

Revision of the genus *Chordodes* (Gordiida, Nematomorpha) from Africa—III: ultrastructural redescription of *Chordodes capensis* Camerano, 1895, *C. clavatus* Linstow, 1906, *C. digitatus* Linstow, 1901, *C. tuberculatus* Linstow, 1901, and reinterpretation of *C. ibembensis* Sciacchitano, 1958 and *C. uncinatus* Sciacchitano, 1958

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Abstract

Six species of the genus *Chordodes* from Africa are investigated in order to certify the taxonomic descriptions and verify the species status. Scanning electron microscopy demonstrates that the males of *Chordodes clavatus* and *C. digitatus* have five types of areoles, while the females of *C. clavatus* have seven areolar types and the females of *C. digitatus* have six areolar types. *Chordodes capensis* also shows this sexual dimorphism, as males have four types of areoles and females have five areolar types. The cuticle of *Chordodes tuberculatus* contains three areolar types. *Chordodes ibembensis* and *C. uncinatus* are synonymized with *C. clavatus*, because no differences can be detected that justify these species as valid.

Keywords: Africa, *Chordodes*, *Nematomorpha*, scanning electron microscopy

Introduction

The nematomorph genus *Chordodes* occurs, with few exceptions, only in tropical and subtropical regions. Taxon sampling has to be considered incomplete, making it possible that the approximately 90 species described to date represent only a fraction of the complete diversity of this genus. Many species' descriptions do not comply with current standards for taxonomic descriptions. Recent investigations have shown that careful

investigations of cuticular structures in different regions of the worm (e.g. dorsal–ventral–lateral), and careful documentation by scanning electron microscopy (SEM), are essential in gaining a more reliable picture of *Chordodes* diversity.

A review of African *Chordodes* species has commenced, and two parts have been published to date (Zanca et al. 2006a, 2006b); this is the third publication in this series, reporting the investigation of a further six *Chordodes* species. For the terminology of cuticular structures (areoles), see Zanca et al. (2006a, 2006b).

Material and methods

Holotypes and paratypes of *Chordodes capensis* (from the National Museum of Natural History of Leiden; RMNH), of *C. clavatus*, *C. digitatus* and the holotype of *C. tuberculatus* (from Museum für Naturkunde, Berlin; ZMB) and the holotypes of *C. ibembensis* and *C. uncinatus* (from the Africa Museum Tervuren, Belgium (Koninklijk Museum voor Midden-Afrika); AMT) have been re-examined.

All specimens investigated were prepared for SEM, but the posterior end of specimens (RMNH Vermes 837 and 837a) were only investigated under light microscopy and photographed under a stereomicroscope. For SEM, parts of the central region of the body (about 5 mm in length) and the posterior end were dehydrated in an increasing ethanol series, critical point-dried, mounted on bronze blocks and gold sputter-coated. Observations were performed using a JEOL JSM 6360 LV scanning electron microscope. All preparations, i.e. the SEM stubs, are stored together with the preserved specimen in the respective museums.

Body measurements were made with outstretched worms using a ruler. Diameters were measured under dissecting microscope using a calliper ruler.

Results

Chordodes capensis Camerano, 1895

(Figure 1)

Chordodes capensis Camerano 1895, p 12, Figures 28, 28a.

Material

Holotype: 1♂, Cape of Good Hope. Specific locality unknown (Camerano 1895) (RMNH Vermes 837). Paratype: 1♀, from type locality (RMNH Vermes 837a).

Material examined. Holotype and paratype, SEM of midbody cuticle and LM posterior end.

Host

Undetermined mantid (De Beauchamp 1923; Baylis 1927), undetermined *Blatta* (Sciacchitano 1933). In one man (Baylis 1927; Coombs and Crompton 1991).

Description

The colour of the body is variable, dark brown (male) and yellowish brown (female). The male is 222 mm long, with a maximum diameter of 1 mm. The female is 224 mm in length

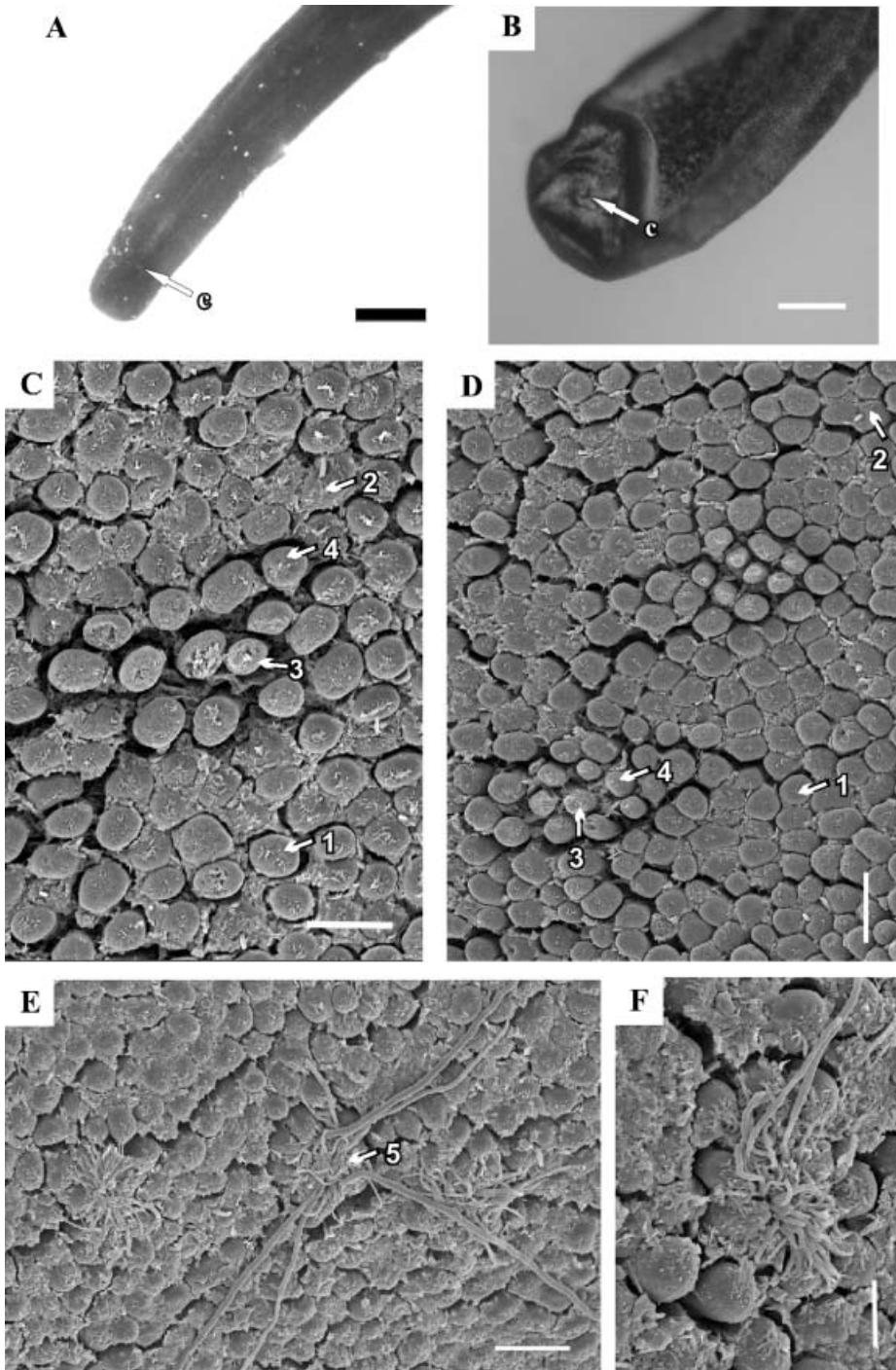


Figure 1. *Chordodes capensis*. (A) Stereo microscopy, ventral view of male posterior end; (B) stereo microscopy, female posterior end; (C, D) SEM of male cuticle, image of midbody cuticle showing simple (1), tubercle (2), crowned (3), and circumcluster areoles (4); (E, F) SEM of female longitudinal ventral groove crowned areoles with long filaments (5). Scale bars: 16.6 μm (A, B); 20 μm (C–E); 10 μm (F).

and 1.7 mm in diameter. A white cap and a dark calotte are not present. The male posterior end is undivided (Figure 1A). The female posterior end is round (Figure 1B).

The male cuticle contains four types of areoles. Simple areoles (Figure 1C) are rounded, low (10 µm), and have fine and minute bristles on their apical surface. Simple areoles are the most abundant type and among these there are scattered tubercle areoles with a short tubercle on top (5.3 µm). Crowned areoles occur in clusters on the cuticle (Figure 1C). These clusters are composed of two crowned areoles, in combination with another type of areole, the circumcluster areoles. The filaments of the crowned areoles are short. Circumcluster areoles (about 11–15 areoles) resemble simple areoles with apical fine bristles, but more elevated (15 µm) and arranged around the crowned areoles. The interareolar furrow is narrow.

The cuticle of the female includes all four types of areoles as in the males (Figure 1D), but another type of crowned areole with very long projections (124 µm) occurs along the ventral midline. These crowned areoles are surrounded by 8–10 circumcluster areoles (Figure 1E, F).

Comments

This study by SEM allows confirmation of the original description by Camerano (1895) of *C. capensis*, where the cuticle bears four areolar types and the female differs from the male in having two types of crowned areoles, with short filaments and with long filaments at the apical centre.

Chordodes clavatus Linstow, 1906

(Figures 2, 3A, B)

Chordodes clavatus Linstow 1906, p 246, Figure 16.

Material

Holotype: 1♂, Republic of Cameroon, Jaunde (ZMB Vermes 4446). Paratypes: 2♀♀, from type locality (ZMB Vermes 4446a).

Material examined. Holotype and paratype, SEM from midbody. Holotype, SEM posterior end.

Host

Unknown.

Description

The body colour of male is dark brown. The body length is 191 mm; diameter in the middle region is 0.99 mm. The anterior end is whitish, white cap and dark collar are not present. The posterior end is undivided (Figure 2A). The cloacal opening is oval and surrounded by slender spines. Anterolateral of the cloacal opening are two straight and narrow rows of bristles (Figure 2B).

The cuticular surface is structured into areoles belonging to five types (Figure 2C). The most abundant type is a rounded or oval areole (the simple areoles; Figure 2D). They are

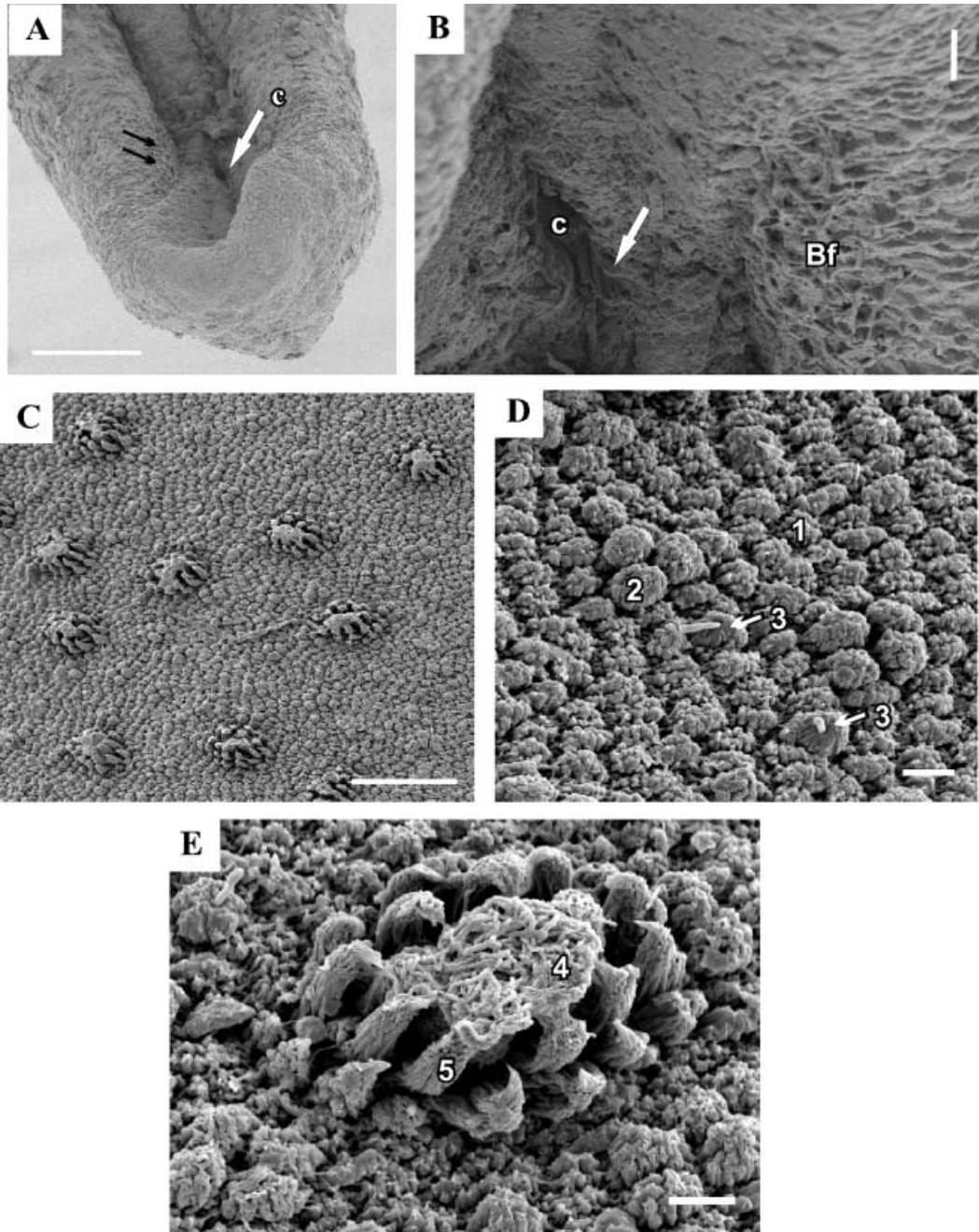


Figure 2. *Chordodes clavatus*, male, SEM. (A) Posterior end with subterminal cloacal opening (c) and bristlefields (black arrows); (B) detail of the posterior end showing the bristlefields (Bf), the cloacal opening (c) and circumcloacal spines (white arrow); (C) general view of the midbody cuticle; (D) detail of the midbody cuticle with simple (1), bulging (2), and tubercle areole (3); (E) midbody cuticle with clusters of crowned areoles (4) surrounded by circumcluster areoles (5). Scale bars: 100 μm (A, C); 10 μm (B, D, E).

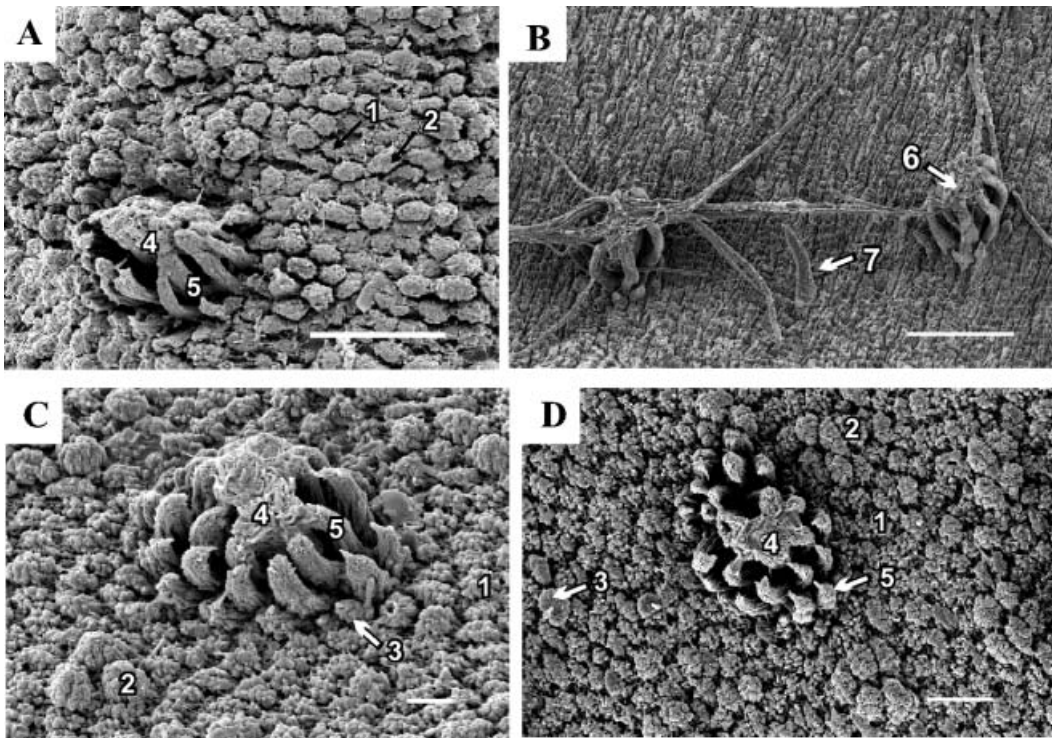


Figure 3. (A, B) *Chordodes clavatus*, female, SEM: (A) general view of the body cuticle showing simple (1), bulging (2), crowned areoles with short filaments (4), and circumcluster areoles (5); (B) crowned areoles with long apical filaments (6) and thorn areole (7) from the ventral midline posterior end. (C) [*Chordodes ibembensis*], cuticle of the holotype showing simple (1), tubercle (2), bulging (3), crowned areoles (4), and circumcluster areoles (5). (D) [*Chordodes uncinatus*], cuticle with the same types of areoles as [*Chordodes ibembensis*]. Scale bars: 20 μm (A); 50 μm (B); 10 μm (C, D).

low (4.4–5.2 μm), and have a warty surface, reminiscent of a blackberry. Bulging areoles (Figure 2D) resemble simple areoles but are more elevated (8.4–9.1 μm) and occur in clusters of two to five. Scattered in distribution are areoles with a finger-like projection on top (9.3 μm high), the tubercle areoles (Figure 2D). The two remaining areolar types occur in clusters of two crowned areoles surrounded by about 12–16 elevated areoles (the circumcluster areoles; Figure 2E). Circumcluster areoles are elevated (19.1–26.9 μm), curved towards the centre and contain apically a tuft of bristles. Crowned areoles resemble the circumcluster areoles in elevation (27.5–28.8 μm), but contain a crown of moderately short filaments on top. The interareolar furrow is narrow, lacking spiniform structures.

The body length of the females varies between 238 and 267 mm. Diameter is 1.14–1.78 mm. The body colour is dark brown. The posterior end is rounded. The ventral midline is darkly pigmented.

Although the cuticle in both females investigated was covered with detritus, the same five types of areoles as seen in the male could be identified (Figure 3A). The noticeable difference from the males is that two further areolar types are evident in the longitudinal ventral furrow of the body of the females. One of these are the thorn areoles, which are areoles with solid spines on top (Figure 3B). Thorns are distinguished from tubercles by

their pointed tip and are usually much more solid and higher (42.2 μm). The other type are crowned areoles with long filaments (60–223.3 μm) surrounded by circumcluster areoles (Figure 3B). It may be concluded that *Chordodes clavatus* females differ from males in having seven areolar types.

Comments

Linstow (1906) recognized only two areolar types in the original description of *C. clavatus*, small oval areoles distributed throughout the cuticle and groups of elevated conical areoles with clear filaments at the apex. These areolar types correspond to simple areoles, and to clusters formed by circumcluster and crowned areoles from the present investigation.

[*Chordodes ibembensis* Sciacchitano, 1958]

(Figure 3C)

Chordodes ibembensis Sciacchitano 1958, p 39, Figures 33, 34.

Material

Holotype: 1♂, Republic of the Congo, Province Uele, Ibembo (AMT 30093).

Material examined. Holotype, SEM from midbody.

Host

Mantis religiosa (Sciacchitano 1958).

Description

The specimen is 111 mm long, with diameter of 1 mm. Body colour is light brown. The anterior end narrows slightly towards apex and has a white calotte. The posterior end is undivided. The ventral longitudinal groove is evident.

The body cuticle has five types of areoles (Figure 3C). Simple areoles are low with varying shape and warty surface like a blackberry (Figure 3C). Clusters of two to five areoles (bulging areoles), with the same surface as simple areoles but taller. Rarely, there are isolated tubercle areoles. Two further types of areoles occur in clusters, circumcluster areoles that contain apically a tuft of bristles and surround two crowned areoles with a crown of filaments on top (Figure 3C).

Comments

In the original description, Sciacchitano (1958) described the cuticle of *Chordodes ibembensis* with three areolar types. This reinvestigation revealed five areolar types. Types 1, 2, and 3 from Sciacchitano (1958) correspond to simple, bulging, and circumcluster areoles, respectively, in the present investigation. By SEM it was revealed that simple and bulging areoles have a roughly structured surface, which was not observed by Sciacchitano (1958). Two more areole types may be added: the crowned areoles and tubercle areoles. No characteristics separate this species from *Chordodes clavatus*. Therefore, *Chordodes*

ibembensis is regarded as a synonym of *Chordodes clavatus*.

[*Chordodes uncinatus* Sciacchitano, 1958]

(Figure 3D)

Chordodes uncinatus Sciacchitano 1958, p 33, Figure 24.

Material

Holotype: 1♂, Republic of the Congo Bidua, Lisala (AMT 21141).

Material examined. Holotype, SEM midbody.

Host

Unknown.

Description

The body dimensions of the holotype are 160 mm in length and 1 mm in diameter. The colour of the body is dark brown. The anterior end is tapered and has a white calotte, the posterior end is undivided.

The cuticle (Figure 3D) shows five areolar types: simple areoles and bulging areoles with structured surface (blackberry-like). Bulging areoles form clusters of two to five areoles. Additionally, there are tubercle areoles with a tubercle on top and crowned areoles that form clusters together with circumcluster areoles. Crowned areoles occur in pairs and have moderately short filaments at the apex. This cuticular pattern shows the same characteristics observed in *Chordodes clavatus*.

Comments

Sciacchitano (1958) described *Chordodes uncinatus* with four areolar types. These areolar types correspond to the simple, bulging, circumcluster, and crowned areoles in our reinvestigation. Sciacchitano (1958) points out that both areolar types, type 1 (simple areoles) and type 2 (bulging areoles), have a tubercle in the middle. In this reinvestigation by SEM, the presence of tubercles could only be confirmed in the tubercle areoles, which are irregularly distributed. The features of the cuticle of *Chordodes uncinatus* are coincident with those described for the holotype of *C. clavatus*; therefore, *C. uncinatus* is regarded as a synonym of *C. clavatus*.

Chordodes digitatus Linstow, 1901

(Figures 4, 5)

Chordodes digitatus Linstow 1901, p 417, Figure 18.

Material

Holotype: 1♂, Tanzania, Unyika plateau (ZMB Vermes 4017). Paratypes: 2♀♀, from type locality (ZMB Vermes 4017a).

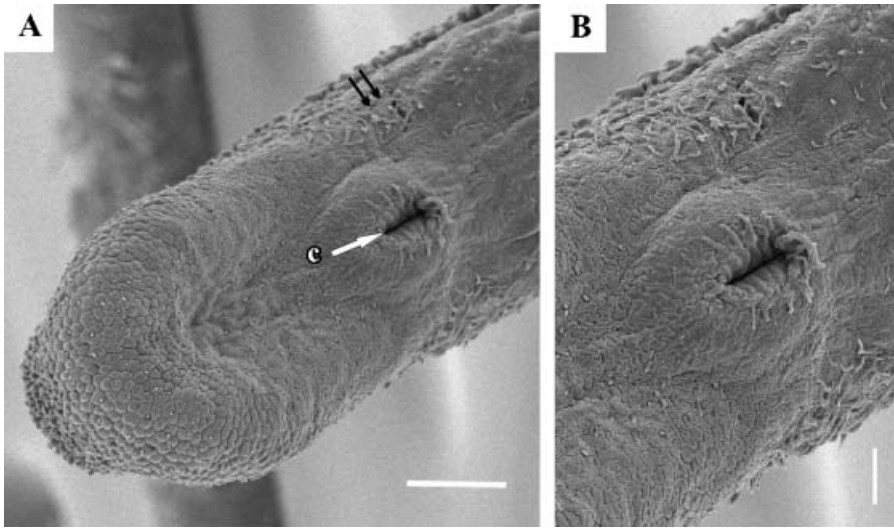


Figure 4. *Chordodes digitatus*, holotype, SEM male posterior end. (A) View of the cloacal opening (c) lying on the central cuticular protuberance and surrounded by circumcloacal spines. Lateral to the cloacal opening are two rows of bristles (the bristlefield, arrow); (B) detail of the posterior end. Scale bars: 50 μm (A); 20 μm (B).

Material examined. Holotype and paratypes, SEM midbody. Holotype, SEM posterior end.

Host

Unknown.

Description

The body colour of the male is dark brown. The body length is 110 mm and 0.5 mm in diameter. The anterior end is tapered and a dark collar is lacking. The posterior end is undivided and has a median ventral groove (Figure 4A). The cloacal opening lies on a central cuticular protuberance and is situated ventrally at about 210 μm from the posterior margin of the animal. The cloacal opening is oval (32.4 μm in length) and surrounded by circumcloacal spines. These spines are about 12.7 μm long and unbranched. Lateral to the cloacal opening are two straight rows of bristles (Figure 4A, B). They reach up to 79 μm in length. Around the cloacal opening, the cuticle is smooth and contains scattered small bristles spreading over the ventral side (Figure 4A).

The cuticle of the male contains five areolar types. Simple areoles are the most abundant, they are rounded or oval in shape, low (6.5 μm), and have a smooth surface. Irregular minute projections are distributed on the apical surface (Figure 5A). Among these are scattered areoles with the same shape but with a tubercle on top (tubercle areoles). The tubercle is about 4.5 μm long. Another type of areole has a solid spine (thorn) on top (thorn areoles). The thorn is longer than the tubercles (7.6 μm) and originates in an eccentric depression in the areole, which is round or horseshoe-like in shape (Figure 5A, B). Clusters of 11–13 of circumcluster areoles (8.6–9.5 μm high) with short filaments on the apex surround three crowned areoles (Figure 5B). Crowned areoles (9.6–10.5 μm high) have extremely short apical filaments. The interareolar furrow is wide (2.7–6.4 μm) and structured into cord-like ridges.

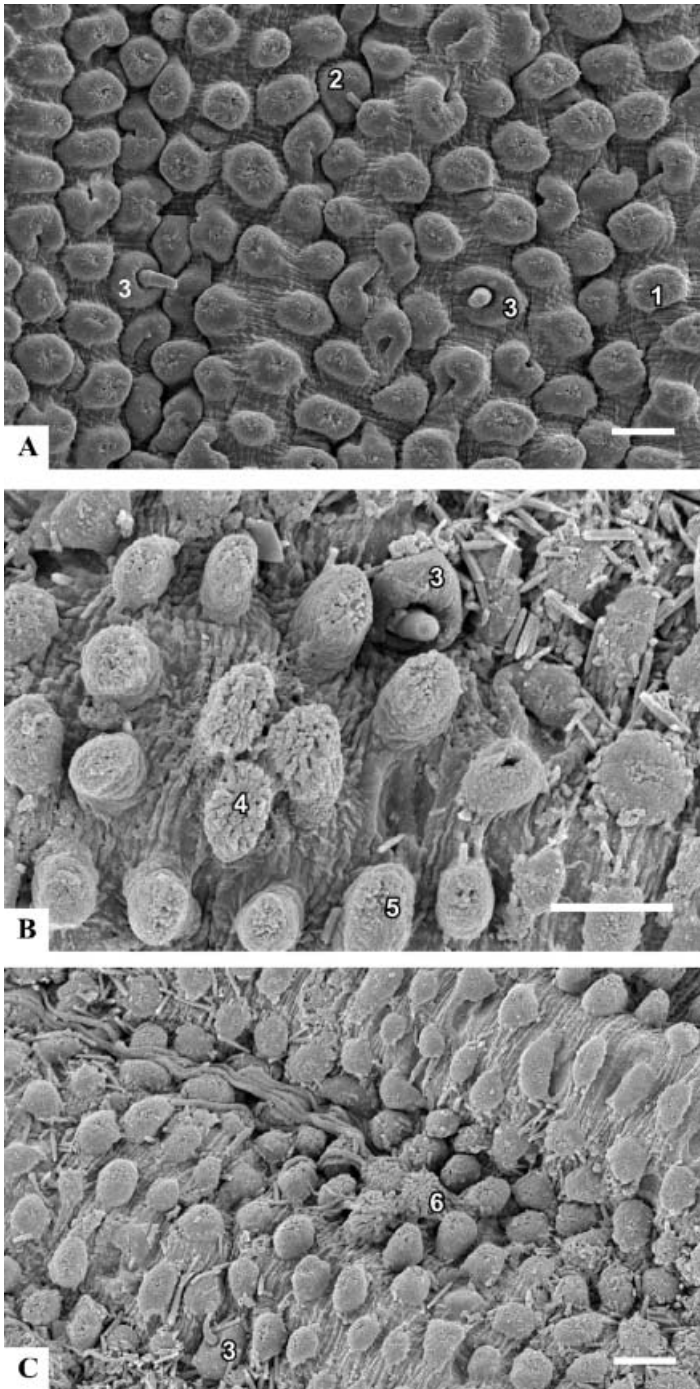


Figure 5. *Chordodes digitatus*. (A, B) SEM male midbody cuticle: (A) cuticle with simple (1), tubercle (2) and thorn areoles; (B) midbody cuticle showing thorn areole (3) and clusters of crowned areoles (4) surrounded by circumcluster areoles (5). (C) SEM of female longitudinal ventral groove: thorn areole (3) and crowned areoles with long filaments (6). Scale bars: 10 μ m.

The female body length varies between 120 and 140 mm, the diameter varies between 0.4 and 0.8 mm. The anterior end is tapered, a white tip or dark collar are not present. The body colour is brown.

The cuticle contains the same five types of areoles as in the male, but on both sides along the ventral midline there is another type of crowned areole (Figure 5C). These crowned areoles have a crown of long filaments (78.1 μm) on top and occur in clusters of three and are surrounded by 9–10 circumcluster areoles.

Comments

In the original description of *Chordodes digitatus*, Linstow (1901) provided measurements of the specimens without specifying to which sex each corresponded. Camerano (1915) mentioned this fact, noting the importance of this information. The present information by SEM reveal that the type specimens of *C. digitatus* correspond to one male and two females. Linstow (1901) described the cuticle of *C. digitatus* with three areolar types: types 1 and 2 correspond to the simple and tubercle areoles, respectively, in the present reinvestigation. The areoles described by Linstow (1901) as type 3 are considered to correspond to circumcluster and crowned areoles.

Chordodes tuberculatus Linstow, 1901

(Figure 6)

Chordodes tuberculatus Linstow 1901, p 417, Figure 17.

Material

Holotype: 1♂ from Tanzania, lake Malawi (original location as lake Nyassa, near Langenburg) (collected at 160 m altitude) (ZMB Vermes 4021).

Material examined. Holotype, SEM from midbody and posterior end.

Host

Unknown.

Description

The body colour is medium brown with numerous darker brown patches all over the body (“leopard pattern”; see Schmidt-Rhaesa et al. 2003). Measurement of the body length is 195 mm and the diameter is 0.48 mm. The posterior end (Figure 6A) is round and wide (223 μm). The cloacal opening (Figure 6A, B) is slit-like (73.1 μm long) and is surrounded by slender spines (circumcloacal spines). The cloacal opening is situated ventrally at 126.9 μm distance from the posterior margin of the body. Around the cloacal opening, the cuticle is smooth and structured by fine furrows into irregularly shaped compartments. Lateral to the cloacal opening are two rows of bristles called bristlefields (Figure 6A, C). The bristlefields are up to 77 μm long.

The body cuticle contains three areolar types (Figure 6D–F). Simple areoles (Figure 6E, F) are rounded or oval, low (9.1 μm high), and have a surface covered with short bristles. Scattered among these areoles are tubercle areoles that carry an eccentric finger-like

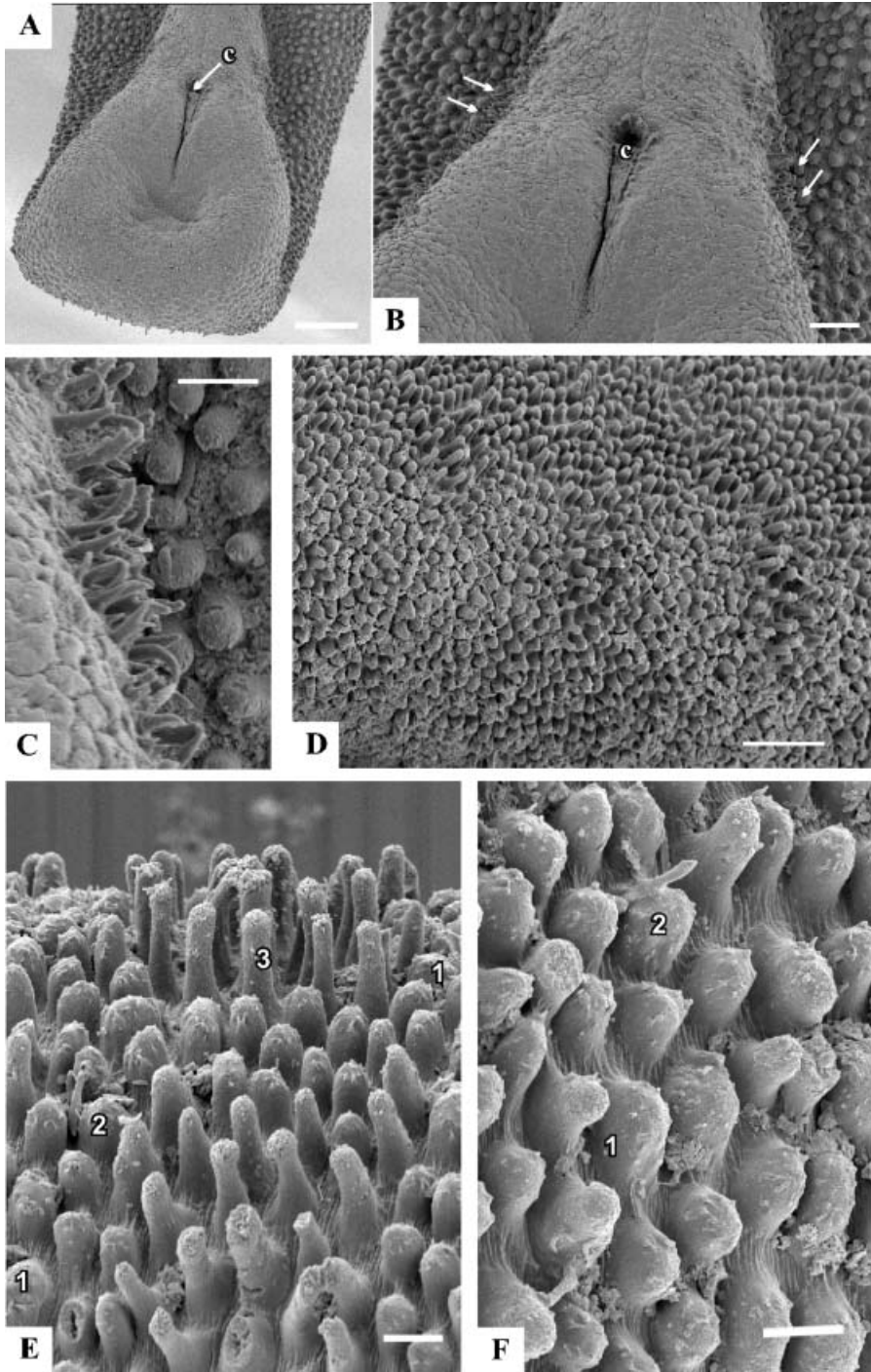


Figure 6. *Chordodes tuberculatus*, holotype. (A–C) Posterior end: (A) general view showing the cloacal opening (c); (B) detail of the cuticle, cloacal opening (c) and bristlefields (arrow) of the terminal end; (C) detail of the bristlefields. (D–F) Midbody cuticle: (D) general view; (E) cuticle with simple (1), tubercle areoles (2) and clusters of crowned areoles (3); (F) detail of simple (1) and tubercle areoles (2). Scale bars: 50 μ m (A, D); 20 μ m (B); 10 μ m (C, E, F).

tubercle (10.9 µm long). The most prominent type of areole is elevated (14.5–17.8 µm high) with several short apical filaments (crowned areoles) (Figure 6D–F). Crowned areoles appear clustered in groups very close together or more or less isolated from each other.

Comments

In the original description, Linstow (1901) considered the holotype of *C. tuberculatus* to be female, but reinvestigation reveals it to be male (see Figure 6). It is possible that Linstow (1901) erroneously determined the holotype as female due to the fact that it is unusual for males to have the posterior end round and wide. Linstow (1901) described the cuticle of *C. tuberculatus* with four areolar types. The first areolar type described by Linstow corresponds to the simple areoles described here. The areoles described by Linstow (1901) as types 2 and 3 are considered to crowned areoles, while his type 4 corresponds to tubercle areoles. Camerano (1915), on the basis of Linstow's (1901) figures, stated that the elevated type 2 and 3 areoles are arranged in groups, corresponding with the dark spots of the cuticle. Present observations agree with Camerano (1915), numerous groups of crowned areoles are visualized as superficial spots.

Discussion

The cuticular characteristics shown by *Chordodes capensis*, *C. clavatus*, *C. digitatus*, and *C. tuberculatus* allow them to be considered as valid species. The males of *Chordodes clavatus* and *C. digitatus* show five types of areole, while the females of *C. clavatus* have seven areolar types and the females of *C. digitatus* have six areolar types. *Chordodes capensis* also shows this sexual dimorphism, as males have four types of areoles and females have five areolar types. This sexual dimorphism has been previously pointed out for other species of *Chordodes* from Africa (Zanca et al. 2006a, 2006b), where the females, besides presenting crowned areoles with short filaments over the whole cuticle, possess crowned areoles with long filaments only on each side along the ventral midline. In the females of *C. clavatus* thorn areoles were also observed, as well as the crowned areoles with long filaments.

The cuticle of *Chordodes tuberculatus* resembles *C. brasiliensis* Janda, 1894 from South America (De Villalobos et al. 2004), as both of them have the same three areolar types, but differ because in *C. brasiliensis* the simple areoles have a roughly structured surface. Additionally, in *C. brasiliensis* the crowned areoles, although occurring abundantly, rarely form clusters of up to four areoles and are randomly distributed among the simple areoles.

Chordodes ibembensis and *C. uncinatus* are synonymized with *C. clavatus*, because no differences can be detected that justify the retention of these species as valid species.

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