wall (Cobb, 1933). *Denticulella* was previously considered in Chromadorinae (Wieser, 1954), in an intermediate position between *Chromadorita* and *Dichromadora* considering the cuticle and the teeth shape. In that same work, Wieser transferred *Chromadora polydonta* Schulz, 1932 and *Dichromadora stygia* Gerlach, 1952 to *Denticulella*, ending up with three species in the genus. Subsequently, *Denticulella stygia* (Gerlach, 1952) was transferred to *Parachromadorita* by Blome (1974) based on the loop-shaped amphideal fovea instead of having a slit-like amphideal fovea as originally described by Cobb (1933). More recently two additional species were described by Dashchenko (2002).

Diagnosis (modified from Tchesunov 2014): Cuticle ornamentation heterogeneous along the body, lateral differentiation of larger dots not arranged in longitudinal rows; in the region of the buccal cavity, a grid-like pattern may be present. Six small outer labial setae or papillae and four cephalic setae in separate circles. Two circles of labial setae are conspicuous in *D. pellucida*. Somatic setae may be present. Amphideal fovea transverse slit-like and loop shaped. Buccal cavity with a dorsal tooth, two smaller ventrosublateral teeth and numerous additional denticles. Pharynx extending from a peribuccal tissue with asymmetrical dorsal swelling related to the size of dorsal tooth, to a single end bulb. Males with cup-shaped precloacal supplements. Marine.

Number of valid species: 4
Genus *Denticulella* Cobb, 1933
VALID SPECIES
1. *Denticulella benthica* Dashchenko, 2002 (NW Pacific, Sea of Japan)
2. *Denticulella boreala* Dashchenko, 2002 (White Sea)
3. *Denticulella pellucida* Cobb, 1933 (USA, Massachusetts)
4. *Denticulella polydonta* (Schulz, 1932) Wieser, 1954 (Germany, Kiel Bay)
Syn. *Chromadora polydonta* Schulz, 1932

Genus *Dichromadora* Kreis, 1929

The genus *Dichromadora* was first established by Kreis (1929) as part of Chromadorinae to accommodate *D. microdonta* Kreis, 1929 and six species of *Chromadora*: *Chromadora cephalata* Steiner, 1916 (the type species), *Chromadora cricophana* Filipjev, 1922, *Chromadora geophila* (de Man, 1876), *Chromadora parapoecilosoma*, *Chromadora sabulicola* Filipjev, 1918 and *Chromadora setosa* Bütschli, 1874. Kreis (1929) distinguished *Dichromadora* from *Chromadora* based on the cuticle with two longitudinal rows of dots, the presence of a spherical pharyngeal bulb, reflexed and symmetrical paired ovaries. Later, *Dichromadora* was differentiated by having a dorsal triangular and acute tooth, different from the S-shaped tooth known for *Hypodontolaimus* (Wieser 1954). Gerlach & Riemann (1973) presented a list of sixteen species, including *D. serrata*, renamed later to *Chromadora serrata* by Timm (1978).

After Gerlach & Riemann (1973), *D. antarctica* (Cobb, 1914) was transferred from *Spilophora*, and other 13 valid species were described (*D. cucullata* Lorenzen, 1973; *D. amphidiscoides* Kito, 1981; *D. abyssalis* Bussau, 1993; *D. gathuai* Muthumbi & Vincx, 1998; *D. loiseae* Muthumbi & Vincx, 1998; *D. longicaudata* Muthumbi & Vincx, 1998; *D. quadripapillata* Muthumbi & Vincx, 1998; *D. parasimplex* Dashchenko, 2002; *D. parva* Vermeeren, Vanreusel & Vanhove, 2004; *D. polaris* Vermeeren, Vanreusel & Vanhove, 2004; *D. polarsternis*

Vermeeren, Vanreusel & Vanhove, 2004; *D. southernis* Vermeeren, Vanreusel & Vanhove, 2004 and *D. weddellensis* Vermeeren, Vanreusel & Vanhove, 2004). Huang & Zhang (2010) described *D. major*, *D. multisetosa* and *D. sinica* and reviewed *Dichromadora*, considering 32 valid species. *D. abyssalis* was described by Bussau (1993) in his PhD thesis and despite its description being of good quality it should be considered as *nomen nudum* following the International Code of Zoological Nomenclature. The last addition to *Dichromadora* was the description of *D. rigida* by Thanh *et al*. (2016). Today we recognize 32 valid species.

Diagnosis (modified from Huang & Zhang 2010 and Tchesunov 2014): Cuticle with homogeneous ornamentation and a pronounced lateral differentiation of two longitudinal rows of enlarged dots. Six outer labial papillae and four cephalic setae in separate circles. Amphideal fovea transverse slit-like and loop shaped. Buccal cavity with a triangular hollow dorsal tooth or a large dorsal tooth and two additional ventrosublateral ones; denticles can be present. Peribuccal pharyngeal tissue not swollen anteriorly or with an asymmetrical dorsal swelling; a distinct posterior pharyngeal bulb. Precloacal supplements present or absent. Marine.

Number of valid species: 32

Genus *Dichromadora* Kreis, 1929

VALID SPECIES

1. *Dichromadora abnormis* Gerlach, 1953 (Italy, San Rossore and Tirrenia beaches)
2. *Dichromadora amphidiscoides* Kito, 1981 (Japan, Oshoro Bay)
3. *Dichromadora antarctica* (Cobb, 1914) Timm, 1978 (Cape Royd, Antarctica)
Syn. *Spilophora antarctica* Cobb, 1914
4. *Dichromadora apapillata* Timm, 1961 (Indian Ocean, Bay of Bengal)
5. *Dichromadora arcospiculum* Timm, 1961 (Indian Ocean, Bay of Bengal)
6. *Dichromadora cephalata* (Steiner, 1916) Kreis, 1929 (Arctic Ocean, Barents Sea)
Syn. *Chromadora cephalata* Steiner, 1916
Chromadora cricophana Filipjev, 1922
7. *Dichromadora cucullata* Lorenzen, 1973 (North Sea, Baltic Sea, Helgoland)
8. *Dichromadora dissipata* Wieser, 1954 (Chile, Seno de Reloncaví)
9. *Dichromadora gathuai* Muthumbi & Vincx, 1998 (Indian Ocean, Kenyan coast)
10. *Dichromadora geophila* (de Man, 1876) Kreis, 1929 (North Sea, Netherlands)
Syn. *Chromadora canadensis* (Cobb, 1914) Micoletzky, 1922
Chromadora geophila (de Man, 1876) Micoletzky, 1922
Hypodontolaimus geophilus (de Man, 1876) Wieser, 1954
Spiliphera geophila de Man, 1876
Spiliphera canadensis Cobb, 1914
Spiliphera spectabilis Allgén, 1929
11. *Dichromadora gracilis* (Kreis, 1929) Wieser, 1954
Syn. *Spilophorella gracilis* Kreis, 1929
12. *Dichromadora hyalocheile* De Coninck & Schuurmans Stekhoven, 1933 (Belgium, Oostende)
13. *Dichromadora islandica* Kreis, 1963 (Iceland, Eyjafjörður)
14. *Dichromadora loiseae* Muthumbi & Vincx, 1998 (Indian Ocean, Kenyan coast)
15. *Dichromadora longicaudata* Muthumbi & Vincx, 1998 (Indian Ocean, Kenyan coast)
16. *Dichromadora major* Huang & Zhang, 2010 (China, Yellow Sea, intertidal sandy sediment)
17. *Dichromadora microdonta* Kreis, 1929 (France, English Channel)
18. *Dichromadora multisetosa* Huang & Zhang, 2010 (China, Yellow Sea)
19. *Dichromadora parasimplex* Dashchenko, 2002 (New Guinea, Astrolabe Bay)
20. *Dichromadora parva* Vermeeren, Vanreusel & Vanhove, 2004 (Antarctic Sea, Halley Bay)
21. *Dichromadora polaris* Vermeeren, Vanreusel & Vanhove, 2004 (Antarctic Sea, Halley Bay)
22. *Dichromadora polarsternis* Vermeeren, Vanreusel & Vanhove, 2004 (Antarctic Sea, Halley Bay)
23. *Dichromadora punctata* Schuurmans Stekhoven, 1950 (Mediterranean, Villefranche Bay)
24. *Dichromadora quadripapillata* Muthumbi & Vincx, 1998 (Indian Ocean, Kenyan coast)
25. *Dichromadora rigida* Thanh, Tu & Gagarin, 2016 (Vietnam)
26. *Dichromadora scandula* Lorenzen, 1966 (North Sea)

27. *Dichromadora simplex* Timm, 1961 (Indian Ocean, Bay of Bengal)
28. *Dichromadora sinica* Huang & Zhang, 2010 (China, Yellow Sea)
29. *Dichromadora southernis* Vermeeren, Vanreusel & Vanhove, 2004 (Antarctic Sea, Halley Bay)
30. *Dichromadora strandi* Allgén, 1940 (Norway, Knivskjaerodden)
31. *Dichromadora tobaensis* Schneider, 1937 (Sumatra)
32. *Dichromadora weddellensis* Vermeeren, Vanreusel & Vanhove, 2004 (Antarctic Sea, Halley Bay)
NOMEN NUDUM
1. *Dichromadora abyssalis* Bussau, 1993 (SE Pacific, Peru Basin)

Genus *Hypodontolaimus* de Man, 1886

The genus *Hypodontolaimus* was erected by de Man (1886) to accommodate *Spilophora inaequalis* (Bastian, 1865). Wieser (1954) proposed the synonimization of *Iotadorus* Cobb, 1920 and *Ptycholaimellus* with *Hypodontolaimus*, and divided the genus in two groups according to the length of cephalic and somatic setae and the type of the inner labial papillae. In the same study two new species were described (*H. steineri* and *H. dimorphus*), and the species *H. minor* and *H. norvegicus* were transferred to *Chromadorita*. Wieser (1954) also presented a key with 16 valid species. *H. heymonsi* (Steiner, 1921) was subsequently considered *species inquirendum* since males were not described (Wieser & Hopper, 1967). Later, 23 species were considered valid by Platt & Warwick (1988), including *H. heymonsi*, which was already considered as *species inquirendum* by Wieser & Hopper (1967). After Platt & Warwick (1988), five species were described in the genus (*H. kiseloevi* Baranova & Dashchenko, 1992; *H. plurisetus* Baranova & Dashchenko, 1992; *H. marleenae* Muthumbi & Vincx, 1998; *H. antarcticus* Andrássy & Gibson, 2007 and *H. ventrapophyses* Huang & Gao, 2016). *H. sivertseni* is considered as *species inquirendum* due to the lack of detailed description of the cuticle (there is no mention to the longitudinal rows of larger dots which is diagnostic character of *Hypodontolaimus*). We recognize 26 valid species within this genus. The recent work of Huang & Gao (2016) presents an identification key for all valid species, except *H. golikovi* Platonova, 1971; *H. kiseloevi*; *H. plurisetus* and *H. punctulatus* (Cobb, 1920). The authors did not consider *H. punctulatus* a valid species stating that this species is known only from females but this is a mistake as there are males in the original description made by Cobb (1920). The other three species were left out without any explanation.

Hypodontolaimus is differentiated from *Dichromadora* and *Ptycholaimellus* by having a large muscular buccal bulb and a sclerotized dorsal apophysis at the level of the dorsal tooth (Inglis 1969 and Muthumbi & Vincx, 1998a). Although the differences among these genera are meagre, many authors still recognize them as valid genera (Decraemer & Smol 2006; Andrássy & Gibson 2007 and Tchesunov 2014).

Diagnosis (modified from Andrássy & Gibson 2007 and Tchesunov 2014): Cuticle with homogeneous punctations, interrupted only on the body sides with two longitudinal rows of larger dots. Six small outer labial setae or papillae and four cephalic setae in separate circles. Inner labial sensilla may be conspicuous in some species (*H. galapagensis* Blome, 1985 and *H. setosoides* Blome, 1982). Somatic setae may be present. Amphideal fovea transverse slit-like. Buccal cavity with a dorsal apophyses and a very prominent S-shaped dorsal tooth; in front of the stoma there is a heavily cuticularized dorsal thickening. Small ventrosublateral teeth may be present. Peribuccal pharyngeal tissue swollen, symmetrically or asymmetrically, in the latter case surrounding the dorsal tooth; the terminal bulb single. The excretory cell conspicuous and large. Males usually with precloacal supplements. Mostly marine genus, but four species were also recovered in brackish waters [*H. angelae* Inglis, 1961*, H. antarcticus, H. balticus* (Schneider, 1906) and *H. inaequalis*].

Number of valid species: 26
Genus *Hypodontolaimus* de Man, 1886
Syn. *Iotadorus* Cobb, 1920
VALID SPECIES
1. *Hypodontolaimus abyssalis* Allgén, 1933 (Sweden, Röberg)
2. *Hypodontolaimus angelae* Inglis, 1961 (South Africa, Kleinemonde River)
3. *Hypodontolaimus antarcticus* Andrássy & Gibson, 2007 (East Antarctica, Vestfold Hills)

4. *Hypodontolaimus balticus* (Schneider, 1906) Filipjev, 1918 (Baltic Sea)
Syn. *Chromadora baltica* Schneider, 1906
Hypodontolaimus buetschlii Filipjev, 1918
Hypodontolaimus striatus Ditlevsen, 1918
Spilophorella paradoxa sensu Coles, 1960
5. *Hypodontolaimus colesi* Inglis, 1962 (France, Banyuls-sur-mer)
6. *Hypodontolaimus dimorphus* Wieser, 1954 (Chile, Tenglo Island)
7. *Hypodontolaimus galapagensis* Blome, 1985 (Ecuador, Archipelago of Galapagos)
8. *Hypodontolaimus golikovi* Platonova, 1971 (Sea of Japan, Bay of Possjet)
9. *Hypodontolaimus inaequalis* (Bastian, 1865) de Man, 1886 (Norway, Oslofjord)
Syn. *Spiliphera inaequalis* Bastian, 1865
10. *Hypodontolaimus interruptus* Wieser & Hopper, 1967 (USA, Virginia Key)
11. *Hypodontolaimus kiseloevi* Baranova & Dashchenko, 1992 (Pacific Ocean, Coral Sea)
12. *Hypodontolaimus longiseta* (Allgén, 1933) Wieser, 1954 (Norway, port of Ilen)
Syn. *Dichromadora longiseta* Allgén, 1933
13. *Hypodontolaimus marleenae* Muthumbi & Vincx, 1998 (Indian Ocean, Kenyan coast)
14. *Hypodontolaimus mediterraneus* (Brunetti, 1949) (Italy, Marina di Pisa)
15. *Hypodontolaimus obtusicaudatus* Allgén, 1947 (USA, San Pedro harbour)
16. *Hypodontolaimus pilosus* (Hopper & Meyers, 1967) (USA, Biscayne Bay)
17. *Hypodontolaimus plurisetus* Baranova & Dashchenko, 1992 (Pacific Ocean)
18. *Hypodontolaimus pumilio* Gerlach, 1956 (Brazil, Pernambuco)
19. *Hypodontolaimus punctulatus* (Cobb, 1920) Filipjev, 1934 (Pacific coast of Costa Rica, Punta Arenas)
Syn. *Iotadorus punctulatus* Cobb, 1920
20. *Hypodontolaimus reversus* Hopper, 1968 (Canada, Prince Edward Island)
21. *Hypodontolaimus schuurmansstekhoveni* Gerlach, 1951 (North Sea, Germany)
22. *Hypodontolaimus setosoides* Blome, 1982 (Germany, Sylt)
23. *Hypodontolaimus setosus* (Bütschli, 1874) Wieser, 1954 (Kiel Bay, Germany)
Syn. *Spiliphera setosa* Bütschli, 1874
24. *Hypodontolaimus solivagus* Hopper, 1963 (USA, Gulf of Mexico)
25. *Hypodontolaimus steineri* Wieser, 1954 (Chile, Tenglo Island)
26. *Hypodontolaimus ventrapophyses* Huang & Gao, 2016 (Dongshan Island, East China Sea)
SPECIES INQUIRENDA
1. *Hypodontolaimus heymonsi* (Steiner, 1921) Filipjev, 1930 (Canary Islands)
Syn. *Spiliphera heymonsi* Steiner, 1921
2. *Hypodontolaimus sivertseni* Allgén, 1951 (Norway, Tautra island)

Genus *Innocuonema* Inglis, 1969

The genus *Innocuonema* was erected by Inglis (1969) to accommodate *Graphonema amokuroides*, *Graphonema clivosa*, *Graphonema flaccida* and *Graphonema tentabunda*, since they share a dorsal onchium controlled by a massive development of the dorsal pharyngeal musculature, a posterior pharyngeal bulb and a small gubernaculum. The species *I. norwegicum* (Allgén, 1932), *I. paraheterophyum* (Allgén, 1932), *I. pusillum* (Allgén, 1947), *I. spectabile* (Allgén, 1932) and *I. suillum* (Allgén, 1947) were considered as *species dubia*. *Graphonema amorukoides* was renamed as *Innocuonema chilense* Inglis, 1969. Later, *I. asymmetricum* Blome, 1985 was described and *I. chitwoodi* (Wieser, 1954) was considered synonym of *I. tentabunda* (Blome 1985). Although the uniqueness of the cuticle and buccal cavity of *Innocuonema* has been recognized, all the remaining diagnostic characters are shared with *Dichromadora* and *Chromadorita* (Table 3) (Decraemer & Smol 2006 and Tchesunov 2014).

Diagnosis (modified from Tchesunov 2014): Cuticle punctuated and heterogeneous, with no lateral differentiation. Anterior sensilla in three separate circles with four terminal cephalic setae. First circle (inner labial setae) conspicuous in two species [*I. clivosum* (Wieser, 1959) and *I. flaccidum* (Wieser, 1959)]. Somatic setae

present. Amphideal fovea transverse, slit-like. Buccal cavity with a large dorsal tooth. Dorsal apophyses and a tiny ventrosublateral tooth may be present. Peribuccal pharyngeal tissue slight swelling in dorsal. Pharynx with a single posterior bulb. Precloacal supplements absent. Marine.

Number of valid species: 5
Genus *Innocuonema* Inglis, 1969
VALID SPECIES
1. *Innocuonema asymmetricum* Blome, 1985 (Galapagos, Ecuador)
2. *Innocuonema chilense* Inglis, 1969 (Campbell Island, New Zealand)
Syn. *Graphonema amokuroides* sensu Wieser, 1954
Spiliphera amokuroides Allgén, 1927
3. *Innocuonema clivosum* (Wieser, 1959) Inglis, 1969 (Richmond Beach, USA, 0.15 m)
Syn. *Graphonema clivosum* Wieser, 1959
4. *Innocuonema flaccidum* (Wieser, 1959) Inglis, 1969 (Richmond Beach, USA, 0.75-1.65 m)
Syn. *Graphonema flaccidum* Wieser, 1959
5. *Innocuonema tentabunda* (de Man, 1890) Inglis, 1969 (Chorao Island, India, mangrove)
Syn. *Chromadorita chitwoodi* Wieser, 1954
Chromadorita crassa Timm, 1952
Innocuonema chitwoodi (Wieser, 1954) Inglis, 1969
Spiliphera tentabunda de Man, 1890
SPECIES INCERTA SEDIS
1. *Innocuonema norwegicum* (Allgén, 1932) Inglis, 1969 (Herdla Island, Norway)
Syn. *Spiliphera norwegica* Allgén, 1932
2. *Innocuonema paraheterophyum* (Allgén, 1932) Inglis, 1969 (Campbell Island, New Zealand)
Syn. *Chromadora paraheterophya* Allgén, 1932
3. *Innocuonema pusillum* (Allgén, 1947) Inglis, 1969 (Bay of Panama, Panama)
Syn. *Spiliphera pusilla* Allgén, 1947
4. *Innocuonema spectabile* (Allgén, 1932) Inglis, 1969 (Campbell Island, New Zealand)
Syn. *Chromadora spectabilis* Allgén, 1932
5. *Innocuonema suillum* (Allgén, 1947) Inglis, 1969 (Bay of Panama, Panama)
Syn. *Chromadora suilla* Allgén, 1947

Genus *Karkinochromadora* Blome, 1982

The genus *Karkinochromadora* was erected by Blome (1982) to accommodate *Chromadora lorenzeni*. It can be distinguished from other genera of Chromadoridae by a peculiar combination of characters like the unusual arrangement of two consecutive teeth and the heterogeneously ornamented cuticle with lateral differentiation.

Diagnosis (modified from Blome 1982 and Tchesunov 2014): Cuticle with a heterogeneous ornamentation, with lateral differentiation of two and four longitudinal rows of enlarged dots. Six outer labial papillae and four cephalic setae in separate circles. Presence of somatic setae. Amphideal fovea rounded loop shaped. Buccal cavity with an unusual arrangement of the two consecutive dorsal teeth (a small anterior and a larger posterior) and two small ventrosublateral teeth. Peribuccal pharyngeal tissue swollen dorsally. Presence of a pear-shaped pharyngeal bulb. Weak precloacal supplements present with grouped distribution in males. Marine.

Number of valid species: 1
Genus *Karkinochromadora* Blome, 1982
VALID SPECIES
1. *Karkinochromadora lorenzeni* (Jensen, 1980) Blome, 1982 (Denmark Sound, Arctic)
Syn. *Chromadora lorenzeni* Jensen, 1980
Genus *Megodontolaimus* Timm, 1969

The genus *Megodontolaimus* was established by Timm (1969) to accommodate *M. coxbazari* and *M. sonadiae*

from the Bay of Bengal. It was considered as closely related to *Hypodontolaimus* differing from it in the buccal cavity: with a large ventral tooth and two-pronged dorsal teeth and the possession of a crescent apophysis on the dorsal side of the anterior part of the pharynx.

Diagnosis (modified from Tchesunov 2014 and Datta *et al.* 2017): Cuticle with larger dots toward the extremities of the body or only anteriorly, and with lateral differentiation of larger dots at the borders of the lateral field; two or six alae are present, showing fine cross bars. Anterior sensilla in *M. coxbazari* in two circles (6+10): one circle with six short setiform inner labial setae and one circle with six shorter outer labial setae and four longer cephalic setae. In *M. sonadiae* anterior sensilla in three circles. Presence of somatic setae. Amphideal fovea transverse slit-like shaped. Buccal cavity with crescent thickening along the buccal wall, with two-pronged dorsal tooth and a large ventral tooth with hooked tip. Peribuccal pharyngeal tissue asymmetrically swollen and with an expanded apophysis on the dorsal side; bulb double. Males lack precloacal supplements. Gubernaculum with lateral sleeve. Marine.

Number of valid species: 2
Genus *Megodontolaimus* Timm, 1969
VALID SPECIES
1. *Megodontolaimus coxbazari* Timm, 1969 (Cox's Bazar, East Pakistan)
2. *Megodontolaimus sonadiae* Timm, 1969 (Cox's Bazar, East Pakistan)

Genus *Neochromadora* Micoletzky, 1924

The genus *Neochromadora* was established by Micoletzky (1924) to accommodate *Chromadora poecilosoma* (de Man, 1893) (designed as the type species), *Chromadora craspedota* (Steiner, 1916) and *Chromadora poecilosomoides* (Filipjev, 1918). Micoletzky (1924) considered *Neochromadora* as close to *Euchromadora*, but distinct in the complex structure of the cuticle. After Micoletzky (1924), 7 species were added to *Neochromadora* [*N. izhorica* (Filipjev, 1929); *N. trichophora* (Steiner, 1921); *N. tecta* Gerlach, 1951; *N. attenuate*; *N. complexa* Gerlach, 1953; *N. amembranata* Wieser, 1954 and *N. brevisetosa* Wieser, 1954]. Wieser (1954) proposed two subgenera, *Trichodorina* and *Neochromadora*, based on the morphology of dorsal tooth, pharyngeal bulb and measurements of cervical and somatic setae. He also transferred *Spiliphera aberrans* Cobb, 1930, *Chromadora craspedota* Steiner, 1916 and *Chromadora sabulicola*, and described two new species of *Neochromadora* (*N. calathifera* and *N. lateralis*), adding up to 15 species in his key. *N. attenuata* was later renamed as *Prochromadorella attenuata*. After Wieser (1954), 11 new valid species were described to *Neochromadora* (*N. bonita* Gerlach, 1956; *N. coudenhovei* Wieser, 1956; *N. notocraspedota* Allgén, 1958; *N. appiana* Wieser, 1959; *N. pugilator* Wieser, 1959; *N. alatocorpa* Hopper, 1961; *N. nitida* Timm, 1961; *N. munita* Lorenzen, 1972; *N. paratecta* Blome, 1974; *N. paramunita* Boucher, 1976 and *N. angelica* Riemann, 1976). Timm (1978) transferred *Spilophera edentata* to *Neochromadora* and suggested *Neochromadora izhorica* as synonym of *N. (Neochromadora) edentata*. After Timm (1978), six other new species were described in the genus (*N. bilineata* Kito, 1978; *N. oshoroana* Kito, 1981; *N. orientalis* Lemzina, 1982; *N. lineata* Pastor de Ward, 1985; *N. papillosa* Pastor de Ward, 1985 and *N. nicolae* Vincx, 1986). *Neochromadora trilineata* was described by Schneider (1943) but later was considered a synonym of *Punctodora ohridensis* by Gerlach & Meyl (1957). However, subsequently, Hopper (1963) removed the synonym of *Neochromadora trilineata* to *P. ohridiensis* and considered the former species as *incertae sedis* since there was no material available for further investigation. The species *N. paramunita* was synonymized with *N. munita* by Vincx (1986). We recognize 31 species as valid.

Diagnosis (modified from Tchesunov 2014): Cuticle ornamentation heterogeneous and complex, with lateral differentiation visible as two or three longitudinal rows of large dots. Six small outer labial setae or papillae and four cephalic setae in separate circles. Inner labial sensilla may be conspicuous in one species (*N. munita*). Presence of somatic setae in some species. Amphideal fovea transverse slit-like and loop shaped. Buccal cavity with a dorsal tooth and two ventrosublateral teeth, in some species the dorsal one being larger than the others. Denticles can be present. Pharynx anteriorly not swollen or swollen next to the dorsal tooth. Pharynx with a single well-developed posterior bulb. Male usually with numerous precloacal supplements. It is mainly a marine genus, but one species was recovered in freshwater (*N. orientalis*) and three were recovered in brackish water (*N. bonita*, *N. complexa* and *N. izhorica*) habitats.

Number of valid species: 31

Genus *Neochromadora* Micoletzky, 1924

VALID SPECIES

1. *Neochromadora aberrans* (Cobb, 1930) Wieser, 1954 (Antarctic, Commonwealth Bay)

Syn. *Spiliphera aberrans* Cobb, 1930

2. *Neochromadora alatocorpa* Hopper, 1961 (USA, Alabama)

3. *Neochromadora amembranata* Wieser, 1954 (Mediterranean Sea)

4. *Neochromadora angelica* Riemann, 1976 (Helgoland (Germany)

5. *Neochromadora appiana* Wieser, 1959 (USA, Washington)

6. *Neochromadora bilineata* Kito, 1978 (Japan, Hokkaido)

7. *Neochromadora bonita* Gerlach, 1956 (Brazil, Cananeia)

8. *Neochromadora brevisetosa* Wieser, 1954 (Mediterranean Sea)

9. *Neochromadora calathifera* Wieser, 1954 (Chile, Seno Reloncavi)

10. *Neochromadora complexa* Gerlach, 1953 (Chile, Seno Ultima Esperanza)

11. *Neochromadora coudenhovei* Wieser, 1956 (Greece, Piraeus)

12. *Neochromadora craspedota* (Steiner, 1916) Wieser, 1954 (Arctic Ocean, Barents Sea)

Syn. *Chromadora craspedota* Steiner, 1916

13. *Neochromadora edentata* (Cobb, 1914) Timm, 1978 (Antarctic, Cape Royds)

Syn. *Nygmatonchus edentata* (Cobb, 1914) Wieser, 1954

Spiliphera edentata Cobb, 1914

14. *Neochromadora izhorica* (Filipjev, 1929) Schuurmans Stekhoven, 1935 (Baltic Sea, Neva Bay)

Syn. *Chromadorella izhorica* Filipjev, 1929

15. *Neochromadora lateralis* Wieser, 1954 (Seno Reloncavi, Chile)

16. *Neochromadora lineata* Pastor de Ward, 1985 (Argentina, Deseado river)

17. *Neochromadora munita* Lorenzen, 1972 (North Sea)

Syn. *Neochromadora paramunita* Boucher, 1976

18. *Neochromadora nicolae* Vincx, 1986 (North Sea)

19. *Neochromadora nitida* Timm, 1961 (Indian Ocean, Bengal bay)

20. *Neochromadora notocraspedota* Allgén, 1958 (Uruguay)

21. *Neochromadora orientalis* Lemzina, 1982 (Kyrgyzstan, Lake Issyk-Kul)

22. *Neochromadora oshoroana* Kito, 1981 (Japan, Oshoro Bay)

23. *Neochromadora papillosa* Pastor de Ward, 1985 (Argentina, Deseado river)

24. *Neochromadora paratecta* Blome, 1974 (North Sea)

25. *Neochromadora poecilosoma* (de Man, 1893) Micoletzky, 1924 (North Sea, English Channel)

Syn. *Chromadora poecilosoma* de Man, 1893

26. *Neochromadora poecilosomoides* (Filipjev, 1918) Micoletzky, 1924 (Black Sea)

Syn. *Chromadora poecilosomoides* Filipjev, 1918

27. *Neochromadora pugilator* Wieser, 1959 (USA, Washington)

28. *Neochromadora sabulicola* (Filipjev, 1918) Wieser, 1954 (Kruglaya Bay and Georgievskii Monastery Bay)

Syn. *Chromadora sabulicola* Filipjev, 1918

29. *Neochromadora tecta* Gerlach, 1951 (Germany, Amrum island)

30. *Neochromadora torquata* Wieser, 1954 (Seno Reloncavi, Chile)

31. *Neochromadora trichophora* (Steiner, 1921) Gerlach, 1951 (Canary Islands)

Syn. *Spiliphera trichophora* Steiner, 1921

Neochromadora longisetosa Schuurmans-Stekhoven, 1935

SPECIES INCERTAE SEDIS

1. *Neochromadora trilineata* Schneider, 1943

Genus *Panduripharynx* Timm, 1961

The genus *Panduripharynx* was established by Timm (1961) to accommodate the species *P. ornata* from the Bay of Bengal. It is distinguished from other genera of the sub-family Hypodontolaiminae on the basis of the structure of the stoma and pharynx, and the cuticular ornamentation. Belogurov *et al.* (1985) described *P. pacifica* but

Dashchenko (1989) transferred *P. bidentatus* and *P. unidentatus* from *Spilophorella* and synonymized *P. pacificus* with *P. unidentatus*.

Diagnosis (modified from Tchesunov 2014): Cuticle heterogeneous and complex with lateral differentiation of larger dots bordering the lateral field. Anterior sensilla in three separate circles. Amphideal fovea transverse slit-like shaped. Buccal cavity broad, with large dorsal tooth with small apophysis, two smaller ventrosublateral teeth, and solid denticles; well-cuticularized walls. Peribuccal pharyngeal tissue swollen dorsally; bulb double, massive, panduriform, with heavy internal sclerotizations. No precloacal supplements in males. Marine.

Number of valid species: 3

Genus *Panduripharynx* Timm, 1961

VALID SPECIES

1. *Panduripharynx bidentatus* (Platonova, 1971) Dashchenko, 1989 (West Pacific, Sea of Japan, Bay of Posjet)

Syn. *Spilophorella bidentata* Platonova, 1971

2. *Panduripharynx ornata* Timm, 1961 (Indian Ocean, Bay of Bengal)

3. *Panduripharynx unidentatus* (Platonova, 1971) Dashchenko, 1989 (West Pacific, Sea of Japan, Bay of Posjet)

Syn. *Panduripharynx pacifica* Belogurov, Dashchenko & Fadeeva, 1985 (West Pacific, Sea of Japan)

Spilophorella unidentata Platonova, 1971

Genus *Parachromadorita* Blome, 1974

The genus *Parachromadorita* was erected by Blome (1974) to accommodate *Dichromadora stygia*. Before that, Wieser (1954) transferred this species to *Denticulella* considering it as closely related to *Denticulella pellucida*. *Denticulella stygia* was then transferred to *Parachromadorita* by Blome (1974) based on the loop-shaped amphid. *Parachromadorita* is considered close to *Chromadora*, *Chromadorita* and *Dichromadora*, but it is distinguished by the morphology of the buccal cavity, the type of lateral differentiation of the cuticle and the shape of the amphideal fovea.

Diagnosis (modified from Tchesunov 2014): Cuticle homogenous with lateral differentiation of irregular larger dots not arranged into longitudinal rows. Anterior sensilla in three separate circles. Amphideal fovea loop shaped. Buccal cavity with a large dorsal tooth, two smaller ventrosublateral teeth and a field of denticles. Peribuccal pharyngeal tissue swollen dorsally; pharynx ending in a single and pear-shaped bulb. Males with precloacal supplements. Marine.

Number of valid species: 1

Genus *Parachromadorita* Blome, 1974

VALID SPECIES

1. *Parachromadorita stygia* (Gerlach, 1952) Blome, 1974 (North Sea, Kiel Bay)

Syn. *Dichromadora stygia* Gerlach, 1952

Denticulella stygia (Gerlach, 1952) Wieser, 195

Genus *Ptycholaimellus* Cobb, 1920

The genus *Ptycholaimellus* was established by Cobb (1920) when the type species *P. carinatus* was collected in Indonesia. Gerlach (1955) proposed *Ptycholaimellus* as subgenus of *Hypodontolaimus* once he considered *Hypodontolaimus ponticus* Filipjev, 1922 and *Ptycholaimellus carinatus* closely related. Wieser & Hopper (1967) transferred *H. macrodentatus* Timm, 1961 and *H. pandispiculatus* Hopper, 1961 to this group. Later, *Ptycholaimellus* was considered as a valid genus (Inglis 1969, Decraemer & Coomans 1978). Jensen & Nehring (1992) transferred *Chromadorissa inaequibulba* to *Ptycholaimellus*, renaming to *P. inaequibulbus*, and regarded 14 species as belonging to *Ptycholaimellus*. More recently, other eight species have been described (*P. jenseni* Muthumbi & Vincx, 1998; *P. penninae* Muthumbi & Vincx, 1998; *P. sindhicus* Turpeenniemi, Nasira & Maqbool, 2001; *P. ocellatus* Huang & Wang, 2011; *P. areniculus* Nguyen Vu Thanh, Nguyen Dinh Tu, Gagarin, Tchesunov &

Nguyen Thanh Hien, 2012; *P. brevisetosus* Nguyen Vu Thanh, Nguyen Dinh Tu, Gagarin, Tchesunov & Nguyen Thanh Hien, 2012; *P. longibulbus* Wang, An & Huang, 2015 and *P. pirus* Huang & Gao, 2016). The recent work of Huang & Gao (2016) presents an identification key for all valid species.

Diagnosis (modified from Jensen & Nehring 1992 and Muthumbi & Vincx 1998a): Cuticle with homogeneous and heterogeneous ornamentation of two longitudinal rows of larger dots. Anterior sensilla in three circles (6+6+4) or in two circles. Only the cephalic setae are conspicuous in some species (*P. hibernus* Eskin & Hopper, 1985; *P. ocellatus*; *P. penninae* and *P. ponticus*). Cephalic setae are inserted on protrusible vestibulum region, distinguinshing this genus from all other Hypondolaiminae genera. Presence of somatic setae in some species. Amphideal fovea transverse slit-like shaped. Buccal cavity with a large S-shaped dorsal tooth. Small ventrosublateral denticles may be present. Peribuccal pharyngeal tissue swollen dorsally; presence of a double pharyngeal bulb. Males without supplements. It is mainly a marine genus, but two species were recovered in brackish water (*P. pandispiculatus* and *P. ponticus*) habitats.

Number of valid species: 22

Genus *Ptycholaimellus* Cobb, 1920

VALID SPECIES

1. *Ptycholaimellus adocius* Dashchenko & Belogurov, 1984 (Sea of Japan, Posjet Bay)

2. *Ptycholaimellus areniculus* Nguyen Vu Thanh, Nguyen Dinh Tu, Gagarin, Tchesunov & Nguyen Thanh Hien, 2012 (North Vietnam Sea)

3. *Ptycholaimellus boucheri* Jensen & Nehring, 1992 (Mediterranean, North Sea)

4. *Pycholaimellus brevisetosus* Nguyen Vu Thanh, Nguyen Dinh Tu, Gagarin, Tchesunov & Nguyen Thanh Hien, 2012 (North Vietnam Sea)

5. *Ptycholaimellus carinatus* Cobb, 1920 (East Indies, Larat)

6. *Ptycholaimellus hibernus* Eskin & Hopper, 1985 (USA, North Inlet Estuary)

7. *Ptycholaimellus inaequibulbus* (Aminova & Galtsova, 1978) Jensen & Nehring, 1992 (White Sea)

Syn. *Chromadorissa inaequibulba* Aminova & Galtsova, 1978

8. *Ptycholaimellus jacobi* Jensen & Nehring, 1992 (Denmark, Hirsholmene, Ellekilde Hage)

9. *Ptycholaimellus jenseni* Muthumbi & Vincx, 1998 (North Sea)

10. *Ptycholaimellus lizardiensis* Decraemer & Coomans, 1978 (Australia, Lizard Island)

11. *Ptycholaimellus longibulbus* Wang, An & Huang, 2015 (Ximen Island, East China Sea)

12. *Ptycholaimellus macrodentatus* (Timm, 1961) Wieser & Hopper, 1967 (Indian Ocean, Bengal Bay)

Syn. *Hypodontolaimus macrodentatus* Timm, 1961

13. *Ptycholaimellus monodon* (Schuurmans-Stekhoven, 1942) Hopper, 1969 (Mediterranean)

Syn. *Hypodontolaimus monodon* Schuurmans-Stekhoven, 1942

14. *Ptycholaimellus ocellatus* Huang & Wang, 2011 (Yellow Sea, China)

15. *Ptycholaimellus pandispiculatus* (Hopper, 1961) Wieser & Hopper, 1967 (USA, Gulf of Mexico)

Syn. *Hypodontolaimus pandispiculatus* Hopper, 1961

16. *Ptycholaimellus penninae* Muthumbi & Vincx, 1998 (Indian Ocean, Kenyan coast)

17. *Ptycholaimellus pirus* Huang & Gao, 2016 (Dongshan Island, East China Sea)

18. *Ptycholaimellus ponticus* (Filipjev, 1922) Gerlach, 1955 (Black Sea, Kristineberg Bay)

Syn. *Hypodontolaimus ponticus* Filipjev, 1922

Spilophorella dentata Schneider, 1926

Spilophorella baltica Schulz, 1932

Hypodontolaimus zosterae Allgén, 1929

19. *Ptycholaimellus setosus* Pastor de Ward, 1984 (Argentina, Deseado estuary)

20. *Ptycholaimellus sindhicus* Turpeenniemi, Nasira & Maqbool, 2001 (Arabian Sea, Pakistan)

21. *Ptycholaimellus slacksmithi* (Inglis, 1969) (Australia, Shark Bay and Cowaramup Bay)

Syn. *Hypodontolaimus (Ptycholaimellus) slacksmithi* Inglis, 1969

22. *Ptycholaimellus vincxae* Jensen & Nehring, 1992 (North Sea)

Genus *Spilophorella* Filipjev, 1918

The genus *Spilophorella* was erected by Filipjev (1918) to accommodate *Spilophora paradoxa* de Man, 1888 (erected as type species), *Spilophora ceylonensis* Cobb, 1890 and the new species *S. euxina* Filipjev, 1918. Later, 12 species were described (*S. tasmaniensis* Allgén, 1927; *S. campbelli* Allgén, 1928; *S. papillata* Kreis, 1929; *S. candida* Gerlach, 1951; S. *paradoxoides* Timm, 1952; *S. meyerabichi* Gerlach, 1955; *S. tollenifera* Wieser, 1955; *S. aberrans* Timm, 1961; *S. furcata* Murphy, 1963; *S. bidentata* Platonova, 1971; *S. unidentata* Platonova, 1971 and *S. intermedia* Gagarin & Lemzina, 1982). *S. simplex* is cited by Wieser (1959) but this species was never described, consequently it is considered *nomen nudum*. More recently *S. bidentata* and *S. unidentata* were transferred to *Panduripharynx* by Dashchenko (1989).

Diagnosis (modified from Tchesunov 2014): Cuticle with complex heterogeneous punctated ornamentation and lateral differentiation of larger dots arranged in longitudinal rows. Six small outer labial setae or papillae and four cephalic setae in separate circles. Presence of somatic setae in some species. Amphideal fovea transverse slit-like shaped. Buccal cavity deep with a long hollow dorsal tooth and, in some species, a smaller ventral tooth is present (e.g. *S. aberrans* and *S. euxina*). Peribuccal pharyngeal tissue swollen slightly and nearly symmetrical. Elongated posterior double bulb present. Males without supplements. Tail ending with a very conspicuous pointed caudal tube (spinneret). It is a largely marine genus, but two species (*S. intermedia* and *S. meyerabichi*) were recovered in brackish water habitats.

Number of valid species: 13
Genus *Spilophorella* Filipjev, 1918
VALID SPECIES
1. *Spilophorella aberrans* Timm, 1961 (Indian Ocean, Bengal Bay)
2. *Spilophorella campbelli* Allgén, 1928 (New Zealand, Campbell Island)
3. *Spilophorella candida* Gerlach, 1951 (Germany, Amrum island)
4. *Spilophorella ceylonensis* (Cobb, 1890) Filipjev, 1918 (Indian Ocean, Arabian Sea and Ceylon)
Syn. *Spiliphera ceylonensis* Cobb, 1890
5. *Spilophorella euxina* Filipjev, 1918 (Black Sea)
6. *Spilophorella furcata* Murphy, 1963 (USA, Depoe Bay)
7. *Spilophorella intermedia* Gagarin & Lemzina, 1982 (Kyrgyzstan, Lake Issyk-Kul)
8. *Spilophorella meyerabichi* Gerlach, 1955 (San Salvador)
9. *Spilophorella papillata* Kreis, 1929 (English Channel)
10. *Spilophorella paradoxa* (de Man, 1888) Filipjev, 1918 (North Sea)
Syn. *Spiliphera paradoxa* de Man, 1888
Spilophorella tenuicaudata de Man, 1922
Spilophorella mediterranea Micoletzky, 1924
11. *Spilophorella paradoxoides* Timm, 1952 (USA, Chesapeak bay)
12. *Spilophorella tasmaniensis* Allgén, 1927 (Australia, Tasmania)
13. *Spilophorella tollenifera* Wieser, 1955 (Japan, Shirahama-cho)
NOMEN NUDUM
1. *Spilophorella simplex* Wieser, 1959 (Chesapeake Bay)

Polytomous Identification Key for Hypodontolaiminae

The polytomous key below is based on six characters to separate the 13 genera of the sub-family Hypodontolaiminae (Table 4, Figure 5). The buccal cavity can be separated in ten states, the supplements in two types and all the remaining characters in three distinct levels. The sorting of the states of buccal cavity, peribuccal pharyngeal tissue and supplements revealed three groups already indicated in the literature: group 1 composed of *Chromadorissa* and *Spilophorella*; group 2 including *Denticulella* and *Parachromadorita*; and group 3 composed of *Dichromadora*, *Hypodontolaimus* and *Ptycholaimellus*. Additionally, two other groups were identified: group 4 composed by *Chromadorita* and *Neochromadora* and group 5 composed by *Innocuonema*, *Panduripharynx*, *Karkinochromadora* and *Megodontolaimus*. *Chromadorita* was considered very similar to *Innocuonema* by Platt &

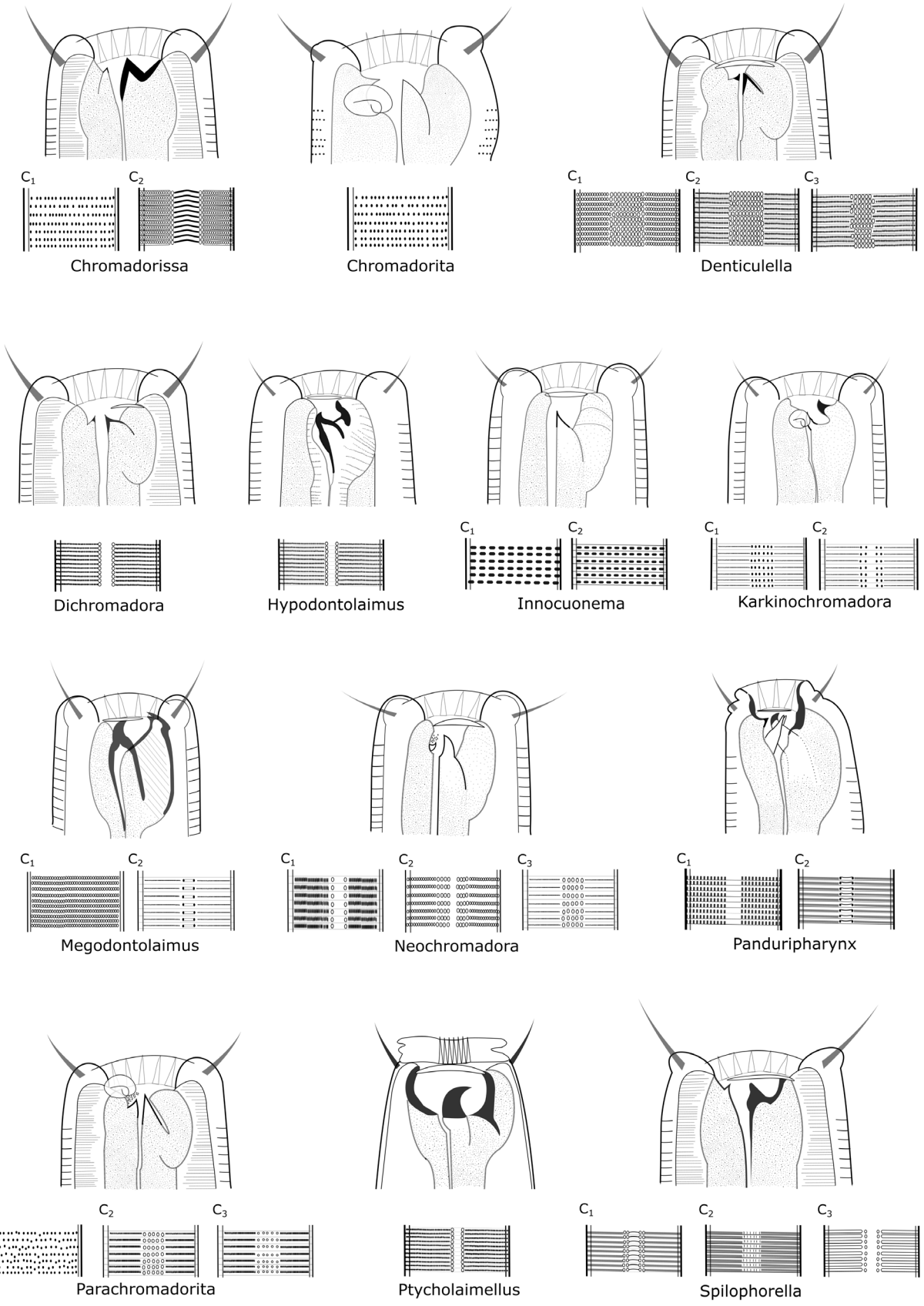

FIGURE 5. Schematic representation of Hypodontolaiminae genera. The draws aim to show head with buccal cavity and amphideal fovea and cuticle ornamentation (general pattern or C1 to C3: variation from anterior to posterior region of the body). In all drawings the right side is the dorsal side of the nematode.

Warwick (1988), but in the present key it is related to *Neochromadora* sharing similar buccal cavity, peribuccal pharyngeal tissue and amphideal fovea. *Innocuonema* is close to *Panduripharynx*, *Ptycholaimellus* and *Hypodontolaimus* mainly based on the peribuccal pharyngeal tissue, supplements and amphideal fovea.

TABLE 4. Polytomous key of Hypodontolaiminae.

	Cuticle	Amphideal fovea	Buccal cavity	Peribuccal pharyngeal tissue	Pharyngeal posterior bulb	Supplements
Chromadorita	1/2	1/2	2/3	2/3	2/3	1/2
Chromadorissa	1	3	1	1	1	1
Denticulella	1	1/2	3	2	2	1
Dichromadora	2	1/2	1/4	2/3	2	1/2
Hypodontolaimus	2	1	5	2/3	2	1/2
Innocuonema	3	1	6	2	2	2
Karkinochromadora	1	2	8	2	2	1
Megodontolaimus	1	1	9	2	1	2
Neochromadora	1	1/2	2/3	2/3	2	1
Panduripharynx	1	1	7	2	1	2
Parachromadorita	2	2	3	2	2	1
Ptycholaimellus	1/2	1	5	2	1	2
Spilophorella	1	1	1	1	1	2

Character states:
Cuticle:
1. Heterogeneous punctated ornamentation with lateral differentiation;
2. Homogeneous punctated ornamentation with lateral differentiation;
4. Heterogeneous ornamentation with obvious punctations but without lateral differentiation.

Amphideal fovea:
1. Transverse slit-like;
2. Rounded loop-shaped;
3. Not described.

Buccal cavity:
1. One large hollow dorsal tooth and one or two smaller ventrosublateral teeth;
2. One indistinct dorsal tooth and one or two ventrosublateral teeth, sometimes tiny denticles may be present;
3. One dorsal tooth, two smaller ventrosublateral teeth and numerous additional denticles;
4. One single S-shaped dorsal tooth; sometimes denticles may be present;
5. One large S-shaped dorsal tooth and a dorsal apophysis, small ventrosublateral teeth may be present;
6. One large S-shaped dorsal tooth, small venrosublateral teeth may be present;
7. One dorsal tooth; dorsal apophysis and a tiny ventrosublateral tooth may be present;
8. One large dorsal tooth with apophysis, two smaller ventrosublateral teeth and denticles;
9. Two consecutive dorsal teeth: a small anterior and a larger posterior and two small ventrosublateral teeth;
10. One large hollow ventral tooth and two-pronged dorsal teeth.

Peribuccal pharyngeal tissue:
1. Symmetrically swollen;
2. Asymmetrical dorsal swelling;
3. Not swollen.

Pharyngeal posterior bulb:
1. Double;
2. Single;
3. Absent.

Supplements:
1. Present;
2. Absent.

Subfamily Spilipherinae

Diagnosis (after Tchesunov, 2014): Cuticle homo- or heterogenous with or without the presence of lateral differentiation of larger dots. Six outer labial setae and four cephalic setae usually in a single circle. Amphidial fovea situated laterally on the head, spiral, i.e., either cryptospiral with a circular outline or a single-loop spiral with at most 1.5 turns. Buccal cavity with three or more solid teeth with or without apophyses. Pharynx with subdivided end bulb. Males with precloacal supplements setose or absent. Tail conical or elongate. All genera in this subfamily are marine, with no records so far in freshwaters.

Genus *Acantholaimus* Allgén, 1933

The genus *Acantholaimus* (Figure 4) was established by Allgén (1933) in the family Comesomatidae Filipev, 1918; subfamily Acantholaiminae Gerlach & Riemann, 1973. Lorenzen (1994) placed *Acantholaimus* within the family Chromadoridae and synonymized the subfamily Acantholaiminae with Spilipherinae. *Acantholaimus* is an abundant and species-rich genus in deep-sea nematode communities. Several *Acantholaimus* species were described by Soetaert (1989) and Bussau (1993) in their PhD thesis and they were included in recent reviews made by Miljutin & Miljutina (2016) and Manoel *et al.* (2017). However, despite their descriptions being of good quality and widespread divulgence (and even redescriptions in case of some of these species), they should be considered as *nomena nuda* following the International Code of Zoological Nomenclature.

Diagnosis (modified from Manoel *et al.* 2017): Cuticle punctate, with transverse rows of dots; lateral differentiation may be present as enlarged dots arranged irregularly, or more sparsely, or in transverse or longitudinal rows. Head sensilla arranged in three circles, posterior two being almost at the same level and usually setiform (sometimes jointed). Anterior sensilla are often papilloid and indistinct. Somatic setae may be present or absent. Amphidial fovea large, round with interrupted posterior rim or nearly comma-shaped (spiral in one species). Buccal cavity armed with three or more solid teeth, teeth minute or large, often eversible. Spicules of a peculiar construction, flattened and strongly broadened proximally. Rod-shaped gubernaculum without apophysis and bifurcated at its distal end. Spermatozoa giant, pear-shaped, often structurally complex. No precloacal supplements. Tail long, filiform. Marine, mostly deep-sea.

Number of valid species: 38.

Genus *Acantholaimus* Allgén, 1933

Syn. *Neochromadorina* Kreis, 1963

VALID SPECIES

1. *Acantholaimus akvavitus* Gerlach, Schrage & Riemann, 1979 (SE Pacific, Peru Basin)
2. *Acantholaimus arminius* Gerlach, Schrage & Riemann, 1979 (SE Pacific, Peru Basin)
3. *Acantholaimus arthrochaeta* Miljutina & Miljutin, 2012 (NE tropical Pacific, Clarion-Clipperton Fracture Zone)
4. *Acantholaimus barbatus* Miljutina & Miljutin, 2012 (NE tropical Pacific, Clarion-Clipperton Fracture Zone)
5. *Acantholaimus calathus* Gerlach, Schrage & Riemann, 1979 (Chiloé Island, South Chile)
6. *Acantholaimus cornutus* Miljutina & Miljutin, 2012 (NE tropical Pacific, Clarion-Clipperton Fracture Zone)
7. *Acantholaimus cyathibucca* Vivier, 1985 (NE Atlantic, Bay of Biscay)
8. *Acantholaimus elegans* Jensen, 1988 (North Atlantic, Norway Sea)
9. *Acantholaimus formosus* Miljutina, Miljutin & Tchesunov, 2013 (SE Atlantic, Angola Basin)
10. *Acantholaimus gathumai* Muthumbi & Vincx, 1997 (Central Western Indian Ocean)
11. *Acantholaimus geraerti* Muthumbi & Vincx, 1997 (Central Western Indian Ocean)
12. *Acantholaimus gigantasetosus* Vivier, 1985 (NE Atlantic, Bay of Biscay)
13. *Acantholaimus heipi* Muthumbi & Vincx, 1997 (Central Western Indian Ocean)
14. *Acantholaimus incomptus* Vivier, 1985 (NE Atlantic, Bay of Biscay)

15. *Acantholaimus invaginatum* Muthumbi & Vincx, 1997 (Central Western Indian Ocean)
16. *Acantholaimus iubilus* Gerlach, Schrage & Riemann, 1979 (SE Pacific, Peru Basin)
17. *Acantholaimus longisetosus* Allgén, 1933 (Norway, Trondheim fjord)
18. *Acantholaimus longistriatus* Gourbault & Vincx, 1985 (SE Atlantic, Walvis Ridge)
19. *Acantholaimus macramphis* Gourbault & Vincx, 1985 (SE Atlantic, Walvis Ridge)
20. *Acantholaimus maks* Gerlach, Schrage & Riemann, 1979 (SE Pacific, Peru Basin)
21. *Acantholaimus marliae* Manoel, Silva & Esteves, 2017 (Potiguar Basin, South Atlantic)
22. *Acantholaimus megamphis* Vivier, 1985 (NE Atlantic, Bay of Biscay)
23. *Acantholaimus microdontus* Gourbault & Vincx, 1985 (SE Atlantic, Walvis Ridge)
24. *Acantholaimus minutus* (Vitiello, 1970) Gerlach, Schrage & Riemann, 1979 (Mediterranean, Gulf of Lion)
Syn. *Acantholaimus minima* (Vitiello, 1970) Gerlach, Schrage & Riemann, 1979
Spiliphera minima Vitiello, 1970
Spiliphera minuta Vitiello, 1972
25. *Acantholaimus obviatus* Vivier, 1985 (NE Atlantic, Bay of Biscay)
26. *Acantholaimus polydentatus* Gerlach, 1951 (Baltic Sea, Kiel Bay)
Syn. *Acantholaimus ewensis* Platt & Zhang, 1982
Acantholaimus pilosus (Kreis, 1963) Hope & Murphy, 1972
27. *Acantholaimus quadridentatus* Jensen, 1985 (Central West Atlantic, Gulf of Mexico).
28. *Acantholaimus quintus* Gerlach, Schrage & Riemann, 1979 (SE Pacific, Peru Basin)
29. *Acantholaimus robustus* Miljutina & Miljutin, 2012 (NE tropical Pacific, Clarion-Clipperton Fracture Zone)
30. *Acantholaimus septimus* Gerlach, Schrage & Riemann, 1979 (SE Pacific, Peru Basin)
31. *Acantholaimus setosus* Vitiello, 1970 (Mediterranean, Gulf of Lion)
32. *Acantholaimus sieglerae* Miljutina & Miljutin, 2012 (NE tropical Pacific, Clarion-Clipperton Fracture Zone)
33. *Acantholaimus skukinae* Miljutina, Miljutin & Tchesunov, 2013 (SE Atlantic, Angola Basin)
34. *Acantholaimus spinicauda* (Vitiello, 1970) Gerlach, Schrage & Riemann, 1979 (NE Atlantic, Bay of Biscay)
Syn. *Spiliphera spinicauda* Vitiello, 1970
35. *Acantholaimus tchesunovi* Miljutina & Miljutin, 2012 (NE tropical Pacific, Clarion-Clipperton Fracture Zone)
36. *Acantholaimus veitkoehlerae* Miljutina & Miljutin, 2012 (NE tropical Pacific, Clarion-Clipperton Fracture Zone)
37. *Acantholaimus vermeuleni* Muthumbi & Vincx, 1997 (Central Western Indian Ocean)
38. *Acantholaimus versheldi* Muthumbi & Vincx, 1997 (Central Western Indian Ocean)
NOMENA NUDA
1. *Acantholaimus aequisetosus* Soetaert, 1989 (Mediterranean)
2. *Acantholaimus aheneus* Bussau, 1993 (SE Pacific, Peru Basin)
3. *Acantholaimus angustus* Bussau, 1993 (SE Pacific, Peru Basin)
4. *Acantholaimus caecus* Bussau, 1993 (SE Pacific, Peru Basin)
5. *Acantholaimus coruscus* Bussau, 1993 (SE Pacific, Peru Basin)
6. *Acantholaimus crenatus* Soetaert, 1989 (Mediterranean)
7. *Acantholaimus effilatus* Soetaert, 1989 (Mediterranean)
8. *Acantholaimus filicaudatus* Soetaert, 1989 (Mediterranean)
9. *Acantholaimus mirabilis* Soetaert, 1989 (Mediterranean)
10. *Acantholaimus occultus* Bussau, 1993 (SE Pacific, Peru Basin)
11. *Acantholaimus pygmaeus* Soetaert, 1989 (Mediterranean)
12. *Acantholaimus tectus* Bussau, 1993 (SE Pacific, Peru Basin)
13. *Acantholaimus vasicola* Soetaert, 1989 (Mediterranean)

Genus *Spiliphera* Bastian, 1865

The genus *Spiliphera* (Figure 4) is poorly known and described, with many invalid, synonymized species or *species inquirenda*. *Spilophora* Bastian, 1865 nec Boheman, 1850 is an impermissible emendation, and *Spilophorium* Cobb, 1933 an impermissible substitution to *Spiliphera.* However, many authors used the

emendation *Spilophora* (Gerlach & Riemann 1973). Wieser (1954) synonymized *Statenia* Allgén, 1930 with *Spiliphera*. Originally this genus was established by Bastian (1865) to accommodate four species (*S. elegans* Bastian, 1865; *S. inaequalis*; *S. robusta* Bastian, 1865 and *S. costata* Bastian, 1865), from which the last three are now included in other three different genera (*Hypodontolaimus*, *Halichoanolaimus* and *Monoposthia*, respectively). The fourth species, *S. elegans*, the type species of *Spiliphera*, is insufficiently described and it was never recorded again, therefore it was considered doubtful species by Wieser (1954) and it is mentioned as *species inquirendum* by Gerlach & Riemann (1973). *S. elegans* was the type species of *Spiliphera*, therefore another, valid species of the genus should be proposed to ICZN as a replacement type species. *S. dolichura* de Man, 1893 and *S. gracilicauda* de Man, 1893 described from the English Channel are the only well-known representatives of *Spiliphera*. Over 30 species originally described as *Spiliphera* (or *Spilophora, Spilophorium* and *Statenia*) belong now to other genera. Here we list only those with dubious taxonomic positions. *S. punctata* is poorly known and according to Gerlach (1964) probably belongs to *Halichoanolaimus*, but until further examination it should be considered *species inquirendum*. *S. longiseta* and *S. tenuicauda*, both poorly described by Allgén (1951) and based only on females, according to Wieser (1954) probably should be members of Comesomatidae and *Prochromadorella*, respectively, but until further examination they are considered here as *species inquirenda*. *S. australis*, *S. gracilis* and *S. falklandiae* are poorly described by Allgén (1959), the first two are based only on a single female specimen and the last lacks drawings, therefore all these three species are considered as *species inquirenda*.

Diagnosis (modified from Wieser 1954 and Tchesunov 2014): Cuticle homogeneous, consisting of more or less irregular dots with lateral differentiation present or absent. Amphideal fovea in shape of an open-looped spiral. Head sensilla arranged in three circles (6+6+4), anterior two minute and posterior setiform. Three solid teeth with posterior apophyses which project backwards into the oesophageal lumen. Pharyngeal bulb pyriform. Spicules not expanded proximally. Tail long, filiform.

Number of valid species: 2.

Genus *Spiliphera* Bastian, 1865

Syn. *Spilophora* Bastian, 1865 nec Boheman, 1850
Statenia Allgén, 1930
Spilophorium Cobb, 1933

VALID SPECIES

1. *Spiliphera dolichura* de Man, 1893 (English Channel)

Syn. *Spiliphera gracilicauda dolichura* de Man, 1893
Spiliphera giardi Rouville, 1903
Spiliphera trichophorella Wieser, 1954
Spiliphera tricophora (Allgén, 1932) Wieser, 1954
Spiliphera trichura (Allgén, 1930) Wieser, 1954
Statenia tricophora Allgén, 1932
Statenia trichura Allgén, 1930

2. *Spiliphera gracilicauda* de Man, 1893 (English Channel)

Syn. *Spiliphera gracilicauda dolichura* sensu Allgén, 1951
Spiliphera gracilicauda breviseta Allgén, 1959

SPECIES INQUIRENDA

1. *Spiliphera australis* Allgén, 1959 (Fuegian Archipelago)
2. *Spiliphera elegans* Bastian, 1865 (English Channel)
3. *Spiliphera falklandiae* Allgén, 1959 (Falkland Islands)
4. *Spiliphera gracilis* Allgén, 1959 (Falkland Islands)
5. *Spiliphera punctata* Linstow, 1900 (Bear Island)
6. *Spiliphera longiseta* (Allgén, 1951) Wieser, 1954 (Hawaii)
7. *Spiliphera tenuicauda* (Allgén, 1951) Wieser, 1954 (Hawaii)

Comments about some dubious/invalid genera of Chromadoridae

Genus *Algoanema* Heyns & Furstenberg, 1987

The genus *Algoanema* was described by Heyns & Furstenberg (1987) with *A. aestuariense*, found in South Africa. According to Heyns & Furstenberg (1987) *Algoanema* is close to *Ptycholaimellus* and *Spilophorella* in the structure of buccal cavity (with S-shaped dorsal tooth), pharynx and absence of precloacal supplements, but differs from them in not presenting lateral differentiation of the cuticle. There is no mention of *Algoanema* in the recent review of Tchesunov (2014) and we did not find any other reference or discussion about the status of *Algoanema* apart from the original description. In our opinion the structure of buccal cavity with the strong S-shaped dorsal tooth is a very remarkable character of *Ptycholaimellus* and *Spilophorella* and the difference in the cuticle is not sufficient to separate *Algoanema* from these genera. *Algoanema* is probably a junior synonym of either *Ptycholaimellus* or *Spilophorella* but until further studies and examination of the type species we prefer to consider it as a dubious genus.

Genus *Algoanema* Heyns & Furstenberg, 1987

1. *Algoanema aestuariense* Heyns & Furstenberg, 1987 (Port Elizabeth, South Africa)

Genus *Chromanema* Khera, 1975

The genus *Chromanema* was described by Khera (1975) based in a single male from a freshwater pond in India. Apparently Khera (1975) compared *Chromanema* only to those genera of Chromadoridae also found in freshwater habitats. The author stated that *Chromanema* is close to *Chromadorella* in having a pharynx without distinct bulb, however differs from it in having a single dorsal tooth. The description of the only species, *C. solitarium* Khera, 1975, presents some strange details, such as an anterior circle of sensilla with eight setae, which can be misinterpretation of what the author saw. There is no mention of *Chromanema* in Lorenzen (1994) and Tchesunov (2014) and we prefer to consider this genus as dubious due to the poor and questionable description based on a single male.

Genus *Chromanema* Khera, 1975

1. *Chromanema solitarium* Khera, 1975 (India)

Genus *Dasylaimus* Cobb, 1933

The genus *Dasylaimus* was established by Cobb (1933) when *D. nudus* Cobb, 1933 was described based on a single female. The description is poor in details and did not present any illustration. Wieser (1954) included *Dasylaimus* in his identification key for Chromadoridae genera but later Hope & Murphy (1972) regarded this genus as dubious. Kulikov & Dashchenko (1991) and Lorenzen (1994) also cited *Dasylaimus* as dubious genus and it was not mentioned by Tchesunov (2014). For these reasons, *Dasylaimus* is considered here as invalid genus.

Genus *Dasylaimus* Cobb, 1933

1. *Dasylaimus nudus* Cobb, 1933 (Massachusetts, USA)

Genus *Deltanema* Kreis, 1929

The genus *Deltanema* was described by Kreis (1929) in subfamily Desmodorinae Filipjev, 1922 (at that time this subfamily belonged to Chromadoridae), based on a single female, when he found the new species *D. parvum* Kreis, 1929 in the English Channel. Kreis (1929) argued that *Deltanema* is close to *Chromadorina* and *Chromadorita* but distinguished from these genera by the well-developed teeth. Hope & Murphy (1972) synonymized *Deltanema* with *Metalinhomoeus* but nevertheless Lorenzen (1994) recognized it as a valid genus in Hypodontolaiminae. Smol & Decraemer (2006) and Tchesunov (2014) argued that *Deltanema* has limited description and poor illustrations, therefore it should be considered a dubious genus. We agree with them and also consider *Deltanema* here as a dubious genus.

Genus *Deltanema* Kreis, 1929

1. *Deltanema parvum* Kreis, 1929 (English Channel)

Genus *Dicriconema* Steiner & Hoeppli, 1926

The genus *Dicriconema* is known from a single species, *Dicriconema tenuis* Steiner & Hoeppli, 1926; described based on a single immature female. Steiner & Hoeppli (1926) described the cuticle in details but gave little information about internal organs stating that they are unable to complete the generic diagnosis due to the thick

cuticle which obscured the internal structures. Wieser (1954) regarded *Dicriconema* as a dubious genus considering it closely related to *Euchromadora*, distinguishable only by some differences in the cuticle. Inglis (1969) reviewed *Euchromadora* and similar genera comparing cuticle and other characters. The author considered *D. tenuis* as *species inquirenda* stating that *Dicriconema* cannot be unequivocably recognized. Nevertheless, both Gerlach & Riemann (1973) and Lorenzen (1994) considered it as valid genus of Euchromadorinae without any discussion. Kulikov & Dashchenko (1991) presented an identification key to genera of Euchromadorinae and considered *Dicriconema* as dubious using the same argumentation as Inglis (1969). More recently Tchesunov (2014) omitted *Dicriconema* without any explanation and we consider it invalid based on Inglis (1969) and Kulikov & Dashchenko (1991).

Genus *Dicriconema* Steiner & Hoeppli, 1926

1. *Dicriconema tenue* Steiner & Hoeppli, 1926 (Japan, Pacific Coast)

Genus *Euchromanema* Kulikov & Dashchenko, 1991

Kulikov & Dashchenko (1991) established *Euchromanema* when describing *E. cervicornia* Kulikov & Dashchenko, 1991 and *E. paracervicornia* Kulikov & Dashchenko, 1991 from the Sea of Japan. There is no mention of *Euchromanema* in the recent review of Tchesunov (2014) and we did not find any other reference or discussion about the status of this genus apart from the original description. Kulikov & Dashchenko (1991) stated that the new genus is comparable with *Endeolophos* and *Actinonema* by the size of dorsal tooth, position of head setae and presence of lateral differentiation of cuticle. According to the authors, *Euchromanema* differs from the genera mentioned above by the prominent pharyngeal posterior bulb and relatively simple ornamentation of cuticle. However, in our opinion the prominent bulb is not sufficient to unequivocally differentiate *Euchromanema* from *Actinonema* as in the last there are species with different stages of development of the bulb. In fact, the bulb seems to be double in the illustration of *E. cervicornia* provided by Kulikov & Dashchenko (1991) and this character is present in other genera of Chromadoridae such as *Chromadorissa* and *Megodontolaimus*. Furthermore, *Euchromanema* can not be distinguished from *Endeolophos* based on the simple ornamentation of the cuticle, as this genus also has a relatively simple ornamented homogenous cuticle. Considering all information presented here, we prefer to consider this genus as dubious.

Genus *Euchromanema* Kulikov & Dashchenko, 1991

1. *Euchromanema cervicornia* Kulikov & Dashchenko, 1991 (Sea of Japan)

2. *Euchromanema paracervicornia* Kulikov & Dashchenko, 1991 (Sea of Japan)

Genus *Odontocricus* Steiner, 1918

The genus *Odontocricus* is a monospecific genus first established as subgenus of *Euchromadora*, with the description of *Euchromadora* (*Odontocricus*) *hupferi* by Steiner (1918), and later erected to genus status by Cobb (1933). Wieser (1954) regarded *Odontocricus* as a dubious genus considering it closely related to *Euchromadora* from which is distinguished by some differences in the cuticle morphology. Coles (1965) transferred *Odontocricus hupferi* to *Euchromadora* and commented that *O. hupferi* has a cuticle with different markings when compared to other *Euchromadora* species. The author considered it as *species inquirendum* due to poor and inadequate description. Inglis (1969), when comparing cuticle and other characters in his review of *Euchromadora* and similar genera, considered *Odontocricus* as dubious genus. Later, Lorenzen (1994) also regarded *Odontocricus* as dubious genus and it is not mentioned in the recent review of Chromadorida by Tchesunov (2014). For all these reasons, *Odontocricus* is considered here as invalid genus and its only species is not listed here [it is listed as *species inquirendum* in *Euchromadora* considering transfer made by Coles, (1965)].

Genus *Paradichromadora* Dashchenko, 1991

Dashchenko (1991) established *Paradichromadora* when describing *P. brevicula* Dashchenko, 1991 associated with the sponge *Adocia cinerea* Grant, 1826 from Sea of Japan. There is no mention of *Paradichromadora* in the recent review of Tchesunov (2014) and we did not find any other reference or discussion about the status of this genus apart from the original description. Dashchenko (1991) states that the characteristic feature of this genus is the heterogeneous ornamentation of cuticle: smooth cuticle rings and those with simple dots interchange with cuticle rings with serrated strips of merged dots. According to the author *Paradichromadora* is most similar to *Neochromadora* and *Dichromadora* but it differs from the first by the "absence of rasp brims in the stoma", no

pharynx dilatation in the stoma region and presence of non-ornamented cuticle ring and from the second by more complicate ornamentation and weak development of pharyngeal bulb. In our opinion *Paradichromadora* description resembles *Chromadorita* which is a genus with large variation of cuticle ornamentation and bulb development among the species. It is probably a junior synonym of *Chromadorita* but until further studies and examination of the type species we prefer to consider it as a dubious genus.

Genus *Paradichromadora* Dashchenko, 1991

1. *Paradichromadora brevicula* Dashchenko, 1991 (Sea of Japan)

Genus *Trichromadorita* Timm, 1961

The genus *Trichromadorita* was established by Timm (1961) when the type species *T. mobilis* was described based in a single male. Timm (1961) considered this genus similar to *Chromadorita* but different based on the presence of a pharynx with three bulbs. According to this author the first bulb is much smaller than the posterior two. Khan (1991) described a second species, *T. marinus*, based only on females and considered it different from *T. mobilis* based mainly on the different body length. Khan (1991) also presented an emended diagnosis of the genus mentioning length of >1mm but this size would exclude *T. mobilis* with only 0.8 mm. Both Timm (1961) and Khan (1991) illustrate multispiral amphids for their species, without futher comments, which is more characteristic to other families such as Comesomatidae Filipjev, 1918; or if in Chromadoridae it is a diagnostic character of subfamily Spilipherinae.

Lorenzen (1994) considered *Trichromadorita* as a valid genus of Spilipherinae but Tchesunov (2014) omitted it without explanation. We believe that the bulbs of *Trichromadorita* can be a misinterpretation and it is particularly difficult to distinguish *T. marinus* from *T. mobilis*. Considering all information known until now, we consider *Trichromadorita* as dubious genus until new records and more detailed descriptions are available.

Genus *Trichromadorita* Timm, 1961

1. *Trichromadorita marinus* Khan, 1991 (Lyari River, Pakistan)

2. *Trichromadorita mobilis* Timm, 1961 (Bay of Bengal)

Genus *Tridentellia* Gerlach & Riemann, 1973

The monospecific genus *Tridentellia* was described by Filipjev (1946) under the name *Tridentella* from New Siberian Islands and was never recorded again. Later this genus was renamed by Gerlach & Riemann (1973) to avoid homonymy with a Crustacean. The only species known, *T. crenopharynx* Filipjev, 1946, was based on a single poorly described immature female. In the description, Filipjev (1946) considered *Statenia* as the closest genus, which was synonymized with *Spiliphera* by Wieser (1954), who did not mention *Tridentellia* in his review. Gerlach & Riemann (1973) recognized *Tridentellia* as a valid genus in sub-family Acantholaiminae (family Comesomatidae) but Lorenzen (1994) transferred this genus (together with *Acantholaimus*) to Spilipherinae considering position of ovaries in relation to intestine and presence of a single anterior testis—characters which are holapomorphies of Chromadoridae. In the description of *Tridentellia* by Filipjev (1946) there is no mentioning about the position of ovaries in relation to intestine and as it was based in a female there is no data about testis. In the recent review of Tchesunov (2014) *Tridentellia* was omitted without explanation and considering all information presented here we consider it an invalid genus.

Genus *Tridentellia* Gerlach & Riemann, 1973

1. *Tridentellia crenopharyncx* Gerlach & Riemann, 1973 (New Siberian Islands)

Syn. *Tridentella crenopharyncx* Filipjev, 1946

Phylogeny of Chromadoridae

A total of 28 sequences of 18S rDNA were retrieved from the GenBank (Appendix 1). These sequences covered 11 genera, of which only nine were identified to species level. The 18S-based molecular phylogenetic tree recovered three monophyletic clades with high support (Figure 6), which correspond to the subfamilies Spilipherinae, Chromadorinae and Hypodontolaiminae. The sequence of *Prochromadorella septempapillata* Platt, 1973, currently classified within the Chromadorinae was grouped with species of Hypodontolaiminae, and the inverse occurred with a *Dichromadora* sequence (AY854209). The tree did not recover the monophyly of most genera. In the case of

Chromadorita, *C. tentadunbum*, a misspelling of *Chromadorita tentabunda* de Man, 1890, is considered as a complex *Chromadorita/Innocuonema* by Platt & Warwick (1988). The molecular data corroborated the hypothesis that this species does not belong to *Chromadorita* and may be classified as *Innocuonema tentabunda* (de Man 1890). *Chromadorina* also showed a difficult taxonomy with many species synonymized or transferred from other genera (see discussion in the Taxonomic session). The high divergence between these sequences and their phylogenetic position suggests that this genus needs a careful re-evaluation. Sequences of *Dichromadora*, *Neochromadora*, *Atrochromadora* and *Chromadora* that were not clustered together with congeneric species probably are misidentified sequences in the GenBank. Problems of misidentification in genetic data banks are common across taxa (Vilgalys 2003) and have a negative effect on the resolution of molecular phylogenies (Holovachov 2016). The *Dichromadora* sequence (AY854209), for example, is identical to the *Atrochromadora microlaima* sequence (AY854204).

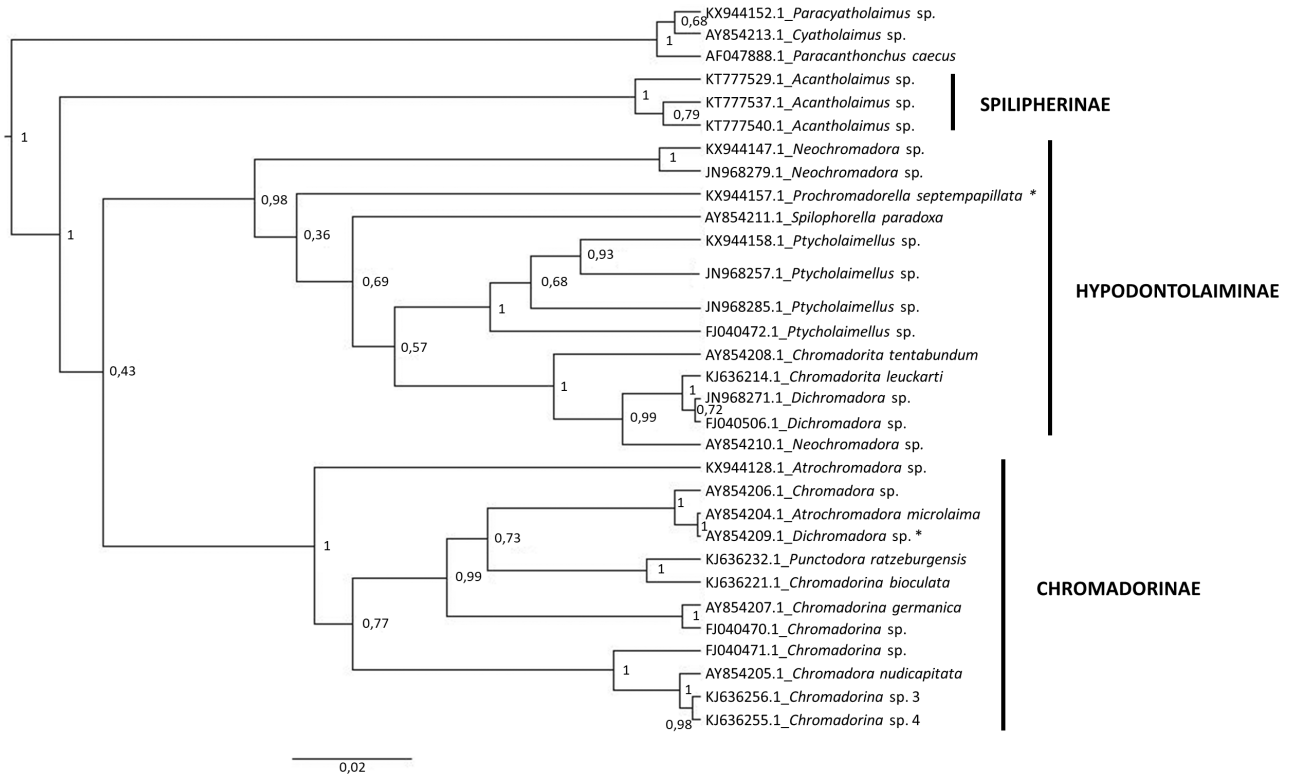

FIGURE 6. Bayesian tree inferred by 18S sequences. The species are coloured based on current classification: *Species currently classified in a subfamily different from that which was grouped by Bayesian analysis. The posterior probabilities are given on each node. The scale represents substitutions per site.

From 28S rDNA region, a total of 11 sequences were obtained covering eight genera and four nominal species (Appendix 1). Once again, the analyses recovered three monophyletic clades roughly corresponding to the three subfamilies (Figure 7). The sequences of *Dichromadora* and *Chromadorina* were grouped into Chromadorinae and Hypodontolaiminae, respectively, contradicting their current classification. This could be another case of misidentified sequences, since these sequences were not identified to species level.

Despite the absence of defined synapomorphies for the subfamilies, the molecular phylogenies were able to recover the classification recognized by Lorenzen (1994) and Tchesunov (2014). It is worth noting that the clade Spilipherinae was represented by a single genus and there are no sequences available for Euchromadorinae and Harpagonchinae. The addition of new data will clarify the systematics within the family. Along with this, the material deposited in the GenBank exemplifies how problematic it is the identification of Chromadoridae species. This is a common issue among marine nematodes and is a consequence of the poorly described species, large number of unknown species and scarcity of specialists. Validation of species lists (e.g. Venekey *et al.* 2014), integrative taxonomical descriptions (e.g. Cunha *et al.* 2013, Leduc *et al.* 2017), and systematics reviews (e.g. Miljutin & Miljutina 2016) are urgently needed within this group.

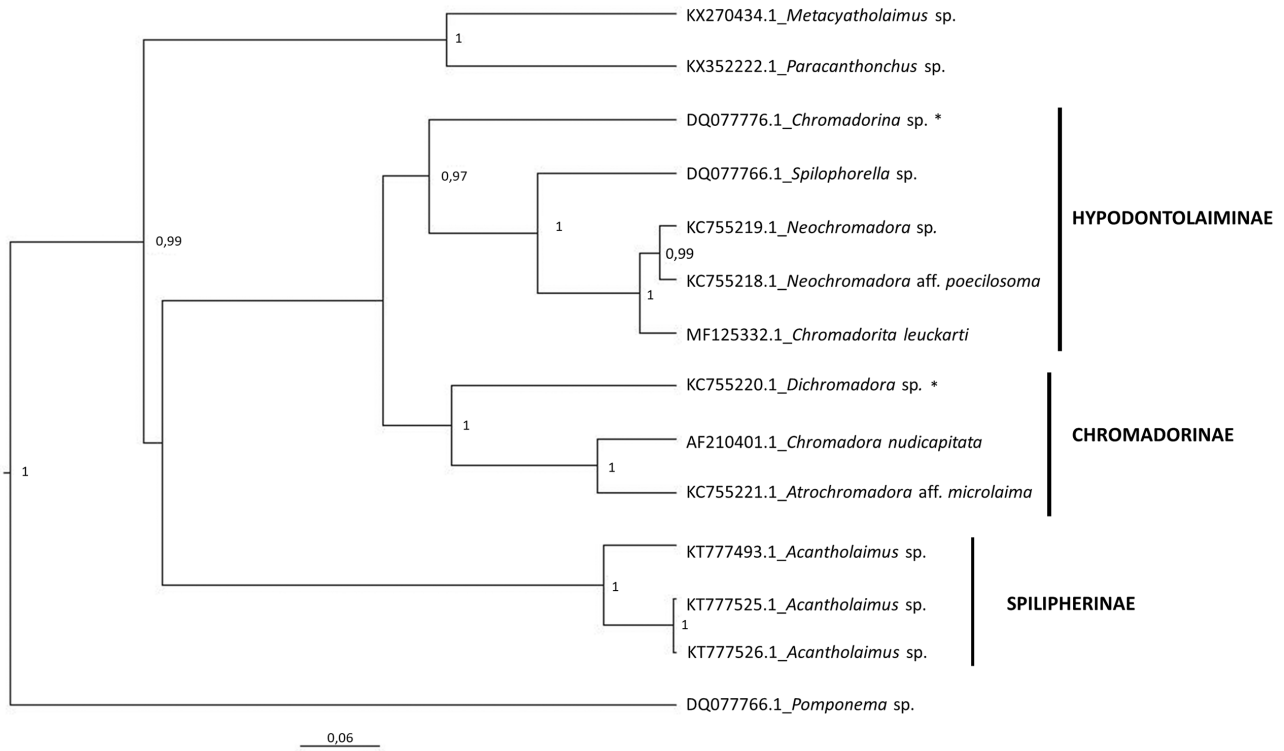

FIGURE 7. Bayesian tree inferred by 28S sequences. The species are coloured based on current classification: *Species currently classified in a subfamily different from that which was grouped by Bayesian analysis. The posterior probabilities are given on each node. The scale represents substitutions per site.

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APPENDIX 1. Sequences retrieved from GenBank. The table shows the classification in subfamilies recognized by Lorenzen (1994) and Tchesunov (2014).

Accession	Species	Classification	Region
AF047888.1	*Paracanthonchus caecus*	OUTGROUP	18S
AY854213.1	*Cyatholaimus* sp.	OUTGROUP	18S
KX944152.1	*Paracyatholaimus* sp.	OUTGROUP	18S
AY854204.1	*Atrochromadora microlaima*	Chromadorinae	18S
AY854205.1	*Chromadora nudicapitata*	Chromadorinae	18S
AY854206.1	*Chromadora* sp.	Chromadorinae	18S
AY854207.1	*Chromadorina germanica*	Chromadorinae	18S
AY854208.1	*Chromadorita tentabundum*	Hypodontolaiminae	18S
AY854209.1	*Dichromadora* sp.	Hypodontolaiminae	18S
AY854210.1	*Neochromadora* sp.	Hypodontolaiminae	18S
AY854211.1	*Spilophorella paradoxa*	Hypodontolaiminae	18S
FJ040470.1	*Chromadorina* sp.	Chromadorinae	18S
FJ040471.1	*Chromadorina* sp.	Chromadorinae	18S
FJ040506.1	*Dichromadora* sp.	Hypodontolaiminae	18S
FJ040472.1	*Ptycholaimellus* sp.	Hypodontolaiminae	18S
JN968257.1	*Ptycholaimellus* sp.	Hypodontolaiminae	18S
JN968271.1	*Dichromadora* sp.	Hypodontolaiminae	18S
JN968279.1	*Neochromadora* sp.	Hypodontolaiminae	18S
JN968285.1	*Ptycholaimellus* sp.	Hypodontolaiminae	18S
KJ636214.1	*Chromadorita leuckarti*	Hypodontolaiminae	18S
KJ636221.1	*Chromadorina bioculata*	Chromadorinae	18S
KJ636232.1	*Punctodora ratzeburgensis*	Chromadorinae	18S
KJ636255.1	*Chromadorina* sp.	Chromadorinae	18S
KJ636256.1	*Chromadorina* sp.	Chromadorinae	18S
KT777529.1	*Acantholaimus* sp.	Spilipherinae	18S
KT777537.1	*Acantholaimus* sp.	Spilipherinae	18S
KT777540.1	*Acantholaimus* sp.	Spilipherinae	18S
KX944128.1	*Atrochromadora* sp.	Chromadorinae	18S
KX944147.1	*Neochromadora* sp.	Hypodontolaiminae	18S
KX944157.1	*Prochromadorella septempapillata*	Chromadorinae	18S
KX944158.1	*Ptycholaimellus* sp.	Hypodontolaiminae	18S
KX270434.1	*Metacyatholaimus* sp.	OUTGROUP	28S
KX352222.1	*Paracanthonchus* sp.	OUTGROUP	28S
DQ077766.1	*Pomponema* sp.	OUTGROUP	28S
AF210401.1	*Chromadora nudicapitata*	Chromadorinae	28S
DQ077766.1	*Spilophorella* sp.	Hypodontolaiminae	28S
DQ077776.1	*Chromadorina* sp.	Chromadorinae	28S
KC755218.1	*Neochromadora* aff. *poecilosoma*	Hypodontolaiminae	28S
KC755219.1	*Neochromadora* sp.	Hypodontolaiminae	28S
KC755220.1	*Dichromadora* sp.	Hypodontolaiminae	28S

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APPENDIX 1. (Continued)

Accession	Species	Classification	Region
KC755221.1	*Atrochromadora* aff. *microlaima*	Chromadorinae	28S
KT777493.1	*Acantholaimus* sp.	Spilipherinae	28S
KT777525.2	*Acantholaimus* sp.	Spilipherinae	28S
KT777526.3	*Acantholaimus* sp.	Spilipherinae	28S
MF125332.1	*Chromadorita leuckarti*	Hypodontolaiminae	28S