A new free-living nematode species, *Terschellingia didistalamphida* sp. nov. (Nematoda: Linhomoeidae), with female intersexuality from West Bengal, India

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Abstract. A new species of free-living soil nematode, *Terschellingia didistalamphida* sp. nov., is described from paddy field in West Bengal, India. It is characterized by moderate body length (L=1.0–3.5 mm), possesses two amphids, only four cephalic setae. Amphideal fovea distant from the anterior end, stoma small and narrow, pharynx with well-developed terminal bulb. Females with amphidelphic ovaries. Males with paired testes, ventrally arcuate, short and stout spicules, gubernaculum with clearly developed dorso-caudal apophysis. Tail long and filiform, similar in both sexes. Fourteen female intersexes of *Terschellingia didistalamphida* sp. nov., with a prominent female reproductive structure and a less conspicuous male reproductive system, were found. These female intersexes are with well-developed vulva and prominent spicules, however, lack apophysis. A checklist for known cases of intersex across various nematode orders has been appended.

Keywords. New species, new records, female intersex, soil nematodes, meiofauna, Monhysterida.

INTRODUCTION

The members of the family Linhomoeidae Filipjev, 1929, are primarily found in marine habitats. However, *Terschellingia* de Man, 1888, is an exception within this family, as it includes mostly freshwater and some marine species (Abebe *et al.* 2006, Armenteros *et al*. 2009). De Man (1888) initially identified the genus *Terschellingia* based on characteristics such as a narrow buccal cavity (when present), four cephalic setae, anterior amphids, a pharynx with a well-developed basal bulb, and amphidelphic ovaries in females. Males of this genus possess robust spicules and a gubernaculum with a prominent dorso-caudal apophysis. The tail may or may not have a filiform expansion.

Amenteros *et al.* (2009) made an extensive review of 38 species of the genus *Terschellingia* described by various authors over the past century and concluded only 15 odds among them as valid species.

Intersexuality has been observed in various forms of nematodes, including those that are insect-parasitic (Hirschmann & Sasser 1955, Steiner 1923), free-living, animal-parasitic (Hirschmann *et al.* 1955), and plant-parasitic (Chitwood 1949, Jairajpuri *et al.* 1977, Triantaphyllou & Hirschmann 1964). Among the reported cases of intersex nematodes, the majority are female intersex, exhibiting fully developed female reproductive structures and rudimentary male reproductive systems (Renubala *et al.* 1992); while a few are

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male intersex, having matured male reproductive organs. Some species display both types of intersexuality (Zhuo *et al*. 2009).

It has been stated in earlier literature that intersexuality is comparatively rare among plant-parasitic forms (Zhuo *et al*. 2009). In addition to recording the descriptions of a new species *Terschellingia didistalamphida* sp. nov., we performed an exhaustive literature review and prepared a comprehensive checklist of records of intersexuality in nematodes across all ecological categories available to date.

MATERIALS AND METHODS

Soil samples (mud) were collected from a depth of 0–15cm from a paddy field in Purba (East) Midnapore district (22.1375°N, 88.0799° E), West Bengal, India. Nematodes were then extracted by processing the mud samples following the modified Baermann funnel technique (Jana *et al*. 2010). Nematodes were fixed in hot (90°–100°C), diluted FAA (formalin acetic acid: 4:1, i.e., 10 parts 40% formalin, 1 part acetic acid, and 89 parts distilled water) solution. Nematodes were then picked up into glycerin-alcohol (5 parts 1.5% glycerin in 95 parts of 30% alcohol) and kept inside a desiccator containing anhydrous calcium chloride ($CaCl_2$). After 4–8 weeks of desiccation, slides were prepared by mounting nematodes into glycerin. The morpho-taxonomic descriptions were made from glycerin mounts using light microscopy. Line drawings were made either using a Dewinter microscope fitted with a drawing tube or digitally drawn using Adobe CS 2021 software from captured images. Imaging was done with an optical microscope (Carl Zeiss Axio Vert. A1 with Zeiss Zen Pro software, Carl Zeiss, Jena, Germany) equipped with an advanced camera (Axiocam 305 Color) sensor and IC measure application.

TAXONOMY

Order Monhysterida Filipjev, 1929

Superfamily Siphonolaimoidea Filipjev, 1918

Family Linhomoeidae Filipjev, 1922

Genus *Terschellingia* de Man, 1888

Diagnosis. Moderate body length Linhomoeidae (L = 1.0–3.5 mm), with transversely striated cuticle. Only four cephalic setae present. Stoma small and narrow. Pharynx with well-developed terminal bulb. Female with amphidelphic ovaries. Testes paired. Spicules short and stout, ventrally arcuate. Gubernaculum with clearly developed caudal apophyses. Pre-anal, mid-ventral genital papillae present in some species. Tail long and filiform. Mostly marine, few found in freshwater.

Type species: *T. communis* de Man, 1888

Terschellingia didistalamphida sp. nov.

(Figures 1–4)

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Type locality and habitat. Soil samples were collected in June 2019 from a paddy field at Haldia (22.1375°N, 88.0799°E), East Midnapore, West Bengal, India.

Type material. Five females (one holotype and four paratypes), four males and fourteen intersex specimens were collected from the study site. Statistical calculations on the morphometric parameters were performed on the basis of all the specimens collected except for the intersexes (seven intersex specimens were used for calculation) as mentioned in Table 1.

Type designation and deposition. Specimens are deposited in the Nemathelminthes Section of the National Zoological Collections (NZC) of ZSI, Kolkata, West Bengal, India. Holotype, Reg. No. WN4130/1 (Female), Paratypes, Reg. No. WN4130/2, WN4130/3 and WN4130/4 (female, male & intersex specimens).

Measurements. Measurements of the new species are given in Table 1. (following de Man's formulae)

Diagnosis. Terschellingia didistalamphida sp. nov. is morphologically close to *Terschellingia lutosa* Gagarin & Nguyen, 2014 (Gagarin & Nguyen 2014) and *Terschellingia rivalis* Gagarin &

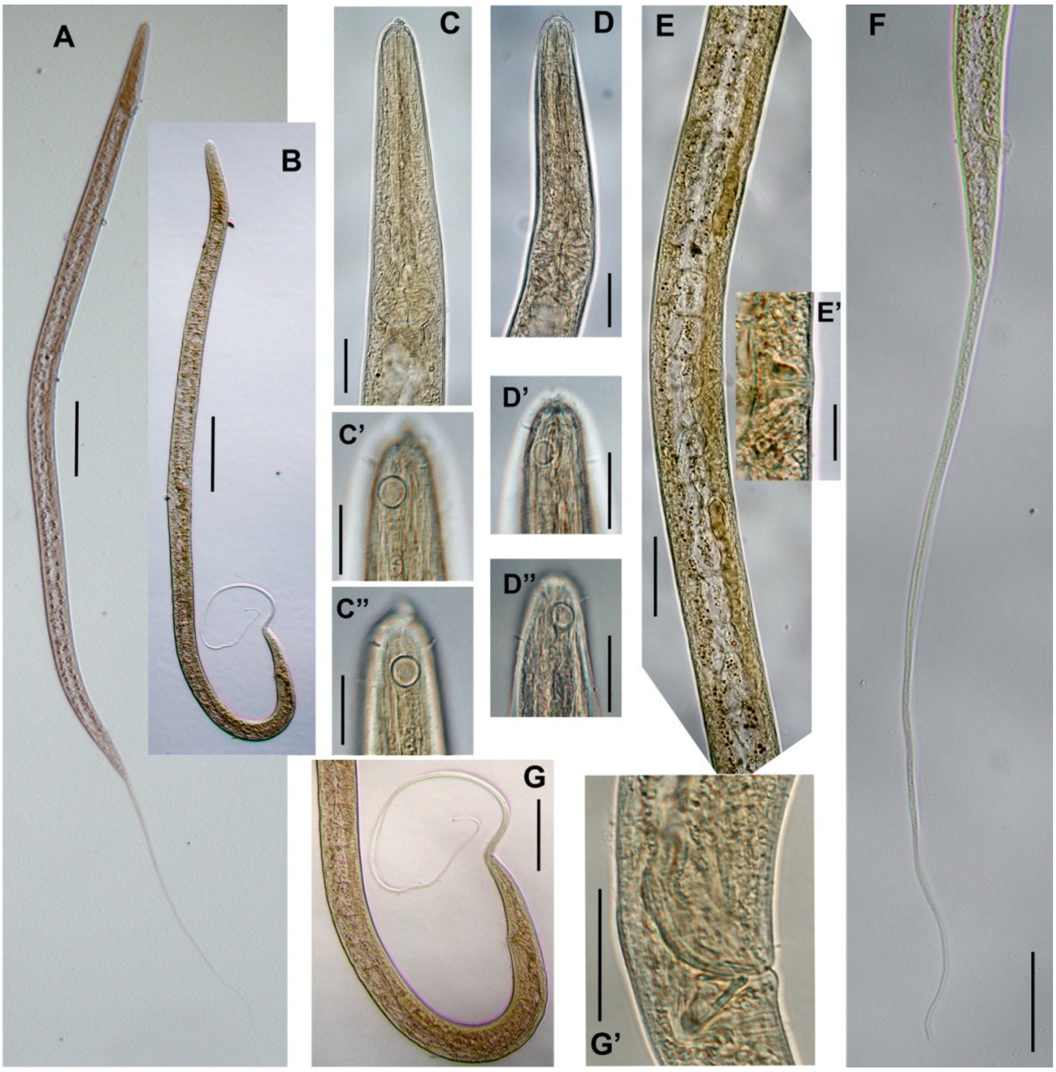


Figure 1. Photographs of *Terschellingia didistalamphida* sp. nov. holotype female and paratype male. Whole body– **A.** female **B.** male; **C.** Anterior end of female showing distinct basal bulb and cardia [**C' & C"–**enlarged view at different focal planes to show the amphids and cephalic setae]; **D.** Anterior end of male [**D' & D"** – enlarged view to show the amphids at different focal planes]; **E.** Gonads with vulva [**E'** – enlarged view to show vulval lips]; **F.** Tail region with anus in female; **G.** Tail region of male with spicules and **G'**. enlarged view to show the spicules. **Scale bars**: **A** & **B** : 100µm; **C**, **C'**, **C"**, **D**, **D'**, **D"** & **G'**: 20µm; **E**: 40µm; **E'**: 10µm and **F** & **G**: 50µm.

Thanh, 2009 (Gagarin & Thanh 2009). However, the new species differs significantly from *T. lutosa* in total body length (1165–1562.5 µm in *T. didistalamphida* sp. nov. vs. 1924–2235 µm in *T. lutosa*) and tail length (c'12–25.87 vs. c'7–8.8). It also differs from *T. rivalis* in tail length (c'12–25.87 in *T. didistalamphida* sp. nov. vs. c'32–33 in *T. rivalis*); the ratio of total body length and GBD also vary significantly (a 31.62–48.06 vs. a 66–83) and in V% (32.58–41.2 vs. 26.4–30.5).

Terschellingia didistalamphida sp. nov. shows some similarities to *T. distalamphida* Juario, 1974 (Portnova 2009) but can be distinguished by many morphological and morphometric features. The female specimens strikingly differ in body length when compared with *T. distalamphida* (1307.5–1467.5 µm in *T. didistalamphida* sp. nov. vs. 750–937.5 µm in *T. distalamphida*). A single circular amphid (6 µm in diameter) is present at a distance of 13–14 µm from the anterior end in case of *T.*

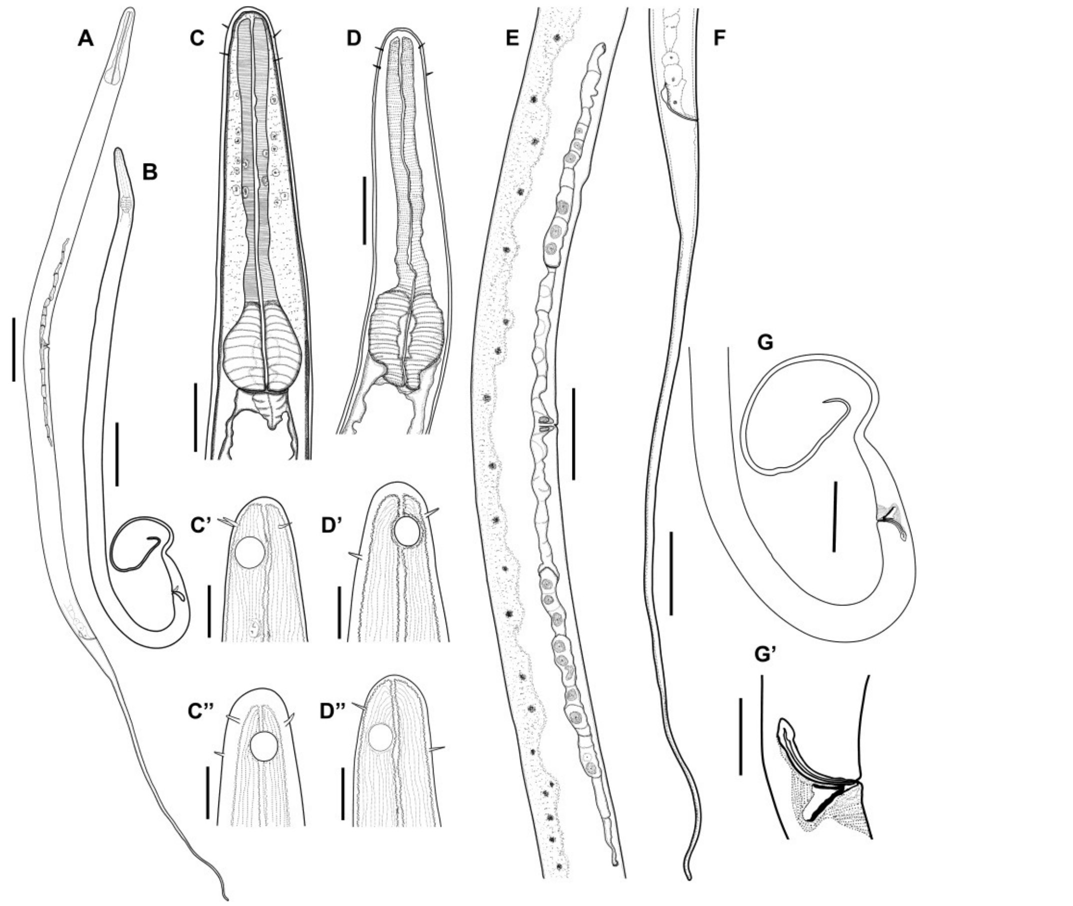
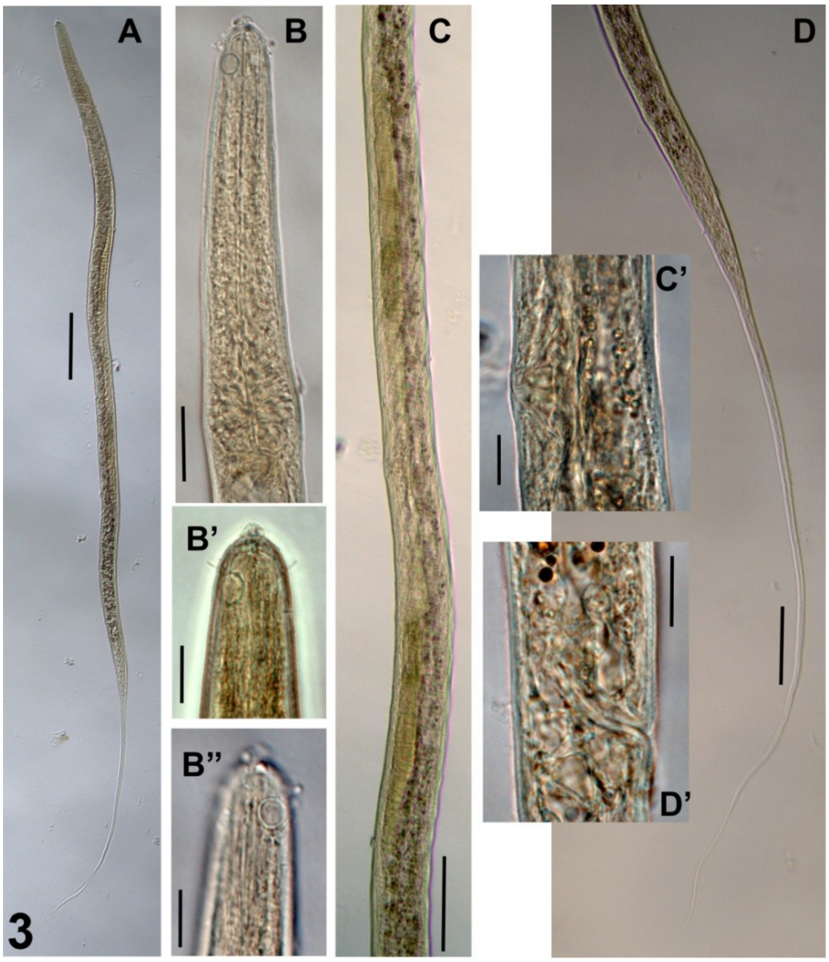


Figure 2. Drawing of *Terschellingia didistalamphida* sp. nov. holotype female and paratype male. Whole body– **A**. female **B**. male; **C**. Anterior end of female showing distinct basal bulb and cardia [**C' & C"**–drawn from images of different focal planes to show the amphids and cephalic setae]; **D.** Anterior end of male [**D' & D"** – drawn from images of different focal planes to show the amphids]; **E.** Gonads with vulva; **F**. Tail region with anus in female; **G.** Tail region of male with spicules and **G'**. enlarged view of the spicules. **Scale bars**: **A** & **B**: 100µm; **C**, **D** & **G'**: 20µm; **C'**, **C"**, **D'**& **D"**: 10µm and **E**, **F** & **G**: 50µm.

distalamphida whereas, there are two amphids (4–6 µm in diameter) in this new species. Two amphids are not placed at the same plane in the newly reported species. In *T. distalamphida*, no cervical setae found, but the novel species possesses prominent setae, including cervical setae.

Description. *Female* (Figs.1, 2) (Table 1). Elongated body with a long filiform tail (437.5–512.5 µm). The female is longer than the male. Body almost straight following heat fixation. Cuticle appears thin and smooth under light microscope. Four prominent cephalic setae, paired round amphids, measuring 5.4–6.4 µm in diameter, are located at the anterior end. Pharynx with a large muscular basal bulb and a small cardia. Ovary amphidelphic and reflexed. Vulva transverse with well-developed pars distalis. The filiform part of the tail is distinctively longer than the conical part. A few random caudal setae and cervical setae present.

Male (Fig.1, 2) (Table 1). The male exhibits an elongated body with a long filiform tail (362.5–437.5 µm). Following heat fixation, the body assumes a "J" shape or becomes almost straight. Cuticle appears thin and smooth under light microscope. Pharynx with a large muscular terminal bulb and a small cardia. Testes paired and reflexed. Spicules slightly curved at the anterior end and with a very prominent dorso-caudal apo-



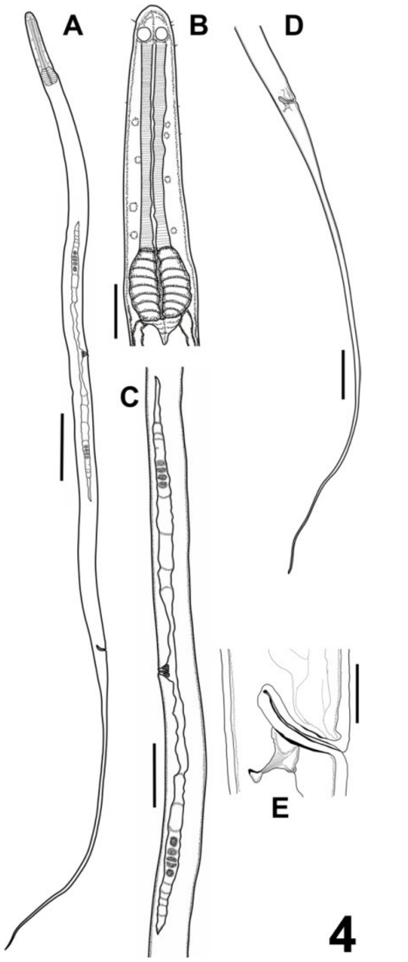


Figure 3. Photographs of *Terschellingia didistalamphida* sp. nov. intersex. **A**. Whole body; **B**. Anterior end showing distinct basal bulb and cardia; **B' & B''**. Enlarged view showing amphids and cephalic setae; **C**. Gonads with vulva; **C'**. Enlarged view showing vulva; **D**. Tail region with spicules; **D'**. spicules. **Scale bars**: **A**: 100µm; **B**: 20µm; **B'**, **B''**, **C'** & **D'**: 10µm; and **C** & **D**: 50µm.

Figure 4. Drawings of *Terschellingia didistalamphida* sp. nov. intersex. **A**. Whole body; **B**. Anterior end showing distinct basal bulb, cardia and cephalic setae; **C**. Gonads (ovaries) with vulva; **D.** Tail region with spicules; **E**. Spicules without apophysis. **Scale bars**: **A**: 100µm; **B**: 20µm; **C** & **D**: 50µm; **E**: 10µm.

physis. The filiform part of the tail is very long and bears a few distinct caudal setae.

Female intersex. (Fig.3, 4) (Table 1). Moderate body length with a very long, filiform tail (337.5–512.5 µm). Cuticle thin and smooth under light microscope. Four cephalic setae, very short and thin, measuring 2–3 µm in length. Amphids round, 5.4–6.4 µm in diameter and located 8–10 µm away from the anterior end; stoma narrow and tiny. Pharynx with large muscular basal bulb. Nearly rounded, small cardia with a diameter of 7.5–12.5 µm. Ovary amphidelphic and reflexed, while the vulva transverse with well-developed pars distalis. Spicules slightly curved at the anterior end and without any gubernaculum. No caudal apophysis is developed, being a female intersex. The filiform part of the tail is very long and contains caudal setae.

Etymology. The newly reported species shows similarity with previously described *Terschellingia distalamphida* Juario, 1974 that is characterized by a single distant amphid. However, in this new species 'two' amphids are present distantly from the anterior end compared to other species under the genus-*Terschellingia,* hence the name *'didistalamphida'* (Greek word, '*di'* derived '*two'*; '*distal'* came from Latin word '*distere'* meaning distant and '*amphid'* comes from greek word '*amphidia'*).

DISCUSSION

Previously described female intersex (Renubala *et al.* 1992, Zhuo *et al*. 2009) were found to possess a well-developed female reproductive system and prominent spicules as the only male reproductive part. However, in our study, we found *T. didistalamphida* sp. nov. with a well-developed amphidelphic ovary, and a prominent vulva but no testes. Based on these characteristics, we can conclude that it is a female intersex individual. This finding represents the first-ever recorded instance of intersex in the genus *Terschellingia*.

As mentioned earlier, all previous reports state that intersex specimens are typically uncommon in plant nematodes (Zhuo *et al*. 2009). However, after a thorough review of available literature, we found intersexuality is most commonly reported in plant nematodes and, rather, rare among free-living forms as reflected in the checklist (Table 2). Our study also uncovered another aspect, a surprisingly high number of female intersex individuals, 14 in total, during a relatively small sampling effort. This abundance cannot be dismissed as a mere coincidence, nor can it be attributed to developmental deformities, as none of the other nematode species examined at the same sites exhibited this phenomenon (unpublished data). Understanding why such a substantial number of female intersex individuals occur and the potential selective advantages conferred by nature to these intersex forms over normal females presents an intriguing question. Furthermore, it would be of interest from a developmental perspective to elucidate the mechanisms by which these individuals deviate from the regular developmental pathway. Additionally, the potential role of the environment in sex determination in this species cannot be disregarded (Hodgkin 2002). Substantial research is required to address these questions, which lie beyond the scope of our current work.

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Table 1. Morphometric characteristics of *Terschellingia didistalamphida* sp. nov., Measurements recorded in micrometer and in the form of mean±standard deviation (range). Number of specimens used for statistical calculation is mentioned within parentheses in the Table header.

Characters	Holotype female	Paratype females (n=4)	Paratype males (n=4)	Paratype female intersexes (n=7)
Body length	1509.5	1441.88±53.71 (1382.5–1512.5)	1165.62±174.43 (905–1207)	1374.28±54.03 (1307.5–1467.5)
Greatest body diameter	39.5	35.63±4.73 (32.5–425)	35±6.12 (27.5–40)	34.64±3.65 (30–40)
a	38.31	40.92±4.69 (33.94–44)	33.48±3.02 (31.37–37.92)	40.05±4.56 (34.25–46.25)
b	12.96	12.71±0.68 (12.1–13.6)	11.006±1.87 (8.22–12.32)	12.33±0.89 (10.46–13.07)
c	3.25	2.95±0.17 (2.81–3.16)	2.89±0.51 (2.23–3.46)	3.12±0.18 (2.85–3.26)
c’	20.80	21.18±1.57 (19.44–22.77)	18.47±0.65 (18–19.44)	20.57±0.93 (18.88–21.87)
V (%)	33.30	36.30±169 (34.44–36.51)	–	36.21±2.46 (33.19–37.11)
Length of gonad	527.76	523.13±24.36 (492.5–550)	456.87±53.99 (390–512.5)	520.71±60.47 (462.5–615)
Distance of amphids from anterior end	8.70	8.13±1.25 (7.5–10)	8.75±1.44 (7.5–10)	8.92±1.33 (7.5–10)
Amphids diameter	5.60	5.97±0.43(5.4–6.4)	5.88±0.44 (5.4–6.3)	5.97±0.40 (5.4–6.4)
Pharynx length	116.43	113.75±9.24 (105–125)	106.25±4.33 (100–110)	111.78±7.17 (102.5–125)
Vulva–anus distance/tail	1.08	0.88±0.07 (0.80–0.942)	–	0.98±0.09 (0.81–1.09)
Vulval body diam.	37.56	31.25±4.79 (27.5–37.5)	–	30.35±4.19 (27.5–37.5)
Anal body diam.	22.28	28.13±1.25 (22.5–25)	21.87±1.25 (20–22.5)	21.78±1.21 (20–22.5)
Tail length	463.61	489.38±34.96 (437.5–512.5)	404.37±31.18 (362.5–437.5)	440.35±24.59 (402.5–467.5)
Lenth of spicules	–	–	22.5±2.5 (12.5–15)	23.21±4.26 (17.5–30)
Length of apophysis	–	–	13.75±1.44 (12.5–15)	–

Table 2. Checklist of reported intersex in nematodes
(Categorization of the species mentioned in this list is given as per the original references only)

Order	Species	Reported from and its Habitat	Ecological status	Type of intersexuality	Reference
Aphelenchida	*Aphelenchoides brassicae*	Canada, Corn field	Plant parasitic	Female intersex	(Edward & Misra 1969)
	Aphelenchoides composticola	Canada, Corn field	Free-living	Female intersex	(Anderson & Kimpinski 1977)
	Aphelenchoides parietinus	California	Plant parasitic	Female intersex	(Krall 1959)
	Aphelenchoides saprophilus	–	Plant parasitic	Female intersex	(Braasch 1987)
	Aphelenchoides sp.	–	Both Plant parasitic & Free-living	Female intersex	(Slepetiene 1962)
	Aphelenchoides sp.	West Bengal, India Rhizosphere of paddy	Both Plant parasitic & Free-living	Female intersex	(Khera & Chaturvedi 1971)
	Aphelenchoides subparietinus	–	Plant parasitic	Male intersex	(Gruzdeva 1980)
Tylenchida	*Ditylenchus triformis*	China, Soil around the rhizosphere of plants	Plant parasitic	Female intersex	(Weizhi & Qingli 2002)
	Tylenchorhynchus capitatus	New Zealand, tobacco fields	Plant parasitic	Female intersex	(Wouts 1966)
	Tylenchorhynchus nilgiriensis	southern Alberta, Potato field	Plant parasitic	Female intersex	(Seshadri *et al.* 1967)
	Tylenchorhynchus sp.	–	Plant parasitic	Female intersex	(Dalmasso 1966)
	Heterodera trifolii	Germany, soil-root samples from a Pasture	Plant parasitic	male intersex	(Wouts 1978)
	Meloidogyne incognita	Japan	Plant parasitic	Male and Female intersex	(Ishibashi 1965)
	Meloidogyne incognita	India	Plant parasitic	Male intersex	(Martin 1970)
	Meloidogyne thamesi	Australia, Grape root	Plant parasitic	Male intersex	(McLeod & Khair 1973)
	Meloidogyne javanica	–	Plant parasitic	Male intersex	(Sheng-Fu & Yong-Fang 1998)
	Meloidogyne javanica	Philippines, Tomato plant root	Plant parasitic	Female intersex	(Davide & Triantaphyllou 1967)
	Helicotylenchus indicus	India	Plant parasitic	Female intersex	(Renubala *et al.* 1992)
	Hirschmanniella oryzae	India, Paddy field	Plant parasitic	male intersex	(Zhuo *et al.* 2009)
	Hirschmanniella shamimi	China, Paddy field	Plant parasitic	Female intersex	(Zhuo *et al.* 2009)
	Tyleptus striatus	India, around the roots of *Saccharum ravennae*	Plant parasitic	Female intersex	(Jairajpuri & Siddiqi 1964)
Mermithida	*Mermis mirabilis*	–	Insect parasitic	–	(Hirschmann & Sasser 1955)
	Mermis sp.	–	Insect parasitic	–	(Hirschmann & Sasser 1955)
	Paramermis fluviatilis	–	–	–	(Hirschmann & Sasser 1955)

	Agamermis decaudata	–	Insect parasitic	Female intersex	(Steiner 1923)
	Agamermis albicans	–	Insect parasitic	Female intersex	(Steiner 1923)
	Pseudomermis vanderlindei	–	Parasitic	Female intersex	(Steiner 1923)
Rhabditida	*Tetanonema strongylurus*	–	Animal parasite (Fish)	Female intersex	(Steiner 1923)
	Porrocaecum heteroura	–	Animal parasite (Bird)	–	(Hirschmann & Sasser 1955)
Enoplida	*Enoplus communis*	Marine	Free-living	–	(Hirschmann & Sasser 1955)
	Enoplus michaelseni	Marine	Free-living	Female intersex	(Steiner 1923)
	Thoracostoma figuration	Marine	Free-living	Female intersex	(Steiner 1923)
	Trilobus diversipapillatus syn. Trilobus longus	–	Free-living	Female intersex	(Hirschmann & Sasser 1955)
	Trilobus gracilis	Freshwater	Free-living	Female intersex	(Hirschmann & Sasser 1955)
Chromadorida	*Chromadora poecilosoma*	Marine	Free-living	–	(Hirschmann & Sasser 1955)
Dorylaimida	*Longidorus africanus*	Israel, avocado roots	Plant parasitic	Female intersex	(Zhuo *et al.* 2009)
	Longidorus distinctus	South-eastern Slovakia, rhizosphere of plum trees	Plant parasitic	Female intersex	(Lišková 2007)
	Longidorus elongates	Scotland, Soil	Plant parasitic	Female intersex	(Raschké & Boag 1981)
	Longidorus helveticus	Serbia, rhizosphere of black-berry	Plant parasitic	Female intersex	(Barsi & De Luca 2005)
	Longidorus macrosoma	–	Plant parasitic	–	(Abouleid & Coomans 1966)
	Aquatides thornei	India, near the roots of *Oryza sativa*	Plant parasitic	Female intersex	(Jairajpuri *et al.* 1977)
	Leptonchus obtusus	Missouri, Soil collected from wooded area	Plant parasitic	Female intersex	(Goseco & Ferris 1973)
	Xiphinema attorodorum	France, Sandy soil	Plant parasitic	Female intersex	(Luc 1961)
	Xiphinema ingens	–	Plant parasitic	Female intersex	(Lamberti *et al.* 1983)
	Xiphinema insigne	India	Plant parasitic	male intersex	(Bajaj & Jairajpuri 1977)
Desmodorida	*Desmodora porosum*	Deep sea, Atlantic	Free-living	Female intersex	(da Rocha Moura *et al.* 2014)
Monhysterida	*Terschellingia didistalamphida sp. nov.*	Soil, paddy field, India	Free-living	Female intersex	Current study