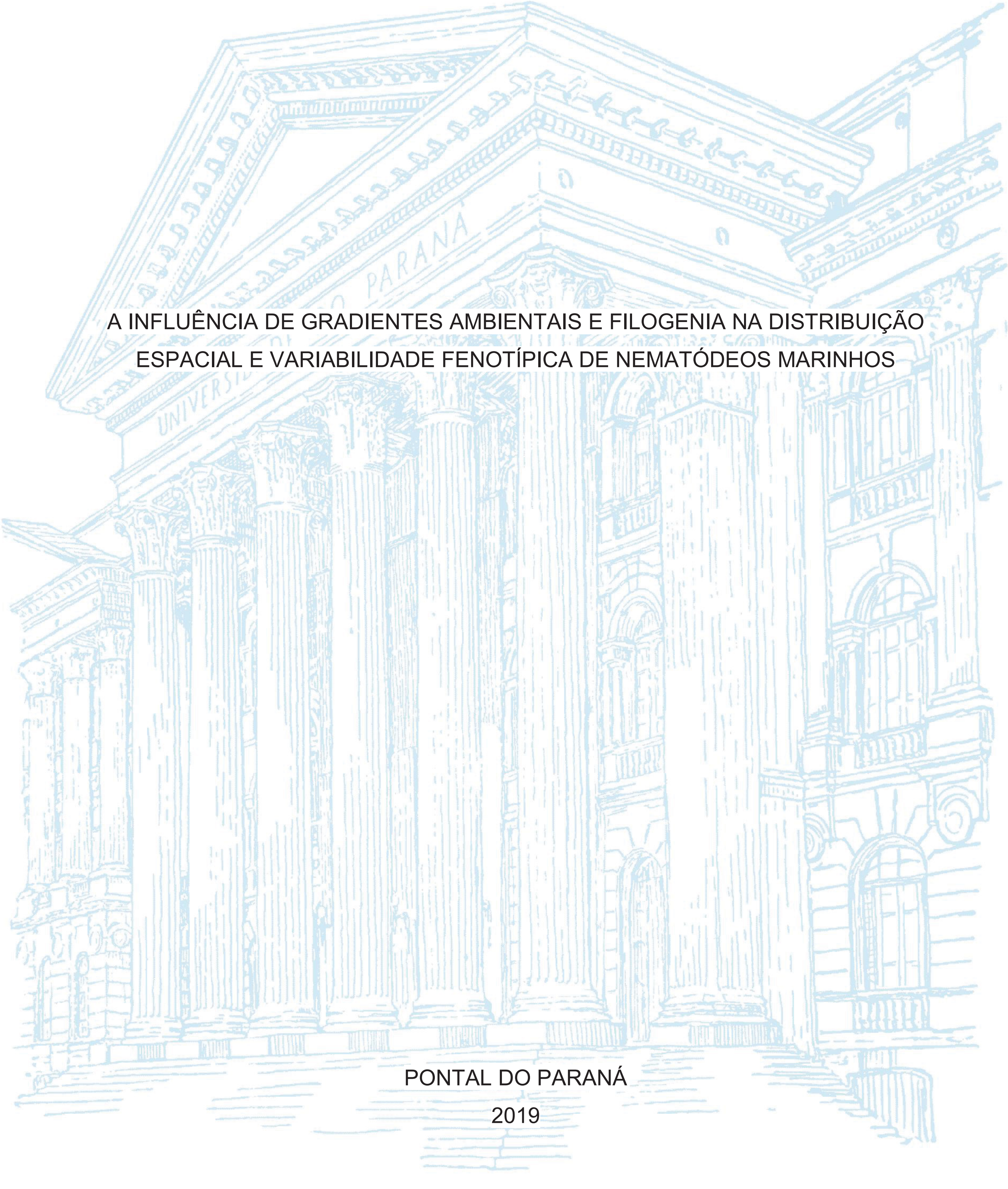
UNIVERSIDADE FEDERAL DO PARANÁ

ANA CAROLINA VILAS-BOAS



A INFLUÊNCIA DE GRADIENTES AMBIENTAIS E FILOGENIA NA DISTRIBUIÇÃO ESPACIAL E VARIABILIDADE FENOTÍPICA DE NEMATÓDEOS MARINHOS

PONTAL DO PARANÁ
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Tese apresentada ao curso de Pós-Graduação em Sistemas Costeiros e Oceânicos, Centro de Estudos do Mar, Universidade Federal do Paraná, como requisito parcial à obtenção do título de Doutor(a) em Sistemas Costeiros e Oceânicos.

Orientador: Prof. Dr. Gustavo Fonseca

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TERMO DE APROVAÇÃO

Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação em SISTEMAS COSTEIROS E OCEÂNICOS da Universidade Federal do Paraná foram convocados para realizar a arguição da Tese de Doutorado de **ANA CAROLINA VILAS-BOAS**, intitulada: **A INFLUÊNCIA DE GRADIENTES AMBIENTAIS E FILOGENIA NA DISTRIBUIÇÃO ESPACIAL E VARIABILIDADE FENOTÍPICA DE NEMATÓDEOS MARINHOS**, após terem inquirido a aluna e realizado a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.

A outorga do título de Doutor está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

Curitiba, 27 de Maio de 2019.

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RESUMO

As dimensões taxonômicas, funcionais e filogenéticas da biodiversidade.são indicadores relevantes para o entendimento das contribuições de processos ecológicos e evolutivos moldando assembleias de organismos. O objetivo geral desta tese foi testar previsões a partir das dimensões da biodiversidade mapeadas em relação a habitats costeiros na inferência de processos ecológicos e evolutivos. O primeiro capítulo é uma revisão sistemática de Chromadoridae, uma das maiores famílias de Nematoda. Este artigo integra e atualiza revisões anteriores para orientar identificações de espécies, descrições taxonômicas e estudos filogenéticos futuros. O capítulo um está publicado no periódico Zootaxa. O capítulo dois fornece uma árvore filogenética informal para Nematoda. Ela consiste em uma hipótese das relações de todos os gêneros marinhos válidos através da análise do conhecimento atual, e serve como base para sugerir a revisão sistemática de táxons e explorar as relações evolutivas em estudos ecológicos. No capítulo três, assembleias de nematódeos marinhos foram usadas para testar se a distinção ambiental entre três habitats costeiros diferentes tem impulsionado distintos processos eco-evolutivos atuando sobre os animais. Os padrões de superdispersão e subdispersão da riqueza de espécies, distinções filogenéticas e funcionais dos nematódeos sugerem diferentes mecanismos evolutivos e ecológicos moldando as assembleias. Portanto, cada uma das três dimensões da biodiversidade utilizadas nesta tese (taxonômica, filogenética e funcional) interage diferentemente com o ambiente e pode apresentar limitações operacionais. Entretanto, quando integradas, fornecem inferências mais robustas sobre os processos eco-evolutivos atuando na estruturação das assembleias de organismos.

Palavras-chave: Ecologia. Filogenia. Nematódeos. Processos evolutivos. Sistemática.

ABSTRACT

The understanding of the relative contributions of ecological and evolutionary processes shaping assemblages is provided by gathering taxonomic, functional and phylogenetic dimensions of biodiversity. The overall purpose of this thesis was to test predictions of dimensions of biodiversity in relation of coastal habitats in the inference of ecological and evolutionary processes shaping assemblages. The first chapter is a systematic review of Chromadoridae, one of the largest families of Nematoda. This paper integrates and updates previous reviews to guide future species identifications, taxonomic descriptions and phylogenetic studies. This chapter is published in Zootaxa. The chapter two provides an informal supertree for Nematoda. It consists in a phylogenetic hypothesis of the relationships of all the valid marine genera through analysing the currently knowledge and serves as the basis to suggest systematics re-examination of taxa and to explore the evolutionary relationships in ecological studies. In the chapter three, the assemblages of nematodes were used to test whether the environmental distinction among three different coastal habitats have driven distinct eco-evolutionary processes acting on the animals. The overdispersion and underdispersion patterns of species richness, phylogenetic and functional distinctness of nematodes suggest different evolutionary and ecological mechanisms shaping assemblages. Therefore, the three different dimensions of biodiversity used in this thesis (taxonomic, phylogenetic and functional dimensions) differently interact with the environment. Each of these dimensions may exhibits operational limitations, but when connected, they provide more robust inferences about eco-evolutionary processes acting on the compositions of assemblages.

Keywords: Ecology. Phylogeny. Nematoda. Evolutionary processes. Systematics.

SUMÁRIO

GENERAL INTRODUCTION

The relative contributions of ecological and evolutionary processes shaping assemblages is provided by the integration of taxonomic, functional and phylogenetic dimensions of biodiversity. Species richness is one of the main indicators of community's patterns but fail in considering species as functional and phylogenetically similar, hampering a detailed comprehension of the dynamics of communities (Dreiss et al., 2015). Thus, the inference of processes has been accessed by correlating phylogenetic diversity (PD), functional diversity (FD) and species richness (S), in which it is expected that increasing the number of species will increase phylogenetic and functional diversities until a limit (Figure 1a). However, PD and FD are limited by different sampling efforts and for not consider the uniqueness of a species in relation to other species in a community (Clarke & Warwick, 2001). These gaps are surpassed by phylogenetic and functional distinctness (PDist and FDist). In this sense, relating functional distinctness with phylogenetic distinctness allow to infer eco-evolutionary mechanisms structuring local communities, like rapid trait evolution hypothesized by functional overdispersion (Figure 1b; Mayfield & Levine, 2010; Safi et al. 2011).

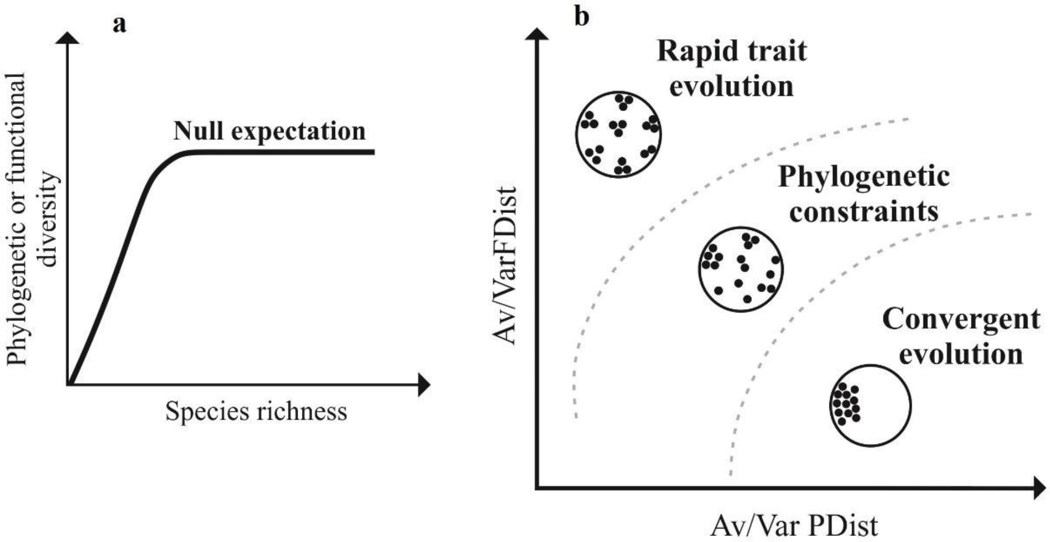


Figure 1. Theoretical models for relationships between (a) phylogenetic or functional diversity and species richness, and (b) functional distinctness components with phylogenetic distinctness components (Adapted from: Cisneros et al., 2014).

The functional distinctness is the average resemblance among species traits in a sample (Somerfield et al., 2008), commonly calculated through pairwise trait-based dissimilarities matrices that generate functional dendrograms connecting species (Kondratyeva et al., 2019). Selecting traits is a relevant step because adding or subtracting traits may change the overdispersion/clustering patterns, and consequently, the conclusions (Saito et al., 2016). Besides, selected traits must be related to ecosystem functioning, like those chosen for marine nematodes, which represent physiological, behavioral and ecological features, and are commonly used in ecological studies (Schratzberger et al., 2007; Alves et al., 2014; Kalogeropoulou et al., 2014).

The phylogenetic distinctness represents the uniqueness of a species in terms of its evolutionary history among the species of the communities (Jarzyna e Jets, 2016; Podani et al., 2018). This measure has been evaluated from supertrees for vascular plants (Purschke et al., 2013), aquatic insects (Saito et al., 2016) and mammals (Cisneros et al., 2014; Hidasi-Neto et al., 2015; Thuiller et al., 2015; Presley et al., 2018). Although Nematoda is probably one of the most successful group of metazoa on earth, a supertree has not been constructed for the phylum so far, hampering an integrated analysis between species richness, PD and FD.

Constructing supertrees consists of reviewing molecular and morphological phylogenies, which may cover particular genetic markers and sets of taxa. These individual studies provide detailed characterization of taxa that facilitate in-depth analyses (Smith & Brown, 2018), being able to discuss the congruences between molecular and morphological data. Thus, systematic reviews are very relevant tools that validate species based on detailed descriptions, which allow accurate identifications. Besides, these reviews guide future taxonomic and phylogenetic studies, as well as subsidize ecological and evolutionary studies.

Therefore, this thesis has three main objectives, each presented as a separated chapter: 1) to elaborate a systematic review of an important family of marine nematodes, 2) to construct a supertree for Nematoda, and 3) to infer ecological and evolutionary processes from phylogenetic and functional distinctness of marine nematodes. The order of the chapters is according to the linearity of systematic knowledge to serving as a foundation to functional and phylogenetic matrices of eco-evolutionary studies.

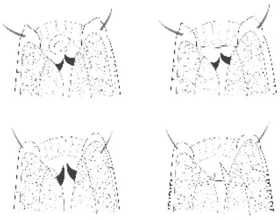
Chapter Overview

Chapter 1 provides a systematic review of one of the largest families of Nematoda, Chromadoridae. This paper integrates and update previous reviews, like the species lists of Gerlach & Riemann (1973) and the genus diagnosis of Tchesunov (2014), to guide future species identifications, taxonomic descriptions and phylogenetic studies. Thus, we present a historical background, diagnosis and list of valid species for each genus, polytomous keys for genera of the three major subfamilies using the most important diagnostic characters, and a phylogenetic analysis based on rDNA sequences currently available in the GenBank. This chapter is published in Zootaxa.

Chapter 2 presents an informal supertree for Nematoda, analysing the currently knowledge of phylogenetic relationships from all the valid marine genera. The construction of the supertree was based on complementing the most inclusive phylogenetic tree for the phylum (van Megen et al., 2009) by references indicated in the GenBank and descriptions of valid taxa. Polytomies were assumed when phylogenetic relationships were absent. The supertree suggests two new orders, one new suborder, four new superfamilies, one new family and many changes in the traditional classification. Therefore, it is a relevant basis to determine phylogenetic relationships among nematodes, to suggest systematics re-examination of taxa and explore the evolutionary relationships in ecological studies.

Chapter 3 test whether the environmental distinction among coastal habitats have driven distinct eco-evolutionary processes. Overdispersion and underdispersion patterns of species richness, phylogenetic and functional distinctness suggest different evolutionary and ecological mechanisms shaping communities. The convergent evolution is a common process acting on marine communities, since the coastal habitats are constantly submitted to selective pressures. However, these habitats are environmental different and, consequently, the selective pressures differ across the habitats. Given these differences, we hypothesized that the power of convergent evolution across the coastal habitats would be higher for homogeneous than for heterogeneous habitats, since heterogeneous habitats have a higher niche-breadth.

Lastly, I present a discussion about the relevance of integrating taxonomy, systematics, phylogeny and ecology, based on the obtained results, highlighting their limitations and their advances for the scientific knowledge.



CHAPTER 1

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

Virag Venekey[1], Paula F. Gheller[2], Noelia Kandratavicius[3], Beatriz Pereira Cunha[4], Ana Carolina Vilas-Boas[5], Gustavo Fonseca[5] & Tatiana F. Maria[6]

[1]Universidade Federal do Pará, Grupo de Estudos de Nematoda Aquáticos, Laboratório de Pesquisa em
Monitoramento Ambiental Marinho, Av. Augusto Corrêa, 01. Guamá—Belém—PA, Brazil. CEP: 66075-110
[2]Universidade de São Paulo (USP), Instituto Oceanográfico, Praça do Oceanográfico, 191. CEP: 05508-120.
Cidade Universitária. São Paulo—SP. Brazil
[3]Universidad de La Republica, Laboratorio de Oceanografía y Ecología Marina, Facultad de Ciencias, Igua 4225, CP:11400.
Montevideu. Uruguay
[4]Universidade Estadual de Campinas, Instituto de Biologia, Programa de Pós-graduação em Biologia Animal, Rua Monteiro Lobato, 255. CEP 13083-862, Cidade Universitária Zeferino Vaz. Campinas—SP. Brazil
[5]Universidade Federal de São Paulo, Campus Baixada Santista, Instituto do Mar. R. Carvalho de Mendonça, 144 CEP: 11070-100. Ponta da Praia. Santos-SP. Brazil
[6]Universidade Federal do Estado do Rio de Janeiro (UNIRIO), Instituto de Biociências Departamento de Ecologia e Recursos Marinhos. Av. Pasteur, 458, sala 411. CEP: 22290-240. Urca. Rio de Janeiro-RJ. Brazil

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[7]Corresponding author. E-mail: venekey@ufpa.br, virag_venekey@yahoo.com.br

1.1 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 constructed for the subfamilies and for the genera of the three major subfamilies (Chromadorinae, Euchromadorinae and Hy-podontolaiminae) 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 de-fined 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

1.2 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 m2 (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.

1.3 MATERIAL AND METHODS

1.3.1 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.

1.3.2 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/).

1.4 RESULTS AND DISCUSSION

1.4.1 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 valid genus by Lorenzen (1994), but although Tchesunov (2014) included it in his review, he considered it dubious. Smol & Decraemer (2006) and Tchesunov (2014) argumented 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.

1.4.2 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 “basketweave”. 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.

1.4.3 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 can not 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 latteral differentiation;
5. Lateral alae present.

Anterior sensilla pattern:

1. 2 circles;
2. 3 circles.

Outer labial sensilla shape:

1. Papiliform;
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.

1.4.4 Comments about valid genera of Chromadoridae

Subfamily Chromadorinae

Diagnosis (modified from Tchesunov, 2014): Cuticle homo- or heterogenous with or without latteral 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 detailes 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 Chromadora 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 punctateion 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 cupshaped 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: 4

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

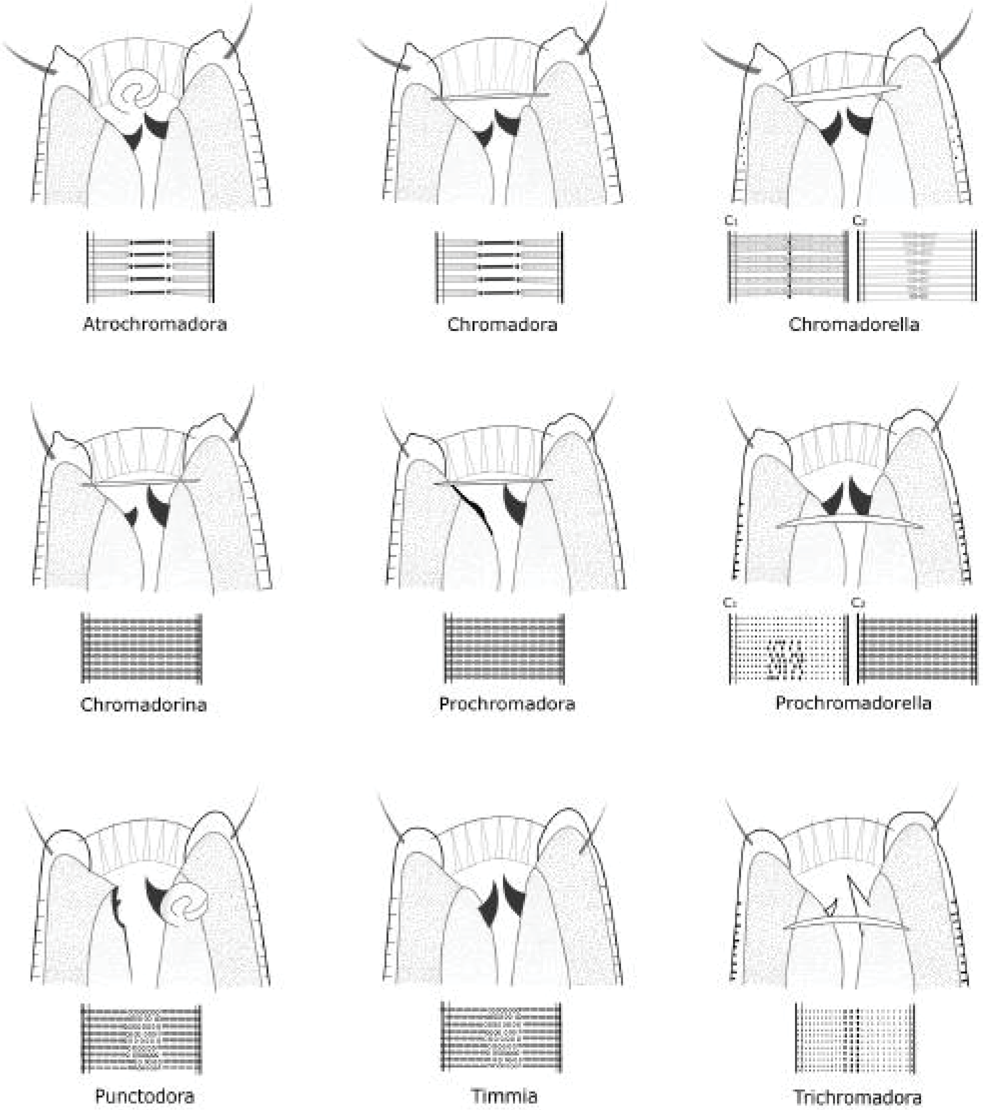

Figure 1. Schematic representation of Chromadorinae genera. The drawings aim to show head with buccal cavity and amphideal fovea, and cuticle ornamentation (general pattern or C1 at anterior body level and C2 at posterior body level). In all drawings the right side is the dorsal side of the nematode.

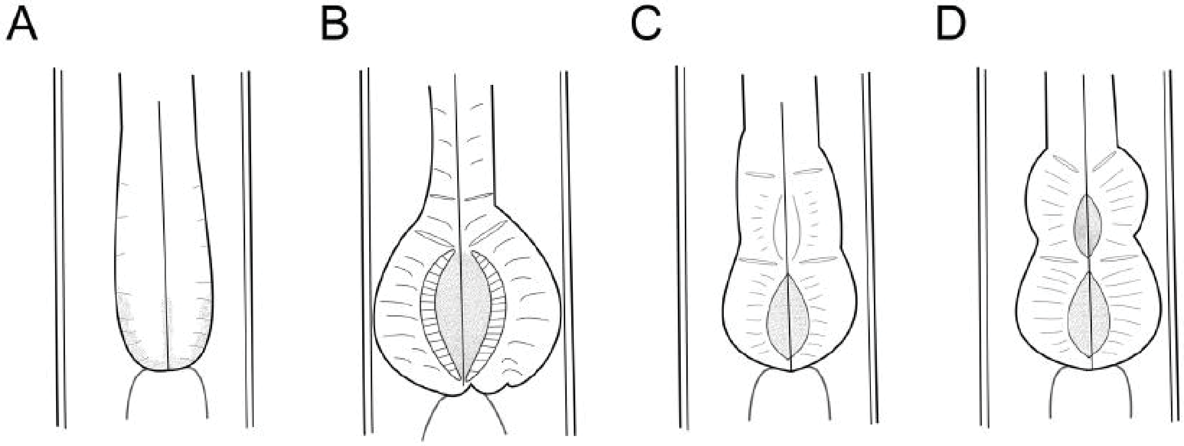

Figure 2. Schematic representation of the pharynx states. A: cylindrical. B: single pharyngeal bulb. C: single pharyngeal bulb, but plasmatic interruptions ressemble a double bulb. D: double pharyngeal bulb.

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:

Cutice:

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 definied 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 loose 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 ringe. 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.

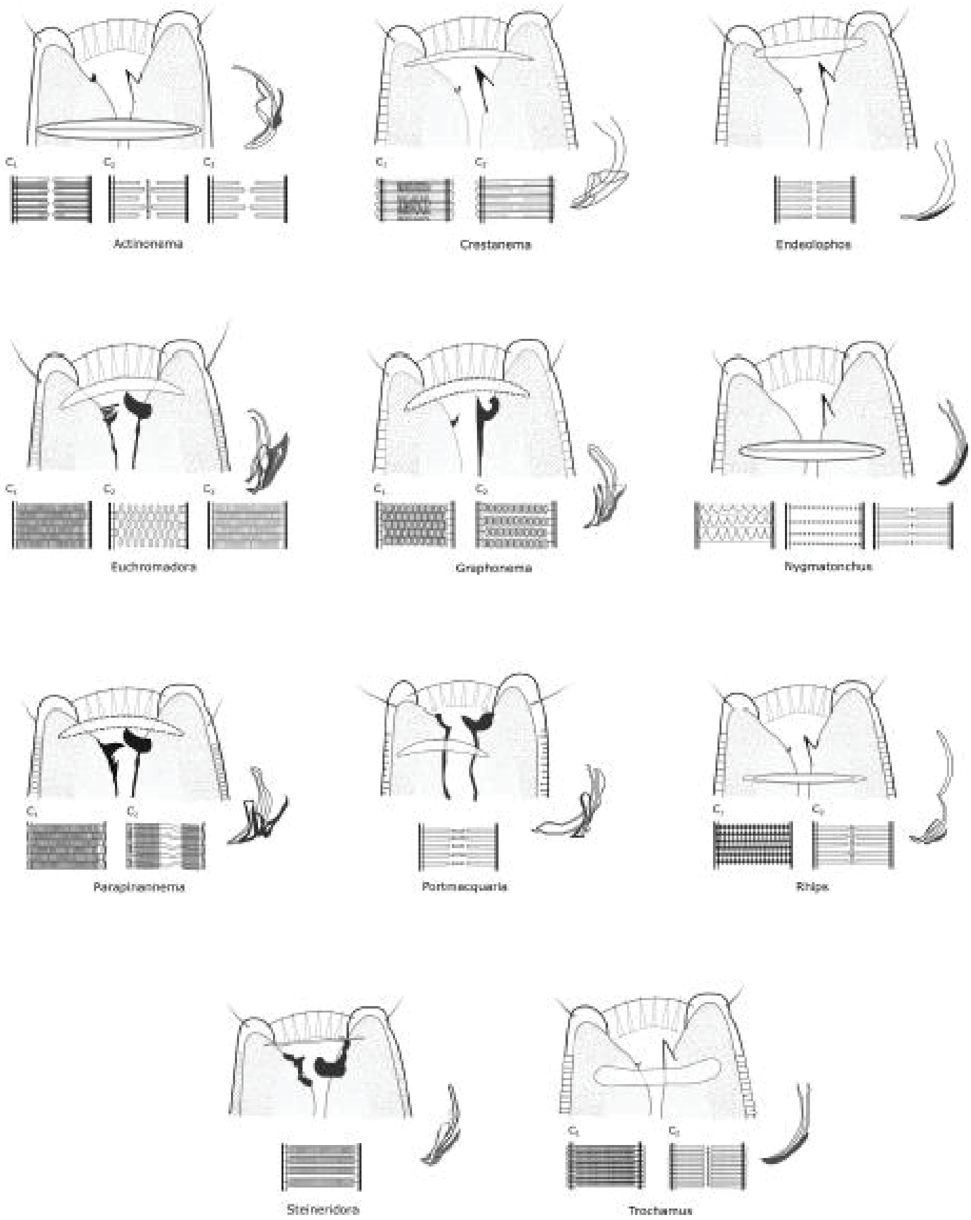

Figure 3. Schematic representation of Euchromadorinae genera. The drawings aim to show head with buccal cavity and amphideal fovea, cuticle ornamentation (general pattern or C1 to C3: variation from anterior to posterior region of the body) and coppulatory apparatus. In all drawings the right side is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

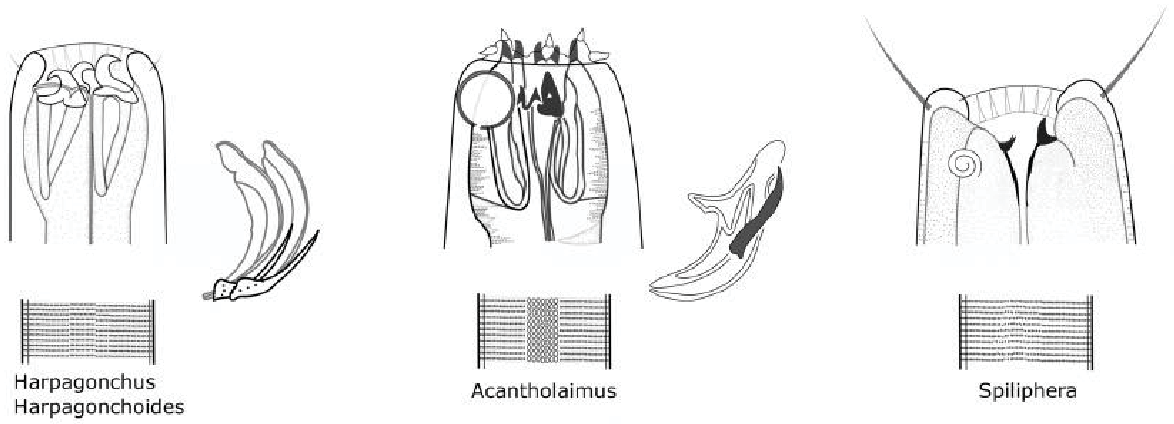

Figure 4. Schematic representation of Harpagonchinae and Spilipherinae genera. The drawings aim to show head with buccal cavity and amphideal fovea and cuticle ornamentation (general pattern). For Harpagonchus, Harpagonchoides and Acantholaimus the copulatory apparatus is also presented. In all drawings 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 subantarctic 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. Chromadorita 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 meager, 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 cuticularised 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 it has been recognized the singularity of the cuticle and buccal cavity of Innocuonema, 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 & 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.

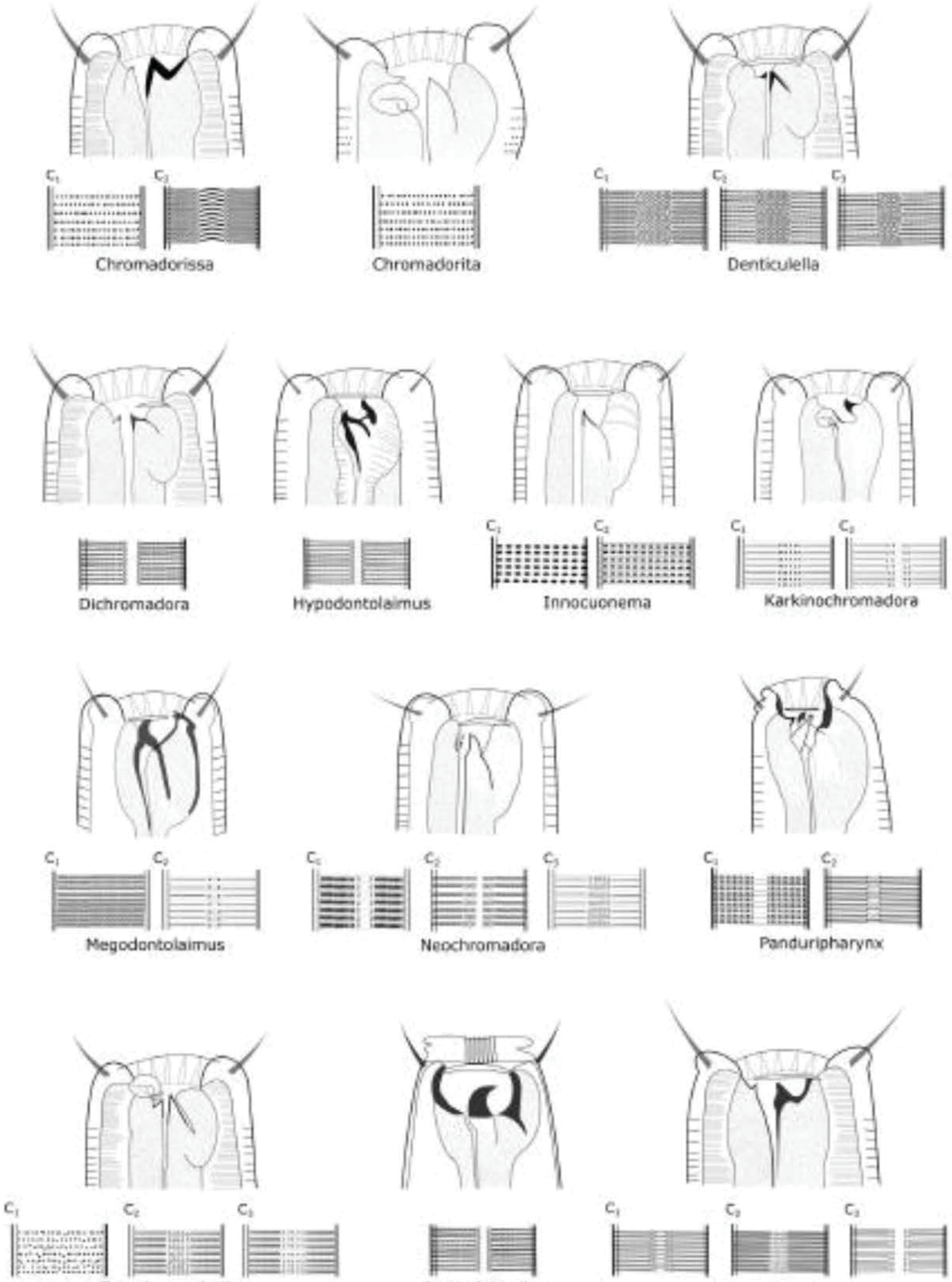

Figure 5. Schematic representation of Hypodontolaiminae genera. The draws aim to show head with buccal cavity and amphideal fovea and cuticle ornamentation (general pattern or C1 to C3: variation from anterior to posterior region of the body). In all drawings the right side is the dorsal side of the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

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;
3. 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 latteral 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, dispite 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 an other, valid, species of the genus should be indicated to substitute it as 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) argumented 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) argumented 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 can not 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 unequivocably 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 pharingeal bulb. In our opinion Paradichromadora description resembles Chromadorita which is a genus with large variation of cuticle ornamentation and bulb development among the species. Its 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 boy 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

1.4.5 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 occured 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).

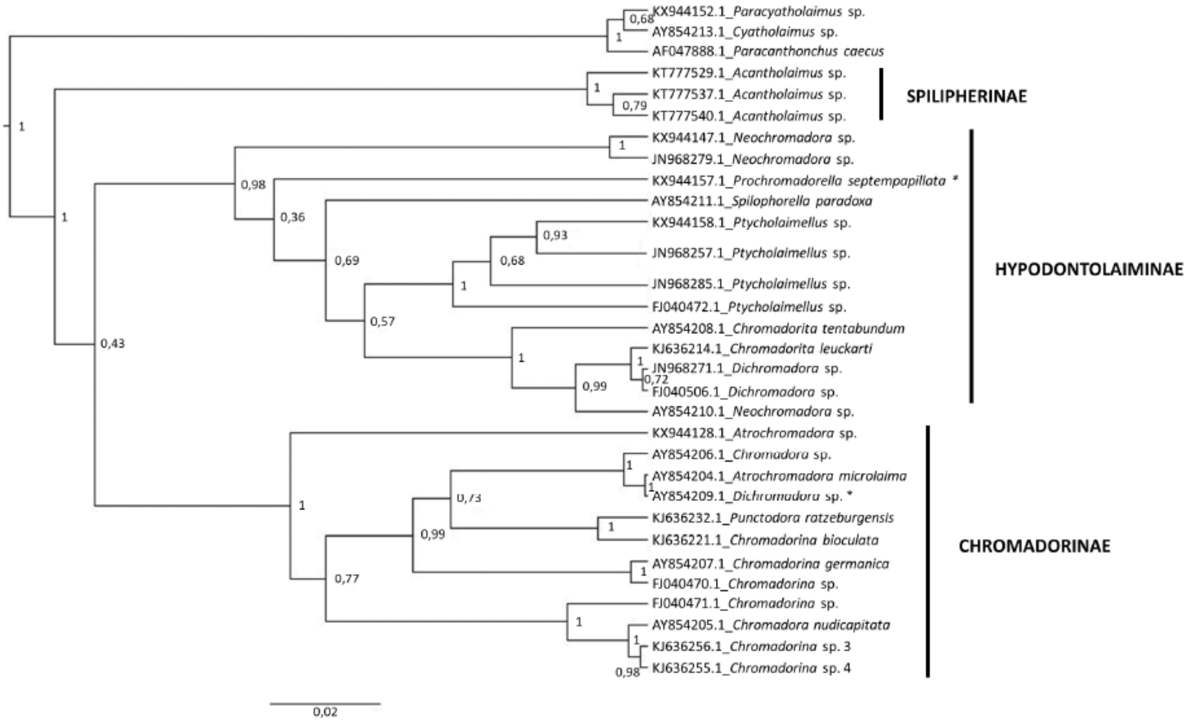

Figure 6. Bayesian tree inferred by 18S sequences. The species are colored based on current classification: Spilipherinae in blue, Chromadorinae in green and Hypodontolaiminae in red. *Species currently classified in a subfamily different from that which was grouped by Bayesian analysis. The posterior 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.

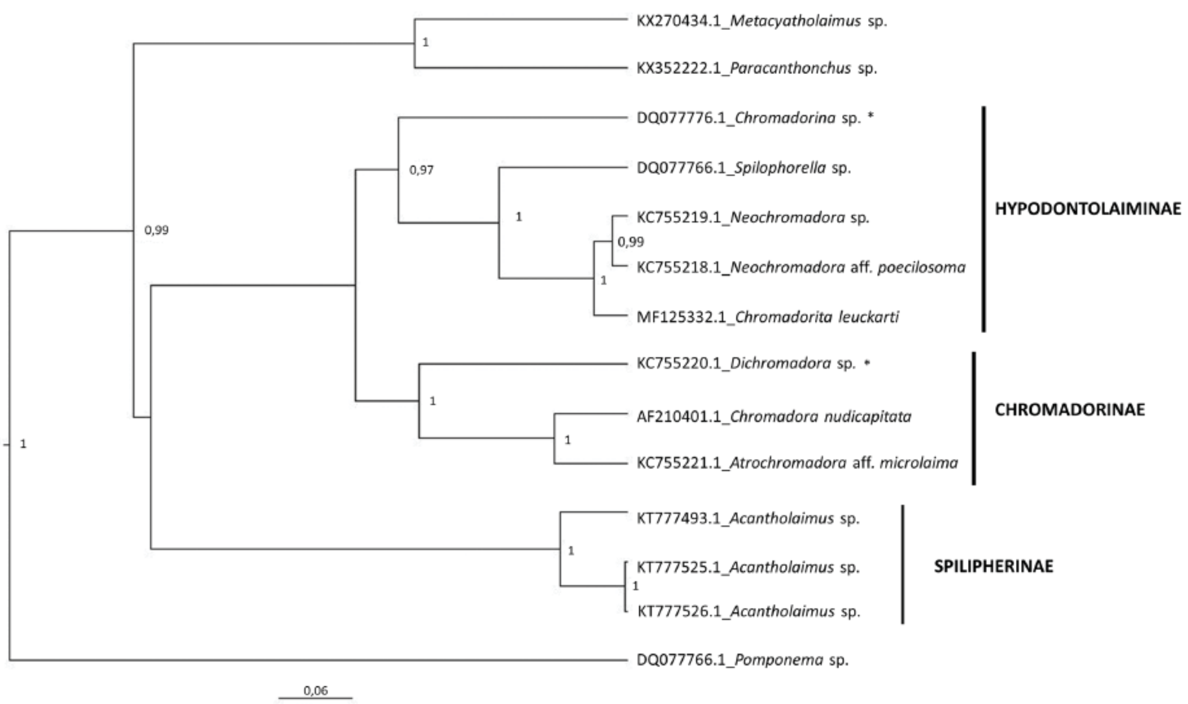

Figure 7. Bayesian tree inferred by 28S sequences. The species are colored based on current classification: Spilipherinae in blue, Chromadorinae in green and Hypodontolaiminae in red. *Species currently classified in a subfamily different from that which was grouped by Bayesian analysis. The posterior probabilities are given on each node. The scale represents substitutions per site.

1.5 ACKNOWLEDGEMENTS

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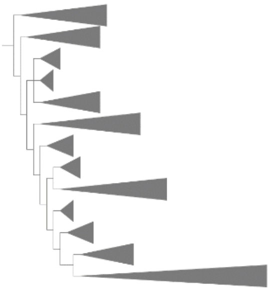
1.6 APPENDIX 1

Sequences retrived 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
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
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



CHAPTER 2

A supertree of Nematoda: implications for the systematics of marine taxa

Ana Carolina Vilas-Boas [1, 2*]; Gustavo Fonseca[2]

[1]Pós-graduação em Sistemas Costeiros e Oceânicos, Centro de Estudos do Mar, Universidade Federal do Paraná, Avenida Beira Mar s/n, Pontal do Sul, CEP 83255-976, PO Box 61, Pontal do Paraná, Paraná, Brazil
[2]Laboratory of Aquatic Ecology, Instituto do Mar, Universidade Federal de São Paulo, Rua Carvalho de Mendonça, 144, Santos, São Paulo, Brazil

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*Corresponding Author. E-mail: ananinanina@hotmail.com

2.1 ABSTRACT

This study aimed at constructing an informal supertree of Nematoda, analysing the currently knowledge of phylogenetic relationships from all the valid marine genera, including the unsequenced ones. The supertree was based on references indicated in the GenBank and the descriptions of taxa considered valid from WoRMS. When phylogenetic information was not available, or it was contradictory among the references, polytomies (uncertainties) were assumed. Only 32% of the marine genera have molecular sequences deposited in the GenBank and were included in phylogenetic studies. Based on cladistic studies and phylogenies from four genes (COI, ITS, 18S, 28S), the supertree ended with thirteen major clades, encompassing 11 orders and the subclass Dorylaimia. The other clades include Haliplectidae and *Prodesmodora* (clade 4), and Siphonolaimoidea together with Axonolaimidae (clade 11). An important proposed change supported by molecular and morphological evidences is to consider the genera of Enchelidiidae as a terminal group within Oncholaimidae. The supertree showed that polytomies are mainly at subfamilies and genera level due to incipient amount of sequences in public depositories, the paraphyletic conditions in molecular phylogenies and the lack of cladistic analysis. The current supertree serves as a basis to determine phylogenetic relationships among nematodes, to improve systematics classification through the re-examination of taxa, guide future species descriptions and explore the evolutionary relationships in ecological studies.

Keywords: Enchelidiidae - marine nematode - polytomies - Siphonolaimoidea - systematics

2.2 INTRODUCTION

Nematoda is probably one of the most successful group of metazoan on earth, since they occupy diverse habitats, making them of significant ecological and economic relevance (De Ley, 2006; Kim et al., 2017). Today, the phylum is composed by 23 orders and about 27.000 described species (Schmidt-Rhaesa, 2014). The most inclusive phylogenetic tree for the phylum is based on the small-subunit ribossomal RNA 18S gene (or SSU rRNA) and covers approximately 1.200 taxa from 15 orders (van Megen et al., 2009). Since its publication, the phylogeny of the phylum has undergone through constant modifications deeply changing the understanding of their evolution and diversification (Armenteros et al., 2014; Kiewnick et al., 2014; Kim et al., 2017; Park et al., 2011). Nevertheless, these recent studies have each considered a particular set of taxa and genetic marker, hampering an overall picture of the phylogenetic tree of the phylum. On top of that, the coverage of the molecular studies is meager in face of the number of described species within the phylum. Although newly phylogenetic analyses and nematode species descriptions are being published, little attention has been given to synthesize the information into a single and encompassing phylogenetic tree.

There are different approaches used to integrate the existing phylogenetic knowledge into a large phylogeny: supermatrix, supertree and grafting (Beaulieu et al., 2012). In the supermatrix approach, separate characters are combined into a single phylogenetic matrix and analysed simultaneously (Bininda-Emonds, 2004; de Queiroz & Gatesy, 2007). Therefore, all the character evidence is used - including phylogenetically non-informative characters - however, some data cannot be combined, and subjective decisions must be made (Davis & Page, 2014). Supertree stands out as an approach that combines the information from existing phylogenetic tree topologies, rather than the character data, in a single and encompassing tree (Creevey & McInerney, 2005; de Queiroz & Gatesy, 2007). The “grafting approach” is a concatenation of hierarchically nested trees from independent studies into a backbone tree, combined to systematic knowledge (Beaulieu et al., 2012; Hinchliff et al., 2015). This procedure can be done manually (Tree of Life Web Project) or through algorithms (Open Tree of Life) resulting in a synthetic tree which can change as new studies are published.

Particularly for those clades with insufficient molecular data, supertrees provide a reasonable representation of relationships between sequenced and ‘unsequenced’ taxa (Hedrick et al., 2015; Wiens et al., 2010). In parallel, for well sequenced clades, supertrees can help to solve uncertain relationships resultant from different phylogenetic hypothesis (Rangel et al., 2015). While some branches of an informal supertree might be derived from robust statistical analysis, others are constructed without statistical inferences and are based on systematic studies. Therefore, the supertree is an important approach to propose new phylogenetic hypothesis, to visualize gaps in data collection, to orient taxonomical studies, as well as to serve as basis of evolutionary ecological studies (Davis & Page, 2014).

Supertrees have been used to obtain the best evolutionary hypothesis for a variety of taxa, such as birds (Davis & Page, 2014), angiosperms (Baker et al., 2009; Davies et al., 2004), mammals (Beck et al., 2006; Nyakatura & Bininda-Emonds, 2012) and insects (Davis et al., 2010). Specifically, informal supertrees suggested evolutionary rate shifts between flight structures and taxonomic diversification of birds (Benson & Chroniere, 2013), as well as to understand the evolutionary responses of dental morphology of ungulates to dietary changes (Famoso et al., 2016).

Within the phylum Nematoda, the marine taxa encompass about 11.400 described species, 6.900 being of free-living (Appeltans et al., 2012). Most of the information of the marine taxa are restricted to the morphological data, which do not provide strong support to deeper relationships (Blaxter et al., 2016). Besides, the position of certain taxa within the phylogenetic trees are paraphyletic, meaning that either the systematic classification of the group is not phylogenetically informative or that the sequences used to infer the phylogenetic tree was misidentified (Fonseca et al., 2018). Thus, the objective of this study is to construct an informal supertree of Nematoda, including all the marine genera described so far.

2.3 METHODS

The study consisted in reviewing the phylogenetic relationships of all clades that included at least one marine genus and graft them into a tree. The relationships presented by van Megen et al. (2009) was considered the backbone tree. This tree also contains terrestrial and parasitic forms that was kept in the present supertree.

Genera were considered marine from records obtained in Lorenzen (1994), Schmidt-Rhaesa (2014) and WoRMS (last access: 26/04/2018).

The survey of molecular phylogenetic articles was done in the GenBank, following the references indicated after each sequence. It is important to note that some genera/species have sequenced segments deposited in the GenBank, but they were not used in phylogenetic studies (eg. *Gonionchus* Cobb, 1920 is represented by two unpublished sequences of large-subunit ribossomal RNA 28S gene). For these cases, their phylogenetic relationships are established from the systematic studies. When inserting a genus in the supertree, it was observed its sister group, the branch support value, the year of publication and the molecular marker type. When available, branch support is represented by Boot (bootstrap replicates) and BPP (Bayesian posterior probability) values taken from the molecular phylogenetic papers using four genes: COI (Cytochrome Oxidase c Subunit 1), ITS (Internal Transcribed Spacer), 18S and 28S. After each branch support, a reference number of the citing article is given between brackets. The reference list of the supertree is in Table 2. Thus, a clade may contain data in which the relationships were stablished from different studies using different genes (e.g. articles using COI, 18S and 28S were considered for Enoplida, while only one article using 18S was considered for Triplonchida). In cases of conflicts or uncertainties between phylogenetic relationships, polytomies are assumed for the most basal branch of the target clade. This was done to avoid unsupported evolutionary steps. Uncertainties have arisen from low branch support values, conflicting relationships among genera due to incomplete sampling of species or misidentification of specimens. The unsequenced genera, considered valid from WoRMS, were also consulted in the Lorenzen (1994) and Schmidt-Rhaesa (2014), and cladistic studies published after 1994 were also considered in this review. When phylogenetic information was not inferred from these references, polytomies were assumed. Genera considered *inquirenda* (eg. *Metadesmodora* Schuurmans Stekhoven, 1942) are not included in the supertree. Genera considered *nomen nudum* (eg. *Cricohalalaimus* Bussau, 1993) are included in the supertree.

The informal supertree was transcribed into the Newick format through the Notepad++ program (version 7.4.2), considering the genera as terminal taxa, and checked through the FigTree program (version 1.4.2).

2.4 RESULTS AND DISCUSSION

2.4.1 The data set

A total of 185 genera, among the 575 valid genera of marine nematodes, have sequences deposited in the GenBank and were used in phylogenetic studies (Table 1). There are additional 28 genera which have sequences in the GenBank, but their phylogenetic positions have not been yet explored. The most used genetic marker from the surveyed references was the 18S (Table 2). This reflects its facility of amplification and wide phylogenetic resolution, from genus to deep phylogenetic relationships (Bik et al., 2010; Blaxter & Koutsovoulos, 2015; De Ley et al., 2005). Most of the surveyed trees were inferred through Bayesian inference and Maximum Likelihood methods. Both methods are character-based methods, which simultaneously compares all the sequences in the alignment considering the mutational events accumulated on the sequences, therefore avoiding loss of information (Patwardhan et al., 2014; Yang & Ranalla, 2012). Given the small size of the molecular data set, it is important to note that the accuracy of the relationships inferred from the molecular phylogenetic hypothesis is susceptible to change from the collection of new data (Wiens & Tiu, 2012). For nematodes these inferences are especially important given the small number of fossil records and unclear morphological characters to differentiate closely related taxa (Bik et al., 2010; Leduc & Sinniger, 2018).

2.4.2 The supertree

The proposed supertree of nematodes has 882 tips separated into 13 major clades (Figure 1), in which several reallocations of genera are proposed. From the 66 families of marine nematodes, 12 families, each with 1 or 2 genera, have 100% of the genera sequenced (Table 1). Sixteen families have no molecular record. For the most species rich families (eg. Chromadoridae Filipjev, 1917 and Desmodoridae Filipjev, 1922), less than half of the genera are included in phylogenetic trees.

According to 18S rDNA, the first split in the supertree separates Enoplia Pearse, 1942 (Clade 1) as the most basal branch of the tree (van Megen et al., 2009). The second split considers Dorylaimia Inglis, 1983 (Clade 2) as a sister group of chromadoreans (Holterman et al., 2006; van Megen et al., 2009). An evolutionary hypothesis is that the first major diversification event separating Enoplia within Nematoda occurred after the emergence of vascular plants, about 440 million years ago (Quist et al., 2015). This hypothesis corroborates the possible marine origin of the phylum, however it is still not definitive since the phylogenetic signal is weak (Blaxter & Koutsovoulos, 2015) and the relationship between Dorylaimia and Chromadoria Pearse, 1942 does not have high branch support (van Megen et al., 2009). Several morphological characters of dorylaims are apomorphic and/or autapomorphic, like their buccal cavity and the connection of the intestine with the rectum, proving them as a monophyletic and distinct group from the other nematodes (Peña-Santiago, 2014). Their relationship with chromadoreans has been suggested by embryogenesis analyses. Both taxa are characterized by the lack of a nuclear membrane in mature spermatozoa, a plesiomorphic character present in many members of Enoplida Filipjev, 1929 (Justine, 2002; Yushin & Malakhov, 2014). Moreover, developmental studies with species of Enoplida, Triplonchida Cobb, 1920, Dorylaimia and Plectida Malakhov, 1982 revealed a gradual evolution in the mode of establishment of a germline: from only a single cell lineage in *Enoplus* Dujardin, 1845 to a partially lineage-independent cell specification in *Plectus* Bastian, 1865 (Schierenberg & Sommer, 2014).

The third split corresponds to the monophyletic Chromadoria, a well resolved clade supported by 18S analyses, and characterized by a diverse morphology in several characters like the buccal cavity, the cuticle and amphideal fovea (De Ley & Blaxter, 2004; Decraemer et al., 2014). Within Chromadoria, the supertree separates Microlaimida Leduc, Verdon & Zhao, 2018 (Clade 3), Haliplectidae and *Prodesmodora* (Clade 4), and Chromadorida Chitwood, 1933 (Clade 5) from the rest of the supertree (4th split; Figure 1). Most phylogenies based on the 18S suggested the monophyly of these clades (Meldal et al., 2007; Holterman et al., 2008; van Megen et al. 2009; Leduc, Verdon & Zhao, 2018; Leduc, Zhao, Verdon & Xu, 2018). Nevertheless, the relationships between them are still unresolved (Holovachov et al., 2012). The erection of the clade four is to accommodate *Haliplectus* Coob, 1913 and *Prodesmodora* Micoletzky, 1923 as suggested by the 18S phylogeny (Boot = 100 in van Megen et al. 2009). Haliplectidae Chitwood, 1951 have been considered *incertae sedis* by the traditional classification (Holovachov, 2014a). *Prodesmodora* and Haliplectidae share similar cuticle, posterior bulb of the pharynx and arcuate spicules (Holovachov, 2014a; Tchesunov, 2014b). On the other hand, Microlaimida is considered more closely related to Chromadorida than any other order within Chromadoria (BPP = 85 in Leduc, Verdon & Zhao, 2018). The three orders share ornamented cuticle and a pharyngeal bulb, or a posteriorly widened pharynx, nevertheless these characters are not restricted to them, and the molecular inferences still need to be supported by more detailed morphological data.

The 5th split of the supertree points the order Desmodorida De Coninck, 1965 (Clade 6) as a sister group of Chromadoria (Leduc, Verdon & Zhao, 2018; van Megen et al. 2009). The relationship of this order with Chromadorida and Desmoscolecida Filipjev, 1929, forming “nested series”, is corroborated by taxonomic (Decraemer & Smol, 2006) and molecular studies (Holovachov, Rodrigues, Zbinden & Duperron, 2013; van Megen et al. 2009), but sequences from Desmoscolecida taxa are rare (Decraemer & Rho, 2014). The monophyly of Desmodorida in molecular phylogenies (Leduc, Verdon & Zhao, 2018; Leduc, Zhao, Verdon & Xu, 2018) is corroborated by the autapomorphy of the anterior testis (Lorenzen, 1994), except for *Onepunema* Leduc & Verschelde, 2013 with two testis.

The next split (6th split; Figure 1) separates Desmoscolecida (Clade 7) from the rest of the supertree with high branch support the (Holovachov et al., 2012; Holovachov, Rodrigues, Zbinden & Duperron, 2013; Hwang et al., 2009). The position of this taxon within Nematoda is still debated (Decraemer & Rho, 2014). The presence of four cephalic setae inserted on peduncles and the vesicular amphideal fovea situated on the head to shortly behind it supports the monophyly of the group (Decraemer & Smol, 2006).

The orders Araeolaimida De Coninck & Schuurmans Stekhoven, 1933 and Monhysterida Filipjev, 1929 appears as a monophyletic group (Clades 8 and 9; 7th split; Figure 1) after the reallocation of the families Fusivermidae Tchesunov, 1996, Linhomoeidae Filipjev, 1922, Siphonolaimidae Filipjev, 1918 and Axonolaimidae Filipjev, 1918 to other clade (see discussion below: Clades 8 to 11). Recent molecular phylogenies points Araeolaimida and Monhysterida as non-monophyletic (Holovachov, Rodrigues, Zbinden & Duperron, 2013; Hwang et al., 2009; Leduc, Verdon & Zhao, 2018; Leduc, Zhao, Verdon & Xu, 2018; van Megen et al. 2009), different from the current systematic classification. This inconsistency can be attributed to incomplete taxonomic descriptions hampering a detailed cladistic analysis of some taxa within these orders (Fonseca & Decraemer, 2008; Fonseca & Bezerra, 2014a; 2014b).

Molecular studies suggest with high branch support (Boot = 100) that the next bifurcation (8th split; Figure 1) separates Isolaimiida Cobb, 1920 as a monophyletic group (Clade 10). This order includes the families Isolaimiidae Timm 1969 and

Aulolaimidae Jairajpuri & Hopper 1968 (Holterman et al., 2008; van Megen et al., 2009). Originally, Isolaimiidae belongs to Isolaimiida and Aulolaimidae to Plectida, but both phylogenetic positions are uncertain (Holovachov, 2014a). Their close relationship is corroborated by several morphological characters, like the strongly elongated buccal cavity, inconspicuous pore-like amphids and reflexed ovaries (Holterman et al., 2008). An important observation however is that the sequences used by van Megen et al. (2009) for these clades were shorter when compared to the sequences of the other clades used in the analyses (Holovachov, 2014a).

In the next split (9th; Figure 1), Siphonolaimoidea together with Axonolaimidae are suggested as a sister group of the terminal dichotomy of the supertree, based on the high branch support from molecular data (BPP = 100) (Holterman et al., 2008; Holovachov, Rodrigues, Zbinden & Duperron, 2013; Leduc, Verdon & Zhao, 2018). The morphological similarities between these taxa are mainly related to the reproductive system, often two gonads, opposed and outstretched, and a gubernaculum with an apophyses oriented caudally (Fonseca & Bezerra, 2014b).

The final bifurcation separates Plectida (Clade 12) from Rhabditida Chitwood, 1933 (Clade 13) according to 18S phylogenies (Holovachov et al., 2012; Holovachov, Boström, Tandingan De Ley, Robinson, Mundo-Ocampo, & Nadler, 2013; Holovachov, Rodrigues, Zbinden & Duperron, 2013). The order Plectida covers the suborders Ceramonematina Cobb, 1933 and Plectina Malakhov, Ryzhikov & Sonin, 1982, but in the present supertree, Ceramonematina is reallocated to Desmoscolecida. Plectida is a well-supported clade (Holovachov, 2014b) which shares with Rhabditida a similar structure of the pharynx (Lorenzen, 1994). Rhabditida is mainly represented by species associated with arthropods and some mammals (Sudhaus, 2014). Therefore, except for the addition of the marine genus *Litoditis* Sudhaus, 2011, this clade is similar represented to Rhabditida in van Megen et al. (2009).

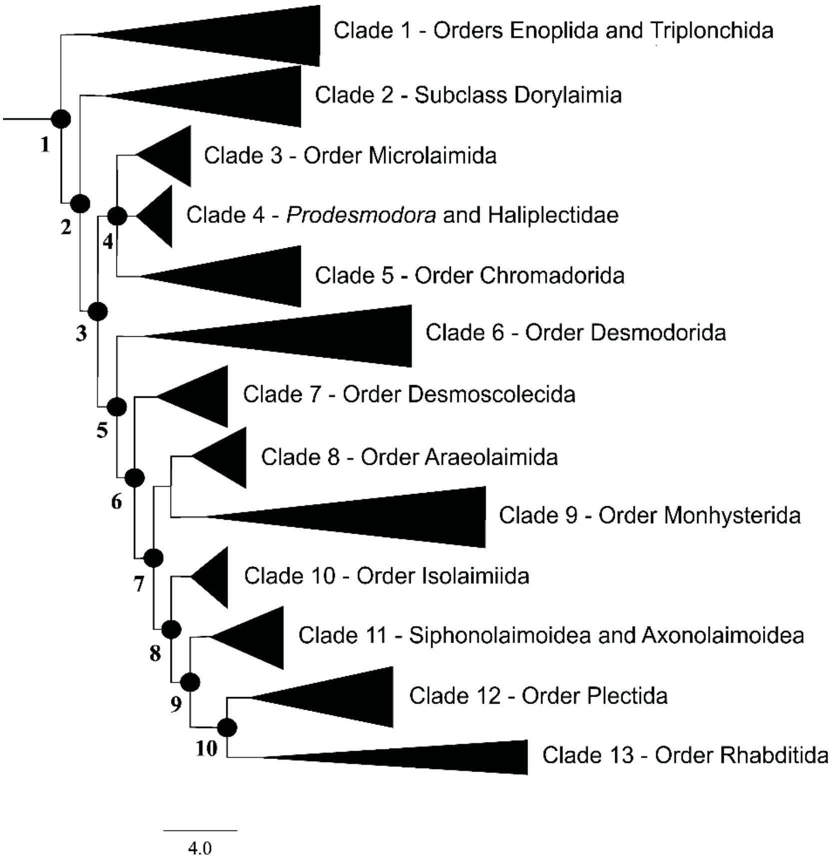

Figure 1. Synthetic supertree of Nematoda with branches collapsed into orders.

CLADE 1 – ORDERS ENOPLIDA AND TRIPLONCHIDA

Enoplida and Triplonchida are considered monophyletic orders according to the 18S gene phylogenies (Leduc, Verdon & Zhao, 2018; Smythe, 2015; van Megen et al., 2009). The molecular studies suggested that Enoplida is subdivided in 3 clades, representing the suborders Ironina, Oncholaimina, and Enoplina (Figures 2 to 4), and Triplonchida, which is formed by a single clade (Figure 5) (Bik et al., 2010; Leduc, Verdon & Zhao, 2018; van Megen et al., 2009).

CLADE 1.1. Suborder Ironina Siddiqi 1983 (Figure 2)

Based on the molecular data, this suborder includes four superfamilies: Campydoroidea, Ironoidea, Tripyloidoidea and Trefusioidea. Till now, the traditional classification considered Campydorina, Tripyloidina De Coninck, 1965 and Trefusiina as suborders and Ironina formed by a single superfamily (Smol et al., 2014).

Superfamily Campydoroidea Jairajpuri 1976

This superfamily comprises two families: Rhabdolaimidae Chitwood, 1951 and Campydoridae (Thorne, 1935) Clark, 1961. Based on 18S phylogenies, the genera *Rhabdolaimus* de Man, 1880, *Syringolaimus* de Man, 1888 and *Campydora* Cobb, 1920 are considered a cluster with high branch support, confirming the monophyly of the superfamily (Bik et al., 2010; Smythe, 2015; van Megen et al., 2009). *Syringolaimus* and *Campydora* share a posterior bulb in the pharynx, character that is absent in other enoplids (Smol et al., 2014). *Syringolaimus* has been classified as Ironidae de Man, 1876 according to the presence of two solid teeth in the buccal cavity (Smol et al., 2014). The reallocation of *Syringolaimus* to Campydoridae implies that the presence of two solid teeth is a convergence within Nematoda. *Rogerus* Hoeppli & Chu, 1934, is also included in Campydoroidea based on its morphological similarities with *Rhabdolaimus* (Holovachov, 2014b).

Superfamily Ironoidea de Man 1876

According to the high branch support from molecular data (BPP = 0.97), this superfamily is formed by the families Alaimidae Micoletzky, 1922, traditionally classified as the only family of Alaimoidea Micoletzky, 1922, and Ironidae de Man, 1876 (Bik et al., 2010; Smol et al., 2014). Other studies suggested that the families Leptosomatidae Filipjev, 1916 and Oxystominidae Chitwood, 1945 should be transferred to the suborders Enoplina and Oncholaimina, respectively (Bik et al. 2010; Leduc, Verdon & Zhao, 2018; Smythe, 2015). Alaimidae is further separated in the three morphological subfamilies (Alaiminae Micoletzky, 1922, Amphidelinae Andrássy, 2002 and Cristamphidelinae Andrássy, 2002) based on the differences in the morphology of the cuticle, amphids, female gonads and spicules (Smol et al., 2014). Ironidae is formed by two subfamilies: Ironinae de Man, 1876 (*Ironus* Bastian, 1865) and Thalassironinae Andrássy, 1976. These subfamilies are also separated by habitat, *Ironus* being limnetic, while Thalassironinae is marine (Smol et al., 2014).

Superfamily Tripyloidoidea Filipjev 1928

The family Rhabdodemaniidae Filipjev, 1934 has been placed within the order Triplonchida, but this placement was considered “provisional”, since there is no a precise description of the spicule’s protractor muscle of this family (Holovachov & Shoshin, 2014). The morphology of two capsule-like structures surrounding the anterior part of each spicule of the spicule’s protractor muscles is considered unique in Triplonchida. Rhabdodemaniidae and Tripyloididae Filipjev, 1928 are here considered sister families due to the high branch support based on different methods of reconstruction which analysed 28S gene (Boot = 97 and 74 in Pereira et al., 2010). Besides, the proximity of *Rhabdodemania* Baylis & Daubney, 1926 to Ironidae was suggested as a homology between the movable odontia of both families (Smythe, 2015). The genera *Tripyloides* de Man, 1886 and *Bathylaimus* Cobb, 1894 are polytomic, since no subfamilies were proposed to Tripyloididae in the recent literature and only them have sequenced material.

Superfamily Trefusioidea Gerlach 1966

The families Trefusiidae Gerlach, 1966 and Trischistomatidae Andrássy, 2007 are considered sister families, since the relation among *Trefusia* de Man, 1893, *Rhabdocoma* Cobb, 1920 and *Trischistoma* Cobb, 1913 was presented with high branch support in molecular phylogenies (Bik et al., 2010; Smythe, 2015; van Megen et al., 2009). It is also known that these families have similar spicule characteristics, intestinal tract and muscles arrangement (Prado-Vera et al., 2016). These two families are traditionally grouped with Xenellidae de Coninck, 1965, Lauratonematidae Gerlach, 1953 and Simpliconematidae Blome & Schrage, 1985 as the superfamily Trefusioidea (WoRMS). Trefusiidae is represented by a dichotomy corresponding to the subfamilies Trefusiinae Gerlach, 1966 and Halanonchinae Wieser & Hopper, 1967, this last including *Rhabdocoma* (Shi & Xu, 2018). This genus was considered closer to *Africanema* Vincx & Furstenberg, 1988 than to *Trefusia*, in line with high branch support (Shi & Xu, 2018). Besides, *Rhabdocoma* possess a single posterior ovary, different from the didelphic genera of Trefusiinae. The genera *Tripylina* Andrassy, 1974 and *Trischistoma* are grouped in Trischistomatidae, a family accepted within Enoplida, by sharing a single ovary (Prado-Vera et al., 2016).

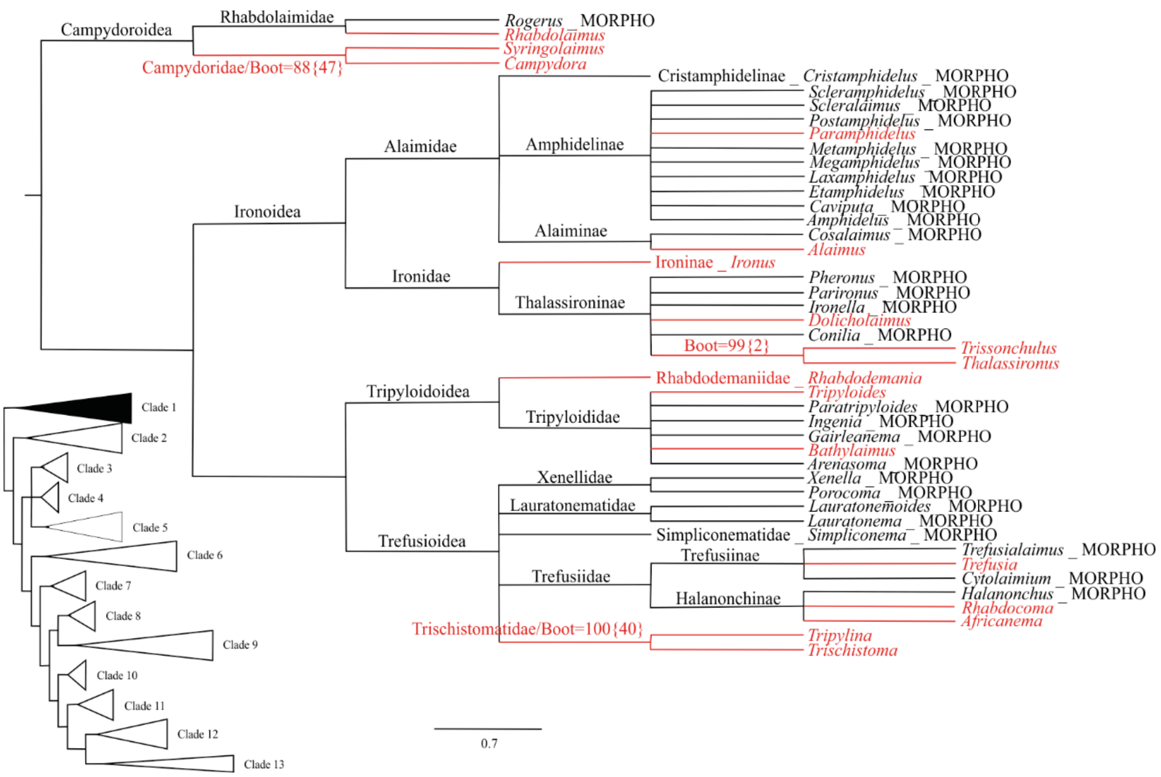

Figure 2. Representation of the Order Enoplida (suborder Ironina) of the supertree of Nematoda. The clades supported by molecular data are marked in red. The number between brackets corresponds to the number of reference in the list of consulted molecular studies.

Clade 1.2. Suborder Oncholaimina De Ley & Blaxter, 2002 (Figure 3)

Different from previous classification, molecular phylogenies indicated that the families Enchelidiidae, Oncholaimidae and Oxystominidae form a clade (BPP = 0.97 and 94, respectively) (Bik et al., 2010; Leduc, Zhao, Verdon & Xu, 2018; van Megen et al., 2009), which is supported by the presence of orthometanemes with a caudal filament (Lorenzen, 1994). From the morphological point of view, Oxystominidae has been classified within Ironina based in many characters as the shape of the buccal cavity and pharynx (Smol et al., 2014).

Family Oxystominidae Chitwood, 1935

This family does not have a known apomorphy (Lorenzen, 1994). The traditional classification considers three subfamilies (Oxystomininae Chitwood, 1935, Halalaiminae De Coninck, 1965 and Paroxystomininae De Coninck, 1965) within it. Nevertheless, only the subfamily Paroxystomininae (represented by *Maldivea* Gerlach, 1962 and *Paroxystomina* Micoletzky, 1924) is recovered in the supertree, corroborating the observed instability in the relationships among the genera within Oxystominidae (Bik et al., 2010; Leduc, Verdon & Zhao, 2018). The genus *Oxystomina* Filipjev, 1918 (Oxystomininae) is occasionally placed close to Campydorina Jairajpuri, 1983 (van Megen et al., 2009) or is grouped with *Halalaimus* de Man, 1888 (Halalaiminae) in line with a high branch support (BPP = 0.9) from a 18S tree (Bik et al., 2010). The deep-sea *Rhaptothyreus* Hope & Murphy, 1969 (Rhaptothyreidae Hope & Murphy, 1969), previously belonging to Rhaptothyreida Tchesunov, 1995, is placed within Enoplida. This decision considers the similarity of the amphid and the arrangement of the cephalic sensilla with some species of Oxystominidae, and the high branch support (BPP and Boot = 100) shared with *Halalaimus* in a 28S tree (Leduc, Verdon & Zhao, 2018). *Wieseria* Gerlach, 1956 and *Nemanema* Cobb, 1920 are included in the polytomy with *Oxystomina*, since they belong to Oxystomininae, according to the morphological descriptions (Smol et al., 2014). The clade containing *Cricohalalaimus* Bussau, 1993, *Litinium* Cobb, 1920 and *Thalassoalaimus* de Man, 1893 is well-separated from *Oxystomina* and *Halalaimus* (Bik et al., 2010; Leduc, Verdon & Zhao, 2018).

Family Oncholaimidae Filipjev, 1916

Originally, the superfamily Oncholaimoidea is firmly considered as a monophyletic taxon that covers the families Oncholaimidae and Enchelidiidae Filipjev, 1918 (Bik et al., 2010). However, Oncholaimidae has been considered paraphyletic by molecular studies, since the clade corresponding to Enchelidiidae appears as a derived group within it (Avó et al., 2017; Bik et al., 2010; Smythe, 2015; van Megen et al., 2009). This family covers only the subfamily Enchelidiinae, since Lorenzen (1994) synonimized the other subfamilies, and considering it as a subfamily of Oncholaimidae could solve the paraphyletic condition of the family. Based on this classification, the three large teeth are a plesiomorphic feature in Oncholaimidae (Shi & Xu, 2016).

Oncholaimidae is composed by seven subfamilies: Adoncholaiminae Gerlach & Riemann, 1974, Pontonematinae Gerlach & Riemann, 1974, Pelagonematinae De Coninck, 1965, Krampiinae De Coninck, 1965, Oncholaiminae Filipjev, 1926, Oncholaimeliinae Fiipjev, 1916 and Octonchinae De Coninck, 1965. Part of the phylogenetic relationships within the family are not all resolved and are presented as polytomic. The genera *Adoncholaimus* Filipjev, 1918 and *Admirandus* Belogurov & Belogurova, 1979 form a polytomy with the other genera of Adoncholaiminae which has no sequenced material (Mordukhovich et al., 2015; Smol et al., 2014; van Megen et al., 2009). *Meyersia* Hopper, 1967, previously classified in this subfamily, is within Oncholaiminae based on morphological and molecular data (Smol et al., 2014; Smythe, 2015). In Oncholaiminae, *Oncholaimus* and *Metoncholaimus* are considered sister genera (Pereira et al., 2010), while for the remaining genera no molecular data or cladistic study is available. The subfamily Octonchinae and Enchelidiidae are considered a terminal clade, supported by molecular and morphological evidences. Members of these taxa possess three large and multiple additional teeth (Shi & Xu, 2016). The phylogenetic relationships among the genera of Enchelidiidae followed Fônseca-Genevois et al. (2009), except for *Enchelidium* Ehrenberg, 1836 and *Polygastrophoroides*. *Enchelidium* is included in the supertree as a sister group of *Abelbolla* Huang & Zhang, 2004 and *Lyranema* Timm, 1961, since it is a doubtful genus (Smol & Coomans, 2006; Wieser, 1953). *Polygastrophoroides* Sun & Huang, 2016 is considered polytomic to *Polygastrophora* and *Belbolla*, given the several morphological resemblances with *Polygastrophora* (Sun & Huang, 2016).

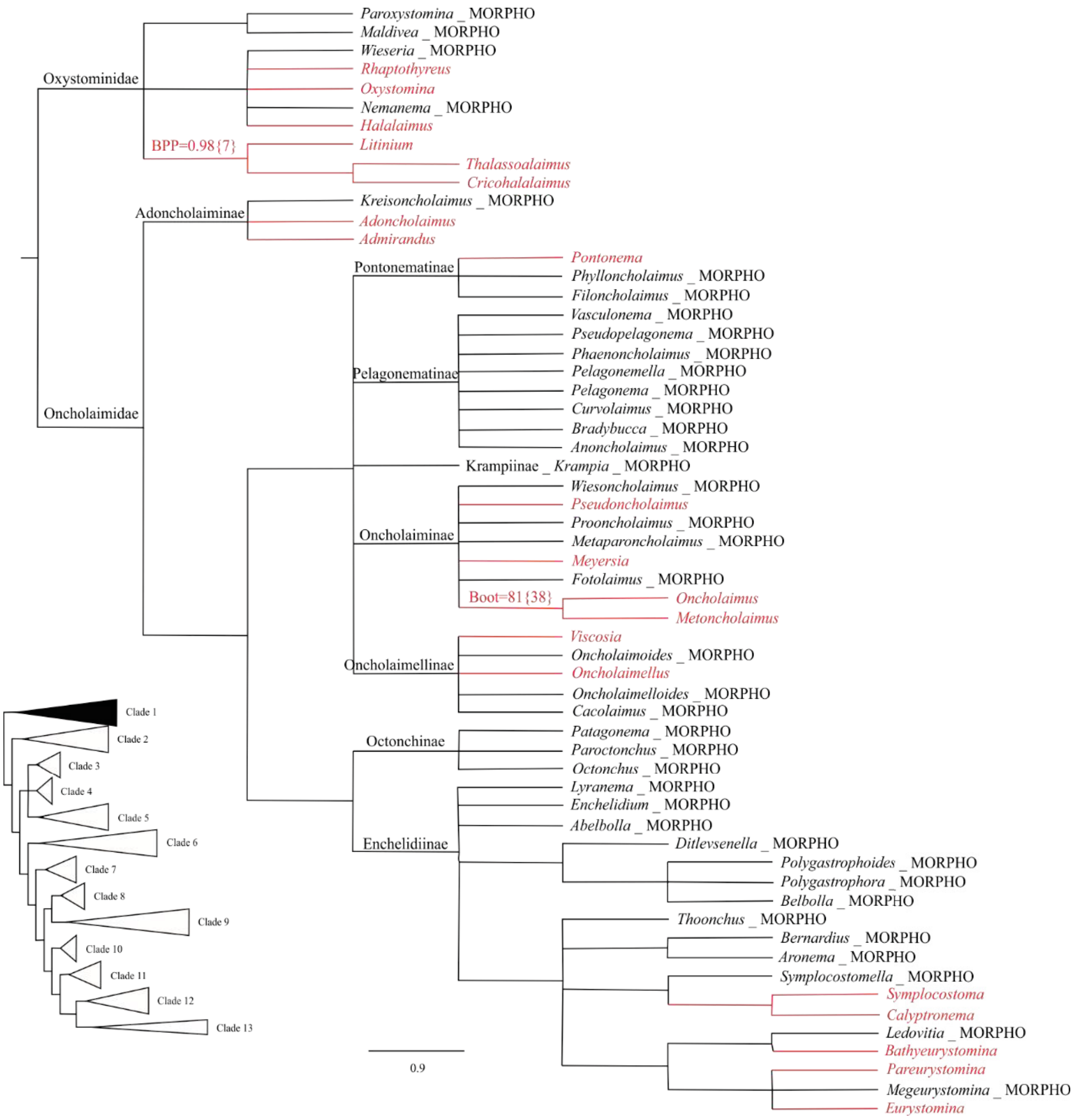

Figure 3. Representation of the Order Enoplida (suborder Oncholaimina) of the supertree of Nematoda. The clades supported by molecular data are marked in red. The number between brackets corresponds to the number of reference in the list of consulted molecular studies.

Clade 1.3. Suborder Enoplina Chitwood & Chitwood, 1937 (Figure 4)

The monophyly of this suborder is partially corroborated by morphological characters. Members of Enoplina have the caudal glands positioned beyond the caudal extension (Lorenzen, 1994), however this character is also present in species of Oncholaimina (Smol et al., 2014). According to molecular data, Enoplina includes three clades: one including Anoplostomatidae Gerlach & Riemann, 1974 and Pandolaimidae Belogurov, 1980, which arised from the separation of Anoplostomatidae from

Enoploidea and the closer relationship of Leptosomatidae. Some studies demonstrated a difficulty in distinguishing some species of Anticomidae Filipjev, 1918 and Leptosomatidae, since they have similar cephalic capsule and buccal cavity (Lorenzen, 1994). The second clade consists of Marimermithidae Rubtzov & Platonova, 1974 and Leptosomatidae. The adult marimermithids, although similar to Leptosomatidae, have morphological adaptations to the parasitic habit and form a monophyletic group (Miljutin, 2014). The third clade is the superfamily Enoploidea (Bik et al., 2010; Leduc, Verdon & Zhao, 2018; Smythe 2015).

Anoplostomatidae and Pandolaimidae

Pandolaimidae is considered close related to Anoplostomatidae due to the morphological similarity between *Pandolaimus* Allgén, 1929 and *Anoplostoma* Bütschli, 1874 (Jensen, 1976). Although *Chaetonema* Filipjev, 1927 and *Anoplostoma* were suggested as independent lineages in different positions along phylogenetic analyses (Bik et al., 2010; Leduc, Verdon & Zhao, 2018; Smythe, 2015), they are considered morphologically sister genera. These genera share similar buccal cavity and cephalic capsule, which are considered unique in “Enoploidea” (Lorenzen, 1994).

Marimermithidae and Leptosomatidae

Marimermithids, previously classified as a separated order, are placed close to Leptosomatidae as the family Marimermithidae, based on morphological and molecular studies (Miljutin, 2014). In molecular phylogenies, the family Leptosomatidae has been mostly suggested to be placed as a sister group of Thoracostomopsidae Filipjev, 1927, Enoplidae Dujardin, 1845, Phanodermatidae Filipjev, 1927 and Anticomidae Filipjev, 1918 (Leduc, Verdon & Zhao, 2018; Smythe 2015). Within the family, the first split separates the subfamilies Barbonematinae Platonova, 1976 (genus *Barbonema* Filipjev, 1927) and Leptosomatinae Filipjev, 1916 from the others (Smythe, 2015). The other branch represents the subfamilies Platycominae Platonova, 1976, Cylicolaiminae Platonova, 1970, Synonchinae Platonova, 1970 and Thoracostomatinae De Coninck, 1965, but their monophyly is not confirmed by morphological studies (Lorenzen, 1994). The genus *Proplatycoma* Platonova, 1976 corresponds to Platycominae, *Cylicolaimus* de Man, 1889 and

Synonchus Cobb, 1894 form a separated dichotomy, but belong to different subfamilies, as well as *Thoracostoma* Marion, 1870 and *Deontostoma* Filipjev, 1916, both within Thoracostomatinae (Armenteros et al., 2014; Smythe, 2015). The last two genera are morphologically similar to each other, solely differing by the presence of ocelli in *Thoracostoma* but not always present in *Deontostoma* (Oliveira et al., 2012; Smol et al., 2014), corroborated by the high branch support in a COI gene tree (Armenteros et al., 2014).

Enoploidea Dujardin, 1845

This superfamily is monophyletic and includes four of the five families from the traditional classification (Smol et al., 2014), since Anoplostomatidae is placed as a separated group within Enoplina. The relationships between Anticomidae, Thoracostomopsidae, Phanodermatidae and Enoplidae are based on the high branch support values of molecular phylogenies (Bik et al., 2010; Smythe, 2015). In Anticomidae, only *Cephalanticoma* Platonova, 1976 and *Anticoma* Bastian, 1865 has been sequenced and therefore all genera are considered polytomic. In Thoracostomopsidae, the subfamilies Enoplolaiminae De Coninck, 1965, Thoracostomopsinae Filipjev, 1927 and Trileptiinae Gerlach & Riemann, 1974 are not supported by molecular studies. The family is still largely polytomic, since *Thoracostomopsis* Ditlevsen, 1918 and *Trileptium* Cobb, 1933 were found within Enoplolaiminae (Pereira et al., 2010; Smythe, 2015). In Phanodermatidae, the dichotomy including *Metaphanoderma* Platonova, 1984 and *Phanoderma* Bastian, 1865 is according to the subfamily Phanodermatinae Filipjev, 1927, distinct from Crenopharynginae Platonova, 1976 by the well-developed cephalic capsule (Smol et al., 2014).

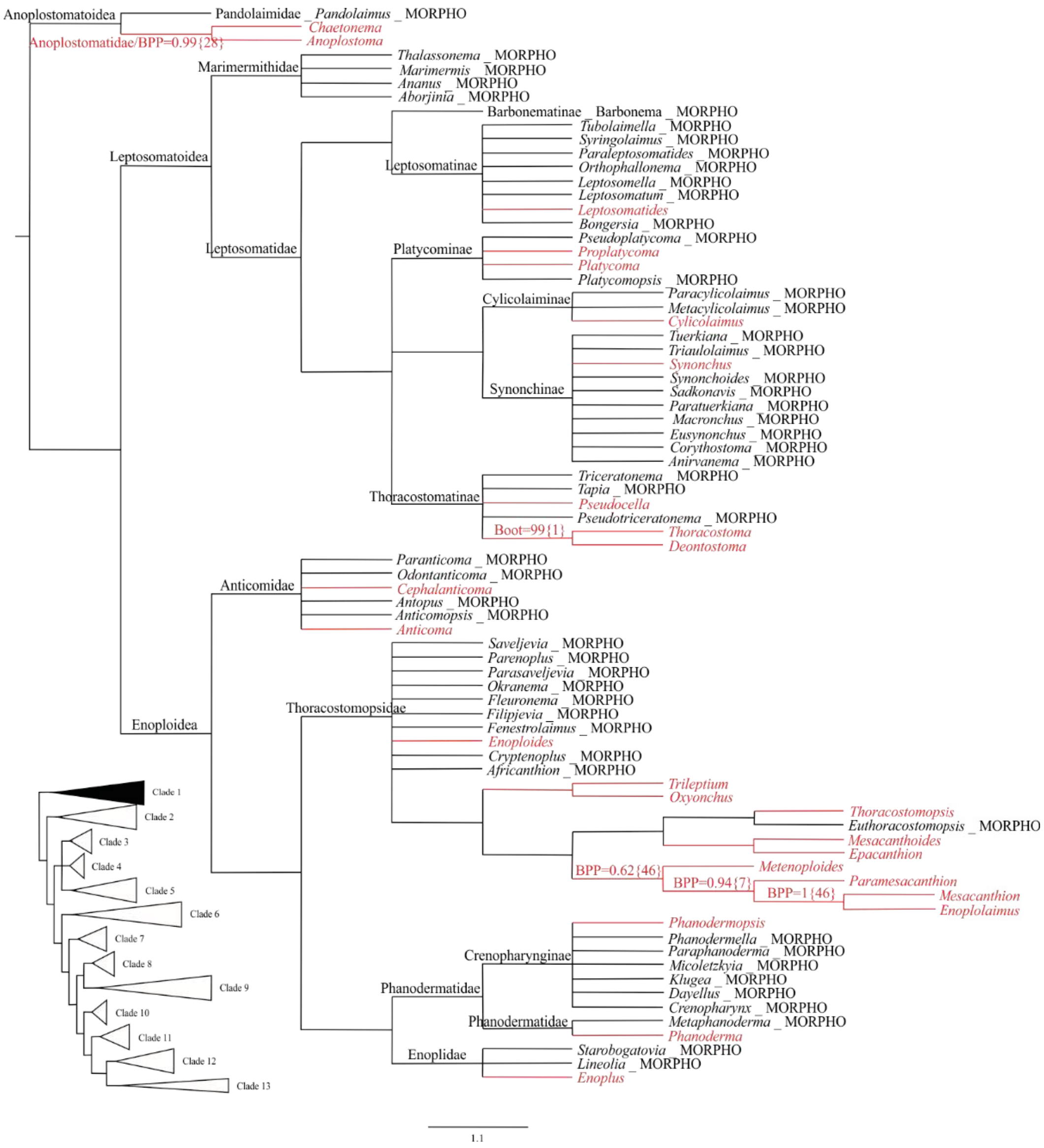

Figure 4. Representation of the Order Enoplida (suborder Enoplina) of the supertree of Nematoda. The clades supported by molecular data are marked in red. The number between brackets corresponds to the number of reference in the list of consulted molecular studies.

Clade 1.4. Order Triplonchida (Figure 5)

Most of the species of the order Triplonchida inhabits the freshwater and terrestrial habitats. *Triodontolaimus* de Man, 1893, a marine genus, has not been sequenced and in the morphological description no phylogenetic relationship has been discussed (Holovachov & Shoshin, 2014). Given the lack of phylogenetic information, a polytomic position is assumed within this clade. For the remaining taxa the phylogenetic position proposed by van Megen et al. (2009) is considered.

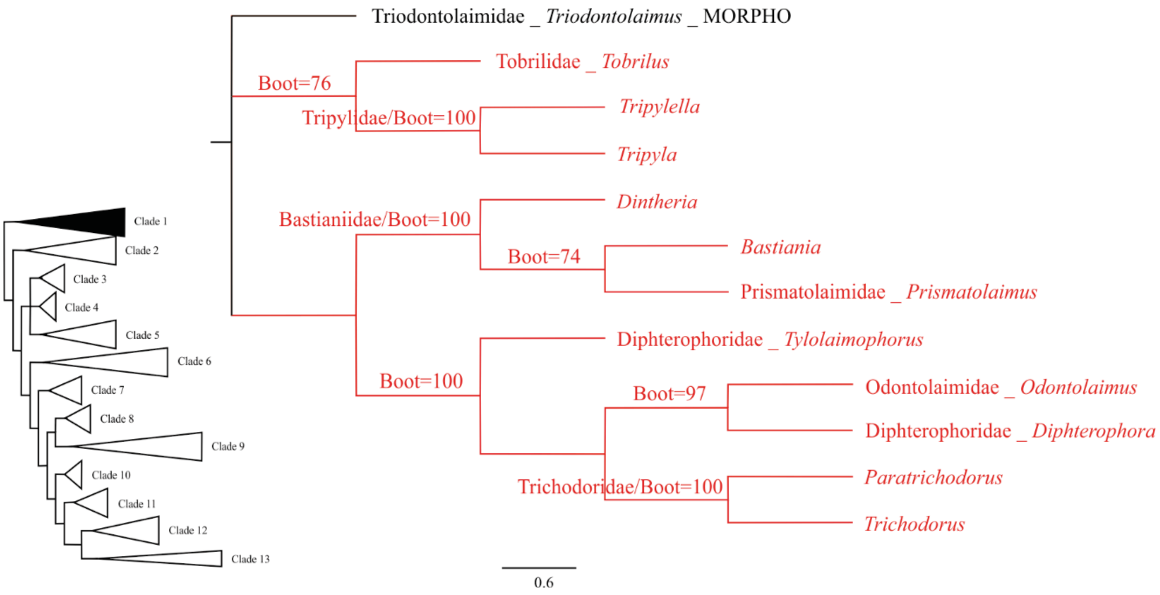

Figure 5. Representation of the Order Triplonchida of the supertree of Nematoda. The clades supported by molecular data are marked in red.

CLADE 3 – ORDER MICROLAIMIDA LEDUC, VERDON & ZHAO, 2018 (Figure 6)

This order was recently suggested by Leduc, Verdon & Zhao (2018) and encloses the superfamily Microlaimoidea Micoletzky, 1922 which is composed by four families: Aponchiidae Gerlach, 1963, Monoposthiidae Filipjev, 1934, Microlaimidae Micoletzky, 1922 and Molgolaimidae Jensen, 1978. The first split form a polytomy, since there is no molecular data to Aponchiidae. The position of Monoposthiidae, traditionally classified in Microlaimoidea, is different along phylogenetic trees. In 18S gene phylogenies, *Nudora* Cobb, 1920 and *Monoposthia* de Man, 1889 are close related to the clade formed by *Microlaimus* de Man, 1880, *Calomicrolaimus* Lorenzen, 1976 and *Molgolaimus* Ditlevsen, 1921 (Holterman et al., 2008; Hwang et al., 2009), which was corroborated by Leduc, Verdon & Zhao (2018). Nevertheless, within Monoposthiidae, a polytomy has to be assumed, since there is no molecular data for *Rhinema* Cobb, 1920 and *Monoposthioides* Hopper, 1963. According to molecular and morphological data, *Microlaimus* and *Calomicrolaimus* are sister genera close to *Molgolaimus* (Holterman et al., 2008, Leduc, Verdon & Zhao, 2018; Leduc & Zhao, 2016a). *Bolbolaimus* Cobb, 1920 have no molecular data on the GenBank, but a phylogenetic relationship with high branch support was found with *Microlaimus* (Derycke et al., 2010).

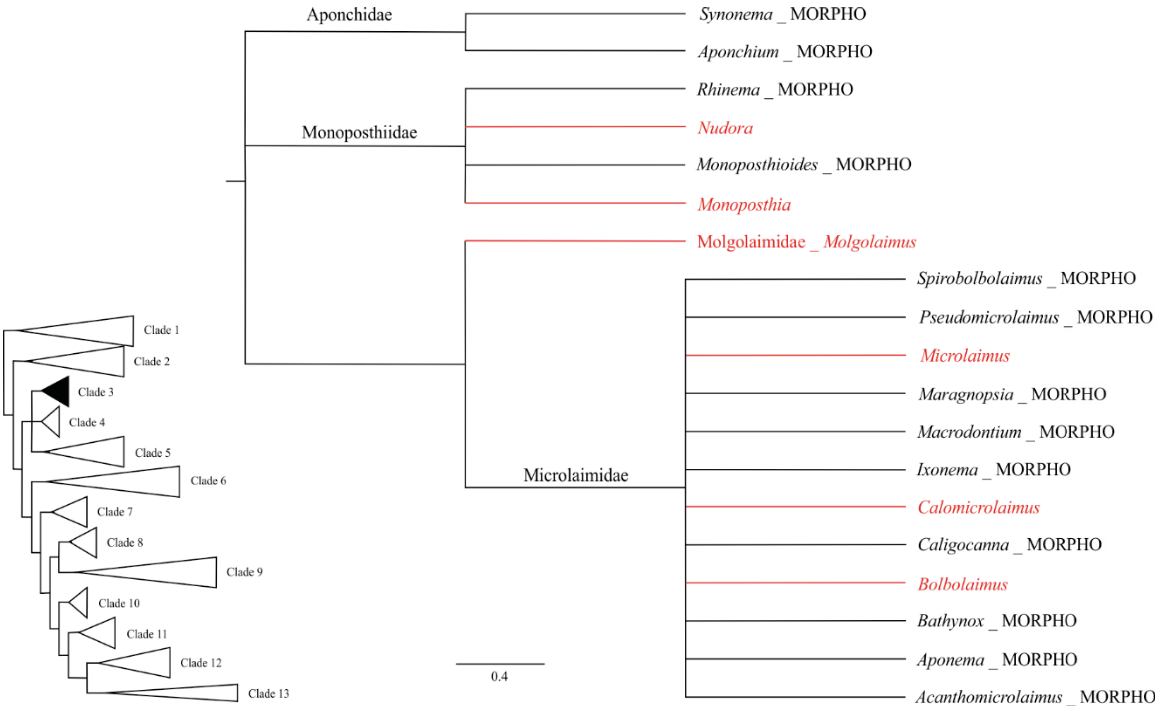

Figure 6. Representation of the Order Microlaimida of the supertree of Nematoda. The clades supported by molecular data are marked in red. The number between brackets corresponds to the number of reference in the list of consulted molecular studies.

CLADE 4 – *PRODESMODORA* AND HALIPLECTIDAE (Figure 7)

The family Haliplectidae is traditionally considered by systematists as *incertae sedis*, but, in molecular studies forms an independent clade, a sister group of Chromadorida (Holovachov, 2014b; Holovachov et al., 2012; van Megen et al., 2009). This family is characterized by the circular amphid and the unique shape of the pharynx, slightly muscular in the anterior part, with a small bulb in the middle section and a large muscular bulb in the posterior section (Lorenzen, 1994). This family has three genera. According to systematic reviews, *Prodesmodora* has been classified as a subfamily within Desmodoridae, but based on molecular studies it is close related to *Haliplectus* (Boot = 100; Leduc & Zhao, 2016a; van Megen et al., 2009). Like members of the Haliplectidae, this genus has an annulated cuticle, a circular amphid and a resembling pharynx, except for the bulb in the middle.

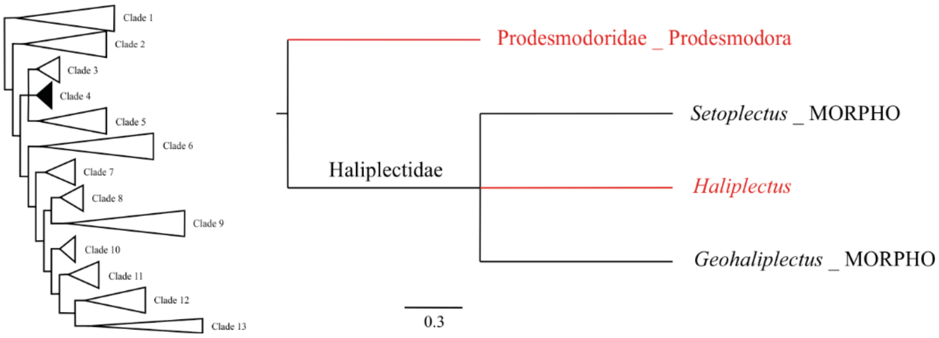

Figure 7. Representation of the clade four, including *Prodesmodora* and Haliplectidae, of the supertree of Nematoda. The clades supported by molecular data are marked in red.

CLADE 5 – ORDER CHROMADORIDA CHITWOOD, 1933 (Figure 8)

In the supertree this order is monophyletic and include three clades: the first consists of Paramicrolaimidae Lorenzen, 1981 and Selachinematidae Cobb, 1915; the second corresponds to Chromadoroidea; and the third covers Ethmolaimidae, Neotonchidae, Cyatholaimidae and Acromadoridae. The combination of punctated cuticle with transverse striae and the reflexed ovaries of females was indicated as an apomorphic character to establish the monophyly of Chromadorida (Lorenzen, 1994). However, the cuticle of *Paramicrolaimus* Wieser, 1954 is different (Leduc, Verdon & Zhao, 2018). The relationships between Paramicrolaimidae Lorenzen, 1981, Selachinematidae Cobb, 1915, Chromadoridae Filipjev, 1917, Ethmolaimidae Filipjev & Schuurmans Stekhoven, 1941, Neotonchidae Wieser & Hopper, 1966, Cyatholaimidae Filipjev, 1918 and Achromadoridae Gerlach & Riemann, 1973 are not well resolved in recent molecular phylogenies (Holovachov et al., 2012; Holovachov, Rodrigues, Zbinden & Duperron, 2013; Leduc, Verdon & Zhao, 2018; Leduc, Zhao, Verdon & Xu, 2018), therefore polytomies are assumed.

Paramicrolaimidae and Selachinematidae

The phylogenetic position of Paramicrolaimidae has changed along the studies due to an unusual morphology (Lorenzen, 1994; Holovachov, 2014b), but the combination of molecular and morphological data indicated that the punctuations of the cuticle may have been lost over time (Leduc, Verdon & Zhao, 2018). The position of Selachinematidae within Chromadoria is also debatable. Evidences in favor of including it have considered it a sister group of other chromadorids, but without a branch support (van Megen et al., 2009), while other 18S phylogenies placed some genera of Selachinematidae close to Araeolaimida, Monhysterida and Plectida, making it a paraphyletic group (Holterman et al., 2008; Leduc, Verdon & Zhao, 2018; Leduc, Zhao, Verdon & Xu, 2018). Considering that this family is monophyletic based on the radial-symmetry of the buccal cavity containing rhabdions (Lorenzen, 1994; Tchesunov, 2014a), it is kept in Chromadorida until a further revision.

According to buccal cavity development, the traditional classification divides the family Selachinematidae in two subfamilies: Choniolaiminae Schuurmans-Stekhoven & Adam, 1931 and Selachinematinae Cobb, 1915, but the molecular data do not support the monophyly of them (Leduc & Zhao, 2015; 2016a; Tchesunov, 2014a). *Cheironchus* Cobb, 1917 (Selachinematinae) is closer to *Latronema* Wieser, 1954 and *Choanolaimus* de Man, 1880 (Choniolaiminae) than to *Pseudocheironchus* Leduc, 2013 and *Synonchiella* Cobb, 1933 (Selachinematinae). The relationships present in the supertree are based on the LSU tree with high branch support (Leduc & Zhao, 2016a). For the unsequenced genera no phylogenetic relationship is available and therefore is presented as a polytomy.

Chromadoroidea Filipjev, 1917

The second branch refers to the superfamily Chromadoroidea, including only the family Chromadoridae. This family is morphologically subdivided in five subfamilies, of which Spilipherinae Filipjev, 1918, Harpagonchinae Platonova & Potin, 1972 and Euchromadorinae Gerlach & Riemann, 1973 are assumed as separate clades, once there are no phylogenetic studies for them (Decraemer & Smol, 2006). Some molecular phylogenies did not separate the genera traditionally classified in Chromadorinae Filipjev, 1917 and Hypodontolaiminae de Coninck, 1965, since *Chromadorella* Filipjev, 1918 and *Prochromadorella* Micoletzky, 1924 are closer to *Dichromadora* Kreis, 1929 than to *Chromadora* Bastian, 1865 (Avó et al., 2017; Derycke et al., 2010). However, Venekey et al. (2019) analysed the phylogenetic relationships from the existing sequences and corroborated the classification of the subfamilies, suggesting a probable misidentification of the deposited sequence of *Prochromadorella* in the Genbank.

Ethmolaimidae, Neotonchidae, Cyatholaimidae and Acromadoridae

The separation of Ethmolaimidae from the remaining families is based on two 18S phylogenies (Holovachov, Rodrigues, Zbinden & Duperron, 2013; van Megen et al., 2009). The families Neotonchidae, Cyatholaimidae and Achromadoridae form a polytomy, due to records of Neotonchidae related to Cyatholaimidae (Armenteros et al., 2014; Leduc, Verdon & Zhao, 2018), and Cyatholaimidae related to Achromadoridae (Holovachov et al., 2012; Holovachov, Rodrigues, Zbinden & Duperron, 2013; Holterman et al., 2008). Neotonchidae does not present an apomorphy, but it was here kept in the rank of a family (Lorenzen, 1994). It can be distinguished by a combination of morphological features, which individually also appear in Chromadoridae, Cyatholaimidae and Ethmolaimidae (e.g. neotonchids have a multispiral amphideal fovea situated posterior to the cephalic setae, like Cyatolaimidae, and cup-shaped supplements, like those of Chromadoridae) (see detailed discussion in Lorenzen, 1994). Achromadoridae has a well-supported relationship with Cyatholaimidae, in both, molecular and morphological grounds (Holterman et al., 2008; Tchesunov, 2014a; van Megen et al., 2009).

Cyatholaimidae has five subfamilies which are paraphyletic and need to be revised (Lorenzen, 1994): Nyctonematinae Bussau, 1993, Xenocyatholaiminae Gerlach & Riemann, 1973, Pomponematinae Gerlach & Riemann, 1973, Cyatholaiminae Filipjev, 1918 and Paracanthonchinae De Coninck, 1965 (Armenteros et al., 2014; Leduc & Zhao, 2018; van Megen et al., 2009).

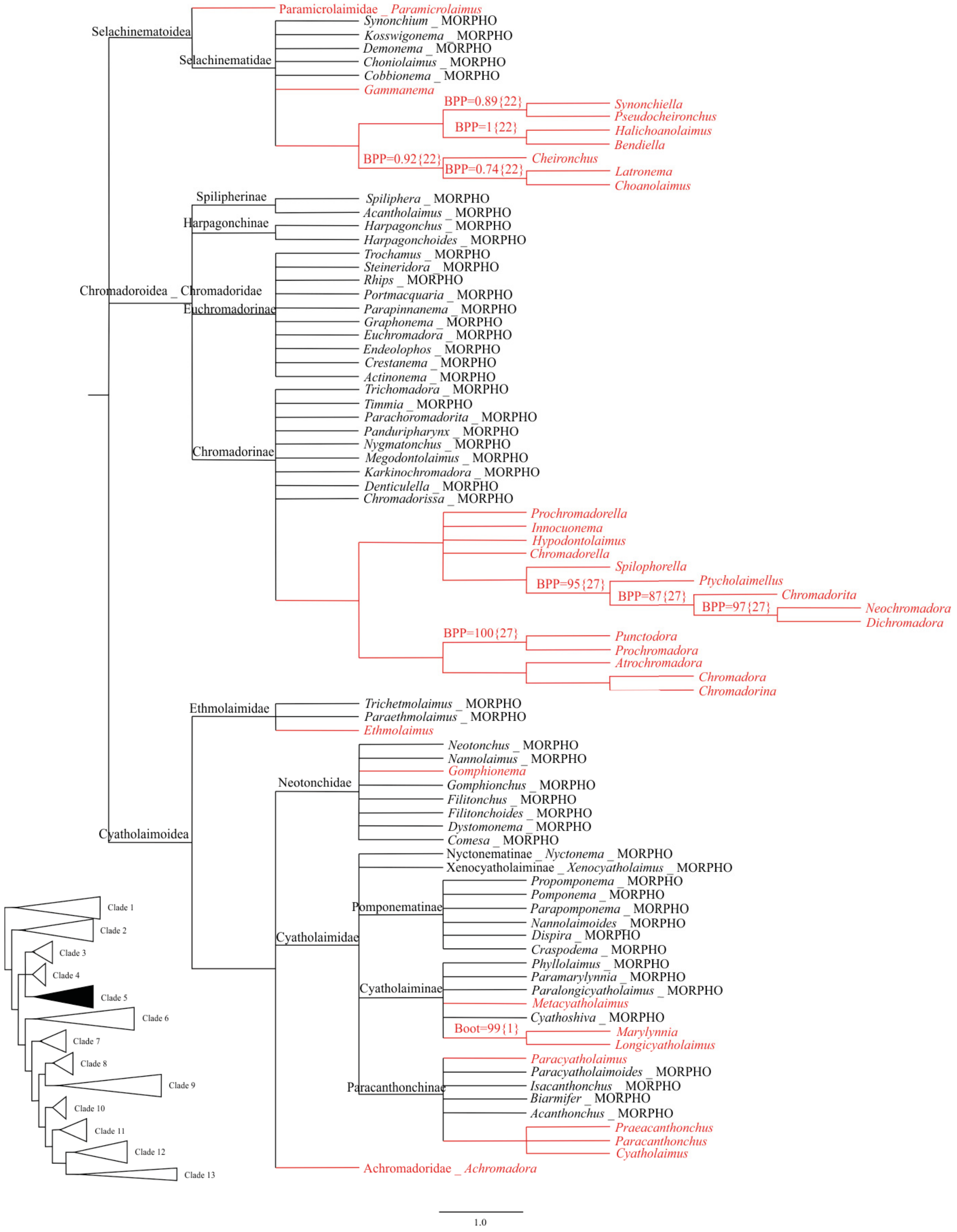

Figure 8. Representation of the Order Chromadorida of the supertree of Nematoda. The clades supported by molecular data are marked in red. The number between brackets corresponds to the number of reference in the list of consulted molecular studies.

CLADE 6 - ORDER DESMODORIDA DE CONINCK, 1965 (Figure 9)

The order Desmodorida originally includes two superfamilies, Desmodoroidea Filipjev, 1922 and Microlaimoidea (Tchesunov, 2014b). Nevertheless, this classification is not supported by molecular data. As already discussed, Microlaimoidea is in the order Microlaimida (Clade 3). In the supertree, Desmodorida only covers the clade Desmodoroidea, which is monophyletic by the presence of a single anterior testis (Lorenzen, 1994). This clade is separated in two monophyletic families: Epsilonematidae Steiner, 1927 and Desmodoridae Filipjev, 1922 (Tchesunov, 2014b). The relationships among the genera of Epsilonematidae follow the tree constructed with non-additive characters proposed by Neira et al. (2005).

Desmodoridae includes three subfamilies, Pseudonchinae Gerlach & Riemann, 1973, Desmodorinae Filipjev, 1922 and Stilbonematinae Chitwood, 1936. The genera of Richtersiidae Kreis, 1929 and Draconematidae Filipjev, 1918 are placed within Desmodoridae (De Ley et al., 2005; Holovachov et al., 2012; Leduc & Zhao, 2016a; Lins et al., 2017). The draconematids is a terminal clade within Desmodorinae and are characterized by distinct morphological synapomorphies: an open “S” body shape; presence of adhesive setae on the dorsal side of the anterior end; stilt setae - where adhesive glands open - lateroventral and subventrally situated in the posterior region of the body; and ovaries situated anterior to the dorsal curvatures of the body - anterior to the stilt setae (Lorenzen, 1994). Furthermore, in many species of *Desmodora*, as well as in more derived forms of epsilonematids and draconematids, there is a difference in body thickness between body regions, the ovaries and the vulva lie well posterior to the middle of the body, and the cuticle has coarse annules (Lorenzen, 1994). Apart from the draconematids, relationships within Desmodoridae remains largely unresolved (Armenteros et al., 2014).

The phylogenetic position of *Richtersia* Steiner, 1916 is controversial in the literature assuming an intermediate position between Selachinematidae, close to *Cheironchus* and *Paramicrolaimus* (Leduc, 2013; Leduc & Zhao, 2015), and Desmodoroidea, close to *Metachromadora* Filipjev, 1918 and *Desmodorella* Cobb, 1933 (De Ley et al., 2005; Lins et al., 2017). Among the phylogenetic hypothesis the highest branch support for *Richtersia* is close to *Desmodorella* (Boot = 20 to 47), from only two 28S sequences (Lins et al., 2017).

The relationships between draconematids are according to morphological and molecular studies (Decraemer et al., 1997; Leduc & Zhao, 2016a; Rho et al., 2011). In Stilbonematinae, the most complete phylogenetic tree suggested that *Eubostrichus* Certes, 1899, *Laxus* Cobb, 1894, *Robbea* Gerlach, 1956 and *Stilbonema* Cobb, 1920 are paraphyletic (Armenteros et al., 2014) and, therefore, till further revision, the relationships within this subfamily remains unresolved.

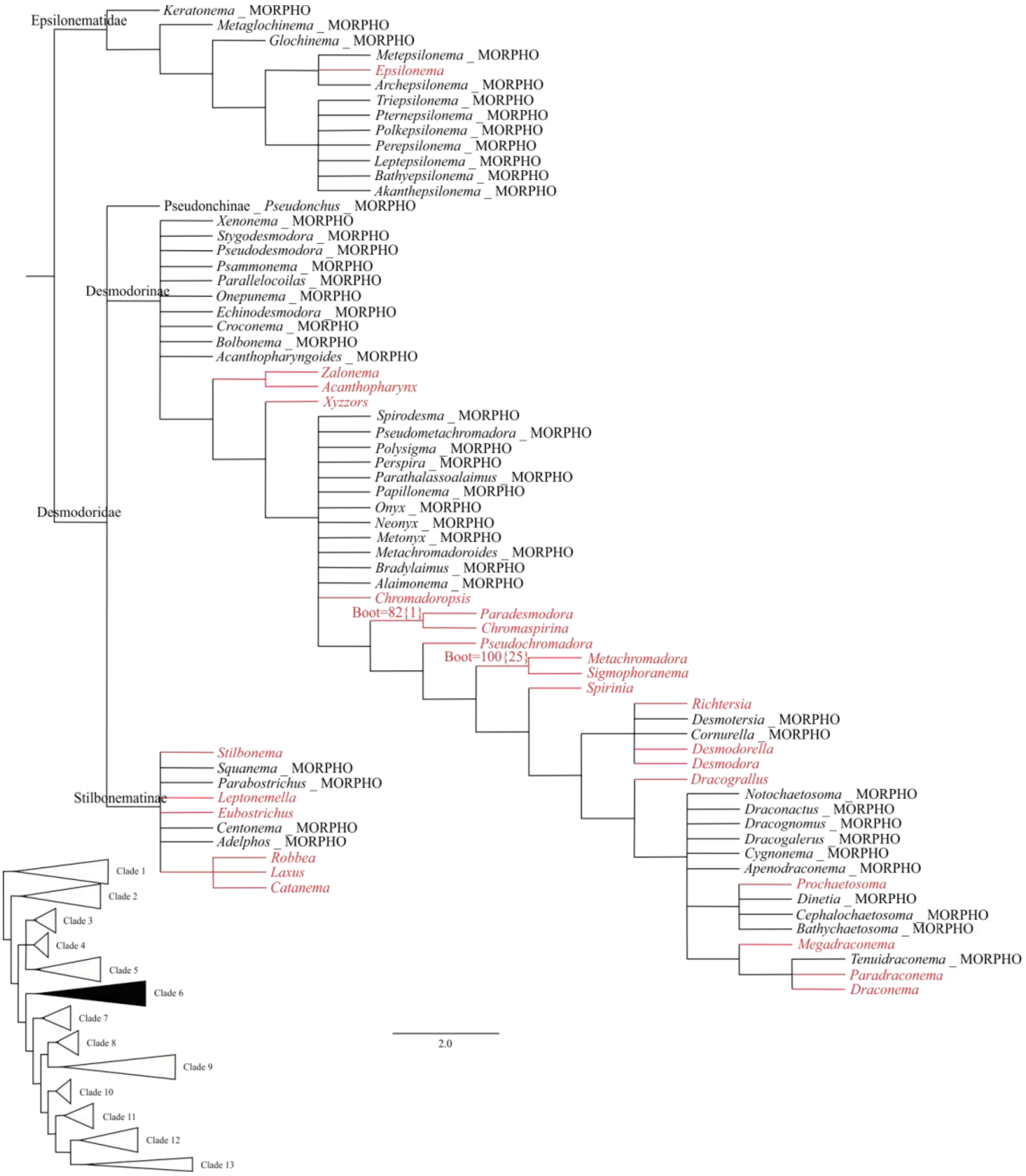

Figure 9. Representation of the Order Desmodorida of the supertree of Nematoda. The clades supported by molecular data are marked in red. The number between brackets corresponds to the number of reference in the list of consulted molecular studies.

CLADE 7 – ORDER DESMOSCOLECIDA FILIPJEV, 1929 (Figure 10)

This clade includes the suborders Ceramonematina Cobb, 1933, originally placed within the order Plectida (Holovachov, 2014b), and Desmoscolecina Filipjev, 1934. Both suborders are phylogenetic related based on the relationships between *Ceramonema* Cobb, 1920, *Pselionema* Cobb, 1933 and *Tarvaia* Allgén, 1934 with the genera of Desmoscolecidae Shipley, 1986 (Holovachov et al., 2012; Lins et al., 2017; Litvaitis et al., 2000). These studies showed that the branch of the genus *Tarvaia* is close to that of *Tricoma* Cobb, 1894, *Paratricoma* Gerlach, 1956 and *Desmoscolex* Claparèrede, 1863, and that *Ceramonema*, *Pselionema*, *Paratricoma* and *Tricoma* are close, relationships with high branch support. Therefore, Ceramonematina is maintained as a monophyletic clade, considering the similar morphology of *Tarvaia* and *Ceramonema* (Holovachov, 2014b), but transferred from Plectida to Desmoscolecida.

Suborder Ceramonematina Cobb, 1933

This clade includes the families Aegialoalaimidae Lorenzen, 1981, Tubolaimoididae Lorenzen, 1981, Tarvaiidae Lorenzen, 1981, Diplopeltoididae Tchesunov, 1990 and Ceramonematidae Cobb, 1933. Although the relationships between the five families are not well defined, their genera have similar structures of the anterior end and of the digestive system (Holovachov, 2014b). Ceramonematidae is divided in two subfamilies, Pselionematinae De Coninck, 1965 and Ceramonematinae Cobb, 1933 based on the features of body cuticle annulation and the type of outer labial and posterior cephalic setae (Holovachov et al., 2008; Tchesunov & Miljutina, 2002).

Suborder Desmoscolecina Filipjev, 1934

This is a well-supported clade considering the morphological characters and molecular phylogenies (Holovachov et al., 2012; Holovachov, Rodrigues, Zbinden & Duperron, 2013; Hwang et al., 2009). Desmoscolecina covers the families Eophasmidae Poinar, 2011, Meyliidae De Coninck, 1965 and Desmoscolecidae Shipley, 1896. The relationships among them are still subject of debate (Decraemer &

Rho, 2014). Therefore, until the emergence of new molecular and morphological data, the families form a polytomy in the supertree. The dichotomy within Desmoscolecidae corresponds to the distinct subfamilies Desmoscolecinae Shipley, 1896 and Tricominae Lorenzen, 1969, corroborated by a 18S rDNA tree (Hwang et al., 2009).

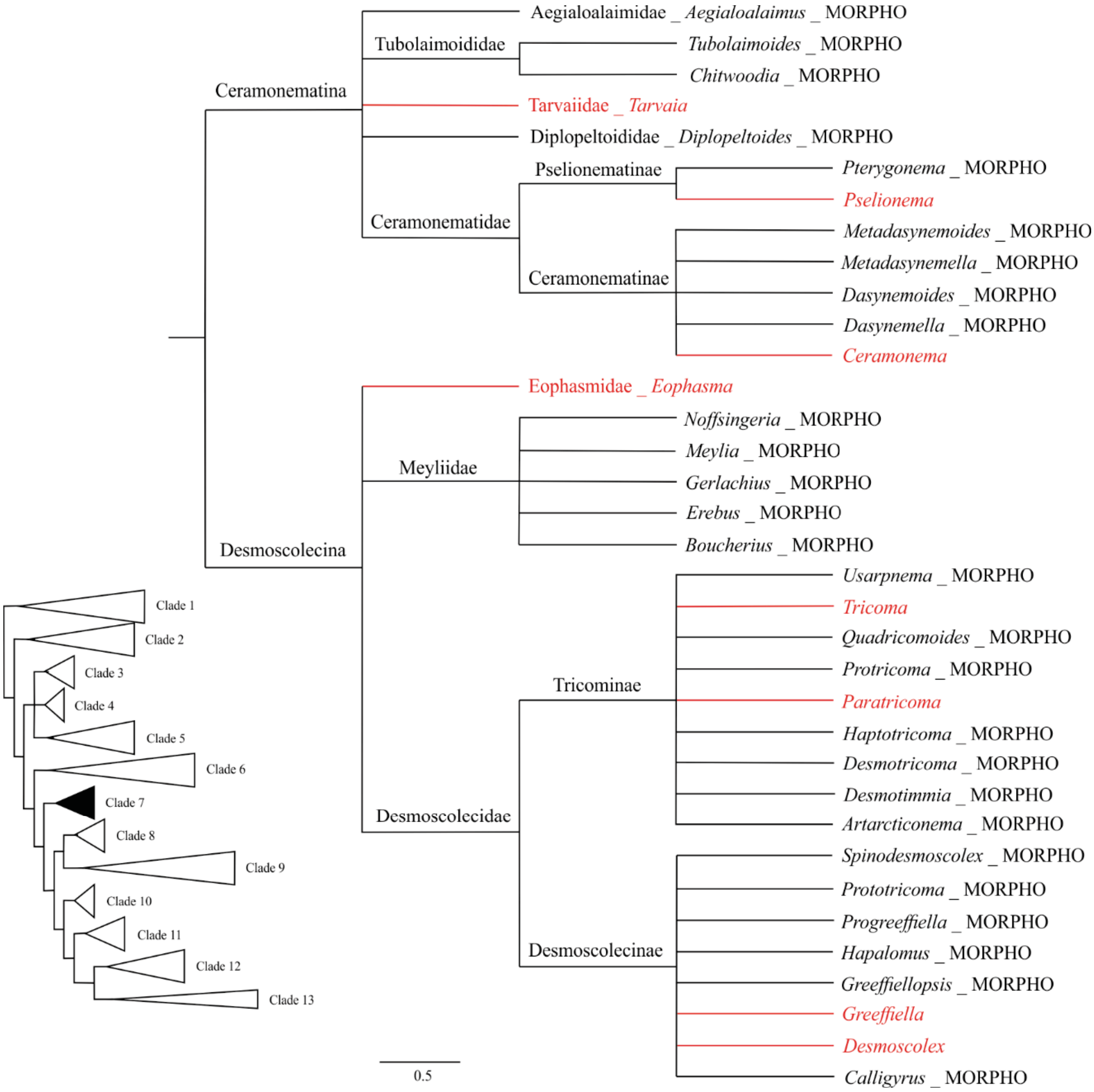

Figure 10. Representation of the Order Desmoscolecida of the supertree of Nematoda. The clades supported by molecular data are marked in red.

CLADE 8 – ORDER ARAEOLAIMIDA DE CONINCK & SCHUURMANS STEKHOVEN, 1933 (Figure 11)

Till now, molecular and morphological studies have pointed that the order Araeolaimida is paraphyletic with Monhysterida (Holovachov, Rodrigues, Zbinden & Duperron, 2013; Hwang et al., 2009; Leduc, Verdon & Zhao, 2018; van Megen et al., 2009). These studies placed Comesomatidae Filipjev, 1918 (Araeolaimida) next to Monhysteridae de Man, 1876. Additionally, the genus *Terschellingia* de Man, 1888 (Monhysterida: Linhomoeidae) has been placed next to *Cyartonema* Cobb, 1920 (Cyartonematidae Tchesunov, 1989: Araeolaimida) (Hwang et al., 2009; Leduc, Verdon & Zhao, 2018). All molecular studies also pointed that Diplopeltidae Filipjev, 1918 formed a separated clade from Monhysterida. For the two remaining families within Araeolaimida, Coninckiidae Lorenzen, 1981 and Bodonematidae Jensen, 1991, only morphological data is available.

Within the order Araeolaimida, the families Coninckiidae, Bodonematidae and Diplopeltidae compose a polytomic clade due to the lack of phylogenetic information. Diplopeltidae is now considered monophyletic, since we have considered *Cylindrolaimus* de Man, 1880 next to Axonolaimidae according to morphological (Lorenzen, 1994; Muthumbi & Vanreusel, 2006) and molecular data (Holovachov, Rodrigues, Zbinden & Duperron, 2013; Hwang et al., 2009; Leduc, Verdon & Zhao, 2018; van Megen et al., 2009). Given that *Terschellingia* was frequently placed as a sister group of comesomatids with high branch support (Boot = 99 and 100) from 18S phylogenies (Bhadury et al., 2008; Holterman et al., 2008; Hwang et al., 2009), we have replaced it within Cyartonematidae. Morphological systematics considered this family close to Meyliidae, in Desmoscolecida, based on the following combination of characters: 1) pharynx with a posterior bulb containing pharyngeal glands; 2) presence of pseudocoelomocytes along the pregonadal midgut; 3) blind intestine; 4) oocytes diminish successively in size from the vagina; 5) type of cephalic setae; 6) amphids; 7) triangular head shape; 8) number and position of the male gonads; 9) copulatory apparatus; 10) tail shape and aperture of the caudal glands (Tchesunov, 1994). Nonetheless, these characters are not exclusive of this clade. *Terschellingia*, *Cyartonema* and *Paraterschellingia* Kreis in Schuurmans-Stekhoven, 1935 share a similar buccal cavity, which can be absent, minute or narrow and tubular, and a didelphic female reproductive system (Decraemer & Smol, 2006; Fonseca & Bezerra, 2014a; 2014b; Gerlach, 1951; Juario, 1972). Based on the molecular and morphological evidences, the order Araeolaimida in the supertree encompass the four families mentioned above.

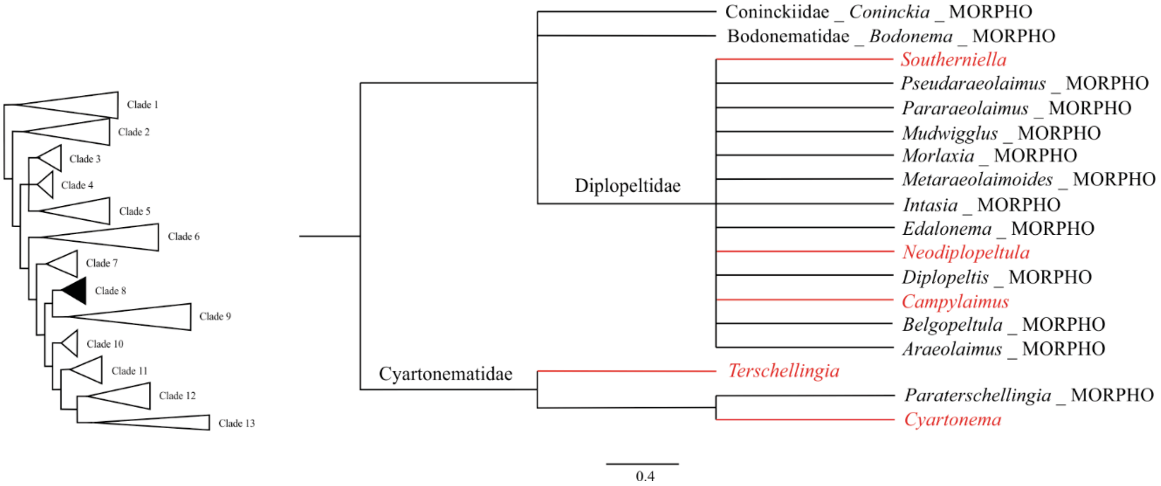

Figure 11. Representation of the Order Araeolaimida of the supertree of Nematoda. The clades supported by molecular data are marked in red.

CLADE 9 - ORDER MONHYSTERIDA FILIPJEV, 1929 (Figure 12)

This order encloses two main clades, one including the family Comesomatidae, traditionally classified in Araeolaimida (see Clade 8), and the other encompassing the suborder Monhysterina De Coninck & Schuurmans Stekhoven, 1933, which consists of the superfamilies Sphaerolaimoidea Filipjev, 1918 (Sphaerolaimidae Filipjev, 1918 and Xyalidae Chitwood, 1951) and Monhysteroidea Filipjev, 1929 (Monhysteridae). The inclusion of Comesomatina in Monhysterida is according to the high branch support (Boot = 71 to 96) observed in molecular phylogenies (Holovachov et al., 2012; Leduc, Verdon & Zhao, 2018; van Megen et al., 2009). It has been suggested that Comesomatidae is close to Monhysteridae and Xyalidae. The clade Siphonolaimoidea is now placed in an aftermost clade (see Clade 11). The outstretched ovaries are considered the apomorphy of Monhysterida - reflexed ovaries just occur in one species of *Hopperia* Vitiello, 1969 - a character that can also be found in comesomatids but independently emerged in other taxa (Fonseca & Bezerra, 2014a; 2014b; Lorenzen, 1994).

Comesomatidae

The basal split separates this family from Monhysterina (Holovachov et al., 2012; Leduc, Verdon & Zhao, 2018; van Megen et al., 2009). There are several morphological characters separating these two clades (Fonseca & Bezerra, 2014a). Comesomatidae is traditionally divided in three subfamilies according to the buccal cavity, copulatory apparatus and cephalic sensilla: Comesomatinae Filipjev, 1918, Dorylaimopsinae De Coninck, 1965 and Sabatieriinae Filipjev, 1934 (Jensen, 1979). However, 18S phylogenies suggested *Dorylaimopsis* Ditlevsen, 1918 within Sabatieriinae (Bhadury et al., 2008; Holterman et al., 2008; Leduc, Verdon & Zhao, 2018), questioning the subfamilies proposed by Jensen (1979).

Monhysterina De Coninck & Schuurmans Stekhoven, 1933

This suborder includes two morphologically distinct superfamilies Sphaerolaimoidea (Sphaerolaimidae and Xyalidae) and Monhysteroidea (Monhysteridae) (Fonseca & Bezerra, 2014a). These superfamilies are distinct from each other based on a combination of cuticle type, anterior setae, number and position of the gonads and tail shape (Coomans & Eyualem-Abebe, 2006). Within Sphaerolaimidae, the relationships among genera are restricted to morphology and each branch corresponds to the subfamilies Parasphaerolaiminae Lorenzen, 1978, Metasphaerolaiminae Gourbault & Boucher, 1982 and Sphaerolaiminae Filipjev, 1918 (Fonseca & Bezerra, 2014a). The relationships within Xyalidae followed morphological (Nicholas & Trueman, 2002) and molecular data (Armenteros et al., 2014; Derycke et al., 2010; Neres et al., 2010; van Megen et al., 2009). For most of the genera no phylogenetic information is available. A cladistic analysis of 31 genera out of the 48 valid genera of Xyalidae suggested the presence of seven clades (Nicholas & Trueman, 2002). However, five genera were polyphyletic in their analyses: *Daptonema* Cobb, 1920, *Xyala* Cobb, 1920, *Gonionchus*, *Filipjeva* Ditlevsen, 1928 and *Cobbia* de Man, 1907. In order to avoid a paraphyletic classification, we have recognized three polytomic clades. The position of these five genera were based on the similarities of the morphological characters (Fonseca & Bezerra, 2014a).

Monhysteroidea is formed by a single family, Monhysteridae, which is morphologically subdivided in two subfamilies, Diplolaimellinae Jacobs, 1987 and

Monhysterinae de Man, 1876 (Fonseca & Decraemer, 2008; Jacobs, 1987). However, these subfamilies have not been recognized in molecular phylogenies (Holovachov et al., 2012; Leduc, Verdon & Zhao, 2018; van Megen et al., 2009). Instead, two clades are recognized with high branch support, one grouping *Anguimonhystera* Andrássy, 1981, *Halomonhystera* Andrássy, 2006, *Eumonhystera* Andrássy, 1981, *Tridentula* (Eyualem - Abebe & Coomans, 1995), and *Monhystera* Bastian, 1865, and a second grouping *Tripylium* Cobb, 1920, *Monhystrium* Cobb, 1920, *Diplolaimelloides* Meyl, 1954 and *Diplolaimella* Allgén, 1929. In two 18S phylogenies, *Geomonhystera* Andrássy, 1981 is separated from these two clades with high branch support (Holovachov, Rodrigues, Zbinden & Duperron, 2013; van Megen et al., 2009). Therefore, all genera without sequenced data were consider polytomic to *Geomonhystera*.

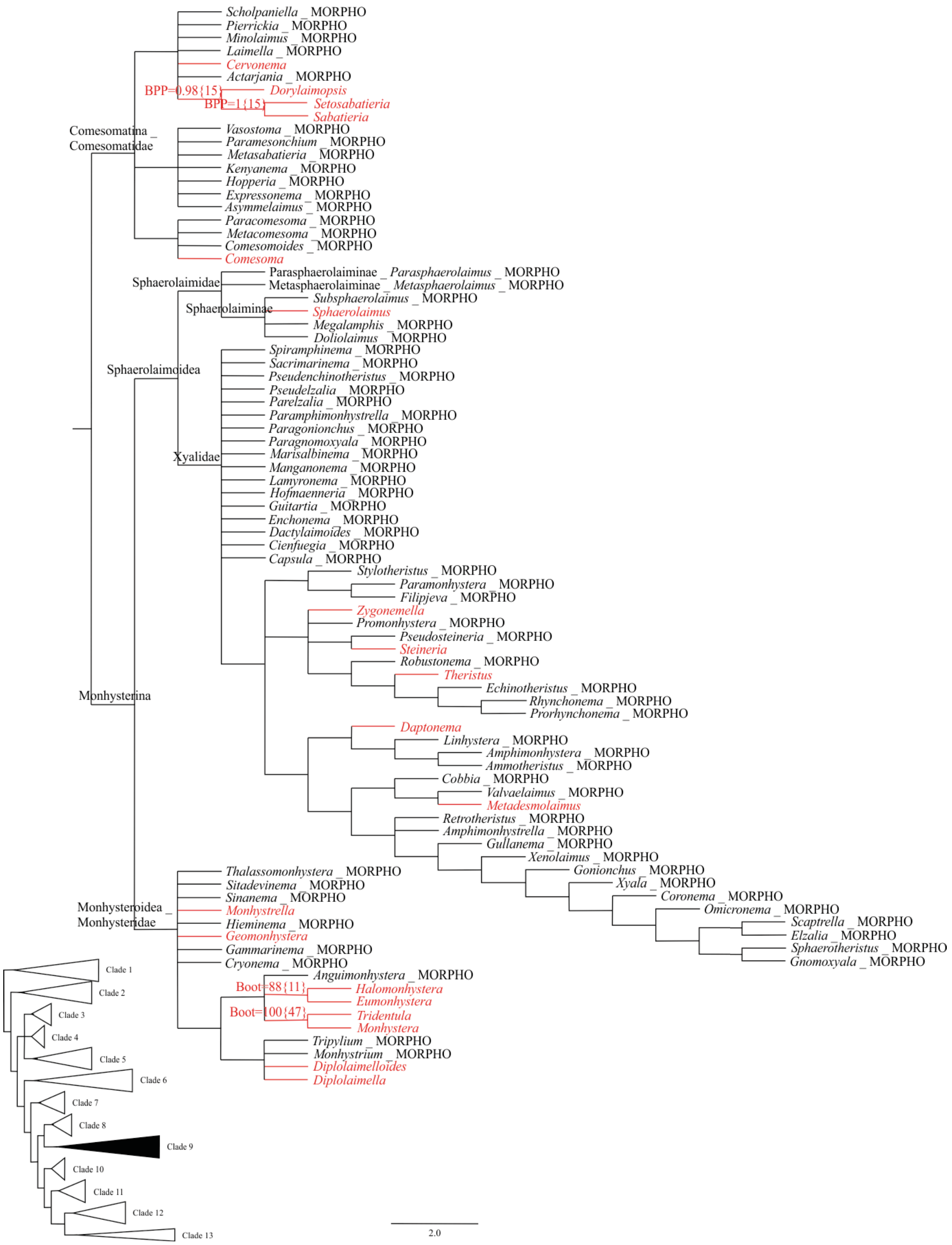

Figure 12. Representation of the Order Monhysterida of the supertree of Nematoda. The clades supported by molecular data are marked in red. The number between brackets corresponds to the number of reference in the list of consulted molecular studies.

CLADE 10 - ORDER ISOLAIMIIDA COBB, 1920 (Figure 13)

Isolaimiida is a monotypic order, originally classified within Dorylaimia, that includes the single genus *Isolaimium* Cobb, 1920, of which its exact phylogenetic position is still subject of debate (Holovachov, 2014a). This genus is close to *Aulolaimus* de Man, 1880 in a separated branch with high branch support (Boot = 100) (van Megen et al., 2009). The family Aulolaimidae Jairajpuri & Hopper, 1968 is considered *incertae sedis* due to the morphological intrageneric diversity of *Aulolaimus* and the difficulty in establish the most distinctive characters (Abolafia & Peña-Santiago, 2018; Holovachov, 2014a). Therefore, the molecular hypothesis was adopted until new data come to light.

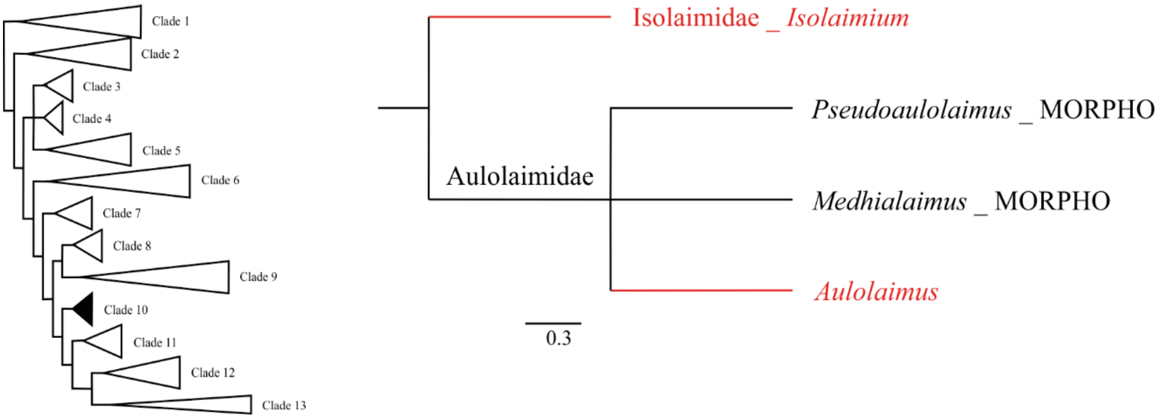

Figure 13. Representation of the Order Isoolaimiida of the supertree of Nematoda. The clades supported by molecular data are marked in red.

CLADE 11 – SIPHONOLAIMOIDEA AND AXONOLAIMOIDEA (Figure 14)

This clade includes the superfamilies Siphonolaimoidea (families Fusivermidae Tchesunov, 1996, Siphonolaimidae Filipjev, 1918 and Linhomoeidae Filipjev, 1922), which was separated from Monhysterida, and Axonolaimoidea (family Axonolaimidae Filipjev, 1918), traditionally classified in Araeolaimida, from molecular phylogenies (Holovachov et al., 2012; Holovachov, Rodrigues, Zbinden & Duperron, 2013; Holterman et al., 2008; Hwang et al., 2009; Leduc, Verdon & Zhao, 2018; Leduc, Zhao, Verdon & Xu, 2018; van Megen et al., 2009). There is no apomorphy to this clade (Fonseca & Bezerra, 2014b).

Superfamily Siphonolaimoidea Filipjev, 1918

The marine family Fusivermidae form a polytomy with Siphonolaimidae and Linhomoeidae since the relationships within Siphonolaimoidea are unclear (Lorenzen, 1994). Siphonolaimidae is subdivided in the two subfamilies Astomonematinae Kito & Aryuthaka, 2006 and Siphonolaiminae Filipjev, 1918 according to the disposition of the anterior sensilla (Fonseca & Bezerra, 2014a). The family Linhomoeidae is divided in four branches corresponding to the subfamilies Desmolaiminae G. Schneider, 1926, Thelonematinae Bussau, 1993, Eleutherolaiminae Gerlach & Riemann, 1973 and Linhomoeinae Filipjev, 1922.

Superfamily Axonolaimoidea Filipjev, 1918

There is no apomorphy to establish the monophyly of Axonolaimidae (Fonseca & Bezerra, 2014b). The only molecular record for *Araeolaimus* de Man, 1888 places it close to *Odontophora* Bütschli, 1874, but they are morphologically distinct genera, mainly regarding to the buccal cavity. Therefore, *Araeolaimus* was maintained in Diplopeltidae. In phylogenetic analysis, *Parodontophora* Timm, 1963 was related to *Enoploides* Saveljev, 1912, order Enoplida (Bhadury et al., 2008). Nevertheless, they are morphologically distinct genera concerning the buccal cavity, pharynx and reproductive system. Moreover Badhury et al. (2008) mentioned some relations found in the 18S tree could be the result of misidentification. For the present supertree, *Parodontophora* was kept within Axonolaimidae.

The genera *Odontophora*, *Axonolaimus* de Man, 1889 and *Ascolaimus* Ditlevsen, 1919 form a polytomy since *Ascolaimus* was suggested to be close to *Odontophora* and *Axonolaimus* (Holovachov, Boström, Tandingan De Ley, Robinson, Mundo-Ocampo, & Nadler, 2013; Hwang et al., 2009; van Megen et al., 2009). Unlike *Araeolaimus*, *Cylindrolaimus* is a sister group of this polytomy (Hwang et al., 2009). The shape of the buccal cavity of *Cylindrolaimus* (long and tubular) resembles that of *Ascolaimus* and *Axonolaimus* (conical); besides, the very characteristic odontia of Axonolaimidae are insignificant in these two genera but present in *Odontophora*. All these genera have also outstretched ovaries (Fonseca & Bezerra, 2014b). Therefore, *Cylindrolaimus* was reallocated from Diplopeltidae to Axonolaimidae.

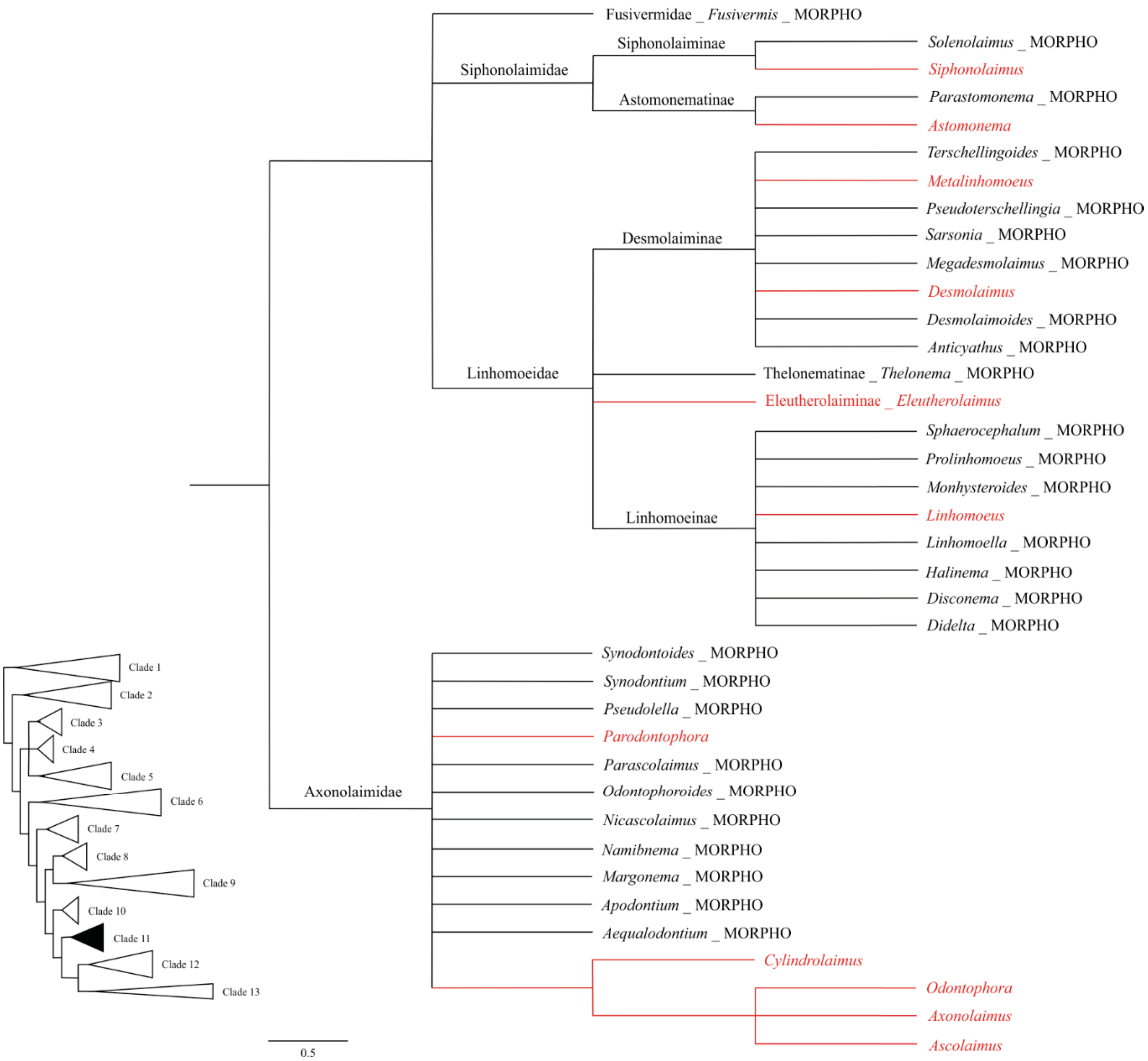

Figure 14. Representation of the Axonolaimida ord. nov. of the supertree of Nematoda. The clades supported by molecular data are marked in red.

CLADE 12 - ORDER PLECTIDA GADEA, 1973 (Figure 15)

The order Plectida was originally divided in two suborders, Ceramonematina Cobb, 1933 and Plectina Malakhov, Ryzhikov & Sonin, 1982, and not considered monophyletic (Holovachov, 2014b). In the supertree, Ceramonematina is within the order Desmoscolecida (clade 7), leaving Plectida with a single suborder, Plectina. This clade includes the families Rhadinematidae Lorenzen, 1981, Metateratocephalidae Eroshenko, 1973, Benthimermithidae Petter, 1980, Ohridiidae Andrássy, 1976, Creagrocercidae Baylis, 1943, Chronogastridae Gagarin, 1975, Leptolaimidae Örley, 1880, Aphanolaimidae Chitwood, 1936, Camacolaimidae Micoletzky, 1924 and

Plectidae Örley, 1880, of which Benthimermithidae and Creagrocercidae are not included in a recent morphological compendium (Holovachov & Boström, 2010).

The first split originates a polytomy, since there is no sequenced material to Rhadinematidae so far (Holovachov, Boström, Tandingan De Ley, Robinson, Mundo-Ocampo, & Nadler, 2013; Holterman *et al*., 2008; van Megen *et al*., 2009). The second split separates Plectidae from the other families.

Based on molecular data, the family Benthimermithidae, originally positioned in the order Benthimermithida Tchesunov, 1995, is polytomic. This clade considers *Trophomera* Rubtzov & Platonova, 1974 (Benthimermithidae) close to *Domorganus* Goodey, 1946, *Creagrocercus* Baylis, 1943, *Chronogaster* Cobb, 1913, Leptolaimidae and Camacolaimidae (Holovachov, Rodrigues, Zbinden, & Duperron, 2013). The insufficient 18S rRNA sequences obtained for this family and the scarcity of morphological features makes the positioning of benthimermithids possible to change in future phylogenetic analysis (Holovachov, Rodrigues, Zbinden, & Duperron, 2013; Miljutin, 2014). At the present, we propose to consider Benthimermithidae within Plectida until the emergence of new data. Ohridiidae and Creagrocercidae form a well-supported dichotomy according to molecular data (Holovachov, Boström, Tandingan De Ley, Robinson, Mundo-Ocampo, & Nadler, 2013).

Leptolaimidae and Aphanolaimidae are considered sister families, but *Paraplectonema* Strand, 1934 would make Leptolaimidae paraphyletic (Holovachov, Boström, Tandingan De Ley, Robinson, Mundo-Ocampo, & Nadler, 2013; van Megen *et al*., 2009). Therefore, we suggest transferring this genus to Aphanolaimidae, since it has no excretory ampulla and its excretory duct is very long and opens at the midpharynx or between subventral lips. All these characters are shared with Aphanolaimidae (Holovachov, 2014b). In Leptolaimidae, *Manunema* Gerlach, 1957 and *Anomonema* Hopper, 1963 are sister genera according to the “somatic pore” type of sensilla on male tail, the somatic setae type and presence of a single testis (Holovachov & Bostrom, 2004).

The genera within Aphanolaimidae are divided in two subfamilies, Aphanolaiminae Chitwood, 1936 and the monotypic Anonchinae Andrássy, 1973, with *Anonchus* Cobb, 1913 (Zullini *et al*., 2002). The genus *Paraplectonema*, originally classified in Leptolaimidae, was considered as a sister group of the genera of Aphanolaimidae (Holovachov, Boström, Tandingan De Ley, Robinson, Mundo-Ocampo, & Nadler, 2013; Holovachov, Rodrigues, Zbinden, & Duperron, 2013; van

Megen *et al*., 2009). Common to *Paraplectonema* and Leptolaimidae is the absence of an excretory ampulla and the long excretory duct, that opens either at level of midpharynx or between subventral lips (Holovachov, 2014b). The relationships of Camacolaimidae followed morphological (Holovachov & Bostrom, 2004) and molecular data (Holovachov, Boström, Tandingan De Ley, Robinson, Mundo-Ocampo, & Nadler, 2013).

In Plectidae, the three branches correspond to the subfamilies, Pakirinae Inglis, 1983, Plectinae Örley, 1880 and Wilsonematinae Chtiwood, 1951, except for *Cynura* Cobb, 1920 that is placed as a sister group of Plectinae and Wilsonematinae, suggesting that the pharyngeal valvular apparatus - one of the two characters used to transfer *Cynura* to Chronogastridae - may have undergone a simplification (Holovachov, Boström, Tandingan De Ley, Robinson, Mundo-Ocampo, & Nadler, 2013).

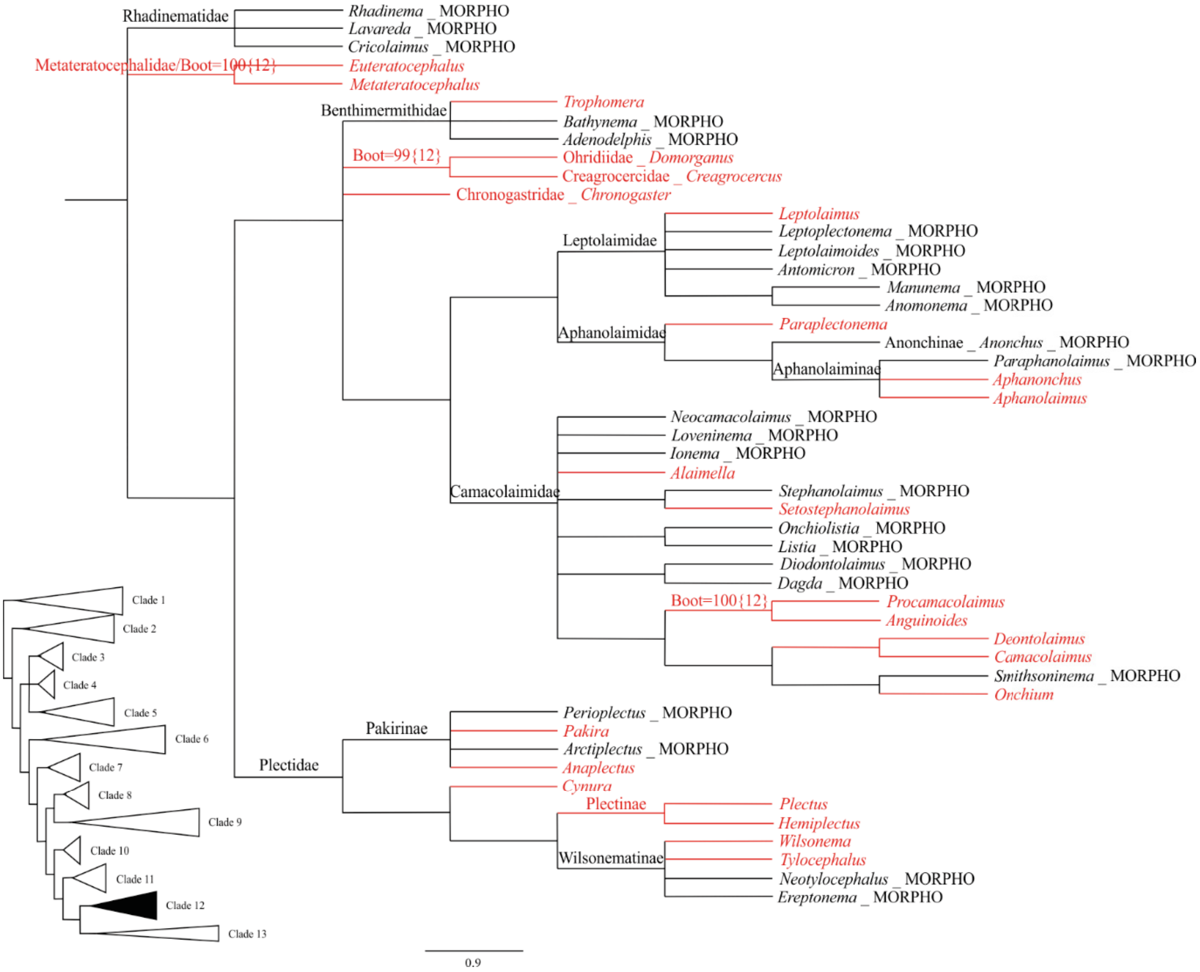

Figure 15. Representation of the Order Plectida of the supertree of Nematoda. The clades supported by molecular data are marked in red. The number between brackets corresponds to the number of reference in the list of consulted molecular studies.

2.5 CONCLUSION

The proposed supertree is the first attempt to synthesize the phylogenetic relationships of nematodes based on the congruence of morphological and molecular phylogenies. After merging morphological and molecular trees across the phylum it became evident that there are several congruences among them, but also, some important divergences to be considered. The proposed changes presented in the supertree should be seen as a starting point for further research, many nodes along the tree are poorly resolved needing more information. An important advance of having such supertree is that all the research areas (phylogenetics, taxonomy and systematics, and ecology) uses the same tree to infer evolutionary and ecological processes.

The main drawback of the Nematoda systematics is the fact that most of the taxa (genera to classes) have been erected based on a combination of morphological characters and not based on synapomorphies and apomorphies. Therefore, the molecular data plays an important role in inferring phylogenetic relationships among taxa. The phylogenetic inference is stronger when multiple studies, genes and morphology, point to the same direction. Particularly for Nematoda, the success of the supertree approach is therefore tightly linked with the amount of molecular data available across the taxa. For marine nematodes, almost 70% have nor molecular data and were not included in any type of phylogenetic analyses, creating a high level of uncertainty (polytomy) within the supertree. Since this uncertainty is now mapped across the tree, it is possible to direct the investigations towards these unsolved nodes. Moreover, it is now possible to transfer these uncertainties to evolutionary and ecological analyses when calculating ecological indices that considers phylogenetic relationships.

Most of the polytomies in the supertree occurred at subfamilies and genera level, reflecting the incipient amount of sequences in public depositories, the paraphyletic condition of many taxa through the molecular phylogenies, and the lack of cladistic analysis. Thoracostomopsidae, for example, is polytomic since molecular studies suggested that *Thoracostomopsis* and *Trileptium* are within Enoplolaiminae. On top of that, half of the genera within this family are unsequenced. Polytomies also exist among families but are less common (e.g. Desmoscolecina). Based on the molecular evidences and morphological considerations it was possible to better organize the taxa into new clades. For instance, Selachinematidae and Paramicrolaimidae form a separated clade within Chromadorida, since the systematic position of the latter family has changed due to an unusual morphology. This grouping indicated that Paramicrolaimidae may have lost the punctuations of the cuticle over time. The reallocation of Siphonolaimoidea and Axonolaimidae as a separated clade recognizes Araeolaimida and Monhysterida as monophyletic orders. Additional changes that are proposed here are that enchelidiids are grouped as a terminal clade of Oncholaimidae, and marimermithids are placed as a family close to Leptosomatidae. Desmodoridae includes three subfamilies, Stilbonematinae, Pseudonchinae and Desmodorinae, this latter including *Richtersia* and draconematids. The families Haliplectidae and Aulolaimidae, and the order Isolaimiida have been traditionally considered *incertae sedis*, but molecular phylogenies indicated they could be placed as independent lineages in the supertree. Specifically, in Aulolaimidae, the morphological intrageneric diversity of *Aulolaimus* hampers to establish the most distinctive characters of the genus. Therefore, in the supertree, the molecular hypothesis was considered until new data come to light.

In many other Phyla, the controversy between molecular and morphological trees have provoked taxonomists to search for phylogenetic informative characters (e.g. osteology in fishes) which were not analysed by previous studies. Therefore, the existence of evolutionary lineages based on molecular evidences may point to the need of constant re-examination of the systematics in a search of morphological synapomorphies. It will also provoke improvements in taxa diagnoses and species descriptions, as well as explore evolutionary processes in ecological data.

2.6 ACKNOWLEDGMENTS

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2.7 APPENDICES

Table 1. Number of sequenced genera of marine nematodes obtained from phylogenetic studies and total number of genera per family. The classification is according to that proposed in the supertree. Molecular data obtained from the GenBank and number of valid genera obtained from WoRMS at 26/04/2018. Daggers represent families with cladistic analysis from morphological characters and after Lorenzen (1994).

	Molecular	**Total**	**%**
Achromadoridae Gerlach & Riemann, 1973	1	1	100%
Aegialoalaimidae Lorenzen, 1981	0	1	0%
Anoplostomatidae Gerlach & Riemann, 1974	2	2	100%
Anticomidae Filipjev, 1918	2	6	33%
Aphanolaimidae Chitwood, 1936	3	5	60%
Aponchiidae Gerlach, 1963	0	2	0%
Axonolaimidae Filipjev, 1918	5	15	33%
Benthimermithidae Petter, 1980	1	3	33%
Bodonematidae Jensen, 1991	0	1	0%
Camacolaimidae Micoletzky, 1924	7	16	44%
Camallanidae Railliet & Henry, 1915	2	3	67%
Campydoridae (Thorne, 1935) Clark, 1961	1	1	100%
Ceramonematidae Cobb, 1933	2	7	29%
Chromadoridae Filipjev, 1917	14	37	38%
Chronogastridae Gagarin, 1975	1	1	100%
Comesomatidae Filipjev, 1918	5	20	25%
Coninckiidae Lorenzen, 1981	0	1	0%
Cyartonematidae Tchesunov, 1989	2	3	67%
Cyatholaimidae Filipjev, 1918	7	23	30%
Desmodoridae Filipjev, 1922†	24	62	40%
Desmoscolecidae Shipley, 1986	4	17	24%

Diplopeltidae Filipjev, 1918	3	13	23%
Diplopeltoididae Tchesunov, 1990	0	1	0%
Enoplidae Dujardin, 1845	1	3	33%
Eophasmidae Poinar, 2011	0	1	0%
Epsilonematidae Steiner, 1927†	1	13	8%
Ethmolaimidae Filipjev & Schuurmans Stekhoven, 1941	1	3	33%
Fusivermidae Tchesunov, 1996	0	1	0%
Gnathostomatidae Railliet, 1895	1	2	50%
Haliplectidae Chitwood, 1951	1	3	33%
Ironidae de Man, 1876	3	7	43%
Lauratonematidae Gerlach, 1953	0	2	0%
Leptolaimidae Örley, 1880	1	6	17%
Leptosomatidae Filipjev, 1916	8	32	25%
Linhomoeidae Filipjev, 1922	4	18	22%
Marimermithidae Rubtzov & Platonova, 1974	0	4	0%
Meyliidae De Coninck, 1965	0	5	0%
Microlaimidae Micoletzky, 1922	3	12	25%
Molgolaimidae Jensen, 1978	1	1	100%
Monhysteridae de Man, 1876	8	17	47%
Monoposthiidae Filipjev, 1934	2	4	50%
Neotonchidae Wieser & Hopper, 1966	1	8	13%
Ohridiidae Andrássy, 1976	1	1	100%
Oncholaimidae Filipjev, 1916†	14	49	29%
Oxystominidae Chitwood, 1945	6	10	60%
Pandolaimidae Belogurov, 1980	0	1	0%
Paramicrolaimidae Lorenzen, 1981	1	1	100%
Phanodermatidae Filipjev, 1927	2	9	22%
Plectidae Örley, 1880	2	2	100%
Prodesmodoridae fam. nov.	1	1	100%

Rhabditidae Örley, 1880	2	3	67%
Rhabdodemaniidae Filipjev, 1934	1	1	100%
Rhabdolaimidae Chitwood, 1951	1	1	100%
Rhadinematidae Lorenzen, 1981	0	3	0%
Selachinematidae Cobb, 1915	8	13	62%
Simpliconematidae Blome & Schrage, 1985	0	1	0%
Siphonolaimidae Filipjev, 1918	2	4	50%
Sphaerolaimidae Filipjev, 1918	1	6	17%
Tarvaiidae Lorenzen, 1981	1	1	100%
Thoracostomopsidae Filipjev, 1927	10	20	50%
Trefusiidae Gerlach, 1966	3	6	50%
Triodontolaimidae De Coninck, 1965	0	1	0%
Tripyloididae Filipjev, 1928	2	6	33%
Tubolaimoididae Lorenzen, 1981	0	2	0%
Xenellidae De Coninck, 1965	0	2	0%
Xyalidae Chitwood, 1951†	5	48	10%
Total	**185**	**575**	**32%**

Table 2. List of molecular studies consulted. Abbreviations: SSU – small subunit; COI - cytochrome c oxidase 1; LSU – large subunit; ML - maximum likelihood; MP - maximum parsimony; NJ - neighbour joining; BI - Bayesian inference.

Number of the author		**Year**	**Gene**	**Iinference Method**	**Taxa**
1	Armenteros *et al*.	2014	18S rDNA (586 bp), COI mtDNA (393 bp)	ML	Desmodoridae Filipjev, 1922 and Nematoda
2	Avó *et al*.	2017	18S rRNA (~998 bp) and COI mtDNA (~362 bp)	ML	Nematoda
3	Bayer *et al*.	2009	18S rDNA	MP	*Robbea* Gerlach, 1956 and Desmodorida De Coninck, 1965
4	Bhadury *et al*.	2006	18S rRNA (~345 bp)	NJ	Nematoda
5	Bhadury *et al*.	2007	18S rRNA (~345 bp)	NJ	Nematoda
6	Bhadury *et al*.	2008	18S rRNA (~926 bp)	NJ	*Terschellingia* de Man, 1888, Enoplida Filipjev, 1929, Desmodorida De Coninck, 1965, Chromadorida Chitwood, 1933 and Monhysterida Filipjev, 1929
7	Bik *et al*.	2010	18S (1600 bp), 28S rRNA (600 bp) and COI mtDNA (~400 bp)	ML	Enoplida Filipjev, 1929

8	De Ley *et al*.	2005	18S rDNA (D2-D3) (~500 bp)	MP and NJ	Nematoda
9	Derycke *et al*.	2010	COI mtDNA (I3M11 and M1M6)	NJ	Nematoda
10	Holovachov *et al*.	2009	18S rDNA	MP, ML and NJ	Plectida Malakhov, 1982, Rhabditida Chitwood, 1933, Araeolaimida De Coninck & Schuurmans Stekhoven, 1933, Monhysterida Filipjev, 1929 and Ceramonematidae Cobb, 1933
11	Holovachov *et al*.	2012	18S rDNA	BI	*Tarvaia* Allgén, 1934 and Chromadoria Pearse, 1942
12	Holovachov *et al*.	2013	18S rRNA	BI	*Cynura* Cobb, 1920 and Plectida Malakhov, 1982
13	Holovachov *et al*.	2013	18S rDNA (~900 bp and ~1700 bp)	BI	*Trophomera* Rubtzov & Platonova, 1974 and Chromadorida Chitwood, 1933
14	Holterman *et al*.	2006	18S rDNA	BI, MP and NJ	Nematoda
15	Holterman *et al*.	2008	18S rDNA	BI and ML	Nematoda
16	Hwang *et al*.	2009	18S rDNA	MP, ML, NJ and BI	Nematoda

17	Kampfer *et al*.	1998	18S rDNA	MP and NJ	Nematoda
18	Kim *et al*.	2017	mtDNA (COI and rrnS)	BI and ML	*Plectus* Bastian, 1865, Enoplea and Chromadorea
19	Koehler *et al*.	2016	18S rRNA (~1600 bp) and COI mtDNA (~240 bp)	ML and BI	Spiruromorpha De Ley & Blaxter, 2002, Dracunculoidea Stiles, 1907, Ascaridomorpha De Ley & Blaxter, 2002 and Oxyuridomorpha De Ley & Blaxter, 2002
20	Kumari & Subbotin	2012	18S rRNA, 28S rRNA (D2-D3)	BI	Trichodoridae Thorne, 1935
21	Leduc & Zhao	2015	18S rDNA and 28S rDNA (D2-D3)	BI	Selachinematidae Cobb, 1915
22	Leduc & Zhao	2016c	18S rDNA and 28S rDNA (D2-D3)	BI	Selachinematidae Cobb, 1915
23	Leduc & Zhao	2018	18S rDNA (~600 bp) 28S (D2-D3) (~300 bp)	BI	Cyatholaimidae Filipjev, 1918
24	Leduc & Zhao	2016b	18S (~700 bp) and 28S (D2-D3) (~400 bp)	BI	Desmodoridae Filipjev, 1922
25	Leduc & Zhao	2016a	18S rDNA (~700 bp) and 28S rRNA (D2-D3)	BI and ML	Desmodoroidea Filipjev, 1922 and Microlaimoidea Micoletzky, 1922

26	Leduc & Sinniger	2018	18S rDNA and 28S (D2-D3) rDNA	BI and ML	Stilbonematinae Chitwood, 1936
27	Leduc et al.	2018	18S (>1200 bp) and 28S (D2-D3) rDNA	BI and ML	*Paramicrolaimus* Wieser, 1954 and Chromadorea
28	Leduc *et al*.	2018	18S (>1200 bp) and 28S (D2-D3) rDNA (>500 bp)	BI and ML	*Rhaptothyreus* Hope & Murphy, 1969 and Nematoda
29	Lins *et al*.	2017	18S rDNA	ML and BI (*Halalaimus*)	Nematoda
30	Litvaitis *et al*.	2000	28S rDNA (D3) (~300 bp)	MP and NJ	Nematoda
31	Markmann & Tautz	2005	28S rRNA (D3-D5)	NJ	Nematoda
32	Matsushita *et al*.	2015	18S rDNA	NJ	Nematoda
33	Meldal *et al*.	2007	18S rDNA	BI	Nematoda
34	Mordukhovich *et al*.	2015	28S rRNA (~500 bp) and COI mtDNA (~300 bp)	ML	*Adoncholaimus* Filipjev, 1918, *Admirandus* Belogurov & Belogurova, 1979, *Viscosia* de Man, 1890
35	Neres *et al*.	2010	18S rRNA	NJ, MP and BI	*Zygonemella* Cobb, 1920, Monhysterida Filipjev, 1929 and

					Desmodorida De Coninck, 1965
36	Oliveira *et al*.	2012	28S rDNA - D2-D3 (~714 bp) and ITS (~1149 bp) - and COI (~396 bp)	NJ	*Thoracostoma* Marion, 1870
37	Ott *et al*.	2014	18S rRNA	BI and ML	*Robbea* Gerlach, 1956 and Stilbonematinae Chitwood, 1936
38	Pereira *et al*.	2010	18S rDNA (324 bp) and 28S rDNA (D2-D3) (794 bp)	MP, ML and NJ	Enoplida Filipjev, 1929
39	Prado-Vera *et al*.	2012	18S rDNA	BI	*Tripylina* Andrassy, 1974 and Tripylidae de Man, 1876
40	Prado-Vera *et al*.	2016	18S rDNA	BI	*Trischistoma* Cobb, 1913, *Tripylina* Andrassy, 1974 and Enoplida Filipjev, 1929
41	Prado-Vera *et al*.	2016b	18S rDNA	BI	*Tripylella* Brzeski & Winiszewska-Slipinska, 1993, Triplonchida Cobb, 1920, Trefusioidea Gerlach 1966 and Enoplida Filipjev, 1929
42	Rho *et al*.	2011	18S rRNA	MP, ML and BI	Draconematidae Filipjev, 1918

43	Sharma *et al*.	2006	18S rDNA (~600 bp)	MP	Comesomatidae Filipjev, 1918, Linhomoeidae Filipjev, 1922, Tobrilidae De Coninck, 1965, Sphaerolaimidae Filipjev, 1918, Desmodoridae Filipjev, 1922, Chromadoridae Filipjev, 1917 and Oncholaimidae Filipjev, 1916
44	Shi & Xu	2018	18S rDNA (~1275 bp)	ML and BI	*Africanema* Vincx & Furstenberg, 1988, Tripyloididae Filipjev, 1928 and Trefusiidae Gerlach, 1966
45	Shokoohi *et al*.	2013	18S rDNA (~900 bp)	BI	*Ironus* Bastian, 1865 and Enoplida Filipjev, 1929
46	Smythe	2015	18S rRNA (~1600 bp)	BI and ML	Enoplida Filipjev, 1929 and Triplonchida Cobb, 1920
47	van Megen *et al*.	2009	18S rDNA (1700 bp)	ML	Nematoda
48	Vogt *et al*.	2014	28S rDNA (D2-D3)	NJ	Nematoda

49	Xu *et al*.	2015	18S rDNA and LSU rDNA (D2-D3)	BI	*Trischistoma* Cobb, 1913 and *Tripylina* Andrassy, 1974
50	Zhang & Zhou	2012	18S rRNA (~900 bp)	NJ	*Enoplus* Dujardin, 1845

CHAPTER 3

The convergent evolution across coastal habitats

Ana Carolina Vilas-Boas[1, 2*], Gustavo Fonseca[2] & Fabiane Gallucci[2]

[1]Pós-graduação em Sistemas Costeiros e Oceânicos, Centro de Estudos do Mar, Universidade Federal do Paraná, Avenida Beira Mar s/n, Pontal do Sul, CEP 83255-976, PO Box 61, Pontal do Paraná, Paraná, Brazil
[2]Instituto do Mar, Universidade Federal de São Paulo, Rua Carvalho de Mendonça, 145 Santos, São Paulo, Brazil

*Corresponding Author. E-mail: ananinanina@hotmail.com

3.1 ABSTRACT

The distribution patterns of biodiversity on Earth are the results of a combination of evolutionary and ecological processes. The assumption is that, within a given habitat, biogeographical historical processes shapes the phylogenetic relatedness of co-occurring species, while ecological processes will select particular functional groups. The relationship between these parameters give us indication of the mechanisms structuring ecological communities over the evolutionary time scale. In order to test whether the environmental distinction among coastal habitats have driven distinct eco-evolutionary processes, we analyzed the average and variation in phylogenetic distinctness (AvPDist and VarPDist), the average and variation in functional distinctness (AvFDist and VarFDist) and their relationships with species richness (S) of marine nematode assemblages across estuarine tidal flats, mangroves and sandy beaches. We hypothetize that species of sandy beaches and mangroves will be more influenced by convergent evolution than the transitional tidal flats. This means that AvFDist will increase with S, but VarFDist will decrease with S, given the expected narrow range of functional traits within those habitats. Convergent evolution also represents that VarFDist and VarPDist are positively correlated with each other and below the relationship expected by a random selection. Mangroves were the most species rich habitat, totalizing 101 species, while sandy beaches and estuarine tidal flats showed respectively 85 and 67 species. Sandy beaches were significantly different from mangroves and tidal flats in terms of species composition, PDist and FDist. The assemblages of sandy beaches had a higher variation and a lower AvPDist and AvFDist than mangroves and tidal flats. Mangroves and tidal flats differed from each other in terms of species composition but not in relation to PDist and FDist. FDist and PDist components were not related to S, but they were positively related to each other at all habitats. These results corroborated that the assemblages of the three coastal habitats are influenced by convergent evolution, specially from the sandy beaches, but suggested that limiting similarity may also be occurring on the assemblages. Therefore, both average and variation in taxonomic distinctness are relevant in inferring processes shaping the communities of coastal habitats.

3.2 INTRODUCTION

Analysing biodiversity patterns from different diversity measures is relevant to shed light on the relative importance of evolutionary and ecological processes shaping communities (Safi et al., 2011). The inference of evolutionary and ecological processes has been accessed by correlating three main parameters: phylogenetic diversity (PD), functional diversity (FD) and species richness (S) (Purschke et al., 2013; Cisneros et al., 2014; Presley et al., 2018). It is expected that, under a random selection of species from a regional pool, as more the species richness increases the phylogenetic and functional diversity will also increase in a local pool (Sax et al., 2007; Kluge & Kessler, 2011). However, these relationships are asymptotic, since the probability of adding new characteristics declines with the increase of the number of species (Fig. 1a). It is also expected that the both PD and FD are positively correlated, in which less closely related species are functionally different (Fig 1b; Safi et al. 2011). Deviations from this scenario correspond to eco-evolutionary processes like environmental filtering or interclade competition suggested by functional underdispersion (Presley et al., 2018), or limiting similarity and rapid trait evolution hypothesized by functional overdispersion (Fig 1b; Mayfield & Levine, 2010). The main assumption of this approach is that distinct communities (in terms of species composition) may show distinct trait evolution patterns if they had enough time to go through evolutionary divergence and differentiate, for example, in the use of resources (Schumacher & Roscher, 2009). So far eco-evolutionary studies have approached this issue by calculating the average PD or FD. These measures are limited by different sampling efforts and for not consider the uniqueness of a species in relation to other species in a community (Clarke & Warwick, 2001). The phylogenetic and functional distinctness (PDist and FDist) overcome these limitations and also reflect the richness in higher hierarchies. However, the components of phylogenetic and functional distinctness, the average (AvDist, Δ^+) and variation (VarDist, Λ^+), as well as their relationship, has been underexplored in evolutionary and ecological studies (Warwick & Clarke, 1998; Somerfield et al., 2008).

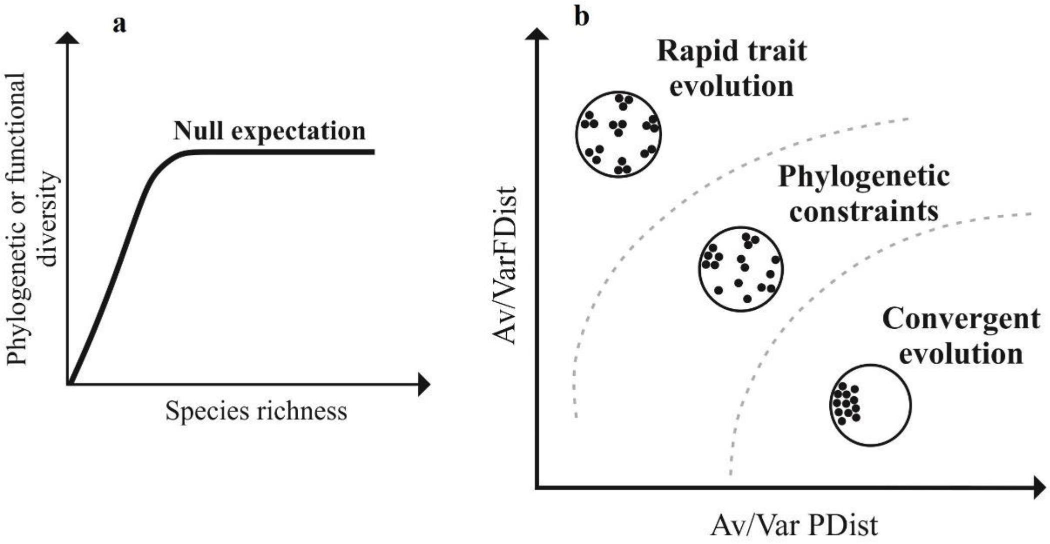

Figure 1. Theoretical models for relationships between (a) phylogenetic or functional diversity and species richness, and (b) functional distinctness components with phylogenetic distinctness components (Adapted from: Cisneros et al., 2014).

According to the eco-evolutionary perspective, AvDist and VarDist give us complementary information. A very harsh environment, for instance, may favour few species of a particular functional group (low average of functional distinctness) which could be a result of the success of a particular clade that lack trait "evolvability" (low variation in phylogenetic distinctness or VarPDist) or from multiple clades (high VarPDist) suggesting convergent evolution (Cadotte et al., 2013). The variation depicts the dispersion of species in evolutionary and functional space through the differences in the structure of the species relationships, analysing from higher ranks, like a taxonomic order or a broader functional group, to terminal groups (Clarke & Warwick, 2001).

Marine populations are submitted to different selective pressures, making common the convergent evolution of morphological structures of co-occurring species (Lindgren et al., 2012). This functional clustered pattern of species co-occurring more than expected by random selection indicate environmental filtering, while species with functional overdispersed patterns (i.e. divergent) co-occurring less than expected by chance indicate limiting similarity, both filters being frequently considered in community assembly studies (Botta-Dukát & Czucz, 2016; Saito et al., 2016).

In the marine realm, the transition between the terrestrial and marine environments creates particular habitats with strong environmental gradients. The intertidal zone of sandy beaches, for instance, shows a decreasing humidity gradient, exposure to wave action, tidal forces and oxygen concentrations, and an increasing temperature variation from the lower to the upper tidal zone (McLachlan & Turner, 1994). Estuarine tidal flats are transitional habitats mainly in relation to salinity and tidal waves (Day Jr. et al., 2012). Mangroves are constantly subjected to variation in salinity, high deposition of organic matter and fine sediments, reducing the quantity of oxygen in the sediment. It is known that these contrasting conditions among coastal habitats provides them to have a unique set of species (Fonseca & Netto 2015; Brustolin, 2018), a very important condition to the conservation of the regional pool of species (Mayfield et al., 2010). Nevertheless, it remains an open question, whether these habitats share similar eco-evolutionary processes.

Given that mangroves, tidal flats and sandy beaches are singular habitats, the objective of this study is to test whether the environmental distinction among coastal habitats have driven distinct eco-evolutionary processes. Overall, we expect that the PDist and FDist components are positively correlated with species richness for the habitats, considering each habitat has a unique set of species. We also hypothetize that species of sandy beaches and mangroves will be more influenced by convergent evolution than the transitional tidal flats. This means that AvFDist will increase with S, but VarFDist will decrease with S, given the expected narrow range of functional traits within those habitats. Convergent evolution means that VarFDist and VarPDist are positively correlated with each other and below the relationship expected by a random selection.

To test the generalization of these hypotheses we have investigated the marine nematode assemblages from distinct coastal habitats, namely: sandy beaches, mangroves and estuarine tidal flats. The convergent morphological evolution is well known within Nematoda, for example, when identifying that parasitic groups do not constitute a monophyletic group in the phylogeny of the phylum (Blaxter et al., 1998). Most of the species of Nematoda are members of marine meiofauna, where they stand out as one of the most abundant and diverse group, living from intertidal to abyssal zones (Nicholas, 1975; Riemann, 1988). Their high diversity makes them an important ecological unit, noticeable through the different feeding mechanisms or different cuticle morphologies (Heip et al., 1982).

3.3 METHODS

3.3.1 Study area and sampling design

A total of 96 samples of sandy beaches, mangroves and estuarine tidal flats were obtained using a nested sampling design along the littoral zone of São Paulo State (Brazil). One campaign was carried out in four exposed locations, 100 kilometers distant, and at each location, two plots were randomly selected, 100 meters distant. At each plot, four samples of sediment, 10 meters distant and down to a depth of five centimeters, were collected using a 2.5 centimeters core. The samples were fixed in 4% folmaldehyde.

3.3.2 Trait data

We have selected six traits. These traits are related to the ecosystem functioning, representing physiological, behavioral and ecological features. The description of each traits and its categories follow below:

Body size and *body shape* are considered relevant to metabolic rates, to the tolerance to chemical stress, to the ability to move or migrate through the sediment and to the vulnerability to predation (Soetaert et al., 2002; Losi et al., 2013). The *body size* was divided in < 1 millimeters (mm), 1 to 2 mm, 2 to 4 mm and > 4 mm (Schratzberger et al., 2007), while *body shape*, that is the length/width ratio, was divided in stout (< 18), slender (from 18 to 72), and thin (> 72) (Soetaert et al., 2002). Slender and thin animals have greater mobility, but may be vulnerable to predation, whereas stout animals have reduced mobility and low vulnerability to the predation pressure.

The *buccal cavity*, linked to feeding strategy, was classified in four categories: 1A, for animals named as selective deposit feeders that consume bacteria and small-sized organic particles small with an absent buccal cavity without teeth; 1B, for animals named as non-selective deposit feeders with medium or large buccal cavity without teeth, which also feed on organic deposit but targeting larger-sized particles; 2A, for animals named as epigrowth/epistrate feeders with a small or medium cavity that use their teeth to scrap food off surfaces or to tap objects; and 2B for animals commonly known as predators, which use their buccal armature (teeth/mandibles) to feed on nematodes or other small invertebrates (Wieser, 1953).

The *life history* follows the c-p scale, ranging from 1 for “colonizers” to 5 for “persisters” (Bongers, 1990). Thus, colonizers have short generation time, high reproduction rates, high colonization ability and high metabolic activity, making them tolerant against various types of disturbance (r-strategist sensu lato); while persisters have comparably long life-cycles, low colonization ability, low metabolic activity and few offspring, making them more vulnerable to disturbance (K-strategists sensu lato) (Bongers & Bongers, 1998; Bongers & Ferris, 1999).

The *tail shape* is separated into four categories. This character is important for foraging, locomotion and reproduction, and is divided, from more mobile to hemisessile animals, in short or round, with a blunt end, clavate, initially conical with an extension to the tip, conical with a pointed tip, and elongated or filiform, which is longer than five times the width of the body (Thistle & Sherman, 1985). Lastly, the *long somatic setae* contribute to locomotion, protection and reproduction behavior, therefore being grouped as present or absent (Kalogeropoulou et al., 2015).

In sum, each nematode species was grouped into these 6 traits, totalizing 22 possible combination of functional groups.

3.3.3 Phylogenetic data

The phylogenetic distances among species of nematodes were estimated from the genus-level supertree proposed by Vilas-Boas & Fonseca (subm.), in the chapter 2 of this thesis, which contains all genera found in the study area. This supertree was based on cladistic studies and previously published phylogenies from four genes (COI, ITS, 18S and 28S). The branch lengths and node ages are not available in this phylogeny, thus their values were considered equal.

3.3.4 Diversity measures and data analysis

We analysed four measures of diversity: AvPDist, VarPDist, AvFDist and VarFDist. The average value represents the mean path length through the tree connecting every pair of species within a sample (Warwick & Clarke, 1998). The AvDist, or $\Delta+$, is: $[\Sigma\ \Sigma i<j\ \omega ij]/[s(s-1)/2]$, where s is the number of species present, the

double summation is over $\{i = 1, \ldots s; j = 1, \ldots s$, such that $i < j\}$, and ωij is the "distinctness weight" given to the path length linking species i and j in the hierarchical classification (Clarke & Warwick, 2001; Wu et al., 2016). VarDist, or $\Lambda+$, is the pairwise path lengths reflecting the unevenness of the tree: $[\Sigma\ \Sigma i<j\ (\omega ij - \Delta^{+})^{2}]/[s(s-1)/2]$ (Clarke & Warwick, 2001).

The average distinctness and the variation in distinctness (Clarke & Warwick, 1998; 2001) were calculated for both phylogenetic and functional data using a constant step length (equal to one) between each classification level. We used a dendrogram with 17 classification levels to estimate the AvPDist and VarPDist from the supertree for each sample of the habitats, and 14 classification levels to calculate the AvFDist and VarFDist from a functional dendrogram for the species of each sample. To build the functional dendrogram, we created a triangular resemblance matrix using Euclidean distances from a presence/absence matrix for each trait category. These indices were tested under the null hypothesis that the species from the samples has a representative structure of the full biodiversity under study (Clarke & Warwick, 2001). Just the significant clades, tested by means of SIMPROF, were recognized as distinct functional groups. The observed $\Delta+$ and $\Lambda+$ of each sample were compared with the $\Delta+$ and $\Lambda+$ from 1000 randomizations of the full list species, determining if the true values fall within the 95% confidence limits in a funnel plot. Rarefaction curves were calculated for each habitat in order to compare the representation of the local species richness to the total species pool of the habitat. The contribution of species to the observed spatial variability was identified through the similarity percentage technique (SIMPER, Clarke, 1993). Plots were produced from species abundance log $(x + 1)$ transformed and ranked in similarity matrices based on Bray-Curtis measures. The non-metric Multi-Dimensional Scaling (nMDS, Clarke & Green, 1988) ordination was applied to visualize the geographic patterns in nematode assemblages from phylogenetic and functional distances.

Analysis of covariance (ANCOVA) were used to test whether the relationships between species richness, FDist and PDist components were dependent on the habitats. When significant differences among habitats were detected Tukey's HSD test as post hoc was performed. When significant differences in the interaction factor was observed, the results for each habitat were graphically presented by means of the linear regression.

3.4 RESULTS

3.4.1 Community structure

A total of 16.481 individuals of 145 species, 98 genera, 33 families and 11 orders of nematodes were recorded. Mangrove was the most species richness habitat, totalizing 87 species, of which 34 species occurring only in this habitat. Sandy beaches showed 70 species with, 36 unique species and in estuarine tidal flats its was found 67 species were recorded, of which 13 were unique to this habitat. Sandy beaches and tidal flats are closer of a sufficient sampling of the total species richness than mangroves (Fig. 2). The most abundant species were *Desmodora cazca* (Desmodoridae), *Terschellingia longicaudata* (Cyartonematidae) and *Omicronema* sp.1 (Xyalidae). SIMPER values show that each of these species are dominant in each habitat, *D. cazca* in tidal flats, *Omicronema* sp.1 in sandy beaches and *T. longicaudata* in mangroves (Table 2).

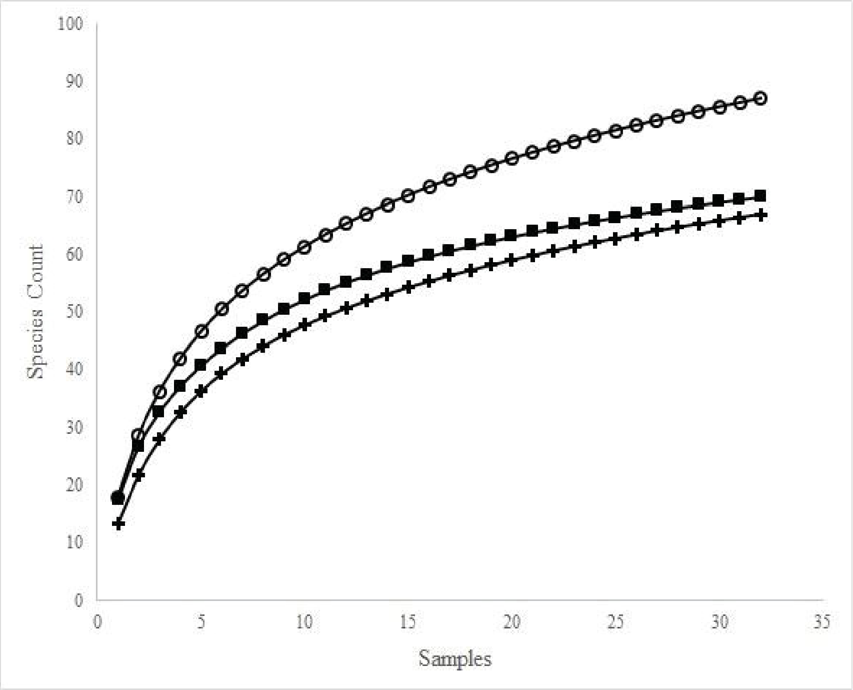

Figure 2. Species rarefaction curves for samples of mangroves (open circles), sandy beaches (filled squares) and estuarine tidal flats (crosses).

Table 2. Results of SIMPER (similarity percentage) for nematode communities along the habitats.

Order	Family	Species	Av. Abund.	Contrib. %
Tidal flats				
Desmodorida	Desmodoridae	*Desmodora cazca*	51.38	44.11
Monhysterida	Xyalidae	*Daptonema* sp.5	12.97	15.98
Enoplida	Oncholaimidae	*Viscosia* sp.1	12.28	11.20
Mangroves				
Araeolaimida	Cyartonematidae	*Terschellingia longicaudata*	49.69	42.38
Enoplida	Anoplostomatidae	*Anoplostoma subulatum*	17.06	19.85
Haliplectida	Haliplectidae	*Haliplectus floridanus*	18.06	7.61
Sandy beaches				
Monhysterida	Xyalidae	*Omicronema* sp.1	40.13	32.05
Chromadorida	Cyatholaimidae	*Paracanthonchus cochlearis*	23.63	13.24
Monhysterida	Xyalidae	*Pseudosteineria marcorum*	10.56	6.81

3.4.2 Distinctness measures

3.4.2.1 Phylogenetic distinctness

The MDS, based on the taxonomic matrix, shows that there is a spatial pattern of the samples, in which the three habitats have distinct communities, with tidal flats and mangroves sharing more species in common when compared to sandy beaches (Fig. 3).

The scatter plot of Λ+ and Δ+ values distributions shows a negative correlation between them (Fig. 3). Sandy beaches showed significantly lower Δ+ values and the highest Λ+ values among the three habitats.

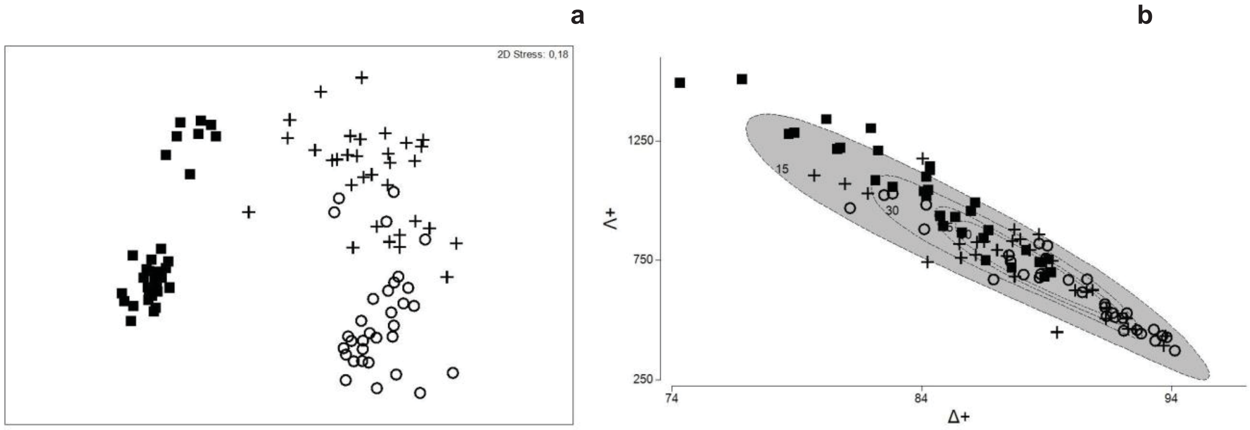

Figure 3. Two-dimensional MDS ordination about phylogenetic distinctness based on the log transformed abundance of nematode species (**a**); and scatter plot of Λ+ against Δ+ of the habitats from the phylogenetic distinctness, in relation to 1000 simulations for a range of 10 to 60 species (**b**). Crosses (+), open circles (○) and filled squares (■) represent estuarine tidal flats, mangroves and sandy beaches respectively.

3.4.2.2 Functional distinctness

As in phylogenetic distinctness analysis, the MDS also displays the spatial pattern of the samples, in general the three habitats having distinct communities (Fig. 4).

The scatter plot of Λ+ and Δ+ distributions of the habitats also shows a negative correlation between the values (Fig. 4). The same pattern for sandy beaches of lowest Δ+ values but the highest Λ+ values among the three habitats is displayed.

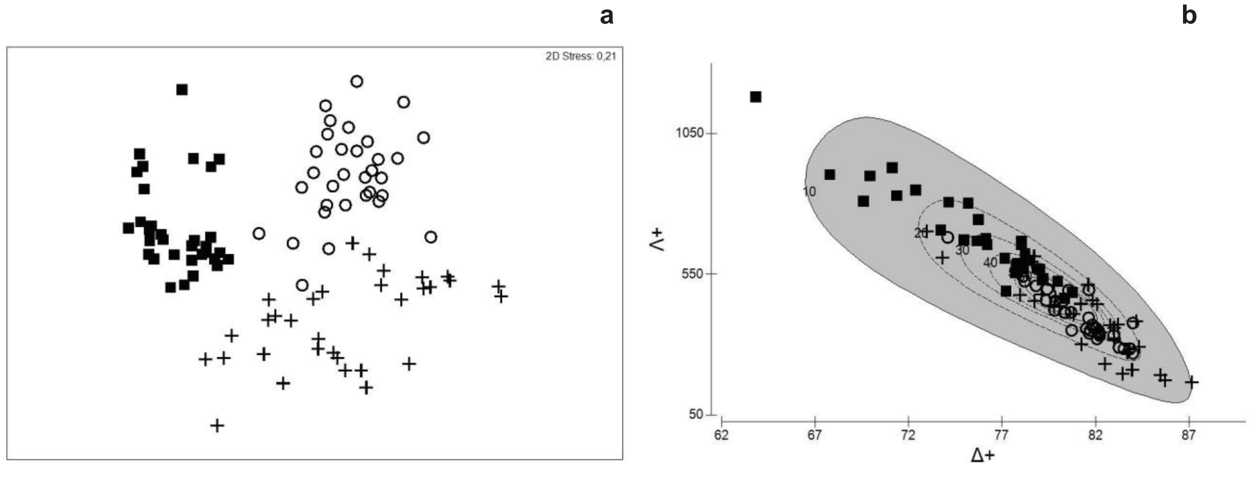

Figure 4. Two-dimensional MDS ordination about functional distinctness based on the log transformed abundance of nematode functional groups (**a**); and scatter plot of Λ+ against Δ+ of the habitats from the functional distinctness, in relation to 1000

simulations for a range of 10 to 60 species (**b**). Crosses (+), open circles (○) and filled squares (■) represent estuarine tidal flats, mangroves and sandy beaches respectively.

3.4.2.3 Relationships among Species Richness, Functional Distinctness and Phylogenetic Distinctness components

The results of ANCOVA showed significant effect of S on AvFDist and VarFDist – as well as AvPDist with AvFDist and VarPDist with VarFDist – but the effects were dependents of the habitat (Table 3; Fig. 5). Specifically for sandy beaches, the comparison of AvFDist in relation to S exhibits a crescent pattern, while there is a lack of pattern for the other habitats (Fig. 5a). On the other hand, the comparison of VarFDist and S exhibits a opposite pattern verified in AvFDist in relation to S, in which the variation decreases to a certain level with the species richness increasing (Fig. 5d). Tukey's tests revealed significant differences between sandy beaches and the other two habitats among all the relationships of S and FDist components (Table 3).

Table 3. Results of ANCOVAs testing the relationships of species richness, PDist and FDist components, considering the habitats as fixed factors and post hoc comparisons among habitats using Tukey HSD test (AvPDist - average phylogenetic distinctness; AvFDist - average functional distinctness; df - degrees of freedom; Est - estuarine tidal flats; Man - mangroves; MS - mean of squares; S - species richness; San Bea - sandy beaches; SS - sum of squares; VarPDist - variation in phylogenetic distinctness; VarFDist - variation in functional distinctness).

	df	*SS*	*MS*	*F*	*p*	*Post hoc*
AvFDist-S						
habitat	2	669	334.5	46.95	**<0.001**	San Bea < Man, Est
S	1	137.2	137.2	19.26	**<0.001**	
habitat:S	2	138.1	69	9.69	**<0.001**	
Residuals	90	641.2	7.1			
VarFDist-S						
habitat	2	1745768	872884	66.75	**<0.001**	San Bea < Man, Est
S	1	258796	258796	19.79	**<0.001**	

habitat:S	2	207290	103645	7.93	**<0.001**	
Residuals	90	1176880	13076			
AvPDist-S						
habitat	2	531.3	265.66	20.48	**<0.001**	
S	1	6.6	6.56	0.51	0.48	
habitat:S	2	6.4	3.19	0.25	0.78	
Residuals	90	1167.4	12.97			
VarPDist-S						
habitat	2	2588319	1294160	29.45	**<0.001**	
S	1	38721	38721	0.88	0.35	
habitat:S	2	10436	5218	0.12	0.89	
Residuals	90	3954726	43941			
AvPDist-AvFDist						
habitat	2	531.3	265.66	22.88	**<0.001**	San Bea < Man, Est
AvFDist	1	91.3	91.28	7.86	**<0.01**	
habitat:AvFDist	2	44.2	22.09	1.90	0.16	
Residuals	90	1044.8	11.61			
VarPDist-VarFDist						
habitat	2	2588319	1294160	38.13	**<0.01**	San Bea < Man, Est
VarFDist	1	919222	919222	27.08	**<0.01**	
habitat:VarFDist	2	30040	15020	0.44	0.64	
Residuals	90	3054621	33940			

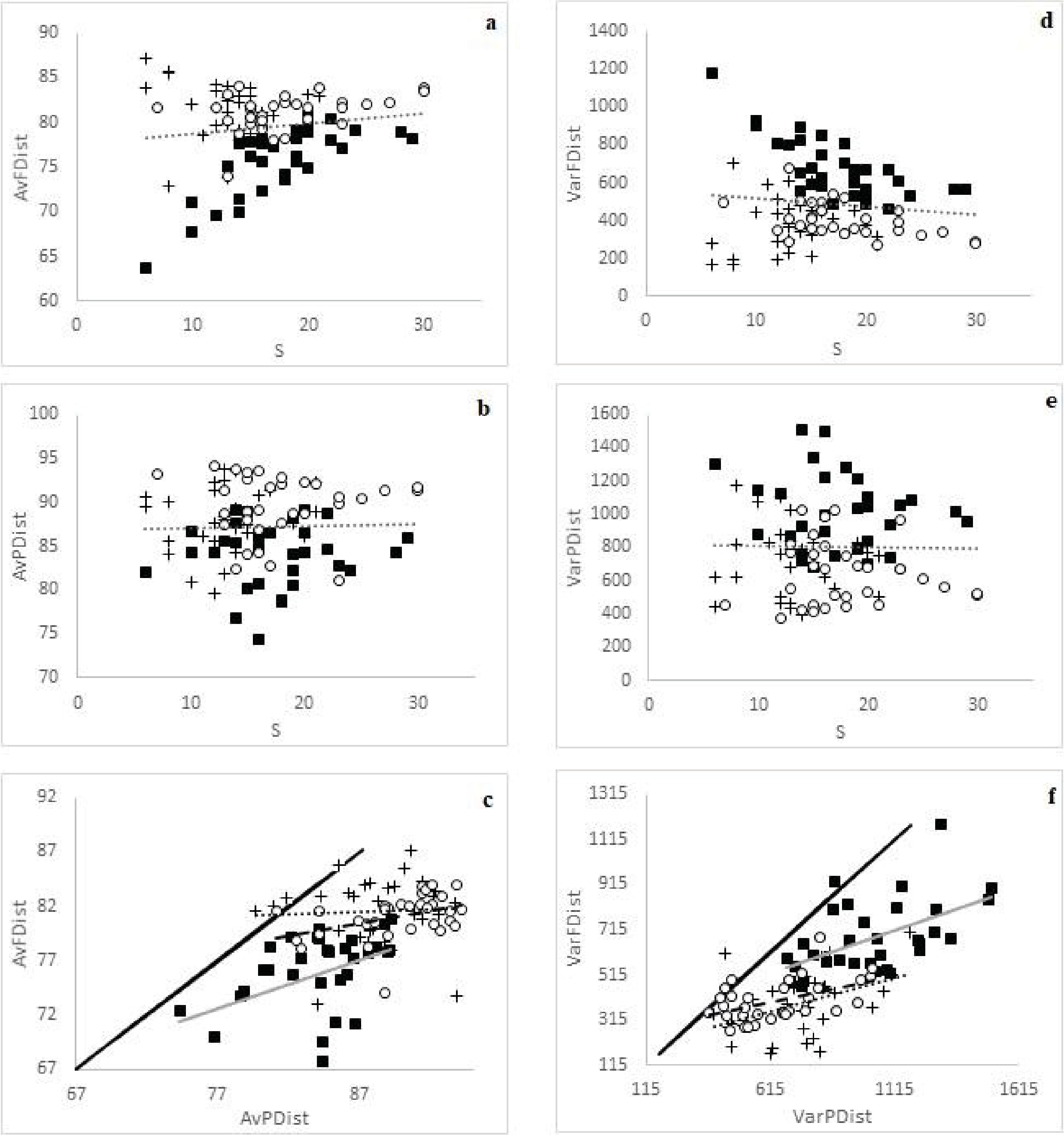

Figure 5. Plots of the relationships among the species richness (S), phylogenetic and functional distinctness components (AvFDist - average functional distinctness; AvPDist - average phylogenetic distinctness; VarFDist - variation in functional distinctness; VarPDist - variation in phylogenetic distinctness). Crosses (+), open circles (○) and filled squares (■) represent estuarine tidal flats, mangroves and sandy beaches respectively. Tendency lines: black dots - estuarine tidal flats; black dash - mangroves; solid gray - sandy beaches.

3.5 DISCUSSION

Coastal habitats with different physical characteristics are characterized by singular benthic assemblages, in which organisms are capable to move and adapt to the environmental conditions (Bernardino et al., 2015). The assemblages of nematodes were markedly different among sandy beaches, tidal flats and mangroves, of which mangroves and sandy beaches had the highest total species richness and highest single species records. Mangroves provide abundant food resource and refuge to development of species of nematodes (Netto & Gallucci, 2003), however are subject to fluctuations of salinity, oxygen and water levels (Giri et al., 2011), restricting the range of tolerant species richness. Sandy beaches, in turn, are homogeneous and high-energy environments in which oxygenated layers can reach great depths (Romer, 1990; Vieira & Fonseca, 2013). These conditions of sandy beaches act in the selection of more similar traits (Weiher & Keddy, 1995), as the predominant slender body shape related to vertical migration (Schratzberger et al., 2007).

Correlating the species richness, functional and phylogenetic distinctness allows to comprehend the relative importance of ecological and evolutionary processes operating at different local and regional scales (Cavender-Bares et al., 2009; Saito et al., 2016; Presley et al., 2018). The deviations from the null expectations are usually called as overdisperion and underdispersion patterns. Overdispersion patterns represent more phylogenetic and functional distinctness than expected by random, while the opposite is expected for underdispersion patterns. Thus, higher phylogenetic and functional distinctness are compatible with competition within clades, niche partitioning, limiting similarity or character displacement. On the other hand, lower phylogenetic and functional distinctness are compatible with competition among clades and environmental filtering (Kluge & Kessler, 2011).

The correlations of PDist and FDist components with species richness along the habitats exhibited weak significant patterns, except for the correlations of AvFDist and VarFDist with species richness for sandy beaches. The increase of AvFDist and the decreasing of VarFDist in relation to species richness indicate that functionally distinct and more closely related species may be arriving sandy beaches, also corresponding to the increasing of the species richness.

The available niches along the ecological habitats is another relevant aspect when analysing underdispersion or overdispersion of functional and phylogenetic distinctness (Ricotta & Moretti, 2011). The niche differentiation is required through evolution of habitat choices and local adaptation for species to co-occur, which enhance local fitness, facilitate the specialization and promote diversity (Kohyama & Takada 2009; Mason et al. 2011). Higher variability in resources favor wider niche breadths and may also influence the responses of organisms to the environment (Wu et al., 2016). Sandy beaches are more homogeneous habitats due to the highly dynamic characteristic thus offering narrower niche breadth. Therefore, corroborating the expected, sandy beaches were dominated by colonizers (c-p 2), species tolerant to various types of disturbance. On the other hand, tidal flats and mangroves are more heterogeneous habitats, with wider niche breadth, in which both colonizers and persisters (c-p 2 and 3) occurred.

The negative correlations between VarPDist and AvPDist as well as VarFDist and AvFDist indicate that the main process shaping the nematode assemblages of all the habitats is convergent evolution. The trait convergence was more noticeable in sandy beaches. This is in part due to the lowest AvPDist and AvFDist and highest VarFDist and VarPDist values compared to the other habitats, and because the dominant species are functionally closer to each other. The dominant species *Omicronema* sp1*, Paracanthonchus cochlearis, Pseudosteineria marcorum* and *Sabatieria* sp 1 are mainly colonizers and non-selective deposit feeders with a slender body shape. For mangroves and tidal flats, higher trait diversity represented by the dominant species suggest that co-occurring species may be exploring different resources.

Considering that a lower surrogacy between ecological and evolutionary dissimilarities is possible by differences in the evolutionary processes concerning each trait under consideration (Diniz-Filho et al., 2013), and that mangroves and tidal flats may shelter a mosaic of habitats, we can infer that the assemblages of these habitats may being shaped by another ecological processes beyond convergent evolution, as limiting similarity. This process is based on the limit of the attributes similarity for species to co-occur in the same habitat, causing a niche differentiation (Stubbs & Wilson, 2004). In parallel, the VarFDist values of mangroves and tidal flats were lower than that of sandy beaches, which may correspond to a consequence of a possible interspecific competition homogenizing the distance among species in the trait space (Botta-Dukát & Czúcz, 2016).

Analysing the dispersion of PDist and FDist components from a single statistic test, and from a single null-model, usually indicate exclusive effects of habitat filtering and limiting similarity, and can mask their simultaneous effects, in variable scales, on assemblages (Weiher et al., 2011; de Bello et al., 2010). Sandy beaches are more influenced by convergent evolution than limiting similarity, with the crescent pattern of the AvFDist in relation to species richness until the environmental constraint (Fig. 6). Functionally and phylogenetically diverse species may be constantly arriving in this habitat, but those without adaptations to establish in this harsh and homogeneous habitat, like the stout body shape, will not persist in sandy beaches. Mangroves and tidal flats are more influenced by limiting similarity, since the relationship between AvFDist and species richness do not significantly change (Fig. 6). These heterogeneous habitats favor a higher diversity of niches, in consequence, the existence of a wide range of functional traits from different clades. The figure 6 is a schematic framework comparing the three coastal habitats and summarizing the conclusions inferred from the results obtained in this study.

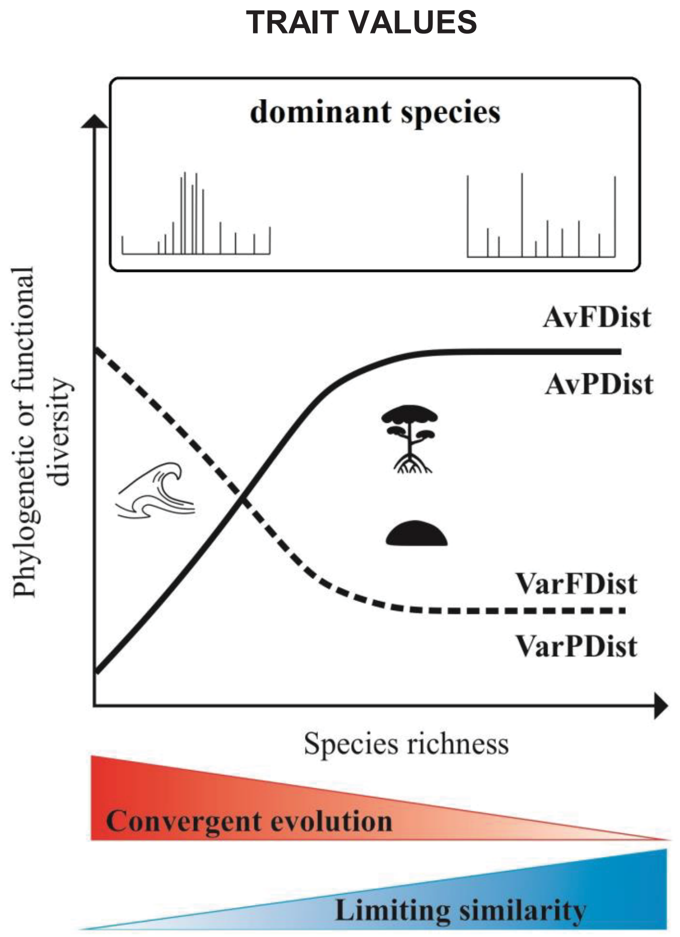

Figure 6. Representation of the process operating on coastal habitats.

3.6 CONCLUSION

Both average and variation in taxonomic distinctness are relevant in inferring processes shaping the communities of coastal habitats. They corroborated the well-known convergent evolution acting on marine communities, but also pointed out for the limiting similarity influencing the distribution of marine nematodes. These results refine the general framework that communities are separated by over- and underdispersion of functional and phylogenetic components, but highlight that processes defined by over- and underdispersion patterns may simultaneoulsy occur whithin communities. Sandy beaches stand out among the coastal habitats, in which the convergent evolution was more pronounced. The diversity measures obtained in sandy beaches were significantly different than the other two habitats, consisting of adaptations of organisms to establish in this harsh and homogeneous habitat.

GENERAL DISCUSSION

Systematic revisions aim to discover synonyms, catalogue valid species, propose keys, organize classifications and update taxonomic diagnoses of poorly described species (Appeltans et al., 2012). The incomplete identifications hamper distinguishing species, which may favor mistakes in specimens' identifications that can be replicated on databases, like GenBank. By consequence, misidentifications may imply in erroneous positionings of taxa within phylogenies, like in the *chapter 1*, in which a sequence of *Dichromadora* was grouped with genera of Chromadorinae, that could mean Hypodontolaiminae as a non-monophyletic clade, but a careful comparison revealed it is similar to a sequence of *Atrochromadora*. Lastly, identification errors in ecological and evolutionary studies may generate wider misinterpretations, like biasing species extinction dynamics (Miller et al., 2011).

Eco-evolutionary studies rely on a single phylogenetic hypothesis as the supertree proposed in the *chapter 2*. This tree is the first hypothesis about the evolutionary history of Nematoda, in which the mapped polytomies is one of the main points of the article. They are common among marine nematodes, since synapomorphies are not easily defined and only about 30% of the genera are included in phylogenetic studies from molecular data. In this sense, relying on a single phylogenetic hypothesis makes polytomies common not only in Nematoda but also in other groups like hummingbirds and seed plants (Rangel et al., 2015; Smith & Brown, 2018). However, more important than the fact of being a limitation for phylogenetic analysis, polytomies are relevant to demonstrate the need for data collection and to guide future systematic revisions, as the revision of Chromadoridae.

Therefore, the three different dimensions of biodiversity used in this thesis (taxonomic, phylogenetic and functional dimensions) differently interact to the environmental gradients. When individually analyzed, each of these dimensions may exhibits operational limitations that can bias the explanations for communities patterns (Saito et al., 2016). Thus, integrating taxonomic, phylogenetic and functional dimensions at the same approach provides more robust inferences about eco-evolutionary processes affecting the compositions of communities (Pavoine & Bonsall, 2011).

The marine environment embrace a rich diversity of organisms living under convergent evolution pressure, but whose diversity of physiological, behavioural and morphological patterns is still poorly known. These scenario is also equally true for marine invertebrates, that are characterized by multiple potentially convergent characters due to continued habitat shifts and diversification (Lindgren et al., 2012). Meiofauna, including the nematodes analysed along this thesis, is a very abundant and diverse group of distantly related eukaryotic lineages living in marine intersticial environments, that may provide deepest insights about fundamental ecological and evolutionary processes (Rundell & Leander, 2010). The results of the *chapter 3*, therefore, contributes in many aspects to studies in nematology, but also contributes to the comprehension of processes shaping marine animals, as the convergent evolution. Furthermore, many other interesting issues besides convergent evolution can be addressed from the results of this thesis.

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