REVIEW

A morphometric analysis of the genus *Terschellingia* (Nematoda: Linhomoeidae) with redefinition of the genus and key to the species

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The cosmopolitan and often ecologically dominant genus Terschellingia *(Nematoda: Linhomoeidae), with 38 nominal species, is taxonomically a problematic taxon. Its species show high morphological plasticity, possess few diagnostic characters and identification keys are lacking. A revision of the genus was carried out based on morphological and morphometric data from the literature and from observations of specimens collected in Cienfuegos Bay, Caribbean Sea, Cuba. The diagnosis of the genus* Terschellingia *is emended. Of the current 38 nominal species, 15 are considered as valid species based on morphological characters related to size and position of amphidial fovea, presence/position of cephalic and cervical setae, presence/size/shape of pharyngeal bulb, shape of spicular apparatus and shape of tail. Tabular and pictorial keys were provided based on these characters. Three sympatric species:* T. communis, T. gourbaultae *and* T. longicaudata *were redescribed based on recently collected Cuban specimens. Each of them showed relatively large differences in body size in comparison with the respective type specimens, suggesting possible variation due to local environmental differences. The highest intraspecific variation pertains for the most widely spread cosmopolitan species* T. longicaudata*, suggesting that morphological plasticity enhanced adaptation to different environmental conditions. The notable taxonomic inflation within the genus (14 species* inquirendae, *9 junior synonyms), probably also present in other highly specious genera of marine nematodes, can lead to an overestimation of the alpha-diversity.*

Keywords: morphometric analysis, genus, *Terschellingia*, redefinition of genus, key to species

INTRODUCTION

The genus *Terschellingia* (Nematoda: Linhomoeidae) was erected by de Man (1888) on the basis of the following features: four cephalic setae, buccal cavity small or absent and circular amphidial fovea located far forward on the head region. The etymology of the genus refers to the origin of the type specimens i.e. collected at Terschelling Island in The Netherlands. In general, species pertaining to this genus are cosmopolitan and very often numerically dominant in muddy subtidal bottoms (Heip *et al.*, 1985). Therefore, they play an important ecological role in the sedimentary environment where they inhabit. Despite the notable presence of

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individuals belonging to the genus *Terschellingia* in samples from benthic studies, currently, identification to species level remains problematic.

The valuable compilation of free-living marine nematodes by Gerlach & Riemann (1973) indicated 28 valid species of *Terschellingia* and six synonymies. The present study describes 38 nominal species and a possible substantial taxonomic inflation (*sensu* Alroy, 2002). Most of the descriptions of *Terschellingia* species were carried out by pioneers of nematology (e.g. Cobb, de Man, Filipjev, Gerlach and Timm) dating from more than 50 years ago. This implies the lack of holotypes, the statement of new species on the basis of one or two specimens, often females with relatively few features of taxonomic value. The relatively slow flow of information among researchers in those years and the reduced access to some journals also enhanced the existence of a plethora of synonymies. Three taxonomic keys have been elaborated (Wieser,

1956; Gerlach, 1963; Austen, 1989), however, these keys do not cover all species of the genus and they are not updated.

The problematic assessment of the genus *Terschellingia* fits in the larger gap about the taxonomic status of the family Linhomoeidae. The last revision of this family was published by Gerlach (1963) and no further revision has been carried out since. Lorenzen (1994), in his cladistic phylogenetic outline about free-living nematodes, recognized that more extensive analyses are still needed before relationships can be determined.

The 'ideal' taxonomic assessment of any taxon should be based on a phylogenetic approach, combining molecular techniques, like DNA sequence analysis, with morphological data to constitute an appropriate basis for studies of diversity of nematodes (De Ley, 2000; Nadler, 2002). However, the promising application of molecular techniques for delimitation of species currently rests on a preliminary morphological approach (Derycke *et al.*, 2005). A framework of nearly 40 species of *Terschellingia*, most of them poorly described and morphologically similar, is not the best scenario for: (i) developing an easier way for identification and classification of relevant taxa in order to reduce the taxonomic impediment (De Ley, 2000); and (ii) applying a molecular approach to the taxonomy of the genus. Currently, the exhaustive revision of any taxon of free-living marine nematodes based exclusively on morphology appears in general not enough for a conclusive statement about taxonomy and relationships though it provides a basis for readdressing future studies on particular morph-species and phylogenetic relationships.

The genus *Terschellingia* possesses relatively few characters of diagnostic value. For example, labial sensilla are reduced (= small), cuticularized structures in buccal cavity as rings or teeth are absent or rarely present, precloacal supplements are rarely present, and the body cuticle lacks ornamentations such as pores or spines. The high morphological plasticity within species of this genus biases to clear identification of morph-species, and is surely related to the cosmopolitan distribution and numerical dominance of the genus in soft bottom habitats. Several appealing features within the genus, such as sperm dimorphism in *T. glabricutis* (Yushin, 2008) and possible presence of cryptic species in *T. longicaudata* (Bhadury *et al.*, 2008), are an incentive for the continuation of the studies about the genus *Terschellingia*. The 'classical' morphological characters used for the diagnosis of species (e.g. relative position of amphidial fovea in the head region,

the pattern of somatic setae and tail length) are clearly not sufficient and other morphometric characters were explored in order to refine species diagnoses.

Ecological studies in subtidal muddy bottoms from Cienfuegos Bay, Cuba, Caribbean Sea indicated a notable numerical dominance of the genus *Terschellingia* in the sediments. Three sympatric species are redescribed in the present study. The aims of this research are: (1) to identify the most important diagnostic features of the genus *Terschellingia* de Man 1888 and redefine the genus diagnosis; (2) to provide a comprehensive diagnosis of the valid species within the genus; and (3) to construct a pictorial key to species level. Additional information is provided for known species collected in Cuba.

MATERIALS AND METHODS

Samples were taken in February 2006 in six subtidal stations from Cienfuegos Bay, Caribbean Sea (22°07′ N 80°22′ W). The bay is a semi-enclosed body of water with relatively high organic content in sediment and predominance of muddy bottoms. Samples were collected using hand-held cores and preserved in 8% buffered formalin. Sediment samples were processed by sieving over two sieves with 500 μm and 45 μm mesh size and specimens were extracted by the flotation technique using a high-density sugar solution (1.16 g cm^{-3}). Sorted animals were transferred to anhydrous glycerol and mounted on glass slides. The description (including measurements) of the three identified species (*T. communis, T. gourbaultae* and *T. longicaudata*) was performed with a contrast phase microscope Leica DMR (maximum magnification 1000 X) with drawing tube.

Most of the data of the species were collected from original descriptions using the NeMys database (www.nemys.ugent.be; Deprez *et al.*, 2004). From species of which original descriptions lacked relevant morphometric data, measurements were obtained directly from the illustrations. Measuring was carried out by a curvimeter for curvilinear (e.g. body length) and a ruler for straight measurements (e.g. body diameter); the maximum accuracy was 0.5 μm in 1000 X. We used a rule for measurement of cephalic sensilla length in order to obtain the maximum possible accuracy.

The set of morphometric features considered of taxonomic relevance was mainly based on ratios (Table 1). Ratios were

Table 1. Morphometric features defined for the analysis of the genus *Terschellingia*.

Code	Measurement	Calculation
L	Body length (μm)	
a, b, c	de Man's ratios	
Amp	Position of amphidial fovea	Distance of end to anterior border of fovea/diameter of fovea
Acbd	Size of amphidial fovea	Diameter of fovea expressed in corresponding body diameter
Nerv %	Position of nerve ring	Expressed as percentage of pharynx length
Excp %	Position of excretory–secretory pore	Expressed as percentage of pharynx length
Bar	Shape of pharyngeal bulb	Length of bulb/width of bulb
T %	Length of male reproductive system	Expressed as percentage of body length
V %	Position of vulva	Distance of end to vulva expressed as percentage of body length
G1 %	Length of anterior genital branch	Length of branch expressed as percentage of body length
G2 %	Length of posterior genital branch	Idem for posterior genital branch
Spicl	Length of spicule along arc	Length of spicule along arc/anal body diameter
Spicar	Shape of spicule	Length of spicule as curve/length of spicule as cord
c′	Tail length	Length of the tail/anal body diameter
Tcon %	Length of conical portion of the tail	Length of conical portion of the tail/total length of the tail

considered more convenient for comparisons than absolute measurements due to large variability (Fortuner, 1990) and because they were more accurately assessed from original drawings. A set of six morphological features was defined for comparison among species: presence of teeth, position/presence of cephalic setae, position/presence of cervical setae, presence of pharyngeal bulb, development of gubernaculum apophysis and shape of the tail (conical portion less or larger than 50% of total length).

The great difference in number of described specimens for each species (i.e. replicates) prevented the application of statistical comparisons and the complete evaluation of the intraspecific variability. For the species reported from the literature only the measurements correspondent to holotype were used, therefore, statistical significance among species could not be tested.

RESULTS AND DISCUSSION

The genus *Terschellingia* de Man, 1888

The genus belongs to the family Linhomoeidae (Monhysterida), a taxon of heterogeneous nature without known holapomorphy (Lorenzen, 1994). Three subfamilies are recognized: Desmolaiminae Schneider, 1926, Eleutherolaiminae Gerlach & Riemann, 1973 and Linhomoeinae Filipjev, 1922. The genus *Terschellingia* belongs to the Desmolaiminae, a subfamily mainly characterized by (modified from Schneider, 1926): cuticle smooth or faintly annulated, second and third circle of anterior sensilla close (6 + 10) or separate (6 + 6 + 4), amphidial fovea circular, buccal cavity conical and presence of cardia between pharynx and intestine.

Terschellingia, *emended diagnosis*. Desmolaiminae. Cuticle faintly striated (may appear smooth under light microscope);

amphidial fovea rounded. Buccal cavity absent or minute, cuticularized structures (i.e. teeth) rarely present. Pattern of anterior sensilla: 6 + 6 + 4; the labial sensilla only detectable in larger specimens at high magnification and they are almost in the same level that cephalic sensilla; the four cephalic sensilla setiform, submedian and non-jointed. Pharynx shape variable (with or without set off bulb). Cardia valve rather well developed. Secretory–excretory pore located posterior to the nerve ring. Male diorchic, posterior testis reflexed; spicules curved; gubernaculum with apophyses (poorly developed in one species). Female didelphic–amphidelphic (rarely monodelphic–prodelphic), ovaries outstretched, vulva at about mid-body. Tail anteriorly largely conical, posterior part cylindrical and tail tip rounded, without terminal setae.

Type species: *Terschellingia communis* de Man 1888.

Evaluation of taxonomic diagnostic characters among *Terschellingia* species

The examination of six morphological (=qualitative) and 17 morphometric features allowed to detect the characters of diagnostic value within the genus. Scatter plots of selected morphometric features were analysed in order to look for those which discriminate among groups of species (Figure 1). The features related to body size (length and de Man's ratios a and b) not only showed poor discrimination among species but also tend to show high correlation (Fortuner, 1990). In addition, the significant relationship between body dimensions and food availability (dos Santos *et al.*, 2008) suggested the lesser diagnostic value. Features related to relative position and size of amphidial fovea, length of the tail (relative to anal body diameter) and length and shape of spicules allowed discrimination of groups of species (Figure 1) and were therefore considered of diagnostic value.
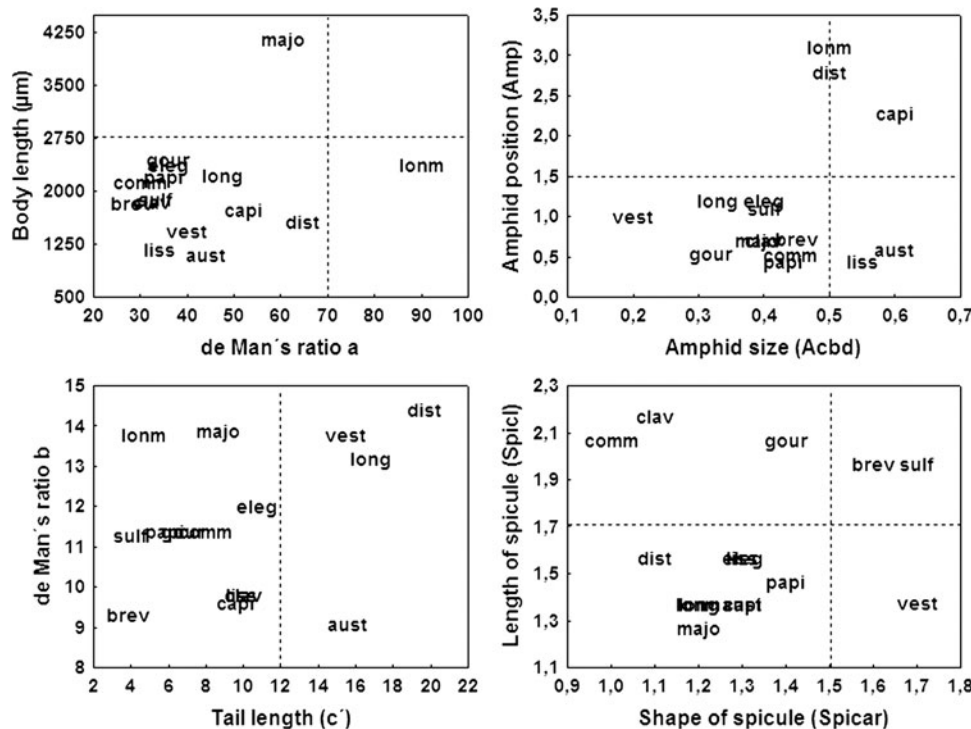

Fig. 1. Scatter plots of morphometric features of valid species of the genus *Terschellingia*. Measurements correspond to holotype. Labels defined as 3–4 first types of the specific names in Table 3 (except for *T. longisoma* = lonm). Dashed lines indicate possible cut-values for discriminating among species.

Morphological characters would be highly useful in diagnosis of species. We selected six features: presence/absence of teeth, shape of cephalic setae (papilliform and setiform), presence/position of cervical setae (absent, at level of or posterior to amphidial fovea), presence/absence of pharyngeal bulb, developed/reduced apophysis and shape of the tail (conical portion less or more than 50% of total length of tail). The number of developed ovaries appears to be a feature with taxonomic value, but it is not always described, mainly in old studies. The presence/pattern of precloacal supplements has been used extensively as a taxonomic character; although supplements are present in at least one species (*T. longicaudata*) they are hard to observe with light microscope, and thus less useful as a diagnostic character.

Discrimination of species within the genus *Terschellingia*

Within the genus, 38 nominal species have been described. However, according to our results only 15 of them are considered as valid. From the 23 non-valid species, 14 are species *inquirendae* and nine are junior synonyms of one of the valid former species (see Table 2 for explanations). Pictorial (Figure 2) and tabular (Table 3) keys summarize the main diagnostic characters for discrimination among valid species of *Terschellingia* and an explanation follows below.

The presence of small teeth in the buccal cavity is the main taxonomic feature that distinguishes *T. elegans* and *T. sulfidrica* from the other species of the genus. Both species can be differentiated from one another by shape and length of spicules (more curved and larger in *T. sulfidrica*; Figures 1 & 2), tail shape (>50% conical in *T. sulfidrica* versus >50% filiform in *T. elegans*), and the presence of a single ovary in *T. sulfidrica*. According to Gagarin & Vu-Thanh (2003), *T. elegans* closely resembles *T. supplementata* (here synonymized with *T. longicaudata*) but mainly differs from it and in extension also from *T. longicaudata* by the presence of a tooth, the shorter cephalic setae and the absence of cervical setae.

Three species of *Terschellingia* have the amphidial fovea located relatively far from the anterior body end: *T. capitata*, *T. distalamphida* and *T. longisoma* (Figures 1 & 2). *Terschellingia distalamphida* can be distinguished from the other two species by the presence of cervical setae and a filiforme tail (<50% conical and more than 12 anal diameters length). *Terschellingia capitata* is characterized by a large and muscular pharyngeal bulb (bar 3.4 versus 1.3 and 1.9 in *T. distalamphida* and *T. longisoma* respectively). *Terschellingia longisoma* is characterized by a very long and thin body (total length holotype: 2156 μm, a = 90); also it has a tail very poorly attenuated to the terminus (Gagarin & Vu-Thanh, 2006).

Terschellingia papillata is the only species of the genus with cephalic setae papilliforme. The spicules of *T. papillata* are very similar to those in *T. longicaudata* (Figure 2), but the former lacks the cervical setae and it has a larger conical portion of the tail.

On the basis of presence/absence of pharyngeal bulb, two groups of species can be distinguished: a group of ten species with clear set-off pharyngeal bulb (six of them already characterized above). The remaining four species (i.e. *T. communis, T. lissa, T. longicaudata* and *T. vestigia*)

differ from each other by a combination of characters (Table 3).

Terschellingia lissa can be differentiated from the other three *Terschellingia* species by a larger size of amphidial fovea (>0.5 cbd), conical portion of the tail is less than 50% of total length and lack of cervical setae. In addition *T. lissa* has a relatively small body length within the genus (<1000 μm).

The main differences between *T. communis* and *T. longicaudata* rest on the length of the conical portion of the tail. The length of the tail appears to be useful for differentiating most of the specimens (i.e. *T. communis* c': <12; *T. longicaudata* c': >12; Figure 1). However, we recorded in Cienfuegos Bay some unusually large male specimens of *T. longicaudata* with 'short tail' (c': 5.5 – 8.8); and some females of *T. communis* can have a relatively long tail (c': 10 – 12). The original description by de Man (1888) of *T. communis* showed a completely conical tail with pointed tip, not found in any other description of the species; the latter feature was discussed by Timm (1962) as 'problematic'. Reviewing the literature and based upon our own material, we found that the tail tip is rounded. The length of spicules appears to be an important feature for differentiating between the holotypes of *T. communis* and *T. longicaudata* (Figure 1). However, there are not clear differences between *T. communis* and *T. longicaudata* regarding spicule length on the basis of the few studies including absolute measurements: 54 – 61 μm (1.6 – 1.9 abd) versus 47 – 48 μm (1.7 abd) in Warwick *et al.* (1998); 38 – 44 μm (1.2 – 1.4 abd) versus 38 – 113 μm (1.4 – 1.9 abd) in specimens from Cienfuegos Bay. However, since Figure 1 shows a clear cut-value around 1.7 abd for holotypes, we include the spicule length as a useful character for diagnosis.

Other important, but more difficult to standardize, differences between *T. communis* and *T. longicaudata* are regarding to cervical setae, shape of cardia, and shape of spicules and gubernaculum apophysis. So far, the main difference with respect to the pattern of cervical setae is the position (at level of amphidial fovea in *T. longicaudata*; posterior to the fovea in *T. communis*). However, the number of cervical setae and their relative position in the anterior region is variable in specimens of *T. longicaudata* as has been reported by other authors (e.g. Chitwood, 1951; Timm, 1961; Wieser & Hopper, 1967; Bhadury *et al.*, 2008) and from specimens from Cienfuegos Bay. The cardia is larger, rounded and without pericardiac cells in *T. communis* versus cylindrical and rounded by intestinal cells in *T. longicaudata*; nevertheless the shape would be affected by the processes of preservation and mounting for the specimen. In relation to accessorial reproductive structures, *T. communis* has a proximal end of spicules non-cephalated and the apophysis of gubernaculum wide and cuticularized in ventral border; *T. longicaudata* has a cephalated spicule with central septum in manubrium and a narrower apophysis of the gubernaculum. However, intraspecific variability in spicule shape and gubernaculum has been observed (i.e. compare *T. communis* in Figures 2E & 3E).

The high number of junior synonymies of *T. longicaudata* (in total five; see Table 2) could be explained by: (i) high abundance and cosmopolitan distribution leading to numerous descriptions by different authors; and (ii) high morphological plasticity. There are, for instance: large variation in body habitus (de Man's ratio a ranged 29 – 40 after Timm, 1962),

Table 2. Outline of non-valid *Terschellingia* species. Abbreviations: sp. inq., species *inquirenda*; syn., synonymy. For additional abbreviations see Table 1. The numbers of specimens used in the original descriptions are indicated.

| Species	Conclusion	Comment
T. antonovi Filipjev, 1922	syn. *T. longicaudata* (by Gerlach, 1963)	8 ♂, 9 ♀, 11 j; original descriptions match very well with current diagnosis of *T. longicaudata*
T. baltica Schulz, 1932	sp. inq. (new)	1 ♂ poorly described, Timm (1962) synonymized it to *T. longicaudata*, but original description is not sufficient for determination beyond doubt
T. baylisi Allgén, 1959	sp. inq. (by Gerlach, 1963)	1 ♂ poorly described; cephalic sensilla not depicted
T. exilis Cobb, 1888	sp. inq. (new)	1 ♀ poorly described, no illustration included
T. falklandiae Allgén, 1959	sp. inq. (by Gerlach, 1963)	2 ♂ poorly described; cephalic sensilla not depicted
T. gerlachi Inglis, 1968	syn. *T. longicaudata* (new)	1 ♂, originally differentiated from *T. longicaudata* just upon length of cephalic setae and presence of precloacal supplements
T. glabricutis Platonova, 1971	sp. inq. (new)	10 ♂, 10 ♀, absence of body setae appears to be a misinterpretation due to mounting techniques used (glycerine/gelatine)
T. heteroseta Schuurmans-Stekhoven, 1950	syn. *T. longicaudata* (by Gerlach, 1963)	6 ♂; species diagnosis based on highly variable characters (length of tail, size of cephalic setae and the amphidial fovea); description matches closely *T. longicaudata*
T. heterospiculum Allgén, 1933	syn. *T. communis* (new)	1 ♂, after Gerlach (1963) syn. of *T. longicaudata*; but position of cervical setae behind amphidial fovea and the shape and length of tail did not support this statement
T. longispiculata Wieser & Hopper, 1967	syn. *T. longicaudata* (new)	The difference with *T. longicaudata* was longer spicules (122 μm), however the shape is closely similar. 2 ♂ from Cienfuegos Bay with long spicules (113 μm) underlined that this character is highly variable
T. longissimicaudata Timm, 1962	sp. inq. (new)	1 ♂; the specimen resembles *T. lissa*; the only difference lies in the 4 cervical setae behind the amphids in *T. longissimicaudata*
T. magna Timm, 1962	sp. inq. (new)	1 ♀. The synonymy of *T. communis* described by Gerlach (1955) is not valid due to differences in the amphidial fovea, cheilostome, cervical setae and tip of the tail
T. maldivensis (Gerlach, 1963) Austen, 1989	sp. inq. (new)	1 ♂, sp. inq. because a single male was described, and the only reliable diagnostic character was the absence of pharyngeal bulb
T. minima Platonova, 1971	sp. inq. (new)	6 ♂, 5 ♀, the description does not contain information on pharyngeal bulb and ovaries. Also absence of setae appears to be a misinterpretation due to employed techniques
T. monohystera Wieser & Hopper, 1967	syn. *T. communis* (new)	A pseudo-monodelphic condition is not enough to state a new species since in specimens of *T. communis* we recorded this condition (see Table 4). Other characters match to *T. communis*
T. mora Gerlach, 1956	syn. *T. communis* (new)	1 ♂, 1 ♀, specimens resemble *T. communis* by Timm (1962) but differed from the holotype in the absence of cervical setae; these may be stout and therefore hard to detect
T. parva Vitiello, 1969	syn. *T. communis* (new)	3 ♂, 2 ♀, 3 j. The diagnostic character was the short body length (649–873 μm); but the description of *T. communis* by Timm (1962) indicated a similar size (780 μm). The high plasticity of *Terschellingia* suggests the low diagnostic value of the total length of body
T. paxi Schneider, 1939	sp. inq. (new)	1 ♀; poorly described. Species *inquirenda* because of absence of male specimens, poor description and lack of discussion
T. polaris Cobb, 1914	sp. inq. (new)	1 ♂, 1 ♀, poorly described. Amphidial fovea far from anterior end, double wings in the cuticle, small size (730–800 μm). Probably those specimens did not belong to the genus *Terschellingia*
T. pontica Filipjev, 1918	sp. inq. (new)	1 ♀, description closely resembles *T. longicaudata*; however the author stated that apparently the ends of ovaries were reflexed
T. similis Allgén, 1933	sp. inq (new)	1 j, the original description of the juvenile specimen resembles closely *T. longicaudata*
T. supplementata Tchesunov, 1978	syn. *T. longicaudata* (new)	4 ♂, 3 ♀, specimens resemble *T. longicaudata*, only difference is presence of precloacal supplements, but they have been reported by Warwick *et al.* (1998), Pastor De Ward (1989) and in present study
T. viridis Timm, 1961	sp. inq. (by Timm, 1962)	1 ♀, after Timm (1962) the specimen probably belongs to another genus due to the far posterior location of the amphidial fovea (1.6 Amp), and a cardia very different from other species of *Terschellingia*
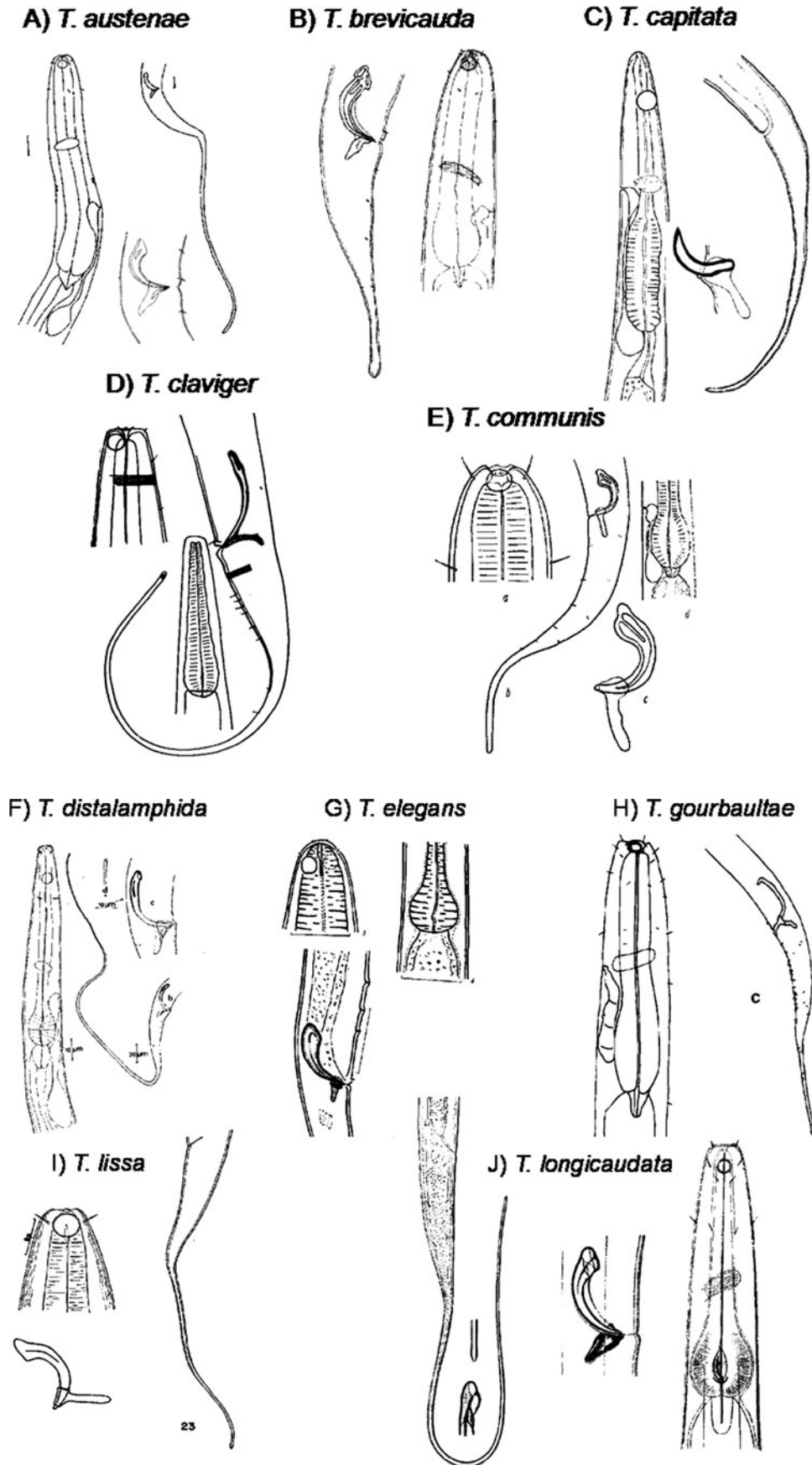
Fig. 2. Outline of 15 valid species of the genus *Terschellingia*. Drawings not to same scale and reproduced from original description (except for *T. communis*, reproduced from Gerlach, 1963).
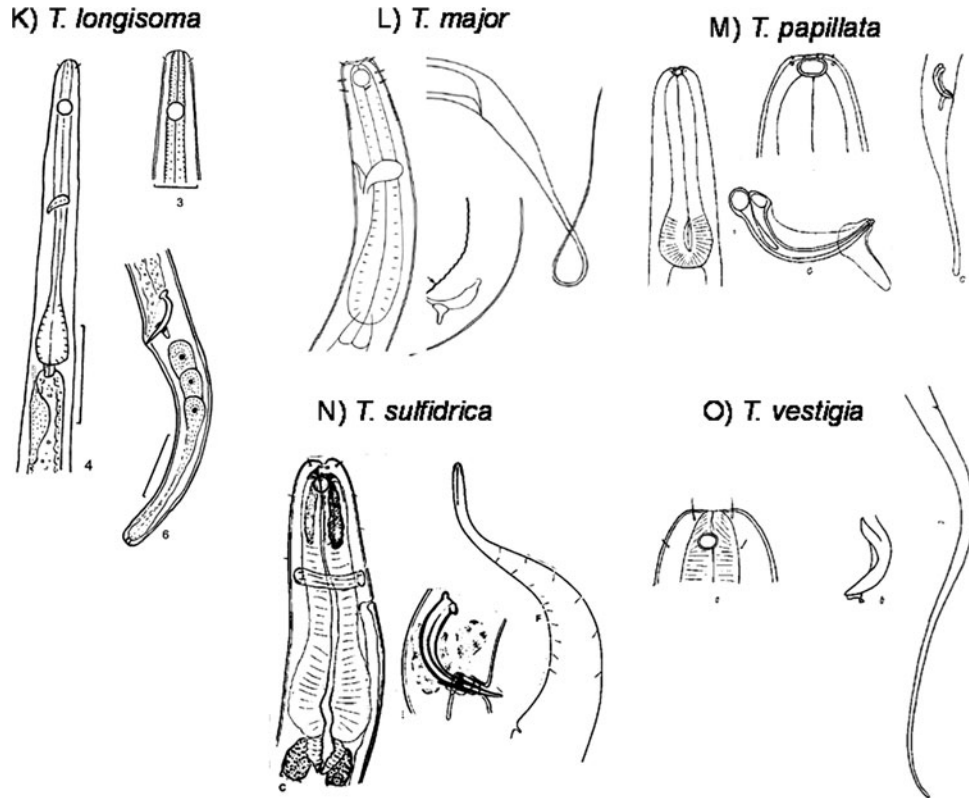
(*Continued*)

K) *T. longisoma*   L) *T. major*   M) *T. papillata*

N) *T. sulfidrica*   O) *T. vestigia*

Fig. 2. (Continued)

sexual dimorphism in size of amphidial fovea (♂ 0.3 cbd; ♀ 0.5 cbd after Wieser, 1956) and in relative position of amphidial fovea (Amp ♂ 0.5; ♀ 0.9 after Vitiello, 1969), different aspect of spicular apparatus (Vitiello, 1969) and presence or absence of precloacal supplements.

The diagnosis of *T. vestigia* is based on the presence of a reduced dorsal apophysis of the gubernaculum. However, since only one male was described, putative intraspecific variability cannot be assessed. We prefer to maintain this species as valid given that it is relatively easy to check this diagnostic character.

Five species of *Terschellingia* lack a set-off pharyngeal bulb; the table elaborated by Austen (1989) and summarizing main differences among these species has been updated by Guo & Zhang (2000) and Huang & Zhang (2005) with addition of one species respectively but without further discussion. We found that some of the proposed diagnostic characters are less useful for species differentiation. Length-related measurements (total body length, de Man's ratio a and tail length) were notably overlapping among species. The body length is not a good main diagnostic character, even for species with extreme body sizes (*T. austenae* <950 μm; *T. major* >

Table 3. Main diagnostic characters differentiating the valid species of the genus *Terschellingia* de Man 1888. Abbreviations in Table 1; additional abbreviations: ceph. setae, shape of cephalic setae; cerv. setae, presence/position of cervical setae (first somatic setae) with respect to amphidial fovea; phar. bulb, pharyngeal bulb; post., posterior. States of character: 0 = absence; 1 = presence. *No females described.

| Species	Teeth	Amp	Acbd	Ceph. setae	Cerv setae	Phar bulb	Tcon%	Spicl	Apo-physis	Post ovary
T. austenae Guo & Zhang, 2000	0	<1.5	>0.5	setiform	at level	0	<50	<1.7	developed	1
T. brevicauda Ott, 1972	0	<1.5	≤0.5	setiform	behind	0	>50	>1.7	developed	1
T. capitata Vitiello, 1969	0	>1.5	>0.5	setiform	absent	1	>50	<1.7	developed	*
T. claviger Wieser, 1956	0	<1.5	≤0.5	setiform	behind	0	<50	>1.7	developed	*
T. communis de Man, 1888	0	<1.5	≤0.5	setiform	behind	1	>50	>1.7	developed	1
T. distalamphida Juario, 1974	0	>1.5	≤0.5	setiform	behind	1	<50	<1.7	developed	1
T. elegans Gagarin & Vu-Thanh, 2003	1	<1.5	≤0.5	setiform	absent	1	<50	<1.7	developed	1
T. gourbaultae Austen, 1989	0	<1.5	≤0.5	setiform	at level	0	>50	>1.7	developed	1
T. lissa Timm, 1962	0	<1.5	>0.5	setiform	absent	1	<50	<1.7	developed	1
T. longicaudata de Man, 1906	0	<1.5	≤0.5	setiform	at level	1	<50	<1.7	developed	1
T. longisoma Gagarin & Vu-Thanh, 2006	0	>1.5	>0.5	setiform	absent	1	>50	<1.7	developed	1
T. major Huang & Zhang, 2005	0	<1.5	≤0.5	setiform	at level	0	>50	<1.7	developed	1
T. papillata Gerlach, 1955	0	<1.5	≤0.5	papilliform	absent	1	>50	<1.7	developed	1
T. sulfidrica Pastor de Ward, 1989	1	<1.5	≤0.5	setiform	behind	1	>50	>1.7	developed	0
T. vestigia Gerlach, 1963	0	<1.5	>0.5	setiform	at level	1	<50	<1.7	reduced	1
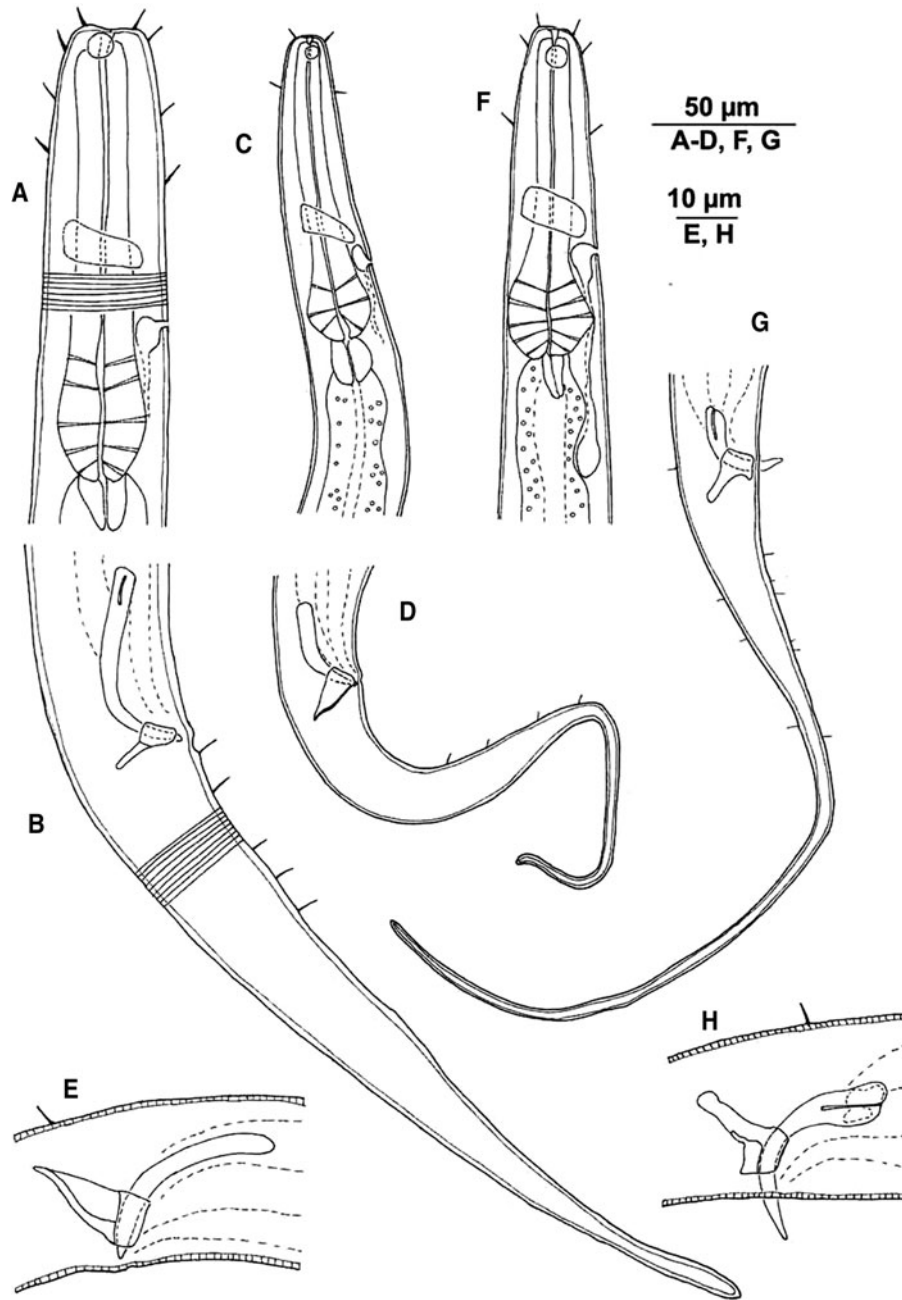
Fig. 3. Species of the genus *Terschellingia* recorded in Cienfuegos Bay, Caribbean Sea. *T. gourbaultae*: (A) anterior part; (B) tail; (G) spicular apparatus; *T. communis*: (C) anterior part; (D) tail; (E) spicular apparatus; *T. longicaudata*: (F) anterior part; (G) tail; (H) spicular apparatus.

3436 μm) since in some monhysterids, body size is influenced by environmental factors such as food availability (dos Santos *et al.*, 2008). In addition, the length of spicules in five specimens of *T. gourbaultae* from Cienfuegos Bay was shorter ($59–66$ μm) than specimens from the Tamar Estuary, England reported by Austen (1989) ($80–88$ μm), suggesting high variability in this character.

Two species (*T. austenae* and *T. claviger*) have less than 50% of total tail length conical, with the distal third portion filiforme. These species can be differentiated from each other by the relative size of amphidial fovea and the position of cervical setae; in addition, the length and shape of spicules and apophysis of gubernaculum would be useful diagnostic characters (Table 3).

Differences among *T. brevicauda*, *T. gourbaultae* and *T. major* are more subtle on the basis of taxonomic characters currently proposed. Austen (1989) pointed out that the shorter tail in *T. brevicauda* (c' $3.5–4.3$) allows its differentiation from other species; the tail of *T. gourbaultae* is effectively larger (c': $5.5–8.0$ after Austen; $5.1–9.4$ in specimens from Cienfuegos Bay). An additional feature, maybe less variable (and so more useful), is the position of the cervical setae (Table 3). The spicular apparatus is different in appearance (Figure 2) and in absolute measures (spicule length: $47–53$ μm for *T. brevicauda* versus $80–88$ μm for *T. gourbaultae*), but other morphometric measures such as relative length and shape of spicules failed to show differences (Figure 1). The unique record of *T. brevicauda* in North

Carolina, USA (Ott, 1972) does not allow to assess possible intraspecific variability.

Two conspicuous features allow to identify specimens belonging to *T. major*; i.e. large body size (>3000 μm), and presence of precloacal supplements (>30). The latter character has been recorded in *T. sulfidrica*; but in specimens described from several geographical regions (e.g. *T. longicaudata*) the presence and number of supplements appeared variable. On the basis of the proposed differential diagnosis for species of *Terschellingia* (Table 3) the discrimination between *T. gourbaultae* and *T. major* would become problematic if high intraspecific variability exists in the latter species. The differences in relative length of spicules between holotypes suggest the usefulness of this feature for discrimination (Figure 1).

Description of *Terschellingia* species from Cienfuegos Bay

For most of the features measured on specimens from Cienfuegos Bay they were relatively different from the data for the holotypes. This suggests a continuum in the size of body structures and a high morphological plasticity in the three species analysed. The high morphological plasticity in some nematode genera with numerical dominance (e.g. *Daptonema*, *Sabatieria* and *Terschellingia*) could adjust in a more general model relating morphological plasticity and ecological success (Hollander, 2008 and references herein). It should be interesting to assess the level of intraspecific variability (i.e. morphological plasticity) in rarer species of nematodes; and also to test for relationships between morphological plasticity and ecological dominance in free-living marine nematodes.

The morphometric data are presented in Table 4 and illustrations in Figure 3. We only include in this section those features with some variation compared to older descriptions of the species.

TERSCHELLINGIA COMMUNIS DE MAN, 1888

Material measured: 3 ♂; 4 ♀; 2 j

Remarks. Body length of juveniles: 1000–1125 μm; differentiation between juvenile stages could not be determined beyond doubt. The degree of development of ovaries was variable either anterior ovary more developed than posterior one, reverse or equally developed. The shape of the spicules and gubernaculum apophyses shows variability in some details among the descriptions by de Man (1888), Timm (1962), Gerlach (1963) and our observations. A conspicuous feature is presence of a developed cardia between pharynx and intestine (however, the shape sometimes appears to be affected by preservation or physiological condition of the specimen). This character has not been pointed out by the earlier descriptions of the species but could be a useful character for identification.

TERSCHELLINGIA GOURBAULTAE AUSTEN 1989

Material measured: 5 ♂; 3 ♀; 4 j.

Remarks. *T. gourbaultae* has been described relatively recently and was recorded only in British and French estuaries. Body length of juveniles: 767–2125 μm; differentiation

Table 4. Morphometric data (minimum–maximum) for males and females of Cuban specimens of the genus *Terschellingia*. Abbreviations in Table 1; additional abbreviations: amph Ø, diameter of amphidial fovea; amp.dist, distance of amphidial fovea to anterior end; gubern., gubernaculum; spic.arc and spic.cor, length of spicules as arc and cord respectively.

Feature	*T. communis*		*T. gourbaultae*		*T. longicaudata*	
	3 ♂	4 ♀	5 ♂	5 ♀	10 ♂	5 ♀
Body length (μm)	1313–1400	1125–2000	1563–2063	1563–2500	1367–2438	1267–1750
A	31.1–32.8	22.0–38.9	25.9–31.2	21.6–33.5	25.9–44.9	27.8–45.0
b	12.4–13.8	12.0–14.4	9.6–11.5	9.6–3.3	11.5–13.9	12.0–14.7
c	5.0–5.6	4.5–8.9	5.2–7.8	4.6–6.0	2.2–7.8	2.5–3.5
Cephalic setae (μm)	4–6	4–6	4–8	4–9	2–7	5–8
Amph Ø (μm)	4–5	4–5	9–12	7–10	7–9	5–10
Acbd	0.3	0.2–0.3	0.3	0.2–0.3	0.3–0.5	0.3–0.5
Amp.dist (μm)	4–5	2–5	5–10	4–12	3–8	2–6
Amp	1.0	0.5–1.3	0.5–1.0	0.6–1.6	0.4–1.0	0.3–0.9
Nerv %	55–65	47–69	34–57	39–54	40–61	44–58
Excp %	78–83	69–75	50–79	61–71	57–76	65–68
Tail length (μm)	233–275	225–263	233–333	313–433	313–488	367–688
ć	8.0–8.9	6.1–11.9	5.1–6.5	6.5–9.4	5.5–18.0	15.5–23.1
Tcon %	55–73	50–72	58–79	44–71	17–62	18–42
Testis length (μm)	733–767		938–1267		533–1313	
T %	55–65		47–68		39–51	
Spic.arc (μm)	38–44		75–88		38–113	
Spicl	1.2–1.4		1.4–1.9		1.4–1.9	
Spic.cor (μm)	31–33		59–66		25–86	
Spicar	1.2–1.3		1.1–1.5		1.4–1.6	
Gubern. length (μm)	10–11		11–13		5–21	
Apophysis length (μm)	14–18		17–24		13–29	
G1 %		5–19		7–31		5–14
G2 %		5–15		5–29		5–14
V %		44–62		45–48		38–47

between juvenile stages could not be determined beyond doubt. The pattern of cervical setae described for holotype (i.e. three circles of cervical setae each one with eight setae) was common; but presence of only a single circle also occurred as well as a reduction in number of setae per circle (to 4–6). The specimens from Cienfuegos Bay closely resemble the holotype, except for the proximal end of the spicule. This suggests that morphological details of accessory reproductive structures have to be interpreted with caution since they can vary among populations.

TERSCHELLINGIA LONGICAUDATA DE MAN 1906

Material measured: 10 ♂, 5 ♀, 6 j.

Remarks. The specimens of *T. longicaudata* collected at Cienfuegos Bay closely resemble the original description of the holotype. Total length of juveniles: 733–1188 μm. Main differences are with regard to the pattern of cervical setae and shorter length of cephalic setae in juveniles. The intestine is often filled with conspicuous green granules all over its length. Precloacal supplements present, visible as small pits (6–7 in number) in large specimens using light microscopy; in smaller specimens only visible by scanning electron microscopy (results not shown). Two large-sized male specimens (4280 and 4800 μm) of *Terschellingia* were described by Murphy (1965) who suggested that they belong to *T. communis*. However, those specimens were similar to *T. longicaudata* in the habitus, pattern of anterior sensilla, and shape and size of spicules; the main difference was the length of the tail (c′: 7). We also collected two large males (2375 and 2438 μm) with tail unusually short (c′:5.5 and 8.6) and large spicules (113 μm both specimens). A recent study (Bhadury *et al.*, 2008), combining morphological and molecular tools points to the presence of cryptic species of *T. longicaudata*. In our study, the exploration of ultrastructure-based characters by SEM (as suggested by Bhadury *et al.*, 2008) did not add any additional character of diagnostic value for discrimination among putatively cryptic species of *T. longicaudata*. Therefore, future refining of molecular techniques on this species (in combination with morphological analysis) is the most promising way forward for dealing with this taxonomically problematic species.

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