

Horsehair worms from Panguana – first record in Peru with description of a new species

(Nematomorpha)

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29 specimens of horsehair worms (Nematomorpha) were collected at the Private Protected Area and Biological Field Station ACP Panguana, which is located in the evergreen lowland rainforests of Peruvian Amazonia. This is the first record for Nematomorpha in Peru. Specimens belong to a minimum of eight species. From these 18 specimens belong to the genus *Chordodes* Creplin, 1847 and were assigned with different degrees of confidence to six species, among which a new species is described within this study. Ten specimens belong to the genus *Gordius* Linne, 1758, but could not be determined in detail due to the lack of diagnostic characters. One female specimen belongs to the genus *Paragordius* Camerano, 1897. The specimens, except the holotype, are stored in the SNSB – Bavarian State Collection of Zoology, *Vertebrata varia* section in Munich, Germany.

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Introduction

The knowledge about the geographic diversity of Nematomorpha is patchy. About 360 species are known to date (Schmidt-Rhaesa 2012) and new species are constantly reported. Nematomorphs, or more precisely the taxon *Gordiida* Vejdovsky, 1886, which includes all but 5 marine species, are parasites of insects, which leave their host for reproduction within fresh water (e. g. Hanelt et al. 2005). In most cases they are collected in this free living stage, but as this phase of the life cycle is comparably short, nematomorphs are not abundantly reported.

Parts of South America, in particular Argentina, are quite well known concerning their nematomorph fauna (De Miralles & De Villalobos 1993). From other parts of the continent few, if any records are known. One such country is Peru, from which no single nematomorph specimen has been recorded to date (see description of one new species by Schmidt-

Rhaesa & Piper 2021, in this volume). It is highly unlikely that the absence of records does indicate a low nematomorph diversity in Peru and several species have to be expected. We report here the first findings from collections around the Biological Station Panguana over a number of years.

To identify gordiids morphological comparisons including the general body outlines and the cuticular structures are used. Males and females are distinguished by the position of the cloacal opening, which is ventral in males and terminal in females. In both sexes, the posterior end may be roundish or divided into two or three lobes. The cuticle is smooth in some species, but mostly contains fine structures called areoles. The type, shape and distribution of areoles is characteristic for genera and species. The cuticular structure in species of the genus *Chordodes* is diverse in comparison to other nematomorph genera. The terminology for areoles was standardized (Schmidt-Rhaesa et al. 2008) and includes maximally

six types: simple, tubercle, thorn, bulging, crowned, and circumcluster areoles. The genus includes more than 100 known species, and is distributed mainly in the tropics and subtropics. The presence, shape, and distribution of these areoles is important for the identification of *Chordodes* species. Another species-rich genus is *Gordius*, which includes species that are very poor in diagnostic characters and therefore difficult to determine. This accounts in particular to female specimens, as most of the few characters important for identification are found in the male posterior end (Schmidt-Rhaesa 2010).

Many new species, including the one in this study, are described from single specimens. Although it is desirable to have more material available for a species description, the collection of nematomorphs is often random, resulting in single or few specimens. A consequence of this fact is also that very little is known about character variability within species. However, with distinct morphological character differences it appears justified to describe new species.

Material and methods

Specimens were collected at the Private Protected Area and Biological Field Station ACP Panguana, Departamento de Huánuco, Provincia de Puerto Inca, Distrito de Yuyapichis (9°37'S 74°56'W), 230 m a.s.l. All specimens except the holotype of *Chordodes dilleri* sp. nov. are deposited in the SNSB – Bavarian State Collection of Zoology, Evertabrata varia section, Munich, Germany. Accession numbers and collecting data are given below for each individual. For SEM investigation, about 1 mm long complete sections from the midbody region were cut out, in male specimens also the posterior end (1–2 mm pieces) was taken for SEM. Cut sections were dehydrated in an increasing ethanol series, critically point dried, and mounted on stubs. In *Chordodes* specimens, some pieces were longitudinally cut, the internal structures (gonads, intestine, musculature) removed and the remaining cuticle spread flat on the stub.

Specimens were sputtered with gold and investigated with a LEO Scanning Electron Microscope 1524. All specimens were collected and exported legally (see table).

Results

Specimens from this investigation belong to three genera, *Chordodes* (18 specimens), *Gordius* (10 specimens), and *Paragordius* (1 specimen). Only two of the 29 specimens were identified with some certainty to species level. The identification of the other specimens is uncertain to some degree, either due to insufficiently preserved structures or due to the rarity or absence of diagnostic characters.

Chordodes balzani Camerano, 1896

Material examined. Female specimen ZSM20190902 collected by E.-G. Burmeister between September 20 and October 9, 2007.

Description

The female is 370 mm long and has a diameter of 1.4 mm. It has a dark brown colour and a white anterior tip. The simple areoles are not well preserved, but appear to have a rough surface without further structures such as bristles. Tubercle areoles are present (Fig. 1B), thorn areoles were not observed. Crowned areoles occur in clusters with a pair of crowned areoles in the center and a larger number (>20) of circumcluster areoles surrounding them (Fig. 1B). Pairs of elevated bulging areoles are present among the simple areoles (Fig. 1B). In the ventral midline, crowned areoles with long apical filaments are present (Fig. 1A).

Taxonomic remarks. The observed characters correspond well with the SEM investigation of this species by De Villalobos et al. (2004) and drawings

Table 1. Collection permits. INRENA, Instituto Nacional de Recursos Naturales; DGFFS, Dirección General Forestal y de Fauna Silvestre; ERFOR, Servicio Nacional Forestal y de Fauna Silvestre

Year	Months	Collecting permit number	Export permit number	Issued by (authority)
2005	IX / X	No. 073-2005-INRENA-IFFS-DCB	No. 006298-AG-INRENA	INRENA
2007	IX / X	No. 097-2007-INRENA-IFFS-DCB	No. 010670-AG-INRENA	INRENA
2008	XI / XII	No. 124-2008-INRENA-IFFS-DCB	No. 011855-AG-INRENA	INRENA
2009	X	No. 334-2009-AG-DGFFS-DGEFFS	No. 001075-AG-DGFFS	DGFFS
2013	IX / X	No. 0276-2013-AG-DGFFS-DGEFFS	No. 000521-MINAGRI-DGFFS	DGFFS
2015	IV / X	No. 007-2014-SERFOR-DGGSPPFS (permit for 5 years)	No. 0001757-SERFOR	SERFOR
2017	IX / X	No. 007-2014-SERFOR-DGGSPPFS	No. 003214-SERFOR	SERFOR

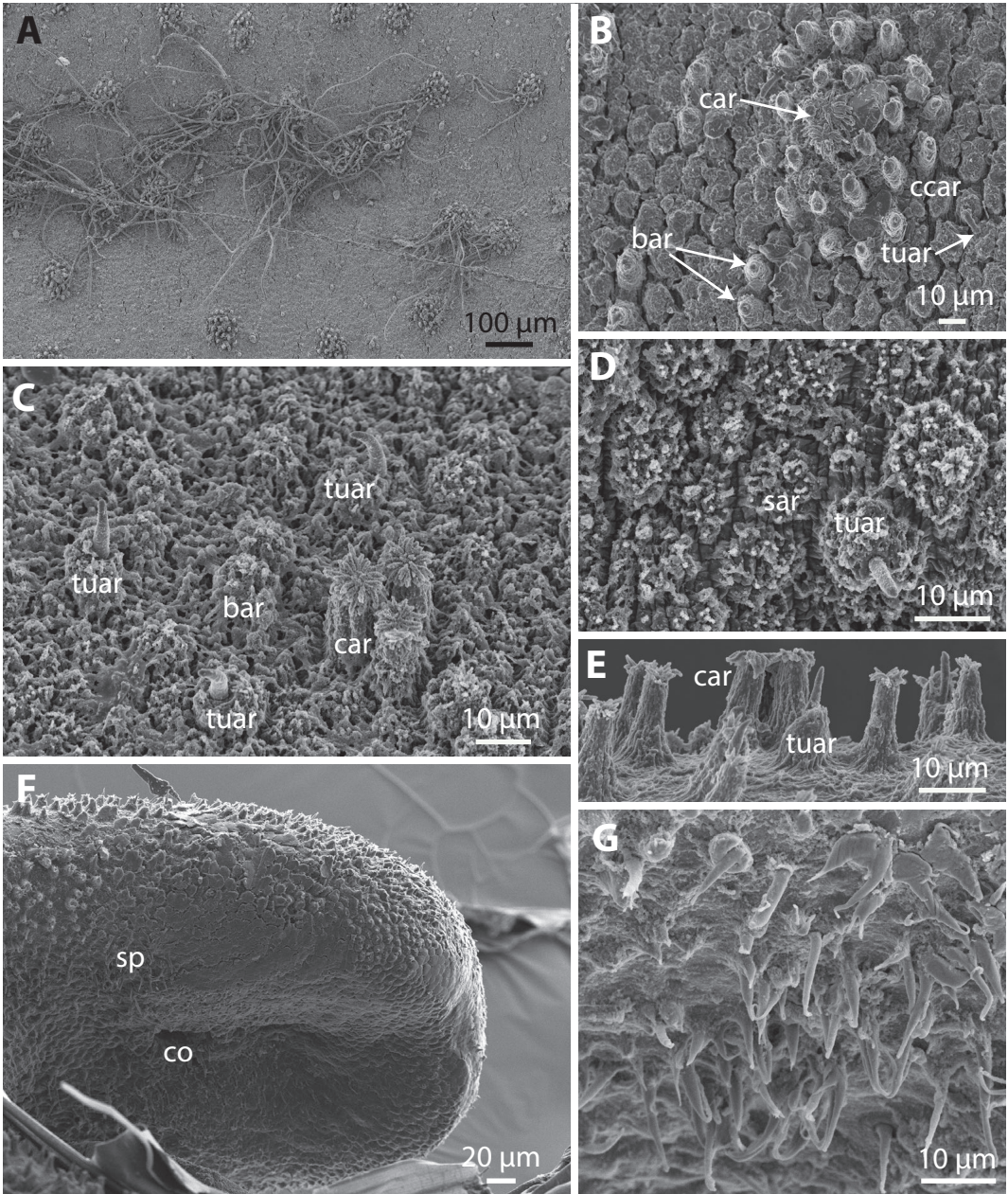


Fig. 1. **A,B.** *Chordodes balzani*, ZSM20190902. **A.** Overview on the cuticle showing clusters or crowned areoles and circumcluster areoles on the cuticle. Along the ventral midline, crowned areoles have very long apical filaments. **B.** Five types of areoles are present: simple areoles (not labelled), crowned areoles (car) surrounded by circumcluster areoles (ccar), tubercle areoles (tuar) and bulging areoles (bar). **C-G.** *Chordodes ecuatoriensis*, ZSM20190907. **C,D.** Cuticle with simple areoles (sar), tubercle areoles (tuar), bulging areoles (bar) and crowned areoles (car). **E.** Lateral view in the posterior body region with crowned and tubercle areoles. **F.** Ventral view on the posterior end of the male specimen with cloacal opening (co) and anterolateral spines (sp). **G.** Magnification of spines on the posterior end.

of Camerano (1897) and Carvalho & Feio (1950). This species has been reported from several South American countries: Bolivia (Camerano 1896), Brazil (Carvalho & Feio 1950), Argentina (De Miralles 1969, De Miralles & De Villalobos 1993), Venezuela (De Villalobos et al. 2004) and Trinidad (De Villalobos et al. 2004).

Chordodes ecuatoriensis De Villalobos,
Zanca & Yanez, 2009

Material examined. Male specimen ZSM20190907 collected by E.-G. Burmeister between September 18 and October 3, 2005.

Description

The male is 170 mm long and has a diameter of 0.5 mm. It has a light brown colour in general and a “leopard pattern”, i. e. darker brown patches on light brown ground. The simple areoles on the cuticle have a warty (“blackberry”) surface (Fig. 1C,D). Tubercle areoles are present (Fig. 1D,E), they have the warty structure of simple areoles with a tubercle on top. Some areoles are higher elevated than the simple areoles, these are bulging areoles (Fig. 1C). Crown areoles occur in clusters of two or three (Fig. 1C,E). They are elevated higher than bulging areoles and have an apical crown of short filaments. They are not surrounded by circumcluster areoles. Crown areoles with long filaments and thorn areoles were also not observed. The posterior end is comparable to that of other *Chordodes* species, with a slit-like ventral cloacal opening and several spines anterolateral of this opening (Fig. 1F,G).

Taxonomic remarks. The characters correspond well with the ones described for *C. ecuatoriensis* (De Villalobos et al. 2009). This species has only been found in Ecuador (De Villalobos et al. 2009).

Chordodes cf. bouvieri (Villot, 1885)

Material examined. Five specimens, all females: ZSM20190905 from host Ensifera, (Orthoptera) and ZSM20190914, both collected by E.-G. Burmeister between September 20 and October 9, 2007; ZSM20190919 from host Tettigonidae (Ensifera, Orthoptera), collected by E.-G. Burmeister between October 2 and 18, 2009; ZSM20190928 and ZSM20190929, both collected by S. Friedrich, F. Wachtel, D. Hauth and T. Lehmann between September 22 and October 10, 2017.

Additional specimens. In further six specimens, all females, the cuticular characters were not well observed, but the few characters that were documented correspond with characters of *C. bouvieri*. Therefore, we treat these determinations with some caution. Specimens are:

ZSM20190911 and ZSM20190912, collected by E.-G. Burmeister between September 18 and October 3, 2005; ZSM20190915 and ZSM20190916, collected by E.-G. Burmeister between September 20 and October 9, 2007; ZSM20190920 collected by E.-G. Burmeister between May 10 and 28, 2013, host was a mantid; ZSM20190925 collected by E.-G. Burmeister between September 20 and October 7, 2013, host was a cockroach (Ectobiidae, Blattodea).

Description

Specimen ZSM20190905 is 160 mm long and 0.9 mm wide, it is light brown and has slightly darker patches (leopard pattern). Specimen ZSM20190914 is 155 mm long and 0.3 mm wide, it is medium brown with darker brown patches. Specimen ZSM20190919 is 190 mm long and 0.9 mm wide, it is light brown with medium brown patches. Specimen ZSM20190928 is 290 mm long and 1.7 mm wide, it is dark brown with even darker patches. Specimen ZSM20190929 is 250 mm long and 1.0 mm wide it is medium brown with darker brown patches.

The cuticle is not well preserved in the five specimens. In some cases, elevated areoles appear as being covered by a layer (Fig. 2A) and in one case this layer was shed, revealing the “adult” cuticle below it (Fig. 2B). The layer covering the adult cuticle therefore is the larval cuticle. When recognizable, simple areoles have a rough surface without further apical structures (Fig. 2C). Tubercle areoles were only found in ZSM20190929 (Fig. 2F), thorn areoles were present in specimens ZSM20190905 and ZSM20190914 (Fig. 2C,D). In all specimens, crowned areoles are grouped in clusters of 2 to 4 areoles, without being surrounded by circumcluster areoles (Fig. 2C–E).

Taxonomic remarks. The absence of circumcluster areoles strongly restricts the number of potential species, with *C. bouvieri* being closest in the structure of the cuticular pattern. This species has been described from several South American countries: Argentina (Carvalho & Feio 1950), Colombia (Camerano 1915), Ecuador (Camerano 1897, De Villalobos et al. 2009), and Venezuela (Camerano 1915). The SEM investigation of Ecuador specimens shows simple areoles with a smooth surface, tubercle areoles that sometimes may also be slender thorn areoles and crowned areoles in small clusters.

Chordodes cf. corderoi Carvalho, 1946

Material examined. Female specimen ZSM20190926 collected by E.-G. Burmeister between October 9 and October 10, 2017.

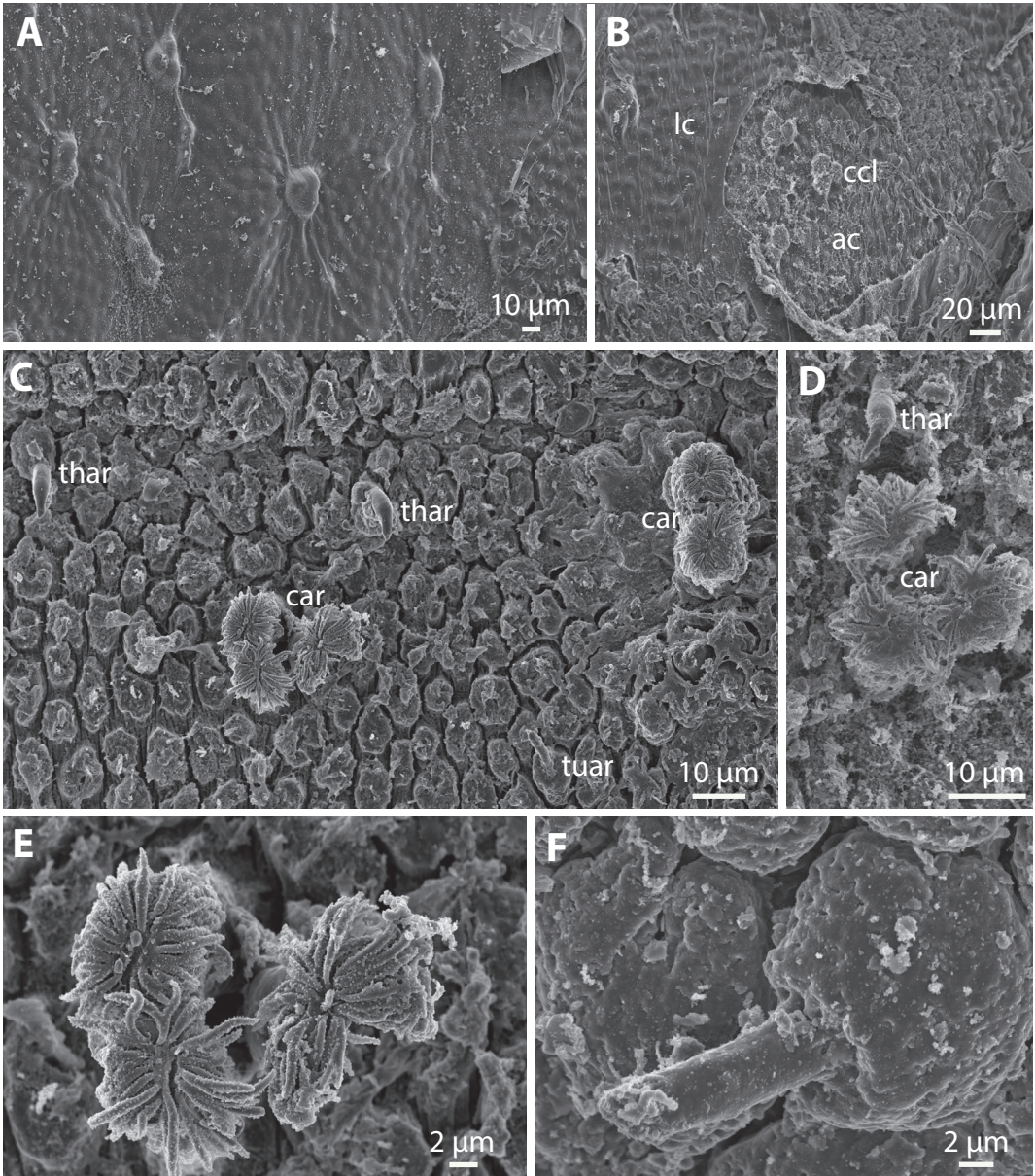


Fig. 2. *Chordodes cf. bouvieri*. **A.** (Adult) cuticle covered by larval cuticle in specimen ZSM20190911. **B.** Partwise shedding of the larval cuticle (lc) in the same specimen, revealing the adult cuticle (ac) with crowned areole clusters (ccd). **C, D.** Areolar types are simple areoles (not labelled), tubercle areoles (tuar), thorn areoles (thar) and crowned areoles (car). **E, F.** Magnification of tubercle areole. **C, E,** specimen ZSM20190919, **D, F,** specimen ZSM20190905, **F,** specimen ZSM20190929.

Additional specimen. ZSM20190930 collected by S. Friedrich, F. Wachtel, D. Hauth and T. Lehmann between September 22 and October 10, 2017. The very small specimen is in the state of emerging from a cockroach (Ectobiidae, Blattodea) (Fig. 3A,B). It remains unsexed, because the posterior end is still inside the host. The preservation of the cuticle is not well, but from what can be observed it seems to correspond to the description below.

Description

The female specimen is 65 mm long and has a width of 0.4 mm. The colour is medium brown. Three types of areoles are present on the cuticle. Simple areoles have a distinct tuft of bristles on top (Fig. 3C,D). Crowned areoles are present in pairs or as three areoles among the simple areoles (Fig. 3C,D). They are more elevated than the simple areoles and have an apical tuft or crown of short filaments that hardly extend in length over the diameter of the areole. Rarely seen are tubercle areoles (Fig. 3C,D). These areoles appear as a combination of a simple and a tubercle areole, because it has the tuft of bristles of simple areoles and, basally to it, a tubercle.

Taxonomic remarks. The description fits well with the description of *C. corderoi*, a species described from Venezuela by Carvalho (1946). The single female described by Carvalho is the only specimen known from this species so far. Simple areoles and crowned areoles look very similar in the Venezuela and in the Peru specimen, but there are two differences. Tubercle areoles are described in the Venezuela specimen as a tubercle on a semispherical areole, without the apical tuft of a simple areole of the Peru specimen. Crowned areoles with very long apical filaments are described from the Venezuela specimen, but were not observed in the Peru specimen. Low numbers of crowned areoles among simple and tubercle areoles are not a common pattern among *Chordodes* species, as very often crowned areoles are either combined into larger clusters or, more often, pairs of crowned areoles are surrounded by another type of areole, the circumcluster areoles.

? *Chordodes* cf. *cornuta* De Villalobos & Camino, 1999

Material examined. Two specimens, both females: ZSM20190918 from host *Ensifera*, (Orthoptera), collect-

ed by E.-G. Burmeister between September 20 and October 9, 2007; ZSM20080137 collected by E. Diller between September 20 and October 7, 2007.

Description

The two females each measure 140 mm, their diameter is (in the order listed above) 0.4 and 0.8 mm. The colour is medium brown or light brown with a slight leopard pattern. On the cuticle, three, possibly four types of areoles are present. Simple areoles were not well preserved in specimen ZSM20190918, they are covered with few scattered bristles in specimen ZSM20190937 (Fig. 3F). Among the simple areoles are crowned areoles. These have short apical filaments (hardly extending over the diameter of the areole) (Fig. 3E,F). Crowned areoles are clustered in groups of up to three (ZSM20190937; Fig. 3F) or about 7 (ZSM20190918; Fig. 3E). Tubercle areoles were rarely observed in specimen ZSM20190918. In specimen ZSM20190937 thorn areoles were found (Fig. 3F).

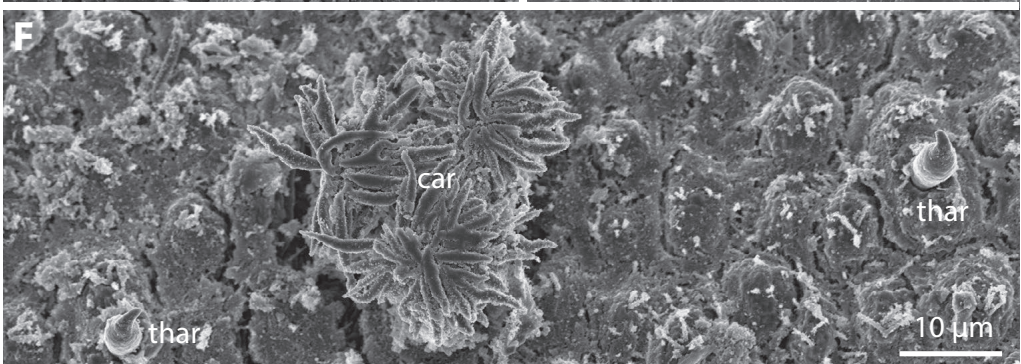
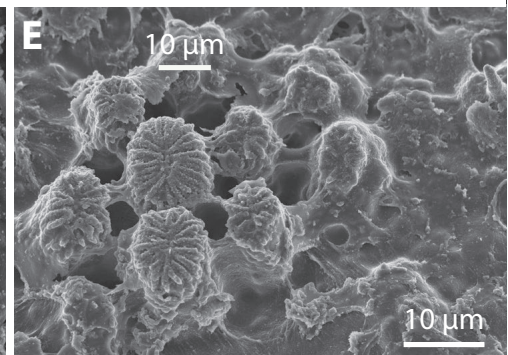
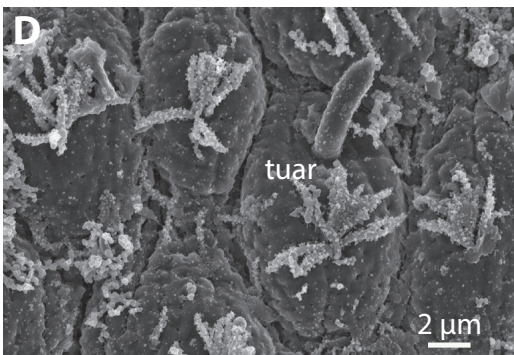
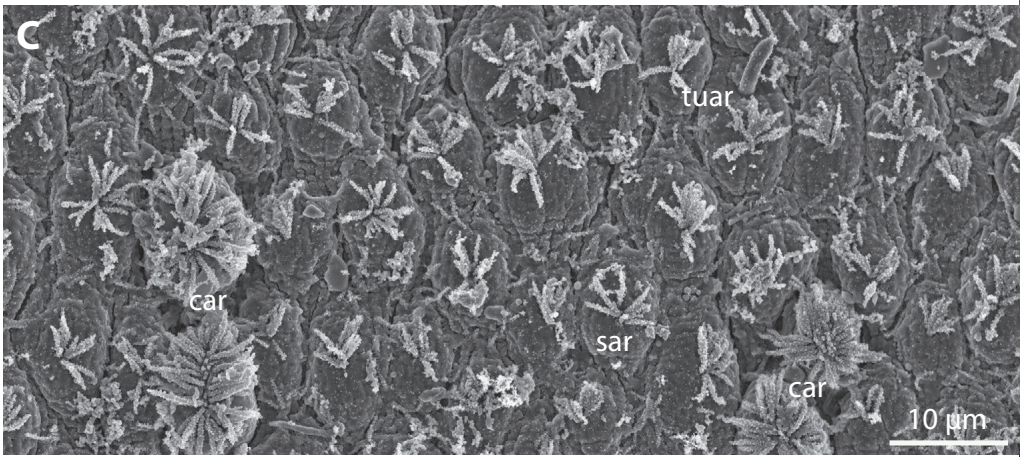
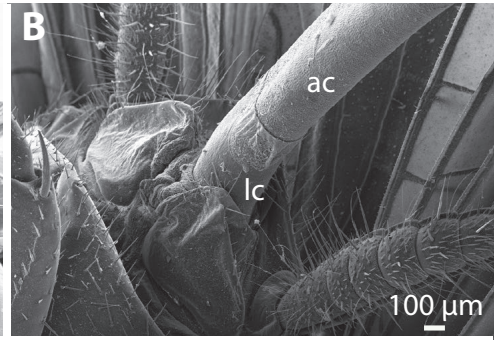
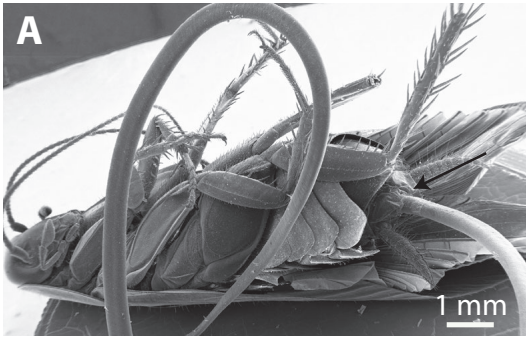
Taxonomic remarks. The two specimens listed here correspond in the absence of circumcluster areoles and in clusters of crowned areoles being composed of more than a pair of areoles. However, the number of crowned areoles in these clusters and the nature of tubercle areoles differ among the three specimens. In specimen ZSM20190918 the cuticle appears to be covered by some material, which makes observation of most structures uncertain. The described characters fit best to *Chordodes cornuta*, which was described with one male specimen from Northern Argentina (Salta) (De Villalobos & Camino 1999). In this species, medium sized clusters of crowned areoles are present, but tubercle and thorn areoles are not described.

Chordodes dilleri sp. nov.

Material examined. One female specimen collected from a Malaise trap, by K. Schönitzer, F. Glaw and F. Wachtel between November 23 and December 11, 2008. The holotype is deposited in the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM-INV4652).

Etymology. The name honours Erich Diller, who has collected some of the worms at the Panguana Station. The input of Juliane and Erich Diller for the station is also appreciated. Dr. Juliane Diller is head of Panguana

Fig. 3. A–D. *Chordodes* cf. *corderoi*, ZSM20190930. A. Host cockroach (Ectobiidae) with worm emerging (black arrow). B. Magnification of the site of emergence. The worm sheds its larval cuticle (lc), exposing the adult cuticle (ac). C. Areolar types are simple areoles (sar), tubercle areoles (tuar) and crowned areoles (car). D. Magnification of tubercle areole. E,F. ?*Chordodes* cf. *cornuta*. E. Crowned areole cluster in specimen ZSM20190918. F. Crowned areoles (car) and thorn areoles (thar) in specimen ZSM20080137. ▷



and was until 2020 vice director of the Bavarian State Collection of Zoology.

Description

The female measures 40 mm, the diameter is 0.2 mm. The colour is light brown with a slight leopard pattern. The cuticle is uniformly covered by one type of areole (Fig. 4A–D). These areoles are hemispherical and carry a tuft of apical bristles that originate from a slit-like depression (Fig. 4B,C). In one region, putatively along the ventral midline (indicated in Fig. 4A) the areoles are quite close to each other, while in the other, putatively lateral, regions they are in some distance to each other. In the ventral areoles, the tuft is not as marked as in the lateral areoles and fewer filaments originate from the center of the areoles (Fig. 4D). Some further fine bristles are present in other parts of the areole (Fig. 4D). Tubercle areoles are present, they are more or less the same areolar type as described above with a tubercle (Fig. 4B,C). One additional structure was observed, this is a small conical structure with a fine extension on the apex (Fig. 4E).

Taxonomic remarks. Crowned areoles are a defining character for the genus *Chordodes*. They are usually defined as areoles with a stem and an apical crown of bristles or filaments. In most species, crowned areoles can be easily recognized, but there are some problematic cases. In some species, simple areoles and/or circumcluster areoles can also carry apical bristles and therefore resemble crowned areoles to some degree (see, e.g. *C. cf. corderoi* above). In some species, e.g. in *C. morgani* Montgomery, 1898, the apical filaments are extremely short and resemble areoles which occur in the genus *Spinochordodes* Kirjanova, 1950 and which are not named crowned areoles (see Schmidt-Rhaesa et al. 2003, Schmidt-Rhaesa 2012). In all such cases, the crowned areoles can be distinguished from other areoles, because different types of areoles can still be recognized. The present specimen is different, as there is no clear distinction between simple and crowned areoles. The differences between the areoles in the ventral area and the lateral area are present, but gradual. Consequently, it cannot be decided whether the areoles are simple areoles resembling crowned areoles or crowned areoles in the absence of simple areoles.

Tubercle areoles are another type of areoles, which are exclusively found in *Chordodes*. Resem-

bling simple areoles, they have an additional projection named the tubercle. Tubercle areoles are present in this specimen and the tubercle also originates on a base that resembles the other areoles. Therefore, in this specimen the presence of tubercle areoles is the main indication for its inclusion in the genus *Chordodes*.

The only species of *Chordodes*, to which the Peruvian specimen can be compared in some regard is *Chordodes lenti* Carvalho, 1944, from which only one male from Brazil (Viçosa, Minas Gerais) is known (Carvalho 1944). In this species, areoles do also not border each other directly. Crowned areoles are less conspicuous than in most other species, but they are clearly recognizable as such and clearly distinguished from the simple areoles (Carvalho 1944).

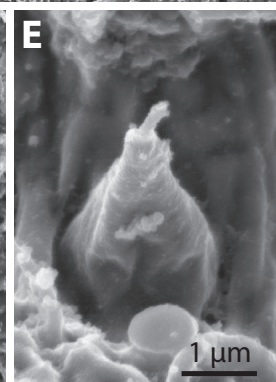
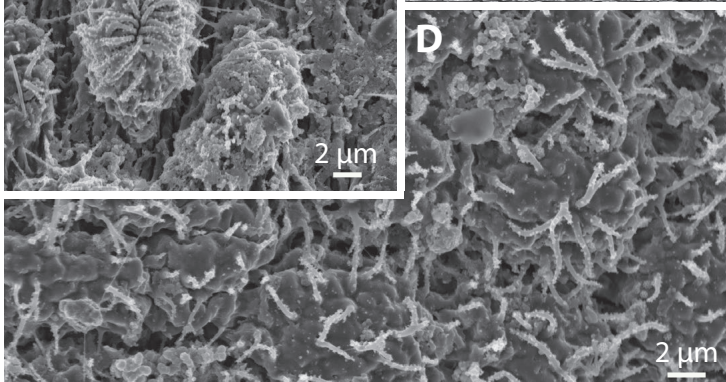
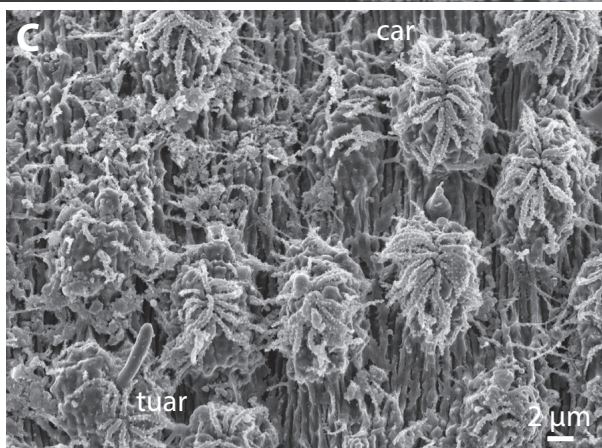
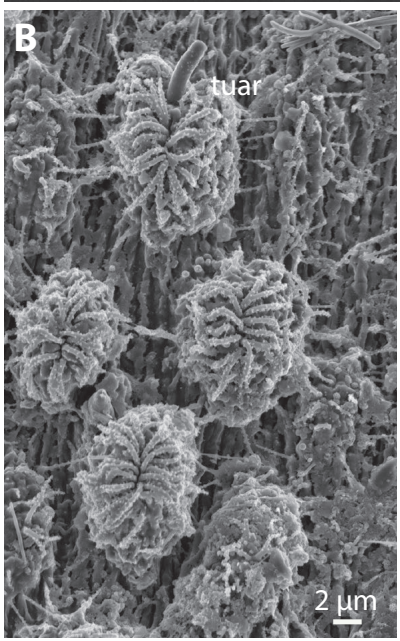
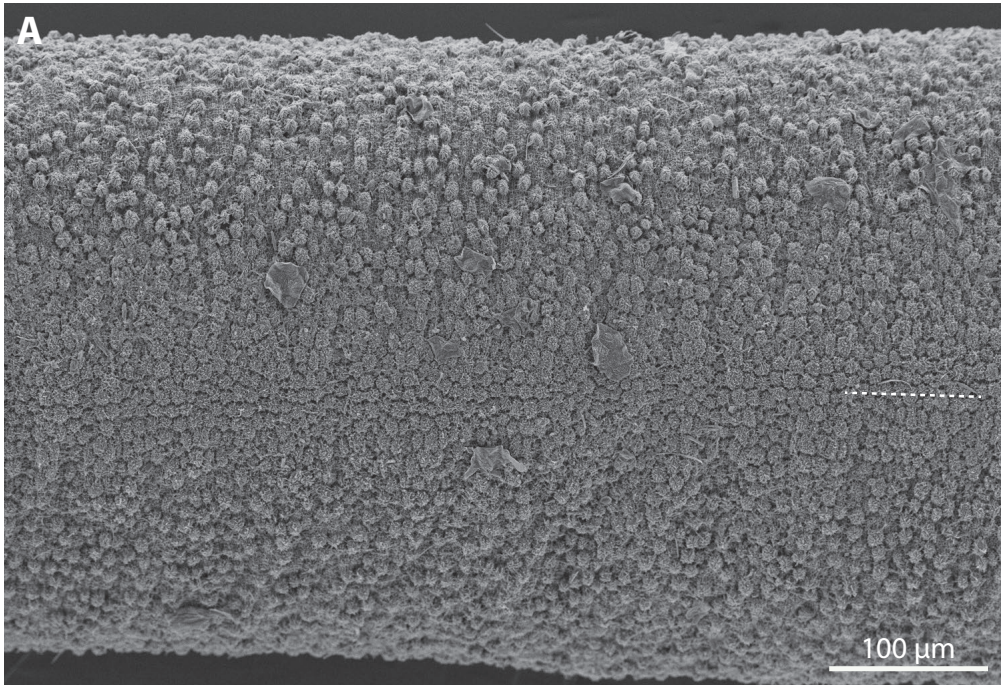
Gordius sp.

Material examined. 10 specimens. ZSM20190903 (female), collected by E.-G. Burmeister between September 20 and October 9, 2007; ZSM20190904 (male) from host Mantodea, collected by E.-G. Burmeister between September 20 and October 9, 2007; ZSM20190908 and ZSM20190909 (both females), collected by E.-G. Burmeister between September 18 and October 3, 2005, second specimen found together with potential host *Camponotus* sp. (Formicidae, Hymenoptera); ZSM20190910 (female), collected in a Malaise trap by E. Diller between May 1 and 20, 2015; ZSM20190917 (female), collected by J. Monzón on May 20, 2015; ZSM20190921 (female), collected by E.-G. Burmeister between October 2 and 18, 2009 from host Tettigonidae (Ensifera, Orthoptera); ZSM20190922 and ZSM20190923 (both females), collected by E.-G. Burmeister between September 28 and October 6, 2000 in a Malaise trap; ZSM20190927 (sex uncertain), collected by S. Friedrich, F. Wachtel, D. Hauth and T. Lehmann between September 22 and October 10, 2017 from host Tettigonidae (Ensifera, Orthoptera).

Description

The cuticle of all specimens is smooth, without any trace of areoles or other cuticular structures (Fig. 5B,C). In some specimens (ZSM20190910, ZSM20190921) the surface appears finely porous. Specimen ZSM20190921 has few very fine bristles on the cuticular surface (Fig. 5D). The only male specimen, ZSM 20190904, has the posterior end not in good shape (Fig. 5A). The region around the cloacal opening is deeply depressed. The postcloacal

Fig. 4. *Chordodes dilleri* sp. nov, female holotype, MUSM-INV4652. **A.** Entire piece of the midbody region showing a dense arrangement of areoles in the putative ventral midline (dashed line) and more loosely arranged in the lateral areas. **B,C.** Magnifications of areoles and tubercle areoles (tuar) from the lateral regions. **D.** Magnification of areoles from the ventral region. **E.** Small cone-like structure.



crescent is semicircular and extends slightly onto the tail lobes. The tail lobes appear to have a more or less sharp ventral edge. There are few bristles on the posterior end, but characteristic patterns of bristles were not observed.

Taxonomic remarks. *Gordius* is a genus with very few diagnostic characters, which makes determination very difficult. There are several species with a smooth cuticle (see Schmidt-Rhaesa 2010), therefore the smooth cuticle of the females does not indicate a certain species. Fine bristles on the otherwise smooth cuticle were observed in some species, but were probably overlooked in others (see Schmidt-Rhaesa 2010). In the posterior end, males have a few more potential characters for identification, but these are usually characteristic patterns of bristles, which were not observed in the Peru specimen. Therefore, none of the *Gordius* specimens could be determined to species level.

Paragordius sp.

Material examined. Female specimen ZSM20190924, collected by E.-G. Burmeister between September 28 and October 6, 2000 in a Malaise trap.

Description

The specimen is 85 mm long and has a diameter of 0.4 mm. The colour is medium brown. The cuticle is smooth and has knob-like structures in regular distances along the entire cuticle (Fig. 5F,G). The posterior end includes, as characteristic for females in this genus, a narrower dorsal and paired broader ventrolateral tail lobes (Fig. 5F,G). Along the outer rim of the tail lobes the cuticle changes structure and is covered by spine-like structures, some of which can have a quite long tip (Fig. 4H). In the center of the inner side of the dorsal lobe is a short groove, which is bordered by hair-like cuticular structures (Fig. 5I).

Taxonomic remarks. Five species of *Paragordius* are known from South America. *Paragordius andreasii* Zanca & De Villalobos, 2006 and *P. minusculus* Carvalho, 1944 differ in the cuticular structure from the Peruvian specimen (see Zanca & De Villalobos 2006 for SEM investigation of both species). *Paragordius flavescens* Linstow, 1906 is reported to have areoles,

but the documentation is not very good and no SEM reinvestigation is available. The two remaining species, *P. esavianus* Carvalho, 1944 and *P. varius* Leidy, 1851 have structures on the cuticle like the Peruvian specimen (see De Villalobos et al. 2000 and Zanca & De Villalobos 2006 for *P. esavianus*). *Paragordius varius* (Leidy, 1851) is a broadly distributed species in North, Central and South America. The cuticle as documented for North American specimens (see Schmidt-Rhaesa et al. 2003) does correspond well with the one in the Peruvian specimen. SEM Documentations of South American specimens either correspond (Zanca & De Villalobos 2006) to this description or deviate somewhat (De Villalobos et al. 2000, De Villalobos & Ronderos 2003). At least for females, there seem to be no clear differences between *P. esavianus* and *P. varius*, therefore the specimen from Peru could not be assigned with certainty to one particular species.

Discussion

The reasons for the different levels of identification (to species, probably to species, to genus) are diverse. In some specimens the fine structural preservation is not good enough to allow a detailed comparison to other documentations. In some cases, the cuticle was covered by an unstructured layer, which most likely represents the larval cuticle (see below). In some cases, especially in female specimens of the genus *Gordius* with a smooth cuticle, further identification is not possible due to a paucity of diagnostic characters (see Schmidt-Rhaesa 2010). Finally, it is sometimes difficult to compare older descriptions with a documentation of characters by drawings. This is due to higher magnifying methods of investigation (SEM has become the standard tool) and for larger areas of surface that are investigated. While earlier often just pieces of cuticle were removed by superficial cuts, now often entire pieces from the midbody region are investigated. This is especially important in the genus *Chordodes*, where there may be regional differences of areoles, which may be overlooked by a superficial section. Finally, the extent of intraspecific variation is hardly known and therefore it can be difficult to decide, whether smaller differences fall within the range of intraspecific variation or not.

Fig. 5. A-D. *Gordius* sp. **A.** Ventral view on posterior end of specimen ZSM20190904, showing region of cloacal opening (co; covered by sperm or other material), the postcloacal crescent (pcc) and two tail lobes (tl). **B, C.** Smooth cuticle in specimens ZSM20190908 (B) and ZSM20190921 (C). **D.** Fine bristles on the cuticle of specimen ZSM20190921. **E-I.** *Paragordius* sp. (specimen ZSM20190924). **E.** Entire posterior end of female with dorsal (dl) and two ventrolateral (vl) tail lobes. Rectangles indicate the position of figures H and I. **F,G.** Structure of the cuticle in different magnifications. **H.** Spine-like structures on the outer edge of a ventrolateral tail lobe. **I.** Hair-like cuticular structures on the inside of the ventral tail lobe.

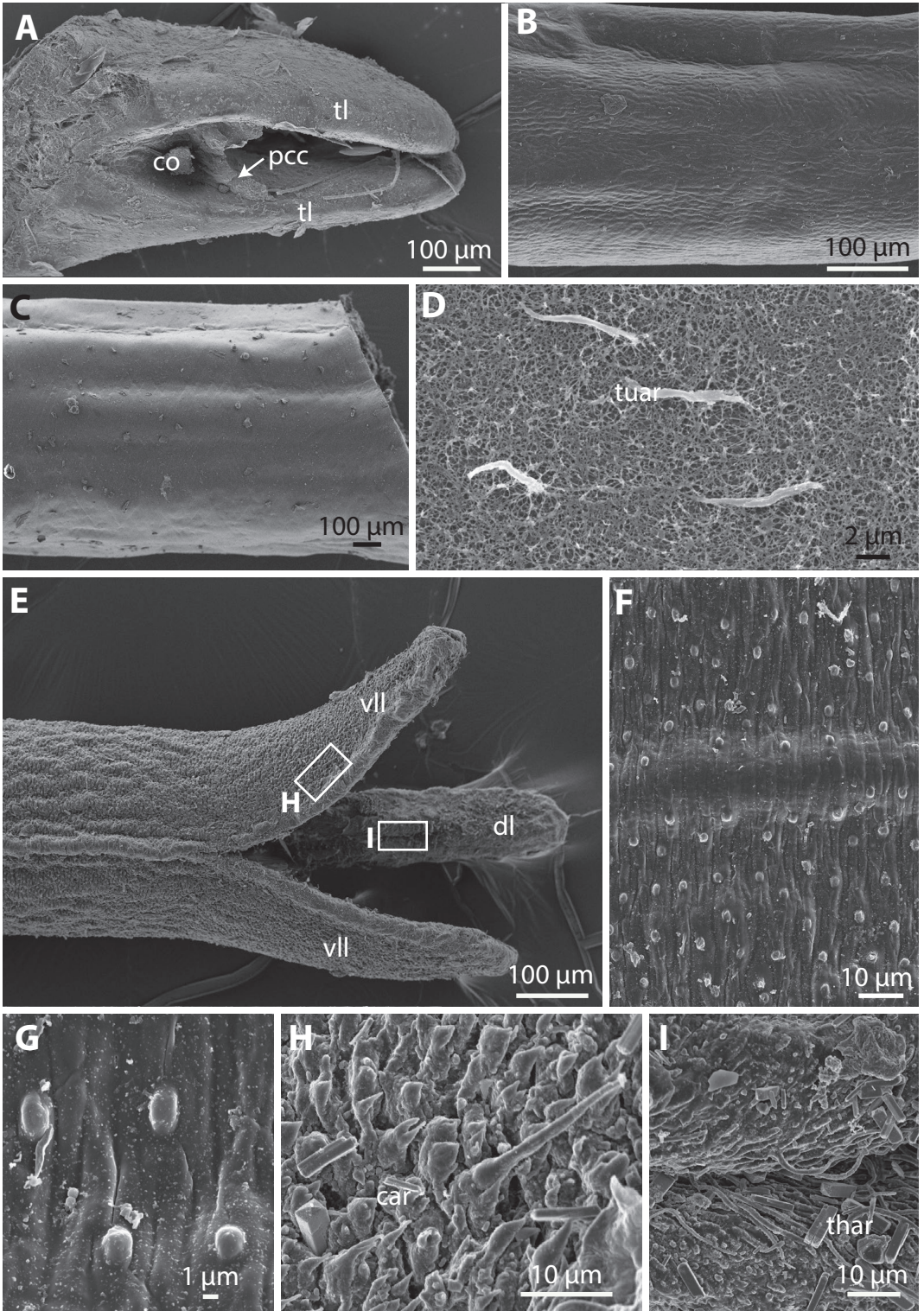


Table 2. Cuticular characters in the *Chordodes* species described above. * Areoles in *C. dilleri* sp. nov. could be simple or crowned areoles (see above).

	Simple areoles	Tubercle areoles	Thorn areoles	Bulging areoles	Crowned areoles	Circum-cluster areoles	Crowned areoles with long filaments
<i>C. balzani</i>	with rough surface	+	–	+	+	+, >20	+
<i>C. ecuatoriensis</i>	warty surface	+	–	+	+	–	–
<i>C. cf. bouvieri</i>	rough surface	+	+	–	+	–	–
<i>C. cf. corderoi</i>	with tuft of bristles	+	–	–	+	–	–
<i>C. cf. cornuta</i>	with scattered bristles	+	+	–	+	–	–
<i>C. dilleri</i> sp. nov.	??*	+	–	–	??*	–	–

Two of the described specimens are in the process of molting. Nematomorpha belong to the Ecdysozoa, therefore molting of the cuticle is not a surprising fact. There is evidence for only one molt during the development of nematomorphs (see Schmidt-Rhaesa 2012) and this takes place around the emergence of worms from their hosts. Usually ecdysis seems to take place within the host, but occasionally specimens are found which retain the old cuticle or parts of it after emergence. This is supported by the two specimens, which either shed their old cuticle in the process of emerging (*Chordodes* cf. *corderoi*, ZSM20190930) or somewhat after emergence (*Chordodes* cf. *bouvieri*, ZSM20190911). The cuticular layers have been named “adult cuticle” and “larval cuticle”, the latter because it seems to be the case that this layer is present from the tiny larva to the fully grown juvenile (see Schmidt-Rhaesa 2012).

For comparison, the cuticular characters of the six *Chordodes* species (discussed above under “taxonomic remarks”) are listed in tabular form (Table 2).

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