Central American and Caribbean species of horsehair worms (Nematomorpha), with the description of three new species

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Abstract
We describe new records of horsehair worms (Nematomorpha) from Central America and islands of the Caribbean Sea, provide updated descriptions including scanning electron microscopy and include a list of all species known from this region. Three new species are described: Pseudochordodes bulbareolatus from Mexico and Guatemala, Neochordodes chordodides from Costa Rica and Belize, and Chordodes polytuberculatus from Costa Rica. From Belize and Trinidad (Gordius robustus), nematomorphs are reported for the first time. Further records include species known from North America (Pseudochordodes manteri, Neochordodes occidentalis) or from South America (Pseudochordodes meridionalis). The actual number of species known from continental Central America is 22 species from five genera, and from Caribbean islands five species from three genera are known.

Keywords: Caribbean, Central America, horsehair worms, Nematomorpha

Introduction
While the nematomorph (horsehair worms) fauna of North America (Schmidt-Rhaesa et al. 2003) and southern South America (e.g. de Miralles and de Villalobos 1993) have been investigated intensively, reports from northern South America and Central America are only fragmentary (see Table I). A better knowledge would, however, be of interest in order to compare the fauna of both continents and to understand better distribution patterns of American nematomorphs. For example, species of the genera Neochordodes and Pseudochordodes occur in South America and in the south-western USA. This might reflect a northward migration of South American species after the connection of the South and North American continents. Migrations in the other direction are not so obvious, but might be discussed for the genus Paragordius, from which one species, P. varius, occurs in both North and South America.

In this paper, we consider continental Central America from Mexico to Panama and all islands in the Caribbean Sea. Twenty species of freshwater Nematomorpha (Gordiida) in six genera have previously been reported from this region (Table I). Sixteen species from
Table I. Reports of nematomorph species from Central America.

| Country   | Species                                           | Locality, if specified                        | Author                  |
|-----------|---------------------------------------------------|-----------------------------------------------|-------------------------|
| Belize    | *Neochordodes chordoidides*                       | Cayo                                          | This investigation      |
| Costa Rica| *Chordodes polytuberculatus*                      | Rio Tempisqueito                               | This investigation      |
|           | *Neochordodes chordoidides*                       | Santa Rosa                                    | Heinze 1935             |
|           | *Paragordius diversolobatus* (Heinze, 1935)       |                                               |                         |
|           | *Paragordius varius* (Leidy, 1851)                |                                               |                         |
| Cuba      | *Chordodes cubanensis* (Montgomery, 1898)         |                                               |                         |
|           | *Parachordodes capitosulcatus* (Montgomery, 1898) |                                               |                         |
| Hispaniola| *Parachordodes ciferrii* (Sciacchitano, 1932)     | Haina (W of Santo Domingo), Dominican Republic| Sciacchitano 1932       |
| Guatemala | *Chordodes gestri* (Camerano, 1904)               | Quezaltenango                                 | Camerano 1904           |
|           | *Gordius guatemalensis* (Linstow, 1902)           | Chiacam                                       | Linstow 1902            |
|           | *Gordius platycephalus* (Montgomery, 1898)        |                                               | Montgomery 1898         |
|           | *Pseudochordodes bulbareolatus*                   |                                               | This investigation      |
|           | *Pseudochordodes guatemalensis* de Miralles, de Villalobos and Rodriguez, 1997 |                                               |                         |
| Honduras  | *Chordodes aurantiacus* (Linstow, 1906)           |                                               |                         |
| Jamaica   | ? *Gordius platyura* (Baird, 1853)                | Gordonstown                                   | Baird 1853              |
| Mexico    | *Chordodes cameranonis* (Montgomery, 1900)        | Mazatlán                                      | Montgomery 1900         |
|           | *Neochordodes nietoi* (Caballero, 1936)           | Estado de México                              | Caballero 1936          |
|           | *Gordius californicus* (Camerano, 1915)           | Guanajuato, Mexico City                       | Camerano 1915           |
|           | *Gordius robustus* (Leidy, 1851)                  | “Distrito Federal”                            | Caballero 1936          |
|           | *Gordius subspiralis* Diesing, 1861               | Nuevo León, Tamaulipas                        | This investigation      |
|           | *Gordius villoti* Rosa, 1882                      | Guanajuato                                    | Camerano 1989           |
|           | *Neochordodes occidentalis* (Montgomery, 1898)    | Mexico-City, Real del Monte, Hidalgo, Guanajuato | Caballero 1936          |
|           | *Paragordius varius* (Leidy, 1851)                |                                               |                         |
|           | *Pseudochordodes bulbareolatus*                   | Veracruz                                      | This investigation      |
|           | *Pseudochordodes dugesi* (Camerano, 1898)         | Altoyac, Vera-Cruz                            | Camerano 1898           |
|           | *Pseudochordodes griffini* (Camerano, 1898)       | Altoyac, Vera-Cruz                            | Camerano 1898           |
|           | *Pseudochordodes manteri* Carvalho, 1942          | Veracruz                                      | This investigation      |
|           | *Pseudochordodes meridionalis* Carvalho and Feio, 1950 | Tamaulipas                                  |                         |
| Panama    | *Chordodes cameranonis* (Montgomery, 1900)        |                                               | Montgomery 1900         |
| Trinidad  | *Gordius robustus* (Leidy, 1851)                  | Mt Samana                                     | This investigation      |

*The worm described by Baird (1853) as *Gordius platyura* was obviously without label, but originated from the collection of Hans Sloane and did therefore likely originate from his journey to Jamaica. bMontgomery (1900) described *Chordodes cameranonis* from a specimen in the Cope collection which he found labelled as “Mazatlán (Mexico) or Panama”.*
five genera are known from the continental region and four species from three genera from islands (Cuba, Jamaica and Hispaniola). Most reports are singular findings, only from Mexico have there been more or less summarizing reports by Camerano (1898) and Caballero (1936). With the exception of the description of *Pseudochordodes guatemalensis* by de Miralles et al. (1997), no report is younger than 1936 or includes documentations of cuticular structures other than by drawings. Now, scanning electron microscopy (SEM), best in combination with light microscopical investigations of cuticular samples, has become the standard technique for the investigation of nematomorphs, because fine structural details can be documented optimally in this way.

We report here new records from Mexico, Belize, Costa Rica, Jamaica, and Trinidad, including the description of three new species, and document these by SEM and light microscopy.

**Materials and methods**

All specimens investigated were preserved in ethanol (70–90%). Specimens were prepared for SEM and some additionally for light microscopy (LM). For SEM, parts of the central region of the body (about 0.5 mm in length) and in some specimens the posterior end were dehydrated in an increasing ethanol series, transferred to liquid CO₂ and dried in a critical point dryer (Balzers CPD 030), coated with gold for 300 s at 30 mA in a sputter coater (Balzers SCD 005), and observed at 15 kV with a Hitachi SEM 450 scanning electron microscope. For LM, complete parts of the body mid-region (about 0.5 mm) were cut longitudinally and internal tissue was removed. The cuticle was mounted in glycerine jelly for permanent storage.

**Results and discussion**

*Pseudochordodes bulbareolatus* nov. sp.

(Figure 1)

Holotype: Mexico, Veracruz, Sumidero de Tlaltenango (1.4 km N Tlaquilpa), 2330 m, one male, coll. 23 March 1995 by C. Savas (Museum für Naturkunde, Berlin, Germany, accession number ZMB Entozoa 7377). Paratype: one male, collection data as holotype (Texas Memorial Museum, Austin, USA, no accession number). Further record: Guatemala (not further specified), one female (Natural History Museum, London, accession number 83.5.24).

**Description**

The two males measure 16 (holotype) and 19.5 (paratype) cm in length and 0.8 and 1.5 mm in diameter, respectively. Their anterior end is white and blends into the medium brown colour of the body. A dark collar, which is present in many other nematomorph species, is not present. There are dark brown patches distributed over the whole cuticle which contrast with the medium brown colour of the cuticle (“leopard pattern”; Schmidt-Rhaesa et al. 2003).

The posterior end of the two males is round, without tail lobes. The cloacal opening is oval and surrounded by short, unbranched spines. There are some short bristles on the ventral side of the posterior end around the cloacal opening.
Figure 1. *Pseudochondodes bulbareolatus* n. sp. (A) Light microscopical preparation of body cuticle showing bulging clusters of areoles; (B–D) SEM overview (B, C) and detail (D) of bulging areolar clusters with areoles in a megareolar pattern in the centre.
The cuticle is structured by rounded to polygonal areoles which are separated by narrow interareolar grooves with short bristles (Figure 1A–D). The surface of these areoles is rough. Among these areoles, few form the megareolar pattern (see Schmidt-Rhaesa 2001), in which two areoles adjoin each other along one side and enclose a short tubercle between them (Figure 1A–D). Rarely, isolated tubercles can also be found in the interareolar grooves. Over the whole cuticle, some regions containing 7–12 areoles, are elevated (Figure 1A–D). In the centre of these elevations are large areoles forming a megareolar pattern. They are surrounded by a varying number of “simple” areoles.

Comments

The presence of elevated regions composed of several areoles is unique and justifies the description of a new species. The characterization of the genus *Pseudochordodes* is as nematomorphs with an undivided male posterior end, in which the cuticle contains two types of areoles (Carvalho 1942). In some species, this is clearly evident (e.g. *P. gordioides*, see Schmidt-Rhaesa et al. 2003), but in others, the recognition of two types of areole is more difficult and species are sometimes assigned to *Neochordodes*, in which only one type of areole is present (Carvalho 1942). In *Pseudochordodes bulbareolatus*, areoles in the bulging clusters are slightly larger than the surrounding ones and occur in a different pattern, which justifies the placement within the genus *Pseudochordodes*.

*Pseudochordodes manteri* Carvalho, 1942

(Figure 2A–C)

*Pseudochordodes manteri* Carvalho 1942: 217–218.

Material studied

Newly reported male from Veracruz, Mexico; LM and SEM.

Description

The male specimen is 19 cm long and has a diameter of 1.2 mm. The body colour is a medium to dark brown. Abundant elevated areoles (see below) create the impression of a finely spotted cuticle. The anterior end is white, a dark collar is not present. The posterior end was lost during preparation and therefore could not be investigated.

The cuticle contains two types of areole (Figure 2A). There are numerous small areoles with varying shape. Usually, they are rounded, but they can also appear in different polygonal shapes. The surface of these areoles is rough. Areoles are separated by narrow interareolar grooves with short bristles (Figure 2B). Few areoles are clustered in the megareolar pattern (Figure 2A; see *P. bulbareolatus*). Among this first type of areole are abundant larger and elevated areoles (Figure 2A–C). They mostly occur in clusters of two. The two neighbouring areoles are partly fused, although the border between them is always visible (Figure 2B, C). Corresponding to the megareolar pattern, these two areoles enclose a central tubercle, which is very short and occurs, due to the partial fusion of the two areoles, in the centre of the suture separating the areoles (Figure 2B, C). The surface of these large areoles is smooth. They are slightly darker in colour than the areoles of the first type. Elevated areoles can also occur individually on the cuticle (Figure 2A), rarely these
individual areoles adjoin the clustered elevated areoles. Very rarely, a clustering of three elevated areoles, surrounding a total of two tubercles, could be observed.

Comments

This specimen of *P. manteri* from Mexico corresponds in all details with the description of a North American specimen (Carvalho 1942). The only difference is that what is termed here a short tubercle (on top of the elevated areoles) was considered to be a pore by Carvalho. This is probably due to differences between light and scanning electron microscopy,
because the short tubercle which is visible with SEM can easily be interpreted as a pore in light microscopical investigation (compare Figure 2A and C). The disjunct reports of this species in Nebraska (USA) and Mexico make it likely that it has a broader distribution than could previously be estimated from the isolated occurrence in Nebraska alone.

**Distribution**

*New record.* **Mexico:** Veracruz, Cueva de Xometta (800 m E Atlalhuilco), 1800 m, one male, coll. 25 March 1995 by P. Sprouse (Texas Memorial Museum, Austin, USA, no accession number).

*Further distribution.* War Bonnet Canyon, Nebraska, USA (Carvalho 1942).

**Pseudochordodes meridionalis** Carvalho and Feio, 1950

(Figure 3)

*Pseudochordodes meridionalis* Carvalho and Feio 1950: 202–203.

*Neochordodes meridionalis:* de Miralles and de Villalobos 1996: 147.

**Material studied**

Newly reported male from Tamanlipas, Mexico; LM and SEM.

**Description**

The newly reported male is 11.5 cm long and has a diameter of 0.4 mm. The body colour is dark brown. Darker, elevated areoles (see below) create a finely spotted pattern of the cuticle. The anterior tip is white, a dark collar is not present. The posterior end is round (Figure 3E). The cloacal opening is slit-like and surrounded by slender bristles. Further bristles are distributed in the ventral region around the cloacal opening (Figure 3E). The ventral face of the posterior end is structured by flat and homogeneous areoles, while the usual pattern of the cuticle starts at the ventrolateral margin of the posterior end. In the lateral and dorsal regions of the posterior end are numerous short tubercles which are lacking in the remaining body.

The cuticle contains two types of areole (Figure 3A–C). The first type is flat and polygonal. Areoles are separated by narrow interareolar grooves with short bristles. Very abundant are larger, darker and elevated areoles which occur either solitary or in clusters (Figure 3A–C). Similar to *P. manteri*, these large areoles often cluster in the megareolar pattern. The neighbouring areoles may fuse almost completely or remain separated by a fine suture or deeper groove (Figure 3B). The surface of the large areoles is smooth. When clusters occur, they are a combination of large areoles in the megareolar pattern and those without this pattern. Clusters may include seven and more areoles. In the ventral midline, there is a loose band of individual large elevated areoles (Figure 3C, D). A megareolar pattern does not occur in this region.

**Comments**

The newly reported specimen corresponds with the description of *P. meridionalis* by Carvalho and Feio (1950). It resembles *P. manteri* in some respects, but individual large
elevated areoles are much more abundant in *P. meridionalis*, and the clusters are larger. De Miralles and de Villalobos (1996) concluded after a reinvestigation that only one type of areole is present in *P. meridionalis* which must therefore belong to the genus *Neochordodes*. However, we observe two kinds of areole, corresponding to the observation of a second type of “vestigial” areole in the first description (Carvalho and Feio 1950) and to such a second type in the figures of de Miralles (1976). Therefore, the specimens investigated by de Miralles and de Villalobos (1996) might represent a different species, although they were sampled, at least in part, in the region where the holotype was collected.

Figure 3. *Pseudochordodes meridionalis*. Light microscopical (A) and SEM (B) image of body cuticle showing clusters of dark and elevated areoles. (C, D). Distribution of areoles along the ventral midline, which is marked by smaller dark areoles (arrows in C). Midline runs from top to bottom in (C) and from left to right in (D). (E) Ventral view of male posterior end, white arrow indicates position of the cloacal opening. The larger white structure is pollution.
**Distribution**

*New record. Mexico:* Tamanlipas, Sótano de San Marcos, one male, coll. 21 March 1998 by P. Sprouse (Texas Memorial Museum, Austin, USA, no accession number).

*Further distribution.* Argentina (Carvalaho and Feio 1950; de Miralles 1976; de Miralles and de Villalobos 1996).

**Neochordodes chordoides** nov. sp.

(Figure 4)

Holotype: Costa Rica, Santa Rosa Field Station, one female, from unidentified cockroach (Blattodea), coll. 16 January 2002 by B. Hanelt (Museum für Naturkunde, Berlin, Germany, accession number ZMB 7382). Paratype (allotype): one male from same location and host as holotype (Museum für Naturkunde, Berlin, Germany, accession number ZMB 7383).

**Description**

The body colour of males is dark brown, females are medium brown. The anterior tip is white, but a following dark collar is absent. The females from Costa Rica measure 55 and 70 mm, the Costa Rica male is 70 mm long, the Belize male 95 mm. Diameters are 0.3 mm (Belize male), 0.4 mm (Costa Rica male), 0.5 and 0.7 mm (Costa Rica females). The posterior end of males is without tail lobes (Figure 4A). In the male from Costa Rica, there is a longitudinal fold on the ventral side anterior of the cloacal opening (Figure 4B), which is probably an artifact. On the ventral surface, around the cloacal opening, are slender, unbranched cuticular spines (Figure 4D).

The cuticle contains, depending on definitions, one or two types of areole (see comments). All areoles are distinctly elevated and have fine bristles on their apical surface (Figure 4C). The size can vary (Figure 4C, E). Several areoles additionally have thicker projections (tubercles). These tubercles are sometimes in the centre of the areole, but are often displaced towards the margin (Figure 4C, E).

**Comments**

The assignment of this new species is not unequivocal. Areoles with apical processes are typical for the genus *Chordodes* (see Schmidt-Rhaesa 2001), but there the processes are often longer or more numerous and are restricted to fewer areoles (the crowned areoles). In some species of *Chordodes*, areoles other than the crowned areoles carry fine apical processes (see e.g. *Chordodes queenslandi* and *C. brevipilus* in Schmidt-Rhaesa 2002). However, as there is no *Chordodes* species without crowned areoles and as crowned areoles are lacking in this new species, an assignment to *Chordodes* is not convincing.

We place this species in the genus *Neochordodes*, because it has one type of areole. Strictly, there are two types, one without and one with tubercles. Two types of areole would support a placement in the genus *Pseudochordodes*, but there is no report of tubercle areoles in *Pseudochordodes*. The difference in areolar types refers to the areolar shape or size, which does not apply in the new specimen.
Distribution

Belize: Cayo, Cebada Cave, one male, coll. 9 May 1986 by G. Veni and C. Zone (Museum für Naturkunde, Berlin, Germany, accession number ZMB Entozoa 7384). Costa Rica: Santa Rosa Field Station, two females (one of them holotype) and one male (allotype), all from one unidentified cockroach (Blattodea), coll. 16 January 2002 by B. Hanelt [Museum für Naturkunde, Berlin, Germany, accession number ZMB 7382 (holotype) and 7383 (allotype), further female in collection of A. Schmidt-Rhaesa, SR 726].

Figure 4. Neochordodes chordodides n. sp. (A) Ventral view of male posterior end from Belize specimen, arrow indicates position of cloacal opening (not visible). (B) Longitudinal fold (arrow) on ventral side of posterior end of the male from Costa Rica. (C) Cuticle in midbody of holotype, some areoles with tubercles (arrows). (D) Long and slender bristles from the ventral side of the male posterior end in the region around the cloacal opening. (E) Light microscopical image of the cuticle. Apical bristles are hardly visible.
Neochordodes occidentalis (Montgomery, 1898)
(Figure 2D, E)

Chordodes occidentalis Montgomery 1898: 50–52.
Neochordodes occidentalis: Poinar and Doelman 1974: 328–330.
Pseudochordodes occidentalis: de Miralles and de Villalobos 1993: 108.

Material studied
Two newly reported males from Mammoth Tusk Cave and Veracruz, Mexico; LM and SEM.

Description
The two male specimens from Mexico measure 16 and 18 cm in length, and 0.9 and 1.1 mm in diameter, respectively. The body colour is a medium brown, the anterior tip is white, a dark collar is not present. The posterior end of the males is round, without tail lobes. The cloacal opening is surrounded by short spines, further, very short spines are distributed in the ventral region around the cloacal opening.

The cuticle contains one type of areole, that varies in shape from rounded to polygonal (Figure 2D, E). The interareolar grooves are very narrow and contain only few bristles (Figure 2E). A megareolar pattern (see P. bulbareolatus) is not clearly visible. In some instances, areoles approach very close, but tubercles could not be observed.

Comments
Previous descriptions of N. occidentalis are heterogeneous (see Schmidt-Rhaesa et al. 2003). It is not quite clear, whether this indicates that N. occidentalis is a polymorphic species or whether more than one species are summarized under this name. However, the newly reported specimens from Mexico correspond in the cuticular ultrastructure to the holotype from California, USA (Montgomery 1898; see also reinvestigation by Schmidt-Rhaesa et al. 2003). Due to the presence of a single type of areole (which is very variable), we follow here the assignment to the genus Neochordodes.

Distribution
New records. Mexico: Mammoth Tusk Cave, San Francisco, one male, coll. 5 January 1976 by D. Lowery and P. Strickland; Veracruz, Sumidero de Tlaltenango (1.4 km N Tlaquilpa), 2330 m, one male, coll. 23 March 1995 by C. Savas (both Texas Memorial Museum, Austin, USA, no accession number).

Further distribution. USA (California, Montana, Nebraska, Nevada, Texas, Utah, Washington, Wyoming; see Schmidt-Rhaesa et al. 2003).

Chordodes polytuberculatus nov. sp.
(Figure 5)

Holotype: female from Costa Rica, Rio Tempisquito, in sandy substratum, coll. 25 February 1999 by B. Hanelt (Museum für Naturkunde, Berlin, Germany, accession number ZMB 7385).
The body colour is light yellow with brown spots. The anterior end is tapering, the posterior end with the terminal cloacal opening is slightly bulging. The specimen measures 29.5 cm in length.

The cuticle contains three types of areoles. The first is relatively flat, with a warty surface (Figure 5B). The second type is very slender and elevated (Figure 5A, B). It is distributed over the whole cuticle and surrounds areoles of the third type (Figure 5A, B). This third type are the so-called crowned areoles which have a base and an apical “crown” of filaments (Figure 5A, B). The apical filaments are numerous, slender and moderately long (Figure 5B). Crowned areoles and areoles of the second type form clusters which are distributed over the whole cuticle without regional differences (Figure 5A). The number of
the second type of areole in these clusters varies around 20. The number of crowned areoles could not be detected, but it seems likely that they are two, as in most other *Chordodes* species.

**Comments**

The very slender form of the second type of areole and their distribution in great abundance over the whole cuticle is not known for other *Chordodes* species, neither from South or Central America nor from other regions and justifies the description of a new species.

*Paragordius varius* Leidy, 1851

*Paragordius varius* is a species with wide distribution in North and South America and has already been reported from Mexico and Costa Rica (see Table I).

**Distribution**

*New records.* **Mexico:** Sótano de la Joya de Salas, Tamps, one female, coll. 6 March 1965 by D. McKenzie et al.; El Sótano de Jerbaritz (22.5 km N Ciudad Valles), San Luis Potosí, one male, coll. 9 January 1970 by S. Wiley (both Texas Memorial Museum, Austin, USA, no accession number).

*Paragordius* sp

One male of *Paragordius* was found in the Botanical Garden of Gordonstown, Jamaica (Natural History Museum, London, accession number 89.4.15.1). Males of *Paragordius* can easily be recognized by their extremely long tail lobes (distinctly longer than body diameter), but the cuticular structures in this specimen from Jamaica were not preserved well enough to allow a further determination.

*Gordius robustus* Leidy, 1851

The genus *Gordius* is the only genus of freshwater nematomorphs which contains species that lack any cuticular structure but have a smooth cuticle. Despite this poverty of taxonomically expressive characters, surprisingly many species are described. However, Schmidt-Rhaesa et al. (2003) regarded several such species (from North America) as synonymous to *Gordius robustus*. This could also account for the Central American and Caribbean species of *Gordius* which have been reported to date: *G. platyura* from Jamaica (Baird 1853), *G. californicus* (Camerano 1915) and *G. subspiralis* from Mexico (Camerano 1898). *Gordius villoti* is a European species and it is likely that the specimens reported by Caballero (1936) from Mexico (see Table I) also belong to *G. robustus*.

**Distribution**

*New records.* **Mexico:** Nuevo León, Pozo del Primero de Septiembre, one male, coll. 25 July 2000 by C. Savvas; Cueva de Oyamel, Conrado Castillo, Tamaulipas, one female, coll.
Conclusion

The species of horsehair worms reported here raise the number of species described from Central America and islands in the Caribbean Sea to 26. First records are provided for one continental country (Belize) and one island (Trinidad). The records confirm that *Paragordius varius* is distributed over the whole of America, with Central American records in Mexico and Costa Rica. This is also true for the North American species *Gordius robustus*, which occurs in Mexico, Costa Rica and Trinidad and has also been reported from Argentina (e.g. de Miralles 1976). Two species from Mexico, *Pseudochordodes manteri* and *Neochordodes occidentalis*, are also reported in North America and one Mexican species, *Pseudochordodes meridionalis*, is elsewhere known from South America.

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