

## Article

# A New Genus of Sminthurididae (Collembola, Symphypleona) from Brazil, with Notes on the Systematics of the Family

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**Abstract:** The Sminthurididae family includes Symphypleona species highly adapted to courtship, with males exhibiting remarkable modifications on their antennae. Here we describe a new Neotropical genus and species of Sminthurididae from a Cerrado-Caatinga ecotonal zone in Brazil. Males of *Parasminthurides spinosus* gen. nov. sp. nov. have highly dimorphic antennal claspers similar to those of *Sminthurides*, but its females have unique strong spiniform chaetae on antennal segments II and III as well, which are possibly accessories for the courtship. The new genus can also be diagnosed by its elongated maxillae, males having large dorsal vesicles between abdomen II and III, ungues I–III with similar morphology and sizes, and interno-apical dental chaetae modified into large spiniform chaetae. We also present the main diagnostic features of all Sminthurididae genera, providing a comparative table and an updated identification key for them. Finally, we discuss the previous and current knowledge on the family's systematics, suggesting some perspectives for future studies in this field.

**Keywords:** Neotropical Region; new species; sexual dimorphism; *Sminthurides*; Sminthuridida



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## 1. Introduction

Sminthurididae represents one of the most peculiar lineages of springtails. The family includes species that are highly adapted to courtship, with males that are notably smaller than females and with complex modified clasping antennae, which are used before mating to hold the opposite sex until the deposition of the spermatophore and posterior insemination. This behavior varies between the few studied species, with males being more active in guiding females to catch the spermatophore in *Sminthurides aquaticus* (Bourlet, 1842) [1]. On the other hand, males of *Denisiella* sp. hold and stimulate females during an energetic courtship, before dropping the spermatophore, which is posteriorly caught by the female alone. In *Sphaeridia pumilis* (Krausbauer, 1898) [2], a direct transfer of the spermatophore by the male with its hind tibiotarsus and ventral tube to the genital opening of the female has been observed [3–5]. In some taxa, such as *Sphaeridia* spp., the specimens can be attached to each other for few days before mating [5]; therefore, it is not uncommon to sample the connected couples, which makes it clear that the individuals belong to the same species. This is particularly useful in relation to the family's taxonomy since females can be quite different from males [4,5].

Sminthurididae, along with the monotypic Mackenziellidae, delimit the suborder Sminthuridida, the sister group of all other Symphypleona, the Appendiciphora [6–8]. Although the systematic placing of Mackenziellidae is still puzzling and has been the

subject of several revisions [9–13], the Sminthurididae are remarkably different from the Appendiciphora due to the sexually dimorphic antennae of males and the absence of the subanal appendage in females [5,6,14]. However, although the morphology supports the splitting of Sminthurididae from the Appendiciphora, the internal relationships of Symphypleona have never been properly studied using modern molecular tools, and preliminary data with limited samples support the notion that Sminthurididae may be an ingroup of Appendiciphora [15–17].

The Sminthurididae are widespread, and there are currently 151 described species distributed in 12 genera within the family. The largest genera are *Sphaeridia* Linnaniemi, 1912 [18]; *Sminthurides* Börner, 1900 [19]; and *Denisiella* Folsom and Mills, 1938 [20], with 69, 56, and 13 nominal species, respectively, whereas all the other genera have only one or two species each [8]. The Neotropical Region represents one of the richest biogeographical zones for the Sminthurididae, with 64 species and five genera recorded [21–23]. However, in Brazil only 25 species have been registered to date, most of them from *Sphaeridia* [24]. This data contrasts with the country's large area in the neotropics and its variety of habitats, suggesting that the Sminthurididae are understudied in Brazil.

Here we describe a new genus and species of Sminthurididae from Piauí state, Brazil. We also survey the main diagnostic features of all Sminthurididae genera, providing a comparative table and an updated identification key for them. Finally, we discuss the previous and current knowledge on the family's systematics and its affinities with other Symphypleona lineages, suggesting some perspectives for future studies in this field.

## 2. Materials and Methods

Fresh specimens of the new species were first preserved in 70% ethanol at 6 °C for a few months. Subsequently, they were clarified in Nesbitt's solution, washed in Arlé's liquid, and mounted in glass slides in Hoyer's medium, following the combined methods of Arlé and Mendonça [25] and Jordana et al. [26]. Morphological studies and raw drawings were made using a Leica DM750 microscope with an attached drawing tube, whereas photographs were taken in the same microscope using a Leica MC170 HD camera and LAS v. 4.12 software. Final figures were vectorized, improved, and assembled in plates with CorelDraw 2021 software.

The terminology used in descriptions mainly follows the works of Massoud and Betsch [27] for the male's antennal chaetotaxy; Cipola et al. [28] for the labral chaetotaxy; Betsch and Waller [29], with adaptations, for the head (including the post-labial region) and anterior large abdomen chaetotaxy; Vargovitsh [30–32] for the posterior large abdomen chaetotaxy, with adaptations; Betsch [33] for the small abdomen chaetotaxy; Nayrolles [34] for the oval and tibiotarsal organs of tibiotarsus III; and Bretfeld [35] for the dorsal dens chaetotaxy. Drawings and observations were made based on the entire type series.

The type material is deposited in the Collembola Collection of the Biosciences Center of the Federal University (CC/UFRN), Natal, Rio Grande do Norte state, Brazil.

The abbreviations used in the text and figures are: Abd—abdominal segment; Ant—antennal segment; and Th—thoracic segment. The presence or absence of chaetae are marked with white arrows; unpaired chaetae on the head and trunk are marked with a “\*”. Head, trunk (thorax + abdomen), and furcal chaetotaxy are given by half body. Chaetae labels are in bold.

## 3. Results

### 3.1. Taxonomic Summary and Genus Diagnosis

Order Symphypleona Börner, 1901 [36]

Suborder Sminthuridida Bretfeld, 1986 [6] sensu Sánchez-García and Engel, 2016 [7]

Superfamily Sminthuridoidea Börner, 1906 [37] sensu Fjellberg, 1989 [13]

Family Sminthurididae Börner, 1906 [37]

Genus *Parasminthurides* gen. nov. Medeiros and Bellini

*Diagnosis of the genus:* Males with highly dimorphic antennae, Ant II with **B1**, **b1–b5**, and **tra1** elements; Ant III with **c1–c3** elements plus up to five small spines between them; **tra2** absent. Females with two apical robust spiniform chaetae on Ant II, and one proximal and two apical robust spiniform chaetae (one of them larger than the others) on Ant III. Ant IV in both sexes undivided, without sensillum-like or large blunt chaetae. Eyes 8 + 8. Post-labial region with **c** chaetae only in females. Head capsule and mandibles without modifications; maxillae elongate. Dorsal Th I with 1 + 1 large vesicles in both sexes; dorsal Th III and posterior large abdomen (Abd II + III region) each with 1 + 1 large dorsal vesicles in males. Dorsal large abdomen posteriorly with long chaetae in both sexes. Small abdomen without appendage-like processes on the dorsal anal valve. Ventral tube corpus regular, without lateral projections or modifications. Tibiotarsi I–II without any clear modification in both sexes; tibiotarsal organ present on distal tibiotarsus III. Leg II without a clasping organ. Ungues I–III subequal in shape and size. Dorso-internal apical chaetae of dens (**J** line) as large spiniform chaetae. Mucro wide and crenulated with three lamellae; mucronal chaeta present.

*Type species:* *Parasminthurides spinosus* gen. nov. sp. nov. Medeiros and Bellini.

*Etymology:* The new genus was named after its resemblance to *Sminthurides* (“para” in Ancient Greek means “next to” or “resembling”).

*Remarks:* To describe the new genus, we revised the most relevant literature on Sminthurididae, circumscribing the main diagnostic features of all genera in Table 1. *Parasminthurides* gen. nov. can be distinguished from all other Sminthurididae especially by the combination of: (1) females’ Ant II and III with robust spiniform chaetae; (2) elongated maxillae; (3) only males with large dorsal vesicles on Abd II–III; (4) unguis I–III with similar morphology and sizes; and (5) apical chaetae of the **J** line on the dens modified into spiniform chaetae. The robust spiniform chaetae on Ant II–III of females have never been reported before to any other member of Sminthurididae (Table 1), and may play a role in courtship, possibly being complementary to the males’ modified antennal elements. At least, the spiniform chaetae on apical Ant III look homologous to the **c2–3** elements of males, and may help couples to remain attached before mating. Modified chaetae on females’ Ant III have also been recorded for *Stenacidia* Börner, 1906 [37]; however, in the latter, females have two blunt chaetae on this segment, which are clearly not homologous to the apical chaetae of the new genus [38]. Furthermore, *Parasminthurides* gen. nov. lacks the **b6** element on males’ Ant II and the blunt chaetae on females’ Ant IV (vs. present), whereas it has elongated maxillae (vs. regular), large dorsal vesicles on the Abd II–III of males (vs. absent), spiniform chaetae on the **J** line of both sexes (vs. only in males), and a wide mucro (vs. a narrow one) [5,38] (Table 1).

**Table 1.** Main diagnostic characters of Sminthurididae genera *sensu* Bellinger et al. [8].

Genera/Characters	Number of Described Species	Ant II Mod. Chaetae (♂)	Ant III Main Mod. Chaetae (♂)	Ant II Mod. Chaetae (♀)	Ant III Mod. Chaetae (♀)	Ant IV Mod. Chaetae (♀)	Ant IV Subdivisions (♀)	Ant IV Subdivisions (♂)	Elongated Maxillae	Th III Dorsal Vesicles (♂)	Abd II–III Dorsal Vesicles	Large Abdomen Dorsal Long Chaetae	Abd V Dorsal Processes (♂)	Mod. Ventral Tube (♂)	Proximal Tibiotarsus I Organ (♂)	Proximal Tibiotarsus II Mod Chaetae	Distal Tibiotarsus III Organ	Leg II Clasping Organ (♂)	Ungues I–II/III Ratio	Dental Spiniform Chaetae (J Line)	Mucro Shape	Mucronal Chaeta
<i>Boernerides</i> [5,39]	1	b1–b6, tra1	c1,c3	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	>?	+	na	–
<i>Debouttevillea</i> [4,27,40]	1	B1, b1–b4, tra1	c1–c3	–	–	–	+	–	–	+	+(♂,♀)	–	–	+	–	+(♀)	–	–	>?	–	wi	+
<i>Denisiella</i> [4,14,20,27,41–45]	13	b1–7, tra1–2	c1,c2(+/-), c3, tra3	–	–	+/(se)	–	–	–	–	–	+/-	–	–	+/-	+/-	–	–	>/=	–	na	+
<i>Pedonides</i> * [46]	1	b1–b5	c1–c3	?	?	?	?	–	–	+	–	–	–	–	+	+	+	+	=	+	na	–
<i>Pseudosminthurides</i> § [7]	1	?	?	?	?	?	?	–	–?	?	?	?	?	?	?	?	?	?	>	?	wi	–
<i>Pygicornides</i> [4,27,47,48]	2	b1–b6, tra1–2	c1–c3	?	?	?	+	+/-	–	+	–	+	+	–	–	–?	+	–	>?	–	wi	+
<i>Sinnamarides</i> [49]	1	B1, b1–b5, tra1	c1–c3	–	–	–	–	–	+	+	–	+	–	–	–	–	+	–	=	–	na	+
<i>Sminthurides</i> [4,5,14,19,27,39,50,51]	56	b1–b6(+/-), tra1, tra2(+/-)	c1–c3	–	–	+/(se)	+/-	+/-	–	+	–	+(♀)	–	–	–	–	+	–	>	-/+	wi/ na	+/-
<i>Sminthuridia</i> [4,27,52]	1	b1–b3	c3	–?	–	+(bl)	+	+	–	+	–	+	–	–	–?	–?	+	–	<	–	wi	+
<i>Sphaeridia</i> [4,5,14,18,27,53–55]	69	b1	c3	–	–	–	–	–	–	–	–	+	–	+	–	–?	–	–	>/=	+/-	na	–
<i>Stenacidia</i> ** [4,5,14,37,38]	1	B1, b1–b6, tra1	c1–c3	–	+(bl)	+(bl)	–	–	–	+	–	+(♂)	–	–	–	–	+	–	</>	+(♂)	na	+
<i>Yosiides</i> [4,27,56,57]	2	b1–b6, tra1(+/-)	c1–c3	–	–	–	+	+	–	–	–	+	–	–	–?	?	+	–	>	–	na	+
<i>Parasminthurides</i> gen. nov.	1	B1, b1–b5, tra1	c1–c3	+(sp)	+(sp)	–	–	–	+	+	+(♂)	+	–	–	–	–	+	–	=	+	wi	+

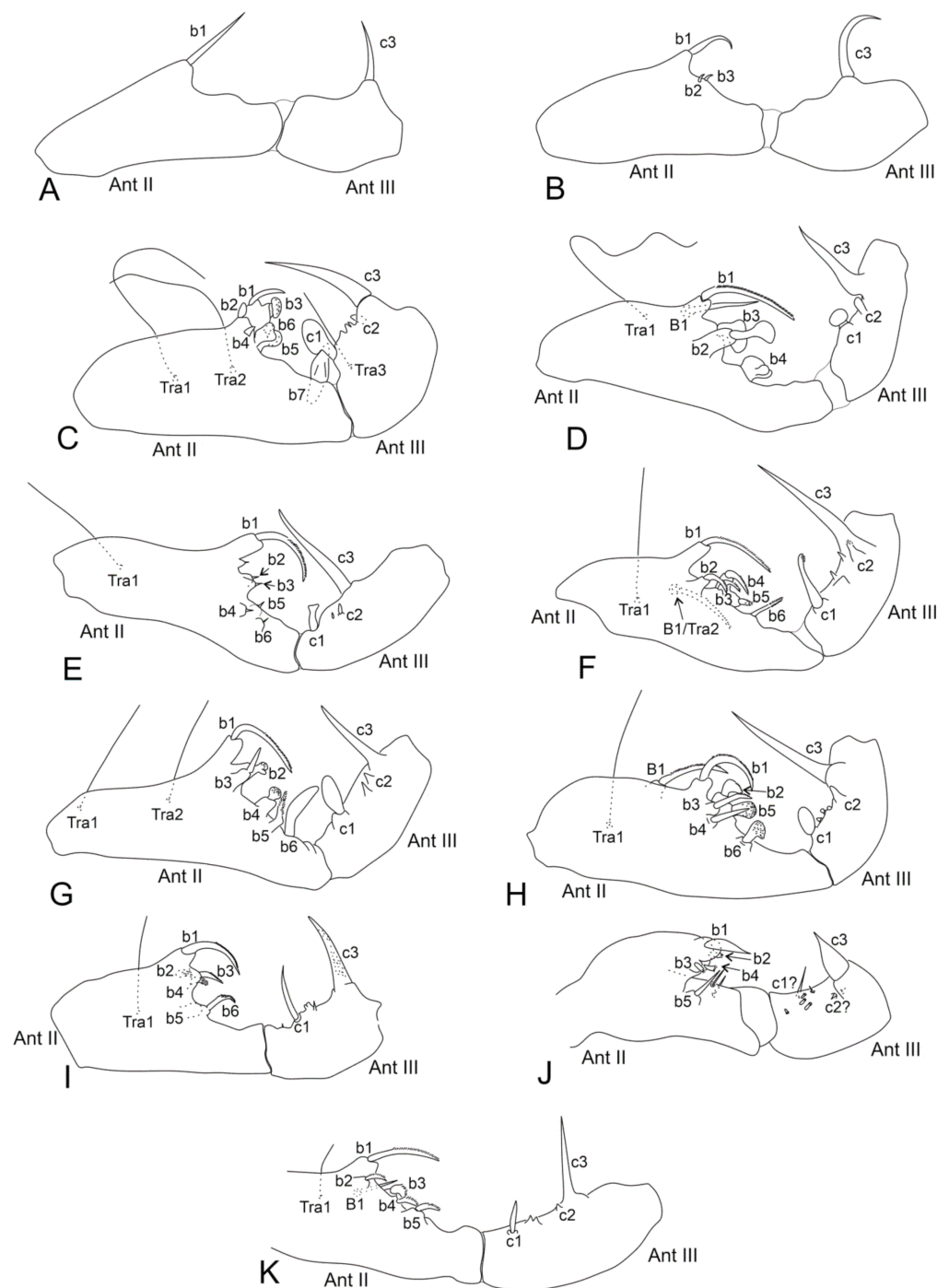
Legends: ‘§’ = extinct; ‘mod’ = modified; ‘+’ = present; ‘/’ = or; ‘-’ = absent; ‘>’ = longer than; ‘<’ = shorter than; ‘=’ = subequal; ‘?’ = unknown/unclear; ‘se’ = sensillum-like; ‘bl’ = blunt chaetae; ‘sp’ = spiniform chaetae; ‘na’ = narrow; ‘wi’ = wide; ‘\*’ = description based on a single male specimen; ‘\*\*’ = we followed Brettfield [5] and considered *Stenacidia stachi* (Jeannelot, 1955) [58] as a junior synonym of *S. violacea* (Reuter, 1881) [59]. Furthermore, *Stenacidia picta* Yosii, 1966 [56] was dismissed from the genus by the author, being *incertae sedis*.

The large dorsal vesicles on Abd II–III have been reported before only for *Debouttevillea* Murphy, 1965 [40], and for both sexes, whereas in *Parasminthurides* gen. nov. this morphology is restricted to the males. The new genus can also be distinguished from *Debouttevillea* by the following elements: males' Ant II with the **b5** element (vs. absent); females with undivided Ant IV (vs. subdivided); presence of elongated maxillae (vs. normal); large abdomen with long dorsal chaetae (vs. absent); ventral tube without modifications (vs. with lateral projections); presence of the tibiotarsus III organ (vs. its absence); and presence of dental spiniform chaetae (vs. their absence) [4,27,40] (Table 1).

The Sminthurididae can be putatively divided in two groups of genera, considering the morphology of the hind legs, having taxa with or without the tibiotarsal organ [5]. *Parasminthurides* gen. nov. belongs to the group in which such organ is present, similarly to *Boernerides* Bretfeld, 1999 [5], *Pedonides* Bretfeld, 2010 [46], *Pygicornides* Betsch, 1969 [48], *Sinnamarides* Betsch and Waller, 1991 [49], *Sminthurides*, *Stenacidia*, *Yosiides* Massoud and Betsch, 1972 [27], and *Sminthuridia* Massoud and Betsch, 1972 [27], while it is missing in *Sphaeridia*, *Denisiella*, and *Debouttevillea* group. All the genera with the tibiotarsal organ, with the exception of *Sminthuridia*, also share a complex morphology of Ant II–III, with at least five modified chaetae on Ant II and with the **c1** element on Ant III (Table 1). Males of *Pygicornides* and *Pedonides* show remarkable autapomorphies, such as enlarged dorsal processes on Abd V in the former and a clasping organ on leg II in the latter, which clearly separate them from all other Sminthurididae, including the new genus [46,48]. Other genera, such as *Boernerides* and *Yosiides*, differ from *Parasminthurides* gen. nov. especially due to the male's Ant II chaetotaxy, with **b6** and lacking the **B1** element (vs. the opposite), regular maxillae (vs. elongated), a narrow mucro (vs. a wide one), and the absence of dental spiniform chaetae in *Yosiides* and of the mucronal chaeta in *Boernerides* (vs. their presence in *Parasminthurides*) [5,27,39,56,57] (further differences are discussed in the previous paragraphs and in Table 1).

The most similar genera to *Parasminthurides* gen. nov. are *Sinnamarides* and *Sminthurides* due to: the absence of modified chaetae on proximal tibiotarsus II; males with a complex chaetotaxy of the Ant II–III and thoracic vesicles, but lacking projections on the ventral tube; and females with elongated chaetae on the dorso-posterior large abdomen. Furthermore, *Sinnamarides* has elongated maxillae, whereas many *Sminthurides* species have a wide mucro, both features seen in the new genus [49–51]. However, *Parasminthurides* gen. nov. can be distinguished from them by: females with spiniform chaetae on Ant II–III (vs. their absence); males with large dorsal vesicles in the Abd II–III region (vs. their absence); t males with elongated dorsal chaetae on the large abdomen (vs. their absence in *Sminthurides*); unguis I–III subequal in shape and size (vs. unguis III shorter and wider than unguis I–II in *Sminthurides*); dens with spiniform chaetae on the J line (absent in *Sinnamarides*), and the presence of a wide mucro (narrow in *Sinnamarides*) [49–51]. In addition, it is worth noting that the spiniform chaetae on the distal dens is a rare condition within *Sminthurides*, apparently having been described for a single species, *S. parvulus* (Krausbauer, 1898) [2] *sensu* Bretfeld, 1999 [5]. Nevertheless, this species does not fit the new genus due to the fact that the females' Ant IV has five subsegments (vs. being undivided), the males' Ant II has a **b6** element (vs. its absence), plus other diagnostic features of *Sminthurides* [5,50,51] (Table 1).

Further comparisons between the Sminthurididae genera are summarized in Table 1, Figure 1, and in the identification key below.



**Figure 1.** General morphology of the modified elements of males' Ant II–III in all previously described extant Sminthurididae genera: (A) *Sphaeridia*; (B) *Sminthuridia*; (C) *Denisiella*; (D) *Debouttevillea*; (E) *Yosiides*; (F) *Sminthurides*; (G) *Pygicornides*; (H) *Stenacidia*; (I) *Boernerides*; (J) *Pedonides*; (K) *Sinnamarides*. Figures based on [27,39,46,49]. We considered the element c2 of Ant III present in *Yosiides*, in contrast with [27].

### 3.2. Identification Key and Distribution of the Extant Genera of Sminthurididae

Below we present an updated key, adapted from Bretfeld [5], to the extant genera of Sminthurididae, including their distribution. We used features of both sexes whenever possible, which made the identification more reliable. However, females of some genera are remarkably similar to each other, whereas in *Pygicornides* they are poorly described, and in *Pedonides* they are completely unknown. Because of this, some steps rely only on the males' morphology. The overall male antennal morphology for the previously described extant genera is represented in Figure 1.

1. Tibiotarsus III distal organ absent . . . . . 2
  - Tibiotarsus III distal organ present . . . . . 4
2. Males' antennal clasper simple, Ant II with only **b1** modified element and without **tra1**, Ant III only with **c3** (Figure 1A), mucronal chaeta absent . . . . . *Sphaeridia* Linnaniemi, 1912 [18]; Worldwide
  - Males' antennal clasper complex, Ant II with **b1–b4**, **tra1** modified elements, Ant III with **c1** and **c3** (Figure 1C,D), mucronal chaeta present . . . . . 3
3. Males' Ant II without **b5–b7** and **tra2** elements (Figure 1D), females Ant IV subdivided, Abd II–III dorsal vesicles present, ventral tube with lateral projections, mucro wide . . . . . *Debouttevillea* Murphy, 1965 [40]; Singapore
  - Males' Ant II with **b5–b7** and **tra2** elements (Figure 1C), females Ant IV undivided, Abd II–III dorsal vesicles absent, ventral tube simple, without lateral projections, mucro narrow . . . . . *Denisiella* Folsom and Mills, 1938 [20]; Americas (including Hawaii), French Polynesia, South Africa, United Arab Emirates
4. Males' leg II with a clasping organ made by opposing strong spines on trochanter and femur . . . . . *Pedonides* Bretfeld, 2010 [46]; Portugal
  - Males' leg II without such morphology . . . . . 5
5. Males' Abd V (small abdomen) dorsally with a pair of large modified processes . . . . . *Pygicornides* Betsch, 1969 [48]; Australia
  - Males' Abd V without such morphology . . . . . 6
6. Males' antennal clasper simple, Ant II with only **b1–b3** modified elements, Ant III with only **c3** (Figure 1B) . . . . . *Sminthuridia* Massoud and Betsch, 1972 [27]; Gambia
  - Males' antennal clasper complex, Ant II with further modified elements than **b1–b3**, Ant III also with **c1** element, usually with extra modified chaetae . . . . . 7
7. Females' Ant II–III with apical robust spiniform chaetae, males with large dorsal vesicles on Abd II–III . . . . . *Parasminthurides* gen. nov.; Brazil
  - Females' antennae without such chaetae, males without vesicles on Abd II–III . . . . . 8
8. Males' Ant III without **c2** element (Figure 1I), mucronal chaeta absent . . . . . *Boernerides* Bretfeld, 1999 [5]; Mediterranean, the Canary Islands
  - Males' Ant III with **c2** element (Figure 1E,F,H,K), mucronal chaeta mostly present . . . . . 9
9. Males with Ant II devoid of **B1** and **Tra2** elements (Figure 1E), Ant IV subdivided, and lacking Th III dorsal vesicles . . . . . *Yosiides* Massoud and Betsch, 1972 [27]; Nepal, China

- Males with **B1** or **Tra2** element present on Ant II (Figure 1F,H,K), Ant IV mostly undivided, and with Th III dorsal vesicles . . . . . 10
- 10. Head and mouthparts elongated, dorso-posterior large abdomen with long chaetae in both sexes . . . . . *Sinnamarides* Betsch and Waller, 1991 [49]; French Guiana
- Head and mouthparts normal, dorso-posterior large abdomen with long chaetae only in one of the sexes . . . . . 11
- 11. Females' Ant III and IV with large blunt chaetae, males with long chaetae on dorso-posterior large abdomen . . . . . *Stenacidia* Börner, 1906 [37]; Holarctic, Cape Verde Islands, Australia, Kerguelen Islands
- Females' Ant III and IV without large blunt chaetae, at most Ant IV with sensillum-like chaetae, males with short chaetae on dorso-posterior large abdomen . . . . . *Sminthurides* Börner, 1900 [19]; Worldwide

### 3.3. *Parasminthurides spinosus* gen. nov. sp. nov. Medeiros and Bellini

*Type material.* Holotype: male on slide, Brazil, State of Piauí, Piracuruca municipality, Sete Cidades National Park, 'Primeira Cidade' (4° 05' 42.53" S; 41° 40' 50.70" W), 168 m, in sandy soil, ecotonal zone between Caatinga and Cerrado biomes, 14/V/2021, A.M.N. Silva col., pitfall traps. Paratypes: one male and five females on slides, with the same data of the holotype.

*Diagnosis of the species.* Males' Ant III with five small spines other than **c1–3**. Dorsal head with a single medial unpaired chaeta (in the **A** line), with 3 + 3 zones without cuticular granulation between the antennae. Prelabral and labral chaetae **m** thick, labrum with well-developed needle-shaped apical papillae. Trochanter II with a multiciliated chaeta only in males. Femur III with a curved chaeta, somewhat spiniform. Ungues I–III without tunica or pseudonychia. Ventral tube and tenaculum each with 1 + 1 chaetae. Dorsal anal valve with three unpaired chaetae (**as1**, **ms1**, and **ps1**). Parafurcal area with 11 chaetae. Two or three spiniform dental chaetae **J**, ventral formula as 2,3,3,2,1,1,1,1 from the apex to the basis.

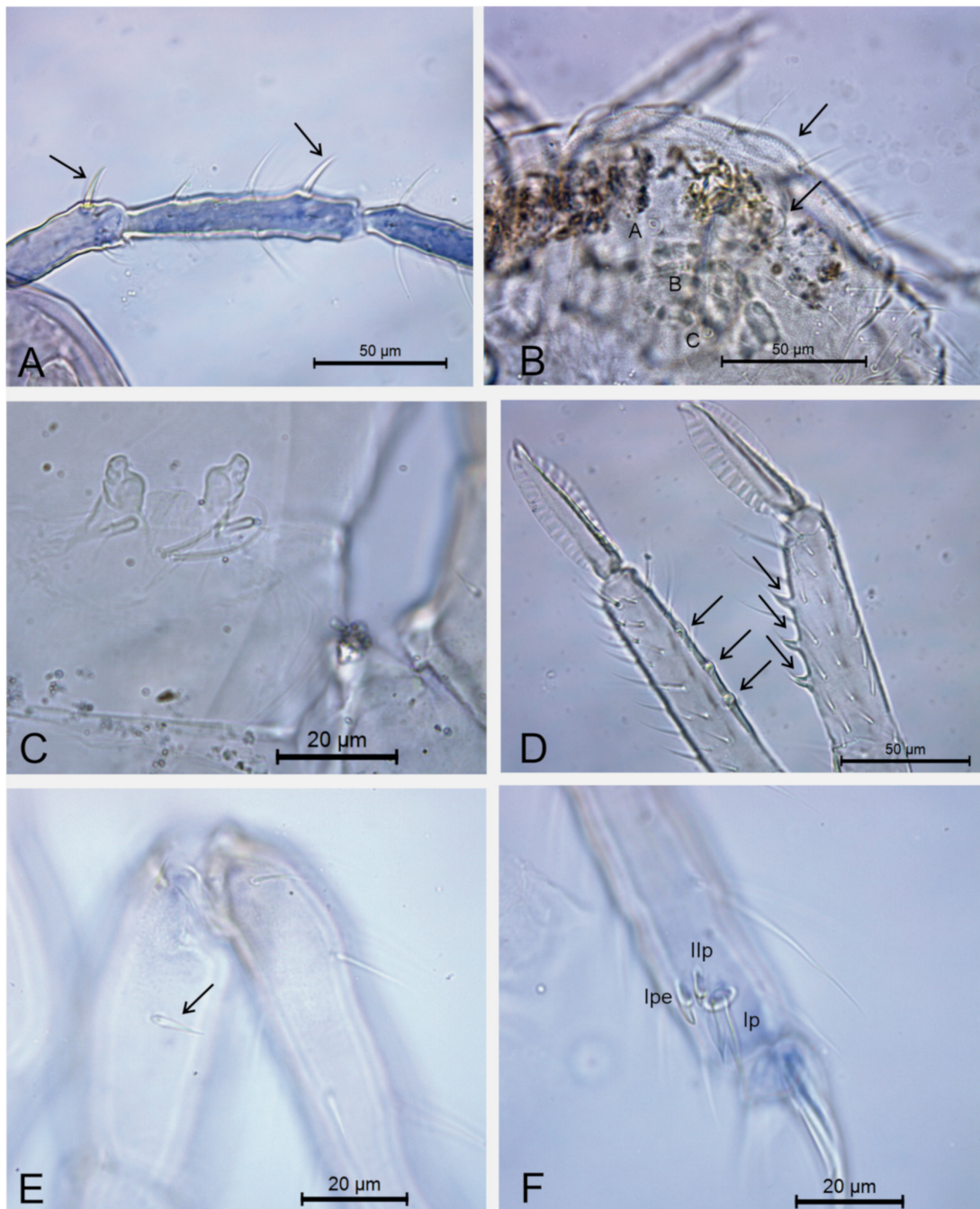
*Description.* Body (head + trunk) length of the type series ranging between 254 and 571 µm, holotype with 254 µm, males' average size = 256 µm, females' average size = 522 µm, entire type series' average size = 386 µm. Specimens mostly dark blue to purplish, legs and furca pale, males darker than females.

Head (Figures 2A, 3 and 4). Antennae length: 204 µm in the holotype. Holotype antennal segment ratio I:II:III:IV as 1:1.63:0.9:1.65. **Males' antenna:** Ant I with seven chaetae, one apical slightly thicker than the others (Figure 3A). Ant II with elements **tra1**, **B1**, **b1–b5**, **B1** as a curved smooth chaeta, **b1** as a large curved chaeta with the outer side serrated on a large papilla, **b2–b5** as small curved chaetae similar in shape to **b1**, all on small papillae, **b5** thicker than **b2–b4**, plus 19 regular chaetae of different sizes (Figure 3B). Ant III with elements **c1–c3** present, **c1** with a rough rounded apex, **c2** as a short strong smooth spine, and **c3** as a long blade-like spine with spiral ornamentation, plus five small spines, two papillae, and 15 regular chaetae; apical organ sensory rods in two independent shallow invaginations, surrounding subapical microsensillum regular (Figure 3C). Ant IV longer than Ant III, undivided, with about 52 chaetae, one of them as a long curved subapical sensillum (Figure 3D). **Females' antenna:** Ant I with seven chaetae, two apical curved and slightly thicker than the others (Figure 3E). Ant II with 12 chaetae, two apical as robust spiniform chaetae (Figures 2A and 3E). Ant III with 16 chaetae, one basal and one apical (the latter possibly homologous to **c2**) as small spiniform chaetae, plus one apical (possibly homologous to **c3**) as a large robust spiniform chaeta; apical organ sensory rods in two independent shallow invaginations, surrounding subapical microsensillum somewhat enlarged and blunt (Figures 2A and 3F). Ant IV longer than Ant III and undivided, with about 60 chaetae, one of them as a long curved subapical sensillum, plus one small cup-shaped sensillum (Figure 3G). **Head capsule (both sexes):** Eyes 8 + 8, head capsule normal

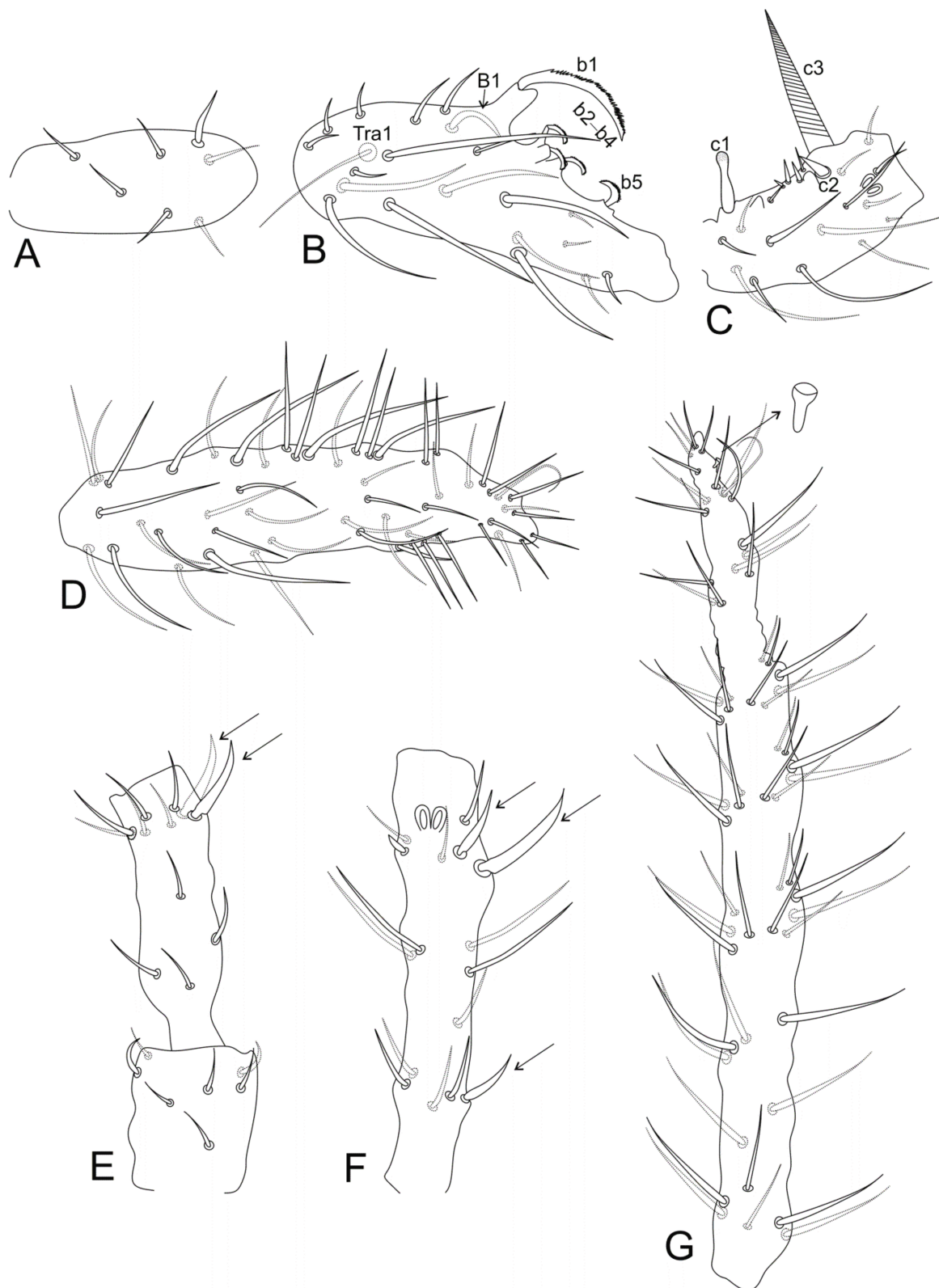


(not elongated) (Figure 4A). Clypeal area **a–f** lines with 7/6/5( $\sigma$ )/8( $\varphi$ )/4/6/6 dorsal + ventral chaetae, respectively, plus one chaeta without clear homology between **d** and **e** lines, dorso-lateral **a** and **b** chaetae thick, **b** line with one dorsal chaeta longer than the others, post-labial (ventral) **c** line only present in females, similarly to *Sminthurides* [51] (Figure 4A,B). Interantennal area  $\alpha$ ,  $\beta$ , and  $\gamma$  lines with 1–2/1–2/1–2 chaetae, respectively; frontal area **A–E** lines with 1(+1)/1/1/1/2 chaetae, respectively; two interocular chaetae present; at least 3 + 3 zones without cuticular granulation present between the antennae and 1 + 1 near the eyes (Figure 4A). Labial basomedian and basolateral fields with four chaetae each (Figure 4B). Six prelabral thick chaetae present, medial chaetae longer, lateral thicker than the others (Figure 4A,C); labral **a**, **m**, and **p** lines with 2(+1), 2(+1), and 2 chaetae, respectively; **m** chaetae thick, **m2** thicker than the others; labrum with 2 + 2 well developed needle-shaped apical papillae (Figure 4C). Mandibles normal (not elongated), almost symmetrical, with 4 + 4 incisive apical teeth (Figure 4D). Maxillae elongated with three smooth teeth and three denticulate lamellae (Figure 4E).

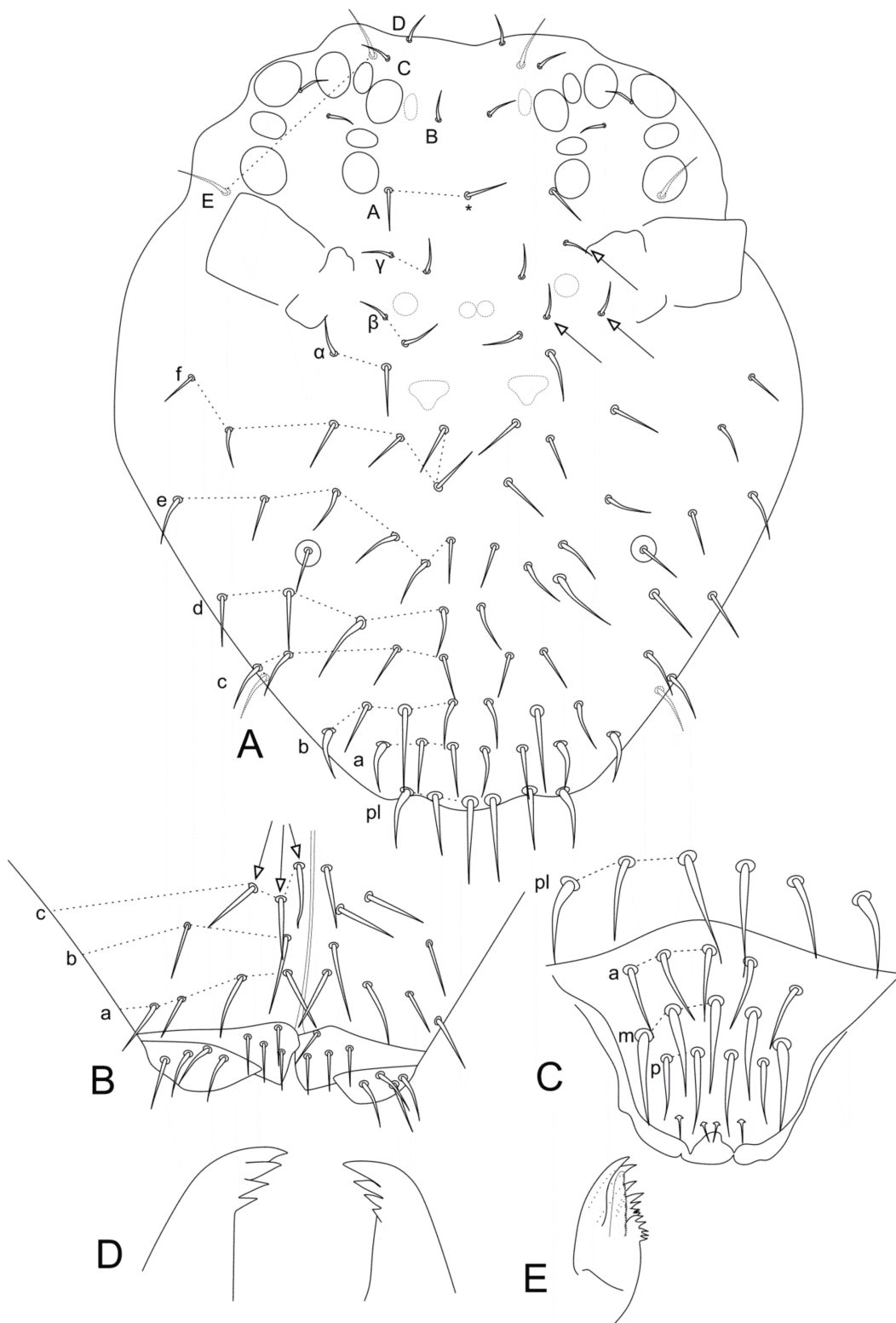
Trunk (Figures 2B, 5 and 6A,B). **Large abdomen:** thorax continuous with the abdomen, without clear segmentations, in both sexes. **Males:** Th I with a large oval vesicle; Th II with one **a** chaeta inside a cavity and one **m**; Th III with one **a** and three **m** chaetae, with a large oval vesicle under the **a** line; Abd I without chaetae; Abd II with bothriotracha **A**, **B**, and **C** slightly misaligned, with two **a**, three **m**, and three **p** regular chaetae near the bothriotracha, with a large dorsal oval vesicle between the **p** line and Abd III; Abd III–IV with two main lines of chaetae above the bothriotrachum **B**: **dII-1** with four, **dIII-1** with four, plus 4–5 lateral chaetae and three under (ventral to) the bothriotrachum **C**. Parafurcal area with four rows of chaetae with four, three, two, and two (total of 11) chaetae, neosminthuroid chaetae absent (Figures 2B and 5A). **Females:** Th I with a large oval vesicle; Th II with one **a** chaeta inside a cavity and one **m**; Th III with one **a** and three **m** chaetae; Abd I without chaetae, about 12 zones lacking cuticular granulation present between Th II and Abd II; Abd II with bothriotracha **A**, **B**, and **C** slightly misaligned, with two **a**, three **m**, and three **p** regular chaetae near the bothriotracha; Abd III–IV with three main lines of chaetae above the bothriotrachum **B**: **dI-1** with three, **dII-1** with four, **dIII-1** with four, plus five lateral chaetae and three under (ventral to) the bothriotrachum **C**. Parafurcal area with four rows of chaetae with four, three, two, and two (total of 11) chaetae, neosminthuroid chaetae absent (Figure 5B). **Small abdomen:** including Abd V–VI in both sexes (Figure 6A,B). **Females:** Abd V with bothriotracha **D** and **E** present, plus 14 regular chaetae, a small medial one unpaired. Dorsal anal valve with **as1–3**, **ms1–4**, and **ps1–2** chaetae, **as1**, **ms1**, and **ps1** unpaired; each ventral anal valve with **aai1**, **ai1–3**, **ami1** (as an oval organ), **mi1–5**, **mpi1**, and **pi1–3** chaetae (Figure 6A). **Males:** Abd V with bothriotracha **D** and **E** present, plus 8 chaetae, a large medial one unpaired. Dorsal anal valve with **as1**, **ms1**, **ms3–4**, and **ps1–2** chaetae, **as1**, **ms1**, and **ps1** unpaired; each ventral anal valve with **ai1–3**, **ami1** (as an oval organ), **mi1–4**, **mpi1**, and **pi1–3** chaetae (Figure 6B). Genital plate unclear in both sexes.



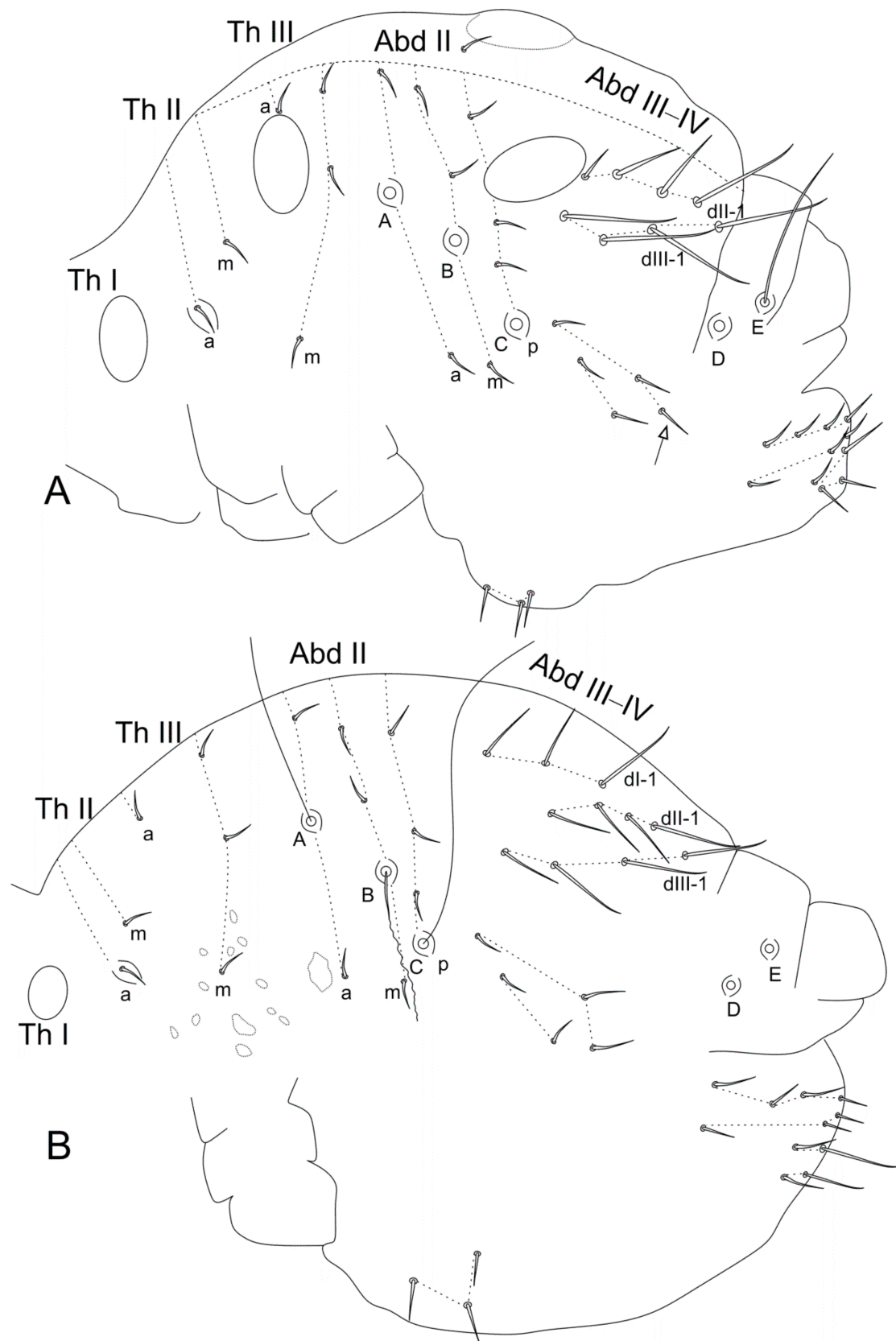
**Figure 2.** *Parasmynthurides spinosus* gen. nov. sp. nov. photographs: (A) female's Ant II–III, with arrows pointing to robust spiniform chaetae; (B) male's large dorsal vesicles on Abd II–III and bothriotricha (A–C); (C) tenaculum; (D) dentes and mucrones, with arrows pointing to spiniform chaetae; (E) femur III, with arrow pointing to curved chaeta; (F) tibiotarsus III organ.



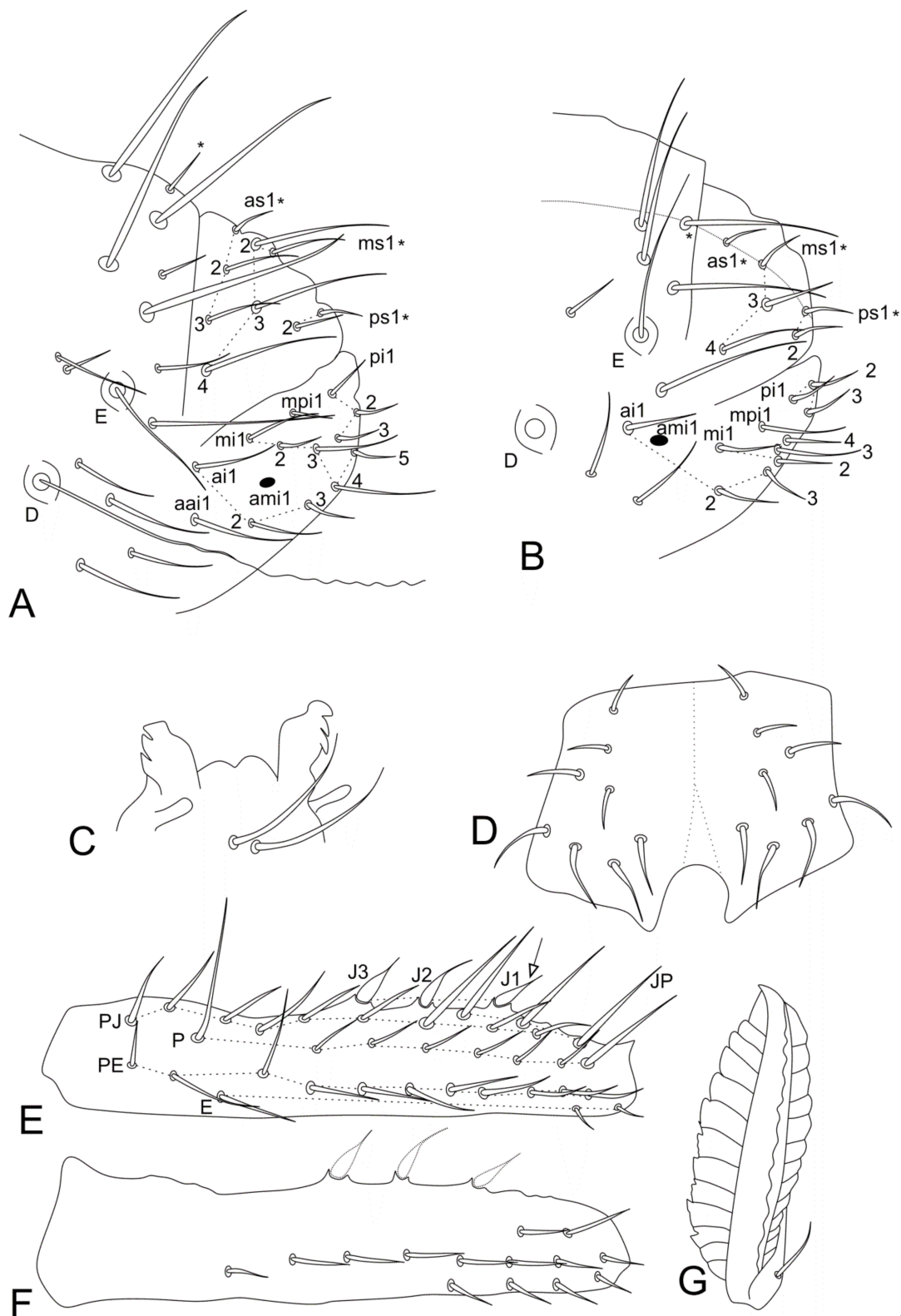
**Figure 3.** *Parasmynthurides spinosus* gen. nov. sp. nov. antennae: (A–D) male’s antenna: (A) Ant I (dorsal view); (B) Ant II (dorsal view); (C) Ant III (ventral view); (D) Ant IV (dorsal view); (E–G) female’s antenna: (E) Ant I–II (dorsal view), with arrows pointing to apical spiniform chaetae on Ant II; (F) Ant III (ventral view), with arrows pointing to spiniform chaetae; (G) Ant IV (dorsal view), a modified apical sensillum in detail.



**Figure 4.** *Parasminthurides spinosus* gen. nov. sp. nov. head: (A) anterior head capsule; circled extra chaetae do not have clear homologies; zones without granulation are marked with dotted thin lines; white arrows point to chaetae present or absent; '\*' marks a single unpaired chaeta; (B) ventral head chaetotaxy, including labial basal chaetae; white arrows point to chaetae which are absent in males; (C) prelabral chaetae and labrum; (D) right and left apices of mandibles (incisive teeth); (E) left maxilla capitulum.



**Figure 5.** *Parasmynthurides spinosus* gen. nov. sp. nov. large abdomen: (A) male, with white arrow pointing to present or absent chaeta; (B) female; zones without granulation are marked with thin dotted lines.



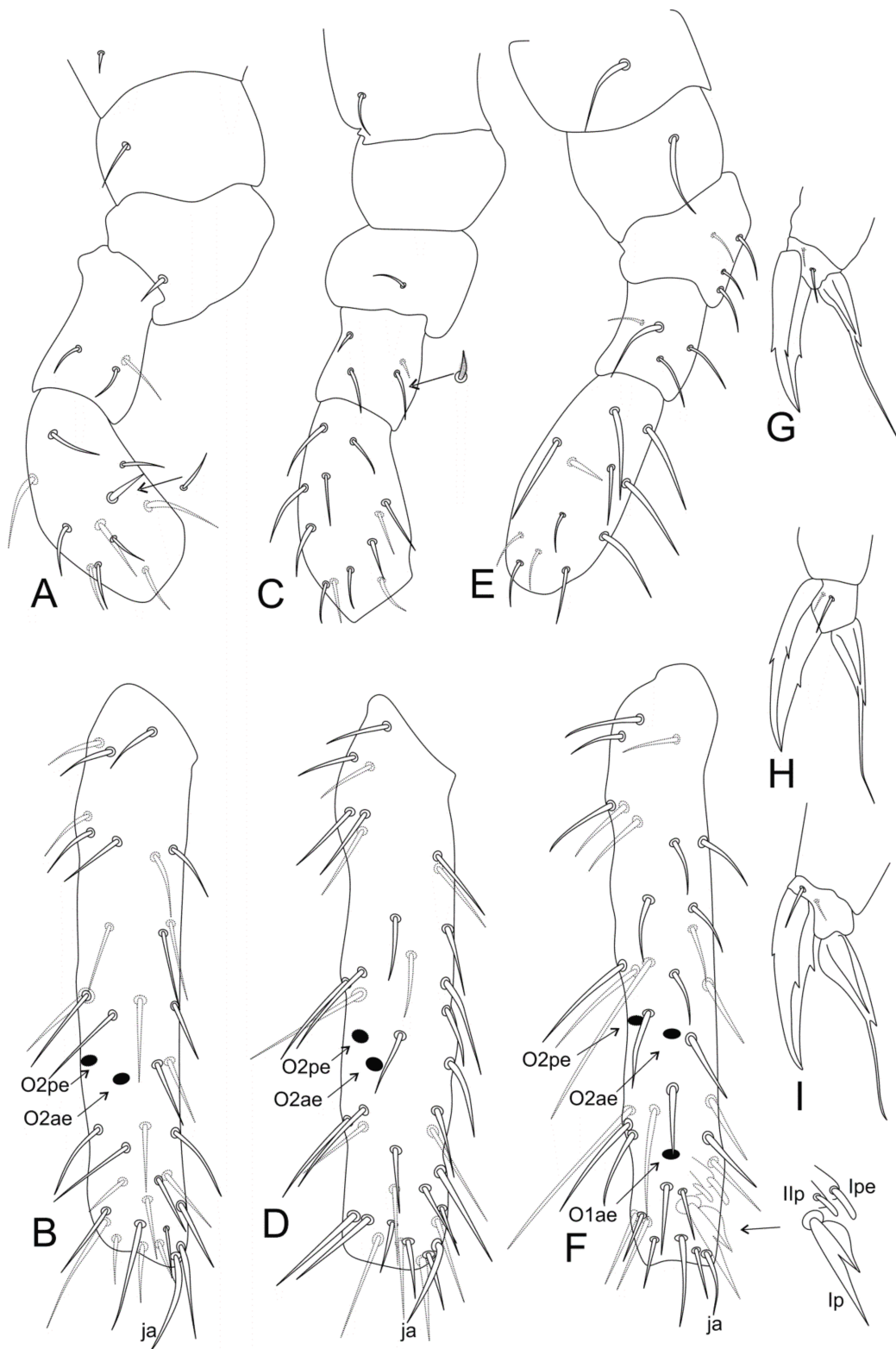
**Figure 6.** *Parasminthurides spinosus* gen. nov. sp. nov. small abdomen and abdominal appendages: (A) small abdomen of the female; (B) small abdomen of the male; ‘\*’ indicates unpaired chaetae; (C) tenaculum; (D) manubrium (dorsal view); (E) dorsal dens chaetotaxy; (F) ventral dens chaetotaxy; (G) mucro.

Abdominal appendages (Figures 2C,D and 6C–G). Ventral tube without lateral projections or other modifications, with 1 + 1 distal chaetae on lateral flaps, sacs short and smooth. Tenaculum ramus with three teeth, plus an apically rounded basal appendix, corpus with 1 + 1 chaetae (Figures 2C and 6C). Manubrium with eight dorsal chaetae (Figure 6D); dens with 36–37 dorsal (posteriorly) chaetae, lines **E/PE/P/PJ/JP/J** with 3/11/8/9/3/2–3 chaetae, respectively; **J** line with strong abruptly acuminate spiniform chaetae; **J2–3** always present; **J1** (the most apical) missing in one dens of one specimen (Figures 2D and 6E); dens ventrally (anteriorly) with 14 chaetae, following the formula from the apex to the base: 2,3,3,2,1,1,1,1 (Figure 6F). Mucro wide, with three crenulated lamellae; mucronal chaeta present (Figure 6G). Mucro:dens:manubrium ratio of the holotype = 1:3:1.2.

Legs (Figures 2E,F and 7). Leg I: epicoxa, subcoxa, and coxa with one chaeta each; trochanter with three chaetae; femur with 11 chaetae, three thicker than the others, plus one curved chaeta, somewhat spiniform (present or modified into a regular chaeta in some specimens); tibiotarsus with 36 chaetae and two oval organs (**O2pe**, **O2ae**), distal whorl with nine chaetae, **ja** thick and curved (Figure 7A,B). Leg II: epicoxa and coxa with one chaeta each, subcoxa without chaetae; trochanter with four chaetae, one of them reduced in females, in males one of them as a multiciliate chaeta; femur with 12 chaetae, three of them thicker than the others; tibiotarsus with 38 chaetae and two oval organs (**O2pe**, **O2ae**), distal whorl with nine chaetae, **ja** thick and curved (Figure 7C,D). Leg III: epicoxa and subcoxa with one large chaeta each, coxa with four chaetae; trochanter with four chaetae, one of them larger than the others; femur with 12 chaetae, most of them thick, one as a short curved chaeta; tibiotarsus with 35 chaetae plus the tibiotarsal organ and three oval organs (**O1ae**, **O2pe**, **O2ae**), distal whorl with nine chaetae, **ja** slightly curved, **Ip** as a bifid spine with a lamella, **Ipe** and **Iip** as short blunt chaetae over papillae (Figures 2E,F and 7E,F). Foot complexes: pretarsi I–III with a long anterior and a short posterior chaetae each; ungues I–III subequal in size and shape, with one pair of lateral teeth, one unpaired internal tooth, and one dorsal unpaired tooth, ungues without tunica and pseudonychia; unguiculi I–III without teeth, with all lamellae smooth, unguiculi filament pre-apical and longer than the ungues in all legs; ratio of ungues I–III in the holotype = 1:0.9:0.9 (Figure 7G–I).

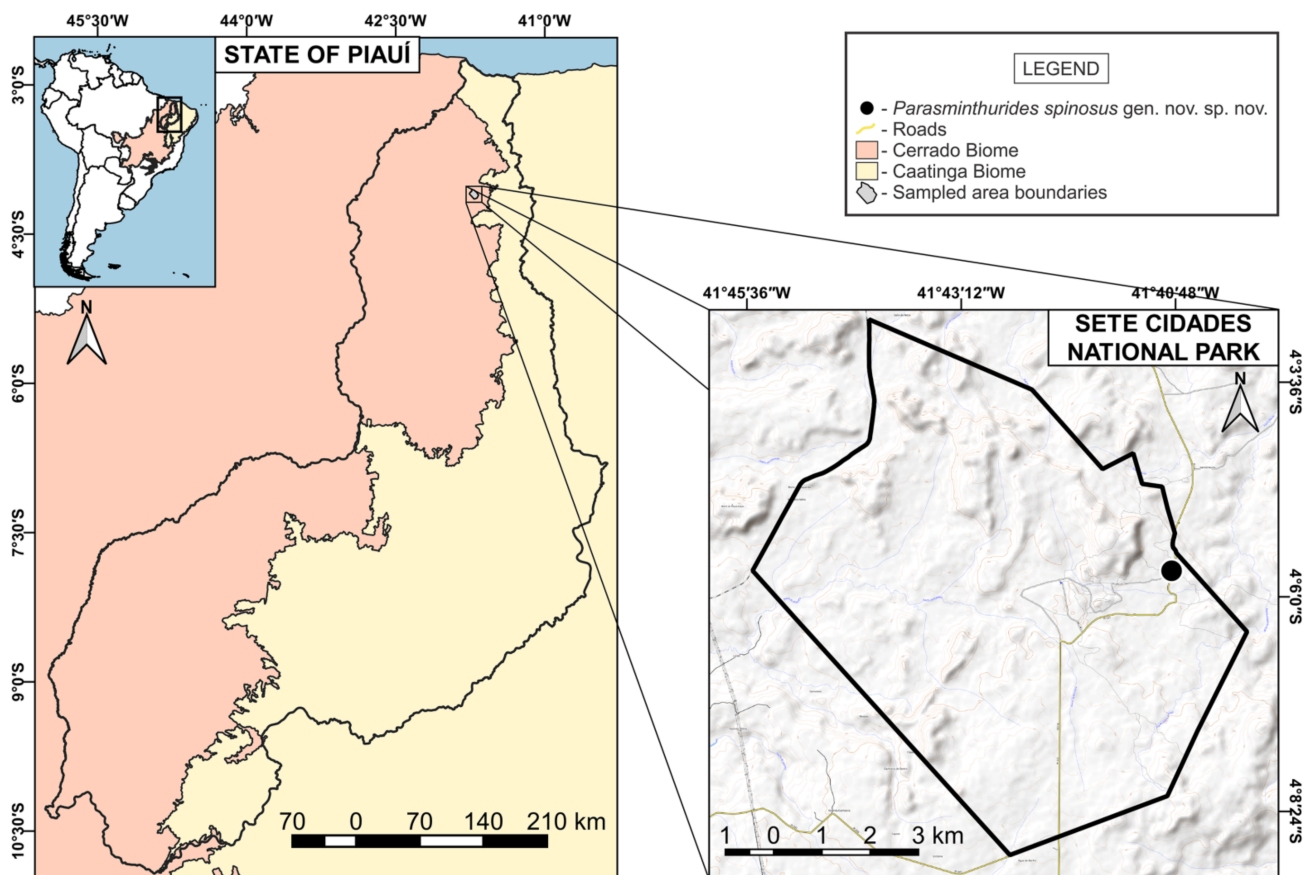
*Etymology.* The new species was named after the spiniform chaetae on the antennae and dens of both sexes.

*Habitat and threats.* Specimens of *Parasminthurides spinosus* gen. nov. sp. nov. were found in an area of Caatinga vegetation in the Sete Cidades National Park, a federal conservation unit with a total area of 6221.48 hectares, located between Piracuruca and Brasileira municipalities, Piauí state, Brazil. The park is located in an ecotonal zone of the Cerrado and Caatinga biomes, with a predominance of the former landscape (Figure 8). The name ‘Sete Cidades’ (Seven Cities) refers to a set of seven peculiar rock formations found in the park, which were named by local residents as ‘Stone Cities’. The Cerrado vegetation of the park forms a mosaic of phytophysionomies composed of a variety of deciduous and semideciduous species, ranging from open grasslands and typical savannas with small gnarled trees and shrubs to denser forest formations where the soil is more fertile and deeper (locally known as ‘cerradão’) (Figure 9A). In places where the soil is shallow and rocky, there are small isolated areas of Caatinga vegetation (Figure 9B), a semiarid biome exclusive to Brazil characterized by the occurrence of species that are highly adapted to long periods of drought and high temperatures throughout the year [60–62].



**Figure 7.** *Parasminthurides spinosus* gen. nov. sp. nov. legs: (A) precoxa, subcoxa, coxa, trochanter, and femur of leg I, and a detailed view of a polymorphic chaeta; (B) tibiotarsus I; (C) precoxa, subcoxa, coxa, trochanter, and femur of leg II, and a detailed view of a multiciliate chaeta seen only in males; (D) tibiotarsus II; (E) precoxa, subcoxa, coxa, trochanter, and femur of leg III; (F) tibiotarsus III, and a detailed view of the tibiotarsal organ; (G) foot complex I, anterior view; (H) foot complex II, anterior view; (I) foot complex III, anterior view.

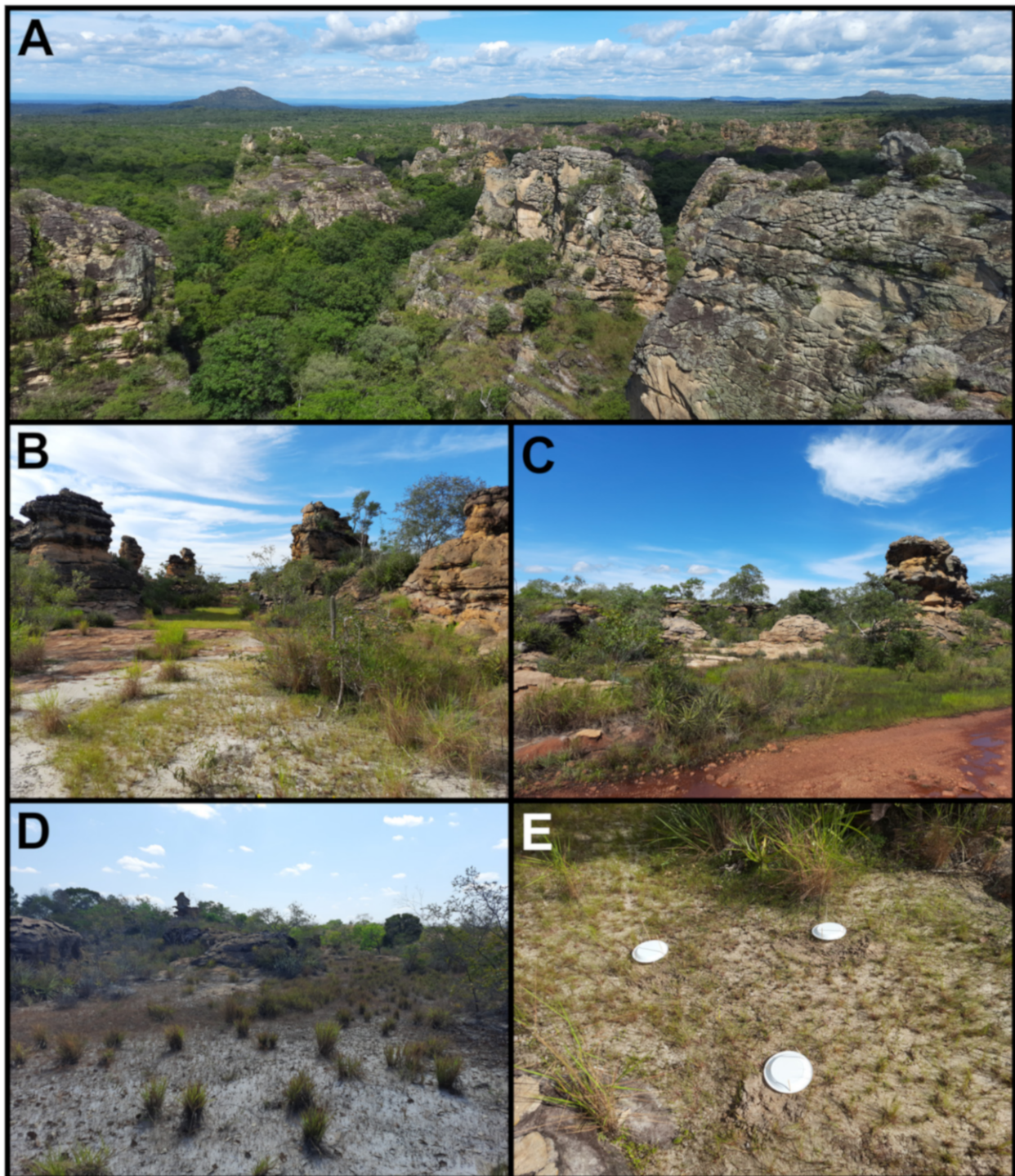




**Figure 8.** Type locality of *Parasmithurides spinosus* gen. nov. sp. nov. in the Sete Cidades National Park, Piauí state, Brazil, highlighting the boundaries between Caatinga and Cerrado biomes in relation to the National Park.

According to the Köppen–Geiger climate classification system, the climate of the region is Aw, tropical with a long dry season and rainy summer, with high temperatures throughout the year [63]. Between 1991 and 2020, the average annual temperature was 29 °C, the maximum recorded temperature was 35 °C, and the minimum was 22 °C, with an average annual insolation of 2800–3000 h. In the same period, the average annual precipitation ranged between 1400 and 1600 mm, mostly concentrated in the three rainiest months—February, March, and April—whereas the average annual evapotranspiration ranged between 2200 and 2400 mm, causing a marked water deficit, which is typical of this Brazilian region [64].

The specific location where the specimens of *Parasmithurides spinosus* gen. nov. sp. nov. were collected is known as ‘Primeira Cidade’ (First City). It is a large outcrop of red sandstones, which can rise about 5–7 m in height (Figure 9B). Between these elevated formations, a rocky floor is formed, with a shallow and sandy soil that is poor in organic matter and widely exposed to solar radiation (Figure 9B). During the rainy season, water accumulates on this same floor, making the soil permanently soggy (Figure 9C), alternating with extremely dry soil during the dry season (Figure 9D). The predominant vegetation of the area is composed mainly of native grasses, small carnivorous plants of the Droseraceae family, and small isolated shrubs and trees, in addition to bromeliads of the genus *Bromelia* and cacti of the genera *Pilosocereus*, *Cereus*, and *Melocactus* over the sandstones. Springtail specimens were collected during the rainy season, using pitfall traps installed in the sandy soil along a 100 m transect (Figure 9E).



**Figure 9.** Typical vegetation and environmental features of the Sete Cidades National Park and of the location where specimens of *Parasmithurides spinosus* gen. nov. sp. nov. were collected: (A) aerial view of the typical vegetation of the Park during the rainy season; (B) collection site of the specimens, highlighting the red sandstone formations, the soil accumulated on the rocky floor, and local vegetation; (C) sandy and soggy soil covered by grasses between the sandstone formations, with the detail of the unpaved road that crosses the place in the lower portion of the image; (D) view of the soil and vegetation during the dry season; (E) pitfall traps used to collect the specimens.

As the known distribution of the new species is limited to its type locality, a well-established federal conservation unit, it suffers few direct threats in the short term. At present, the park is relatively protected from effects caused by the main human activities that threaten the biodiversity in Brazil, especially illegal deforestation to expand agriculture and livestock areas and for charcoal production. The main source of direct impacts on the new species is an unpaved road that crosses the area where the specimens were collected (Figure 8), on which only motorcycles and other small vehicles may pass, most of them belonging to park visitors.

On the other hand, the main threats in the medium and long terms are the sharp and systematic cuts in the transfer of financial resources for the maintenance and inspection of federally protected areas in Brazil. Despite being one of the most visited national parks in the Brazilian northeastern region, protecting a unique level of biological and landscape diversity, in addition to a rich collection of rock art left by pre-Columbian inhabitants, the Sete Cidades National Park, as well as other Brazilian federal conservation units, are currently undergoing a process of dismantlement, with potentially disastrous consequences for the conservation of biodiversity.

*Remarks.* Comparisons between the new species and other Sminthurididae are presented in the remarks on the new genus, Table 1, and the identification key. Since this is the first described species of *Parasminthurides* gen. nov., the genus and species diagnoses should be considered complementary to each other. The description of further species of the genus will provide enlightening information concerning which features can be better regarded as generic of specific traits of this lineage.

We found a single male specimen of *Parasminthurides* gen. nov. from Bahia state, Lençóis municipality, about 940 km away from the type locality of *Parasminthurides spinosus* gen. nov. sp. nov. Its head, antennal, and dental chaetotaxy support it is a new species; however, the poor quality of the specimen and the absence of females prevent us from describe it.

#### 4. Discussion

##### *Systematics of the Sminthurididae: Past, Present, and Future*

Börner's work "*Das System der Collembolen . . .*" [37] was a milestone in the modern systematics of the Collembola. In his study, the subfamily Sminthurinae was erected inside the Sminthuridae (a former synonym of the Symphypleona s. str.) to gather the current Sminthurididae and Katiannoidea genera. Subsequently, the same author relied solely on the use of the morphology of the small abdomen and its chaetotaxy to split the Sminthurinae into two tribes: the Sminthuridini (the current Sminthurididae) and the Katiannini [65]. In 1956, Stach provided a detailed diagnosis of the Sminthuridini, remarking on the importance of the males' antennal clasper and the absence of the subanal appendage in females as the main diagnostic features of the group. The author also disregarded the use of subfamilies of Sminthuridae, arguing that the main feature used to split them, the tenaculum morphology, was of lesser importance [66]. In 1968, Richards provided a new view of the Sminthurinae *sensu* Börner, 1906. First, this author raised the Katiannini to a subfamily status, and rediagnosed the Sminthurinae *sensu* Börner, 1906 [37] using Stach's view of the group [66]. Furthermore, the Sminthuridini *sensu* Börner, 1913 [65] was rethought to gather genera with males' complex antennal clasper—at that time, *Sminthurides*, *Denisiella*, and *Stenacidia* (the latter a subgenus of the former); and Sphaeridiini was proposed to group the Sminthurinae with simpler clasping antennae, originally represented only by *Sphaeridia* [14]. Although the term "Sminthurididae" was arbitrarily used before 1968 as a synonym of Sminthurinae *sensu* Börner, 1906, as in Murphy's studies [40,52], Betsch and Massoud [38] officially raised the Sminthurinae *sensu* Richards, 1968 [14] to the family level, a classification retained until now [8,67]. The authors also dismissed any internal suprageneric subdivisions of the family, a position which was followed by other important revisions [4,5,27], and genera and species descriptions [45,46,49–51,54]. In 1986, Bretfeld [7] proposed a phylogenetic study of the higher taxa of the Symphypleona, suggesting the

name Sminthuridida as a synonym of Sminthurididae, which was subsequently used as a suborder of Symphypleona by Sánchez-García and Engel [7], also encompassing the Mackenziellidae.

Considering the phylogenetics of the Sminthurididae, very few data are currently available. Possibly the first attempt to present and discuss the internal relationships between its genera was provided by Richards [14]. In his tree, *Sphaeridia* was proposed as a basal group and as the sister-group of genera with complex antennal claspers in males. This view was endorsed by Fjellberg [13], who suggested the Mackenziellidae as the sister group of Sminthurididae due to its simpler male antennal clasper, quite possibly homologous to the one seen in *Sphaeridia*. Due to this observation, the author suggested that the simpler clasper was a plesiomorphy of a possible Mackenziellidae + Sminthurididae clade, with the derived Sminthurididae showing more complex male antennae. On the other hand, Betsch's phylogeny [4] suggested that the presence/absence of the tibiotarsus III organ was a more relevant trait in grouping the Sminthurididae genera than the complexity of the antennal clasper.

Regarding the external relationships of the family, Richards [14] provided the first detailed framework of the affinities between the higher taxa of Symphypleona. In his tree, the first main split inside the order separated the Sminthurididae from all other Symphypleona. That author's hypothesis suggested that the Sminthurididae had three main synapomorphies: the male's antennal clasper, the fusion of Abd V and VI, and the suppression of the precoxal process. Nevertheless, the family's ancestor maintained the plesiomorphic states of spherical short sacs on the ventral tube and the absence of the subanal appendage in females, whereas all other lineages of Symphypleona shared modified long sacs of the ventral tube and the subanal appendage [14]. Although Betsch's tree [4] did not show any clear resolution regarding the relationships of Symphypleona families, in 1986 Bretfeld followed Richard's view closely and proposed a name for the clade with the subanal appendage, Appendiciphora, keeping the Sminthurididae (in his study the Sminthuridida) as its sister group [6]. A similar tree was recovered by D'Haese [68]; however, the position of the Katiannidae in relation to the other Symphypleona was not resolved in his study. Yet such vision was not shared by other authors, who considered the current Sminthurididae as an ingroup of the Appendiciphora *sensu* Bretfeld, 1986 [6], based on morphological traits, as in [69–71]. Complementarily, in 1961, Yosii [12] proposed the Mackenziellidae as the sister group of the Symphypleona, whereas Fjellberg [13] suggested this family as an ingroup of the order, closely related to the Sminthurididae.

With the advent of the use of molecular tools to investigate the phylogeny of springtails, the previous hypotheses could be properly tested. Nevertheless, the main limits of the current knowledge in this field are as follows: to date, no study has been able to verify the internal relationships of the Sminthurididae in depth, as they were based on one or two species of the family, each; and no sequences of Mackenziellidae have been used in a phylogenetic study or deposited at the GenBank to date [72]. Thus, it is not entirely clear how *Mackenziella psocodes* Hammer, 1953 [9] relates to other Collembola and whether Fjellberg's [13] and Sánchez-García and Engel's [7] views of the clade Mackenziellidae + Sminthurididae are corroborated by molecular data. On the other hand, recent molecular studies have provided a wide variety of views on the internal organization and validity of the higher taxa of Symphypleona. In D'haese [73] the order was considered basal among the Collembola and paraphyletic, with the Sminthurididae as the most basal branch. A similar result was obtained by Luan et al. [74]; however, in this study, the Sminthurididae were not recovered as a valid family, but were the basal stock of all other Collembola lineages. More recent studies validated the Symphypleona as a monophyletic order, but with different placements for the Sminthurididae. Xiong et al. [75] recovered the Sminthurididae as a monophyletic group, using one species of *Sphaeridia* and another of *Sminthurides*, and as the sister-group of the Appendiciphora. In this phylogeny there was one representative of Katiannidae, *Papirinus prodigiosus* Yosii, 1954 [76], and these results rejected the original systematic view of Börner [37], with the Sminthurididae being related to the Katiannoidea.

Nevertheless, a quite different result was achieved by Yu et al. [15]. The Sminthurididae, also represented by *Sphaeridia* and *Sminthurides*, were not recovered as a monophyletic family, and appeared mixed with the other Symphypleona branches, thus representing a rejection of the hypothesis of Appendiciphora + Sminthuridida proposed by Bretfeld [6]. Contrarily, Nardi et al. [77] endorsed Bretfeld's hypothesis; however, no Katiannidae was included in the analysis. Finally, more recent papers, such as those by Sun et al. [16] and Cucini et al. [17], did not recover the Appendiciphora either, but found the Sminthurididae to be the sister-group of the Katiannidae, similarly to Börner's view, expressed in 1906 [37]. Such discrepant results may be the result of limited and uneven samples and the use of different analysis parameters and markers.

In this scenario, the internal and external affinities of the Sminthurididae are mostly unclear, demanding further investigations. The ideal way to test the previous hypotheses and better comprehend the family's systematics would be to provide a large-scale molecular or morphology-based phylogeny of the Symphypleona, including *Mackenziella psocodes* and representative genera and species of the Sminthurididae. Such studies could verify the validity of the Sminthuridida, Appendiciphora, and the family itself, resolving the positioning of the puzzling Mackenziellidae and putting to test previous hypotheses such as those of Börner [37], Richards [14], Cassagnau [70], Massoud [71], Bretfeld [6], Fjellberg [13], among others. Furthermore, a large study including many species and genera of Sminthurididae could test the phylogenetic signals associated with the males' antennal clasper chaetotaxy, the presence of the tibiotarsus III organ, ventral tube modifications, and other relevant taxonomical traits used to circumscribe genera and species, thus confronting the views of Richards [14] and Betsch [4] regarding the internal organization of the family. Ultimately, a study like this could also test the validity of *Sminthurides*, with a large array of morphologies supporting it is an artificial group (see Table 1). Such variations in morphology have already been used to split the genus into two groups of species, *penicillifer* and *aquaticus* [27,50,51], which have been never properly tested to date in the light of modern phylogenetic tools.

## 5. Conclusions

Here we described *Parasminthurides spinosus* gen. nov. sp. nov. The main features which support the new genus are: females' Ant II and III with robust spiniform chaetae, possibly complementary to the males' clasper elements; males with large dorsal vesicles on Abd II–III; and the interno-apical chaetae of the dens, modified into spiniform chaetae. The genus has many characteristics seen in other taxa, which led us to revise the Sminthurididae, providing a detailed comparison of its genera (Table 1) and an updated key for them. The systematics of Sminthurididae and Symphypleona are mostly unclear, with several hypotheses having been proposed in previous years, which require further testing using molecular phylogenetics.

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