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## Summary of *Chordodes* species (Nematomorpha, Gordiida), with a discussion of their diagnostic characters

**Abstract** More than 100 species of the genus *Chordodes* (Nematomorpha, Gordiida) have been described, but there is no unity in the naming of cuticular structures. This makes the determination of new specimens and the recognition of new species extremely difficult. We summarize here all known *Chordodes* species and list their cuticular characters with a uniform nomenclature. 54 species are considered as being sufficiently described to recognize them again, these species have been integrated into a key. 36 species surely are members of the genus *Chordodes*, but their description is not convincing and reinvestigations are desirable. Further 22 species names are invalid.

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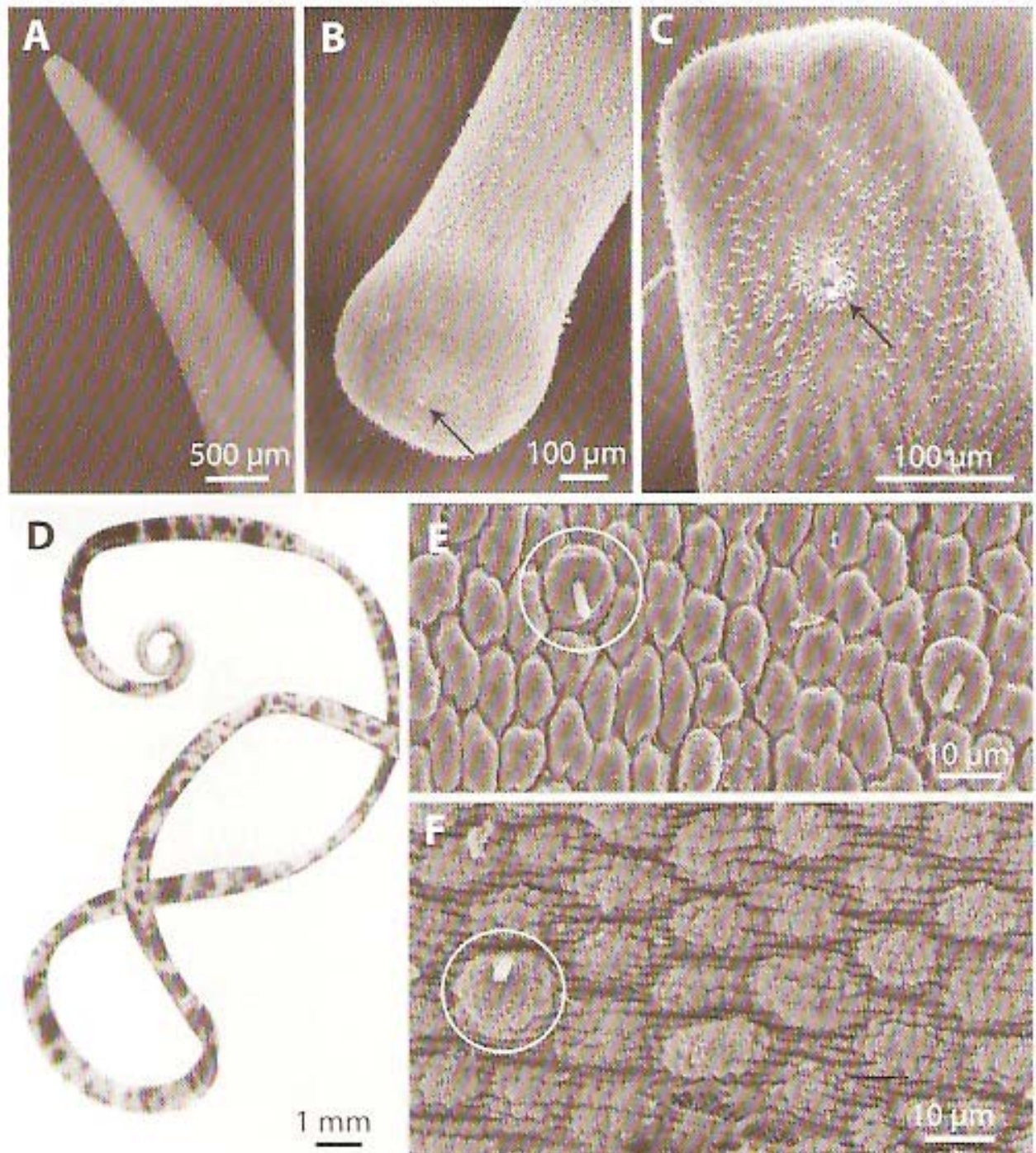
## Introduction

The genus *Chordodes* is the largest among horsehair worms (Nematomorpha) concerning species numbers, with about 100 species described so far. With few exceptions, species are distributed in tropical and subtropical regions. This corresponds to the distribution of their main hosts, praying mantids (SCHMIDT-RHAESA & EHRMANN 2001). The sampling is more or less sporadic and patchy, so that a higher diversity has to be expected.

Measurements such as length and diameter as well as colouration appear to be no reliable tools in determining species within nematomorphs. The diagnostic characters are cuticular structures. The earliest researchers have investigated more or less random pieces of cuticle and made drawings of the structures present. Now the documentation with light microscopy and especially with scanning electron microscopy has become the standard tool in describing the fine structures on the cuticle. Furthermore, it has become evident that the cuticular structures can vary spatially, making it important to investigate the structures in different regions of the body, particularly along the ventral and dorsal midline in comparison to the lateral regions. It was also found that sexual dimorphism occurs in some species. In these cases, males and females differ in the types of areoles present along the ventral and dorsal midline. Taking only random cuticular samples might underestimate the distribution of sexual dimorphism in the genus *Chordodes*. SCHMIDT-RHAESA (2002a) suggested a protocol requiring the investigation of the cuticle from an entire piece of the animal, cut out from the midbody region. However, this is regarded as problematic in the case of rare animals or holotypes, where less destructive methods such as removing smaller parts of the cuticle might be more appropriate.

The cuticle is structured into so-called areoles, which are more or less elevated structures of variable shape. The genus *Chordodes* is richest in areolar diversity, compared to all other nematomorphs. Several types can be distinguished and it appears that there is a standard “set” of areolar types, which are found in the majority of species. Some types of areoles occur abundant, but others only sporadic, therefore the pieces of cuticle investigated should not be too small. The basic differences between species are the particular shape of the types of areoles, their distribution patterns and their abundance or even absence.

Besides the cuticle on the main body, two regions of interest for nematomorph taxonomy are the anterior and the posterior end. The anterior end in all *Chordodes* species is distinctly tapering (Fig. 1A). The anterior tip is whitish in colour, blending into the normal colouration of the remaining body. In many other nematomorphs, such a white tip is separated from the remaining body by a ring-like dark colouration, this is absent in *Chordodes* species. The posterior end of females is often distinctly “swollen” (Fig. 1B). The terminal cloacal opening may be in a slight terminal depression, how-



**Fig. 1** Characteristics of the genus *Chordodes*. A. The anterior end is always tapering. B. The female posterior end is often swollen, the cloacal opening is terminal (arrow). C. Ventral view on the male posterior end, showing cloacal opening (arrow) surrounded by spines and further spines its vicinity. D. Male specimen with "leopard pattern", posterior end is coiled towards the ventral side. E. Almost smooth simple areoles and tubercle areoles (circle). F. "blackberry" simple areoles and tubercle areoles (circle). A-C, E-F with SEM. Organisms: A, C. *modiglianii*, Natural History Museum, London 1946.12.20.75-76. B D. *C. morgani*, collection Schmidt Rhaesa (no. SR 672.1, SR 630, no accession number). E. Undetermined species from Zoological Museum Hamburg (no. V4599). F. Undetermined species from Papua New Guinea, collection Schmidt Rhaesa.

ever, the presence of such a depression may depend on the maturity of the individual, in particular how much of the gametes are already shed. In males, the cloacal opening is on the ventral side, the postcloacal region is not divided into two tail lobes as in some other nematomorph genera (Fig. 1 C). There are spines and bristles around the cloacal opening and in the ventral region around it (Fig. 1 C). Because few *Chordodes* species are known in larger numbers of individuals, few things can be said about colouration patterns. It appears, however, that this is quite variable. This has been shown e.g. for *Chordodes morgani* (SCHMIDT-RHAESA et al. 2003). Often, but not as a constant pattern, the cuticle can contain darkly stained patches on a lighter background (Fig. 1 D). Such a pattern can be present in varying shades of contrast and is also likely to vary intraspecifically.

In describing a *Chordodes* species, most authors choose their own terminology for areolar types and consequently come to very different estimates of the number of different types of areoles. Usually, areoles are numbered (type 1, ...), but this numbering accounts only to particular species. Therefore, areoles of type 1 in one species may be homologous to areoles of type 2 in a second species. An example are the species *Chordodes anthophorus* and *C. aquaeductus*, which were found together in irrigation channels close to the city Pendschikent in Tajikistan and described in one publication by KIRJANOVA (1950). Both possess obviously homologous areolar types. According to the terminology explained below three of these types can be named simple areoles, crowned areoles and circumcluster areoles. While these represent types 2, 6 and 7 in *C. anthophorus*, they are types 1, 4 and 5 in *C. aquaeductus*, respectively.

Recently, several new species are described or reinvestigated (e.g. DE VILLALOBOS et al. 2004a, 2004b, 2007a, 2007b, SCHMIDT-RHAESA & MENZEL 2005, ZANCA & DE VILLALOBOS 2005, ZANCA et al. 2006a, 2006b, SCHMIDT-RHAESA & BRUNE 2008) and this has revealed two problems. First, older species descriptions vary considerably in their information content, making it often extremely hard to assign newly found specimens to already described species. There is a number of descriptions, which do not allow the recognition of this particular species among undetermined material. Second, as has been indicated above, there is a need for a standardized terminology. Such terminology has already been used in recent publications (e.g. DE VILLALOBOS et al. 2007a, SCHMIDT-RHAESA & BRUNE 2008) but we regard it as helpful to apply such a terminology here to all available species descriptions. Finally, previous descriptions often failed to name the structures or patterns characteristic of a particular species or such characteristic features are so weak that they do not stand a thorough comparison with other species.

In summarizing the present status of the description of cuticular structures and translating it to a unified terminology, we hope to set a framework, making the identification and description of new species in the genus *Chordodes* much easier.

## Terminology of areolar types

The cuticle of *Chordodes* species contains different types of areoles. As most of these types occur in almost all species, it makes sense to give them particular names (instead of confusingly number them). The description of different types, however, should not necessarily imply their homology; this is a more difficult task and will be discussed below.

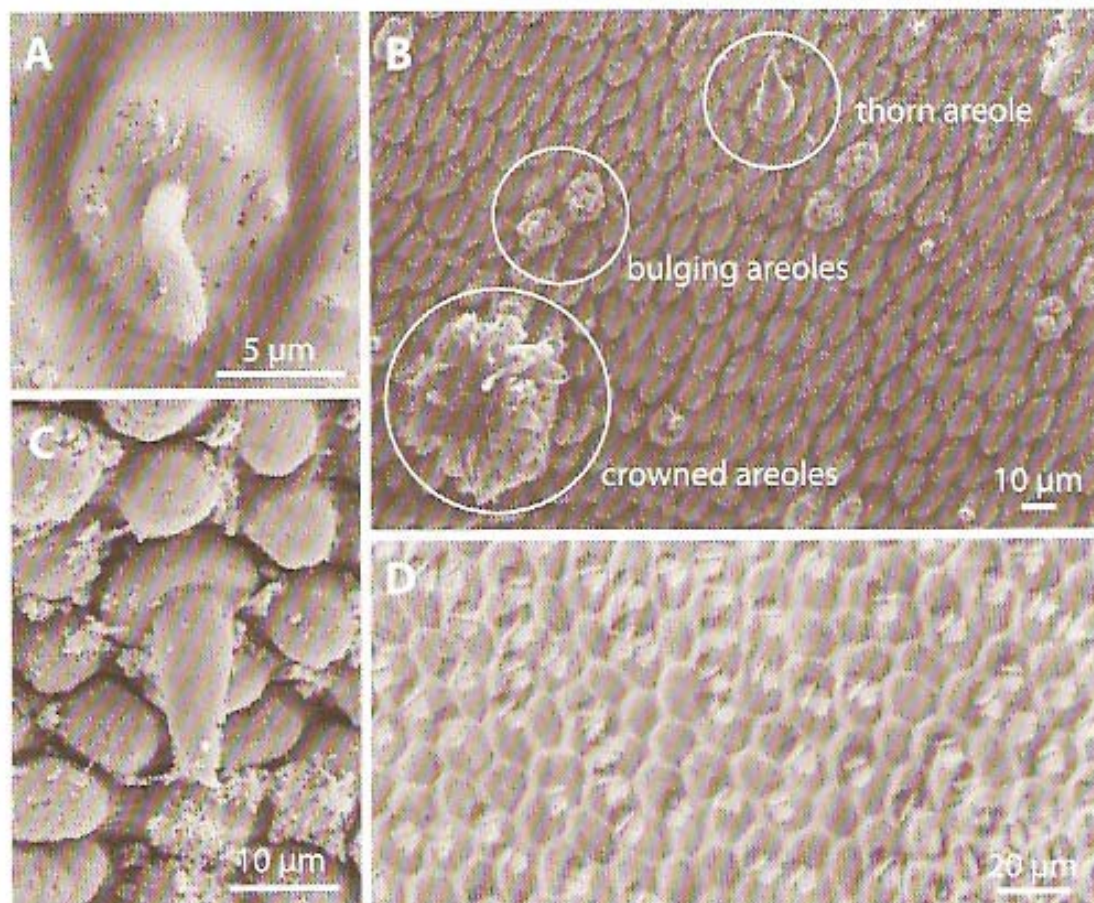
**Simple areoles.** The general pattern is that some "special" types of areoles are embedded into a "carpet" of simply structured, moderately elevated areoles which are called simple areoles (Figs. 1 E, F). This type is always the most abundant one. Simple areoles are flatter than the remaining areolar types, but they can range from very flat to semi spherical. Their outline is often irregular, they may be more rounded or polygonal, attach directly or leave interareolar furrows between neighbours. The surface may be smooth (Fig. 1 E) or irregularly structured. In several species, simple areoles have a warty surface, reminding of a blackberry (therefore they are also named "black berry areoles"; Fig. 1 F). In some species, short, bristlelike projections can be present on the surface of simple areoles.

**Tubercle areoles.** They are characterized by the tubercle, which is a fingerlike projection starting from the apical surface of what resembles a simple areole (Fig. 1 E, F, 2 A). This projection is not distinctly pointed and the tip therefore is more or less rounded. Tubercle areoles have been documented in almost all *Chordodes* species and appear scattered on the entire cuticular surface.

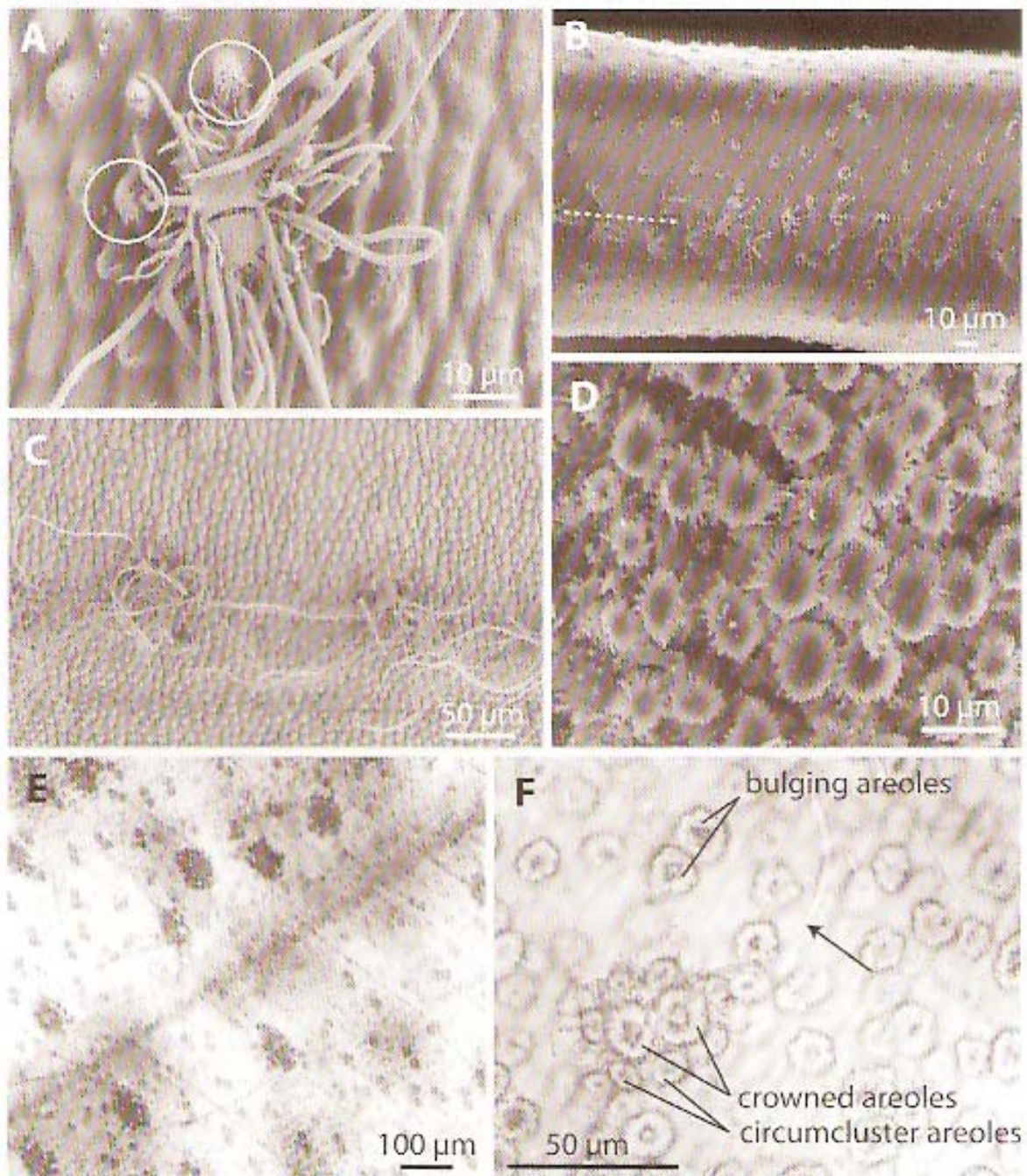
**Thorn areoles.** In many species, distinct thorns have been documented on the cuticle. The thorns are more or less curved and pointed (Fig. 2 B, C), in contrast to the tubercle of tubercle areoles. On closer look they originate from a basal structure that appears to represent an areole, therefore, these thorns are considered to be a type of areoles. Thorn areoles generally occur quite scattered on the cuticular surface and may be overlooked, especially when the cuticular samples investigated are quite small.

**Bulging areoles.** In some species, some areoles which do not belong to the types described above or below occur isolated or in small clusters among the simple areoles (Fig. 2 B). They are distinctly elevated above the simple areoles. Rarely, as for example in *C. brasiliensis* and *C. polytuberculatus* (see below), bulging areoles are very slender and tall, they occur in considerable numbers. Bulging areoles often resemble other areolar types in their structure, either the simple areoles or the crowned or circumcluster areoles described below. This makes it very hard to guess the "nature" of bulging areoles, but for descriptive purposes they are well recognizable and therefore an important type of areoles.

**Crowned areoles.** Crowned areoles are characterized by a basal, elevated trunk, from which numerous filamentous projections arise (Fig. 2B, 3A-F). These filaments are usually arranged in a circle, leading to the name "crowned" areole. The filaments can vary from being extremely short (Fig. 2B) to being considerably long (Fig. 3A). Corresponding to their length, their diameter also varies. Sometimes the apical surface of crowned areoles has the form of a plate, from which the filaments originate (Fig. 3A). In several cases, two types of crowned areoles occur on the cuticle of one and the same animal. In these cases, crowned areoles on the lateral sides of the body have moderately long apical projections, but paired rows of crowned areoles with very long projections occur along the ventral and in some species also along the dorsal midline (Fig. 3 B,C,E,F). It appears that this phenomenon is most distinctive in females, in males it appears to be either absent or the differences are very small (see, e.g., *C. queenslandi*, below).



**Fig. 2** Characteristics of the genus *Chordodes*: A. Tubercle areole. B. Overview on cuticle showing thorn areole, bulging areoles and crowned areole cluster. C. Thorn areole. D. Subcuticular paired structures. A-C with SEM, D with light microscope. A. *C. japonensis*, collection Schmidt Rhaesa. B, C. Undetermined species from Zoological Museum Hamburg (no. V4064 and V5202). D. *C. ferox*, Natural History Museum, London. 1947.5.20.195-198.



**Fig. 3.** Characteristics of the genus *Chordodes*: crowned areoles. A. Cluster of two crowned areoles with surrounding circumcluster areoles. B, C, E. Crowned areoles with long filaments occur along the ventral midline (dotted line in B, dark pigmentation in E). D. Cluster composed only of crowned areoles. F. Crowned areole cluster as visible with the light microscope. Arrow indicates one long apical filament. A-D with SEM, E, F with light microscope. A, C. *C. japonensis*, collection Schmidt-Rhaesa. B, D. Undetermined species from Zoological Museum Hamburg (no. V4064 and V11540). E, F. *C. queenslandi*, Australian National Insect Collection, Canberra, Australia (no. 9500002232).

Crowned areoles occur in clusters on the cuticle. These clusters are composed either only of crowned areoles (e.g. *C. fukuii* and *C. morgani*; Fig. 3D) or, more abundantly, in combination with another type of areole, the circumcluster areoles (see below; Fig. 3A,F). In these cases, usually two crowned areoles are present in the centre of the

cluster, but their number may also be higher. In several cases it has been observed that two crowned areoles closely attach along one side, enclosing a small tubercle between them.

Crowned areoles are an autapomorphy of the genus *Chordodes* (SCHMIDT-RHAESA 2002b). They are known from every species, at least in one sex (they are, e.g. lacking in males of *C. brasiliensis*, DE VILLALOBOS et al. 2004a). In cases where the apical filaments are very few and short, crowned areoles may resemble other elevated areoles with apical bristles, posing questions whether these are really crowned areoles (see discussion below).

**Circumcluster areoles.** Crowned areoles are in most, but not all cases surrounded by elevated areoles which are therefore called circumcluster areoles. In typical cases these areoles are slender and highly elevated, they may be without further substructure or carry apical fine bristles. It is not always possible to distinguish these areoles from simple areoles, because gradual transitions in size can occur. In some species, such as *C. fukuii*, circumcluster areoles are absent and crowned areoles directly border the simple areoles (Fig. 3 A, F).

Several older descriptions mention another cuticular character, conical structures, often occurring in pairs. These are structures within or below the cuticle, most likely cushion-like structures in the distal cuticular layer (see SCHMIDT RHAESA & GERKE 2006). They are not visible on the surface and are therefore no type of areoles (see also Schmidt-Rhaesa 2001).

The function of the diverse types of areoles is still unknown. Several investigations suggest the presence of canals in some areolar types, but it is not known whether they have a glandular or a receptive function. One first line structural insight into the structure of the cuticle of *Chordodes nobilii* (SCHMIDT-RHAESA & GERKE 2006) could add several new observations, but was still unable to answer functional questions.

We suggest that descriptions of species belonging to the genus *Chordodes* should include answers to the following questions:

1. Which of the types of areoles described above are present?
2. Are there further types of areoles?
3. What is the form of the simple areoles?
4. Are circumcluster areoles present and which form do they have?
5. Is there a dimorphism of crowned areoles?
6. What is the shape of crowned areoles? How long are the filaments?
7. How many crowned areoles are in a cluster?

Part of this information might be given in the form of a standardized table, such as the following:

simple areoles	
tubercle areoles	
thorn areoles	
bulging areoles	
crowned areoles	
circumcluster areoles	
dimorphism in crowned areoles?	
form of crowned areole cluster	

## Summary of species

In the following, “Material” summarizes all specimens described in the literature, “Documentation” indicates with which kind of illustrations (drawings, light microscopical image [LM], scanning electron micrograph [SEM]) the description is supplemented and “Distribution” lists the collection sites. Neglected in the following are reports on the host (see SCHMIDT-RHAESA & EHRMANN 2001), body measurements and colouration as well as details from the posterior ends.

### *Chordodes aelianus* (CAMERANO, 1894)

As *Gordius aelianus* by CAMERANO (1894a), transferred to *Chordodes* by CAMERANO (1897a)

**Material** 1 ♂

**Documentation** no drawing in original description (CAMERANO 1894a), drawing in CAMERANO (1897a).

**Distribution** **Indonesia:** Sumatra, Doloc Surugnan (1 ♂, CAMERANO 1894a).

simple areoles	warty surface (“blackberry areole”)
tubercle areoles	present
thorn areoles	not described
bulging areoles	not described
crowned areoles	occurring in pairs, apical filaments short
circumcluster areoles	present, resembling elevated simple areoles
dimorphism in crowned areoles?	not described
form of crowned areole cluster	pair of crowned areoles, surrounded by several circumcluster areoles

Comment on species status: The description and documentation of this species is not detailed enough to recognize characters particular to this species, a fine-structural reinvestigation is required.

*Chordodes aethiopicus* INOUE, 1974

Material 2 ♀♀

Documentation drawing in INOUE (1974)

Distribution Ethiopia: Awash National Park (2 ♀♀, INOUE 1974)

simple areoles	present, smooth surface with few irregular fine bristles
tubercle areoles	rarely present
thorn areoles	not described
bulging areoles	not described
crowned areoles	with short apical filaments
circumcluster areoles	resembling crowned areoles
dimorphism in crowned areoles?	not described
form of crowned areole cluster	the clusters are formed by 10–20 areoles of similar shape. The central pair is largest.

Comment on species status: This species belongs into a group of species in which the clusters are formed by similarly shaped areoles, making a distinction between crowned and circumcluster areoles difficult. *Chordodes aethiopicus* is characterized among this group of species by the presence of a pair of larger areoles in the center of the cluster.

*Chordodes africanus* SCIACCHITANO, 1933Synonyms *Chordodes butensis* (synonymized by ZANCA et al. (2006b))

Material presumably 3 ♂♂

Documentation drawings in SCIACCHITANO (1933, 1958), SEM in ZANCA et al. (2006b).

Distribution Democratic Republic of the Congo: Sankuru, Kondué (1 ♂, [1 ♀?]; SCIACCHITANO 1933, 1958), Buta (1 ♂, as *C. butensis*, SCIACCHITANO 1937); Angola: Dundo (1 ♂; SCIACCHITANO 1961a).

Note: Sciacchitano (1933) gave a very brief description based on a female. In a later publication (SCIACCHITANO 1958), he describes *C. africanus* based on a male specimen from the same locality, with the same collector, same measurements and supplemental information on the cuticle. Although he does not refer to a probable misinterpretation of the sex, we assume that he described only one specimen and assigned the wrong sex to it in the first description. The data below are based on the reinvestigation by ZANCA et al. (2006b)

simple areoles	warty surface ("blackberry areole"), fine bristles on surface
tubercle areoles	not described
thorn areoles	not described

bulging areoles	present, structure like simple areoles, in groups of 2–4
crowned areoles	present, with short apical filaments
circumcluster areoles	not present
dimorphism in crowned areoles?	not described
form of crowned areole cluster	clusters of 28–35 crowned areoles, no circumcluster areoles

Comments on cuticular structure: Two (SCIACCHIANO 1933) or three (SCIACCHIANO 1958) types of areoles are described. One of them are simple areoles and another must be crowned areoles. SCIACCHIANO (1958) describes areoles with an apical ring of bristles in two types, one of them with “granules” (2–3 in number) and one without (20–25 in number). A reinvestigation by ZANCA et al. (2006b) revealed the presence of simple, bulging and crowned areoles.

Comment on species status: This species belongs into a group of species in which the clusters are formed by similarly shaped areoles, making a distinction between crowned and circumcluster areoles difficult. *Chordodes africanus* closely resembles *C. fukuii* and *C. tuberculatus* but is distinguished from the first by the presence of simple areoles clearly elevated above the cuticular surface and from the last by moderately high crowned areoles, these are slender and high in *C. tuberculatus*.

### *Chordodes albibarbatatus* MONTGOMERY, 1898

**Material** 1 ♂, 1 ♀

**Documentation** drawings in MONTGOMERY (1898a, b).

**Distribution** probably Gabon, Ogove river (1 ♂, MONTGOMERY 1898a), Gaboon river (1 ♀; MONTGOMERY 1898b) [both rivers originate in neighbouring countries, Equatorial Guinea and Republic of the Congo, the exact collection site is not indicated].

simple areoles	variable in shape, surface appears to be more or less smooth (♂) or structured into “denticles” and canals (♀)
tubercle areoles	present
thorn areoles	present in females, but rare
bulging areoles	not described
crowned areoles	occurring in pairs, apical filaments moderately long
circumcluster areoles	present as slender areoles, often with more or less pointed tip, fine bristles on top
dimorphism in crowned areoles?	not described
form of crowned areole cluster	pair of crowned areoles, surrounded by 20–30 circumcluster areoles

Comment on species status: This species belongs into a large group in which the simple areoles are smooth or superficially structured, but not as extreme as in the “black berry” areoles. Clusters of crowned and circumcluster areoles are present. Among

these, *C. albibarbatus* is characterized by the presence of tubercle and thorn areoles, but the absence of bulging areoles.

### *Chordodes amboinensis* SCIACCHITANO, 1962

Material 1 ♂

Documentation drawing in SCIACCHITANO (1962).

Distribution **Indonesia:** Ambon (Maluku Islands) (as Amboina) (1♂, SCIACCHITANO 1962)

simple areoles	almost square circumference, surface probably smooth
tubercle areoles	not described
thorn areoles	probably present ("dark areoles, sometimes with tooth")
bulging areoles	probably present as dark isolated areoles or groups of 2-3 moderately dark areoles
crowned areoles	occurring in pairs, length of apical filaments not described
circumcluster areoles	present, fine structure not described
dimorphism in crowned areoles?	not described
form of crowned areole cluster	pair of crowned areoles, surrounded by 8-12 circumcluster areoles

Comments on cuticular structure: SCIACCHITANO (1962) describes four types of areoles: simple areoles, dark areoles, sometimes carrying a "tooth", moderately dark areoles in groups of 2-3 and clusters with areoles surrounding one or two larger areoles. Areoles of this last type are obviously crowned and circumcluster areoles, the second and third type probably are bulging areoles. The documentation is not very detailed.

Comment on species status: The description and documentation of this species is not detailed enough to recognize characters particular to this species, a fine structural reinvestigation is required.

### [*Chordodes annandalei* CAMERANO, 1908]

Material 3 ♂♂, 1 ♀

Documentation NONE

Distribution **Nepal:** Chitlong (2 ♂♂, 1 ♀, CAMERANO 1908a); **India:** Maidan (1♂; CAMERANO 1915).

CAMERANO (1908a, 1915) reports, without documentation in figures, only one type of areoles on the cuticle, which are not crowned areoles. Therefore, *C. annandalei* can not be regarded, on the basis of the available data, as belonging to the genus *Chordodes*.

**[*Chordodes annulatus* (VON LINSTOW, 1906)]****Material** 1♂, 1♀**Documentation** drawing in VON LINSTOW (1906a), LM in SCHMIDT RHAESA (2002a).**Distribution** **Australia:** Queensland (1♂, 1♀, VON LINSTOW 1906a)

This species, described as *Parachordodes annulatus* by VON LINSTOW (1906a) and then transferred to the genus *Chordodes* by CAMERANO (1915), does not have crowned areoles and therefore does not belong to the genus *Chordodes* (see reinvestigation of the holotype by SCHMIDT-RHAESA 2002a)

***Chordodes anthophorus* KIRJANOVA, 1950****Synonyms** *Chordodes aquaeductus*, *C. ferganensis*, *C. oscillatus* (all synonymized by DE VILLALOBOS et al. 2007b).**Material** 21♂♂, 7♀♀**Documentation** drawings in KIRJANOVA (1950), SEM in DE VILLALOBOS et al. (2007b).**Distribution** **Georgia:** Tbilisi (1♀, as *C. oscillatus*, KIRJANOVA 1953); **Tajikistan:** irrigation channel close to Pendschikent (18♂♂, 3♀♀, KIRJANOVA 1950, 1♂, DE VILLALOBOS et al. 2007b, 2♂♂, 1♀ as *C. aquaeductus*, KIRJANOVA 1950); **Uzbekistan:** in puddle close to Fergana (1♀, as *C. ferganensis*, KIRJANOVA & SPIRIDONOV 1989), Samarkand (1♀, DE VILLALOBOS et al. 2007b).

simple areoles	oval or round, sometimes with fine bristles on surface
tubercle areoles	present
thorn areoles	probably absent (mentioned but not figured by KIRJANOVA 1950, not found in reinvestigation by DE VILLALOBOS et al. 2007b)
bulging areoles	probably absent (mentioned but not figured by KIRJANOVA 1950, not found in reinvestigation by DE VILLALOBOS et al. 2007b)
crowned areoles	occurring in pairs, apical filaments moderately long, in ventral and dorsal midline with longer apical filaments
circumcluster areoles	present, with ring of short apical bristles
dimorphism in crowned areoles?	present
form of crowned areole cluster	pair of crowned areoles, surrounded by 12–20 circumcluster areoles

Comments on cuticular structure: KIRJANOVA (1950) describes seven types of areoles, from which five are figured. These correspond to simple, tubercle, crowned and circumcluster areoles. KIRJANOVA's type 3 is probably a large tubercle areole, whether this is a separate type should be cleared in a reinvestigation. Additionally, the nature of KIRJANOVA's types 4 (paired areoles with thorn-like extensions) and 5 (rare, isolated areoles resembling crowned areoles) is not completely clear, but these may represent thorn and bulging areoles. Their presence must, however, be checked in further inves-

tigations, because they were not observed in the reinvestigation by DE VILLALOBOS et al. (2007b).

Comment on species status: This species belongs into a large group in which the simple areoles are smooth or superficially structured, but not as extreme as in the "blackberry" areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes anthophorus* is quite similar to *C. japonensis* and *C. timorensis*, the differences between these species should be made clearer. In *C. anthophorus* two crowned areole clusters are sometimes close together, this might be a potential characteristics of this species.

### [*Chordodes aquaeductus* KIRJANOVA, 1950]

Material 2♂♂, 1♀

Documentation drawings in KIRJANOVA (1950), SEM in DE VILLALOBOS et al. (2007b).

Distribution **Tajikistan**: irrigation channel close to Pendschikent (2♂♂, 1♀, KIRJANOVA 1950).

After a reinvestigation, DE VILLALOBOS et al. (2007) synonymized this species with *Chordodes anthophorus*.

### *Chordodes auranthiacus* VON LINSTOW, 1906

Material 1♀

Documentation drawing in VON LINSTOW (1906a).

Distribution **Honduras**, no further data (1♀, VON LINSTOW 1906a).

The description is very brief, supplemented by an insufficient figure. It can be estimated that simple areoles, tubercle areoles, crowned areoles and circumcluster areoles are present, but details such as the exact structure of simple areoles or the number of crowned areoles are unknown. The crowned areoles figured have very long apical filaments, it remains to be shown if these belong to clusters from the ventral or dorsal midline or whether all crowned areoles have so long filaments.

### *Chordodes balzani* CAMERANO, 1896

Material 3♂♂, 3♀♀

Documentation drawings in CAMERANO (1896a, 1897a), CARVALHO & FEIO (1950) and DE MIRALLES (1976a), SEM in DE VILLALOBOS et al. (2004b).

Distribution **Argentina**: Misiones; **Bolivia**: Basso Beni (1♀, CAMERANO 1896a); **Brazil**: São Pedro do Sul. [CARVALHO & FEIO 1950 report two specimens, 1♂ and 1♀, from Argentina and from São Pedro do Sul, without indicating, which is which. DE MIRALLES (1976a) lists *C. balzani* as an Argentinian species, occurring in Misiones, but it is not clear if she investigated the material mentioned by CARVALHO & FEIO 1950 or if her specimen/speci

mens are new]; **Trinidad and Tobago**: Tamara Cave, Tamara Hill, Central Range Mountains (1♂, 1♀, DE VILLALOBOS et al. 2004b); **Venezuela**: Rio Cuchivero, Las Lomitas Caicara (1♂, DE VILLALOBOS et al. 2004b).

simple areoles	probably dimorphic, male with smooth areoles and fine processes, female with "blackberry" areoles (according to DE VILLALOBOS et al. 2004b)
tubercle areoles	present
thorn areoles	not described
bulging areoles	probably present (see e.g. Fig. 3 in CARVALHO & FEIO 1950)
crowned areoles	in pairs, encircling one tubercle, with short apical filaments; in dorsal and ventral midline with very long filaments
circumcluster areoles	present, slender
dimorphism in crowned areoles?	present
form of crowned areole cluster	2 crowned areoles, surrounded by 9–20 circumcluster areoles

**Comment on cuticular structure:** A sexual dimorphism concerning the structure of simple areoles has not been observed in other species and it will be informative to check if this is really a stable difference between both sexes. Additionally, it should be checked, whether bulging areoles are present or not.

**Comment on species status:** The difference in the form of the simple areoles and the uncertainties concerning the presence of bulging areoles makes it hard to place this species among others and require further reinvestigations.

### *Chordodes baramensis* RÖMER, 1895

**Material** 1 ♀

**Documentation** drawings in RÖMER (1896).

**Distribution** **Malaysia:** Baram river, Sarawak (1 ♀, RÖMER 1895a).

The description of areoles in RÖMER'S (1895a, 1896) descriptions is very superficial, mentioning only "papillae" of varying size, some of them with a tuft of bristles. It is quite evident that at least simple and crowned areoles are present, but nothing is known concerning the fine structure and the distribution patterns. RÖMER (1895a, 1896) notes that larger areoles (probably crowned areole clusters) are regularly arranged along both sides of the ventral and dorsal midline. This might indicate the dimorphism of crowned areoles as known from other species, but this remains to be documented.

*Chordodes betularius* VON LINSTOW, 1904**Material** 3 ♀♀**Documentation** one drawing in VON LINSTOW (1904).**Distribution** from stream running into the Caspian Sea (no further data, 3 ♀♀, VON LINSTOW 1904).

Two types of areoles are indicated, these represent simple areoles and probably crowned areoles with very short apical filaments. However, these filaments are described as “radial rays”, making a reinvestigation of this species desirable.

*Chordodes bipilus* KIRJANOVA, 1957**Material** 2 ♀♀**Documentation** drawings in KIRJANOVA (1957).**Distribution** **Iran:** vicinity of Astrobad (1 ♀) and in puddle in vicinity of Bechbechan (Farsistan province) (1 ♀) (both records KIRJANOVA 1957).

simple areoles	polygonal shape, irregular surface, sometimes with one bristle on top
tubercle areoles	present
thorn areoles	present
bulging areoles	present in pairs, enclosing a tubercle
crowned areoles	in pairs, enclosing a tubercle. Apical filaments of two kinds: abundant short fine filaments and less abundant, longer (reaching the border of the cluster) and thicker filaments.
circumcluster areoles	present, with fine apical bristles
dimorphism in crowned areoles?	appears to be present, Kirjanova reports filaments being longest on the ventral side
form of crowned areole cluster	2 crowned areoles, surrounded by 9–12 circumcluster areoles

Comment on species status: This species belongs into a large group in which the simple areoles are smooth or superficially structured, but not as extreme as in the “black-berry” areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes bipilus* is unique in having two different types of apical filaments.

*Chordodes boulengerii* CAMERANO, 1912**Material** 2 ♂♂, 6 ♀♀**Documentation** no figures in original description, drawing in SCIACCHITANO (1958).**Distribution** **Cameroon:** Dja river near Bitye (1 ♂, 6 ♀♀, CAMERANO 1912a); **Democratic Republic of the Congo:** Ingende (1 ♂, SCIACCHITANO 1958). [CAMERANO 1912a described the species from “the Congo” in the title and from “the Congo river basin” in the text, the river Dja and town Bitye are located in southern Cameroon, which may still be meant to be within the Congo basin].

simple areoles	irregular circumference and surface ("blackberry areole")
tubercle areoles	probably present (areoles with apical process described, but as they are not figured, it remains unclear whether these are tubercle or thorn areoles).
thorn areoles	see tubercle areoles
bulging areoles	probably present as elevated, dark areoles in groups (male: 2-6 areoles according to CAMERANO (1912a), 2-7 according to SCIACCHITANO (1958); female: 3-4 according to CAMERANO 1912a)
crowned areoles	present, but exact form insufficiently described. Apical filaments in males are described as being <i>sometimes</i> very long (CAMERANO 1912a). SCIACCHITANO (1958) figures areoles in the typical cluster of crowned and circumcluster areoles, but does neither mention nor figure apical filaments.
circumcluster areoles	present, exact form not described
dimorphism in crowned areoles?	not described
form of crowned areole cluster	2 crowned areoles, surrounded by circumcluster areoles (male: 25-40 areoles according to CAMERANO 1912a, 10-20 according to SCIACCHITANO 1958; female: 10-15 according to CAMERANO 1912a)

Comments on species status: The description and documentation of this species is not detailed enough to recognize characters particular to this species, a fine structural reinvestigation is required. Reinvestigations should consider the specimens from the type series as well as SCIACCHITANO's male specimen.

### *Chordodes bouvieri* (VILLOT, 1885)

As *Gordius bouvieri* by VILLOT (1885), transferred to *Chordodes* by RÖMER (1895b)

**Material** 5♂♂, 14♀♀

**Documentation** drawings in VILLOT (1886), CAMERANO (1897a), CARVALHO & FEIO (1950) and DE MIRALLES (1976a), LM in CARVALHO & FEIO (1950).

**Distribution** locality of type specimens (2♀♀) unknown (VILLOT 1885, 1886). **Argentina:** Tucuman (1♂, CARVALHO & FEIO 1950); **Colombia:** Gimenez (2♂♂, CAMERANO 1915); **Ecuador:** Gualáquiza (2♀♀, CAMERANO 1897b); **Venezuela:** Merida (1♂, 2♀♀), Chama (1♂, 3♀♀), Escurial (5♀♀) (all CAMERANO 1915).

Additional remark: This species was originally described as *Gordius bouvieri* by VILLOT (1885). SCIACCHITANO (1937) again uses the name *Gordius bouvieri* for the description of a new species from the Democratic Republic of the Congo, which was later (SCIACCHITANO 1958) recognized as being a mermithid nematode. RÖMER (1895b, 1896) added a specimen from Australia (Sydney), but his determination as *C. bouvieri* was later changed to *C. modiglianii* (CAMERANO 1897a, HEINZE 1935) and finally to *C. queen slandi* (SCHMIDT-RHAESA 2002a).

simple areoles	as flat, polygonal areoles
tubercle areoles	present (at least in all available drawings)
thorn areoles	not described
bulging areoles	not described
crowned areoles	present, usually in pairs, probably also isolated or in groups of three (see drawing in CAMERANO 1897a). Numerous fine and short apical filaments
circumcluster areoles	not described
dimorphism in crowned areoles?	not described
form of crowned areole cluster	Crowned areoles appear not to be surrounded by circumcluster areoles

Comment on species status: The description and documentation of this species is not detailed enough to recognize characters particular to this species, a fine structural reinvestigation is required.

### *Chordodes brasiliensis* JANDA, 1894

**Material** 62♂♂, 17♀♀

**Documentation** drawings in JANDA (1894), CAMERANO (1897a), CARVALHO (1946a), CARVALHO & FEIO (1950), DE MIRALLES (1969, 1976a,b, 1993), DE MIRALLES & CAMINO (1983); LM in CARVALHO (1946b), CARVALHO & FEIO (1950); SEM in DE VILLALOBOS et al. (2004a).

**Distribution** **Argentina:** San Lorenzo in Jujuy, Tala in Salta (total of 35♂♂, CAMERANO 1897c), town Salta (1♀, DE VILLALOBOS et al. 2004a), Gualguaychú in Entre Ríos (probably 1♂, 1♀, CARVALHO 1946b), Puerto Bembey in Misiones (2♂♂, CARVALHO & FEIO 1950), Cuña Pirú stream in Misiones (1♀, DE VILLALOBOS et al. 2004a), Iguazú National Park, Base Yawí (1♂, DE VILLALOBOS et al. 2004a), stream La Granja, Alta Gracia in Córdoba (2♂♂, DE MIRALLES 1976b), Alta Gracia in Córdoba (1♂, DE MIRALLES 1984a), town Corrientes (1♂, 1♀, DE VILLALOBOS et al. 2004a), El Reparito, Estancia Grande in San Luis (1♂) (both DE MIRALLES 1976b), Sierra de la Ventana, Cerro Tres Picos in province Buenos Aires (3♂♂, DE MIRALLES & CAMINO 1983), stream El Loto, Río Sauce Grande in prov. Buenos Aires (8♂♂, 4♀♀, DE MIRALLES 1980), Río Las Tipas in Tucumán (1♂, DE MIRALLES 1984b, 1♂, 2♀♀, DE MIRALLES 1993); **Brazil:** no further details (1♂, JANDA 1894), Espírito Santo/Santa Teresa (2♂♂, 3♀♀, CARVALHO 1946a), Rio de Janeiro (1♂, DE VILLALOBOS et al. 2004a), Niterói (1♂, DE VILLALOBOS et al. 2004a), Cachoeira de Macacu (1♀, DE VILLALOBOS et al. 2004a), Minas Gerais (1♀, DE VILLALOBOS et al. 2004a); **Uruguay:** no further details (1♀, CAMERANO 1915), Nueva Palmira (1♂), Tacuarembó (1♂), Mercedes (1♂) (all CARVALHO 1946b).

Note: CAMERANO 1897c reports "numerous" specimens from San Lorenzo and Tala, these were counted by DE VILLALOBOS et al. (2004a) to be 54♂♂ and 1♀. This reinvestigation, however, showed, that only 35♂♂ were determined correctly as *C. brasiliensis*.

simple areoles	with irregular shape and "warty" surface
tubercle areoles	present, with comparably long tubercles
thorn areoles	absent
bulging areoles	see comment below
crowned areoles	see comment below, present as flat areoles along the ventral and dorsal midline, with two kinds of filaments: very long and thick as well as shorter, fine filaments
circumcluster areoles	present only around crowned areoles along ventral and dorsal midline, small and curved
dimorphism in crowned areoles?	present
form of crowned areole cluster	clusters only along dorsal and ventral midline, here flat regions, from which long filaments originate and which are surrounded by 5–6 circumcluster areoles

Comments on cuticular structure: Typical for *C. brasiliensis* are slender areoles, highly elevated above the simple areoles. These have fine bristles on top and have a shape that is present in bulging or circumcluster areoles from several other species. They may well represent bulging areoles, which would mean that crowned areoles are completely absent in the males. In females, the structures along the ventral and dorsal midline must represent modified crowned areoles, which have reduced the "stem", so that the apical filaments more or less directly originate on the surface. Therefore, the crowned areoles, which are so characteristic for the genus *Chordodes*, are present in *C. brasiliensis* only in females along the ventral and dorsal midline.

Comment on species status: The presence of abundant, slender areoles on the cuticle makes this species easily recognizable. The only other species with this character, *C. polytuberculatus*, differs from *C. brasiliensis* by having clusters with crowned areoles on the lateral body sides, such clusters are not present in *C. brasiliensis*.

### *Chordodes brevipilus* SCHMIDT-RHAESA, 2002

Material 1 ♂

Documentation LM and SEM in SCHMIDT-RHAESA (2002a).

Distribution **Australia:** Queensland, Goldsborough State Forest Reserve (1 ♂, SCHMIDT-RHAESA 2002a).

simple areoles	with warty surface, separated by wide interareolar furrows
tubercle areoles	present
thorn areoles	absent
bulging areoles	probably present, some areoles are described as elevated and somewhat resembling crowned areoles with a reduced crown of apical filaments, these may either represent isolated crowned areoles or bulging areoles
crowned areoles	in pairs, enclosing a tubercle; with very short apical filaments
circumcluster areoles	absent

dimorphism in crowned areoles?	not present in male
form of crowned areole cluster	clusters are not present, pairs of crowned areoles are not surrounded by circumcluster areoles

Comment on species status: This species belongs into a group of species characterized by wide spaces between the areoles. *Chordodes brevipilus* is distinguished from the other species in this group by the absence of clear circumcluster areoles and by the presence of warty (instead of smooth) simple areoles.

### *Chordodes bukavuensis* SCIACCHITANO, 1958

Material 1 ♂

Documentation drawings in SCIACCHITANO (1958).

Distribution Democratic Republic of the Congo: Bukavu (1 ♂, SCIACCHITANO 1958).

simple areoles	with irregular shape and surface, separated by wide interareolar furrows
tubercle areoles	present
thorn areoles	not described
bulging areoles	not described
crowned areoles	in pairs (probably also single or in groups of three), moderately long apical filaments (until about border of crowned areole cluster), in female slightly longer than in male
circumcluster areoles	present, fine structure not described
dimorphism in crowned areoles?	not described
form of crowned areole cluster	1-3 crowned areoles, surrounded by circumcluster areoles (approximately 10 in male, 6-8 in female)

Comment on species status: This species belongs into a group of species characterized by wide spaces between the areoles. *Chordodes bukavuensis* is distinguished from the other species in this group by the presence of circumcluster areoles.

### [*Chordodes butensis* SCIACCHITANO, 1937]

Material 1 ♂

Documentation drawings in SCIACCHITANO (1937, 1958), SEM in ZANCA et al. (2006b).

Distribution Democratic Republic of the Congo: Buta (1 ♂, SCIACCHITANO 1937).

In the original description, Sciacchitano described four types of areoles, none of which are crowned areoles. In a new description, he described crowned areoles (SCIACCHITANO 1958). However, no characters specific for *C. butensis* can be identified and ZANCA et al. (2006b) showed in an SEM reinvestigation that the cuticular pattern corresponds to that of *C. africanus*, from which *C. butensis* has to be regarded a synonym.

*Chordodes caledoniensis* (VILLOT, 1874)

As *Gordius caledoniensis* by VILLOT (1874), transferred to *Chordodes* by RÖMER (1896)

**Synonyms** *Gordius sumatrensis*, *Gordius tuberculatus* (synonymised by RÖMER 1896)

**Material** 6 ♀♀

**Documentation** drawings in VILLOT (1874) and DORIER (1946).

**Distribution** **Australia:** Rockhampton, Queensland (as *Gordius tuberculatus*, 4 ♀♀, VILLOT 1874); **Indonesia:** Sumatra, Solok (as *Gordius sumatrensis*, 1 ♀, VILLOT 1892); **New Caledonia** (1 ♀, VILLOT 1874) [VILLOT 1874 described 3 ♀♀, which DORIER 1946 recognized in a re-investigation to be 2 ♀♀ and 1 ♂, from which only 1 ♀ corresponds to the characters described for *C. caledoniensis*].

simple areoles	rounded or polygonal, obviously with smooth surface
tubercle areoles	probably present (see figure 4–2 in Dorier 1946)
thorn areoles	not described
bulging areoles	present, fine structure unknown
crowned areoles	in pairs, with very fine, short apical filaments, along ventral midline with longer and more solid filaments
circumcluster areoles	present, fine structure not described
dimorphism in crowned areoles?	present
form of crowned areole cluster	pair of crowned areoles, surrounded by up to 11 circumcluster areoles

**Comment on species status:** This species belongs into a large group in which the simple areoles are smooth or superficially structured, but not as extreme as in the “black-berry” areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes caledoniensis* is distinguished from the other species in this group by the presence of tubercle areoles, short apical filaments in the crowned areoles and the presence of bulging areoles.

*[Chordodes cameranonis* MONTGOMERY, 1900]

**Material** 1 ♂

**Documentation** drawings in MONTGOMERY (1900).

**Distribution** West coast of Central America, but exact location unknown, MONTGOMERY (1900) indicates Panama or Mazatlan (Mexico) as possible collection sites.

In this species, no crowned areoles are described (MONTGOMERY 1900 particularly states that he has looked for crowned areoles but did not find them) and therefore it can not be included into the genus *Chordodes*. The pattern of distribution of elevated versus flat areoles reminds of patterns present in species of *Spinochordodes* or in *Chordodes morgani* and a reinvestigation using SEM would be helpful in further assigning this species.

*Chordodes capensis* CAMERANO, 1895**Material** 7♂♂, 9♀♀**Documentation** drawings in CAMERANO (1897a) and BEAUCHAMP (1923), SEM in DE VILLALOBOS et al. (2007b).**Distribution** **Angola:** cascades of Cuango Muquè, Alto Chicapa (1♂, SCIACCHITANO 1961a). **Democratic Republic of the Congo:** Mayumbe (1♀, BEAUCHAMP 1923), Bokoto (1♂, SCIACCHITANO 1933), Funda Biabo (1♀, SCIACCHITANO 1933), KUNHUNGI (1♀, SCIACCHITANO 1937), mission Kanzenze (2♂♂, SCIACCHITANO 1955), Uele, Angodia (1♂, SCIACCHITANO 1958), Kisangani (as Stanleyville, 1♀, SCIACCHITANO 1958), Kivu, Kalimabenge (1♀, SCIACCHITANO 1958), Kivu, Mt. Kahuzi (1♀, SCIACCHITANO 1961b), Epulu (1♀, SCIACCHITANO 1961b); **South Africa:** Cape of Good Hope (1♂, 1♀, CAMERANO 1895a); **Tanzania:** Kilo sa (1♂, reported as human parasite, BAYLIS 1927), Moba (1♀, SCIACCHITANO 1958).

Note: BEAUCHAMP (1923) reports one specimen of *C. capensis* to be found together with one specimen of *C. madagascariensis* in one host specimen, an undetermined species of praying mantid. Such report of the parasitism of one host specimen by two gortiid species is unusual and the specimens should be reinvestigated.

simple areoles	roundish, surface smooth and with few fine bristles
tubercle areoles	present
thorn areoles	not described
bulging areoles	not described
crowned areoles	in pairs, with either very short and fine apical filaments or with longer and more solid filaments
circumcluster areoles	similar in structure to simple areoles, but slightly more elevated
dimorphism in crowned areoles?	present, crowned areoles with longer filaments are located along the ventral midline
form of crowned areole cluster	pair of crowned areoles, surrounded by 11–15 circumcluster areoles

**Comment on species status:** This species belongs into a large group in which the simple areoles are smooth or superficially structured, but not as extreme as in the “black-berry” areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes capensis* is quite similar to *C. digitatus* and *C. muelleri*, the differences between these species must be made clearer. All three species are distinguished from other species in this group by the presence of tubercle areoles, short apical filaments in the crowned areoles and the absence of bulging areoles.

*Chordodes capillatus* VON LINSTOW, 1901

Material 1 ♀

Documentation drawings in VON LINSTOW (1901).

Distribution **Tanzania:** Langenburg at Lake Malawi (town was given up with rising level of Lake Malawi and does not exist today) (1 ♀, VON LINSTOW 1901).

The description of this species is not very detailed, indicating simple areoles, circumcluster areoles, crowned areoles and probably thorn areoles, but no fine structure. A reinvestigation is needed for this species.

[*Chordodes carioca* CARVALHO & FEIO, 1950]

Material 1 ♂

Documentation drawing and LM in CARVALHO &amp; FEIO (1950).

Distribution **Brazil:** Rio de Janeiro (1 ♂, CARVALHO & FEIO 1950).

CARVALHO & FEIO (1950) described two types of areoles from this species, neither of which are crowned areoles. Therefore, this species does not belong to the genus *Chordodes*.

*Chordodes carmelitanus* CARVALHO & FEIO, 1950

Material 1 ♀

Documentation drawing and LM in CARVALHO &amp; FEIO (1950), SEM in DE VILLALOBOS et al. (2004a).

Distribution **Brazil:** Fazenda da Algeria, Carmo do Rio Claro, Minas Gerais (1 ♀, CARVALHO & FEIO 1950). [species reported from Argentina as *C. carmelitanus* by DE MIRALLES 1989 were reinvestigated and determined to be *C. nobilii* by DE VILLALOBOS et al. 2004a].

simple areoles	elevated above cuticular surface to differing degrees, with irregular, "warty" surface
tubercle areoles	present
thorn areoles	not described
bulging areoles	not described
crowned areoles	present, but exact form not completely clear; they appear to be quite flat and the origin of the long and solid apical filaments can not exactly be traced
circumcluster areoles	not clear, the areoles surrounding crowned areoles do not differ distinctly from simple areoles
dimorphism in crowned areoles?	appears to be present
form of crowned areole cluster	as areoles surrounding the crowned areoles are not very distinct from simple areoles, it appears that no clusters are present

Comment on species status: Despite the reinvestigation by de Villalobos et al. (2004a), some characters of the cuticle remain unclear. Further investigations should attempt to clarify the fine structure of the crowned and circumcluster areoles.

[*Chordodes carvalhoi* DE MIRALLES & CAMINO, 1983]

Material 1 ♀

Documentation drawing in DE MIRALLES & CAMINO (1983).

Distribution **Argentina**: Río Primero in Córdoba (1 ♀, DE MIRALLES & CAMINO 1983).

No crowned areoles are described from this species, which does therefore not belong into the genus *Chordodes*.

*Chordodes clavatus* VON LINSTOW, 1906

Synonyms *C. ibembensis*, *C. uncinatus* (synonymised by DE VILLALOBOS et al. 2007a).

Material 5 ♂♂, 2 ♀♀

Documentation drawing in VON LINSTOW (1906a), SEM in DE VILLALOBOS et al. (2007a).

Distribution **Angola**: Dundo (as *C. ibembensis*, 2 ♂♂, SCIACCHITANO 1961a); **Cameroon**: Yaoundé (1 ♂, 2 ♀♀, VON LINSTOW 1906a); **Democratic Republic of the Congo**: Uele, Ibembo (as *C. ibembensis*, 1 ♂, SCIACCHITANO 1958), Bidua, Lisala territory (as *C. uncinatus*, 1 ♂, SCIACCHITANO 1958).

simple areoles	with warty surface ("blackberry areole")
tubercle areoles	present
thorn areoles	present only in females along the ventral midline
bulging areoles	resembling simple areoles, but more elevated, in clusters of 2-5
crowned areoles	with moderately long apical filaments (not reaching the border of the cluster or, only along the ventral midline in females, with very long filaments)
circumcluster areoles	slender, elevated, slightly curved towards centre of the cluster, with fine bristles on top
dimorphism in crowned areoles?	present, crowned areoles with long apical filaments present along the ventral midline in females
form of crowned areole cluster	pair of crowned areoles, surrounded by 12-16 circumcluster areoles

Comment on species status: This species belongs into a large group of species, in which the simple areoles are strongly structured into "blackberry" areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes clavatus* is distinguished from the other species in this group by the presence of tubercle and bulging areoles, the absence of thorn areoles and moderately long apical filaments in the crowned areoles.

*Chordodes compactus* SCHMIDT-RHAESA & BRUNE, 2008

Material 6 ♂♂, 1 ♀

Documentation LM and SEM in SCHMIDT-RHAESA & BRUNE (2008).

Distribution **Malaysia**: Cameron highlands, Chegar Peragh (6 ♂♂, 1 ♀, SCHMIDT-RHAESA & BRUNE 2008).

simple areoles	slightly elevated, with roughly structured surface
tubercle areoles	present
thorn areoles	present but rare
bulging areoles	present as isolated areoles resembling crowned areoles
crowned areoles	with slender stem and short apical filaments, the crowns of the areoles in a cluster are very close together, crowned areoles with moderately long apical filaments are present along the ventral midline of the male, those in the female have very long filaments
circumcluster areoles	not present on body sides, in clusters along the ventral midline, crowned areoles with long filaments are surrounded by areoles resembling crowned areoles with short filaments, which may also represent circumcluster areoles
dimorphism in crowned areoles?	present in both sexes, but in males crowned areoles along the ventral midline have moderately long filaments while those in females are very long
form of crowned areole cluster	on body sides, clusters are formed by crowned areoles alone, while along the ventral midline a pair of crowned areoles is surrounded by several areoles resembling crowned areoles with short filaments

Comment on species status: This species belongs into a group of species in which the clusters are formed by similarly shaped areoles, making a distinction between crowned and circumcluster areoles difficult. *Chordodes compactus* is characterized among these by the close association of crowned areoles within the clusters.

### *Chordodes compressus* RÖMER, 1895

**Material** 1 ♀

**Documentation** drawing in RÖMER (1896).

**Distribution** Malaysia; Baram river, Sarawak (1 ♀, RÖMER 1895a).

The cuticle contains simple areoles and crowned areoles, but the description is too superficial to recognize details. RÖMER (1895a, 1896) notes strong resemblances to another nematomorph from the same location, *C. baramensis*, with differences in size and colouration. As these are assumed to be quite variable, both species should be re-investigated. A different pattern of areoles along the ventral midline is indicated in *C. compressus* by RÖMER (1895a, 1896).

### *Chordodes congolensis* SCIACCHITANO, 1933

**Material** 4 ♂♂, 1 ♀

**Documentation** drawings in SCIACCHITANO (1933, 1958).

**Distribution** Democratic Republic of the Congo: Kasai, Ipaihu (1 ♂, SCIACCHITANO 1933, 1958), Flandria (1 ♂, SCIACCHITANO 1933, 1958), Uélé, Tuku (1 ♀, SCIACCHITANO 1933), Bamania (2 ♂♂, SCIACCHITANO 1961b). [The individuals from Kasai and Flandria were described as ♀ by SCIACCHITANO 1933 and recognized as ♂ by SCIACCHITANO 1958].

The description and figures of the cuticle are not sufficient. Simple areoles and probably thorn and bulging areoles appear to be present. Crowned areoles may be pre-

sent with a crown of very short and fine apical filaments, they may occur in clusters composed only of crowned areoles, but all these data need better documentation by a reinvestigation.

### *Chordodes corderoi* CARVALHO, 1946

**Material** 1 ♀

**Documentation** drawings and LM in CARVALHO (1946a).

**Distribution** **Venezuela:** Naiguatá, Los Canales (1 ♀, CARVALHO 1946a).

simple areoles	polygonal, flat areoles, probably all with tuft of fine bristles originating from the centre of the areole
tubercle areoles	present
thorn areoles	not described
bulging areoles	not described
crowned areoles	probably present isolated, with short, fine apical filaments; along dorsal and ventral midline in pairs, with very long filaments
circumcluster areoles	not described
dimorphism in crowned areoles?	present
form of crowned areole cluster	probably no cluster is present, crowned areoles are either in pairs (along dorsal and ventral midline) or singular (in remaining parts)

Comment on species status: Typical for *Chordodes corderoi* is the presence of a tuft of bristles on the simple areoles. Bristles can be present on simple areoles of other species, too, but only in *C. corderoi* and *C. villalobi* they form a tuft. Both species are distinguished by the absence of circumcluster areoles in *C. corderoi*, these are present in *C. villalobi*.

### *Chordodes cornuta* DE VILLALOBOS & CAMINO, 1999

**Material** 1 ♂

**Documentation** SEM in DE VILLALOBOS & CAMINO (1999).

**Distribution** **Argentina:** vicinity of town Salta (1 ♂, DE VILLALOBOS & CAMINO 1999).

simple areoles	with "warty" surface
tubercle areoles	?
thorn areoles	not described
bulging areoles	not described
crowned areoles	isolated or in groups of up to seven areoles; with very short crown of apical filaments
circumcluster areoles	not present
dimorphism in crowned areoles?	not described
form of crowned areole cluster	crowned areoles are either isolated or occur in small clusters, but without circumcluster areoles

Comment on cuticular structure: DE VILLALOBOS & CAMINO (1999) described "type B areoles", which resemble the basal part of a tubercle areole. Whether this means that they represent a tubercle areole which has lost its tubercle is not known.

Comment on species status: This species belongs into a group of species in which the clusters are formed by similarly shaped areoles, making a distinction between crowned and circumcluster areoles difficult. *Chordodes cornuta* is characterized among these by the presence of small clusters (< 7 areoles).

### [*Chordodes cubanensis* MONTGOMERY, 1898]

Material 1♂, 1♀

Documentation drawings in MONTGOMERY (1898c).

Distribution Cuba (not further specified; 1♂, 1♀, MONTGOMERY 1898c).

MONTGOMERY (1898c) describes three types of areoles, which are insufficiently figured. From their distribution pattern, they resemble areoles as described for *C. morgani* or for species of the genus *Spinochordodes*. A reinvestigation is necessary for this species.

### *Chordodes curvicillatus* KIRJANOVA & SPIRIDONOV, 1989

Material 1♀

Documentation drawings, LM and SEM in KIRJANOVA & SPIRIDONOV (1989).

Distribution Indonesia: Sumatra, near Pajacombach (1♀, KIRJANOVA & SPIRIDONOV 1989).

simple areoles	often conical, sometimes with fine bristles on top
tubercle areoles	probably present
thorn areoles	present as slender, hooked process on simple areole
bulging areoles	probably present (see figs 3 and 4 in KIRJANOVA & SPIRIDONOV 1989)
crowned areoles	present, with very short apical filaments on lateral body and with long filaments along midventral and middorsal lines
circumcluster areoles	present, either as pointed areoles with few fine bristles on top (on lateral body) or resembling crowned areoles from lateral body in having a crown of apical fine bristles
dimorphism in crowned areoles?	present
form of crowned areole cluster	on lateral body sides several crowned areoles with short filaments, encircled by pointed circumcluster areoles, sometimes a "thorn" appears to be present in the center; in ventral and dorsal midline, pair of crowned areoles with long filaments, encircled by no so pointed circumcluster areoles with apical filaments or bristles

Comment on species status: This species belongs into a large group in which the simple areoles are smooth or superficially structured, but not as extreme as in the "black-berry" areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes curvicillatus* is unique in having hook-shaped thorn areoles

*Chordodes defilippii* (ROSA, 1881)

As *Gordius* (*Chordodes*) *De Filippii* by ROSA (1881), transferred to *Chordodes* by RÖMEL (1896)

Material 2 ♂♂

Documentation NONE

Distribution **Georgia:** Tibilisi (1 ♂, ROSA 1881), Caucasus (unspecified location, 1 ♂, CAMERANO 1896b).

This species, described as *Gordius* (*Chordodes*) *De Filippii* (ROSA 1881), later cited as *Gordius defilippii* (JANDA 1894) and transferred to the genus *Chordodes* by CAMERANO (1896b) and RÖMEL (1896), as *C. defilippii* or *C. defilippi*, respectively. CAMERANO later (1897a, 1915) used the writing *C. De Filippii*. The species is insufficiently described and lacks documentation by figures. Simple and crowned areoles are indicated in the description, but the fine structure or distribution patterns are unknown.

*[Chordodes delmae* DE VILLALOBOS, 1995]

Material 1 ♂

Documentation SEM in DE VILLALOBOS (1995).

Distribution **Argentina:** Salta, Campo Quijano (1 ♂, DE VILLALOBOS 1995).

There are no crowned areoles in this species, which therefore does not belong to the genus *Chordodes* (it shows the characters of the genus *Pseudochordodes*).

*Chordodes devius* KIRJANOVA, 1950

Material 3 ♀♀

Documentation drawing and LM in KIRJANOVA (1950).

Distribution **Tajikistan:** irrigation channel close to Pendschikent (3 ♀♀, KIRJANOVA 1950).

Note: The documentation includes only a silhouette drawing of anterior and posterior and a low magnification micrograph, from which details of the areoles are not visible, the description below is based on the text description.

simple areoles	only tubercle areoles are described as the most abundant type
tubercle areoles	abundantly present
thorn areoles	present
bulging areoles	present as pairs, enclosing one tubercle
crowned areoles	present in pairs with long and slender apical filaments; they enclose two tubercles
circumcluster areoles	present; with fine apical bristles
dimorphism in crowned areoles?	not described
form of crowned areole cluster	pair of crowned areoles, surrounded by 10–12 circumcluster areoles

Comment on species status: If the description is reliable, *C. devius* is unique in possessing only tubercle areoles and no simple areoles.

*Chordodes digitatus* VON LINSTOW, 1901

**Material** 1♂, 2♀♀ (VON LINSTOW 1901 does not recognize the sex, he additionally reports two fragments, sex was determined by DE VILLALOBOS et al. 2007a).

**Documentation** drawing in VON LINSTOW (1901), SEM in DE VILLALOBOS et al. (2007a).

**Distribution** Tanzania: Unyika plateau, Konde (1♂, 2♀♀, VON LINSTOW 1901).

simple areoles	variable in shape, including horseshoe-shaped and other forms, with fine bristles on top
tubercle areoles	present, sometimes as horseshoe-shaped areoles surrounding a strong tubercle
thorn areoles	not described
bulging areoles	not described
crowned areoles	with very short apical filaments on body sides or, only in females along the ventral midline, with long filaments
circumcluster areoles	elevated above simple areoles, with granular surface
dimorphism in crowned areoles?	present, in females crowned areoles with long apical filaments along the ventral midline
form of crowned areole cluster	three crowned areoles, surrounded in some distance by 11–13 (body sides) or 9–10 (ventral midline in females) circumcluster areoles

Comment on species status: This species belongs into a large group in which the simple areoles are smooth or superficially structured, but not as extreme as in the “black-berry” areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes digitatus* is quite similar to *C. capensis* and *C. muelleri*, the differences between these species must be made clearer. All three species are distinguished from other species in this group by the presence of tubercle areoles, short apical filaments in the crowned areoles and the absence of bulging areoles.

[*Chordodes ferganensis* KIRJANOVA & SPIRIDONOV, 1989]

**Material** 1♀

**Documentation** drawings and SEM in KIRJANOVA & SPIRIDONOV (1989), SEM in DE VILLALOBOS et al. (2007b).

**Distribution** Uzbekistan: in puddle close to Fergaha (1♀, KIRJANOVA & SPIRIDONOV 1989).

After a reinvestigation, DE VILLALOBOS et al. (2007b) synonymized this species with *Chordodes anthophorus*.

*Chordodes ferox* CAMERANO, 1897

**Material** 1♂♀♀

**Documentation** drawings in CAMERANO (1897a) and BEAUCHAMP (1923).

**Distribution** “French Congo” (no further specified location, this region now includes the Republic of

the Congo, Gabon and the Central African Republic; specimen was originally described as *Gordius verrucosus* by Camerano 1893a) (1 ♀, CAMERANO 1897a); **Democratic Republic of the Congo**: Kisantu (1 ♀, BEAUCHAMP 1923), Bas-Uélé, La Kulu, Bondo (1 ♀, SCIACCHITANO 1933), Kisangani (as Stanleyville, 2 ♀ ♀, SCIACCHITANO 1933), Komi, Lodja (3 ♀ ♀, SCIACCHITANO 1933), Boma (1 ♀, SCIACCHITANO 1933), Ingende (1 ♀, SCIACCHITANO 1958).

simple areoles	variable in shape, obviously more or less smooth on surface
tubercle areoles	present
thorn areoles	present
bulging areoles	probably present (see figure in BEAUCHAMP 1923 and description by SCIACCHITANO 1958)
crowned areoles	with long apical filaments (strongly exceeding borders of cluster)
circumcluster areoles	present
dimorphism in crowned areoles?	not described
form of crowned areole cluster	unknown number of crowned areoles, surrounded by 9–13 circumcluster areoles

Comment on species status: The description and documentation of this species is not detailed enough to recognize characters particular to this species, a fine-structural reinvestigation is required.

### *Chordodes festae* CAMERANO, 1897

**Material** 42 ♂♂, 12 ♀♀

**Documentation** no figure in original description (CAMERANO 1897b), drawing in CAMERANO (1897a), SEM in DE VILLALOBOS & ZANCA (2001).

**Distribution** **Ecuador**: Cuenca (34 ♂♂, 7 ♀♀, CAMERANO 1897b [numbers given in reinvestigation of DE VILLALOBOS & ZANCA 2001]); **Venezuela**: Merida (7 ♂♂, 5 ♀♀, CAMERANO 1905); **Democratic Republic of the Congo**: river Kalimabenge (1 ♂, SCIACCHITANO 1958).

simple areoles	polygonal, irregular surface with fine bristles
tubercle areoles	not described
thorn areoles	present, thorns appear to arise more or less directly from cuticle
bulging areoles	not described
crowned areoles	present, with few moderately long apical filaments (reaching the border of the cluster)
circumcluster areoles	present, elevated, with apical bristles
dimorphism in crowned areoles?	not described
form of crowned areole cluster	pair of crowned areoles, surrounded by two rings of 8–10 circumcluster areoles in each ring

Comments on cuticular structure: DE VILLALOBOS & ZANCA (2001) described one type of areoles, occurring singly or in groups up to four areoles. These areoles are elevated

above the simple areoles and have an apical tuft of filaments. They therefore somewhat resemble crowned areoles in their form or, in their distribution, bulging areoles. It is not quite clear, to which type of areoles they are homologous.

**Comment on species status:** This species belongs into a large group in which the simple areoles are smooth or superficially structured, but not as extreme as in the "blackberry" areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes festae* is distinguished from the other species in this group by the absence of tubercle areoles. This is shared only by *C. sanduensis*, which has short apical filaments in the crowned areoles in contrast to *C. festae*, which has moderately long filaments. The reports of this species on two continents must be confirmed, but appear to be not very likely.

### *Chordodes fukuui* INOUE, 1951

- Material** unknown number of specimens, the sex is only given for 1♂ and 4♀.
- Documentation** no figures in original description, drawings in INOUE (1952, 1988), SEM in SCHMIDT-RHAESA 2004).
- Distribution** **Japan:** prefectures Akita, Tochigi, Yamanashi (INOUE 1951), Tokyo (INOUE 1952), Shizuoka (INOUE 1988), Toyama city, Akiuōji (INOUE 1994), vicinity of Lake Biwa Museum, Oroshimo, Kusatsu town (4♀, SCHMIDT-RHAESA 2004), shore of Lake Biwa, Kitahira, Shiga town (1♂, SCHMIDT-RHAESA 2004). [in publications by INOUE, only the distribution in certain prefectures is indicated, no numbers or sex are given].

simple areoles	very flat, surface densely covered with apical granules or short bristles
tubercle areoles	present
thorn areoles	not described
bulging areoles	not described
crowned areoles	areoles in clusters of several are elevated and carry a ring with very short filaments, these probably represent the crowned areoles
circumcluster areoles	not present
dimorphism in crowned areoles?	not described
form of crowned areole cluster	clusters are composed only of crowned areoles, circumcluster areoles are absent. There are 10 or more areoles in a cluster.

**Comment on species status:** This species belongs into a group of species in which the clusters are formed by similarly shaped areoles, making a distinction between crowned and circumcluster areoles difficult. *Chordodes fukuui* closely resembles *C. africanus* and *C. tuberculatus*, but is distinguished from both by the presence of flat simple areoles, these are further elevated in the other species.

*Chordodes furnessi* MONTGOMERY, 1898**Material** 1 ♂, 3 ♀♀**Documentation** drawing in MONTGOMERY (1898a), LM and SEM in SCHMIDT-RHAESA & YADAV (2004).**Distribution** “Borneo” (no further specification, 1 ♂, 1 ♀, MONTGOMERY 1898a), **India**: Shillong (2 ♀♀, SCHMIDT-RHAESA & YADAV 2004, as *Chordodes* cf. *furnessi*).

simple areoles	rounded, with fine apical bristles
tubercle areoles	not described (only tubercles or thorns close to areoles in the interareolar space are present)
thorn areoles	not described
bulging areoles	present as single or few areoles resembling circumcluster areoles
crowned areoles	on body sides with very short apical filaments, along ventral and dorsal midline with long and solid filaments (these were only found in the Indian specimens)
circumcluster areoles	in clusters along ventral and dorsal midline, circumcluster areoles are present and resemble the areoles from clusters on the sides of the body
dimorphism in crowned areoles?	present
form of crowned areole cluster	on body sides only around 20 areoles of one type, resembling crowned areoles. Along ventral and dorsal midline single crowned areoles with very long apical filaments, surrounded by circumcluster areoles with very short filaments

Comment on species status: This species belongs into a group of species in which the clusters are formed by similarly shaped areoles, making a distinction between crowned and circumcluster areoles difficult. *Chordodes furnessi* is characterized by the presence of crowned areole dimorphism in females and by the absence of tubercle areoles.

*Chordodes gariazzi* CAMERANO, 1902**Material** 1 ♂**Documentation** SEM in ZANCA et al. (2006a).**Distribution** **Democratic Republic of the Congo**: unknown locality (1 ♂, CAMERANO 1902a).

simple areoles	with warty surface (“blackberry areoles”) and fine bristles
tubercle areoles	present
thorn areoles	present
bulging areoles	present in clusters of two to four, similar in structure to simple areoles, but more elevated and the fine bristles appear to be clustered together
crowned areoles	with moderately long apical filaments (slightly exceeding the border of the clusters)
circumcluster areoles	slender areoles, slightly curved towards center, with rough apical surface
dimorphism in crowned areoles?	not described
form of crowned areole cluster	pair of crowned areoles surrounded by 12–20 circumcluster areoles

Comment on species status: This species belongs into a large group of species, in which the simple areoles are strongly structured into “blackberry” areoles. Clusters of

crowned and circumcluster areoles are present. *Chordodes gariuzzi* is characterized by the presence of club shaped tubercles in the tubercle areoles. Such tubercles have been found only in *C. heinzei*, which has smooth simple areoles.

### *Chordodes gestri* CAMERANO, 1904

Material 1 ♂

Documentation NONE

Distribution **Guatemala:** Quezaltenango (1 ♂, CAMERANO 1904a).

The original description indicates the presence of simple and tubercle areoles as well as the presence of clusters of 8–10 circumcluster areoles around a pair of crowned areoles. However, as further fine structural descriptions and distribution patterns are lacking, this species requires a reinvestigation.

### *Chordodes guineensis* SPIRIDONOV, 2001

Material 1 ♂, 4 ♀♀

Documentation drawings in SPIRIDONOV (2001).

Distribution **Guinea:** Kankan (in abscess of dog, 1 ♂, 4 ♀♀, SPIRIDONOV 2001).

simple areoles	with granulated surface
tubercle areoles	present
flom areoles	present
bulging areoles	probably absent
crowned areoles	filaments either very short, fine and numerous or very long
circumcluster areoles	present, as elevated areoles with fine bristles on top
dimorphism in crowned areoles?	present, but distribution not clear; according to text, crowned areoles with long filaments occur in the dorsal and lateral side, while those with short areoles occur in the lateral and ventral side
form of crowned areole cluster	pair of crowned areoles with 6–17 circumcluster areoles

Comment on species status: The distribution of the two types of crowned areoles is unusual compared to other species with dimorphic crowned areoles, because areoles with long filaments appear not to occur in the ventral line (which is the case in all other species when long filaments are present). If the dorsal and ventral sides were not confused in this investigation, this is an important diagnostic character of *C. guineensis*. SPIRIDONOV (2001) does not mention whether this description does account to males and females and it should be checked whether the male does also have a crowned areole dimorphism.

### [*Chordodes hamatus* RÖMER, 1895]

- Material** 3♂♂, 2♀♀
- Documentation** drawings in RÖMER (1896).
- Distribution** Gaboon: "Sibanga Farm" (3♂♂, 2♀♀, RÖMER 1895b).

HEINZE (1934) recognized this species to be a mermithid nematode and renamed it *Gordionermis hamatus*.

### *Chordodes hawkeri* CAMERANO, 1902

- Material** at least 6♂♂, 11♀♀
- Documentation** no figures in original description, SEM in ZANCA et al. (2006b).
- Distribution** East Africa, Lake Victoria (as "Victoria Nyanza", not further specified, 1♂, 3♀♀, CAMERANO 1912b); **Democratic Republic of the Congo**: Katanga (unspecified number and sex, CAMERANO 1915); **Kenya**: Mombasa (unspecified number and sex, CAMERANO 1915); **Sierra Leone** (unspecified number and sex, CAMERANO 1915); **South Africa**: probably Grahamstown (as "Grahamstow") (3♂♂, 1♀, CAMERANO 1908b); **Sudan**: White Nile (2♂♂, 7♀♀, CAMERANO 1902b).

simple areoles	irregular structure, roughly structured surface
tubercle areoles	present
thorn areoles	present
bulging areoles	present as elevated, not further structured areoles in groups of 2-10
crowned areoles	probably only present as isolated areoles with very short apical filaments, better described as a crown of granule-like processes
circumcluster areoles	not present
dimorphism in crowned areoles?	not present
form of crowned areole cluster	clusters not present

**Comment on species status:** The description and documentation of this species is not detailed enough to recognize characters particular to this species, a fine structural reinvestigation is required. It should be checked in particular whether the areoles with apical granules can be regarded as crowned areoles.

### *Chordodes heinzei* SCIACCHITANO, 1937

- Material** 1♂, 1♀
- Documentation** drawings in SCIACCHITANO (1937, 1958), SEM in ZANCA et al. (2006a).
- Distribution** **Democratic Republic of the Congo**: Kasai, Luebo (1♂, SCIACCHITANO 1937), Kasai, Makaw (1♀, SCIACCHITANO 1961b).

simple areoles	flat, with irregularly structured surface
tubercle areoles	present, tubercle is large and club-shaped
thorn areoles	not described
bulging areoles	isolated or in clusters of 2–4, slightly conical, with fine bristles on top
crowned areoles	with moderately long apical filaments (not exceeding the borders of the cluster)
circumcluster areoles	slender, curved towards centre of the cluster, with ring of fine bristles on top
dimorphism in crowned areoles?	not described
form of crowned areole cluster	pair of crowned areoles, surrounded by 17–24 circumcluster areoles

Comment on species status: This species belongs into a large group in which the simple areoles are smooth or superficially structured, but not as extreme as in the “black berry” areoles. Clusters of crowned and circumcluster areoles are present. Among these species, *C. heinzei* is characterized by the presence of tubercle and bulging areoles, but the absence of thorn areoles. Additionally, *C. heinzei* has club shaped tubercles, which are elsewhere only known from *C. gariazzi*.

### [*Chordodes ibembensis* SCIACCHITANO, 1958]

Material 3♂♂

Documentation drawing in SCIACCHITANO (1958)

Distribution **Angola:** Dundo (2♂♂, SCIACCHITANO 1961a); **Democratic Republic of the Congo:** Uele, Ibembo (1♂, SCIACCHITANO 1958).

This species was synonymised with *C. clavatus* after a reinvestigation using SEM (DE VILLALOBOS et al. 2007a).

### *Chordodes ikelensis* SCIACCHITANO, 1961

Material 1♀

Documentation drawing in SCIACCHITANO (1961b).

Distribution **Democratic Republic of the Congo:** Ikela, stream Tshuapa (1♀, SCIACCHITANO 1961b).

simple areoles	with irregular circumference
tubercle areoles	probably present (simple areoles with “tooth” are mentioned in text but not figured)
thorn areoles	not described
bulging areoles	present, with solid tubercle on top
crowned areoles	with very long apical filaments
circumcluster areoles	present, according to figure elevated, with more or less flat apical surface, in group diverging from center to periphery
dimorphism in crowned areoles?	not described
form of crowned areole cluster	pair of crowned areoles, surrounded by up to 30 circumcluster areoles

Comment on cuticular structure: Large dark areoles are described with a strong "tooth" on top. They are described to occur isolated or in groups up to four, but the figure only shows isolated areoles. Such areoles resemble bulging areoles, but this is the only case, where bulging areoles carry a tubercle.

Comment on species status: A fine structural reinvestigation of this species will be helpful, but the bulging areoles with a tubercle on top appear to be a unique character for this species.

### *Chordodes insidiator* CAMERANO, 1899

Material 1 ♂

Documentation drawing in CAMERANO (1899).

Distribution Malaysia: Borneo, Sarawak, Cascata del Monte (1 ♂, CAMERANO 1899).

simple areoles	present, flat
tubercle areoles	present
thorn areoles	present
bulging areoles	abundantly present
crowned areoles	present, but exact form unknown
circumcluster areoles	present, but exact form unknown
dimorphism in crowned areoles?	not described
form of crowned areole cluster	two to three crowned areoles are surrounded by an unknown number of circumcluster areoles

Comment on species status: The description and documentation of this species is not detailed enough to recognize characters particular to this species, a fine structural reinvestigation is required.

### *Chordodes iturensis* SCIACCHITANO, 1958

Material 3 ♂♂, 1 ♀

Documentation drawings in SCIACCHITANO (1958).

Distribution Democratic Republic of the Congo: Ituri, Nioka (3 ♂♂, SCIACCHITANO 1958), Urundi, Usumbara (1 ♀, SCIACCHITANO 1958).

simple areoles	irregularly shaped
tubercle areoles	probably present
thorn areoles	not described
bulging areoles	not described
crowned areoles	present with either short fine or very long apical filaments, exact form and distribution pattern are not described

circumcluster areoles	present, but exact form not described
dimorphism in crowned areoles?	present, but distribution pattern not described
form of crowned areole cluster	unknown number of crowned areoles surrounded by unknown number of circumcluster areoles

Comment on species status: The description and documentation of this species is not detailed enough to recognize characters particular to this species, a fine structural reinvestigation is required.

### *Chordodes jandae* CAMERANO, 1895

**Material** 2♂♂, 1♀

**Documentation** drawings in CAMERANO (1897a), LM in SCHMIDT-RHAESA (2002a), SEM in DE MIRALLES & DE VILLALOBOS (1994) and SCHMIDT-RHAESA (2002a).

**Distribution** "stream near Dillu, Timor" probably means **East Timor**: stream near Dili (2♂♂, CAMERANO 1895a); **Australia**: Queensland, Cucania south of Cairns (1♀, DE MIRALLES & DE VILLALOBOS 1994).

simple areoles	flat, with strongly structured surface ("blackberry areole")
tubercle areoles	present, but rare
thorn areoles	present (in Australian specimen)
bulging areoles	present, as "blackberry" areoles with warty surface
crowned areoles	with very short apical filaments
circumcluster areoles	present, either with only moderately structured surface (Australian specimen) or with strong "blackberry" structure (Timor specimens)
dimorphism in crowned areoles?	not described
form of crowned areole cluster	pair of crowned areoles enclosing a central tubercle, surrounded by about 20 circumcluster areoles (in Australian specimen, number may be lower in Timor specimens)

Comment on areolar structure: There are slight differences between the Timor specimens and the better investigated Australian specimen such as the probable absence of thorn areoles in the Timor specimens and differences in the form of circumcluster areoles, the validity of these differences should be tested in a reinvestigation of the Timor specimens. Large "craters" observed by DE MIRALLES & DE VILLALOBOS (1994) probably represent regions, where the clusters have mechanically lost the central crowned areoles (SCHMIDT-RHAESA 2002a).

Comment on species status: This species belongs into a large group of species, in which the simple areoles are strongly structured into "blackberry" areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes jandae* is characterized by the presence of tubercle, thorn and bulging areoles and comparably large crowned areole clusters (> 20).

## *Chordodes japonensis* INOUE, 1952

- Material** numerous specimens of both sexes
- Documentation** drawings in INOUE (1952a,b, 1988), SEM in BAEK (1993) and SCHMIDT-RHAESA (2004).
- Distribution** **Japan:** different locations on Honsyu (49♂♂, 37♀♀, INOUE 1952b), prefectures Tochigi, Saitama, Chiba, Tokyo, Yamanashi, Aichi, Nara (INOUE 1951), Nagano (INOUE 1952a), Kanto (INOUE 1988), Shimosakamoto, Otsu city (1♂, SCHMIDT-RHAESA 2004), Hiyoshidai, Otsu city (1♀, SCHMIDT-RHAESA 2004); **South Korea:** Pakdal, Kyongju-gun, Kyongsangbuk-do (15♂♂, 3♀♀, BAEK 1993), Seoul (1♀, BAEK 1993), Mt. Moak, Chollabuk-do (1♂, 2♀♀, BAEK 1993), Sakimak, Kyunggi-do (1♂, 1♀, BAEK 1993). [in publications by INOUE, if not otherwise indicated, only the distribution in certain prefectures is indicated, no numbers or sex are given].

Note: *Chordodes japonensis* is briefly mentioned with some distribution records already in INOUE (1951). The description of this species was given in parallel in two publications in 1952, from which INOUE (1952a) occurred earlier during the year than INOUE (1952b), although this second description is more detailed.

simple areoles	rounded areoles, moderately elevated above cuticular surface, surface slightly irregular structured
tubercle areoles	present, but rare
thorn areoles	present according to INOUE (1952b), they were not found in SEM investigations by BAEK (1993) and SCHMIDT-RHAESA (2004)
bulging areoles	not present, but simple areoles may have different levels of elevation
crowned areoles	with short, but comparatively solid or (along ventral midline) with very long apical filaments
circumcluster areoles	present, with tuft of apical bristles, areoles with such a bristle form a group of ascending height towards the central crowned areoles
dimorphism in crowned areoles?	present
form of crowned areole cluster	pair of crowned areoles encircling a central tubercle, surrounded by varying number of circumcluster areoles

Comments on cuticular structure: The original description by INOUE (1952a,b) and the SEM reinvestigations differ slightly, these differences were listed by SCHMIDT-RHAESA (2004).

Comment on species status: This species belongs into a large group, in which the simple areoles are smooth or superficially structured, but not as extreme as in the “blackberry” areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes japonensis* is quite similar to *C. anthophorus* and *C. timorensis*, the differences between these species should be made clearer in further investigations.

*Chordodes joyeuxi* DORIER, 1935

- Material** 1 ♀
- Documentation** drawings in DORIER (1935).
- Distribution** **Vietnam:** Langson, Tonkin (1 ♀, DORIER 1935).

simple areoles	with irregular shape and surface ("blackberry areole")
tubercle areoles	present
thorn areoles	present
bulging areoles	not described
crowned areoles	with long apical filaments (exceeding borders of the cluster)
circumcluster areoles	present, but fine structure not described
dimorphism in crowned areoles?	not described
form of crowned areole cluster	pair of crowned areoles encircling a central tubercle, surrounded by 7–10 circumcluster areoles

Comment on species status: This species belongs into a large group of species, in which the simple areoles are strongly structured into "blackberry" areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes joyeuxi* is characterized by the combination of possessing tubercle and thorn areoles and lacking bulging areoles. It is distinguished from *C. shoutedeni*, which also shows this combination, by longer apical filaments in the crowned areoles, these filaments are short in *C. shoutedeni*.

*Chordodes kakandensis* SCIACCHITANO, 1958

- Material** 1 ♀
- Documentation** drawings in SCIACCHITANO (1958).
- Distribution** **Democratic Republic of the Congo:** Lualaba, Kakanda (1 ♀, SCIACCHITANO 1958).

The description and figures of this species are insufficient to make any statements about the species status. Crowned areoles, probably with many fine and short apical filaments are present as well as simple, circumcluster and probably thorn areoles, but their exact form and distribution patterns are unknown.

*Chordodes kallstenii* JÄGERSKIÖLD, 1897

- Material** 1 ♀
- Documentation** drawings in JÄGERSKIÖLD (1897).
- Distribution** **Cameroon:** Ekundu (1 ♀, JÄGERSKIÖLD 1897).

The presence of simple areoles, crowned areoles and thorn areoles is indicated in the original description, but few fine structural details and no distribution patterns are present. Therefore, this species needs a reinvestigation.

*Chordodes kivuensis* SCIACCHITANO, 1958**Material** 1 ♂**Documentation** drawings in SCIACCHITANO (1958).**Distribution** **Democratic Republic of the Congo:** Kivu, Tshibinda (1 ♂, SCIACCHITANO 1958).

This species is insufficiently described. The original description indicates the presence of simple areoles, either tubercle or thorn areoles and clusters with crowned areoles, but these are only described as clusters of 12–15 areoles with a tuft of bristles in the center. A reinvestigation will clear the fine structural details and distribution patterns.

*Chordodes kolensis* SCIACCHITANO, 1933**Material** 9 ♂♂, 15 ♀♀**Documentation** drawings in SCIACCHITANO (1933, 1958), SEM in ZANCA et al. (2006a).

**Distribution** **Angola:** Tsharissoka, on street between Dundo and Camissombo (1 ♂, SCIACCHITANO 1961a); **Democratic Republic of the Congo:** Borobo, Uebi (2 ♀♀, SCIACCHITANO 1933), Kole (1 ♀, SCIACCHITANO 1933), Wangata (1 ♀, SCIACCHITANO 1933), Goquilhatville (1 ♀, SCIACCHITANO 1933), Kahzenze (1 ♀, SCIACCHITANO 1933), Kisangani (as Stanleyville, 2 ♂♂, 3 ♀♀, SCIACCHITANO 1958), Gwange, Busu-Bodua (1 ♂, SCIACCHITANO 1958), Kasai, Sankuru, Lusambo (1 ♂, SCIACCHITANO 1961b), Kivu, Mt. Kahuzi (1 ♂, SCIACCHITANO 1961b), Bokungu in province Equateur Tshuapa (2 ♂♂, ZANCA et al. 2006a), Gemena in province Equateur Ubangi (1 ♂, ZANCA et al. 2006a), Uele, Ibembo (1 ♂, ZANCA et al. 2006a), Yokamba in province Equateur (1 ♂, 4 ♀♀, ZANCA et al. 2006a); **Côte d'Ivoire:** Mont Nimba (1 ♀, ZANCA et al. 2006a); **Kenya:** Nairobi, Katira Forest (1 ♀, ZANCA et al. 2006a) [for some confusion with the individuals described by SCIACCHITANO see ZANCA et al. 2006a].

simple areoles	irregularly shaped, more or less smooth surface
tubercle areoles	not described
thorn areoles	not described
bulging areoles	isolated or in groups of up to three areoles, elevated, smooth surface, neighboring areoles closely touch each other
crowned areoles	with very short apical filaments, in females along the ventral midline with very long filaments
circumcluster areoles	slender, elevated areoles
dimorphism in crowned areoles?	present in females
form of crowned areole cluster	pair of crowned areoles surrounded by 20–26 circumcluster areoles

**Comment on species status:** This species belongs into a large group in which the simple areoles are smooth or superficially structured, but not as extreme as in the “black-

berry" areoles. Clusters of crowned and circumcluster areoles are present. Typical for *C. kolensis* are probably blossom-shaped arrangements of areoles in which four semi-circular areoles surround a central one. Such an arrangement is unknown from other species, a homology to other areolar types is uncertain.

### *Chordodes koreensis* BAEK, 1993

- Material** 12♂♂, 5♀♀
- Documentation** drawings and SEM in BAEK (1993).
- Distribution** **South Korea:** Pakdal, Kyongju gun, Kyongsangbuk-do (1♂), Pakdal, Kyongju-gun (6♂♂, 3♀♀), Mt. Chogye, Chollanam-do (5♂♂, 1♀), Mt. Worak, Choongchungbuk do (1♀) (all reports by BAEK 1993).

simple areoles	flat, strongly "blackberry"-structured
tubercle areoles	present
thorn areoles	not described
bulging areoles	present in clusters of 2–4, smooth surface
crowned areoles	there are typical arrangements corresponding to a pair of crowned areoles and surrounding circumcluster areoles, but the pair of areoles in the centre do not have conspicuous apical filaments, only small central granules (plate 1, fig. 3 in BAEK 1993) or a small central tuft of bristles (plate 1, fig. 4 in BAEK 1993). Therefore, these can be considered as crowned areoles without apical filaments
circumcluster areoles	present, smooth surface with occasional occurrence of few fine bristles
dimorphism in crowned areoles?	not described
form of crowned areole cluster	pair of crowned areoles surrounded by 7–11 circumcluster areoles

**Comment on species status:** This species belongs into a large group of species, in which the simple areoles are strongly structured into "blackberry" areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes koreensis* is characterized by the presence of tubercle and bulging areoles and the absence of thorn areoles. From other species with this character combination it can be distinguished by the very short apical projections on the crowned areoles.

### *Chordodes lefeburei* (SCIACCHITANO, 1937)

As *Parachordodes lefeburi* by SCIACCHITANO (1937), transferred to *Chordodes* by SCIACCHITANO (1958)

- Material** 1♀
- Documentation** drawings in SCIACCHITANO (1937, 1958).
- Distribution** **Democratic Republic of the Congo:** Katanga, Kanzenze (1♀, SCIACCHITANO 1937).

The descriptions of this species, the original description as *Parachordodes lefeburi* (SCIACCHITANO 1937) as well as the redescription as *Chordodes lefeburi* (SCIACCHITANO

1958) are insufficient. Simple areoles of variable shape are present as well as tubercle or thorn areoles and clusters composed of crowned areoles with short apical filaments and up to 20 surrounding circumcluster areoles, but no fine structural details are described or figured.

### *Chordodes lenti* CARVALHO, 1944

**Material** 1 ♂

**Documentation** drawings in CARVALHO (1944).

**Distribution** Brazil: Viçosa, Minas Gerais (1 ♂, CARVALHO 1944).

simple areoles	irregularly distributed, with wide interareolar spaces, smooth surface
tubercle areoles	present
thorn areoles	not described (or confused with tubercle areoles)
bulging areoles	not described
crowned areoles	present, with few (up to 10) moderately long apical filaments
circumcluster areoles	not clear, figures show few areoles in close neighborhood of crowned areoles, these may be circumcluster areoles
dimorphism in crowned areoles?	not described
form of crowned areole cluster	crowned areoles occur in pairs or in clusters of 3, it is not clear whether they are associated with few circumcluster areoles or not

**Comment on species status:** This species belongs into a group of species characterized by wide spaces between the areoles. *Chordodes lenti* is quite similar to *C. moraisi*, the differences between these species have to be made clearer. From other species with wide interareolar spaces *C. lenti/C. moraisi* can be distinguished by the absence of clear circumcluster areoles in combination with the presence of smooth simple areoles.

### [*Chordodes lichyi* SCORZA, 1952]

**Material** 2 ♂♂

**Documentation** drawings in SCORZA (1952).

**Distribution** Venezuela: Cerro Marahuaca, Cunucunuma (2 ♂♂, SCORZA 1952).

The description of this species does not contain any usable information on the structure of areoles. Therefore, a reinvestigation must clear, whether this is a *Chordodes* species at all and if so, describe the fine structure as well as distribution of areoles.

*Chordodes ligasiensis* SCIACCHITANO, 1933**Material** 1♂, 2♀♀**Documentation** drawings in SCIACCHITANO (1933, 1958).**Distribution** **Democratic Republic of the Congo:** Ligasa, Isango (1♂, 2♀♀, originally described as 3♀♀ in SCIACCHITANO 1933, later recognized as 1♂, 2♀♀ by SCIACCHITANO 1958).

The description of this species is insufficient. Simple areoles and clusters composed of 2–4 crowned areoles and up to 20 circumcluster areoles are mentioned and figured with low magnification, but no further details are recognizable.

*[Chordodes liguligerus* RÖMER, 1895]**Material** 1♀**Documentation** drawings in RÖMER (1895b).**Distribution** **India:** Calcutta (1♀, RÖMER 1895b).

This species was recognized to be a mermithid nematode by Heinze (1935)

*[Chordodes longipilus* KIRJANOVA, 1949]

Unfortunately, the description of this species could not be located. It is mentioned briefly in KIRJANOVA (1971), but without giving a reference.

*Chordodes lotus* DE MIRALLES & DE VILLALOBOS, 1997**Material** 1♀**Documentation** SEM in DE MIRALLES & DE VILLALOBOS (1997).**Distribution** **Argentina:** Misiones, Rio Uruguay (1♀, DE MIRALLES & DE VILLALOBOS 1997).

simple areoles	present as moderately elevated areoles with a roughly structured surface (“black-berry areoles”)
tubercle areoles	rarely present
thorn areoles	not described
bulging areoles	not described
crowned areoles	probably present only along the ventral midline, where areoles with apical filaments occur
circumcluster areoles	probably not present
dimorphism in crowned areoles?	probably present (see comment below)
form of crowned areole cluster	clusters are probably not present

Comments on areolar structure: DE MIRALLES & DE VILLALOBOS (1997) include two further areolar types in their description, areoles resembling simple areoles but carry-

ing a longitudinal depression and those with such a depression and short projections. The preservation of the crowned areoles on both sides along the ventral midline is not perfect, but these areoles probably indeed represent crowned areoles. This raises the question whether crowned areoles are also present on the lateral sides of the body and they may be represented by the areoles with a depression and projections. This would indicate a crowned areole dimorphism. Clusters with paired crowned areoles and circumcluster areoles appear not to be present.

Comment on species status: This species belongs to a group of species in which circumcluster areoles are lacking. *Chordodes lotus* is unique among these species in possessing only isolated crowned areoles on the body side.

### *Chordodes maculatus* SCIACCHITANO, 1958

**Material** 1♂, 5♀♀

**Documentation** drawings in SCIACCHITANO (1958).

**Distribution** **Democratic Republic of the Congo:** Kinshasa (as Leopoldville), Kalina (1♂, 2♀♀), lake Leopoldo II (1♀), Ubangi, Bokapo (Lisala) (1♀), Ubangi, Libenge (1♀) (all reports SCIACCHITANO 1958).

simple areoles	flat, lightly coloured areoles
tubercle areoles	either tubercle or thorn areoles appear to be present
thorn areoles	see tubercle areoles
bulging areoles	present as paired areoles enclosing a central tubercle
crowned areoles	probably present with very short apical filaments
circumcluster areoles	present, with fine bristles on top
dimorphism in crowned areoles?	not described
form of crowned areole cluster	probably present, but exact composition unknown. There are clusters, which are composed of elevated and dark areoles. All areoles are reported to have apical bristles, this may indicate a cluster composed only of crowned areoles or more or less inconspicuous crowned areoles in the centre.

Comment on species status: The description and documentation of this species is not detailed enough to recognize characters particular to this species, a fine structural reinvestigation is required. The name giving character are dark patches that may coincide with the occurrence of clusters with elevated areoles (crowned and circumcluster areoles). This colouration pattern, however, the "leopard pattern", occurs in several *Chordodes* species and is therefore not unique to *C. maculatus*.

*Chordodes madagascariensis* (CAMERANO, 1893)

**Material** 13♂♂, 15♀♀

**Documentation** drawings in CAMERANO (1897a), BEAUCHAMP (1916, 1923).

**Distribution** **Angola:** Duido (1♂, SCIACCHITANO 1961a), Calonda (1♂, SCIACCHITANO 1961a); **Democratic Republic of the Congo:** Mission Stappers (1♂, 1♀, BEAUCHAMP 1916), Kasongo (1♀, BEAUCHAMP 1916), Kitempuka (1♀, BEAUCHAMP 1916), Mayumbe (1♀, BEAUCHAMP 1923), Wombali (1♂, BEAUCHAMP 1923), Kananga (as Luluabourg, 1♂, BEAUCHAMP 1923), Lubumbashi (as Elisabethville, 1♂, 1♀, SCIACCHITANO 1932), Bas-Uélé, Gwane (1♀, SCIACCHITANO 1933), Boma (3♀♀, SCIACCHITANO 1933), Sankuru, Kondué (1♀, SCIACCHITANO 1933), Flandria (1♀, SCIACCHITANO 1958), Boende (2♂♂, SCIACCHITANO 1958), Kinshasa (as Leopoldville), Kalina (1♂, SCIACCHITANO 1958), Kinshasa (1♀, SCIACCHITANO 1958), isle Biana, Lokandu, Maniema (1♂, 1♀, SCIACCHITANO 1958), Tshuapa, near Ikela (1♂, SCIACCHITANO 1961b); **Guinea** (as French Guinea): Fouta Oulani (1♂, 2♀♀, CAMERANO 1915); **Madagascar:** Antananarivo (as Annanarivo) (1♂, CAMERANO 1893b).

Note: BEAUCHAMP (1923) reports one specimen of *C. madagascariensis* to be found together in one host specimen, an undetermined species of praying mantis, together with one specimen of *C. capensis*. Such report of the parasitization of one host specimen by two gordiid species is unusual and the specimens should be reinvestigated.

simple areoles	rounded or polygonal, light in colour
tubercle areoles	present
thorn areoles	present
bulging areoles	present, as pairs or clusters of up to four darker areoles
crowned areoles	present, probably with short apical filaments
circumcluster areoles	probably present (see below)
dimorphism in crowned areoles?	not described
form of crowned areole cluster	after CAMERANO (1897a), 10–14 crowned areoles form a cluster, after the drawing of BEAUCHAMP (1923), there is a cluster with a pair of large central areoles, surrounded by several further, darkly coloured areoles, the peripheral of which form a regular circle. The fine structure is not described.

Comment on species status: This species belongs into a large group in which the simple areoles are smooth or superficially structured, but not as extreme as in the “black-berry” areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes madagascariensis* resembles *C. moutoni* and *C. queenslandi*. A reinvestigation should make probable differences between these species clearer.

*Chordodes matensis* DE VILLALOBOS & DE MIRALLES, 1997**Material** 1 ♂**Documentation** SEM III DE VILLALOBOS & DE MIRALLES (1997).**Distribution** **Argentina:** Misiones, stream Chuña-Pirú (1 ♂, DE VILLALOBOS & DE MIRALLES 1997).

simple areoles	roundish, with irregularly structured surface
tubercle areoles	present, with thin or pointed tubercle
thorn areoles	present
bulging areoles	elevated, spherical areoles
crowned areoles	present, with moderately long apical filaments
circumcluster areoles	not present
dimorphism in crowned areoles?	not described
form of crowned areole cluster	crowned areoles occur in pairs, but further clusters are not present

Comment on species status: This species belongs to a group of species in which circumcluster areoles are lacking. *Chordodes matensis* is unique among these species in possessing only pairs of crowned areoles on the body side.

*Chordodes mobensis* SCIACCHITANO, 1958**Material** 1 ♀**Documentation** drawings in SCIACCHITANO (1958).**Distribution** **Democratic Republic of the Congo:** Moba (near Lake Tanganijka, 1 ♀, SCIACCHITANO 1958).

The description of this species is insufficient. Three types of areoles are indicated, the first are simple areoles with a roundish or irregular shape. The second appear to be bulging areoles, which occur in groups of 2–4. The last type is reported to be dark elevated areoles in clusters of 7–12. These probably represent crowned areole clusters, but the fine structure of these areoles is not described or figured and, for example, no apical filaments are evident. Therefore, this species needs a reinvestigation.

*Chordodes modiglianii* (CAMERANO, 1892)

As *Gordius modiglianii* by CAMERANO (1892), transferred to *Chordodes* by CAMERANO (1895a)

**Material** 2 ♂♂, 2 ♀♀**Documentation** drawing III CAMERANO (1897a).**Distribution** **Indonesia:** Enggano Island (as isola di Engano), Bua Bua (1 ♂, CAMERANO 1892), Sulawesi, Gorontalo (1 ♀, CAMERANO 1895a), West Papua, Manokwari, Baia di Dorè (1 ♂, 1 ♀, CAMERANO 1915).

simple areoles	with warty appearance (“blackberry areole”)
tubercle areoles	present
thorn areoles	not described
bulging areoles	not described
crowned areoles	with moderately long apical filaments (according to the drawing in Camerano 1897)
circumcluster areoles	present in unknown number, shape as simple areoles, but higher elevated
dimorphism in crowned areoles?	not described
form of crowned areole cluster	pair of crowned areoles, surrounded by unknown number of circumcluster areoles

Comment on species status: This species belongs into a large group of species, in which the simple areoles are strongly structured into “blackberry” areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes modiglianii* is characterized by the combination of the following characters: presence of tubercle areoles and absence of thorn and bulging areoles. *Chordodes modiglianii* resembles *C. silvestri* and the differences between these species must be made clearer.

### [*Chordodes moluccanus* RÖMER, 1895]

**Material** 2 ♀♀

**Documentation** drawings in RÖMER (1896).

**Distribution** **Indonesia:** Halmahera, Soah Konorah, northeastern coast region (2 ♀♀, RÖMER 1895a).

There are no fine structural data, but as RÖMER (1896) indicates the presence of only one type of areoles (and some kind of bristles or spines), this species may either not belong to the genus *Chordodes* or an areolar diversity was overlooked. A reinvestigation will be helpful in clearing these problems.

### *Chordodes montgomeryi* CAMERANO, 1901

**Material** 1 ♀

**Documentation** none

**Distribution** **Madagascar:** Fort Dauphin (1 ♀, CAMERANO 1901a).

simple areoles	rounded or polygonal
tubercle areoles	probably present
thorn areoles	probably present
bulging areoles	not described
crowned areoles	present
circumcluster areoles	present
dimorphism in crowned areoles?	not described
form of crowned areole cluster	pair of crowned areoles, surrounded by 6–7 circumcluster areoles

Comment on species status: The description and documentation of this species is not detailed enough to recognize characters particular to this species, a fine-structural reinvestigation is required.

### *Chordodes moraisi* (CARVALHO, 1942)

As *Neochordodes moraisi* by CARVALHO (1942), transferred to *Chordodes* by CARVALHO (1944)

**Material** 1 ♂, 1 ♀

**Documentation** drawings in CARVALHO (1944), LM in CARVALHO (1942).

**Distribution** Brazil: Viçosa, Minas Gerais (1 ♀, CARVALHO 1942 and 1 ♂, CARVALHO 1944).

simple areoles	rounded, smooth surface, wide interareolar spaces
tubercle areoles	present
horn areoles	not described
bulging areoles	probably present (see comment below)
crowned areoles	present (described only in male), with moderately long apical filaments
circumcluster areoles	not present
dimorphism in crowned areoles?	not described
form of crowned areole cluster	crowned areoles are in pairs, but circumcluster areoles are obviously absent

Comment on areolar structure: The female, on which the original description was given and which was described as *Neochordodes moraisi* (CARVALHO 1942), has only one type of rounded areoles with wide interareolar spaces. Areoles often attach each other and form pairs, clusters or chains. A male found in the same location shows a similar general arrangement of areoles with wide interareolar spaces and clusters of elevated roundish areoles (CARVALHO 1944), but allows a distinction of different types of areoles including crowned areoles. These are stated to be also present in the female, although not described there (CARVALHO 1944).

Comment on species status: This species belongs into a group of species characterized by wide spaces between the areoles. *Chordodes moraisi* is quite similar to *C. lenti*, the differences between these species have to be made clearer. From other species with wide interareolar spaces *C. moraisi* / *C. lenti* can be distinguished by the absence of clear circumcluster areoles in combination with the presence of smooth simple areoles.

### *Chordodes morgani* MONTGOMERY, 1898

**Material** numerous specimens.

**Documentation** drawings in MONTGOMERY (1898c) and CHANDLER & WELLS (1989), LM in WATERMOLEN & CHANDLER (1993) and SCHMIDT-RHAESA et al. (2003), SEM in CHANDLER & WELLS (1989) and SCHMIDT-RHAESA et al. (2003).

**Distribution** USA: eastern states and Texas (see SCHMIDT-RHAESA et al. 2003 for a list of all locations).

Comments on the areolar structure: This species is particular in not showing the “typical” areolar types. The cuticle contains numerous elevations in different forms, from small knobs over pin-like elevations to distinctly elevated areoles, sometimes forming clusters composed of several areoles which stand more or less close to each other (SCHMIDT-RHAESA et al. 2003). There is obviously a considerable variation in the exact form of the cuticular structures (SCHMIDT-RHAESA et al. 2003). The elevated, clustered areoles may have a smooth surface or have a small crown of apical filaments and therefore represent crowned areoles, which makes *C. morgani* a member of the genus *Chordodes*.

### *Chordodes moutoni* CAMERANO, 1895

**Material** 7♂♂, 7♀♀

**Documentation** drawings in CAMERANO (1897a, 1899) and WU & TANG (1933), LM and SEM in SCHMIDT-RHAESA & BRUNE (2008), SEM in ZANCA & DE VILLALOBOS (2005).

**Distribution** China: Ho Chan in province Ngan Haei (2♂♂, 2♀♀, CAMERANO 1895b), Yünhwo Hsien, Chekiang province (4♂♂, 2♀♀, WU & TANG 1933); Malaysia: Perak (1♀, CAMERANO 1899), Perak, foot of Gunung Inas (1♂, CAMERANO 1903a, SHIPLEY 1903), Kedah (1♀, CAMERANO 1901b), Cameron highlands, 30 km NE of Tapan (1♀, SCHMIDT-RHAESA & BRUNE 2008).

simple areoles	flattest type of areoles, but distinctly elevated above areolar surface, with irregularly structured surface
tubercle areoles	present
thorn areoles	present
bulging areoles	present, but hard to distinguish from simple areoles. They are slightly more elevated than simple areoles and have fine bristles on their surface. They occur isolated or ingroups of up to four
crowned areoles	with moderately long apical filaments (reaching the border of the cluster). Crowned areoles with very long apical filaments are described from the ventral and dorsal midline in females from China.
circumcluster areoles	elevated and with apical tuft of fine bristles
dimorphism in crowned areoles?	present at least in females from China, in female from Cameron highlands, Malaysia, no dimorphism is present
form of crowned areole cluster	pair of crowned areoles, surrounded by 9–15 circumcluster areoles

Comment on areolar structure: The specimens from China differ in small details, such as the exact form of simple and circumcluster areoles, from the Malaysian specimens. These differences were regarded as too minor to separate these as two species by CAM

FRANO (1899), but a more detailed reinvestigation of specimens from both regions would be interesting in this regard.

Comment on species status: This species belongs into a large group in which the simple areoles are smooth or superficially structured, but not as extreme as in the "blackberry" areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes moutoni* resembles *C. madagascariensis* and *C. queenslandi* and the differences between these species should be made clearer. A probable difference between *C. moutoni* and *C. queenslandi* is the height of bulging areoles, in *C. moutoni* these are less prominent than in *C. queenslandi*.

### *Chordodes muelleri* SCIACCHITANO, 1937

[originally described as *C. mulleri* by SCIACCHITANO (1937), named *müllerii* in SCIACCHITANO (1958) and *muelleri* in ZANCA et al. (2006a)]

**Material** 1 ♀ (sex misinterpreted by SCIACCHITANO 1937).

**Documentation** drawing in SCIACCHITANO (1937), SEM in ZANCA et al. (2006a).

**Distribution** Ruanda: Gabiro (1 ♀, SCIACCHITANO 1937).

simple areoles	variable shape, roughly structured surface, irregular base
tubercle areoles	present
thorn areoles	not described
bulging areoles	described by ZANCA et al. (2006a), with more smooth surface, but as simple areoles are very heterogeneous, the differences between simple and bulging areoles are disputable
crowned areoles	with very short apical filaments on body sides or with long filaments along ventral midline
circumcluster areoles	slender, curved towards centre of the cluster
dimorphism in crowned areoles?	present, crowned areoles with long apical filaments occur along the ventral midline
form of crowned areole cluster	pair of crowned areoles, surrounded by 9-12 circumcluster areoles

Comment on species status: This species belongs into a large group in which the simple areoles are smooth or superficially structured, but not as extreme as in the "blackberry" areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes muelleri* is quite similar to *C. capensis* and *C. digitatus*, the differences between these species must be made clearer. All three species are distinguished from other species in this group by the presence of tubercle areoles, short apical filaments in the crowned areoles and the absence of bulging areoles.

*Chordodes nobilii* CAMERANO, 1901

Material	11♂♂, 9♀♀
Documentation	SEM in DE VILLALOBOS et al. (2004a) and SCHMIDT-RHAESA & GERKE (2006).
Distribution	<b>Argentina:</b> province Buenos Aires: Sierra de la Ventana in (3♀♀ as <i>C. carmelitanus</i> , DE MIRALLES 1989, 1♂, DE VILLALOBOS et al. 2004a), stream Sauce Grande in Sierra de la Ventana (4♂♂, DE VILLALOBOS et al. 2004a), Balcarce (1♀, DE VILLALOBOS et al. 2004a); province Córdoba: Cosquín (1♀, CAMERANO 1901c), stream San Lorenzo, Cura Brochero (as <i>C. carmelitanus</i> , 1♀, DE MIRALLES 1989), El Durazno (1♂, DE VILLALOBOS et al. 2004a), not further specified (2♀♀, DE VILLALOBOS et al. 2004a); province San Luis: Carpintería, stream Piedra Blanca in province San Luis (3♂♂ as neo- and paraneotypes, DE VILLALOBOS et al. 2004a), stream San Ignacio, Villa Larca, Aguas Blancas (2♂♂, 1♀, DE VILLALOBOS et al. 2004a).

simple areoles	moderately elevated, with rough surface structure ("blackberry areole")
tubercle areoles	present
thorn areoles	not described
bulging areoles	not described
crowned areoles	present at least along the ventral and dorsal midline in females. The stem of the areole is not clearly recognizable, solid filaments originate from a low structure on the cuticle
circumcluster areoles	not present
dimorphism in crowned areoles?	typical crowned areoles are present only in females, along the ventral and dorsal midlines
form of crowned areole cluster	no cluster appears to be present

Comments on areolar structure: Apart from the simple areoles and the crowned areoles in the female, the cuticle includes another type on the lateral body sides. These are similar to simple areoles, but have a tuft of short bristles on their apical side. Whether these should be regarded as (not distinctly bulging) bulging areoles or as homologues to the crowned areoles is unclear.

Comment on species status: This species belongs into a large group of species, in which the simple areoles are strongly structured into "blackberry" areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes nobilii* resembles *C. modiglianii* and *C. silvestri* in having the following characters: presence of tubercle areoles and absence of thorn and bulging areoles. From *C. modiglianii* and *C. silvestri* it is distinguished by the absence of a distinct stem in the crowned areoles.

*Chordodes ornatus* (GRENACHER, 1868)

As *Goeldius ornatus* by GRENACHER (1868), transferred to *Chordodes* by RÖMÉR (1896)

Material 1 ♀

Documentation drawings in GRENACHER (1868).

Distribution Philippines (no further location, 1 ♀, GRENACHER 1868).

simple areoles	conical in shape
tubercle areoles	not described
thorn areoles	not described
bulging areoles	not described
crowned areoles	with moderately long apical filaments (hardly reaching the border of the cluster) on the body sides and with long filaments in the dorsal and ventral midline
circumcluster areoles	present, but fine structure unknown
dimorphism in crowned areoles?	present. In dorsal midline one row of crowned areoles, ventral midline is flanked by two rows of crowned areoles
form of crowned areole cluster	pair of crowned areoles, surrounded by unknown number of circumcluster areoles

Comment on species status: The description and documentation of this species is not detailed enough to recognize characters particular to this species; a fine structural reinvestigation is required.

*[Chordodes oscillatus* KIRJANOVA, 1953]

Material 1 ♀

Documentation drawing in KIRJANOVA (1953).

Distribution Georgia: Tbilisi (1 ♀, KIRJANOVA 1953).

After a reinvestigation, DE VILLALOBOS et al. (2007b) synonymized this species with *Chordodes anthophorus*.

*[Chordodes parasitus* CREPLIN, 1847]

Material 1 ♀

Documentation NONE

Distribution Brazil (no further location, 1 ♀, CREPLIN 1847).

As JANDA (1894) notes, CREPLIN'S worm is certainly a nematomorph, but nothing further can be said. No areoles are described and so it is even not sure whether it belongs to the genus *Chordodes*, although this is the first species, for which the name was given. A reinvestigation is very desirable.

*Chordodes penicillatus* CAMERANO, 1895**Material** 1 ♀**Documentation** drawings in CAMERANO (1897a).**Distribution** unknown (the label “Cantraine: Italie” is suspected by CAMERANO (1895a) to be wrong. VON LINSTOW (1906a) listed Brazil as the origin for this species, but does not explain, how this information is gained).

simple areoles	slightly oval in shape, with roughly structured surface
tubercle areoles	not described
thorn areoles	not described
bulging areoles	not described
crowned areoles	with very long apical filaments
circumcluster areoles	present, but fine structure unknown
dimorphism in crowned areoles?	not described
form of crowned areole cluster	pair of crowned areoles, surrounded by unknown number of apical filaments

Comment on species status: The description and documentation of this species is not detailed enough to recognize characters particular to this species, a fine-structural reinvestigation is required.

*Chordodes peraccae* (CAMERANO, 1894)

As *Gordius peraccae* by CAMERANO (1894b), transferred to *Chordodes* by CAMERANO (1897a)

**Material** 3 ♀♀**Documentation** drawings in CAMERANO (1897a) and DE MIRALLS (1976a), SEM in DE VILLALOBOS & ZANCA (2001).**Distribution** **Argentina:** San Pablo in province Tucumán (1 ♀, CAMERANO 1894b); **Bolivia:** Aguir-enda (1 ♀, CAMERANO 1897c); **Brazil:** Uruçim (1 ♀, CAMERANO 1901d).

Note: the data in the following table are mainly based on a reinvestigation of the holotype (Argentinian specimen) and the Bolivian specimen by DE VILLALOBOS & ZANCA (2001).

simple areoles	in a variety of shapes: round, oval or horseshoe-shaped, smooth surface
tubercle areoles	present
thorn areoles	not described
bulging areoles	not described
crowned areoles	with either moderately long apical filaments or, along the ventral midline of the Bolivian specimen, with very long filaments
circumcluster areoles	present, with apical tuft of fine bristles
dimorphism in crowned areoles?	present, but described only from the Bolivian specimen
form of crowned areole cluster	pair of crowned areoles, surrounded by 8–10 circumcluster areoles

Comment on species status: This species belongs into a large group in which the simple areoles are smooth or superficially structured, but not as extreme as in the “black-berry” areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes peraccae* roughly resembles *C. anthophorus*, *C. japonensis* and *C. timorensis*, but differs from these by the variable shape of simple areoles.

### *Chordodes pilosus* MÖBIUS, 1855

Material 1 ♀

Documentation drawings in MÖBIUS (1855).

Distribution **Venezuela:** Ciudad Bolívar (1 ♀, MÖBIUS 1855) [sent to the Zoological Museum in Hamburg by a physician in Angostura (now Ciudad Bolívar), this is assumed to be also the collection locality].

simple areoles	present
tubercle areoles	not described
thorn areoles	not described
bulging areoles	not described
crowned areoles	present, at least along ventral midline
circumcluster areoles	not described
dimorphism in crowned areoles?	crowned areoles are clearly present along the ventral midline, whether there is another type is not sure
form of crowned areole cluster	not completely clear

Comments on species status: The description of this species by MÖBIUS (1855) does not include much data on areolar structure or distribution patterns, which led CAMERANO (1897a) to include this under “species inquirendae”. HEINZE (1935) reinvestigated the specimen and concluded that it is a valid species, having three types of areoles. However, he could not clearly demonstrate crowned areoles. These are, however, present along the ventral midline, as a preliminary unpublished investigation shows. The description and documentation of this species, however, is not detailed enough to recognize characters particular to this species, a fine-structural reinvestigation is required.

### *Chordodes pollonerae* CAMERANO, 1912

Material 1 ♂, 1 ♀

Documentation none.

Distribution **India:** Assam (1 ♂, CAMERANO 1912c); **Somalia:** Aodegle (1 ♀, CAMERANO 1915).

simple areoles	with warty surface ("blackberry areole")
tubercle areoles	present
thorn areoles	not described
bulging areoles	present in groups of 2-4, darker and more elevated than simple areoles
crowned areoles	with short apical bristles
circumcluster areoles	present
dimorphism in crowned areoles?	not described
form of crowned areole cluster	pair of crowned areoles, surrounded by 7-8 circumcluster areoles

Comment on species status: This species belongs into a large group of species, in which the simple areoles are strongly structured into "blackberry" areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes pollonevae* is quite similar to *C. staviarskii*, the differences must be made clearer. Both species are characterized by the presence of tubercle and bulging areoles and the absence of thorn areoles.

### *Chordodes polycoronatus* SCHMIDT-RHAESA & BRUNE, 2008

- Material** 1 ♀
- Documentation** LM and SEM in SCHMIDT-RHAESA & BRUNE (2008).
- Distribution** **Malaysia:** Cameron highlands, Chegar Peragh (1 ♀, SCHMIDT-RHAESA & BRUNE 2008).

simple areoles	with granular surface, sometimes with minute projections
tubercle areoles	present
thorn areoles	present but rare
bulging areoles	present isolated or in pairs, resembling crowned areoles
crowned areoles	with very short apical filaments, in females along the ventral midline with longer filaments
circumcluster areoles	present only in clusters along ventral midline in female
dimorphism in crowned areoles?	present in female
form of crowned areole cluster	large clusters with about 40 crowned areoles on body sides, only in females along ventral midline are clusters composed of a pair of crowned areoles, surrounded by circumcluster areoles

Comment on species status: This species belongs into a group of species in which the clusters are formed by similarly shaped areoles, making a distinction between crowned and circumcluster areoles difficult. *Chordodes polycoronatus* is characterized among these by the abundant and large clusters of crowned areoles

*Chordodes polytuberculatus* SCHMIDT-RHAESA & MENZEL, 2005

Material: 1♀

Documentation: SEM in SCHMIDT-RHAESA &amp; MENZEL (2005).

Distribution: Costa Rica: Rio Tempisque (1♀, SCHMIDT-RHAESA &amp; MENZEL 2005).

simple areoles	with irregularly structured surface
tubercle areoles	not present
horn areoles	not present
bulging areoles	as slender elevated areoles with smooth surface, in large numbers
crowned areoles	with moderately long, fine apical filaments
circumcluster areoles	resembling the bulging areoles in structure
dimorphism in crowned areoles?	not described
limit of crowned areole cluster	number of crowned areoles can not be reliably stated, there are probably two in a cluster, surrounded by up to 20 circumcluster areoles

Comment on species status: The presence of abundant, slender areoles on the cuticle is characteristic for this species. It differs from *C. brasiliensis*, the only other species with this character, by having clusters with crowned areoles on the lateral body sides, such clusters are not present in *C. brasiliensis*.

*[Chordodes puerilis* MONTGOMERY, 1898]

The male specimen originally described as *Chordodes puerilis* by MONTGOMERY (1898c) was then discovered to belong to *C. norgeni* (MONTGOMERY 1901, see also SCHMIDT-RHAESA et al. 2003).

*Chordodes puncticulatus* CAMERANO, 1895

Material: 3♂♂, 1♀

Documentation: drawings in CAMERANO (1897a).

Distribution: Indonesia: Sumatra, Deli (1♀, CAMERANO 1895a); Malaysia: Perak (2♂♂, CAMERANO 1899, Kedah (1♂, CAMERANO 1901b).

simple areoles	flat round or oval areoles, surface not heavily structured
tubercle areoles	present
horn areoles	probably present (see fig. 25 in CAMERANO 1897a)
bulging areoles	present, isolated or in small clusters, as elevated, dark areoles, fine structure is unknown
crowned areoles	probably present (see below)
circumcluster areoles	probably present (see below)
dimorphism in crowned areoles?	not described

form of crowned areole cluster	there are clusters composed of up to 26 areoles. According to the descriptions and drawings, it appears as if all areoles in a cluster have fine and short apical bristles. Whether these can be divided into crowned and circumcluster areoles must be shown in a reinvestigation.
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Comment on species status: The description and documentation of this species is not detailed enough to recognize characters particular to this species; a fine structural reinvestigation is required.

### *Chordodes queenslandi* SCHMIDT-RHAESA, 2002

Material 1♂, 2♀♀

Documentation LM and SEM in SCHMIDT-RHAESA (2002a).

Distribution **Australia:** Queensland, Carnarvon Gorge National Park (1♂, 1♀, SCHMIDT-RHAESA 2002a), Sydney (as *C. bouvieri* in RÖMLER 1895b) and as *C. modiglianii* in HEINZE 1935, 1♀, synonymised by SCHMIDT-RHAESA 2002a).

simple areoles	circular or oval, semicircular, with slightly rough surface
tubercle areoles	present, scattered
thorn areoles	present, rare
bulging areoles	present in pairs or in clusters of 3 or 4, elevated above simple areoles, dark colour, apically structured into granules or short processes
crowned areoles	with either moderately long (on body sides) or very long (along dorsal and ventral midlines) apical filaments
circumcluster areoles	structure similar to bulging areoles
dimorphism in crowned areoles?	present in both sexes
form of crowned areole cluster	pair of crowned areoles with a central tubercle, surrounded by 8–12 circumcluster areoles

Comment on species status: This species belongs into a large group in which the simple areoles are smooth or superficially structured, but not as extreme as in the “black berry” areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes queenslandi* resembles *C. madagascariensis* and *C. moutoni* and the differences between these species should be made clearer. A probable difference between *C. queenslandi* and *C. moutoni* is the height of bulging areoles, in *C. queenslandi* these are more prominent than in *C. moutoni*.

*Chordodes rigatus* SCIACCHITANO, 1937**Material** 1 ♂**Documentation** drawings in SCIACCHITANO (1937, 1958).**Distribution** **Democratic Republic of the Congo:** Lubumbashi (as Elisabethville, 1 ♂, SCIACCHITANO 1937).

The description and documentation of areoles in this species is not sufficient. In the original description it is only distinguished between lighter and darker areoles (SCIACCHITANO 1937), later three types of areoles are indicated (SCIACCHITANO 1958). The drawings in both publications differ in some respects. Simple and thorn areoles are present, as well as clusters of elevated areoles. The presence of crowned areoles and circumcluster areoles can be expected, but remains to be demonstrated.

*Chordodes ruandensis* SCIACCHITANO, 1937**Material** 1 ♀**Documentation** drawings in SCIACCHITANO (1937, 1958), SEM in ZANCA et al. (2006a).**Distribution** **Ruanda:** Gabiro (1 ♀, SCIACCHITANO 1937).

simple areoles	round or oval, with roughly structured surface
tubercle areoles	not described
thorn areoles	not described
bulging areoles	not described
crowned areoles	with moderately long apical filaments (slightly exceeding the borders of the cluster)
circumcluster areoles	as elevated areoles with fine bristles on top
dimorphism in crowned areoles?	not described
form of crowned areole cluster	pair of crowned areoles, surrounded by 16–19 circumcluster areoles

**Comment on species status:** Despite a reinvestigation by SEM (ZANCA et al. 2006a), the description and documentation of this species is not detailed enough to recognize characters particular to this species, a fine structural reinvestigation is required.

*Chordodes sajanensis* SPIRIDONOV, 2000**Material** probably 1 ♂**Documentation** drawings in SPIRIDONOV (2000).**Distribution** **Russia:** Guserskii pond in Lugovka river, 30 km from Minussinsk (1 specimen, probably 1 ♂, but posterior end damaged, SPIRIDONOV 2000).

simple areoles	roundish or polygonal
tubercle areoles	not present
thorn areoles	not present
bulging areoles	probably present as isolated larger and darker areoles
crowned areoles	present only on both sides along the ventral midline, with long (up to 300 $\mu\text{m}$ ) and short (10–15 $\mu\text{m}$ ) filaments. In pairs, sometimes isolate
circumcluster areoles	not present
dimorphism in crowned areoles?	not present, crowned areoles only along ventral midline
form of crowned areole cluster	only pairs of crowned areoles are present

Comment on species status: The presence of crowned areoles only along the ventral midline and the occurrence of crowned areoles isolated or in pairs is characteristic for this species.

### *Chordodes sandoensis* SCIACCHITANO, 1937

**Material** 1 ♀ (originally described as a male by SCIACCHITANO 1937, 1958, recognized as a female by ZANCA et al. 2006b).

**documentation** drawings in SCIACCHITANO (1937, 1958), SEM in ZANCA et al. (2006).

**Distribution** Democratic Republic of the Congo: Lulua Sandoa (1 ♀, SCIACCHITANO 1937).

simple areoles	irregular in structure, with more or less smooth surface and some fine bristles
tubercle areoles	not described
thorn areoles	present
bulging areoles	not described
crowned areoles	with very short apical filaments (fig. 4 in SCIACCHITANO 1937 indicates the presence of long filaments, but this is not indicated by SCIACCHITANO 1958 or confirmed by ZANCA et al. 2006b)
circumcluster areoles	as slender, elevated areoles with more or less smooth surface
dimorphism in crowned areoles?	not described
form of crowned areole cluster	pair of crowned areoles is surrounded by 13–15 circumcluster areoles

Comment on species status: This species belongs into a large group in which the simple areoles are smooth or superficially structured, but not as extreme as in the “black-berry” areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes sandoensis* is characterized among these species by the absence of tubercle areoles in combination with the presence of crowned areoles with short apical filaments. However, these characters should be subject of a further reinvestigation of this species.

*Chordodes schoutedeni* SCIACCHITANO, 1933

**Material** 1 ♀ (originally described as a male by SCIACCHITANO 1937, 1958, recognized as a female by ZANCA et al. 2006b).

**Documentation** drawings in SCIACCHITANO (1937, 1958), SEM in ZANCA et al. (2006b).

**Distribution** **Democratic Republic of the Congo:** Kinshasa (as Leopoldville, 1 ♀, SCIACCHITANO 1933).

simple areoles	irregular in shape, with warty surface ("blackberry areole")
tubercle areoles	present
thorn areoles	present
bulging areoles	not described
crowned areoles	with very short apical filaments
circumcluster areoles	slender, slightly curved towards centre of the cluster, some apically smooth, others with granular apical surface
dimorphism in crowned areoles?	not described
form of crowned areole cluster	pair of crowned areoles is surrounded by 23–27 circumcluster areoles

**Comment on species status:** This species belongs into a large group of species, in which the simple areoles are strongly structured into "blackberry" areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes schoutedeni* is characterized among these species by the following character combination: tubercle and thorn areoles present, bulging areoles absent, crowned areoles with short apical filaments.

*Chordodes shipleyi* CAMERANO, 1899

**Material** 1 ♂

**Documentation** drawings in CAMERANO (1899).

**Distribution** **Malaysia:** Sarawak (1 ♂, CAMERANO 1899).

simple areoles	with strong warty surface ("blackberry areoles")
tubercle areoles	present
thorn areoles	present
bulging areoles	present isolated or in groups up to seven, structure as simple areoles, but higher elevated and darker in colour
crowned areoles	with short and fine apical filaments, along ventral midline with very long filaments
circumcluster areoles	correspond in structure to the bulging areoles
dimorphism in crowned areoles?	present
form of crowned areole cluster	pair (or three) of crowned areoles, surrounded by several circumcluster areoles

**Comment on species status:** This species belongs into a large group of species, in which the simple areoles are strongly structured into "blackberry" areoles. Clusters of

crowned and circumcluster areoles are present. *Chordodes shipleyi* resembles *C. jandae* and *C. skorikovi* in many characters, the differences between these species have to be made clearer.

### *Chordodes siamensis* CAMERANO, 1903

**Material** 2♂♂, 4♀♀

**Documentation** drawing in BEAUCHAMP (1923).

**Distribution** **Angola:** near Cassanguidi, Lunda N.E. (1♀, SCIACCHITANO 1961a); **India:** Assam (1♂, CAMERANO 1908a); **Democratic Republic of the Congo:** Ibehubo (1♂, BEAUCHAMP 1923), Kotili (1♀, SCIACCHITANO 1933), probably Bokoro, Kunungu, Funda Biabo (unknown sex, mentioned in a list in SCIACCHITANO 1958 with reference to SCIACCHITANO 1937, where this species does not occur); **Birma:** Pegu (1♀, CAMERANO 1908a); **Thailand** (as Siam): Biserat (1♀, CAMERANO 1903b).

simple areoles	present
tubercle areoles	present
thorn areoles	present (in specimen from Ibehubo)
bulging areoles	probably present
crowned areoles	with either long apical filaments or, scattered, with shorter filaments
circumcluster areoles	present
dimorphism in crowned areoles?	present, but according to the description of CAMERANO (1903b), crowned areoles with long filaments are not only restricted to the ventral and/or dorsal midlines
form of crowned areole cluster	pair of crowned areoles with circumcluster areoles

**Comment on areolar structure:** The occurrence of a *Chordodes* species on two continents is, to the current knowledge, unusual. Although CAMERANO (1903b, 1915) describes the cuticular structure in some detail, we regard this description as not sufficient to reliably state the occurrence of this Asian species in Africa, as BEAUCHAMP (1923) and later SCIACCHITANO (1933, 1958, 1961) did. A reinvestigation, especially of the Asian individuals, will clear this point.

**Comment on species status:** The description and documentation of this species is not detailed enough to recognize characters particular to this species, a fine structural reinvestigation is required.

*Chordodes silvestri* CAMERANO, 1895**Material** 2♂♂, 1♀**Documentation** drawings in CAMERANO (1897a) and INOUE (1952a).**Distribution** **Indonesia:** Borneo (Giappone and Goehong, Kenepai) (1♀, CAMERANO 1895a); **Japan:** no further location (2♂♂, CAMERANO 1895a).

simple areoles	with warty surface ("blackberry areoles")
tubercle areoles	present
thorn areoles	not described
bulging areoles	not described
crowned areoles	with moderately long apical filaments (slightly exceeding the border of the cluster)
circumcluster areoles	present, as elevated and dark areoles, fine structure unknown
dimorphism in crowned areoles?	not described
form of crowned areole cluster	pair of crowned areoles, surrounded by unknown number of circumcluster areoles

**Comment on species status:** This species belongs into a large group of species, in which the simple areoles are strongly structured into "blackberry" areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes silvestri* is characterized by the combination of the following characters: presence of tubercle areoles and absence of thorn and bulging areoles. *Chordodes silvestri* resembles *C. modiglianii* and the differences between these species must be made clearer.

*Chordodes skorikovi* CAMERANO, 1903**Material** 5♂♂, 5♀♀**Documentation** drawing and LM in FERNANDO & DISSANAIKE (1962).**Distribution** **Sri Lanka** (as Ceylon): no further location (1♀, CAMERANO 1903c and 1♀, CAMERANO 1903d), Kandy (1♀, CAMERANO 1903c), Colombo (1♂, FERNANDO & DISSANAIKE 1962); **Thailand** (as Siam): no further location (4♂♂, 2♀♀, CAMERANO 1904b).

simple areoles	with warty surface ("blackberry areoles")
tubercle areoles	present
thorn areoles	present
bulging areoles	present in clusters of 2-4, similar in structure to simple areoles, but more elevated and darker in colour
crowned areoles	with very fine, short apical filaments
circumcluster areoles	similar in structure to the bulging areoles
dimorphism in crowned areoles?	indicated to be present in females by CAMERANO (1904b)
form of crowned areole cluster	pair of crowned areoles, surrounded by 7-8 circumcluster areoles

**Comment on species status:** This species belongs into a large group of species, in which the simple areoles are strongly structured into "blackberry" areoles. Clusters of

crowned and circumcluster areoles are present. *Chordodes skorikovi* is characterized by the presence of tubercle, thorn and bulging areoles and comparably small crowned areole clusters (< 8).

[*Chordodes somaliensis* SCIACCHITANO, 1961]

Material 1 ♂

Documentation drawing in SCIACCHITANO (1961c).

Distribution Somalia: Afgoi dall'Agronomo (1 ♂, SCIACCHITANO 1961c).

SCIACCHITANO (1961c) described two types of areoles on the cuticle of this species. Both are roundish areoles, resembling each other, but one type being darker than the other. No surface structure or appendages are described or figured, therefore it is questionable, whether this specimen belongs to the genus *Chordodes*.

*Chordodes staviarskii* CARVALHO & FEIO, 1950

Material 1 ♀

Documentation drawings and LM in CARVALHO & FEIO (1950).

Distribution Brazil: Rio de Janeiro (1 ♀, CARVALHO & FEIO 1950).

simple areoles	with very irregular surface structure
tubercle areoles	present
thorn areoles	not described
bulging areoles	resembling simple areoles, but more elevated, occurring alone or in pairs
crowned areoles	with either fine, short apical filaments or, in the ventral and dorsal midline, with very long filaments
circumcluster areoles	elevated, structure probably more smooth than bulging areoles
dimorphism in crowned areoles?	present, in ventral and dorsal midline with long apical filaments
form of crowned areole cluster	pair of crowned areoles, surrounded by 6-12 circumcluster areoles, in the ventral and dorsal midline, the clusters are larger, containing 18-22 circumcluster areoles

Comment on species status: This species belongs into a large group of species, in which the simple areoles are strongly structured into "blackberry" areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes staviarskii* is quite similar to *C. polloneriae*, the differences must be made clearer. Both species are characterized by the presence of tubercle and bulging areoles and the absence of thorn areoles.

*Chordodes tenoderæ* KIRJANOVA, 1957

Material 2♀♀

Documentation drawings in KIRJANOVA (1957).

Distribution **China**: lake Taichu in province Tszjansu (2♀♀, KIRJANOVA 1957).

simple areoles	with warty surface ("blackberry areoles")
tubercle areoles	probably present
thorn areoles	probably present
bulging areoles	probably not present
crowned areoles	with either short or long apical filaments
circumcluster areoles	present, with fine bristles on apical surface
dimorphism in crowned areoles?	present, crowned areoles along the dorsal and ventral midline have long filaments, while those on the body sides have short filaments. In the ventral midline, clusters occur regularly and are abundant, in the dorsal midline, they are not as abundant
form of crowned areole cluster	pair of crowned areoles, surrounded by 12 circumcluster areoles

Comment on areolar structure: KIRJANOVA (1957) described a total of nine types of areoles, but not all of them are very clear. The areoles of (her) types 4 and 5 are described as being paired areoles with apical processes. From the figures, the fine structure is not clearly evident. The same accounts to types 8 and 9, which occur on the body sides and form clusters, resembling crowned areole clusters. SEM documentation will certainly help to clear the open questions in this species.

Comment on species status: The description and documentation of this species is not detailed enough to recognize characters particular to this species, a fine structural reinvestigation is required.

*Chordodes timorensis* CAMERANO, 1895

Material 1♂

Documentation drawings in CAMERANO (1897a).

Distribution "stream near Dillu, Timor" probably means **East Timor**: stream near Dili (1♂, CAMERANO 1895a).

simple areoles	flat, rounded, with smooth surface
tubercle areoles	present
thorn areoles	not described
bulging areoles	not described
crowned areoles	with moderately long apical filaments
circumcluster areoles	probably with fine apical bristles
dimorphism in crowned areoles?	not described
form of crowned areole cluster	pair (or 3) of crowned areoles, surrounded by unknown number of circumcluster areoles

Comment on species status: This species belongs into a large group in which the simple areoles are smooth or superficially structured, but not as extreme as in the "blackberry" areoles. Clusters of crowned and circumcluster areoles are present. *Chordodes timorensis* is quite similar to *C. anthophorus* and *C. jandae*, the differences between these species should be made clearer.

### *Chordodes tuberculatus* VON LINSTOW, 1901

Material 1 ♀

Documentation drawing in VON LINSTOW (1901), SEM in DE VILLALOBOS et al. (2007a).

Distribution **Tanzania:** Lake Malawi near Langenburg, 160 m depth (town Langenburg was given up with rising level of Lake Malawi and is not existent today) (1 ♀, VON LINSTOW 1901).

Note: The term "*tuberculatus*" has been used several times to describe nematomorph species and may cause confusion. A species *Gordius tuberculatus* has been described by VILLOT (1874) from Australia, this was later synonymised with *Chordodes caledoniensis* by RÖMER (1896). The name *Gordius tuberculatus* was then used again for the description of a new species from Croatia by ČANADIJA (1956).

simple areoles	conical, variable in shape, with roughly structured surface or short bristles
tubercle areoles	present, but tubercle is eccentric and may even be positioned next to an areole
thorn areoles	not present
bulging areoles	not present
crowned areoles	very slender areoles, with very short apical filaments
circumcluster areoles	not present
dimorphism in crowned areoles?	not described
form of crowned areole cluster	crowned areoles are clustered together, they are not surrounded circumcluster areoles

Comment on species status: This species belongs into a group of species in which the clusters are formed by similarly shaped areoles, making a distinction between crowned and circumcluster areoles difficult. *Chordodes tuberculatus* closely resembles *C. africanus* and *C. fukuui* but is distinguished from the second by the presence of simple areoles clearly elevated above the cuticular surface and from the first by high and slender crowned areoles.

### [*Chordodes uncinatus* SCIACCHITANO, 1958]

Material 1 ♂

Documentation drawing in SCIACCHITANO (1958a)

Distribution **Democratic Republic of the Congo:** Bidua, Lisala territory (1 ♂, SCIACCHITANO 1958).

This species was synonymised with *C. clavatus* after a reinvestigation using SEM (DE VILLALOBOS et al. 2007a).

[*Chordodes undulatus* VON LINSTOW, 1906]**Material** 1 ♀**Documentation** drawing in VON LINSTOW (1906b).**Distribution** Australia: Sydney (1 ♀, VON LINSTOW 1906b).

Two types of areoles are described, but none of them are crowned areoles (see SCHMIDT-RHAESA 2002a). Therefore, this species does not belong to the genus *Chordodes*.

[*Chordodes variopapillatus* RÖMER, 1895]**Material** 1 ♀**Documentation** drawings in RÖMER (1895b).**Distribution** “Bahia” (1 ♀, RÖMER 1895b).

The cuticle of this species is described as having papillae in various forms, but not belonging to different recognizable types. There is no resemblance to any known type of areoles. HEINZE (1935) regarded this to be an artificial elaboration of the cuticle, probably due to a fungal infection.

*Chordodes villalobi* SCHMIDT-RHAESA & BRUNE, 2008**Material** 1 ♀**Documentation** LM and SEM in SCHMIDT-RHAESA & BRUNE (2008).**Distribution** Malaysia: Cameron highlands, Chegar Peragh (1 ♀, SCHMIDT-RHAESA & BRUNE 2008).

simple areoles	conical, with tuft of apical fine bristles
tubercle areoles	present
thorn areoles	present, but rare
bulging areoles	not present
crowned areoles	with short apical filaments on body sides and with very long filaments along the ventral midline
circumcluster areoles	present only in clusters along ventral midline, but resembling crowned areoles with short apical filaments
dimorphism in crowned areoles?	present
form of crowned areole cluster	clusters on the body side are composed only of 15–20 crowned areoles, along ventral midline up to four crowned areoles are surrounded by about 15 circumcluster areoles

Comment on species status: Typical for *Chordodes villalobi* is the presence of a tuft of bristles on the simple areoles. Bristles can be present on simple areoles of other species, too, but only in *C. villalobi* and *C. corderoi* they form a tuft. Both species are distinguished by the absence of clusters with crowned are circumcluster areoles in *C. corderoi*, such clusters are present in *C. villalobi*.

*Chordodes wangi* WU & TANG, 1933

- Material** 1 ♀  
**Documentation** drawings in WU & TANG (1933).  
**Distribution** **China:** Soochow (1 ♀, WU & TANG 1933).

Three types of areoles are indicated in the rudimentary description of this species: simple, tubercle and crowned areoles. The crowned areoles occur in pairs and have short apical filaments, but further information on the presence of other areolar types, for example circumcluster areoles, as well as the fine structure and distribution patterns are lacking.

[*Chordodes weberi* (VILLOT, 1892)]

As *Gordius weberi* by VILLOT (1892), transferred to *Chordodes* by RÖMER (1896)

- Material** 1 ♂, 2 ♀♀  
**Documentation** drawings in CAMERANO (1897a) and SCIACCHITANO (1958).  
**Distribution** **Democratic Republic of the Congo:** Flandria (unknown sex, SCIACCHITANO 1958), Kivu, Uvira (1 ♂, SCIACCHITANO 1958); **Indonesia:** Sumatra, lake near Kaju tanam (1 ♀, VILLOT 1892), Sumatra, Si-Rambé (1 ♀, CAMERANO 1894a).

The descriptions of the two individuals from Sumatra show two types of areoles, simple areoles and areoles with an apical tubercle or thorn. Two publications in German language (JANDA 1894 and RÖMER 1896) mention a crown of apical filaments, but this is obviously a wrong translation. The individuals from Africa appear to correspond to the Sumatra individuals in this respect. However, as no crowned areoles are present, this species does not belong to the genus *Chordodes*.

## Key

We regard it as helpful to present a key leading to those species of *Chordodes* that can be recognized. However, it must be stressed that such a key can only be a working tool, as further investigations might reveal more or other structures than the ones currently known. Therefore, we suggest to use this key as a first help to identify species within the genus *Chordodes* but modify it whenever new information is available.

The key does covers species from all regions, the continents are indicated in parenthesis: Af = Africa, As = Central and Eastern Asia, Aus = Australia, CA = Central America, NA = North America, SA = South America, SEAs = Southeastern Asia (including India).

1. Wide spaces between areoles .....	2
Areoles more or less close together .....	4
2. Crowned areole cluster including circumcluster areoles absent .....	3
Circumcluster areoles present .....	<i>C. bukavuensis</i> (Af)
3. Simple areoles smooth .....	<i>C. lenti</i> (SAm) or <i>C. moroisi</i> (SAm)
Simple areoles warty .....	<i>C. brevipilus</i> (Aus)
4. Simple areoles absent, most abundant type are tubercle areoles .....	<i>C. devius</i> (As)
Simple areoles are present .....	5
5. Simple areoles with tuft of bristles .....	6
Simple areoles with or without bristles, but not forming a distinct tuft .....	7
6. Crowned areole clusters clearly present .....	<i>C. villalobi</i> (SEAs)
Crowned areoles not in clusters .....	<i>C. corderoi</i> (SAm)
7. Bulging areoles high, slender and abundant .....	8
Bulging areoles present or absent, but never slender and high .....	9
8. Crowned areoles present on lateral body sides .....	<i>C. polytuberculatus</i> (CAm)
Crowned areoles absent on lateral body sides .....	<i>C. brasiliensis</i> (SAm)
9. Crowned areole clusters without clear distinction in crowned and circumcluster areoles .....	10
Crowned areole clusters clearly composed of crowned and circumcluster areoles ..	18
10. Two types of crowned areoles present (long and short filaments) .....	11
Only one type of crowned areoles present .....	13
11. Crowned areoles isolated .....	<i>C. lotus</i> (SAm)
Crowned areoles in pairs .....	<i>C. matensis</i> (SAm)
Crowned areoles in larger clusters .....	12
12. Tubercle areoles absent .....	<i>C. furnessi</i> (SEAs)
Crowned areoles very close together .....	<i>C. compactus</i> (SEAs)
Crowned areole clusters very large .....	<i>C. polycoronatus</i> (SEAs)
13. Crowned areoles isolated or in pairs, only along ventral midline ...	<i>C. sajanensis</i> (As)
Crowned areole clusters with central pair of larger crowned areoles	<i>C. aethiopicus</i> (Af)
Crowned areoles may have different sized, but transitions are more gradual .....	14
14. Small clusters (< 7) .....	<i>C. cornuta</i> (SAm)
Larger clusters (≥ 10) .....	15
15. Simple areoles clearly recognizable .....	16
Cuticular structures not clearly recognizable as areoles .....	<i>C. morgani</i> (NAm)
16. Simple areoles flat .....	<i>C. fukuui</i> (As)
Simple areoles more elevated .....	17
17. Crowned areoles moderately high .....	<i>C. africanus</i> (Af)
Crowned areoles slender and high .....	<i>C. tuberculatus</i> (Af)
18. Bulging areoles carry a solid tubercle on top .....	<i>C. ikelensis</i> (Af)
Bulging areoles absent or without a tubercle .....	19

19.	Simple areoles strongly structured into "blackberry" areoles	20
	Simple areoles smooth or roughly structured, but not as "blackberry areoles"	27
20.	Thorn areoles present	21
	Thorn areoles absent	25
21.	Bulging areoles present	22
	Bulging areoles absent	24
22.	Tubercle in tubercle areoles club shaped	<i>C. gariuzzi</i> (Af)
	Thorn areoles only along ventral midline in females	<i>C. clavatus</i> (Af)
	Other characters	23
23.	Large crowned areole clusters (> 20 areoles)	<i>C. jandae</i> (SEAs, Aus)
	Smaller crowned areole clusters (< 8 areoles)	<i>C. skorikovi</i> (SEAs)
24.	Crowned areoles with long apical filaments	<i>C. joyeuxi</i> (SEAs)
	Crowned areoles with short apical filaments	<i>C. shoutedeni</i> (Af)
25.	Bulging areoles present	26
	Bulging areoles absent	<i>C. modiglianii</i> (SAm) or <i>C. silvestri</i> (As, SEAs)
26.	Apical filaments in crowned areoles moderately long	<i>C. clavatus</i> (Af)
	Apical filaments in crowned areoles short	<i>C. polloneræ</i> (SAm, Af) or <i>C. staviarskii</i> (SAm)
	Apical filaments in crowned areoles very short, more like granules	<i>C. koreensis</i> (As)
27.	Tubercle areoles absent	28
	Tubercle areoles present	29
28.	Apical filaments in crowned areoles moderately long	<i>C. festæ</i> (SAm, Af)
	Apical filaments in crowned areoles short	<i>C. sandoensis</i> (Af)
29.	Apical filaments in crowned areoles short	30
	Apical filaments in crowned areoles moderately long	31
30.	Bulging areoles present	<i>C. caledoniensis</i> (Aus, SEAs)
	Bulging areoles absent	<i>C. capensis</i> (Af) or <i>C. digitatus</i> (Af) or <i>C. muelleri</i> (Af)
31.	Thorn areoles present	32
	Thorn areoles absent	34
32.	Bulging areoles present	33
	Bulging areoles absent	<i>C. albibarbatu</i> (Af)
33.	Crowned areoles with two types of apical filaments	<i>C. hipilus</i> (As)
	Crowned areoles with only one type of filament	<i>C. madagascariensis</i> (Af) or <i>C. moutoni</i> (As, SEAs) or <i>C. queenslandi</i> (Aus)
34.	Bulging areoles present	<i>C. heinzei</i> (Af)
	Bulging areoles absent	35
35.	Simple areoles in a variety of shapes	<i>C. peraccae</i> (SAm)
	Simple areoles all more or less roundish or polygonal	<i>C. anthophorus</i> (As) or <i>C. japonensis</i> (As) or <i>C. timorensis</i> (SEAs)

## Discussion

### Historical aspects

The description of nematomorph species started in temperate regions, first using the single genus name *Gordius*. With the starting exploration of tropical regions, the number and diversity of nematomorphs species grew. CREPLIN (1847) introduced a new name, *Chordodes*, for a worm from Brazil (*C. parasitus*). A few years later, MÖBIUS (1855) included a second species from Venezuela, *Chordodes pilosus*, to this genus. The reason for this inclusion were for MÖBIUS a similar external appearance and similarities in the musculature between *C. parasitus* and *C. pilosus*, despite the fact that the cuticular surface differed in being smooth (*C. parasitus*) or rough (*C. pilosus*). The concept for the introduction of a new genus name obviously was not convincing to other researchers, because the next eight species which we today include into *Chordodes* were described as *Gordius* (*ornatus*, *caledoniensis*, *defilippii*, *bouvieri*, *modiglianii*, *weberi*, *madagascariensis* and *aelianus*). This was changed by JANDA (1894), who gave the first characterization of the genus, including the presence of papillae on the cuticle and transferred the species named above to *Chordodes* (including further species that now are transferred to other genera). Since then, the name *Chordodes* was regularly applied to tropical species with a strong diversity in cuticular structures.

Today, a particular cuticular structure named the crowned areoles is recognized to be characteristic for the genus *Chordodes*. As these are conspicuously tall areoles, they are easily recognized already with low magnifications and led to the notion of papillae being present on the cuticle. Some researchers already noted that these papillae were composed of a stem with an apical ring of filaments and this structure was integrated in the definition of the genus by LORENZO CAMERANO, a prominent specialist on Nematomorpha, describing a large number of species including many from expeditions in all parts of the world, in his monography (1897a). The name “crowned areoles” is derived from his “corona di prolungamenti”.

CAMERANO’s descriptions (1892–1912) can be evaluated as being considerably detailed and comparatively well documented. It turned out that this level in the description of species was not always kept by following researchers. The description of *Chordodes* species is very heterogeneous throughout the years. After an intensive time of with many species descriptions by CAMERANO, VON LINSTOV, RÖMER and MONTGOMERY (last publication by CAMERANO 1912), there are no publications until 1933. Between 1933 and 1961, there were several new descriptions, mainly by SCIACCHITANO, INOUE, KIRJANOVA and CARVALHO. The quality of several of these species descriptions is not convincing. It appears as if the growing diversity of *Chordodes* and the absence of summarizing publications evaluating the diagnostic characters created a certain chaos.

As one example, it is incredible, how an unspecific description such as the one of *Chordodes lichyi* by SCORZA (1952) could get published.

After 1961, there was another period, in which, with the exception of INOUE (1974) no species was described until 1989, when a new phase of activity started. Since then, 15 new species have been described.

Methodologically, Scanning Electron Microscopy was a considerable progress for the description of nematomorph species in general and the genus *Chordodes* in particular, because the fine structural details are resolved and documented in a much more reliable way than it was possible before. Additionally, it turned out to be important to observe as large pieces of cuticle as possible, because some structures (such as thorn areoles) can have a very scarce distribution and others (such as crowned areoles) can show distinct differences in different regions of the body. A reinvestigation of the previously described species appears very helpful, as has been shown for example in a series of reexaminations of African species (ZANCA et al. 2006a, b, DE VILLATOROS et al. 2007a).

## Diversity of *Chordodes*

113 species of the genus *Chordodes* are known to us. From these, only the original description of *C. longipilus* was not available. 54 species can be regarded as being sufficiently described, 36 species are regarded as belonging to the genus *Chordodes*, but their species status must be confirmed by further investigations and 22 species are considered either as not belonging to the *Chordodes* or have been synonymised with other species. Therefore, the diversity can be summarized as consisting of 90 species, from which 54 are well described species.

Well-characterized species	<i>C. aethiopicus</i> , <i>C. africanus</i> , <i>C. albibarbatus</i> , <i>C. anthophorus</i> , <i>C. bipilus</i> , <i>C. brasiliensis</i> , <i>C. brevipilus</i> , <i>C. baka-vuensis</i> , <i>C. caledoniensis</i> , <i>C. capensis</i> , <i>C. clavatus</i> , <i>C. compactus</i> , <i>C. corderoi</i> , <i>C. cornuta</i> , <i>C. curvifollatus</i> , <i>C. devius</i> , <i>C. digitatus</i> , <i>C. festae</i> , <i>C. fukuii</i> , <i>C. furnessi</i> , <i>C. gariazzi</i> , <i>C. guineensis</i> , <i>C. heinzei</i> , <i>C. ikelensis</i> , <i>C. jandae</i> , <i>C. japonensis</i> , <i>C. joyeuxi</i> , <i>C. kolensis</i> , <i>C. koreensis</i> , <i>C. lenti</i> , <i>C. lotus</i> , <i>C. madagascariensis</i> , <i>C. matensis</i> , <i>C. modiglianii</i> , <i>C. moraisi</i> , <i>C. morgani</i> , <i>C. moutoni</i> , <i>C. muelleri</i> , <i>C. nobilii</i> , <i>C. peraccae</i> , <i>C. pollonerae</i> , <i>C. polycornutus</i> , <i>C. polytuberculatus</i> , <i>C. queenslandi</i> , <i>C. sajanensis</i> , <i>C. sandoensis</i> , <i>C. schoutedeni</i> , <i>C. shipleyi</i> , <i>C. silvestri</i> , <i>C. skori-kovi</i> , <i>C. staviarskii</i> , <i>C. timorensis</i> , <i>C. tuberculatus</i> , <i>C. villalobi</i> .
Species to be reinvestigated	<i>C. aelianus</i> , <i>C. amboinensis</i> , <i>C. aurantiacus</i> , <i>C. bulzani</i> , <i>C. baramensis</i> , <i>C. betulatus</i> , <i>C. boulengerii</i> , <i>C. bouvieri</i> , <i>C. capillatus</i> , <i>C. carmelitanus</i> , <i>C. compressus</i> , <i>C. congolensis</i> , <i>C. cubanensis</i> , <i>C. defilippii</i> , <i>C. ferox</i> , <i>C. gestri</i> , <i>C. hawkeri</i> , <i>C. insidiator</i> , <i>C. itarensis</i> , <i>C. kakandensis</i> , <i>C. kallstenii</i> , <i>C. kivuensis</i> , <i>C. lefeburei</i> , <i>C. ligasiensis</i> , <i>C. maculatus</i> , <i>C. mobensis</i> , <i>C. montgomeryi</i> , <i>C. ornatus</i> , <i>C. penicillatus</i> , <i>C. pilosus</i> , <i>C. puncticulatus</i> , <i>C. rugatus</i> , <i>C. ruandensis</i> , <i>C. siamensis</i> , <i>C. tenoderae</i> , <i>C. wangi</i> .
Invalid species names	<i>C. amandalei</i> , <i>C. annulatus</i> , <i>C. aquaeductus</i> , <i>C. butensis</i> , <i>C. cuneatus</i> , <i>C. carioca</i> , <i>C. carvalhoi</i> , <i>C. delmae</i> , <i>C. ferganensis</i> , <i>C. hamatus</i> , <i>C. ibembensis</i> , <i>C. lichyi</i> , <i>C. liguligerus</i> , <i>C. mohuccanus</i> , <i>C. oscillatus</i> , <i>C. parasitus</i> , <i>C. paucius</i> , <i>C. somaliensis</i> , <i>C. uncinatus</i> , <i>C. undulatus</i> , <i>C. variopapillatus</i> , <i>C. weberi</i> .

## Comparison of areolar types

When we have distinguished here different types of areoles this implies that each type is clearly recognizable. This is, however, not always the case and a closer look must be taken at transitions between different types. It must be kept in mind that the distinction between different types of areoles is strictly typological.

The structuring of the cuticle into small compartments, named areoles, is a common pattern among gordiids (freshwater Nematomorpha) and is lacking only in some species of the genus *Gordius*, which have a smooth cuticle (SCHMIDT-RHAESA 2002b). With the exception of *Chordodes*, all other gordiids have either one or two types of areoles. One type are flat areoles of varying shape and surface structure, but it appears likely that such areoles (the "simple areoles") are homologous. When a second type of areoles is present (with the exclusion of the genera *Chordodes* and *Spiniochordodes*), such areoles differ from simple areoles in being larger, more elevated and often darker in colour (this includes the megareoles in *Parachordodes* which appear to be a fusion product; see SCHMIDT-RHAESA 2002b). Additionally, such larger areoles often occur in a particular pattern, where two such areoles attach along one side and usually enclose a tubercle (this is named the megareolar pattern; see SCHMIDT RHAESA 2002b). Large areoles with or without being arranged in a megareolar pattern are also found in some *Chordodes* species as the bulging areoles. The evaluation of the presence and arrangement of larger areoles as being homologous or not is and remains to be an open question.

Crowned areoles are the most prominent diagnostic character for the genus *Chordodes* and have been evaluated as an autapomorphy of this taxon (SCHMIDT RHAESA 2002b). However, crowned areoles and their arrangement patterns can vary. This is, besides being a help in determination, of potential value for evolutionary considerations among *Chordodes*. It is also of pronounced importance for the comparison with species from the genus *Spiniochordodes*. Crowned areoles are composed of a stem with an apical ring of filaments. In most cases, this structure is unequivocal to recognize, but there are also cases, in which the filaments can be very short or in which the stem is quite short, creating the appearance of filaments originating from the cuticular surface. Furthermore, bristle-like projections can be present on other areolar types, too. This is the case with simple areoles (e.g. *C. corderoi*, *C. villalobi*), bulging areoles (e.g. *C. brevipilus*, *C. compactus*, *C. polycoronatus*) or circumcluster areoles (e.g. *C. aethiopicus*). This makes it sometimes hard to distinguish areoles from each other, for example deciding whether a particular type of areole represents bulging or crowned areoles. Crowned areoles occur in many species in a particular and conspicuous pattern, as a pair of crowned areoles surrounded by a ring of circumcluster areoles. More problematic are the species, in which this arrangement pattern is not present. In several species, there are clusters of areoles including only crowned areoles. It remains to be

tested whether this means that clusters of crowned and circumcluster areoles evolved from such clusters of only crowned areoles.

A further problem is that crowned areoles in such species with clusters of only crowned areoles make it sometimes hard to recognize their nature as crowned areoles. If we take a look at species such as *C. fukuii* (SCHMIDT-RHAESA 2004) or *C. morgani* (SCHMIDT-RHAESA et al. 2003), the apical filaments are hardly recognizable as such. This is particularly important, because in species of the genus *Spinochordodes* (note that the genera *Pantachordodes* and *Dacochordodes* have been synonymised with *Spinochordodes*; see ZANCA & SCHMIDT-RHAESA 2006) have areoles consisting of a stem that terminates in a ring of short projections. Such areoles occur in large groups forming patches on the cuticle that irregularly alternate with patches of simple areoles (see, e.g. ZANCA & SCHMIDT-RHAESA 2006). This pattern is also present in species such as *Chordodes fukuii* and *C. morgani*, making this transition between *Spinochordodes* and *Chordodes* an important topic for further research.

Tubercle and thorn areoles are known only from *Chordodes* species, but as their occurrence is not in all species, it remains to be shown in phylogenetic analyses whether they are ancestral patterns in this genus.

## Conclusions

We hope that this summary of characters in the genus *Chordodes* and especially the universal terminology of structures will be of help in further investigations concerning this genus. The sampling of nematomorphs in the tropical regions is quite patchy and it is expected that the diversity in this region is higher than currently known. New descriptions or the assignment of newly recorded specimens to known species must be based on an effective comparison with previous descriptions.

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