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Research article

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***Campydoroides manautei* gen. et sp. nov. from New Caledonia and a reappraisal of the suborder Campydorina (Nematoda)**

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Abstract. The new genus and species *Campydoroides manautei* Holovachov gen. et sp. nov. is placed in the suborder Campydorina and is characterised by a transversely striated cuticle without lateral alae, body pores or epidermal glands; somatic sensilla only on pharyngeal region and on tail; a truncate labial region with papilliform inner labial, outer labial and cephalic sensilla; a stirrup-shaped amphid with transverse slit-like opening; a conoid stoma with strongly cuticularised walls and large protrusible dorsal tooth; a cylindrical pharynx with distinct basal bulb but without valves; a large ovoid cardia; didelphic, amphidelphic female gonads with antidromously reflexed ovaries and without spermatheca; a transverse vulva; a straight vagina without *pars refringens vaginae* or epiptygmata; an elongate tail with caudal glands and spinneret. The new genus is similar to the genera *Campydora* Cobb, 1920 and *Udonchus* Cobb, 1913 in having papilliform labial and cephalic sensilla, a stirrup-shaped amphid with a transverse slit-like opening, a stoma with a well-developed protrusible dorsal tooth, and a muscular pharynx with a strongly developed basal bulb, but can be easily separated from both in details of a stoma morphology. The systematics of the suborder Campydorina is revised. *Halirhabdolaimus* Siddiqi, 2012 is synonymised with *Syringolaimus* de Man, 1888.

Keywords. Classification, fauna, morphology, revision, taxonomy.

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Introduction

Due to the remarkable geological history of New Caledonia, the flora and fauna of the archipelago has a high proportion of endemism, which has attracted the attention of taxonomists and biogeographers (Grandcolas *et al.* 2008). As a result, many large groups of organisms are relatively well known, with current research focusing more on the speciation and microendemism and less on the general floristic and faunistic surveys. Nematodes, on the other hand, have been largely overlooked in the past. The few existing taxonomic and faunistic papers list only sixty-nine non-animal-parasitic nematode species known from New Caledonia (Table 1). Of them, thirty-five are marine (Inglis 1968; Gourbault & Decraemer 1991, 1993, 1994a, 1994b; Guo *et al.* 2008), while 34 are found in freshwater and terrestrial habitats (Andrássy 1978; Germani 1990; Germani & Anderson 1991; Yeates 1992; Holovachov 2001;

Table 1. Free-living and plant-parasitic nematode fauna of New Caledonia (originally described from New Caledonia are marked with an asterisk).

	Marine or terrestrial	Distribution in New Caledonia	Reference	Distribution (in addition to New Caledonia)
MONONCHIDA				
<i>Prionchulus punctatus</i>	terrestrial	Mt. Dzumac	Yeates (1992)	cosmopolitan
<i>Clarkus dorsalis</i> *	terrestrial	Port Laguerre, Paita, Mt. Dzumac, Chutes de la Madeleine	Yeates (1992)	putative endemic
<i>Clarkus ouinnensis</i> *	terrestrial	Ouinne Valley, Mt Dzumac	Yeates (1992)	putative endemic
<i>Actus neocaledonensis</i> *	terrestrial	Port Laguerre, La Foa	Yeates (1992)	Vietnam
<i>Mylonchulus ciradi</i> *	terrestrial	Port Laguerre	Yeates (1992)	putative endemic
<i>Mylonchulus vasis</i> *	terrestrial	Port Laguerre	Yeates (1992)	India
<i>Mylonchulus paitensis</i> *	terrestrial	Paita	Yeates (1992)	Pakistan, Iran
<i>Mylonchulus ananasi</i> *	terrestrial	Port Laguerre	Yeates (1992)	putative endemic
<i>Cobbonchus couleensis</i> *	terrestrial	La Coulee	Yeates (1992)	putative endemic
<i>Cobbonchus altitudinarum</i> *	terrestrial	Montagne des Sources, Ouinne Valley, Mt Dzumac	Yeates (1992)	putative endemic
<i>Cobbonchus dzumaci</i> * syn. <i>C. mauritanus</i>	terrestrial	Mt. Dzumac	Yeates (1992)	Mauritius
<i>Cobbonchus orstomi</i> *	terrestrial	Pic du Pin, Montagne des Sources, Champ de Bataille	Yeates (1992)	putative endemic
<i>Iotonchus lacuplanarum</i> *	terrestrial	Pic du Pin, Chutes de la Madeleine	Yeates (1992)	putative endemic
<i>Iotonchus montanum</i> *	terrestrial	Montagne des Sources	Yeates (1992)	putative endemic
<i>Iotonchus candelabri</i> *	terrestrial	Champ de Bataille	Yeates (1992)	Vietnam
<i>Iotonchus recessus</i> *	terrestrial	Montagne des Sources	Yeates (1992)	putative endemic
<i>Iotonchus trichurus</i>	terrestrial	Port Laguerre	Yeates (1992)	cosmopolitan
<i>Mulveyellus monhystera</i>	terrestrial	La Coulee	Yeates (1992)	circumtropical
DORYLAIMIDA				
<i>Xiphinema fagesi</i> *	terrestrial	Mt. Tandji	Germani (1990)	putative endemic
<i>Xiphinema ensiculiferum</i>	terrestrial	not provided	Grandison <i>et al.</i> (2009)	Indo-Malay and Australasian
ENOPLIDA				
<i>Paranticoma caledoniensis</i> *	marine	Baie Saint Vincent	Inglis (1968)	putative endemic
<i>Paramesacanthion barbae</i> *	marine	Baie Saint Vincent	Inglis (1968)	putative endemic
DESMODORIDA				
<i>Nudora nuda</i> *	marine	Baie Saint Vincent, Uvea Lagoon	Inglis (1968); Guo <i>et al.</i> (2008)	Malaysia
<i>Chromaspirina dubia</i> *	marine	Baie Saint Vincent	Inglis (1968)	putative endemic
<i>Croconema mawsonae</i> *	marine	Baie Saint Vincent	Inglis (1968)	putative endemic
<i>Desmodora deconincki</i> *	marine	Baie Saint Vincent	Inglis (1968)	Adriatic Sea
<i>Paradesmodora supplementatis</i> *	marine	Baie Saint Vincent	Inglis (1968)	Tunisia
<i>Xenodesmodora wieseri</i> * syn. <i>Desmodora wieseri</i>	marine	Baie Saint Vincent	Inglis (1968)	putative endemic
<i>Spirinia laevioides</i>	marine	Uvea Lagoon	Guo <i>et al.</i> (2008)	Indo-Malay and Australasian
<i>Eubostriechus parasitiferus</i>	marine	Uvea Lagoon	Guo <i>et al.</i> (2008)	circumtropical
<i>Catanema cobbi</i> * syn. <i>Laxus cobbi</i>	marine	Baie Saint Vincent	Inglis (1968)	putative endemic
<i>Akanthepsilonema helleouetae</i> *	marine	Ilot Signal	Gourbault & Decraemer (1991)	putative endemic
<i>Epsilonema exoticum</i>	marine	Yaté	Gourbault & Decraemer (1994b)	French Polynesia

Table 1 (page 2 of 3).

	Marine or terrestrial	Distribution in New Caledonia	Reference	Distribution (in addition to New Caledonia)
DESMODORIDA (cont.)				
<i>Epsilonema enigmaticum</i> *	marine	Ilot Kouaré	Gourbault & Decraemer (1994b)	putative endemic
<i>Glochinema phaleratum</i> *	marine	Yaté Plage	Gourbault & Decraemer (1993)	putative endemic
<i>Metaglochinema strigosum</i> *	marine	Yaté Plage	Gourbault & Decraemer (1993)	putative endemic
<i>Polkepsilonema firmatum</i> *	marine	Phare Amédée, Ile des Pins, Ilot Signal, Ilot Régnière	Gourbault & Decraemer (1994a)	putative endemic
<i>Draconema eira</i> * syn. <i>Dracograllus eira</i>	marine	Baie Saint Vincent	Inglis (1968)	Papua New Guinea
CHROMADORIDA				
<i>Chromadora macrolaimoides</i>	marine	Uvea Lagoon	Guo <i>et al.</i> (2008)	cosmopolitan
<i>Atochromadora denticulata</i>	marine	Uvea Lagoon	Guo <i>et al.</i> (2008)	North Atlantic
<i>Prochromadorella ditlevseni</i>	marine	Uvea Lagoon	Guo <i>et al.</i> (2008)	cosmopolitan
<i>Prochromadorella septempapillata</i>	marine	Uvea Lagoon	Guo <i>et al.</i> (2008)	North Atlantic, Mediterranean
<i>Euchromadora colesi</i> * syn. <i>Parapinnanema colesi</i>	marine	Baie Saint Vincent, Uvea Lagoon	Inglis (1968); Guo <i>et al.</i> (2008)	putative endemic
<i>Halichoanolaimus unicus</i> *	marine	Baie Saint Vincent	Inglis (1968)	putative endemic
<i>Richtersiella discorda</i> * syn. <i>R. discorda</i>	marine	Baie Saint Vincent	Inglis (1968)	Bay of Bengal
ARAEOLAIMIDA				
<i>Parodontophora xenotricha</i>	marine	Uvea Lagoon	Guo <i>et al.</i> (2008)	Polynesia
<i>Mesonchium angelae</i> *	marine	Baie Saint Vincent	Inglis (1968)	putative endemic
DESMOSCOLECIDA				
<i>Desmoscolex grandiamphis</i> *	marine	Baie Saint Vincent	Inglis (1968)	putative endemic
<i>Tricoma spuria</i> *	marine	Baie Saint Vincent	Inglis (1968)	putative endemic
MONHYSTERIDA				
<i>Elzalia poli</i>	marine	Uvea lagoon	Guo <i>et al.</i> (2008)	Gulf of Mexico
<i>Metalinhomoeus timmi</i> *	marine	Baie Saint Vincent	Inglis (1968)	putative endemic
<i>Theristus pertenuis</i>	marine	Uvea Lagoon	Guo <i>et al.</i> (2008)	Atlantic, Baltic, Mediterranean
<i>Daptonema svalbardense</i>	marine	Uvea Lagoon	Guo <i>et al.</i> (2008)	Svalbard
<i>Siphonolaimus dorylus</i> *	marine	Baie Saint Vincent	Inglis (1968)	putative endemic
<i>Terschellingia gerlachi</i> * syn. <i>T. longicaudata</i>	marine	Baie Saint Vincent	Inglis (1968)	cosmopolitan
PLECTIDA				
<i>Plectus brzeskii</i> *	terrestrial	Mt. Mou	Holovachov (2001)	putative endemic
RHABDITIDA				
<i>Bicirronema caledoniense</i> *	terrestrial	Mt. Ounda, Mt. Mandjéla, Mt. Koghi	Andrássy (1978)	putative endemic
<i>Amphidirhabditis longipapillata</i> *	terrestrial	Mt. Ounda	Andrássy (1978)	putative endemic
<i>Dolichodorus pellegrini</i> *	terrestrial	Mt. Panié	Germani (1990)	putative endemic
<i>Hemicriconemoides scottolamassesei</i> *	terrestrial	Montagne des Sources	Germani & Anderson (1991)	putative endemic
<i>Hemicriconemoides mangiferae</i>	terrestrial	Koumac, Pindai, Col des Roussettes, not provided	Germani & Anderson (1991); Grandison <i>et al.</i> (2009)	cosmopolitan
<i>Helicotylenchus dihystra</i>	terrestrial	not provided	Grandison <i>et al.</i> (2009)	cosmopolitan
<i>Helicotylenchus multincinctus</i>	terrestrial	not provided	Grandison <i>et al.</i> (2009)	cosmopolitan

Table 1 (page 3 of 3).

	Marine or terrestrial	Distribution in New Caledonia	Reference	Distribution (in addition to New Caledonia)
RHABDITIDA (cont.)				
<i>Helicotylenchus pseudorobustus</i>	terrestrial	not provided	Grandison <i>et al.</i> (2009)	cosmopolitan
<i>Tylenchulus semipenetrans</i>	terrestrial	not provided	Grandison <i>et al.</i> (2009)	cosmopolitan
<i>Meloidogyne incognita</i>	terrestrial	not provided	Grandison <i>et al.</i> (2009)	cosmopolitan
<i>Pratylenchus coffeae</i>	terrestrial	not provided	Grandison <i>et al.</i> (2009)	cosmopolitan
<i>Radopholus similis</i>	terrestrial	not provided	Grandison <i>et al.</i> (2009)	cosmopolitan
<i>Rotylenchulus reniformis</i>	terrestrial	not provided	Grandison <i>et al.</i> (2009)	cosmopolitan

Grandison *et al.* 2009), and include plant-parasitic nematodes (Germani 1990; Germani & Anderson 1991; Grandison *et al.* 2009).

Forty-five species of nematodes were originally described from New Caledonia as new to science (Inglis 1968; Andrásy 1978; Germani 1990; Germani & Anderson 1991; Gourbault & Decraemer 1991, 1993, 1994a, 1994b; Yeates 1992; Holovachov 2001). Of these, *Actus neocaledoniensis* Yeates, 1992 and *Iotonchus candelabri* Yeates, 1992 were subsequently recorded from Vietnam (Nguyễn Vũ Thanh 2007; Vu Thi Thanh Tam 2015), *Mylonchulus vasis* Yeates, 1992 was found in India (Tahseen *et al.* 2013), *Mylonchulus paitensis* Yeates, 1992 is known from Pakistan (Tabassum *et al.* 2001) and Iran (Farahmand *et al.* 2009; Mahdikhani-Moghadam *et al.* 2017), *Nudora nuda* Inglis, 1968 from Malaysia (Shabdin *et al.* 2013), *Desmodora deconincki* Inglis, 1968 from the Adriatic Sea (Travizi & Vidaković 1997; Travizi 2010), *Paradesmodora supplementatis* Inglis, 1968 from Tunisia (Beyrem & Aissa 2000; Boufahja *et al.* 2014; Jouili *et al.* 2018), *Dracograllus eira* (Inglis, 1968) from Papua New Guinea (Decraemer 1988), and *Richtersiella discorda* Inglis, 1968 (now in genus *Richtersia* Steiner, 1916) from the Bay of Bengal (Bhanu *et al.* 2017). *Cobbonchus dzumaci* Yeates, 1992 was synonymised with *Cobbonchus mauritanus* (Williams, 1958), a species known from Mauritius. *Terschellingia gerlachi* Inglis, 1968 was recorded from the Adriatic Sea (Travizi & Vidaković 1997), but is now synonymised with *Terschellingia longicaudata* de Man, 1907, a cosmopolitan species. The species listed above are not endemic to New Caledonia, because they have been found in other places. The remaining species have not been found anywhere else in the world and can be preliminary listed as endemic to New Caledonia (Table 1).

The samples were collected during field trips in 2017 and 2018 as part of the *Our Planet Reviewed/La Planète Revisitée* programme – New Caledonia expeditions (2016–2018), which were organized by the Muséum national d’Histoire naturelle (Paris) and the Conservatoire d’Espaces Naturels de Nouvelle-Calédonie. This paper is the first in a series describing new nematode taxa found during these sampling trips.

Material and methods

A total of 230 samples was collected in New Caledonia during 2017 and 2018 (Fig. 1). The majority of the samples was collected in freshwater, limno-terrestrial and terrestrial habitats. Since the nematode fauna of several rivers and lakes included marine elements, additional samples were collected in salt-water habitats (brackish lagoons, mangroves and marine littoral) for comparative purposes. Nematodes from non-marine habitats were extracted from samples using a modification of Whitehead tray extraction technique (Whitehead & Hemming 1965) and immediately fixed in a 4% formaldehyde solution in freshwater or in 95% ethanol. In some cases, the entire sample of substrate was fixed in 4% formaldehyde; in such cases nematodes were extracted from the samples using a decanting and sieving

method (smallest mesh sizes: 45 μm or 70 μm), followed by a centrifugation in Ludox HS-40 (Burgess 2001). For light microscopy, formaldehyde-preserved specimens were transferred to pure glycerine using the rapid method of Seinhorst (1959) as modified by De Grisse (1969). Permanent nematode mounts on the glass slides were prepared using the paraffin wax ring method. All curved structures were measured along the curved median line. Measurements are presented in μm as mean and (range) where appropriate (Table 3). General terminology follows Maggenti (2005). Type specimens are deposited in the collections of the National Museum of Natural History in Paris, France (MNHN) and of the Swedish Museum of Natural History in Stockholm, Sweden (SMNH).

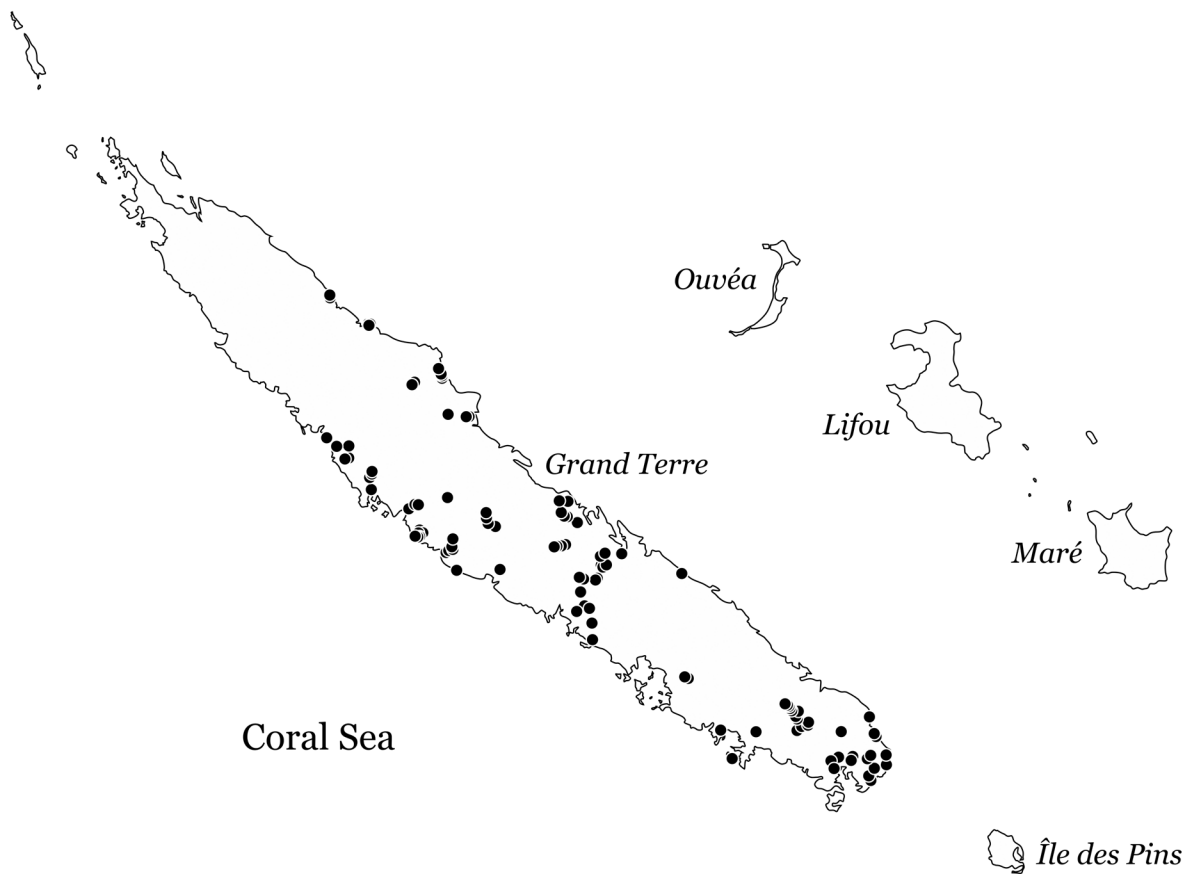


Fig. 1. Map of New Caledonia showing approximate position of sampled locations (modified from a map file available from https://d-maps.com/carte.php?num_car=15257).

Results

New genus and species

Phylum Nematoda Potts, 1932
Class Enoplea Inglis, 1983
Order Enoplida Filipjev, 1929
Suborder Campydorina Jairajpuri, 1983
Superfamily Campydoroidea Thorne, 1935
Family Campydoridae Thorne, 1935

Genus *Campydoroides* Holovachov gen. nov.

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Diagnosis

Cuticle transversely striated. Lateral alae, body pores and epidermal glands absent. Somatic sensilla distinct along anteriormost part of pharyngeal region and on tail. Labial region truncated. Six inner labial papilliform sensilla, located on anterior surface of lips. Six outer labial papilliform sensilla, located on periphery of labial region. Four cephalic papilliform sensilla, located a short distance behind labial region. Amphid stirrup-shaped with transverse slit-like opening. Stoma conoid, stegostom with strongly cuticularised walls and large protrusible dorsal tooth. Pharynx cylindrical anteriorly, with distinct basal bulb; valves absent. Cardia ovoid, partially embedded into intestinal tissue. Secretory-excretory system absent. Female reproductive system didelphic, amphidelphic, ovary branches reflexed antidromously. Vulva a transverse slit. Vagina straight, without *pars refringens vaginae* or epiptygmata. Spermatheca absent. Male reproductive system unknown. Tail elongate. Caudal glands and spinneret present.

Type species

Campydoroides manautei Holovachov gen. et sp. nov. (type by original designation).

Relationships

The new genus shows close affinities to the genera *Campydora* Cobb, 1920 and *Udonchus* Cobb, 1913 in having papilliform labial and cephalic sensilla, stirrup-shaped amphid with transverse slit-like opening, stoma with well-developed protrusible dorsal tooth, and muscular pharynx with strongly-developed basal bulb. The new genus differs from *Campydora* in detailed stoma morphology (conoid with strongly cuticularised walls and large dorsal tooth in *Campydoroides* gen. nov. vs cylindrical with weakly cuticularised walls and small dorsal tooth in *Campydora*), secretory-excretory system (absent in *Campydoroides* gen. nov. vs present in *Campydora*), cuticle (without longitudinal ridges in *Campydoroides* gen. nov. vs with ventral and dorsal ridges in *Campydora*) and tail (caudal glands and spinneret present in *Campydoroides* gen. nov. vs absent in *Campydora*). From *Udonchus* the new genus can also be easily separated by detailed stoma morphology (conoid with strongly cuticularised walls in *Campydoroides* gen. nov. vs cylindrical with weakly cuticularised walls in *Udonchus*) and number of teeth (single dorsal tooth in *Campydoroides* gen. nov. vs three small denticles in *Udonchus*). Further diagnostic characters separating the genus *Campydoroides* gen. nov. from all other genera considered in the suborder Campydorina are listed in the Table 2 and the identification key.

Overall morphology of the anterior end (papilliform labial and cephalic sensilla, stirrup-shaped amphid with transverse slit-like opening, stoma with well-developed dorsal tooth) is similar to that found in the members of the order Mononchida Jairajpuri, 1969 (Peña-Santiago 2014). However, the presence of a basal pharyngeal bulb in *Campydoroides* gen. nov. is a feature never observed in any species of mononchid nematodes. In fact, the basal pharyngeal bulb is rarely present in non-chromadorean nematodes (those

Table 2. Selected diagnostic characters of the genera classified in the suborder Campydorina Jairajpuri, 1983.

Character	<i>Campydora</i> Cobb, 1920	<i>Campydoroides</i> Holoovachov gen. nov.	<i>Udonchus</i> Cobb, 1913	<i>Mediolainus</i> Tahseen <i>et al.</i> , 2012	<i>Rhabdolainus</i> de Man, 1880	<i>Rogerus</i> Hoeppli & Chu, 1934	<i>Syringolainus</i> de Man, 1888
Labial region	cap-like	truncated	truncated	flattened	truncated	truncated	truncated
Cephalic sensilla	papilliform	papilliform	papilliform	papilliform	papilliform	setiform	papilliform
Cephalic sensilla position	on cap-like labial region	posterior to labial region	posterior to labial region	posterior to labial region	posterior to labial region	posterior to labial region	?
Amphid aperture	transverse slit	transverse slit	transverse slit	transverse ovoid	transverse slit	transverse ovoid	transverse slit
Stoma shape	cylindrical	conoid	cylindrical	cylindrical	cylindrical	cylindrical	cylindrical
Teeth/denticles	one	one	three, at two levels	three, at same level	three, at same level	three, at same level	three, at same level
Number of female gonads	two	two	one	two	two	two	two
Ovaries	reflexed	reflexed	reflexed	outstretched	reflexed	outstretched	reflexed
Caudal glands and spinneret	absent	present	present	absent	present	present	present/absent

belonging to *Enoplia* Pearce, 1942 and *Dorylaimia* Inglis, 1983, see Schmidt-Rhaesa 2014), and is here considered one of the diagnostic features of the suborder Campydorina (see below).

Campydoroides manautei Holovachov gen. et sp. nov.

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Figs 2–4; Table 3

Diagnosis

Campydoroides manautei sp. nov. is characterised by a 0.49–0.82 mm long body, papilliform inner labial, outer labial and cephalic sensilla, amphidial opening a transverse slit, strongly cuticularised stoma with single robust dorsal tooth, muscular pharynx with distinct basal bulb, large cardia, didelphic, amphidelphic female gonads, straight vagina, and elongate conoid tail equal to 6.0–9.6 anal body diameters in length.

Etymology

The new species is named in honour of Joseph Manauté, director of the Parc provincial de la Rivière bleue, for his indispensable support during the sampling in the Park.

Type material

Holotype

NEW CALEDONIA • 1 ♀; Yate Province, Parc provincial de la Rivière bleue, station HYNC2372/4680; 22°04.401' S, 166°36.995' E; 18 Jul. 2018; O. Holovachov leg.; virgin forest, soil; MNHN-BN511.

Paratypes

NEW CALEDONIA • 4 ♀♀; Yate Province, Parc provincial de la Rivière bleue, station HYNC2372/4680; 22°04.401' S, 166°36.995' E; 19 Nov. 2017 and 18 Jul. 2018; O. Holovachov leg.; virgin forest, soil; MNHN-BN511, SMNH Type-9167 • 2 ♀♀; Yate Province, Parc provincial de la Rivière bleue, station HYNC2378; 22°05.374' S, 166°38.185' E; 19 Nov. 2017; O. Holovachov leg.; virgin forest, wet soil at the bottom of a stream bed; SMNH Type-9168, SMNH Type-9169.

Additional non-type material

NEW ZEALAND • 2 ♀♀; Napier, Puketitiri, station Z236; 10 Nov. 1988; D. Sturhan leg.; SMNH-175283.

Description

Female

Body cylindrical, tapering slightly along pharyngeal region towards truncated anterior end, tapering more rapidly along tail towards tail tip; straight or ventrally curved upon fixation. Cuticle finely transversely striated along entire body, starting from base of outer labial sensilla and ending near tail tip; striations less than 1 µm; lateral alae absent; any other types of cuticular ornamentation absent. Body pores and epidermal glands absent. Somatic sensilla distinct along anteriormost part of pharyngeal region (cervical setae, see below) and on tail, indistinct or absent along rest of body. Labial region truncated, lips indistinct (fused). Six inner labial sensilla small papilliform, located on anterior surface of lips. Six outer labial sensilla small papilliform, located on outer periphery of labial region, 1.5–5.0 µm from anterior end (5 µm in specimen with everted stoma). Four cephalic sensilla small papilliform, located short distance behind lip region, 4–7 µm from anterior end, at level with dorsal tooth tip (in relaxed specimens, with inverted stoma, see below). Four pairs of cervical sensilla present, papilliform in shape, arranged in one dorsosublateral, one subdorsal and two subventral pairs at level of stoma base. Amphid stirrup-shaped with transverse slit-like opening 3–4 µm wide, located at level with middle of stoma. Oral opening

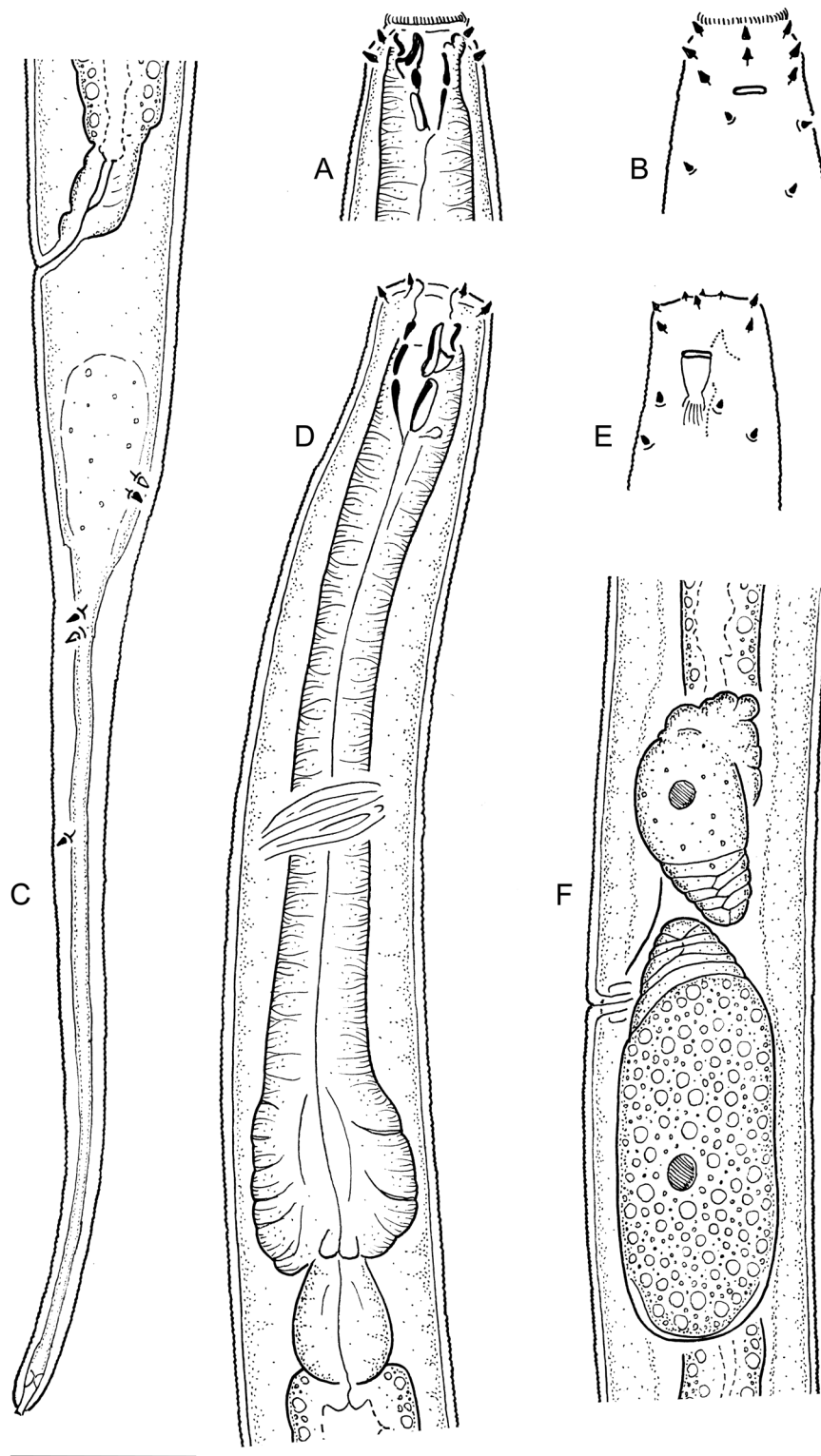


Fig. 2. *Campydoroides manautei* Holovachov gen. et sp. nov. **A–B.** Paratype female (SMNH Type-9167). **C–F.** Holotype (MNHN-BN511). **A.** Female pharyngeal region, median section. **B.** Female anterior end, median section. **C–D.** Female anterior end, surface view. **E.** Female reproductive system. **F.** Female tail. Scale bar: 20 µm.

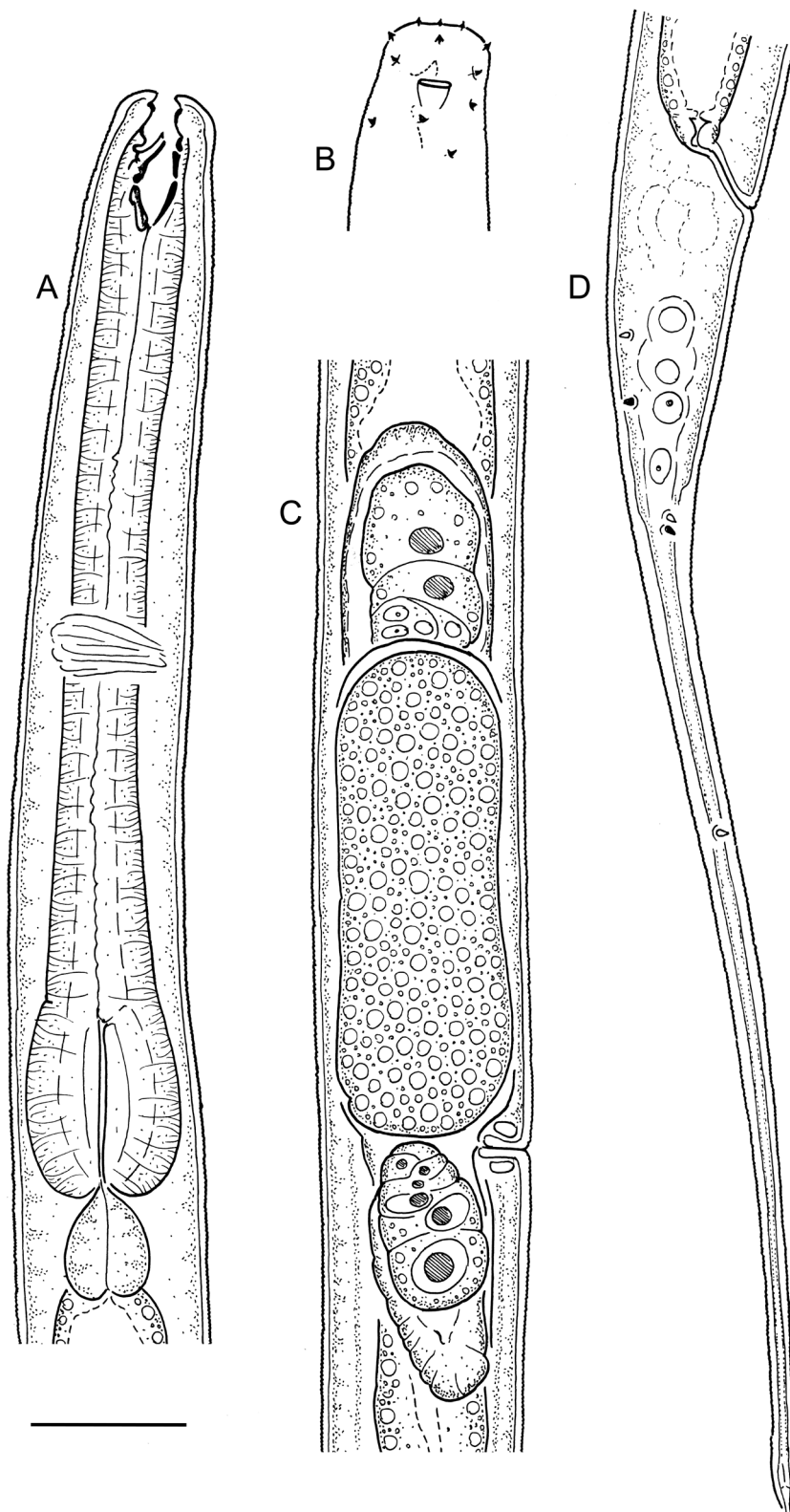


Fig. 3. *Campydoroides manautei* Holovachov gen. et sp. nov., non-type female from New Zealand (SMNH-175283). **A.** Female pharyngeal region, median section. **B.** Female anterior end, surface view. **C.** Female reproductive system. **D.** Female tail. Scale bar: 20 μ m.

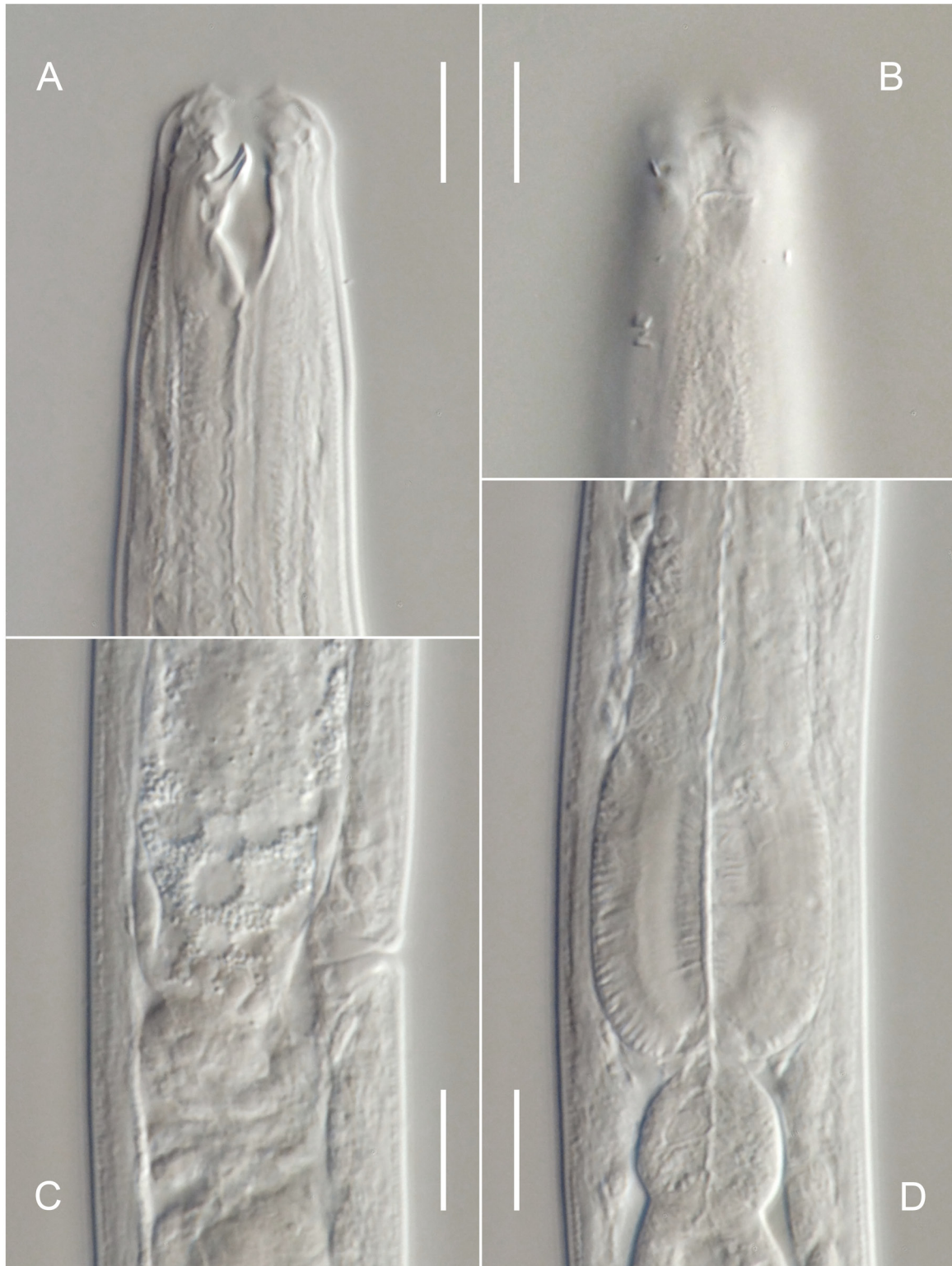


Fig. 4. *Campydoroides manautei* Holovachov gen. et sp. nov., non-type female from New Zealand (SMNH-175283). **A.** Anterior end, median section. **B.** Anterior end, surface view. **C.** Vulval region. **D.** Base of pharynx. Scale bar: 20 μ m.

Table 3. Morphometrics of *Campydoroides manautei* Holovachov gen. et sp. nov. (all measurements are in μm , except for the ratios a , b , c , c' and V).

Character	Holotype female	New Caledonia (n = 7, incl. holotype)	New Zealand (n = 2)
Body length	609	537 \pm 45 (492–609)	786; 817
Body diameter	26	24 \pm 3 (19–28)	25; 28
Pharynx length	110	94 \pm 9 (86–110)	140; 146
Tail length	128	115 \pm 9 (104–128)	173; 178
Anal body diameter	16	16 \pm 1 (15–17)	18; 19
a	23.9	22.7 \pm 2 (19.5–25.5)	31.6; 29.6
b	5.6	5.7 \pm 0.4 (4.9–6.1)	5.6; 5.6
c	4.8	4.7 \pm 0.2 (4.3–5.0)	4.6; 4.6
c'	8.0	7.1 \pm 0.8 (6.0–8.0)	9.6; 9.2
V (%)	40.5	41.4 \pm 1.1 (40.5–43.4)	42.1; 42.6
Labial region diameter	12	12 (12–14)	14; 14
Amphid from anterior end	7	8 (7–9)	9; 8
Stoma length	17	16 (13–17)	19; 17
Stoma width	6	6 (5–6)	6; 6
Nerve ring from anterior end	59	47 \pm 7 (37–59)	75; 76
Basal bulb length	20	21 \pm 2 (17–23)	26; 23
Basal bulb width	19	17 \pm 1 (16–19)	20; 21
Cardia length	14	9 \pm 3 (6–14)	14; 15
Cardia width	10	11 \pm 1 (10–12)	12; 12
Vagina length	7	6 (6–7)	7; 7
Rectum length	15	14 \pm 1 (12–16)	15; 15
Cardia width	10	11 \pm 1 (10–12)	12; 12
Vagina length	7	6 (6–7)	7; 7
Rectum length	15	14 \pm 1 (12–16)	15; 15

apical, surrounded by a fringe of tiny projections, visible only when stoma is everted to the outside (Fig. 2A). Stoma conoid; cheilostom short and weakly cuticularised; gymnostom as long and broad as cheilostom, weakly cuticularised; stegostom with strongly cuticularised walls, distinctly subdivided into three sections by breaks in cuticularised walls, with large dorsal tooth projecting anteriorly from its middle section. Tooth heavily cuticularised, 3–5 μm long, hollow inside, protrusible, its tip is 10–13 μm from stoma base. Pharyngeal tubes absent. Pharynx cylindrical anteriorly, with distinct basal bulb; anterior cylindrical part of pharynx with evenly distributed myofilaments, basal bulb strongly muscularised; pharyngeal lumen uniform in thickness along entire pharynx length; valves absent. Pharyngeal glands and their orifices indistinct. Cardia large, ovoid, partially embedded into intestinal tissue. Nerve ring encircling pharynx at 43–54% of its length. Secretory-excretory system indistinct/absent. Female reproductive system didelphic, amphidelphic, ovary branches reflexed antidromously, usually located on same side of intestine; symmetrical in younger females, asymmetrical in older females when large developing ovocyte or intrauterine egg is present in one of genital tubes. Anterior genital tube 21–91 μm long, equal to 4–13% of total body length, situated to either right (n = 4) or left (n = 3) of intestine; posterior genital tube 23–55 μm long, equal to 4–9% of total body length, situated to either right (n = 3) or left (n = 4) of intestine. Vulva a transverse slit, located anterior to midbody. Vagina straight, equal to 0.2–0.3 body diameters in length, with developed sphincter muscle surrounding its proximal part; *pars refringens vaginae* or epiptygmata absent. Spermatheca absent. Intrauterine egg measuring 64–77 \times 17–21 μm . Rectum short, equal to 0.8–1.2 anal body diameters in length. Tail elongate, distinctly subdivided

into conoid proximal part 26–42 μm in length, and subcylindrical distal part 76–136 μm long. Caudal setae present, one subdorsal pair along proximal conoid part of tail, one subventral pair at level with junction between proximal and distal parts of tail, and single lateral setae on left side of distal cylindrical part of tail. Caudal glands present, opening via small terminal spinneret.

Male

Not found. The species is presumed to be thelytokous.

Remarks

The two female specimens collected in New Zealand match very well the morphology of the type specimens from New Caledonia, except for the larger body size, higher values for some body measurements and longer tail (including higher c' -ratio). Since no qualitative morphological differences were found between the two populations, they both are here considered to belong to the same species.

Notes on the systematics of Campydorina

The unique and poorly understood morphology of the genus *Campydora* hindered understanding of its relationships with other nematodes and resulted in the taxonomic inflation from the genus to the suborder level (Jairajpuri 1983). This decision was followed in subsequent publications, although the suborder was transferred from the order Dorylaimida to the order Enoplida based on the morphological and molecular evidence, and its relationships within the order Enoplida remained unresolved (Siddiqi 1983; Winiszewska 2001; Mullin *et al.* 2003; Zhao *et al.* 2012; Smol *et al.* 2014). Subsequent phylogenetic studies using 18S rDNA sequence suggested close affinities between the genera *Campydora*, *Rhabdolaimus* de Man, 1880 and *Syringolaimus* de Man, 1888, placing these three genera as a monophyletic clade within the unresolved order Enoplida (Meldal *et al.* 2007; van Megen *et al.* 2009; Bik *et al.* 2010; Shokoohi *et al.* 2013; Smythe 2015; Leduc *et al.* 2018). This grouping can be further substantiated by at least one morphological character: the presence of a well-developed basal bulb, not found in any other Enoplida (the genera *Polygastrophora* de Man, 1922 and *Belbolla* Cobb, 1920 have the posterior part of the pharynx modified into a series of bulb-like swellings that are of independent origin). Placement of the genus *Syringolaimus* in the suborder Campydorina is further supported by the monorchic male reproductive system similar to the reproductive system found in the species from the genera *Campydora* and *Rogerus* (Hoepli & Chu 1932; Winiszewska 2001; Tchesunov 2017), while it is diorchic in other genera of *Ironina* Siddiqi, 1983 (Shokoohi *et al.* 2013; Chen & Guo 2015). The revised classification of the suborder Campydorina is given below.

Superfamily **Campydoroidea** Thorne, 1935

Diagnosis (modified from Smol *et al.* 2014)

Cuticle finely striated. Lip region truncated or set off. Inner labial sensilla papilliform, outer labial sensilla and cephalic sensilla usually papilliform, sometimes setiform. Amphid with slit-like or transversely oval aperture and stirrup-shaped fovea. Stoma tubular or conoid, with one to three teeth. Pharynx cylindrical anteriorly, with distinct basal bulb; valves absent. Secretory-excretory pore present or absent. Female reproductive system didelphic, amphidelphic or monodelphic prodelphic. Ovary branches reflexed antidromously or outstretched. Males monorchic, testis outstretched, spicules paired and symmetrical. Caudal glands and spinneret present or absent.

Included families

Family Campydoridae Thorne, 1935.

Family Rhabdolaimidae Chitwood, 1951.

Family **Campydoridae** Thorne, 1935

Diagnosis

As for the superfamily Campydoroidea, except that stoma with single dorsal tooth.

Type genus

Campydora Cobb, 1920.

Included genera

Campydora Cobb, 1920.

Campydoroides Holovachov gen. nov.

Genus *Campydora* Cobb, 1920

Diagnosis (based on Jairajpuri (1983) and Winiszewska (2001), supplemented with personal observations)

Cuticle transversely striated, with dorsal and ventral longitudinal ridges. Lateral alae absent. Somatic sensilla not described. Labial region cap-like. Six inner labial papilliform sensilla, located on anterior surface of lips. Six outer labial papilliform sensilla, located on periphery of labial region. Four small papilliform cephalic sensilla, located just behind outer labial sensilla, on cap-like labial region. Amphid stirrup-shaped with transverse slit-like opening located on cap-like labial region. Stoma cylindrical, with weakly cuticularised walls and large protrusible dorsal tooth. Pharynx cylindrical anteriorly, with distinct basal bulb with strongly cuticularised lumen; valves absent. Cardia conoid, embedded into intestinal tissue. Secretory-excretory system present. Female reproductive system didelphic, amphidelphic, ovary branches reflexed antidromously. Vulva funnel-shaped, with transverse slit-like opening. Vagina straight, without *pars refringens vaginae* or epiptygmata. Spermatheca absent. Male reproductive system monorchic, testis outstretched. Spicules arcuate, symmetrical. Gubernaculum present. Precloacal supplements papilliform, in single midventral row. Caudal alae present. Tail conoid. Caudal glands and spinneret absent.

Type and only species

Campydora demonstrans Cobb, 1920.

Genus *Campydoroides* Holovachov gen. nov.

Diagnosis

See above.

Type and only species

Campydoroides manautei Holovachov gen. et sp. nov.

Family **Rhabdolaimidae** Chitwood, 1951

Diagnosis

As for the superfamily Campydoroidea, except stoma with three denticles.

Included subfamilies

Subfamily Monochromadorinae Andrassy, 1958.

Subfamily Rhabdolaiminae Chitwood, 1951.

Subfamily **Monochromadorinae** Andrásy, 1958

Udonchinae Eyuaem & Coomans, 1996: 213.

Diagnosis

Cheilostom with twelve longitudinal rugae; stoma with three denticles, which are arranged in two separate groups at two levels; female reproductive system monodelphic.

Type and only genus

Udonchus Cobb, 1937.

Genus *Udonchus* Cobb, 1913

Monochromadora Schneider, 1937: 69.

Diagnosis (based on Eyuaem & Coomans (1996) and Tahseen *et al.* (2012))

Cuticle transversely striated. Lateral alae, body pores and epidermal glands absent. Somatic sensilla absent. Labial region truncated, lips fused. Six inner labial papilliform sensilla, located on anterior surface of lips. Six outer labial papilliform sensilla, located on periphery of labial region. Four cephalic papilliform sensilla, located short distance behind lip region. Amphid stirrup-shaped with transverse slit-like opening. Stoma tubular, cheilostom with 12 rugae, stegostom with cuticularised walls and three denticles (dorsal and ventral in anterior and left lateral in posterior parts of stoma). Pharynx cylindrical anteriorly, with distinct basal bulb; valves absent. Cardia conoid, not embedded into intestinal tissue. Secretory-excretory system absent. Female reproductive system monodelphic prodelphic, ovary branch reflexed antidromously. Vulva a transverse slit. Vagina oblique, without *pars refringens vaginae* or epiptygmata. Spermatheca absent. Male reproductive system unknown. Tail elongate. Caudal glands and spinneret present.

Type species

Udonchus tenuicaudatus Cobb, 1913.

syn. *Chromadora monohystera* Micoletzky, 1915.

syn. *Udonchus monohystera* (Micoletzky, 1915).

syn. *Monochromadora monohystera tenuiformis* Koniar, 1955.

syn. *Udonchus monhystera tenuiformis* (Koniar, 1955).

syn. *Monochromadora monhysteroides* Schneider, 1937.

syn. *Monochromadora monhysteroides longicaudata* Schneider, 1937.

Included species

Udonchus crassicauda (Schneider, 1937) Schiemer, 1978.

syn. *Monochromadora crassicauda* Schneider, 1937.

Udonchus merhatibebi Eyuaem & Coomans, 1996.

Subfamily **Rhabdolaiminae** Chitwood, 1951

Rogerinae Andrásy, 1976: 117.

Diagnosis

Cheilostom without rugae; stoma with three denticles arranged in one group, all at the same level; female reproductive system didelphic.

Type genus

Rhabdolaimus de Man, 1880.

Included genera

Mediolaimus Tahseen, Sultana, Khan & Hussain, 2012.

Rogerus Hoeppli & Chu, 1934.

Syringolaimus de Man, 1888.

Genus *Mediolaimus* Tahseen, Sultana, Khan & Hussain, 2012

Diagnosis (after Tahseen *et al.* 2012)

Cuticle transversely striated. Lateral alae absent. Somatic sensilla not described. Labial region flattened. Inner labial sensilla not described. Six outer labial pore-like sensilla. Four cephalic papilliform sensilla. Amphid with elliptical slit-like opening (transverse ovoid). Stoma tubular, cheilostom minute, stegostom with weakly cuticularised walls and three small denticles located at same level at its anterior edge. Pharynx cylindrical anteriorly, with distinct basal bulb; with thickened valve plates. Cardia small. Secretory-excretory system present. Female reproductive system didelphic, amphidelphic, ovary branches outstretched. Vulva a transverse slit. Vagina straight, with weak *pars refringens vaginae*, without epiptygmata. Spermatheca undescribed. Male reproductive system unknown. Tail elongate. Caudal glands and spinneret absent.

Type and only species

Mediolaimus obtusicaudatus Tahseen, Sultana, Khan & Hussain, 2012.

Genus *Rhabdolaimus* de Man, 1880

Pseudorhabdolaimus Soós, 1937: 323.

Diagnosis (modified from Siddiqi 2012)

Cuticle transversely striated. Lateral alae, body pores and epidermal glands absent. Somatic sensilla absent. Labial region truncated, lips indistinct. Inner labial sensilla indistinct. Six outer labial pore-like sensilla, located on periphery of labial region. Four cephalic papilliform sensilla, located just behind labial region. Amphid stirrup-shaped with transverse slit-like opening. Stoma tubular, cheilostom minute, stegostom with weakly cuticularised walls and three small denticles located at same level at its anterior edge. Pharynx cylindrical anteriorly, with distinct basal bulb; valves absent. Cardia small, partially embedded into intestinal tissue. Secretory-excretory system absent. Female reproductive system didelphic, amphidelphic, ovary branches reflexed antidromously. Vulva a transverse slit. Vagina straight, without *pars refringens vaginae* or epiptygmata. Spermatheca absent. Male reproductive system unknown. Spicules arcuate, symmetrical. Gubernaculum, supplements and caudal alae absent. Tail elongate. Caudal glands and spinneret present.

Type species

Rhabdolaimus terrestris de Man, 1880.

syn. *Rogerus rosea* Ali, Suryawanshi & Chisty, 1971.

Included species

Rhabdolaimus alpestris Siddiqi, 2012.

Rhabdolaimus annulatus Siddiqi, 2012.

Rhabdolaimus antiquus Siddiqi, 2012.

Rhabdolaimus aquaticus de Man, 1880.
syn. *Rhabdolaimus terrestris aquaticus* de Man, 1880.
Rhabdolaimus brachyuris Meyl, 1954.
Rhabdolaimus directistomus Gagarin, 2000.
Rhabdolaimus hasani Siddiqi, 2012.
Rhabdolaimus limnophilus (Soós, 1937).
syn. *Pseudorhabdolaimus limnophilus* Soós, 1937.
Rhabdolaimus medius Siddiqi, 2012.
Rhabdolaimus minor Cobb, 1914.
Rhabdolaimus nannus (Hoepli, 1926).
syn. *Chromadora nanna* Hoepli, 1926.
Rhabdolaimus parvulus Siddiqi, 2012.
Rhabdolaimus porifer Siddiqi, 2012.
Rhabdolaimus porosus Siddiqi, 2012.
Rhabdolaimus sclerorectum Tahseen, Chowdhary, Kulsum, Ahmad & Jairajpuri, 2005.
Rhabdolaimus strialaimus Siddiqi, 2012.
Rhabdolaimus thornei Siddiqi, 2012.

Genus **Rogerus** Hoepli & Chu, 1934

Diagnosis

Cuticle transversely striated. Lateral alae, body pores and epidermal glands absent. Somatic sensilla absent. Labial region truncated, lips indistinct. Inner labial sensilla papilliform. Six outer labial sensilla papilliform or setiform, located on periphery of labial region. Four cephalic setiform sensilla, at level with outer labial sensilla. Amphid oval (transverse ovoid). Stoma tubular, cheilostom minute, stegostom with weakly cuticularised walls and three small denticles located at same level at its anterior edge. Pharynx cylindrical anteriorly, with distinct basal bulb; valves absent. Cardia small, partially embedded into intestinal tissue. Secretory-excretory system absent. Female reproductive system didelphic, amphidelphic, ovary branches outstretched. Vulva circular. Vagina straight, without *pars refringens vaginae* or epiptygmata. Spermatheca absent. Male reproductive system monorchic. Spicules arcuate, symmetrical. Gubernaculum, supplements and caudal alae absent. Tail elongate. Caudal glands and spinneret present.

Type and only species

Rogerus orientalis (Hoepli & Chu, 1932).
syn. *Greenia orientalis* Hoepli & Chu, 1932; *Greeninema orientalis* (Hoepli & Chu, 1932).

Included species

Rogerus rajasthanensis Khera, 1966.
syn. *Rhabdolaimus rajasthanensis* (Khera, 1966).

Genus **Syringolaimus** de Man, 1888

Halirhabdolaimus Siddiqi, 2012: 65 syn. nov.

Diagnosis (after Tchesunov 2017)

Cuticle visually smooth or transversely striated. Lateral alae absent. Somatic sensilla undescribed. Labial region truncated. Inner labial sensilla indistinct. Morphology of inner and outer labial sensilla unclear. Four cephalic small papilliform sensilla. Amphid stirrup-shaped with transverse slit-like opening. Stoma

cylindrical, with cuticularised walls and three protrusible bifid teeth located at same level at anterior edge of stegostom. Pharynx cylindrical anteriorly, with distinct basal bulb; valves absent. Cardia large, ovoid, partially embedded into intestinal tissue. Secretory-excretory system present. Female reproductive system didelphic, amphidelphic, ovary branches reflexed antidromously. Morphology of vulva and vagina unknown. Male reproductive system monorchic, testis outstretched. Spicules arcuate, symmetrical. Gubernaculum present. Precloacal supplements papilliform, in single midventral row. Caudal alae absent. Tail elongate. Caudal glands and spinneret present or absent.

Type and only species

Syringolaimus striatocaudatus de Man, 1888.
syn. *Syringolaimus striatocaudatus aberrans* Micoletzky, 1924.
syn. *Syringolaimus striatocaudatus steineri* Micoletzky, 1924.
syn. *Dolicholaimus propinquus* Allgén, 1933.
syn. *Dolicholaimus tenuicaudatus* Allgén, 1932.

Included species

Syringolaimus annae Lima, Lins, Da Silva & Esteves, 2009.
Syringolaimus elegans Tchesunov, 2017.
Syringolaimus filicaudatus Vitiello, 1970.
Syringolaimus loofi Gourbault & Vincx, 1985.
syn. *Halirhabdolaimus loofi* (Gourbault & Vincx, 1985).
Syringolaimus renaudae Gourbault & Vincx, 1985.
Syringolaimus smolae Lima, Lins, Da Silva & Esteves, 2009.
Syringolaimus striatocaudatus de Man, 1888.
Syringolaimus taniae Lima, Lins, Da Silva & Esteves, 2009.

Species inquirenda

Syringolaimus brevicaudatus Micoletzky, 1922.
Syringolaimus caspersi Gerlach, 1951.
Syringolaimus lichenii (Nasira & Turpeenniemi, 2002).
syn. *Trissonchulus lichenii* Nasira & Turpeenniemi, 2002.
Syringolaimus marisalbi Platonova & Mokievsky, 1994.
Syringolaimus smarigodus Cobb, 1928.

Nomina nuda

Syringolaimus gladius Bussau, 1993.
Syringolaimus ingens Bussau, 1993.
Syringolaimus nitidus Bussau, 1993.
Syringolaimus venustus Bussau, 1993.

Remarks

See Tchesunov (2017) for the most recent and comprehensive revision of the genus. The genus *Halirhabdolaimus* was proposed by Siddiqi (2012) for a single species, *Syringolaimus loofi*, and was only compared with the genus *Rhabdolaimus*. However, the author did not compare *Halirhabdolaimus* with *Syringolaimus*. The differential diagnoses of both genera match perfectly and thus the proposal of the new genus was entirely unjustified.

Key to the genera of the suborder Campydorina (see Table 2 for additional diagnostic characters)

1. Stoma with single well developed dorsal tooth2
– Stoma with three denticles3
2. Stoma conoid with large tooth; cephalic sensilla and amphids posterior to labial region; caudal glands and spinneret present*Campydoroides* Hologachov gen. nov.
– Stoma cylindrical with small tooth; cephalic sensilla and amphids on cap-like labial region; caudal glands and spinneret absent*Campydora* Cobb, 1920
3. Denticles located at different levels (dorsal and ventral in anterior and left lateral in posterior parts of stoma); female reproductive system monodelphic*Udonchus* Cobb, 1913
– Denticles located at same level in anterior part of stoma; female reproductive system didelphic4
4. Ovaries outstretched5
– Ovaries reflexed6
5. Cephalic sensilla setiform; caudal glands and spinneret present ...*Rogerus* Hoeppli & Chu, 1934
– Cephalic sensilla papilliform; caudal glands and spinneret absent
.....*Mediolaimus* Tahseen, Sultana, Khan & Hussain, 2012
6. Marine*Syringolaimus* de Man, 1888
– Freshwater and terrestrial*Rhabdolaimus* de Man, 1880

Discussion

The genera grouped in the suborder Campydorina differ from each other in the morphology of the stoma, which in the past was used as a reason to classify them in different orders of the phylum Nematoda. On the other hand, other systems of organs show similar morphology. These include the papilliform labial sensilla, the papilliform or short setiform cephalic sensilla, the stirrup-shaped amphid with transverse ovoid or slit-like aperture, the cylindrical and uniformly muscularised pharynx with a distinct basal bulb without valves or grinder, and the female reproductive system with simple vagina and short uteri. A similar pattern is observed in other groups of nematodes, such as in the families Chromadoridae Filipjev, 1917 and Diplogastridae Micoletzky, 1922, in which the general body plan is conserved, while the morphology of the stoma is extremely diverse (Sudhaus & von Lieven 2003; Venekey *et al.*, in press), reflecting various feeding strategies employed by different species of the same family.

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