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# Three new genera of Schizogyniidae (Parasitiformes: Mesostigmata) from a New Caledonian millipede (Spirobolida)*

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## Abstract

Three new monotypic genera of Schizogyniidae, *Terrogynium* **gen. nov.**, *Xenogynium* **gen. nov.** and *Zygogynium* **gen. nov.**, are described from a spirobolid millipede in New Caledonia. *Terrogynium* has females with chelicerae presumably modified for parasitism, and both sexes have numerous flattened ventral setae, convergent with many Paramegistidae. *Xenogynium* and *Zygogynium* are less-specialised genera with the former appearing closer to *Terrogynium.* Genus relationships are difficult to determine. These three genera are probably most closely related to each other but as a group it lacks convincing unique synapomorphies. Possible synapomorphies may instead reflect convergence for living on hosts, such as their shortened peritremes and loss of pretarsal claws, characters found elsewhere in the Schizogyniidae. The origins of the Schizogyniidae are discussed and a key to genera of Schizogyniidae is provided.

**Key words**: New species, key, sexual dimorphism, sperm transfer modifications, convergent evolution, biogeography

## Introduction

The Schizogyniidae is a small family of Celaenopsoidea comprising five genera and 12 species (Table 1). Trägårdh (1950) established the family based on *Schizogynium*, which he saw as intermediate between the Euzerconidae and Diplogyniidae. This intermediate position primarily relates to the female mesogynal and latigynal shields: in Euzerconidae, they are completely fused to the ventral shield and delimited by a short, inverted Y-shaped incision, but in Diplogyniidae the latigynal shields, and usually mesogynal shield, are completely separate. According to Trägårdh (1950), Schizogyniidae sits between these families by having larger latigynal elements. Otherwise, the form of these shields is identical to the Euzerconidae, although in *Mixogynium* Ryke, 1957 this suture completely separates the latigynal shields from the genitiventral shield.

The Schizogyniidae are found primarily on beetles (Carabidae, Lucanidae, Passalidae, Scolytinae) (Table 1). Two exceptions are *Mixogynium proteae* Ryke, 1957*,* found in flowers, and *Indogynium lindbergi* Sellnick, 1954*,* found on uropeltid snakes. This diversity of hosts is found in the Diplogyniidae, but not in the Euzerconidae, which are found only on passalid beetles. Immature schizogyniid mites are known only for *Choriarchus reginus* Kinn, 1966, which are roaming predators in the tunnels of their scolytine hosts, as are all trigynaspid mites that associate with wood-feeding beetles (*e.g.* Butler & Hunter 1968; Kinn 1966, 1967; Seeman 2000).

Herein, I describe three new monotypic genera of Schizogyniidae found on a large juliform millipede from New Caledonia. The relationships between these genera, other schizogyniid genera and Celaenopsoidea are discussed, including modifications for sperm transfer. Convergence with other millipede-associated taxa is also explored and a key to adult females and males is provided.

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**TABLE 1.** Species of Schizogyniidae, type locality and host, male modifications, and reference.

| Taxon | Type locality | Host family | Male modifications | Reference |
|---|---|---|---|---|
| *Choriarchus reginus* | USA | Scolytinae | Chelicera (finger-like) | Kinn (1966) |
| *Euroschizogynium calvum* | Ukraine (Odessa) | Carabidae (Coleoptera) | Chelicera (finger-like) | Trach & Seeman (2014) |
| *Indogynium lindbergi* | India (Tamil Nadu) | Uropeltidae (Squamata) | Chelicera (scoop-like) | Sellnick (1954) |
| *Mixogynium proteae* | South Africa | Protea flowers | Hypostomal setae (*h1, h2, h3*) | Ryke (1957) |
| *M. ruhmi* | Chile | Scolytinae | Hypostomal setae (*h1, h2, h3*) | Hirschmann (1972) |
| *Paraschizogynium odontokeri* | Philippines (Calabarzon) | Passalidae (Coleoptera) | Hypostomal setae (*h1, h3*) | Hunter & Rosario (1987) |
| *Paraschizogynium plumachela* | China (Guizhou Prov.) | Carabidae, Lucanidae, Passalidae (Coleoptera) | Hypostomal setae (*h1, h3*) | Zhang *et al.* (2017) |
| *Schizogynium africanum* | South Africa (KwaZulu-Natal) | Passalidae (Coleoptera) | Male unknown | Trägårdh (1950) |
| *S. berlesei* | Zambia, Congo, South Africa | unknown | Probably chelicera ("strong accessory digits") | Funk (1970) |
| *S. forcipis* | New Caledonia | Passalidae | Male unknown | Karg (1997) |
| *S. intermedium* | Uganda, South Africa | Passalidae (Coleoptera) | Male unknown | Trägårdh (1950) |
| *S. megisthanoides* | Central America | unknown | Male unknown | Stoll (1893) |
| *Terrogynium* | New Caledonia | millipede | Chelicera (scoop-like); longer corniculi | |
| *Xenogynium* | New Caledonia | millipede | Chelicera (finger-like); longer corniculi | |
| *Zygogynium* | New Caledonia | millipede | Chelicera (finger-like); longer corniculi | |

## Materials and methods

The millipedes were collected by hand into 75% ethanol and their associated mites removed later in the laboratory. Mites were cleared in Nesbitt's fluid, mounted in Hoyer's medium, and examined with a phase contrast (Leica DMLB) and DIC microscope (Nikon Eclipse 80i). Photomicrographs were also taken with the latter system. Some specimens were dissected with mounted micropins to separate the dorsum, venter, gnathosoma and chelicerae. Drawings were made with the aid of a camera lucida, inked by hand, then corrected and improved in Adobe Photoshop 23.1.1™. Leg chaetotaxy follows Evans (1963), body chaetotaxy follows Lindquist & Evans (1965) and is applied cautiously to the central setae only. Abbreviations: MNHN (Muséum National d'Histoire Naturelle, Paris, France), QM (Queensland Museum, South Brisbane, Australia).

## Taxonomy

### Schizogyniidae Trägårdh, 1950

**Type genus:** *Schizogynium* Trägårdh, 1950, by original designation.

**Diagnosis.** See Trach & Seeman (2014), except modified as follows: latigynal shields sometimes extending to level

of posterior coxa III (instead of mid-coxa IV; see *Indogynium, Xenogynium* gen. nov.); paired ventromarginal shields flank ventral shield (sometimes reduced to metapodal platelets, see *Mixogynium*); sometimes with narrow strap-like marginal shield bearing marginal setae (*Choriarchus, Paraschizogynium*). Male sexual dimorphism present in hypostomal setae (*Mixogynium, Paraschizogynium*) or cheliceral excrescences, the latter being either finger-like (*Choriarchus, Euroschizogynium, Xenogynium* gen. nov.*, Zygogynium* gen. nov.; probably *Schizogynium berlesei*) or scoop-like (*Indogynium*, *Terrogynium* gen. nov.).

### *Terrogynium* gen. nov.

Type species: *Terrogynium weatherwaxae* **sp. nov.**

**Diagnosis.** Both sexes: Dorsal shield with about 100 small (< 20 μm), slender setae; tritosternal laciniae fused for about half their length; genitiventrianal shield expanded, opisthosomal section as wide or slightly wider than long, bearing numerous weakly-sclerotised, obovate setae; ventromarginal shields large, triangular, lacking setae; peritreme shortened, reaching mid-coxa II; tarsus II with large hook-like seta; chelicerae lacking large proximal tooth. Female: sternal shield free from metasternal shields, deeply concave posteriorly, *st2* and *st3* on posterior margin; latigynal, mesogynal and anal shields fused with ventral shield; inverted Y-shaped suture delimiting genital shields bearing large membranous areas; chelicerae with movable digit extending well beyond tip of fixed digit, movable digit with several (8–9) small teeth. Male: with sternoventrianal shield; corniculi longer than female's corniculi; movable digit of chelicerae not extending past fixed digit, bearing large scoop-like excrescence.

**Material examined.** Holotype. Female, ex large spirobolid millipede, likely *Spirobolellus* sp., New Caledonia, Pic du Pin, Site 2, 22°14′16″S 166°50′01″E, 25 Nov 2004, S. Wright, day hand collection. Paratypes. 1 female, 2 males, same data as holotype female. Holotype female and paratype male deposited in MNHN, paratype female and male deposited in QM.

**Remarks.** *Terrogynium* presents several impressive autapomorphies, particularly the large membranous areas separating the genital shields and the hook-like setae of tarsus II. Within the Celaenopsoidea, the obovate, paddle-like ventral setae and the female's elongate fixed digit are unique. These features, in combination with the reduced cheliceral dentition, are evocative of a parasitic habit and are reminiscent of the Paramegistidae (Seeman & Baker 2008; Derne *et al.* 2018; see Discussion).

**Etymology.** *Terrogynium* is based on *terror* (L., alarm, fear) and refers to the brutal morphology of the female's chelicerae, while *-gynium* (Gr., female) is a common ending in the Schizogyniidae.

*Terrogynium weatherwaxae* **sp. nov.**
(Figs 1–7)

**Description. Female.**
*Dorsal idiosoma* (Fig. 1). Dorsal shield length 1010 (1020), maximum width 630 (730), covered with fine network of polygonal reticulation comprised of fine lines joined by larger dots. Shield with 24–26 and 22–26 loosely paired podonotal (50 setae) and opisthonotal setae (48 setae), respectively, plus unpaired podonotal seta *j2* (off-centre due to damage in holotype); all setae smooth, short, of subequal length (15–25); lateral margins with numerous pores.

*Ventral idiosoma* (Figs 2, 7a). Tritosternum length 160 (broken), base heavily pilose, laciniae less pilose, separate for about half its length 75 (broken). Sternal shield deeply concave posteriorly, medial length 55 (55), maximum width 285 (280), bearing three pairs of smooth setae and two pairs of lyrifissures; setal lengths: *st1* 30 (50), *st2* 26 (32), *st3* 14 (25). Metasternal shields separate from sternal shield and each other, bearing one pair of lyrifissures and setae *st4*, length 18 (26); region between sternal and metasternal shields weakly sclerotised, with faint reticulation. Endopodal shields narrow, fused posteriorly with peritrematal shields, anteriorly to latigynal shields. Latigynal shields bearing 2–3 pairs of short setae (length 15–20) and several unpaired pores, defined by inverted Y-shaped suture; arms of Y with expanded region of soft cuticle, with 1-2 asymmetrically expressed pores. Vaginal sclerites clavate, lateral margins irregular, heads resting in metasternal shields. Mesogynal region with several pores. Anterior margins of sternal, latigynal and metasternal shields heavily sclerotised.

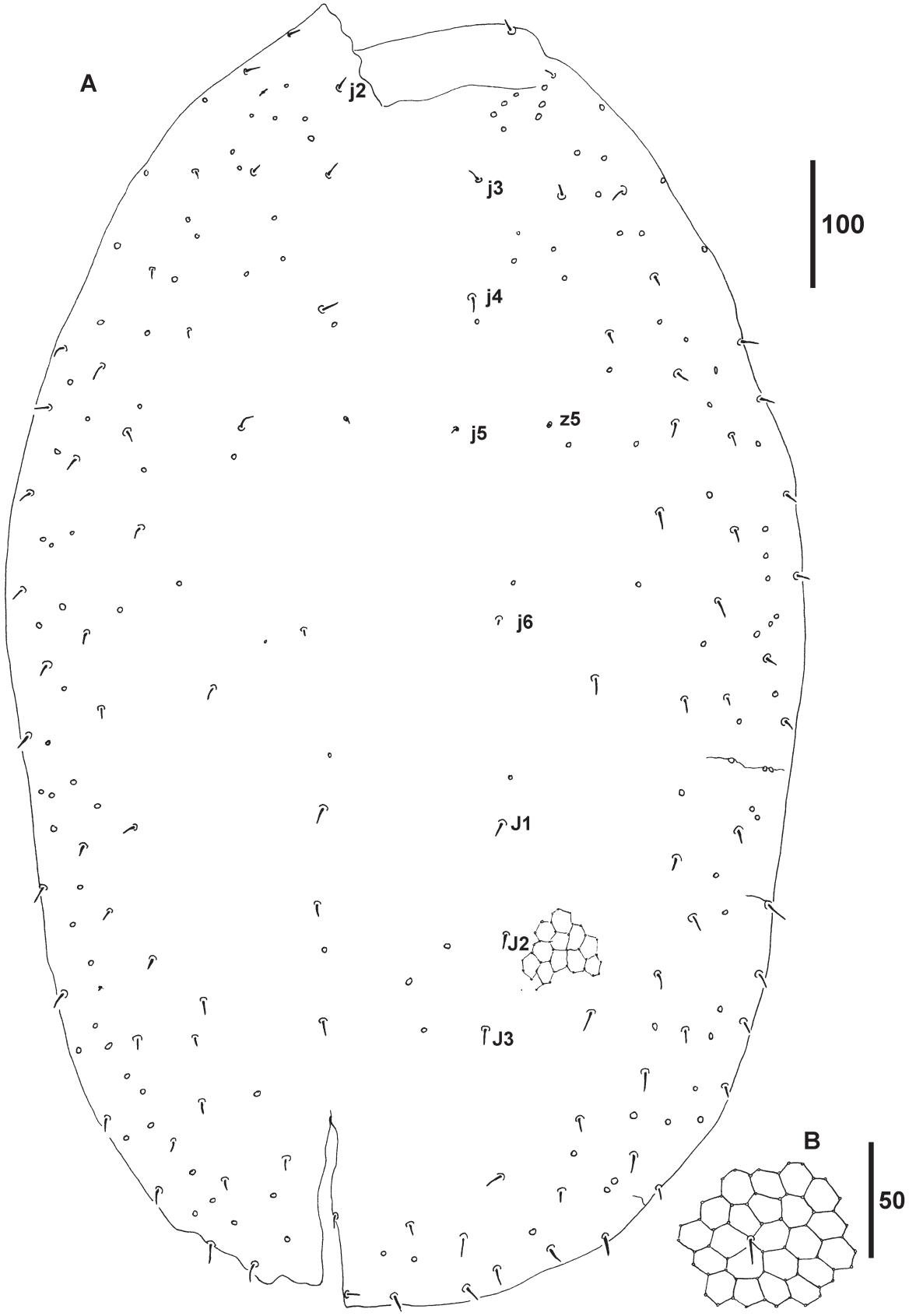


**FIGURE 1.** *Terrogynium weatherwaxae* **sp. nov.** female. (A) dorsum, one patch of ornamentation shown near J2; (B) detail of ornamentation covering entire dorsum. Note: seta j2 displaced to left due to idiosomal damage.

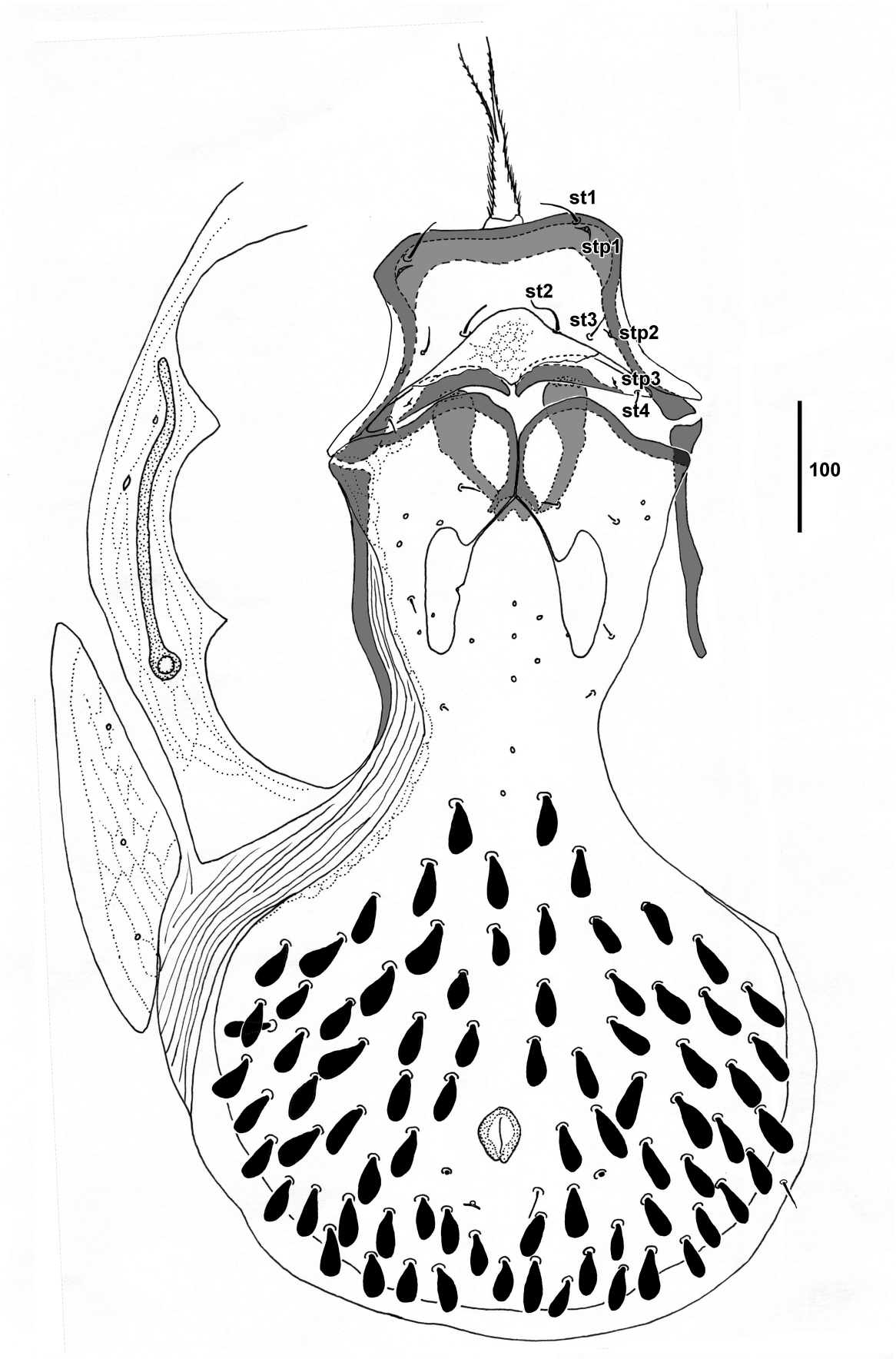


**FIGURE 2.** *Terrogynium weatherwaxae* **sp. nov.** female, venter.

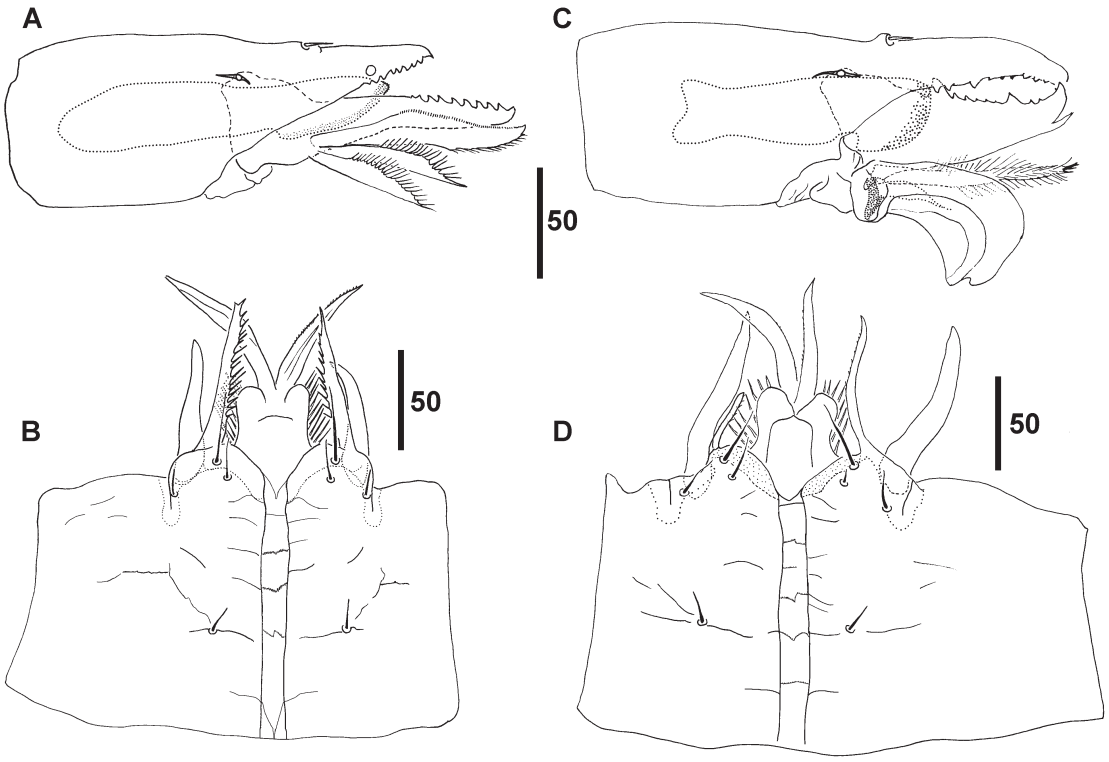


**FIGURE 3.** *Terrogynium weatherwaxae* **sp. nov.** (A–B) female, chelicera and subcapitulum; (C-D) male, chelicera and subcapitulum; note: hypostomal process broken on one side.

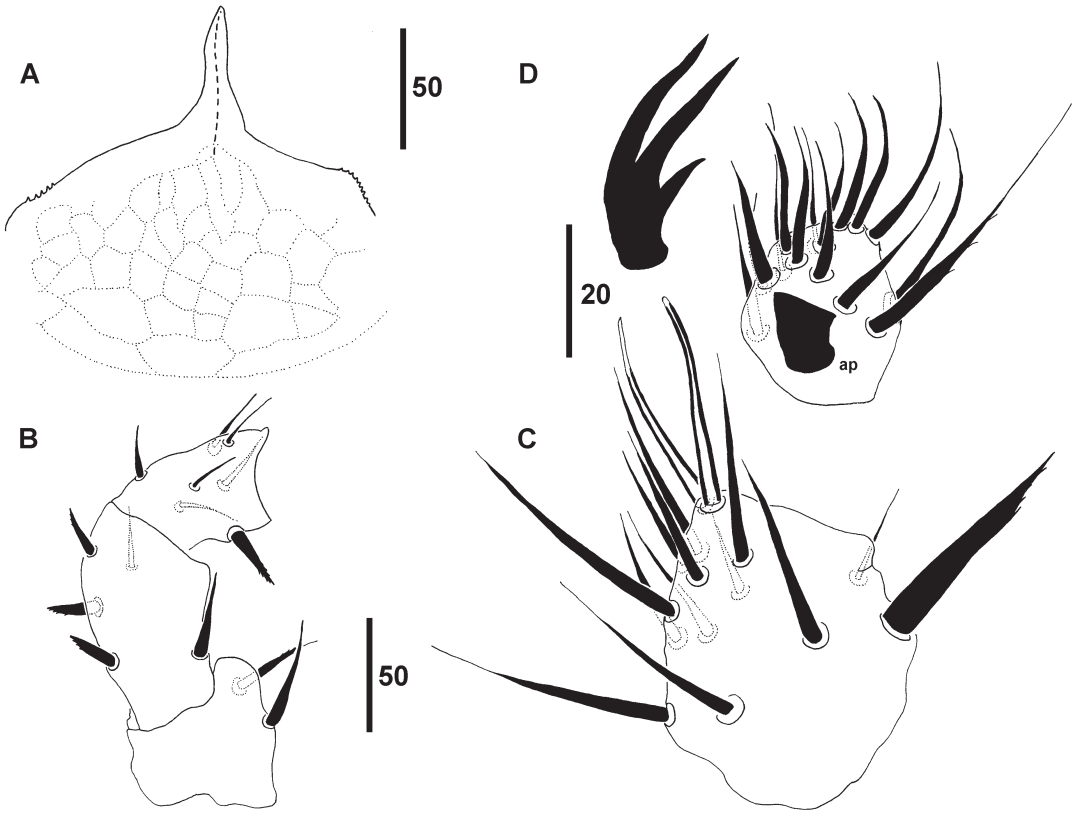


**FIGURE 4.** *Terrogynium weatherwaxae* **sp. nov.** female. (A) gnathotectum; (B) palp trochanter to genu; (C) palp tibia; (D) palp tarsus, apotele (ap) truncated, drawn separately.

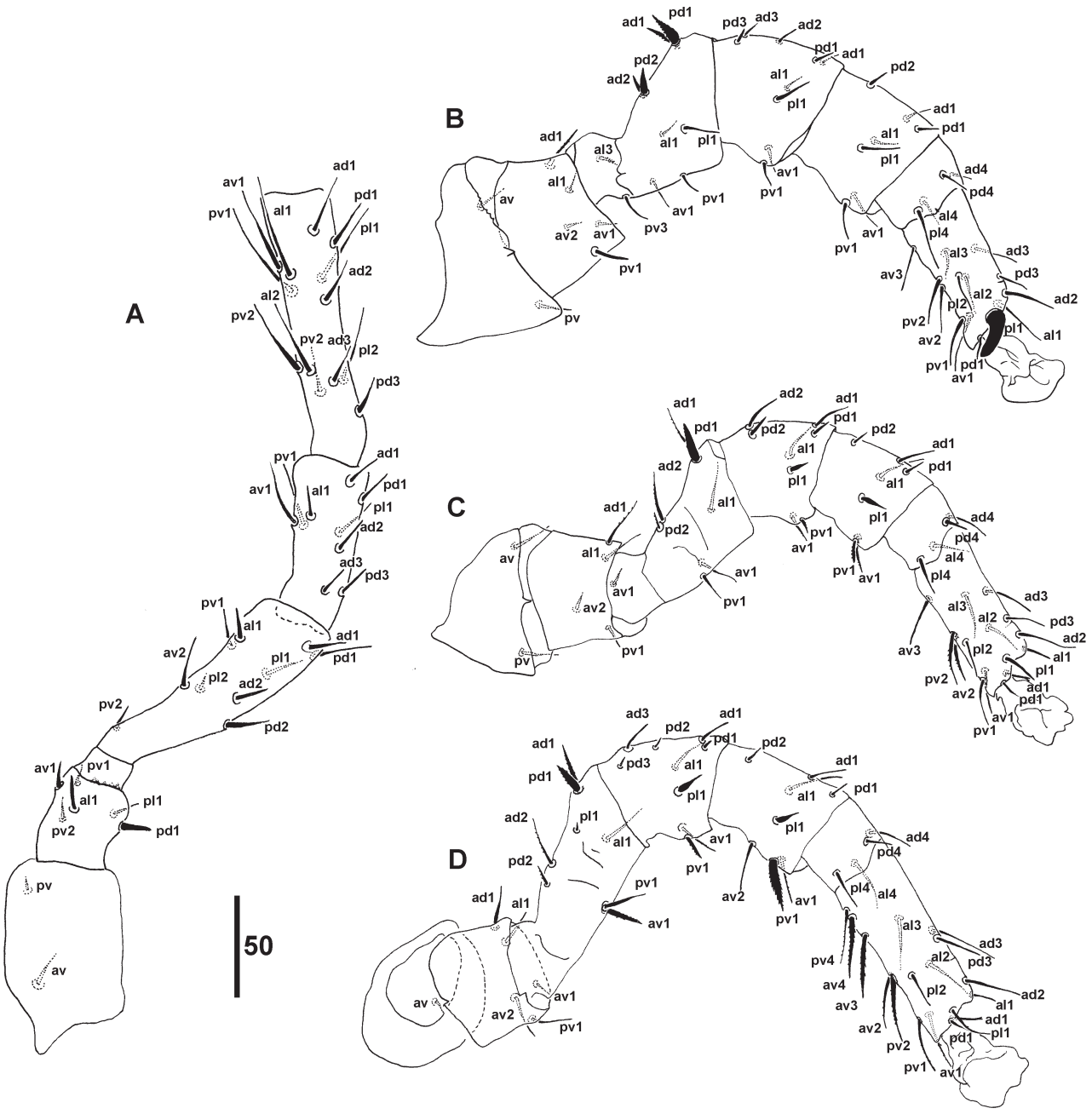


**FIGURE 5.** *Terrogynium weatherwaxae* **sp. nov.** female. (A–D) legs I–IV.

Genitiventrianal shield expanded, covering most of opisthogaster, width 450 (475) bearing 80 (70) smooth, weakly sclerotised obovate setae, plus one pair of simple paranal setae; lateral and posterior margins of shield surrounded overlapped by soft cuticle. Soft cuticle surrounding shield with one pair of simple setae (one lost in dissection; present as pair in other specimens). Ventromarginal shields triangular, reticulate, lacking setae, with three pairs of pores. Peritreme shortened, extending to mid-coxa II; peritrematal shield reticulate, free from dorsal shield.

*Gnathosoma* (Figs 3b, 4). Gnathosoma with four pairs of smooth setae, *h1* 41 (38), *h2* 15 (14), *h3* 19 (broken), palpcoxal seta 13 (16); hypostomal groove hardly distinguishable, with three rows of minute denticles and anterior and posterior lines; corniculi elongate, strong, length 80 (80); internal malae fringed at base, extending to palpgenu; hypostomal processes slender, internally pilose except at base. Gnathotectum thinly acuminate, margin smooth (Figs 5, 12). Palp setal formula: 2-5-7-15-15; trochanter with slight dorso-distal hump, setae *v1* and *v2* slender, lightly barbed; femur with most setae thick, spine-like; genu and tibia with seta *v* thick, spine-like; other genual, tibial and tarsal setae smooth, slender; palptarsal apotele large, 3-tined.

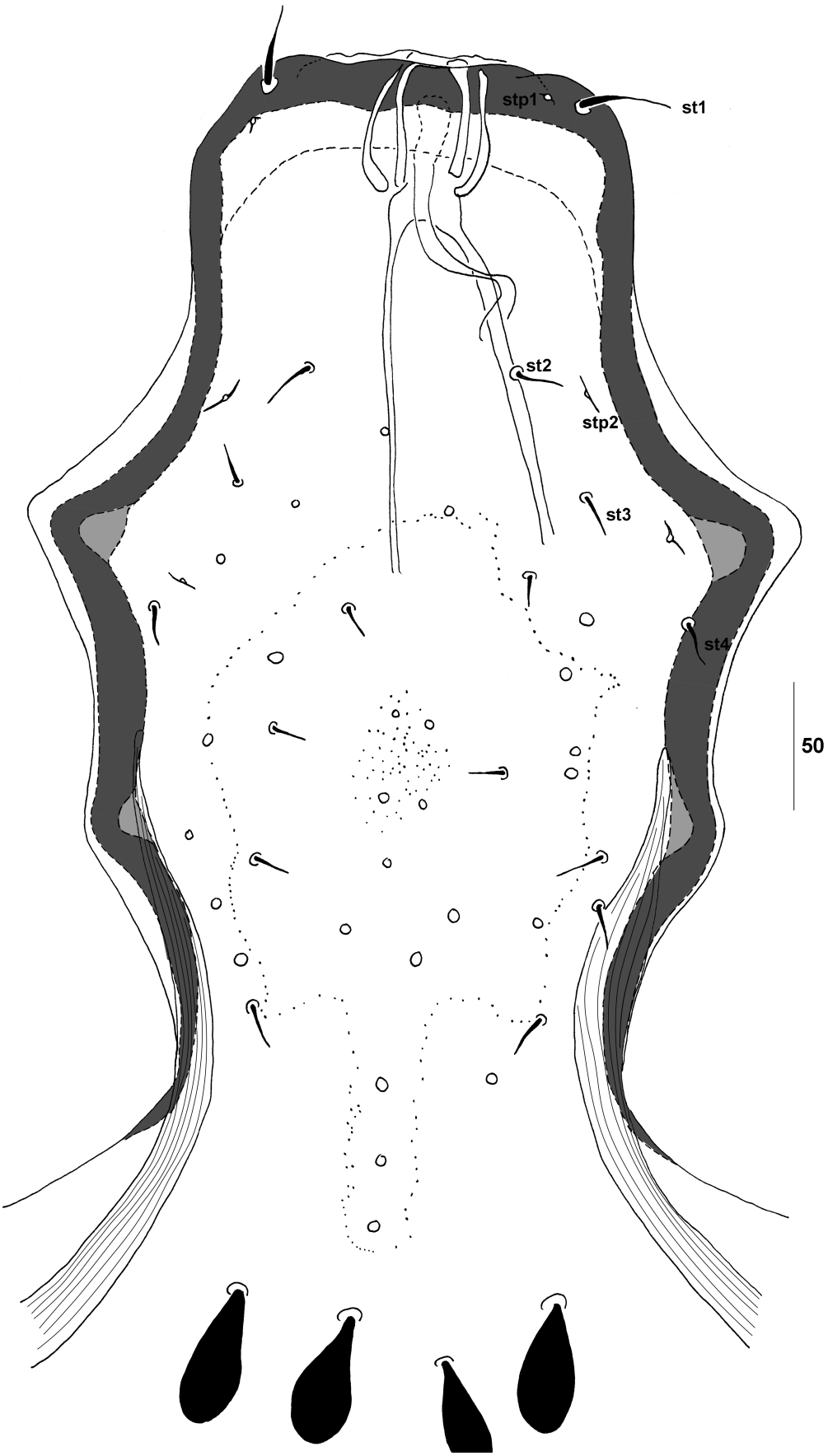


**FIGURE 6.** *Terrogynium weatherwaxae* **sp. nov.** male, sternogenital region.

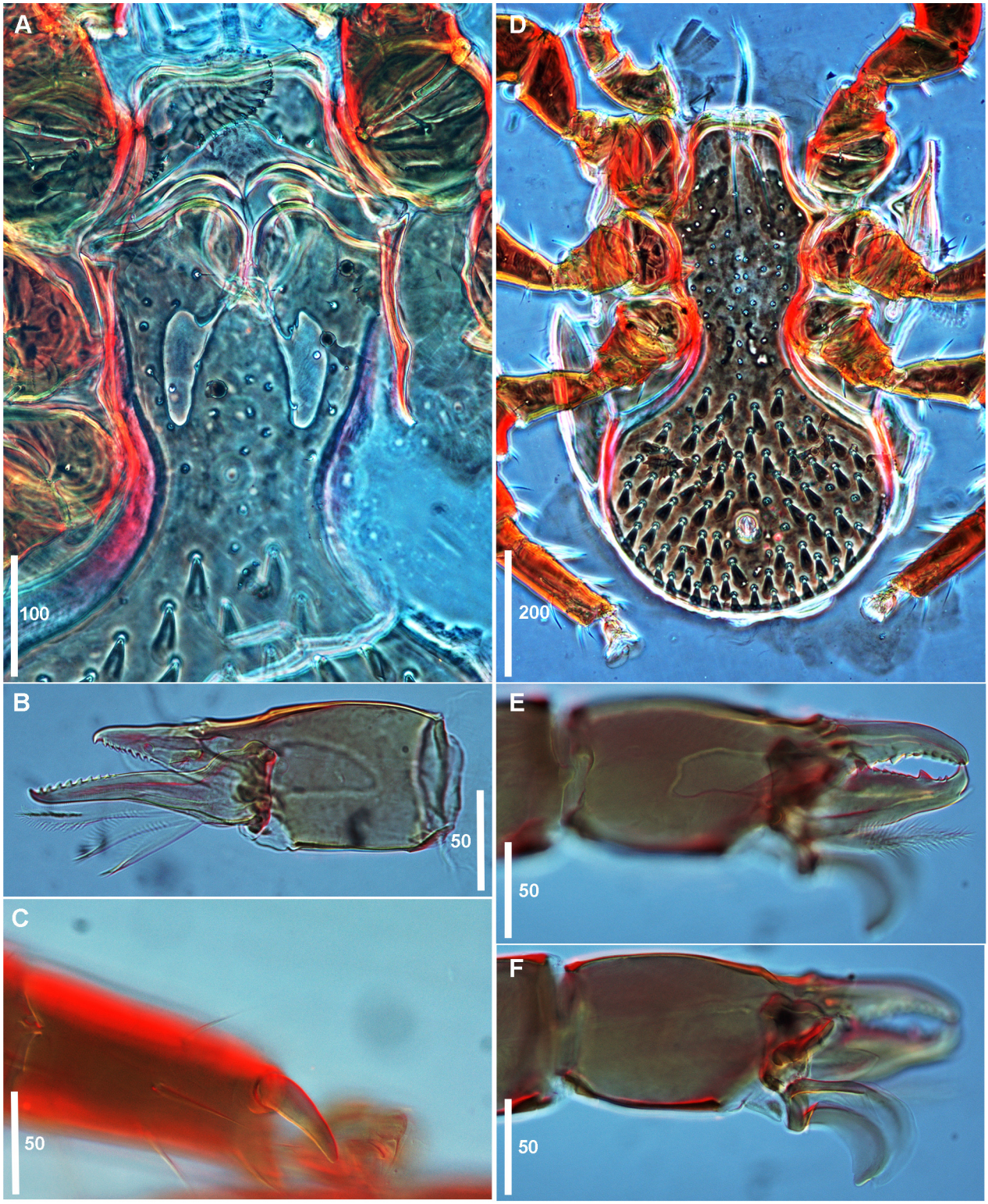


**FIGURE 7.** *Terrogynium weatherwaxae* **sp. nov.** photomicrographs (A–C) female: sternogenital region, chelicera, spur-like seta on tarsus II; note: *Rickia* (Laboulbeniales) thallus partially obscures sternal shield; (D–F) male: venter, chelicera adaxial and abaxial views.

*Chelicerae* (Figs 3a, 7b). Fixed digit length 190 (185), movable digit 125 (125), extending 34 (37) past tip of fixed digit. Fixed digit with 6–8 teeth, pilus dentilis rudimentary; cheliceral seta small 13 (12), appressed to dorsal surface. Movable digit with 8–9 teeth (some broken in holotype on both sides), large proximal tooth absent, with

three excrescences: two with pilose upper margins; other excrescence larger, broader, with pilose ventro-distal margin and finely pilose comb-like upper margin.

*Legs* (Figs 5, 7c). Lengths, excluding ambulacrum, I 960 (970), II 810 (750), III 690 (670), IV 820 (800). Leg I without ambulacrum, claws. Legs II–IV with large ambulacra lacking claws.

Leg chaetotaxy:

Leg I: 2- 6-10 (1 2/1 2/2 2)-9 (1 3/1 2/1 1)-13 (2 3/2 2/2 2)
Leg II: 2-5-10 (2 2/1 2/2 1)-9 (1 3/1 2/1 1)-7 (1 1/1 2/1 1)
Leg III: 2-5-7 (1 2/1 2/1 0)-8 (1 2/1 2/1 1)-7 (1 1/1 2/1 1)
Leg IV: 1-5-8 (1 2/1 2/1 1)-9 (1 2/1 3/1 1)-8 (1 1/2 2/1 1)

Thick spine-like setae: Tr I *pd1*; Fe II *ad1, pd1, pd2*; Fe III *pd1*; Ge III, *pl1*; Ti III, *pl1*; Fe IV *pd1, av1*; Ge IV *pl1*; Ti IV *pl1, pv1*. Tarsi II-IV with 19-19-21 setae, respectively. Tarsus II with *pl1* a large, curved spur (Fig. 7c), tips broken in holotype and male paratypes. Tarsi II-IV with truncate tips, tarsi III–IV with seta *al1* on small apophysis; seta *ad1* small, with bifurcate tips (not seen on tarsus II, possibly obscured), seta *pd1* small, unmodified; both *ad1* and *pd1* difficult to discern. Tarsus IV without intercalary sclerite, setae *av4, pv4* on cuticle distal to tarsal suture.

**Male.**

*Dorsal idiosoma.* Similar to female. Length 940–1090, width 660–720.

*Ventral idiosoma* (Figs 6, 7d). Sternoventrianal shield length 770–850, cuticle lightly punctate, although medial area between coxae III–IV more coarsely punctate; sternal setae *st1* 40–41, closely associated with *stp1,* setae *st2-4* and other intercoxal setae 16–23; nine intercoxal setae (four loose pairs plus asymmetrical additional seta); 24–27 pores, not obviously paired. Opisthogaster and lateral region similar to female.

*Gnathosoma* (Fig. 3b). Similar to female, except corniculi somewhat longer (95–100) and hypostomal processes with fewer, smaller barbs.

*Chelicerae* (Figs 3a, 7e–f). Fixed digit length 215, movable digit 105, not extending past tip of fixed digit. Fixed digit with 11–13 teeth, pilus dentilis rudimentary; cheliceral seta small 10–12, appressed to dorsal surface. Movable digit with 8–9 teeth (third and proximal teeth much larger than others), distally with small finger-like process, proximally with three excrescences: one pilose excrescence (similar to female, except pilosity more extensive), a broad scoop-like excrescence; and a small, heavily sclerotised ventrally deflexed excrescence bearing hyaline lobe extending anteriorly, tapering distally.

*Legs.* Same as female.

**Etymology.** The specific name *weatherwaxae* refers to Esme Weatherwax, a character created by Terry Pratchett, alluding to the one of the three unnamed witches of *Macbeth.*

**Remarks.** The millipede host—which is the host individual of all three new species—is one of the large species of New Caledonian *Spirobolellus* and, following Carl (1926), seems closest to *S. albidicollis*, a large (> 50 mm) species. This genus comprises numerous species in New Caledonia and elsewhere, including Australia, but only two species in New Caledonia are large (Carl 1926).

### *Xenogynium* gen. nov.

Type species: *Xenogynium oggae* **sp. nov.**

**Diagnosis.** Both sexes: Dorsal shield with 86–88 small (< 20 μm), slender setae; tritosternal laciniae fused for about two-thirds their length; genitiventrianal shield expanded, opisthosomal section wider than long, bearing several short, simple setae; ventromarginal shields large, subtriangular, lacking setae; peritremes shortened, reaching posterior coxa II. Female: sternal shield free from metasternal shields, deeply concave posteriorly, *st2* and *st3* on posterior margin; latigynal, mesogynal and anal shields fused with ventral shield; inverted Y-shaped suture delimiting genital shields short, not passing level of coxa IV; chelicerae with movable digit not extending beyond tip of fixed digit, movable digit with numerous (14–15) small teeth. Male: with sternoventrianal shield; corniculi longer than female's corniculi; chelicera with finger-like excrescence bent ventrally midway.

**Etymology.** Based on *xenos* (Gr., strange, guest), referring to the unusual morphology of this genus, and paired with *-gynium* (Gr., female), a common ending in Schizogyniidae.

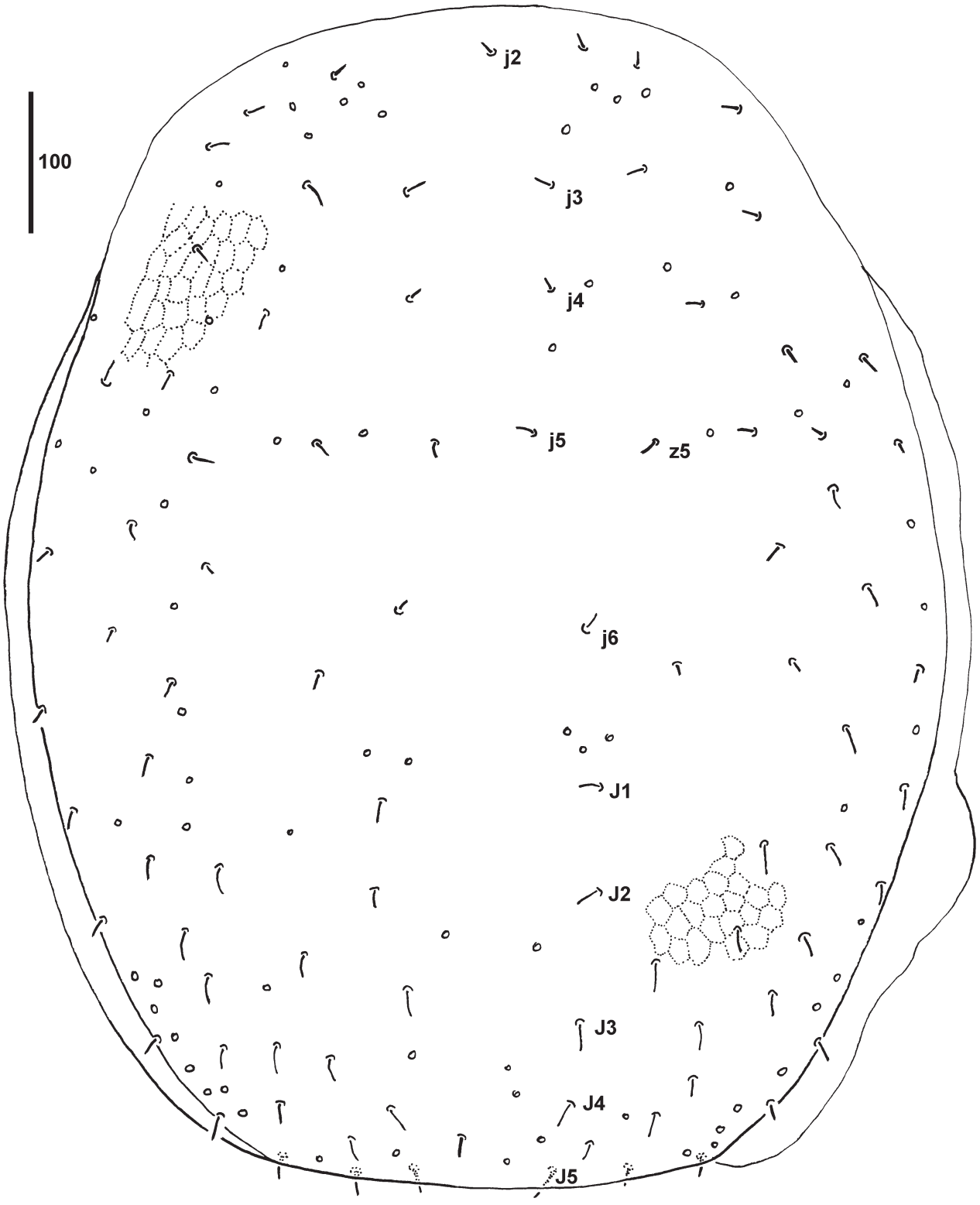


**FIGURE 8.** *Xenogynium oggae* **sp. nov.** female, dorsum.

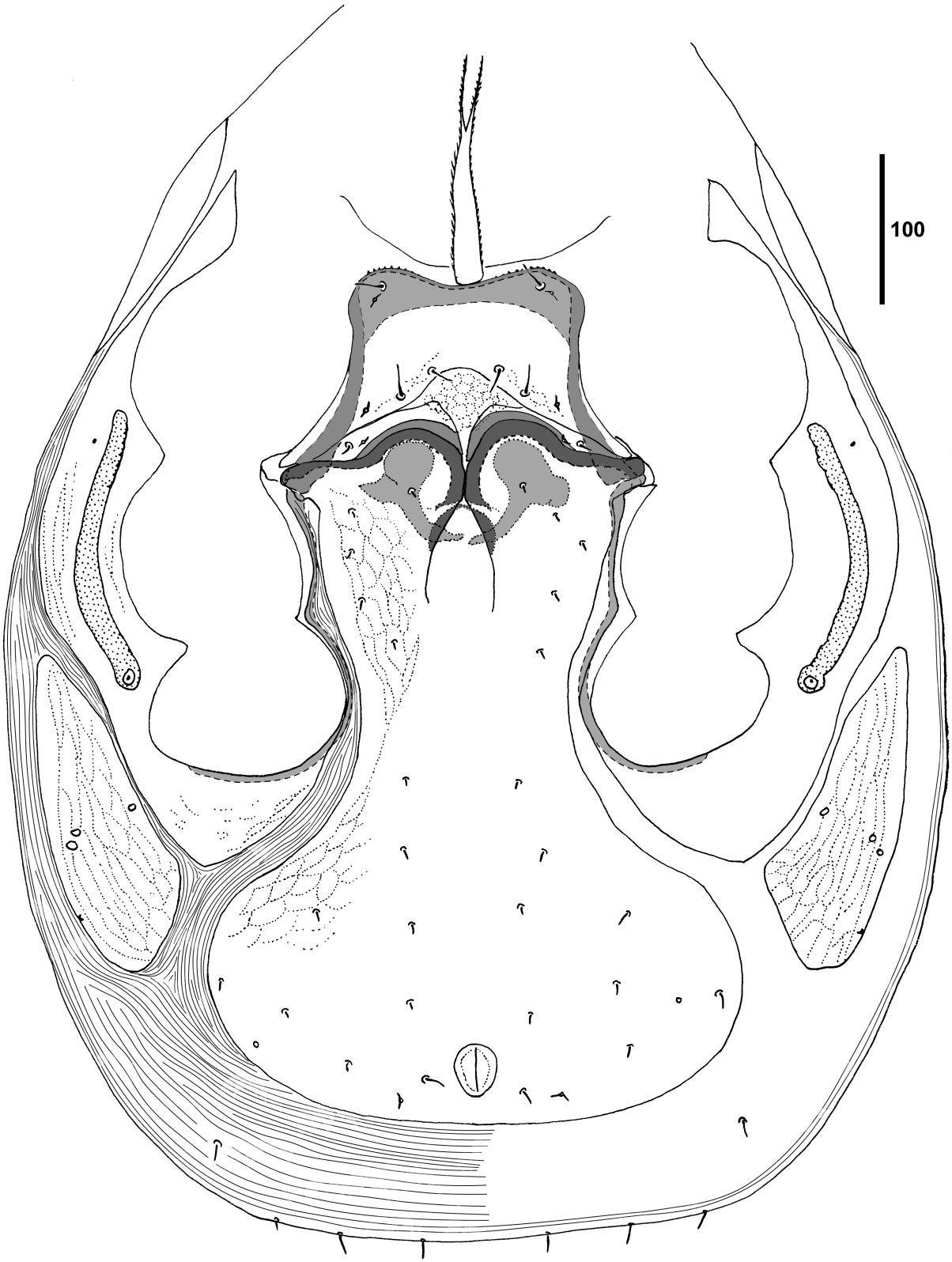


**FIGURE 9.** *Xenogynium oggae* **sp. nov.** female, venter.

***Xenogynium oggae* sp. nov.**
Figures 8–13

**Material examined.** Holotype. Female, ex juliform millipede. New Caledonia, Pic du Pin, Site 2, 22°14′16″S 166°50′01″E, 25 Nov 2004, S. Wright, day hand collection. Paratypes. 1 female, 2 males, same data as holotype female. Holotype female and paratype male deposited in NMHN, paratype female and male deposited in QM.

**Description. Female.**
*Dorsal idiosoma* (Figs 8, 13a). Dorsal shield length 820 (830), maximum width 620 (650), covered with fine network of polygonal reticulation comprised of fine lines joined by larger dots. Shield with 22 pairs of podonotal setae (one unpaired in holotype) plus unpaired *j2,* and 21–22 pairs of opisthonotal setae (plus one unpaired seta in holotype; others loosely paired), all smooth, short, of subequal length (13–25); lateral margins with numerous pores.

*Ventral idiosoma* (Figs 9, 13c). Tritosternum length 145 (160), base and laciniae uniformly and shortly pilose, separate for about two-thirds its length 55 (55). Sternal shield deeply concave posteriorly, medial length 55 (55), maximum width 225 (245), bearing three pairs of smooth setae and two pairs of lyrifissures; setal lengths: *st1* 24 (27), *st2* 23 (23), *st3* 25 (26). Metasternal shields separate from sternal shield and each other, bearing one pair of lyrifissures and setae *st4*, length 17 (13); region between sternal and metasternal shields weakly sclerotised, with faint reticulation. Endopodal shields narrow, fused posteriorly with peritrematal shields, underlying latigynal shields anteriorly. Latigynal shields bearing four pairs of short smooth setae (length 10–23; paratype with 5/7 setae on each shield), lacking pores, defined by inverted Y-shaped suture; intercoxal region with one pair of smooth setae. Vaginal sclerites clavate, lateral margins with irregular processes, heads resting in metasternal shields. Mesogynal region lacking pores. Anterior margins of sternal, latigynal and metasternal shields heavily sclerotised.

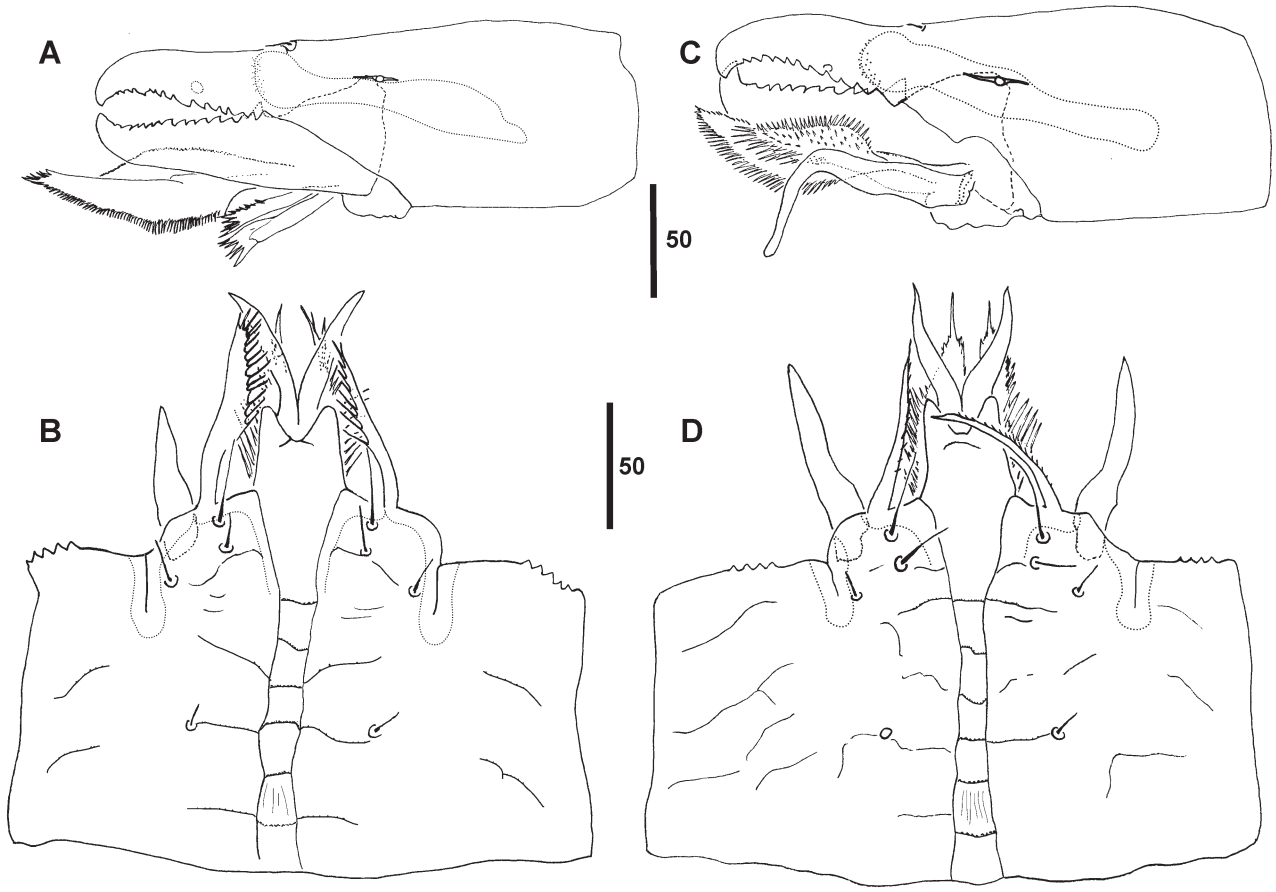


**FIGURE 10.** *Xenogynium oggae* **sp. nov.** (A–B) female, chelicera and subcapitulum; (C–D) male, chelicera and subcapitulum. Note: female, right corniculus broken.

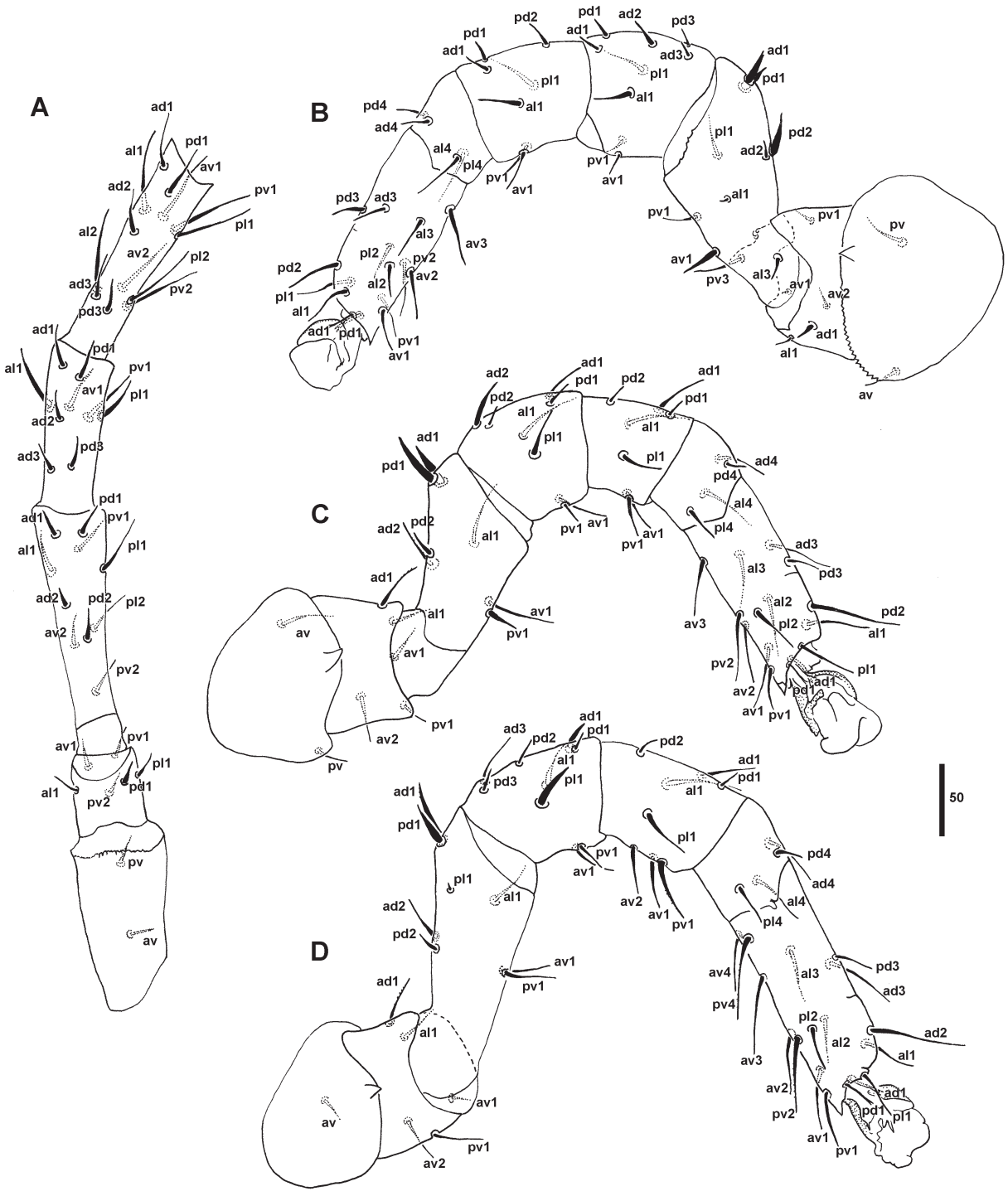


**FIGURE 11.** *Xenogynium oggae* **sp. nov.** female. (A–D) legs I–IV.

Genitiventrianal shield expanded but not covering opisthogaster, width 350 (380) bearing nine pairs (additional one unpaired seta in paratype) of smooth, simple setae, plus one pair of simple paranal setae; most setae very short (5–7) excepting paranal setae (19–20) and lateral shield seta (13–15); lateral and posterior margins of shield surrounded overlapped by soft cuticle. Soft cuticle surrounding shield with one pair of simple setae. Ventromarginal shields triangular, reticulate, lacking setae, with three pairs of pores. Peritreme shortened, extending almost to mid-coxa II; peritrematal shield reticulate, free from dorsal shield.

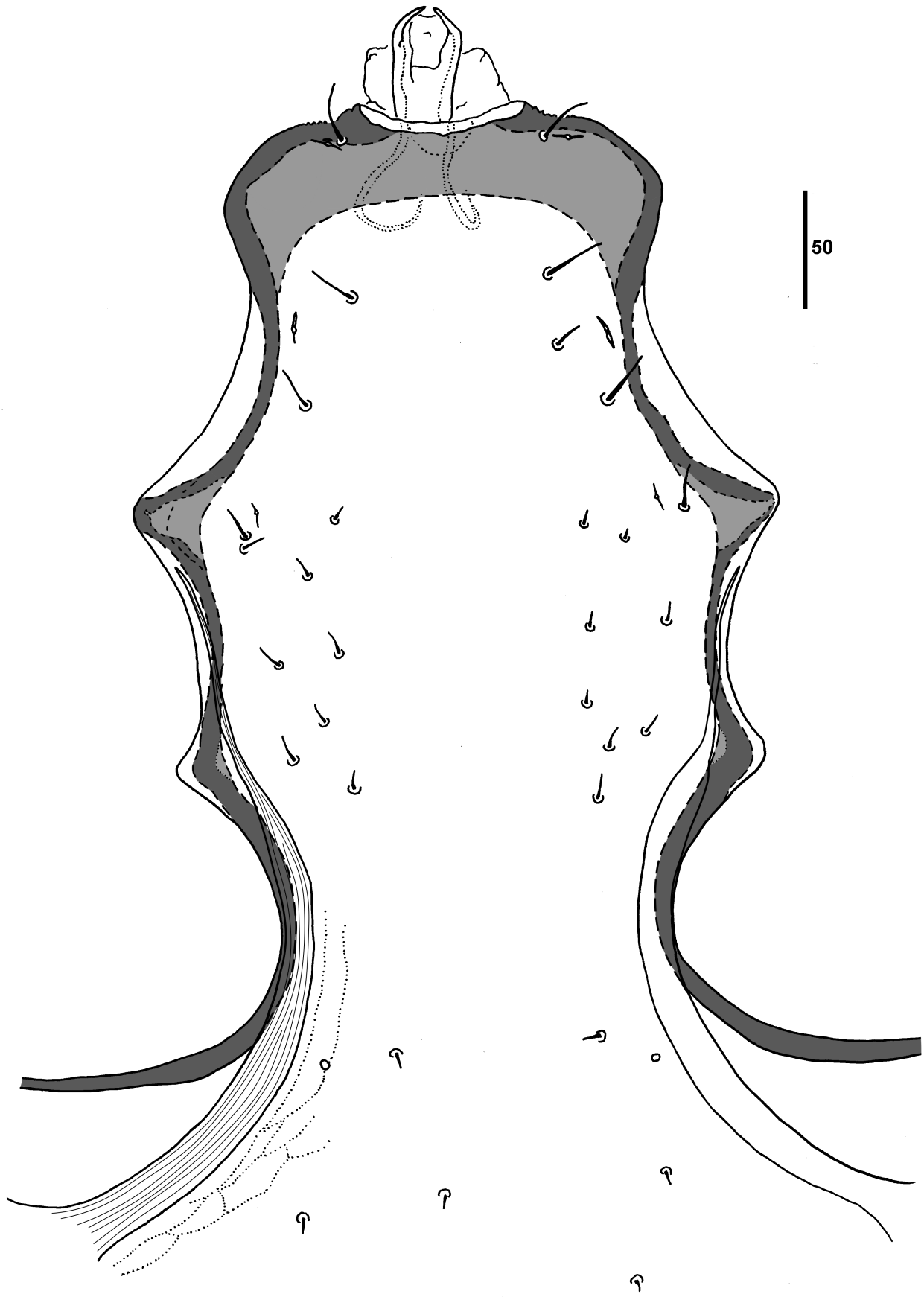


**FIGURE 12.** *Xenogynium oggae* **sp. nov.** male, sternogenital region.

*Gnathosoma* (Fig. 10b). Gnathosoma with four pairs of smooth setae, *h1* 37 (34), *h2* 16 (17), *h3* 21 (22), palpcoxal seta 11 (12); hypostomal groove with six rows of minute denticles; corniculi elongate, strong, length 70 (65), shorter than hypostomal processes; internal malae fringed at base, extending to palpgenu; hypostomal processes slender, internally pilose in distal half. Gnathotectum acuminate, margin smooth. Palp setal formula: 2-5-7-14-15; trochanter with dorso-distal hump, setae *v1* and *v2* slender, *v1* lightly barbed, *v2* smooth; genual, tibial and tarsal setae smooth or slightly barbed apically, slender or slightly thickened; palptarsal apotele large, 3-tined.

*Chelicerae* (Fig. 10a, 13c–d). Fixed digit length 195 (205), movable digit 105 (115), not extending past tip of fixed digit. Fixed digit with 13–14 teeth, pilus dentilis rudimentary; cheliceral seta small 8–10, appressed to dorsal surface. Movable digit with 14–15 teeth, proximal tooth large, with three excrescences: two with pilose upper margins; other excrescence larger, broader, with pilose ventro-distal margin and finely pilose comb-like upper margin.

*Legs* (Fig. 11). Lengths, excluding ambulacrum, I 810 (840), II 580 (600), III 600 (590), IV 690 (710). Leg I without ambulacrum, claws. Legs II–IV with large ambulacra lacking claws.

Leg chaetotaxy same as *Terrogynium.* Thick spine-like setae: Tr I *pd1*; Fe II *ad1, pd1, pd2*; Fe III *ad1, pd1*; Fe IV *ad1, pd1*; Ge IV *pl1*. Tarsi II–IV with truncate tips, tarsi III-IV with seta *al1* on small apophysis; setae *ad1, pd1* small, with bifurcate tips, both setae difficult to discern. Tarsus IV without intercalary sclerite, setae *av4, pv4* on rudiments of sclerite distal to tarsal suture.

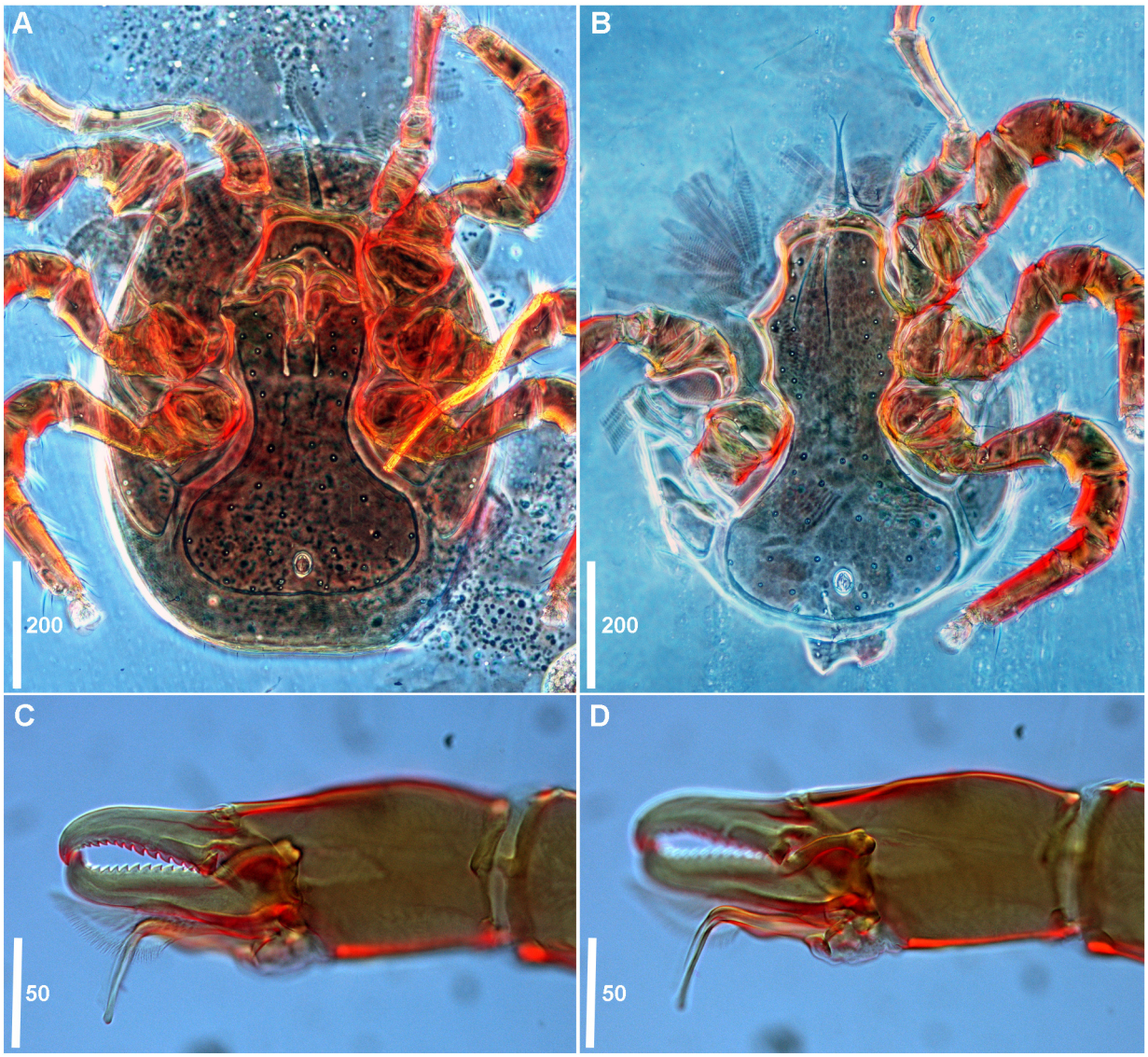


**FIGURE 13.** *Xenogynium oggae* **sp. nov.** photomicrographs (A) female, venter; (B–D) male, venter and chelicera adaxial and abaxial views.

**Male.**

*Dorsal idiosoma.* Similar to female. Length 850–910, width 640–650.

*Ventral idiosoma* (Fig. 12). Sternoventrianal shield length 660–670, cuticle smooth excepting some weak reticulation posterior to coxa IV; sternal setae *st1* 25–28, closely associated with *stp1,* setae *st2-4* 18–25, *stp2* posterolaterad *st2, stp3* close to *st4.* Intercoxal region with 11–16 smaller (length 8–12) setae. Opisthogaster and lateral region similar to female.

*Gnathosoma* (Fig. 10d). Similar to female, except corniculi longer (83–85), as long as hypostomal processes.

*Chelicerae* (Figs 10c, 13c-d). Fixed digit length 205–220, movable digit 105–115, not extending past tip of fixed digit. Fixed digit with 12–14 teeth, pilus dentilis rudimentary; cheliceral seta small 9–10, appressed to dorsal surface. Movable digit with 11–12 teeth, proximal tooth large, with two obvious excrescences: one pilose excrescence (similar to female), the other thin, sclerotised, bent downwards about halfway along its length; additional third excrescence possibly represented by scarcely visible and small non-pilose lobe.

*Legs.* Same as female.

**Etymology.** The specific name *oggae* refers to Nanny Ogg, a character created by Terry Pratchett, alluding to the one of the three unnamed witches of *Macbeth.*

## *Zygogynium* gen. nov.

(Figures 14–19)

Type species: *Zygogynium garlickae* **sp. nov.**

**Diagnosis.** Both sexes: Dorsal shield with 75–77 small to minute (< 15 μm) setae; tritosternal laciniae fused for about three-quarters their length; genitiventrianal shield not expanded, lateral edges almost parallel, opisthosomal section longer than wide, bearing 15–19 slightly thickened setae; ventromarginal shields large, triangular, lacking setae; peritremes shortened, reaching anterior coxa III. Female: sternal shield free from metasternal shields, deeply concave posteriorly, *st2* and *st3* on posterior margin; latigynal, mesogynal and anal shields fused with ventral shield; chelicerae with movable digit not extending beyond tip of fixed digit, movable digit with numerous (12–13) teeth. Male: with sternoventrianal shield; corniculi much longer than female's corniculi; chelicerae with small finger-like excrescence.

**Material examined.** Holotype. Female, ex juliform millipede. New Caledonia, Pic du Pin, Site 2, 22°14′16″S 166°50′01″E, 25 Nov 2004, S. Wright, day hand collection. Paratypes. 2 females, 2 males, same data as holotype female. Holotype female and paratype male deposited in NMHN, two paratype females and paratype male deposited in QM.

**Etymology.** Based on *zygo* (Gr., yoke, paired), alluding to the strong ventromarginal shields flanking the ventral shield, and *gynium* (Gr., female), a common ending in Schizogyniidae.

## *Zygogynium garlickae* sp. nov.

**Description. Female.**

*Dorsal idiosoma* (Fig. 14). Dorsal shield length 660 (660), maximum width 420 (440), covered with fine network of polygonal reticulation comprised of fine lines joined by larger dots. Shield with unpaired *j2* and 18 pairs of podonotal setae (plus an additional unpaired seta in holotype), and 19 pairs of opisthonotal setae (plus one unpaired seta in holotype), all smooth, some marginal and submarginal setae short, of subequal length (8–10), other setae minute, reduced to vestigial stubs; shield with several obvious pores.

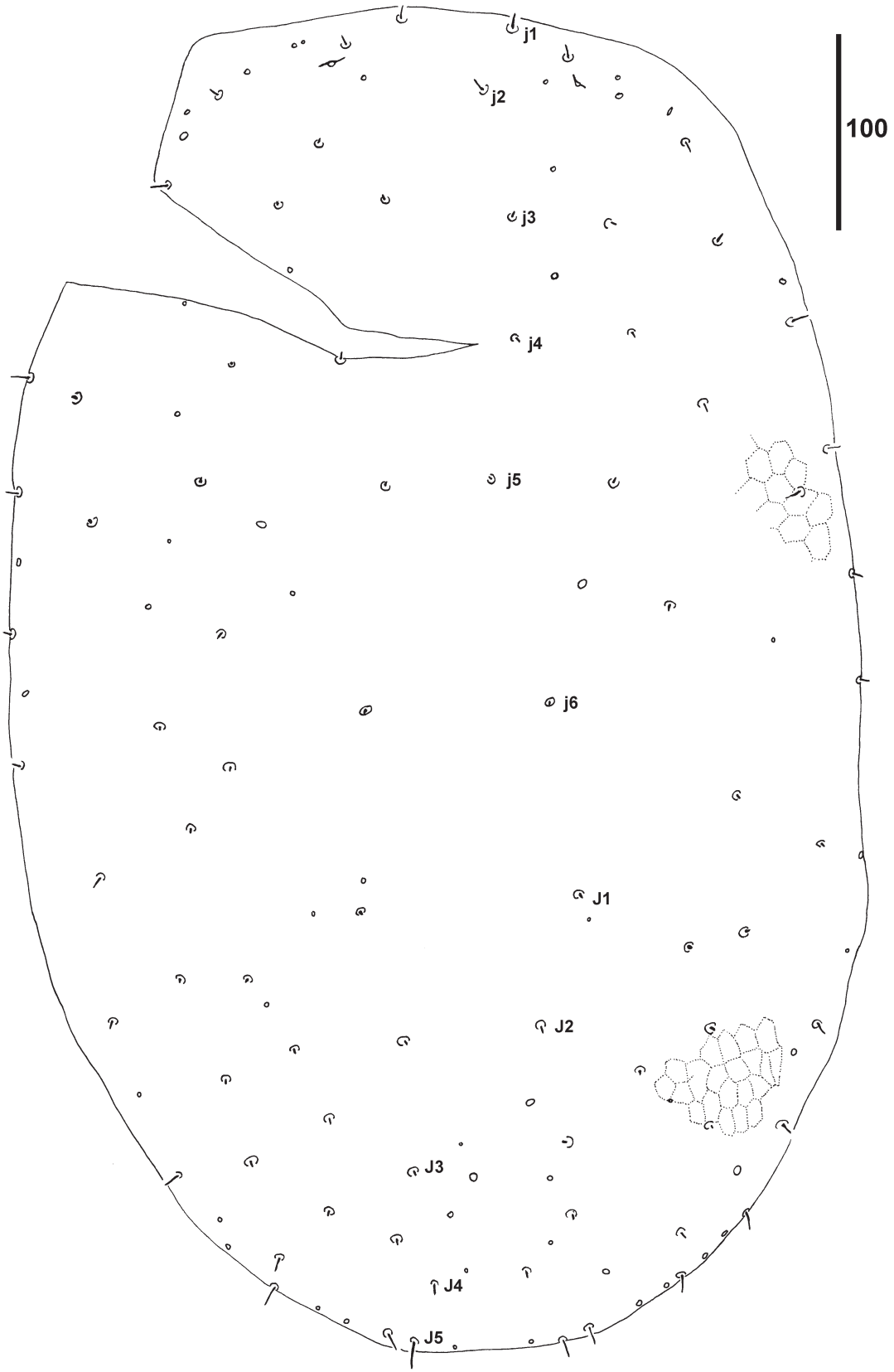


**FIGURE 14.** *Zygogynium garlickae* **sp. nov.** female, dorsum, with *j-J* series designated.

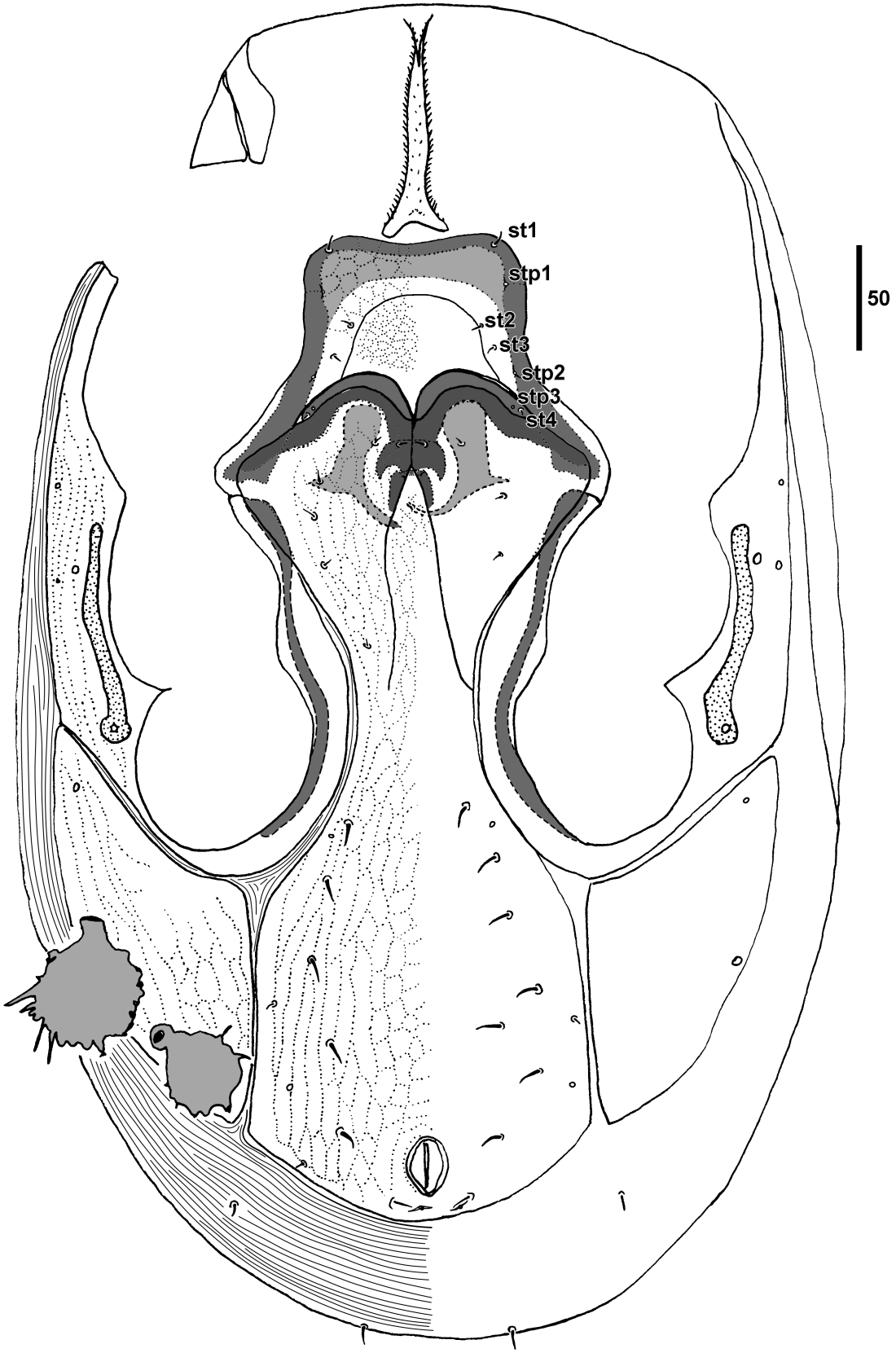


**FIGURE 15.** *Zygogynium garlickae* **sp. nov.** female, venter. Note: *Rickia* (Laboulbeniales) thalli shaded grey.

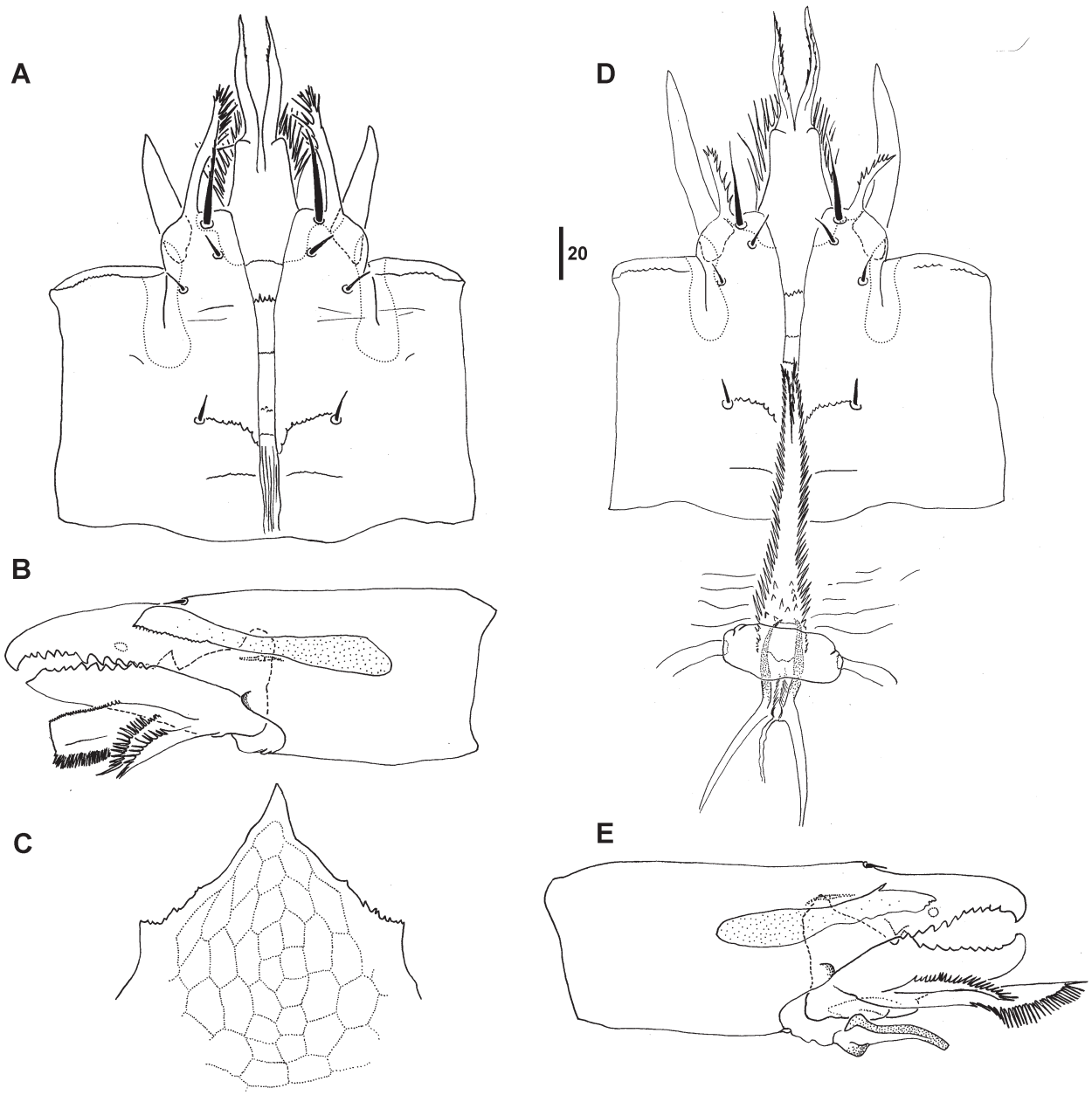


**FIGURE 16.** *Zygogynium garlickae* **sp. nov.** (A–C) female, subcapitulum, chelicera and gnathotectum; note: excrescence severed; (C–D) male, subcapitulum and chelicera.

*Ventral idiosoma* (Figs 15, 19b–c). Tritosternum length 115 (125), base and laciniae uniformly and shortly pilose, separate for about three-quarters its length 30 (37). Sternal shield deeply concave posteriorly, medial length 28 (34), maximum width 200 (180), bearing three pairs of short, smooth setae and two pairs of lyrifissures; setal lengths: *st1* 9 (7), *st2* 7 (7), *st3* 5 (4); seta *st2* expressed asymmetrically in paratype. Metasternal shields separate from sternal shield and each other, bearing one pair of lyrifissures and setae *st4*, length 4 (3); region between sternal and metasternal shields weakly sclerotised, with densely reticulate cuticle. Endopodal shields narrow, fused posteriorly with peritrematal shields, underlying latigynal shields anteriorly. Latigynal shields bearing 4–5 pairs of short setae (length 5–8; expressed asymmetrically in both specimens on different sides), lacking pores, defined by inverted Y-shaped suture; suture asymmetrical in holotype, reaching shield margin on one side; suture straight and not reaching shield in paratype. Vaginal sclerites clavate, lateral margins with irregular processes, heads resting in metasternal shields. Mesogynal region lacking pores. Anterior margins of sternal, latigynal and metasternal shields heavily sclerotised.

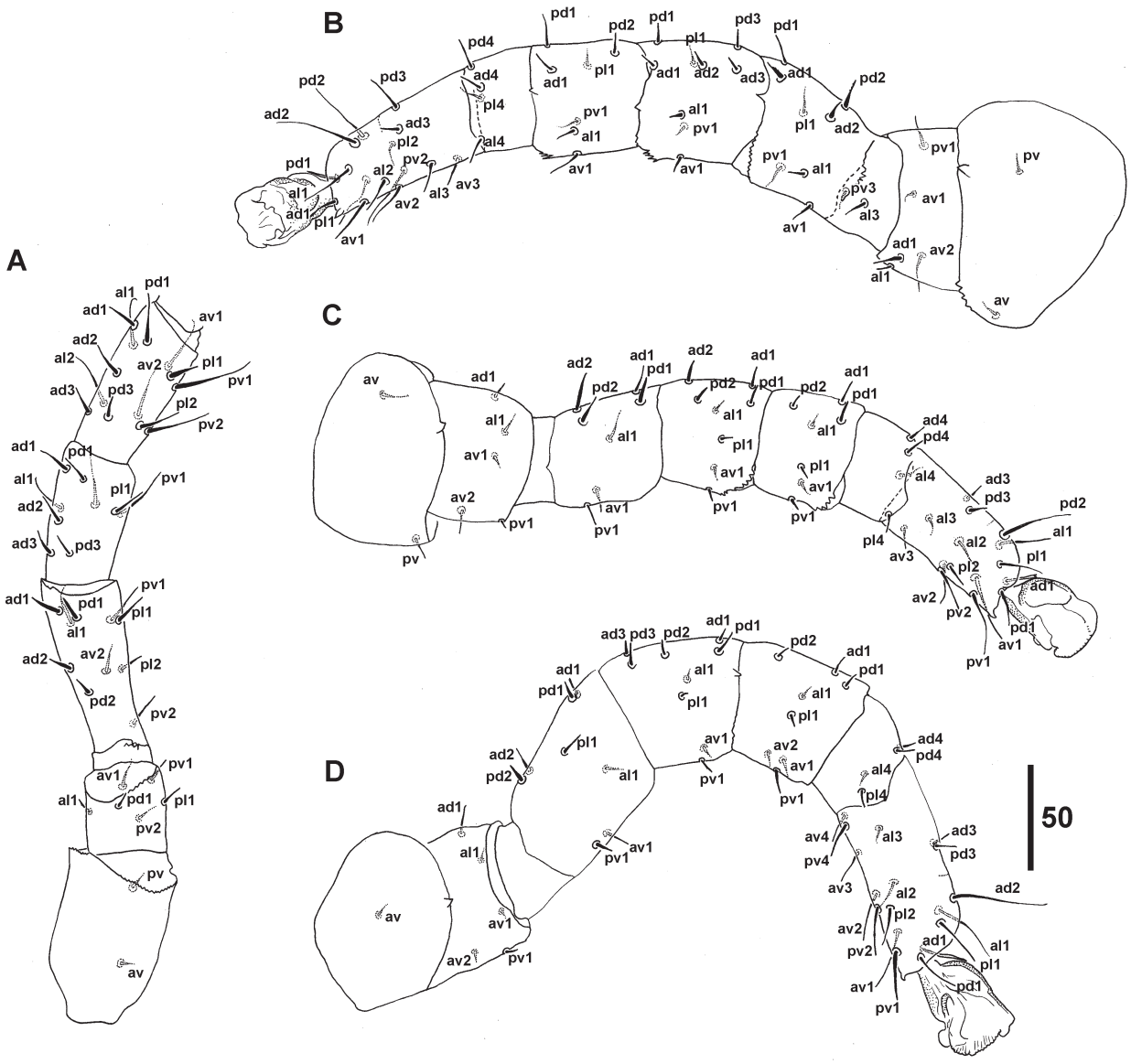


**FIGURE 17.** *Zygogynium garlickae* **sp. nov.** female. (A–D) legs I–IV.

Genitiventrianal shield expanded but not covering opisthogaster, lateral margins straight and almost parallel, width 170 (185), bearing 17 setae (21 in paratype); most setae blade-like (length 13–17) excepting paranal setae (length 14–16) and 3–4 short setae on lateral and posterolateral margins (length 5–7); lateral and posterior margins of shield overlapped by soft cuticle. Soft cuticle surrounding shield with one pair of simple setae. Ventromarginal shields triangular, reticulate, lacking setae, with 2-3 pairs of pores. Peritreme shortened, extending to anterior of coxa III; peritrematal shield reticulate, free from dorsal shield.

*Gnathosoma* (Figs 16a,c). Gnathosoma with four pairs of smooth setae, *h1* 32 (41), *h2* 7 (8), *h3* broken (11), palpcoxal seta 7 (10); hypostomal groove with five rows of minute denticles, groove with striate pattern behind proximal row of denticles; corniculi elongate, strong, length 50 (52), shorter than hypostomal processes; internal malae fringed at base, extending to palptibia; hypostomal processes slender, internally pilose in distal half. Gnathotectum acuminate, margin with few denticles (Fig. 16c). Palp setal formula: 2-5-7-14-15; trochanter with small dorso-distal hump, setae *v1* and *v2* slender, *v1* lightly barbed, *v2* apically barbed; genual, tibial and tarsal setae smooth, slender; palptarsal apotele large, 3-tined.

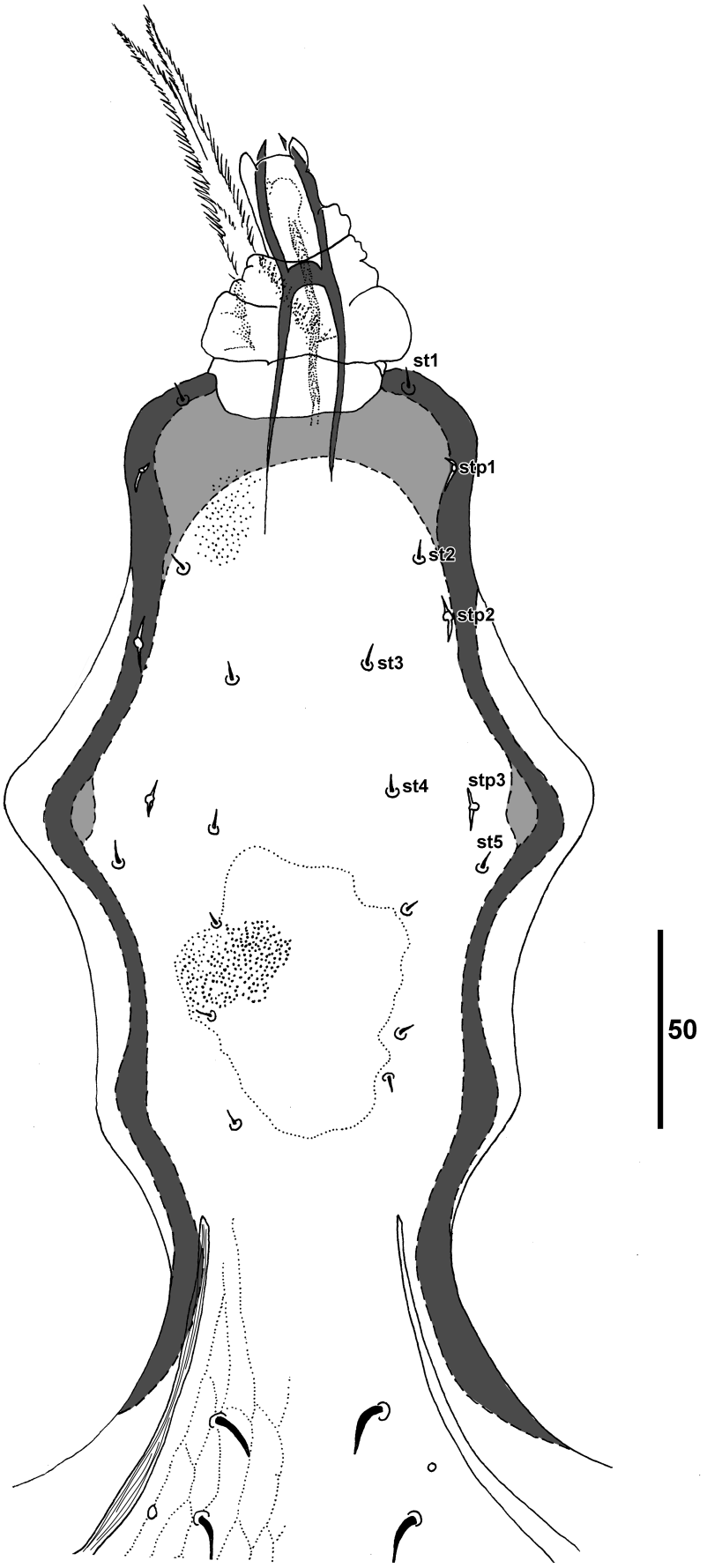


**FIGURE 18.** *Zygogynium garlickae* **sp. nov.** male, sternogenital region.

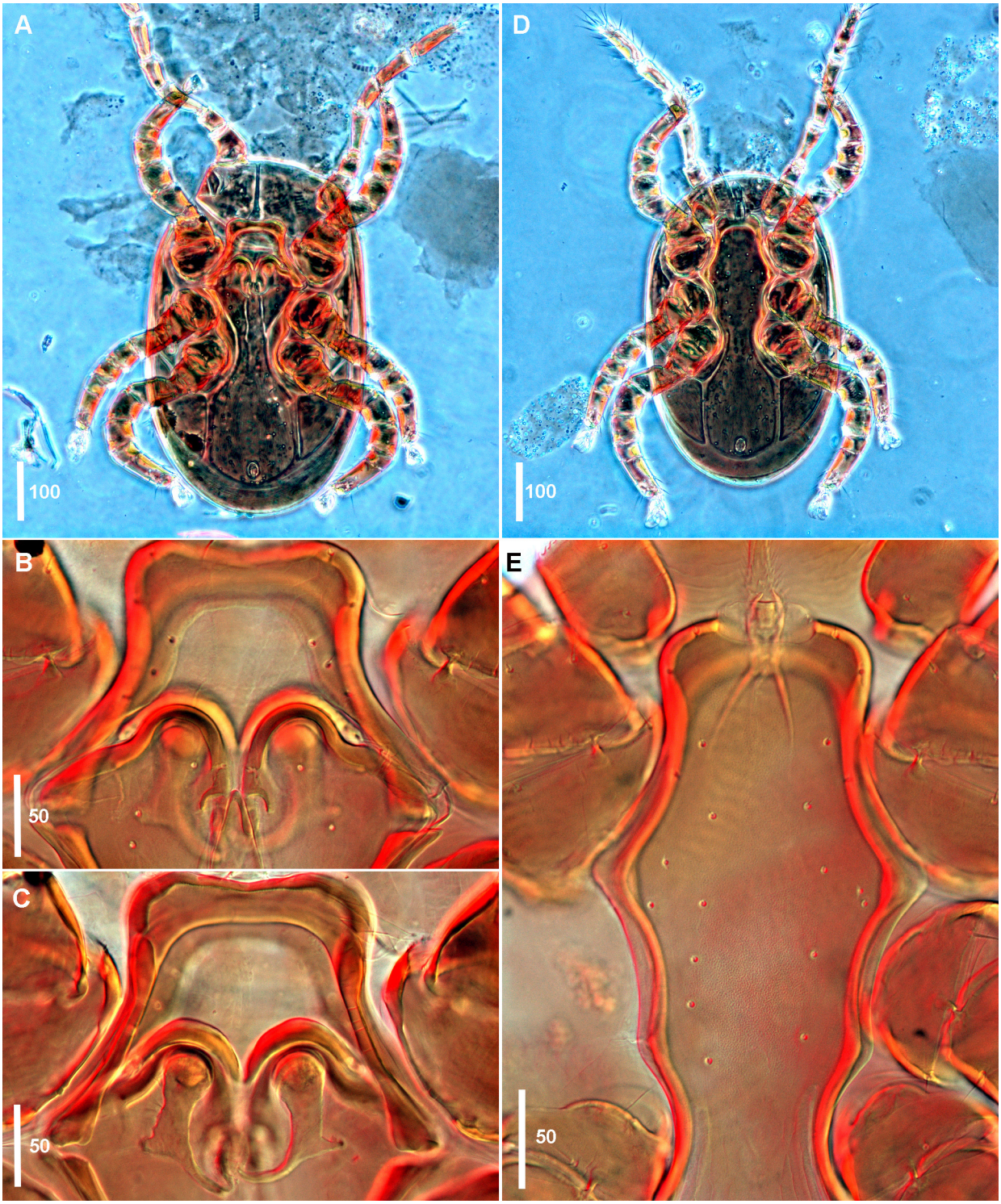


**FIGURE 19.** *Zygogynium garlickae* **sp. nov.** photomicrographs (A–C) female, venter, external sternogenital region, internal sternogenital region showing strong metasternal elements and vaginal sclerites; (D–E) male, venter, sternal region.

*Chelicerae* (Fig. 16b). Fixed digit length 145 (145), movable digit 78 (76), not extending past tip of fixed digit. Fixed digit with 12 teeth (fifth and sixth from base largest), pilus dentilis rudimentary; inner side with micropapillate membranous lobe, length 75–80, distally expanded bearing small papillae on ventral edge; cheliceral seta small (ca. 5), appressed to dorsal surface. Movable digit with 12–13 teeth, proximal tooth large, with three excrescences: two with pilose upper margins; other excrescence larger, broader, with pilose ventro-distal margin and finely pilose comb-like upper margin.

*Legs* (Fig. 17). Lengths, excluding ambulacrum, I 430 (480), II 380 (410), III 350 (360), IV 420 (430). Leg I without ambulacrum, claws. Legs II–IV with large ambulacra lacking claws.

Leg chaetotaxy same as other genera. No leg setae obviously thickened or spine-like; femur III and IV with somewhat thicker setae *ad1*. Tarsi II–IV with truncate tips; setae *ad1, pd1* small, with bifurcate tips. Tarsus IV without intercalary sclerite, setae *av4, pv4* on cuticle distal to tarsal suture.

**Male.**

*Dorsal idiosoma.* Similar to female. Length 590, width 370–380.

*Ventral idiosoma* (Figs 18, 19d–e). Sternoventrianal shield length 465, cuticle lightly punctate, although medial area between coxae III more coarsely punctate; sternal setae *st1* 7–8, well-separated from *stp1,* setae *st2–4* and other intercoxal setae 4–7; six-seven loosely paired additional intercoxal setae (asymmetrical additional seta in one specimen); *stp2-3* present, other pores absent. Opisthogaster and lateral region similar to female.

*Gnathosoma*. Similar to female, except corniculi longer (76–78), much longer than hypostomal processes, which are shorter than female's processes; anterior row of denticles absent.

*Chelicerae* (Fig. 16e; n=1). Fixed digit length 145, movable digit 69, not extending past tip of fixed digit. Fixed digit with 11 teeth, proximal six teeth largest, pilus dentilis rudimentary; cheliceral seta small, 4, appressed to dorsal surface. Movable digit with 10–11 teeth (proximal tooth largest, others becoming smaller distally), with three obvious excrescences: two pilose excrescences (longest similar to female, 65, the other shorter and brush-like, length 50), third excrescence blunt-tipped, finger-like, length 30.

*Legs.* Same as female.

**Etymology.** The specific name *garlickae* refers to Magrat Garlick, a character created by Terry Pratchett, alluding to the one of the three unnamed witches of *Macbeth.*

## Discussion

*The Schizogyniidae and their origins*

Trigynaspid mites show a bewildering array of shield arrangement and setation and, while important for defining families, variation within families is also prevalent (Trägårdh 1950; Kazemi *et al.* 2008). Schizogyniidae are a prime example, possessing genera with their anal shields separate or included into a genitiventrianal shield, metasternal shields fused with or free from the ventral shield, ventromarginal shields ranging from expansive to reduced to metapodal platelets (and sometimes fused to the peritrematal shields), latigynal shields sometimes free from the ventral shield (*Mixogynium*), and sometimes thin strap-like marginal shields.

This conglomerate of features raises questions of identity and monophyly of the Schizogyniidae. On a higher level, the Schizogyniidae belong to the Celaenopsoidea, which is a well-defined superfamily recovered as a strongly supported group in two separate phylogenetic analyses, each based on different character sets (Kethley 1977; Kim 2004), as well as a combined data set of leg setae and body characters (Seeman 2002). Thus, despite some striking similarities with non-celaenopsoid taxa (see later discussion), the Schizogyniidae is undoubtedly part of the Celaenopsoidea. Within the Celaenopsoidea the family-relationships are not so well-resolved. However, one possible major division – reflected in keys but not yet in phylogeny (*e.g.* Kim 2004)—is the presence of free latigynal shields (Costacaridae, Diplogyniidae, Triplogyniidae) versus latigynal shields fused to the sternoventral shields (Celaenopsidae, Euzerconidae, Megacelaensopsidae, Neotenogyniidae, Schizogyniidae). This presumably reflects a major shift in how eggs are laid: from between the latigynal shields, perhaps like a trapdoor, to being pushed out anteriorly, assisted by flexion of the sternogenital region, similar to gamasine mites. In Celaenopsidae, the complete or near-complete fusion of the latigynal shields may be compensated for by the metasternal shields becoming the primary genital opening.

Based on genital shields alone, the Schizogyniidae is closest to Euzerconidae, being distinguished by the length of the latigynal shields, which extend no further than mid-coxa III in Euzerconidae, but reach slightly further—at least to the posterior margin of coxa III—in Schizogyniidae. Although this difference is minor, euzerconid mites are also defined by their serrate corniculi and their males with extraordinarily modified hypostomes (Funk 1980). In the latter respect the Euzerconidae are similar to *Mixogynium* and *Paraschizogynium* which also have males with modified hypostomes (Table 1), although not to the same asymmetric extent of euzerconid mites. Nevertheless,

this modification, if not homoplasious, is suggestive of a close (and possibly paraphyletic) relationship between Euzerconidae and Schizogyniidae. Similar modifications of the hypostome are also found in the Celaenopsidae and Megacelaenopsidae (Kinn 1968; Funk 1974), further grouping these families with the schizogyniid genera *Mixogynium* and *Paraschizogynium*, and are indicative of complex homoplasies (*i.e.* convergent evolution) or paraphyly in the Celaenopsidae, Euzerconidae, Megacelaenopsidae, and Schizogyniidae.

This putative relationship between Schizogyniidae and Euzerconidae is further reinforced by biogeography. The other moderately diverse families of Celaenopsoidea (> 2 species: Celaenopsidae, Diplogyniidae, Triplogyniidae) are found world-wide including Australia and New Guinea (*e.g.* Trägårdh 1950, 1951; Womersley 1958; Seeman & Walter 1997; Seeman 2012). However, the Euzerconidae and Schizogyniidae are absent throughout most of Australia: just one undescribed species of *Paraschizogynium* (a previously South-east Asian genus) occurs on lucanid beetles in Cape York (pers. obs.), perhaps representing a more recent arrival. Also, as geological evidence points to New Caledonia emerging from complete submersion about 37 mya (Grandcolas *et al.* 2008; Cluzel *et al.* 2012; Grandcolas 2017; but also consider Giribet & Baker 2019 and Heads 2019), these new genera probably arrived via a relatively recent and remarkable overseas journey, arriving after the Australian and Indomalayan plates collided. Did these three remarkable genera evolve *in situ* from a common ancestor, or do close relatives exist in Indonesia, the Philippines and other significant stepping-stones such as New Guinea? Obviously, further collecting efforts are required in these localities, as well as New Caledonia, to answer this question.

*The three new genera and their relationships*

The discovery and proposal of three new monotypic genera from a single millipede is extraordinary. Multiple trigynaspid genera from the same family sometimes live on a host species, such as *Fedrizzia* and *Neofedrizzia* on Passalidae (Seeman 2007), but the phenomenon is generally rare. Typically, on a given host species, each family of mites is represented by one or two species in the same genus, such as Diplogyniidae on cockroaches (Seeman 2012). By proposing three new genera, I hypothesise that each genus are representatives of three radiations of these mites on the millipedes of New Caledonia with a likely origin, or multiple origins, from the Indomalayan region or New Guinea.

These three genera all share a similar ventral shield arrangement, and other possible synapomorphies mentioned below, suggesting a close relationship between them. However, when each component of the ventral shields is considered separately, they are all found in other genera: free, separate metasternal shields (also in *Mixogynium, Schizogynium*); short latigynal shields, not extending past coxae III (*Indogynium*); and well-developed ventromarginal shields (all but *Mixogynium*). Other potential synapomorphies are likely to be homoplasious as they present in three different genera and may represent independent adaptations to adult life on a host: *i.e.* the loss of pretarsal claws (*Euroschizogynium*), short peritremes (*Choriarchus*), and loss of setae on ventromarginal shields (*Indogynium*). The only exception linking these three genera is a somewhat ambiguous synapomorphy: the obviously larger corniculi in males which are, where known, at most only slightly longer than those of the females of other genera (see *S. berlesei*). Thus, no solid basis is attainable for a one or two genus concept for these three species.

*Secondary sexual characteristics of the Schizogyniidae*

Modification of the male gnathosoma and chelicerae is widespread in the Celaenopsoidea. As mentioned previously, the modified gnathosoma of *Mixogynium* and *Paraschizogynium* may be analogous with the modified gnathosomas of Euzerconidae, Celaenopsidae and Megacelaenopsidae. In these cases, the male chelicera is similar to that of the female.

In contrast, the other genera of Schizogyniidae have modified cheliceral excrescences like those of the Diplogyniidae. In the three new genera, the male chelicerae of *Terrogynium* bears a scoop-like excrescence, that of *Xenogynium* has a slender finger-like excrescence (which is uniquely bent), while *Zygogynium* has a small finger-like excrescence. Curiously, these variations are all present in Diplogyniidae (*e.g.* Trägårdh 1950; Elsen 1981; Seeman 2012), suggesting considerable evolutionary experimentation with sperm transfer within both families. However, should the male secondary sexual characteristics be synapomorphic, then an evolutionary transition can be proposed for Celaenopsoidea: from minimal secondary sexual modification (Triplogyniidae) to modified chelicerae (Diplogyniidae, some Schizogyniidae) to modified gnathosomas (some Schizogyniidae, Celaenopsidae, Euzerconidae, Megacelaenopsidae).

*Convergence of* Terrogynium *with Heterozerconidae and Paramegistidae*

These new genera of Schizogyniidae, as well as *Indogynium*, share convergent characters with the Paramegistidae and Heterozerconidae, which also live on millipedes (as well as squamates) as adults. These mites have small or minute dorsal setae, numerous spine-like marginal setae (*Indogynium*, Paramegistidae, Heterozerconidae) and tend to have rounded bodies (*Terrogynium*, *Xenogynium,* Paramegistidae, Heterozerconidae). The loss of pretarsal claws in the schizogyniid genera also resembles the weak claws of Paramegistidae. *Terrogynium* is further akin in having broad flattened setae like those found in Paramegistidae, especially *Neomegistus* (Baker & Seeman 2008). Unusually, the genital shield of *Neomegistus* is also identical to that of Schizogyniidae, and the ventral shield arrangement differs only in the separation of *st1* on presternal shields; also, the large proximal tooth, present in most Celaenopsoidea, is lacking in *Terrogynium* (also see *Neotenogynium malkini* Kethley, 1974, which also shares a similar genital shield to Schizogyniidae). The loss of the proximal tooth probably relates to the parasitic nature of *Terrogynium* but the genital shield arrangement seems like a chance convergence that relates to the diversity of female genital shields in trigynaspid mites.

## Key to genera of Schizogyniidae

Modified from the key by Trach & Seeman (2014).

1. Female . . . 2
- Male . . . 10
2. Anal shield free from ventral shield . . . 3
- Anal shield fused with ventral shield . . . 5
3. Latigynal shields free . . . *Mixogynium* Ryke, 1957
- Latigynal shields fused with ventral shield . . . 4
4. Metasternal shields absent, fused with sternal shield; most submarginal and central setae on dorsal shield absent or vestigial; anal shield wide (as wide as sternal shield) . . . *Indogynium* Sellnick, 1954
- Metasternal shields fused but free from sternal shield; dorsal shield setae well developed, hypertrichous; anal shield small (no more than half as wide as sternal shield) . . . *Choriarchus* Kinn, 1966
5. Large pre-anal membranous region present; metasternal shields fused with sternal shield. . . . *Euroschizogynium* Trach & Seeman, 2014
- Pre-anal membranous region absent; single or paired metasternal shields free from sternal shield . . . 6
6. All dorsal setae short; ventromarginal shields lacking setae; latigynal shields short, not extending to mid-coxa IV . . . 7
- At least some marginal and/or dorsal setae long, extending beyond margin of body; ventromarginal shields with setae; latigynal shield longer, extending at least to mid-coxa IV . . . 9
7. Genitiventrianal shield setae obovate, membranous; cheliceral movable digit extending well beyond fixed digit, fixed digit without large proximal tooth; tarsi II–IV each with a thick, claw-like seta . . . *Terrogynium*
- Genitiventrianal shield setae unmodified; cheliceral movable digit not extending beyond fixed digit, fixed digit with large proximal tooth; tarsi II–IV without thick, claw-like setae . . . 8
8. Genitiventrianal shield longitudinally elongated, lateral edges almost straight; ventrianal setae longer, thickened; femur-tibia II–IV with leg setae all short, femur II–IV with some setae only slightly thicker than others. . . . *Zygogynium*
- Genitiventrianal shield broad, lateral edges curved; ventrianal setae short, slender; femur-tibia II–IV with some setae obviously different lengths, femur II–IV with at least *ad1* and *pd1* strongly thickened. . . . *Xenogynium*
9. Metasternal shields fused, broadest medially; opisthosoma with one or two pairs of setae exceptionally long (ca. 10 times longer than other posterior dorsal shield setae); genu III–IV with very long macroseta. . . *Paraschizogynium* Hunter & Rosario, 1987
- Metasternal shields free; opisthosoma with dorsal setae not exceptionally long (at most 5 times longer than other posterior dorsal shield setae); genu III–IV setae not exceptionally long. . . . *Schizogynium* Trägårdh, 1950
10. Male hypostome with highly modified setae; chelicerae similar to female . . . 11
- Male hypostome similar to female; chelicerae with modified excrescences . . . 12
11. Anal shield separate or weakly connected with sternoventral shield, bearing one pair of setae; lateral opisthosoma with metapodal platelets, ventromarginal shields absent; dorsal shield with all setae subequal, short . . . *Mixogynium*
- Anal shield fused with sternoventral shield; lateral opisthosoma with large ventromarginal shields; opisthosoma with one or two pairs of extremely long setae . . . *Paraschizogynium*
12. Male chelicera with large scoop-like excrescence . . . 13
- Male chelicera narrow finger-like excrescence . . . 15
13. Large pre-anal membranous region present . . . *Euroschizogynium*
- Large pre-anal membranous region absent. . . . 14
14. Ventrianal setae obovate, membranous; modified cheliceral excrescence curving ventrally . . . *Terrogynium*
- Ventrianal setae short, fine; modified cheliceral excrescence not significantly curved, directed anteriorly . . . *Indogynium*
15. Anal shield separate from ventral shields; cheliceral excrescences reduced to single, finger-like excrescence . . . *Choriarchus*

- Anal shield absent, incorporated into sternoventrianal shield; cheliceral excrescences, where known, include modified excrescence and two brush-like excrescences typical of female . . . . . 16

16. Pretarsi with claws . . . . . *Schizogynium* (known from *S. berlesei* only)

- Pretarsi lacking claws . . . . . 17

17. Modified cheliceral excrescence long, bending abruptly downwards; anterior sternal setae and about twice length other sternal setae; ventrianal setae short, slender . . . . . *Xenogynium*

- Modified chelicera excrescence short, straight; anterior sternal setae sort, subequal to other sternal setae; ventrianal setae longer, thickened . . . . . *Zygogynium*


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