



Collembola associate with hermit crabs *Coenobita clypeatus* (Crustacea: Paguroidea: Coenobitidae)

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Abstract

This study provides a redescription and new biological information on *Coenaletes caribaeus* (Collembola: Coenaletidae), an obligate commensal springtail associated with terrestrial hermit crabs. Using both scanning electron microscopy (SEM) and light microscopy, we analyze the distinctive morphological characteristics of this genus and the Caribbean species. In addition, we present new records and offer insights into the gastropod shells that serve as hosts.

Keywords Springtail | seashore | terrestrial crabs | commensal | gastropod shells

1 Introduction

Hermit crabs are decapod crustaceans, most of which possess a non-calcified abdomen that require protection from predation. More than 850 species within the superfamily Paguroidea inhabit empty gastropod shells for protection, the majority of which are marine. Hermit crabs are best known from intertidal areas, where they are conspicuous and ecologically important as scavengers and predators. The family Coenobitidae comprises approximately 17 amphibiotic species that live near coastal areas, as their larvae must develop in seawater. The genus *Coenobita* is widely distributed throughout tropical regions, and its members use a variety of gastropod shells for shelter throughout their lifespan.

Approximately 140 species of these crabs have documented biological associations (including parasitism) involving 149

species across nine phyla (McDermott, 2010). A wide range of symbionts attach to, bore into, or live freely within lumen of shells inhabited by hermit crabs, which also serve as hosts for numerous parasites. Some ectosymbiotic mites are obligate associates. Additionally, certain invertebrates act as parasitic castrators, crabs can also have pathogens and function as first or second intermediate hosts.

However, associations involving members of the class Collembola have been largely overlooked.

Springtails (Collembola) are primarily known as inhabitants of soil and leaf litter; however, a few families are restricted to seashore habitats, including Actaletidae (genera *Spinactaletes* and *Actaletes*) and Isotogastruridae (*Isotogastrura*). In addition, some members of Isotomidae (*Archisotoma*, *Axelsonia*), Neanuridae (*Friesea*, *Oudemansia*), Entomobryidae



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(*Seira*), and Hypogastruridae (*Paraxenylla*) also occur in marine littoral environments (Christiansen & Bellinger, 1988; Palacios-Vargas & Vázquez, 1988).

In 1980, a species was identified as a commensal of hermit crabs (Jacquemart, 1980), led Bellinger (1985) to establish the family Coenaletidae. This monogeneric family comprises only two known species: *Coenaletes vangoethemi* (Jacquemart, 1980), from New Guinea, and *C. caribaeus* Bellinger, 1985 from Guadeloupe Island in the Caribbean Sea. Both species are exclusively associated with hermit crabs of the genus *Coenobita* (Crustacea: Decapoda).

Additionally, *C. caribaeus* has been reported from the Dominican Republic (Mari Mutt, 1994) and the Mexican Caribbean (Maldonado-Vargas & Palacios-Vargas, 1999). The aim of this study is to provide a redescription of *Coenaletes caribaeus*, the only known springtail genus that has adapted to life as an obligate commensal of terrestrial hermit crabs. Specimens were examined using

both light and scanning electron microscopy to obtain detailed information on their distinctive morphology. This study also presents new distribution records and discusses aspects of the species' biology, including the shell preferences of its hermit crab hosts.

2 Materials and Methods

The crabs examined were collected from two localities in the state of Quintana Roo, Mexico (Cozumel Island and Xcacel), and from one locality in Bahía Solano, Chocó Province, Colombia. On Cozumel Island, 10 specimens of *Coenobita clypeatus* were collected. In Xcacel, three samplings were conducted: 46 specimens in 1999, six in July 2022, and 20 in March 2024. In Bahía Solano, two specimens of *Coenobita compressus* were collected in 2024.

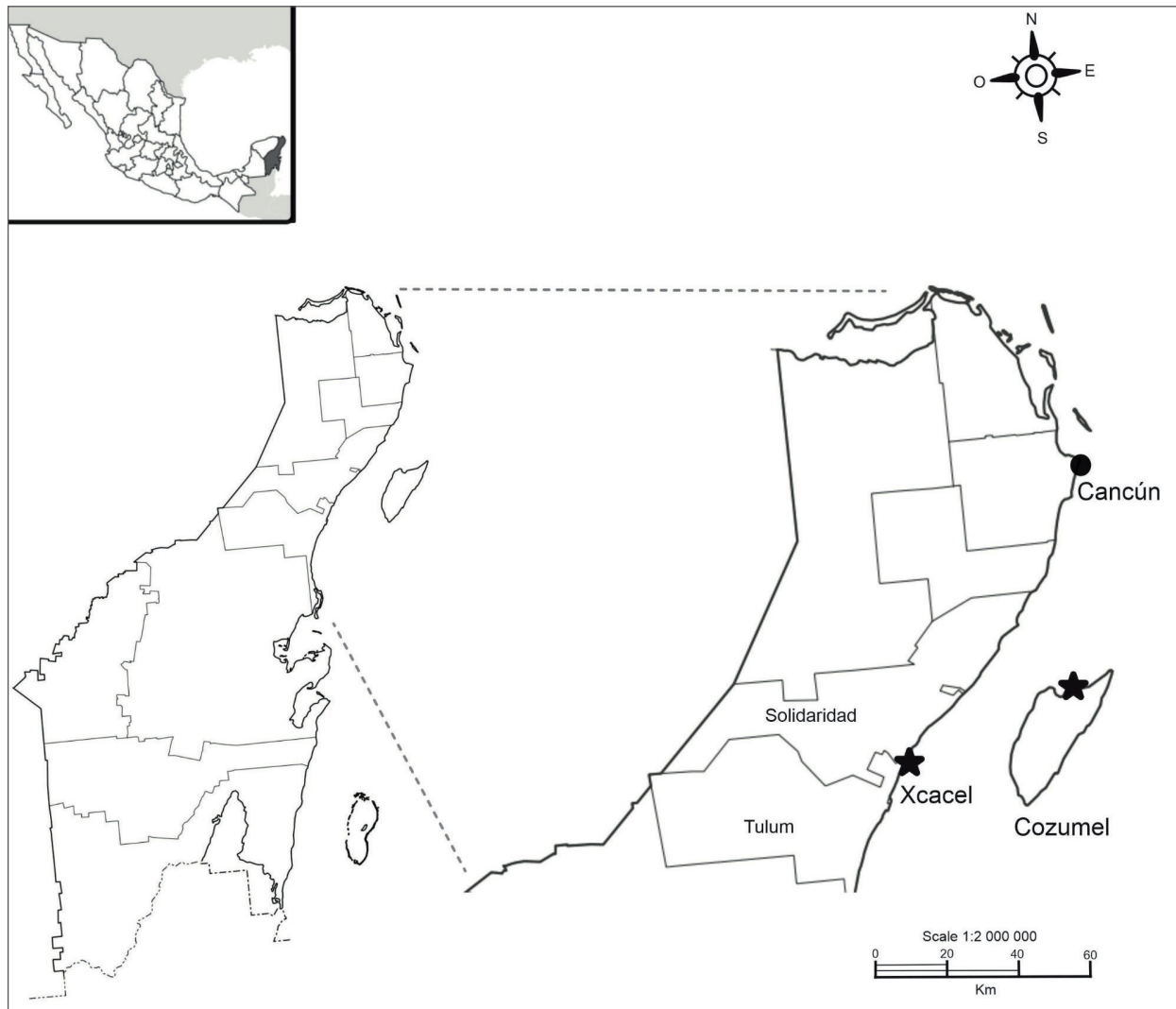


Figure 1. Map showing the two localities.

The area of Cozumel Island where *C. clypeatus* occurs is dominated by dwarf mangroves. The limited growth of these mangroves is attributed to the karstic bedrock, which restricts water exchange and results in calcium-saturated, nutrient-poor water and shallow soils. In Xcacel, *C. clypeatus* inhabits a coastal tropical forest, where it is found in groups. In contrast, Bahía Solano is characterized by tropical rainforest, where *C. compressus* also occurs in large aggregations.

To study the morphology of *Coenaletes caribaeus*, multiple specimens were dissected and mounted on slides in Hoyer's solution after clarification with 10% KOH and lactic acid. Images of various body structures were obtained using a scanning electron microscope (SEM) and a phase-contrast microscope (PCM).

For scanning electron microscopy (SEM), specimens were dehydrated through a graded ethanol series, dried using a Baltec CPD030 critical point dryer, and coated with gold with a Denton Vacuum Desk II ion coater. This method allowed the imaging of previously undocumented structures, including the mandible, maxilla, and foot complex.

2.1 Study area

Specimens of the hermit crab *Coenobita clypeatus* (Fabricius, 1787) were collected from two localities in the state of Quintana Roo state in Mexico: Xcacel beach (20° 20' 25" N 87° 20' 42" W), and the Northern coast of Cozumel Island (20°30'N and -86°57'W) (Fig.1).

2.2 Vegetation

Cozumel is an island located off the coast of Quintana Roo, opposite Playa del Carmen. Its vegetation is predominantly medium subdeciduous forest, although mangroves and coastal dune vegetation are also present. Other plant formations, such as lowland rainforest and halophytic coastal dune vegetation, also occur and the area is colonized by dwarf mangroves (Moreno-Casasola & Infante, 2009).

In Xcacel, the vegetation is characterized by coastal dunes, coastal scrub, mangroves, low subdeciduous forest, and secondary vegetation. In the dune zone, sea grape and coconut palm are common. Red and white mangroves are also present, and tule vegetation occurs in flood-prone areas (Prezas, 1996).

2.3 Methods

In July 2022, specimens of the hermit crab *Coenobita clypeatus* (Fig. 2), were collected manually and placed

in shaded plastic containers for inspection. Population density was not estimated because it exhibits gregarious behavior. The crabs were washed with fresh water, and when springtails floated to the surface (Fig. 3), they were collected with a brush and preserved in 96% ethanol. The hermit crabs placed in water containers were subsequently released back unharmed into their natural habitat, while five individuals were retained in their shells for later examination.

A second expedition was conducted in March 2024, during which several specimens of the hermit crab *Coenobita clypeatus* were collected at Xcacel, Quintana Roo. Springtails were obtained by immersing the



Figure 2. Habitus of *Coenobita clypeatus* in *Cittarium pica* (Linnaeus, 1758)



Figure 3. *Coenaletes caribaeus* floating on freshwater beside the hermit crab.

crabs in freshwater; the Collembola were subsequently preserved, and the hermit crabs were released unharmed into their natural habitat.

On the same date, a pair of hermit crabs were also collected on Cozumel Island and transported early in the morning to the Faculty of Sciences, UNAM, in a plastic container lined with a small towel and containing a small amount of water. By the afternoon, the hermit crabs were still alive, and several springtails were obtained. These springtails survived for up to five hours outside the crabs and were photographed and filmed alive for the first time (Fig. 3).

Preservation of Collembola in 96% alcohol resulted in the adhesion of numerous bacteria to the cuticle, which complicated the acquisition of detailed images of specific body regions using scanning electron microscope. Although bacterial adhesion to the cuticle is uncommon in most soil-dwelling organisms, this condition must be considered in collembolans associated with hermit crabs. Because these collembolans inhabit the interior of gastropod shells and remain in close contact with crab secretions, other microorganisms, such as bacteria, may become associated with their cuticle. This association complicates the cleaning process during specimen preservation.

A total of 22 specimens were examined to assess morphological variation. Thirteen slides were prepared (five females, three juveniles, and five males). Six additional specimens were dissected to obtain detailed drawings and photographs of the mouthparts, and three specimens were prepared for scanning electron microscopy (SEM). For SEM analysis, specimens were dehydrated through a graded ethanol series, dried in a Baltec CPD030 critical point dryer, and coated with gold with a Denton Vacuum Desk II ion coater. Observations were conducted a Carl Zeiss Primo Star phase-contrast microscope.

3 Results

3.1 Redescription

Coenaletes Bellinger, 1985

Diagnosis: Entomobryoidea. Lacking pigment, eyes, and postantennal organ. Mandible with molar plate but without apical teeth; maxilla small, bearing six subequal lamellae. Pronotum reduced; abdominal segments III and IV fused and elongated, remaining trunk segments distinct. Plurichaetotic, ordinary setae conical and acuminate, varying in length. Differentiated setae present only on abdominal tergites II–IV, trochanters and

apices of tibiotarsi. Differentiated spine-like setae occur only on antennal segments and on the lateral margins of thoracic and abdominal tergites in males. Dorsal apex of tibiotarsus excavate at the base of unguis; pretarsal setae borne on papillae. Unguis with greatly enlarged lateral teeth, capable of folding dorsally into a recess at the distal end of the tibiotarsus. Furcula well developed, extending beyond ventral tube; with dens smooth, bearing few setae; mucro falcate and fused to dens.

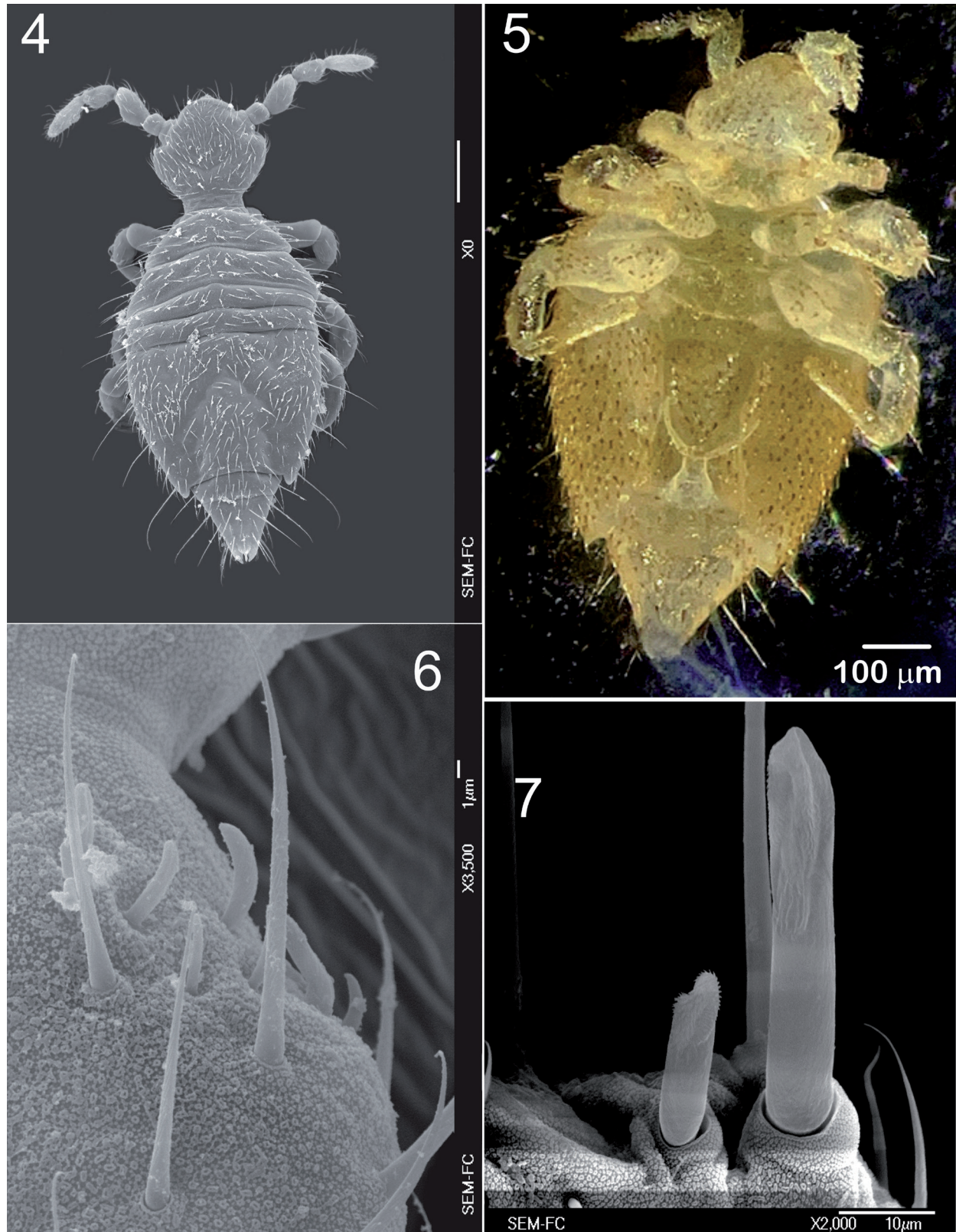
Type species : *Coenaletes vangoethemi* (Jacquemart, 1980).

Coenaletes caribaeus Bellinger, 1985

Female. (Figs 4 and 5). Antennal segment IV in the male with two subapical organs, each borne on a separate minute peg, and additional sensilla located on the apical half. Antennal segment III with eight sensilla of varying size on the outer apical surface (Fig. 6), two similar spines with rounded, truncate apices, and one spiniform seta at the base of the segment; four bothriotrichia present ventrally. Antennal segment II with one blunt seta on outer apical surface, two spines of different sizes with truncate apices and minute serrations, and six bothriotrichia (Fig. 7). Antennal segment I with nine setae arranged in a distal ring and five to six more basal setae; additionally, two setulae and one thick spine with a rounded apex are present on the outer apical surface.

Head slightly wider than long ($204\mu\text{m} \times 232.5\mu\text{m}$) (Figs 4, 5) in both sexes, with the oral region only slightly projecting beyond the anterior curvature of the frons; interantennal distance approximately equal to head length. Mandible with a well-developed molar plate, lacking apical teeth. Maxilla with a compact capitulum bearing six short, curved lamellae, the inner margins finely fringed (Fig. 8); maxillary outer lobe not discernible. Labrum with six small anterior labral setae and six longer prelabral setae, positioned anterior to the ordinary cephalic setae (Fig. 9). Labium with four setae on basomedial area one of which is longer and thicker; basolateral area with 5 setae; proximal area with 3 distal papillae, each bearing 1 apical and 1–2 subapical setae (Fig. 10).

Thorax with short blunt sensory setae: 1 + 1 laterally on abdominal segments II and III, and 2 + 2 located posterior to the inner bothriotrichia of the fused abdominal segments III and IV. Thoracic segment III in males with a group of four differentiated spines at each side. Abdominal segments I–III each with one spine per side, the spine on segment III directed upward, larger, and sharply pointed (Fig. 11). Macrochaetae arranged as follows: 1 + 1 dorsally and 3 + 3 laterally on the fused abdominal segments III and IV; 1 + 1 laterally

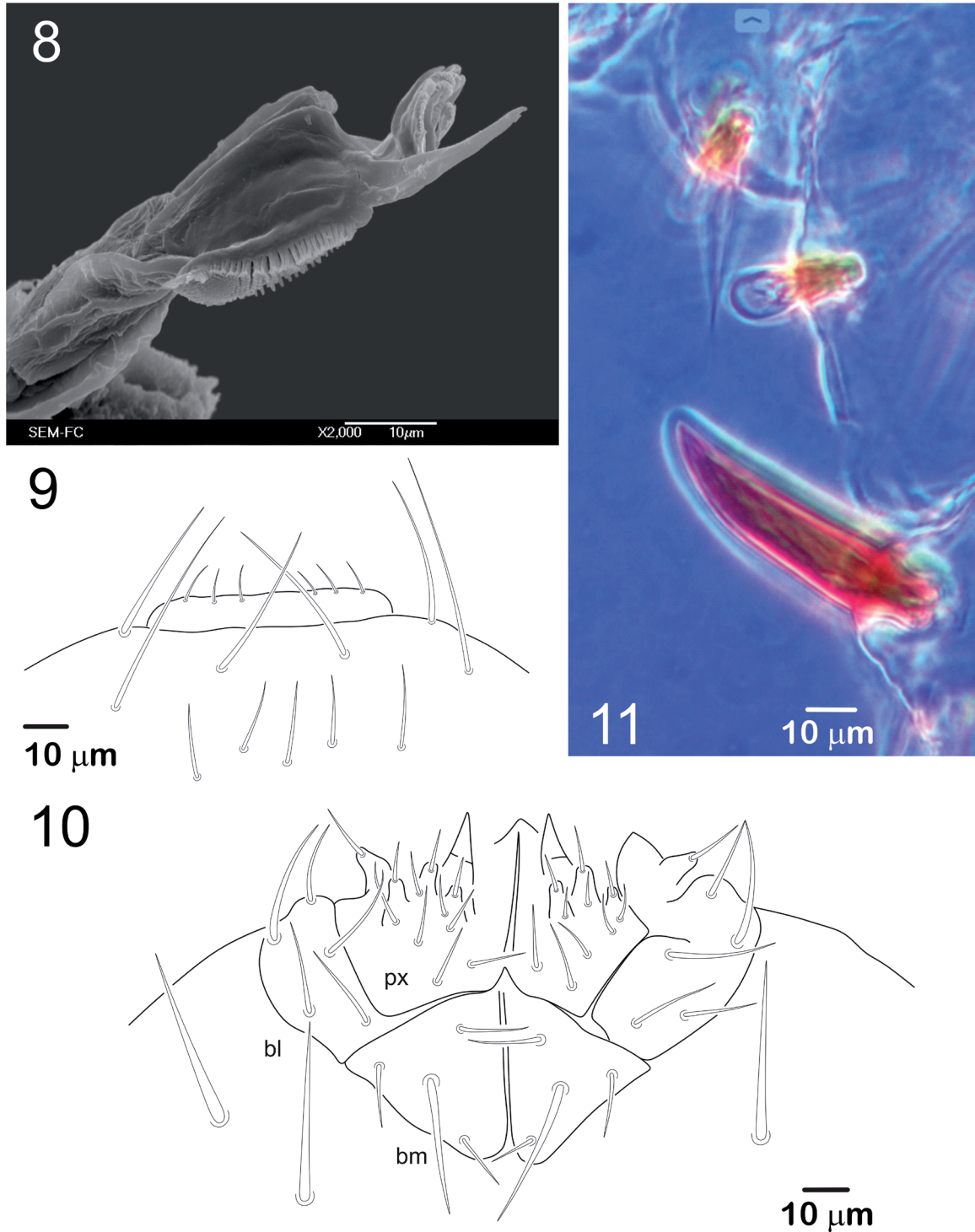


Figures 4–7. (4). Habitus dorsal view (SEM) of female *C. caribaeus*. (5) Ventral view of *C. caribaeus* alive (Phase Contrast Microscopy). (6) Ant. III, sensilla from sensorial organ, (7) Spines and setae of Ant. II of male.

on abdominal segment V; and 5 + 5 very large setae on abdominal segment VI (Fig. 4).

One bothriotrichia present on the inner face of each trochanter. Tibiotarsi (I-III) with acuminate tenent hairs

3, 3, 4 arrangements, respectively (Fig. 12). Dorsal apex of the tibiotarsus concave, accommodating the dorsal base of the unguis. Pretarsus bearing a single lamella comparable in size to the unguis. Dorsal and



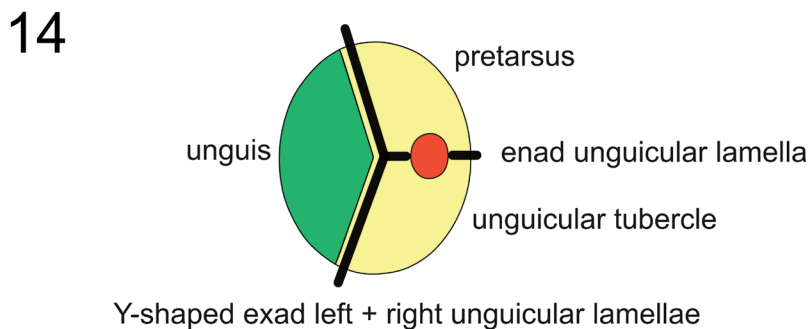
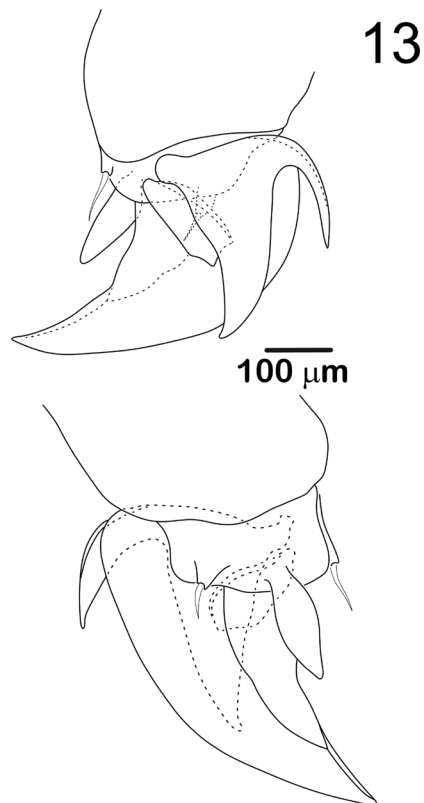
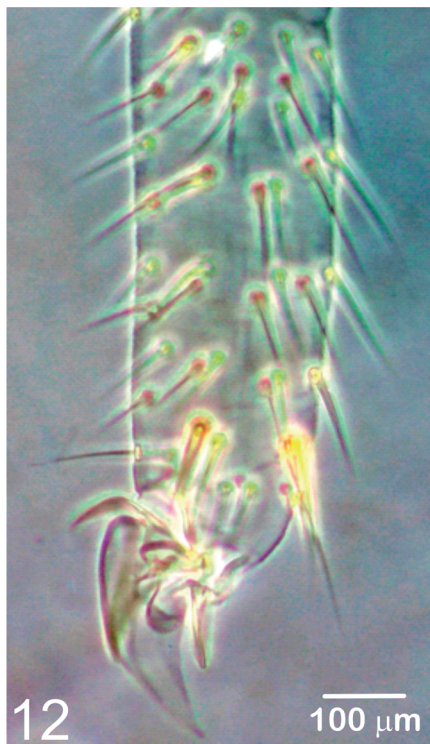
Figures 8–11. (8) Mandible and maxilla of female (SEM), mandible shows molar plate and apical teeth, maxilla with the six lamellae. (9) Labrum showing the labral and prelabral setae. (10) Labium showing the basomedial (bm) and basolateral (bl) plates with 4 and 6 setae respectively and proximal plate (px) with labial papillae. (11) Abd. I-III showing lateral spines, Phase Contrast Microscopy.

posterior teeth of the unguis forming lamellae similar in size to the unguis itself (Fig. 13). Foot complex with asymmetrical unguiculus, its apex usually obliquely truncated. Pretarsal setae borne on papillae (Figs 13 a, b and 14) (Janssens, 2024). The foot complex is notably thin, flexible, and easily distorted in mounted specimens. Pretarsal setae on papillae (Figs 15 and 16). Ventral tube with up to 10 + 10 or 11 + 11 lateral setae and 5 + 5 basal setae (Fig. 17).

Tenaculum bears up to distal 48 setae and 4 + 4 teeth (Fig. 18). The Manubrium has 4 pairs of posterior setae,

basal one longer than others, and anterior surface without setae. The dens are smooth, with 3 posterior setae in basal half. The Mucro is simple, fused to dens, mucro is about 1/9 of its length (Figs 19 and 20).

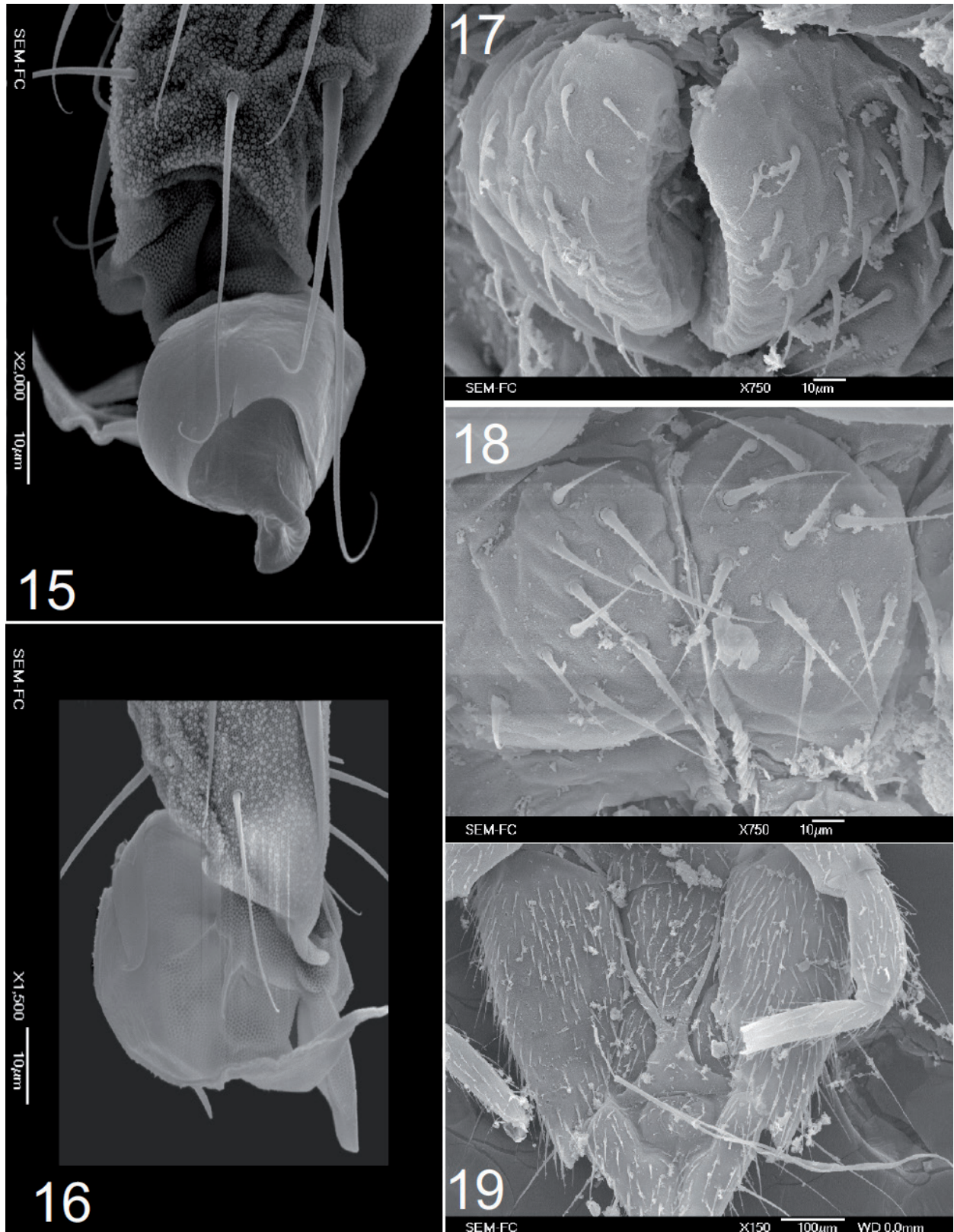
Male genital opening has 10 (9–11) circumgenital setae, 2 pregenital and 2 + 2 eugenital (1 + 1) (Fig. 21). The anal opening is located at the end of abdominal segment VI, showing the lateral anal plates posterior to the dorsal plate (Fig. 22). Specimens exhibit a small concavity in the middle of posterior abdominal segment III-IV (Fig. 4).



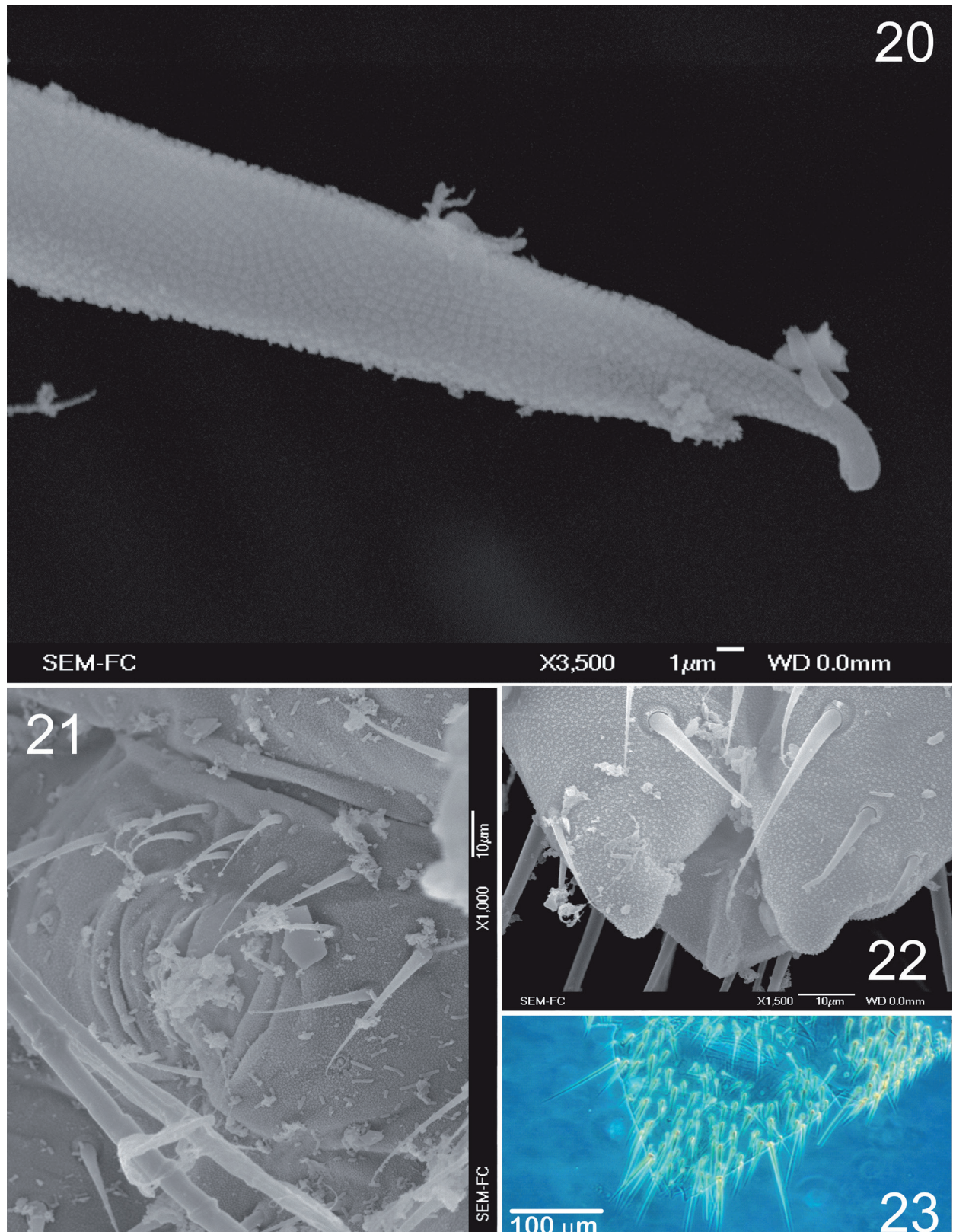
Cross-section of foot

Frans Janssens 2022.09.13

Figures 12–14, (12) Foot complex of leg I. **(13)** Foot complex, a) lateral and b) ventral views. **(14)** Cross section of foot complex interpreted by F. Janssens (2022).



Figures 15–19, (15) Dorsal view of foot complex and the acuminated tenent hairs (SEM). **(16)** Lateral view of foot complex (SEM). **(17)** Ventral tube (SEM). **(18)** Tenaculum (SEM). **(19)** Furcula (SEM).



Figures 20–23, (20) Apical part of dens and mucro (SEM). **(21)** Genital plate of male (SEM). **(22)** Anal opening of male (SEM). **(23)** Anal opening of female (Phase Contrast Microscopy).

Males of *C. caribaeus* can be distinguished from *C. vangoethemi* by their larger body size and longer dens. The number of antennal spines (from antenna I to III) in *C. caribaeus* are 1, 2, 2 and in *C. vangoethemi* are 1, 2, 3. Lateral trunk spines (thorax III and abdominal segments I–III) also differ between the species: 4, 1, 1, 1 in *C. caribaeus* and 3, 1, 2, 1 in *C. vangoethemi*, respectively.

Variation.

Females closely correspond to the description provided by Bellinger (1985). The results of the comparison with the Palacios-Vargas *et al.* (2000) study, show the following variation: present circumgenital setae 9–11, eugenital setae 1 + 1, and 2 + 1 (Fig. 23). Notably, one male exhibited asymmetry, bearing only two spines on thorax III and lacking a lateral spine on abdominal segment I.

Males of *C. caribaeus* are distinguished by their bigger size and longer dens than *C. vangoethemi* (see following key to check differences between species). The number of antennal spines (from antenna I to III). *C. caribaeus* are 1, 2, 2 and in *C. vangoethemi* are 1, 2, 3. The lateral spines on the trunk (thorax III and abdomen I to III) are also different, in *C. caribaeus* are 4, 1, 1, 1 in *C. vangoethemi* are 3, 1, 2, 1. The distribution of this family of Collembola is almost certainly pantropical, mirroring that of its host genus *Coenobita*. The limited records from Mexico, the Caribbean, and New Guinea likely reflect inadequate collecting rather than true distributional limits.

Key to the species of *Coenaletes*











Males with antennal spines (from Antenna I to III) 1, 2, 2; lateral spines on the trunk (Thorax III and Abdomen I to III) 4,1,1,1; dens smooth with 3 posterior setae along the appendix *C. caribaeus*
 Males with antennal spines (from Antenna I to III) 1,2,3; lateral spines on the trunk (Thorax III and Abdomen I to III) 3,1,2,1; dens smooth, bearing 2 posterior setae in basal half *C. vangoethemi*

3.2 Biology

Knowledge of the biology of this springtail is limited. *Coenaletes caribaeus* is a commensal of hermit crabs and shows a clear preference for gastropod shells occupied by *Coenobita clypeatus* (Decapoda: Coenobitidae), specifically those of *Cittarium pica* (Mollusca: Tegulidae). In a previous study, Maldonado and Palacios-Vargas (1999) examined 46 specimens of *C. clypeatus* and recorded 85 Mesostigmata (4.6%), 1,595 Astigmata (91.35%), 10 Prostigmata, and 56 Collembola (3.2%).

Among the Collembola, they were identified *Cyphoderus* sp. (Cyphoderidae), *Seira* sp. (Entomobryidae), and *Coenaletes caribaeus* (Coenaletidae). Notably, among the ten different gastropod species used by the hermit crabs, only those of *Cittarium pica* hosted this springtail (Table 1). The association between *C. caribaeus* and hermit crabs likely arises from the shape of the shell and the crabs.

Table 1. Gastropoda shells used by hermit crabs of genus *Coenobita*

FAMILY	SPECIES
Trochidae	<i>Cittarium pica</i> 
Trochidae	<i>Tegula excavata</i> 
Turbinidae	<i>Lithopoma caelatum</i> 
Neritidae	<i>Nerita peloronta</i> 
Neritidae	<i>Nerita tessellata</i> 
Littorinidae	<i>Cenchritis muricatus</i> 
Cassidae	<i>Cypraecassis testiculus</i> 
Melongenidae	<i>Melongena melongena</i> 
Fasciolaridae	<i>Hemipolygona carinifera</i> 
Fasciolaridae	<i>Leucozonia leucozonalis</i> 

New Records.

This information is relevant for assessing the distribution of the species and underscores the potential for discovering both new species and new locality records.

Material Examined. Ex *Coenobita clypeatus*, from Santo Domingo. Collection of Smithsonian Institution, 1978. Sample 873 from the Crustacean collection of the Institute of Biology, UNAM. *M. J. Rathbun det.*, 1991. One specimen of *Coenaletes caribaeus* was recovered and used for illustrations, although it was old and poorly preserved.

Ex *Coenobita compressus*, Colombia, Cochó: Beach of Utría Cove, from shells of *Tegula atra* Lesson, 1830 (Gasteropoda: Tegulidae). One juvenile specimen of *Coenaletes* sp., collected on 24-XII-2024 by J. G. Palacios-Vargas.

4 Discussion

Palacios-Vargas and Castaño-Meneses (2009) conducted a revision of sexual dimorphism across several families of Collembola and found that, in most cases, pronounced sexual dimorphism is associated with aquatic habitats.

In these environments, males often possess clasping antennae that allow them to hold onto females, reducing the risk of separation caused by water movement. Most interesting is that other families have Antennae II and III modified, such as all Mackenziellidae (now part of Sminthurididae), some Bourletiellidae, all Sminthurididae, some genera of Isotomidae and the two known species from Coenaletidae.

In this latter family, males also bear spines on the thorax and abdomen, although their function remains unknown. Within Entomobryomorpha, pronounced sexual dimorphism is particularly notable in Coenaletidae and resembles that observed in certain Isotomidae, such as the marine littoral species *Axelsonia tubifera*, one of the few Arthropoda species known exhibit sexual dimorphism. The distal part of Antenna III in *Axelsonia*, which contains a characteristic cluster of thick sensilla (about 14), in contrast with *A. littoralis*, which has 9–11 sensilla. Members of *Axelsonia* lack a postantennal organ, and species of Coenaletidae also display 9 sensilla on the distal part of antennal segment III, while lacking both postantennal organs and eyes.

When comparing the morphology of *Coenaletes*, it is noteworthy that *Axelsonia* exhibits smooth trichobothria and numerous sensilla on Antenna III, in addition to the absence of a postantennal organ. Most species of *Axelsonia* inhabit marine littoral environments within the tidal area; however, *A. johnstoni* Jordana in 1997, was described from the gill chambers of terrestrial crabs.

Several morphological similarities are shared by *Axelsonia tubifera* and *Coenaletes caribaeus*, including a tegument covered with acuminate setae measuring 9–50 μm in length and the presence of 2 + 2 very thin sensory setae (approximately 90 μm long) on Abdomen II to IV, with all abdominal segments clearly separated. In contrast, *C. caribaeus* also features 2 + 2 sensory setae on its abdominal segments, but Abdomens III and IV are fused. The tenaculum of *A. tubifera* bears 4 + 4 teeth on each ramus and about 13 setae on the corpus, whereas *A. littoralis* has 16 setae. The furcula of *A. tubifera* is elongate, reaching the ventral tube, with the dens approximately twice the length of the manubrium (1.5–2 times longer).

Interestingly, the furcula of *Podura aquatica* and *C. caribaeus* share a similar in overall appearance, both are elongated and oriented in a “Y” shape. However, in *Podura aquatica*, the furcula is annulated, whereas in *C. caribaeus* it is smooth. The former bears numerous setae, while the latter has only two or three setae on each dens. The mucro also differs markedly between the two species; in *Podura aquatica* it is clearly separated and adapted for jumping on water, while in *C. caribaeus*, it is nearly completely fused to the dens and is hooked. These similarities are best interpreted as the result

convergent evolution between the families Poduridae and Coenaletidae, reflecting analogous adaptations to aquatic or semi-aquatic environments.

Consequently, it is possible that Coenaletidae, an obligated commensal of hermit crabs of the genus *Coenobita* (Crustacea: Paguridae), originated from certain members of *Axelsonia* (Isotomidae). Both groups are associated with marine littoral environments, and at least *A. johnstoni* has been recorded from terrestrial crabs. Recent molecular studies further support this hypothesis by revealing a close phylogenetic relationship between *Axelsonia yinii* and *Coenaletes caribaeus*.

5 Conclusions

Coenaletes caribaeus is an obligate symbiont of tropical terrestrial hermit crabs of the genus *Coenobita* and shows a marked preference for inhabiting gastropod shells of the family Trochidae, particularly *Cittarium pica*. We suggest that the preference of *Coenaletes caribaeus* for shells of *Cittarium pica* is related to the shell's volume and shape, which explains why these springtails are found exclusively in the hermit crab *Coenobita clypeatus*. In a study by Guillén and Osorno (1993) of 945 specimens of *Coenobita compressus* Edwards, 1836 from Isabel Island, Nayarit, it was observed that the crabs preferred shells of *Nerita scabricosta*, likely because of their low weight and relatively large internal volume. Although shells of *Cittarium pica* are comparatively heavy, their large size and spacious interior may similarly account for the preference shown by both the hermit crabs and their associated springtail, *C. caribaeus*.

Apparently, shells of this gastropod provide the greatest benefits to hermit crabs due to their low weight and relatively large internal volume compared to other shell species. Under conditions of high mobility and low predation pressure, *C. compressus* maximize these benefits by selecting lighter shells, thereby reducing the energetic cost of transport. An additional noteworthy record comes from Bahía Solano (Colombia), where a specimen of *Coenaletes* sp. was recovered in *C. compressus*, but inhabiting *Tegula atra* (Tegulidae). This record is particularly relevant because material from the Mexican Pacific coast at Bahía de Banderas (Jalisco) was also examined, yet no springtails were recorded there.

Key morphological features of the genus include antennal segment III bearing eight sensilla and a mandible with a well-developed molar plate but lacking apical teeth. Sexual dimorphism is expressed by the presence of spines on antennal segments II and III, as well as lateral spines on the trunk (thorax III and abdominal segments I–III).

Pronounced hypertrichosis is present on the ventral tube, which bears to 10+10 or 11+11 distal lateral setae and 5+5 proximal setae, and the tenaculum may carry as many as 48 setae. The most remarkable diagnostic character is the highly specialized foot of *C. caribaeus*, which is entirely distinct from that of other known Collembola.

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