Persian J. Acarol., 2024, Vol. 13, No. 2, pp. 189–231.
https://doi.org/10.22073/pja.v13i2.84737
Journal homepage: http://www.biotaxa.org/pja

http://zoobank.org/urn:lsid:zoobank.org:pub:0093BF72-FFD2-46D3-97EB-81C68FE4BC87

Article

Systematics of *Guntheria* Womersley, 1939 and related genera of chigger mites (Acariformes: Trombiculidae)

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ABSTRACT
Chigger mites of the tribe Schoengastiini Vercammen-Grandjean, 1960 having five non-specialized setae on the palpal tarsus and some other genera related to *Guntheria* Womersley, 1939 were reviewed based on literature. Original descriptions and re-descriptions of 283 species were examined. A new classification of *Guntheria* was proposed, with the re-definition of the subgenera *G.* (*Domrowana*) Vercammen-Grandjean & Langston, 1971 and *G.* (*Domrowella*) Vercammen-Grandjean, 1960, and the related genus *Derrickiella* Audy & Domrow, 1957. The subgenus *G.* (*Phyllacarus*) Vercammen-Grandjean, 1967 was re-defined and raised to the genus level. One new subgenus was described — *Phyllacarus* (*Platypacarus*) **subgen. nov.** One previously monotypic genus *Argentinacarus* Goff & Gettinger, 1995 was expanded and included in *Derrickiella* as a subgenus. The genus *Proschoengastia* Vercammen-Grandjean, 1967 previously synonymized with *Herpetacarus* (*Abonnencia*) Vercammen-Grandjean, 1960 was restored. Two new synonyms were established: *Pseudoschoengastia* (*Walchioides*) Vercammen-Grandjean 1960 [= *Guntherana* (*Pseudosusa*) Vercammen-Grandjean, 1960, **syn. nov.**] and *Euryphylla* Vercammen-Grandjean, 1967 **stat. nov.** [= *Eusaperium* Brennan, 1970, **syn. nov.**]. Sixty-six new combinations were proposed in the genera *Guntheria* (3), *Derrickiella* (22), *Susa* Audy & Nadchatram, 1960 (1), *Schoutedenichia* Jadin & Vercammen-Grandjean, 1954 (2), *Phyllacarus* (26), *Pseudoschoengastia* Lipovsky, 1951 (1), *Vanidicus* Brennan & Jones, 1961 (1), *Ornithogastia* Vercammen-Grandjean, 1960 (1), *Perissopalla* Brennan & White, 1960 (1), *Euryphylla* (7), and *Proschoengastia* (1). A key to the genera and subgenera of Schoengastiini with five setae on palpal tarsus was compiled.

KEYWORDS: Australia, chiggers, classification, New Guinea, Schoengastiini.

PAPER INFO.: Received: 15 December 2023, Accepted by: *A. Saboori*, 25 January 2024, Published: 15 April 2024

INTRODUCTION

The genus *Guntheria* Womersley, 1939 originally included one species of chigger mites with expanded sensilla (trichobothria), *Neoschoengastia kallipygos* Gunther, 1939, having paired sclerite plates in the caudal part of the idiosoma (pygosomal plates), which is a unique character within trombiculids. Womersley and Heaslip (1943) proposed a new replacement name *Guntherana* Womersley & Heaslip, 1943 for this genus, assuming that *Guntheria* was a junior homonym, but subsequent detailed studies confirmed the validity of *Guntheria* (Domrow 1971). Early works (e.g. Womersley and Heaslip 1943; Radford 1946a; Womersley 1952) included the type species under the new name *Neoschoengastia bipygalis* Gunther, 1939 (Gunther 1952). Its creation was, however, unnecessary, and *G. kallipygos* remains valid (Domrow 1960).

How to cite: Stekolnikov, A.A. (2024) Systematics of *Guntheria* Womersley, 1939 and related genera of chigger mites (Acariformes: Trombiculidae). *Persian Journal of Acarology*, 13(2): 189–231.

Domrow (1960) significantly expanded the genus by transferring *Euschoengastia* (*Derrickiella*) Audy & Domrow, 1957 to *Guntherana*, including additional species previously described as *Schoengastia* Oudemans, 1910 or *Neoschoengastia* Ewing, 1929, and describing four new species. He recognized two subgenera within *Guntherana* — the nominative and *Derrickiella*. The latter was characterized by the anterolateral scutal setae (AL) shorter than the anteromedian seta (AM) and clavate sensilla, vs. AL much longer than AM and globose sensilla in *G.* (*Guntherana*). The nymphs of *G.* (*Derrickiella*) differed from those of *G.* (*Guntherana*) by a narrow intersensillary space (ASL/SB = 1.5–2.3 vs. 0.8–1.1).

Vercammen-Grandjean and Langston (1971) restricted the nominative subgenus to the seven species having pygosomal plates only and divided the remaining *Guntherana* species into four subgenera. They redefined *Derrickiella* as *Guntherana* having subterminala (ζ) on the palpal tarsus (the formula of palpal tarsus 5BS); this subgenus, in their sense, included 17 species. The species of *Guntherana* without palpal subterminala (5B) and pygosomal plates constituted three subgenera: (1) *Guntherana* (*Ophthalmophila*) Vercammen-Grandjean & Langston, 1971, monotypic, created for an aberrant species *Ascoschoengastia* (*Oculicola*) *scaevola* Domrow, 1960; (2) *Guntherana* (*Ornithogastia*) Vercammen-Grandjean, 1960, a group of five close species parasitizing birds and characterized by the presence of cuticular striations (epiostracal pleats) on the scutum, around the sensillary bases; (3) *Guntherana* (*Domrowana*) Vercammen-Grandjean & Langston, 1971, a large miscellaneous group that included 33 species.

In total, the genus *Guntherana* included 63 species (nine of them were described as new) occurring in Australia and New Guinea. Exceptions were the species of *Ornithogastia* (recorded in Morocco, Iran, Russia, Japan, and the US), *Guntherana* (*Domrowana*) *japonica* Vercammen-Grandjean & Langston, 1971 described from Japan, *G.* (*D.*) *philippensis* (Philip & Woodward, 1946) recorded in Australia and the Philippines, and *G.* (*D.*) *domrowi* Brennan, 1965 known from the islands of the North Pacific Ocean. Previously, Vercammen-Grandjean (1967) transferred *Schoengastia* (*Trombewingia*) Fonseca, 1955 to *Guntherana* and described a new monotypic subgenus *Guntherana* (*Phyllacarus*) Vercammen-Grandjean, 1967, but these taxonomic acts were ignored by Vercammen-Grandjean and Langston (1971). These authors also rejected the inclusion of the genus *Susa* Audy & Nadchatram, 1960 into *Guntherana* proposed by Vercammen-Grandjean (1968).

Later, this genus (already under the name *Guntheria*) was separately reviewed in New Guinea by Goff (1980c) and in Australia by Domrow and Lester (1985). Both these revisions accepted in general the classification proposed by Vercammen-Grandjean and Langston (1971), with the subgenera *Guntheria* characterized by the presence of pygosomal plates and *Derrickiella* with the subterminala on palpal tarsus. Goff (1980c), however, raised *Ornithogastia* to generic rank and synonymized *G.* (*Ophthalmophila*) with *G.* (*Domrowana*). Domrow and Lester (1985) synonymized *G.* (*Domrowana*) with *G.* (*Phyllacarus*), on the ground that the type species of *Phyllacarus* belongs to *Domrowana* and the former name has a priority over the latter one. They supported the synonymization of *Ophthalmophila*, which thus became a synonym of *Phyllacarus*. The genus *Zyzomyacarus* Goff, 1979 characterized by the presence of only slightly expanded sensilla vs. clavate or globose in the majority of *Guntheria* was synonymized with the latter by Lester (1984); Domrow and Lester (1985) included it in the synonyms of *Phyllacarus*.

Since the last revision (Domrow and Lester 1985) did not consider the genus *Guntheria* in full, the subgeneric name *Domrowana* was retained for many species described in New Guinea by Goff. As a result, the checklist compiled by Nielsen *et al.* (2021) combined the systems proposed by Goff (1980c) and Domrow and Lester (1985), with the Australian species included in the subgenus *Phyllacarus* and the New Guinean species in *Domrowana*. In total, 97 valid species are currently associated with the genus name *Guntheria* (Nielsen *et al.* 2021). After the first revision of the genus (Domrow 1960), many new species were described in *Guntheria* by Domrow (1962, 1964, 1971, 1972, 1974, 1978, 1984), Brennan (1965), Nadchatram and Traub (1969), Vercammen-Grandjean

and Langston (1971), Goff (1977a, b, 1978, 1979, 1980a, b, c, 1981a, b, c, d, e, 1982, 1983), Loomis and Goff (1983), Lester (1984), Domrow and Lester (1985), and Fain and Stekolnikov (2004).

The nominative subgenus of *Guntheria* in the recent systems is a group of closely related species possessing pygosomal plates, a similar shape of scutum, globose sensilla, one genuala I (*σ*), nude galeal (deutorostral) seta; almost identical palpal setal formula B/B/NNN(B); a uniform chaetotaxy of idiosoma; and without subterminala on the palpal tarsus. Species from the other subgenera — *Derrickiella* and *Phyllacarus* (or *Domrowana*) — present a wide variety of characters: sensilla from globose to narrow fusiform; scutum of various shapes, similar to that of different groups, for example *Helenicula* Audy, 1954, *Schoengastia*, *Cheladonta* Lipovsky, Crossley & Loomis, 1955, *Herpetacarus* Vercammen-Grandjean, 1960a, and *Schoutedenichia* Jadin & Vercammen-Grandjean, 1954; palpal setal formula varies from N/N/NNN (all setae nude) to B/B/BBB (all setae branched); idiosomal setae from 50–60 in number, with the dorsal setae of post-humeral rows distributed as 6-6-6 or even 4-4-4, to about 350, with indistinct rows (Vercammen-Grandjean and Langston 1971; Goff 1977a; Domrow and Lester 1985). In some species, the dorsal idiosomal and some scutal setae are expanded, lanceolate or leaf-like, with their barbs sometimes modified into large spikes. The setation of legs is mostly standard for the subfamily Trombiculinae, but in a few species reduction of some setae, such as genualae II and/or III (*σ*), tibiala III (*φ*), leg I subterminala (*ζ*), and pretarsala II (*ζ*), can take place. In a few species leg I tarsala (*ω*) occupies a terminal position, near the subterminala.

Because of this diversity, the definition of *Guntheria* becomes uncertain. The only character common for all species currently included in this genus is the presence of five non-specialized setae on the palpal tarsus, in addition to basal tarsala (*ω*). However, species of several other genera of chigger mites with expanded trichobothria can have the same setation of the palpal tarsus, for example, *Colicus* Brennan, 1970 (5BS, like in *Derrickiella*), *Helenicula* (5B in some species), *Pseudoschoengastia* Lipovsky, 1951 (5B), *Kayella* Vercammen-Grandjean, 1960 (5B in some species), *Schoutedenichia* (5B in the subgenus *Pentachia* Vercammen-Grandjean, 1958), and *Susa* (5B) (Brennan and Goff 1977; Kudryashova 1998; Stekolnikov 2018). Although the hypothesis that *Guntheria* is a monophyletic group associated with the Australian zoogeographic realm is possible, its division into several genera seems necessary to make the system of chigger mites more coherent.

Since almost all species of *Guntheria* have complete and well-illustrated descriptions or re-descriptions, its new classification based on the literature seems possible. The recent checklist (Nielsen *et al.* 2021) included synonymies for all its species; the summary works of Vercammen-Grandjean and Langston (1971), Goff (1980c), and Domrow and Lester (1985) included detailed data on the types, synonymy and bibliography, distribution, hosts, and also identification keys for the majority of species. Therefore, it is enough to give here only the diagnoses and lists of species for the genera and subgenera.

Womersley (1952), Domrow (1960), and Domrow and Lester (1985) regarded many species of *Guntheria* as subjective synonyms. In some cases, however, Vercammen-Grandjean and Langston (1971) and Goff (1980c) provided enough grounds for the separation of previously synonymized species (Stekolnikov 2021). As an estimation of the relations between close species would require a special work, possibly with an examination of types, which are not accessible to me now, I refrain here from the definite conclusions and mainly follow only the acts of synonymization recognized by Vercammen-Grandjean and Langston (1971). Other published opinions on the synonymy are given in brackets.

I include also data on other genera of chigger mites — either associated previously with *Guntheria* or having similar traits — in order to place this genus in a wider context and to support its new system. A study of the original descriptions of species and other taxonomic literature on these genera resulted, in addition, in multiple corrections of the current generic placement of species.

MATERIAL AND METHODS

Terminology and illustrations

I use the standard terminology of chigger mites, abbreviations and diagnostic formulas summarized by Goff *et al.* (1982). The words used in different sources to describe the shapes of expanded sensilla (trichobothria) were not terminologically standardized. Following Domrow (1960), Nadchatram and Traub (1971), and Nadchatram and Dohany (1974), I designate the sensillum having a spherical head on a short stalk as globose; the sensillum characterized by a more or less smooth transition from the head to the stalk is termed clavate; a narrow sensillum, usually pointed to the end is named fusiform.

The words "setation standard for Trombiculinae" in the description of legs in diagnoses mean the presence of following specialized setae: pretarsalae I and II (ζ); subterminala (ζ) and nude parasubterminala (z); 2 tibialae I and II, 1 tibiala III (φ); 1 genuala II, 1 genuala III (σ); microtibiala I and microgenuala I (κ).

All illustrations given herein represent an original artwork made on the base of published sources with alterations. The scales for the drawings published without scale lines were approximately reconstructed based on the measurements provided in the same works as the drawings.

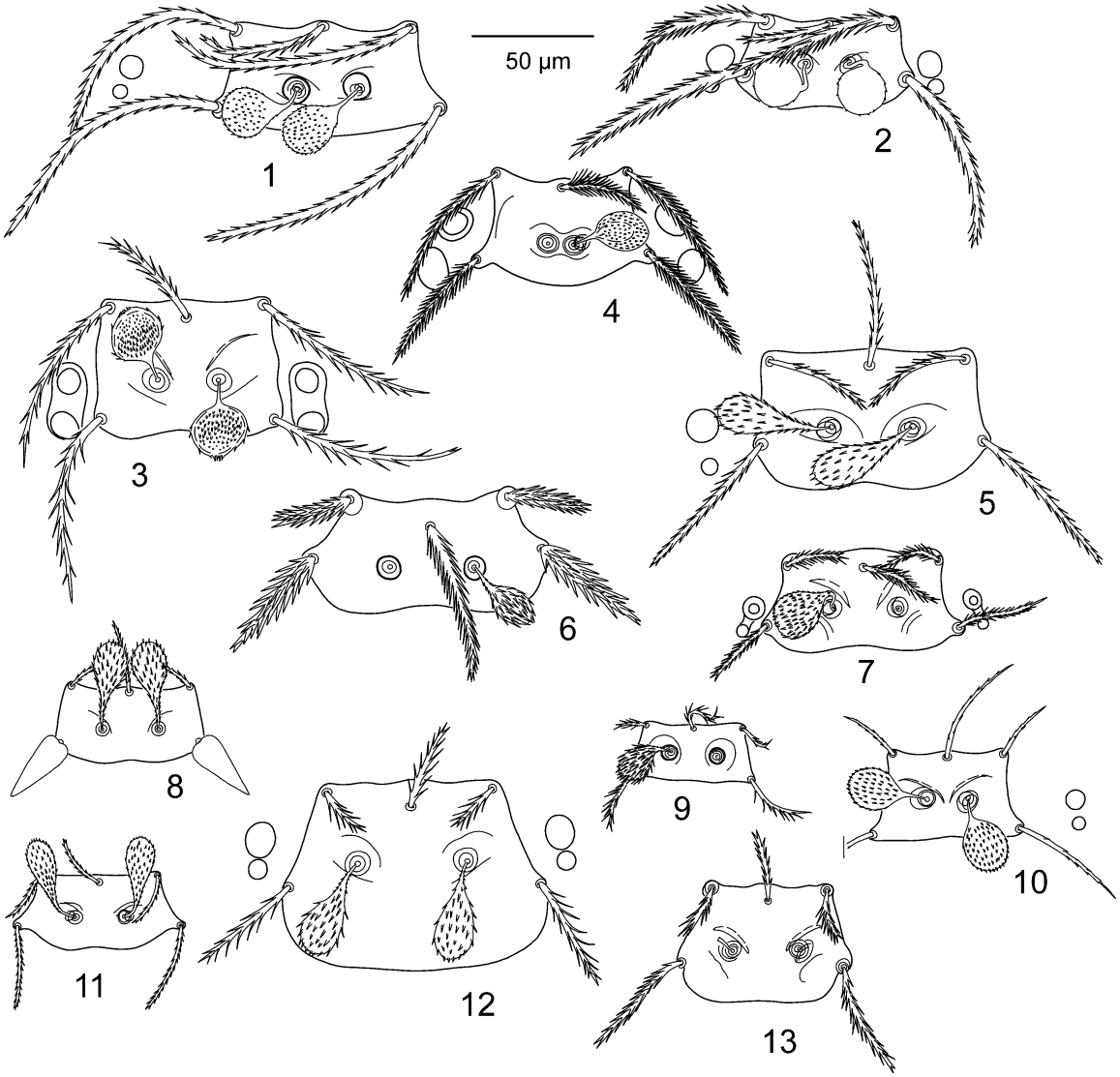
Principles of classification

The presence of the pygosomal plates in the nominative subgenus of *Guntheria* is an evident autapomorphy. All other morphological characters used in the taxonomy of this genus, such as details of the setation of gnathosoma and legs, shape of the posterior scutal margin, shape of sensilla, shapes of scutal and idiosomal setae, could be homoplasies, as well as in other large larval genera of chigger mites (Stekolnikov 2013). I should emphasize that characters of the trombiculid instars other than the parasitic larva, and molecular data, are currently obtained only for a small proportion of chigger species (Antonovskaia 2018; Zajkowska *et al.* 2023). In these circumstances, inferring a complete phylogeny is hardly possible. Nevertheless, we may reveal at least some fragments of the natural system marked by stable combinations of possibly independent morphological characters. For example, *Guntheria* possessing the pygosomal plates have also a series of common traits, such as the presence of only one genuala I (see above). Sometimes even a purely morphometric approach can help to find or confirm the groups of evidently related chigger species (Stekolnikov 2013).

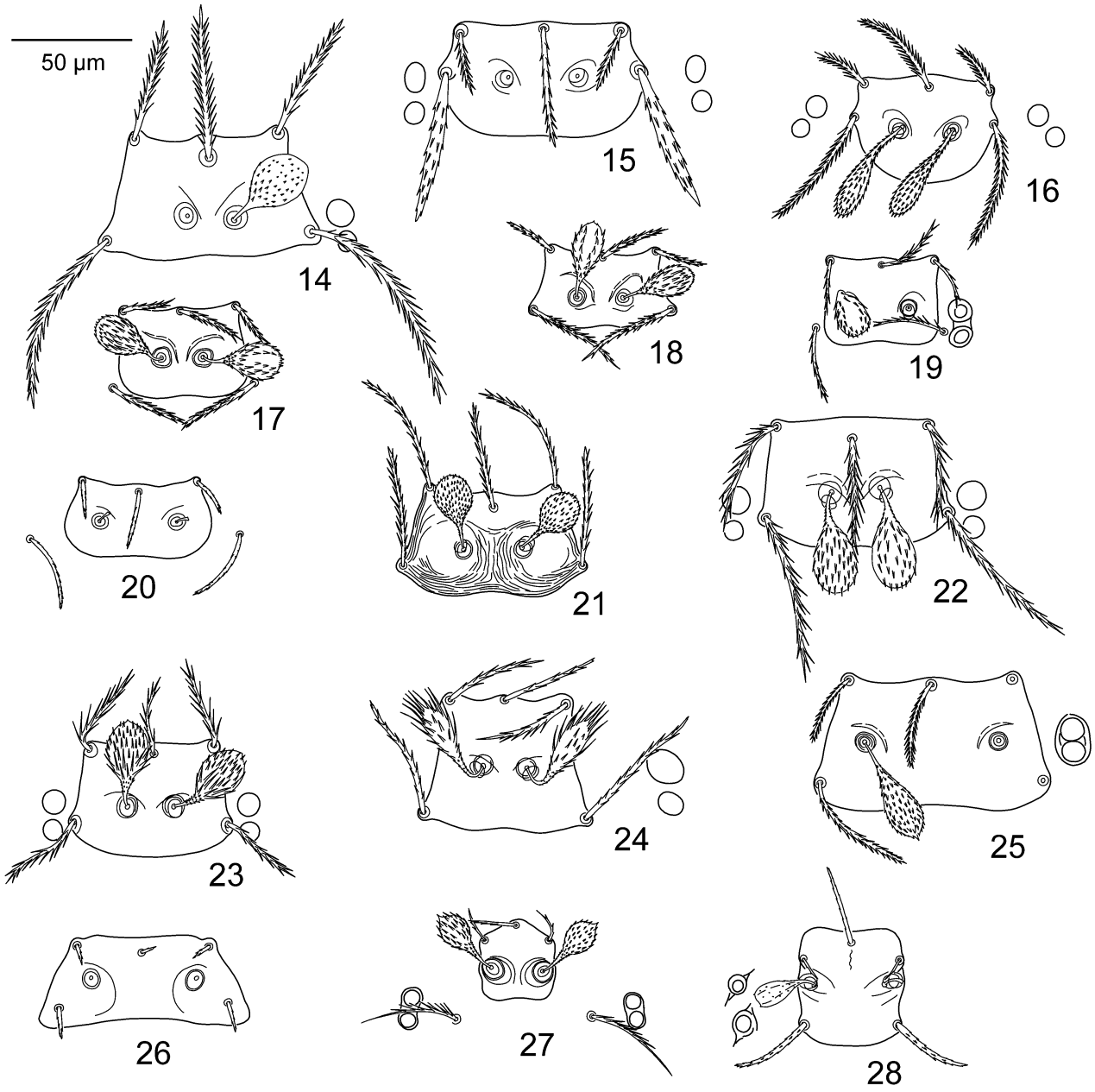
The classification approach proposed by Vercammen-Grandjean and Langston (1971) and accepted by Goff (1980c) and Domrow and Lester (1985), where the largest and most variable part of *Guntheria* was divided by two groups based on the presence or absence of palpal subterminala (ζ), looks artificial. This division is not supported by any other trait. At the same time, an independent reduction (and probably restoration) of this seta seems probable. The genus *Schoutedenichia* presents an example of a random distribution of the palpal subterminala among species (Vercammen-Grandjean 1958). Another example is the genera *Ericotrombidium* Vercammen-Grandjean, 1966 and *Hypotrombidium* Vercammen-Grandjean, 1966, which are indistinguishable by all traits, except for the presence of the palpal subterminala in the former genus (Vercammen-Grandjean and Langston 1976; Stekolnikov 2018). I suggest a return to the taxonomic decision introduced by Domrow (1960) for the classification of *Guntheria* that implied using the ratio of the lengths of AL and AM setae, together with the shape of trichobothria, as a stronger difference. In addition, I use the following details of the scutal shape: 1. A relative distance between the sensillary bases: close to each other — omorostigmal scutum (Figs. 4, 14); closer to the lateral scutal margins than to each other — telostigmal scutum (Figs. 15, 25, 26); 2. Shape of the posterior scutal margin: weakly projected (Figs. 1, 3, 9, 10, 14, 24); projected and bilobate (Figs. 5–7); greatly projected and rounded (Fig. 16); greatly projected, straight in center and deeply rounded at edges (Figs. 12, 13, 15).

The general appearance of the scutum, which combines the details of the scutal shape and sculpture, position and shape of sensilla, and relative lengths and shapes of the scutal setae, allows an immediate recognizing of the chigger mite genera. Characters of the gnathosoma and the leg setation

can usually only confirm the identification. The good examples are the large and variable genera *Leptotrombidium* Nagayo *et al*., 1916, *Microtrombicula* Ewing, 1950, and *Schoutedenichia*. At the same time, the scutal characters taken separately may expose a continuous variation that hampers their use in identification keys. Thus, one can observe a continuous gradation between the definitely omorostigmal and the definitely telostigmal scutum for a large set of different species. I, therefore, prefer to define a scutum as omorostigmal or telostigmal only in the most striking cases, such as the genus *Helenicula* (definitely omorostigmal scutum) and the subgenus *Schoutedenichia* (*Pentachia*) (definitely telostigmal scutum), and to use the vaguer definitions "not omorostigmal" and "not telostigmal" for other groups.



Figures 1–13. Scutum – 1. *Guntheria* (*Guntheria*) *kallipygos* (Gunther, 1939), after Domrow and Lester (1985); 2. *Guntheria* (*Domrowana*) *cassiope* (Womersley, 1952), after Domrow and Lester (1985); 3. *Guntheria* (*Domrowella*) *antipodiana* (Hirst, 1929), after Domrow and Lester (1985); 4. *Helenicula amicula* Nadchatram & Traub, 1971, after Nadchatram and Traub (1971); 5. *Derrickiella* (*Derrickiella*) *smithi* (Womersley, 1939), **comb. nov.**, after Domrow and Lester (1985); 6. *Derrickiella* (*Argentinacarus*) *expansus* (Goff & Gettinger, 1995), **comb. nov.**, after Goff and Gettinger (1995); 7. *Derrickiella* (*Argentinacarus*) *kolebinovae* Kudryashova, Neronov & Farhang-Azad, 1978, after Kudryashova *et al.* (1978); 8. *Cordiseta mexicana* (Hoffmann, 1954), after Hoffmann (1954); 9. *Susa* (*Susa*) *debilis* (Gater, 1932), after Audy and Nadchatram (1960); 10. *Susa* (*Ophthalmophila*) *scaevola* (Domrow, 1960), **comb. nov.**, after Domrow and Lester (1985); 11. *Kayella lacerta* (Brennan, 1948), after Brennan (1948); 12. *Phyllacarus* (*Platypacarus*) *wongabelensis* (Womersley, 1952), **comb. nov.**, after Domrow and Lester (1985). 13. *Phyllacarus* (*Platypacarus*) *ornithorhynchi* (Fain & Stekolnikov, 2004), **comb. nov.**, after Fain and Stekolnikov (2004).



Figures 14–28. Scutum – 14. *Guntheria* (*Domrowella*) *quatuor* Domrow, 1972, after Domrow and Lester (1985); 15. *Phyllacarus* (*Phyllacarus*) *pseudomys* (Womersley, 1952), **comb. nov.**, after Domrow and Lester (1985); 16. *Phyllacarus dasycerci* (Hirst, 1929), **comb. nov.**, after Domrow and Lester (1985); 17. *Pseudoschoengastia* (*Pseudoschoengastia*) *extrinseca* Brennan, 1960, after Brennan (1960); 18. *Pseudoschoengastia* (*Walchioides*) *inevicta* Brennan, 1960, after Brennan (1960); 19. *Vanidicus tricosus* Brennan & Jones, 1961, after Brennan (1973); 20. *Fauranius atecmartus* Brennan & Lukoschus, 1971, after Brennan and Lukoschus (1971); 21. *Ornithogastia paenitens* (Brennan, 1952) (syn.: *Neoschoengastia kohlsi* Brennan, 1951), after Brennan (1951); 22. *Colicus icomi* Brennan, 1970, after Brennan (1970b); 23. *Boshellia hirsuta* (Boshell & Kerr, 1942), after Brennan and Vercammen-Grandjean (1970); 24. *Perissopalla barticonycteris* Brennan, 1969, after Brennan (1969); 25. *Schoutedenichia* (*Pentachia*) *rouchoni* (Abonnenc, 1955), after Vercammen-Grandjean (1958); 26. *Polylopadium kramisi* Brenann & Jones, 1961, after Brennan and Jones (1961b); 27. *Kymocta zulia* Brennan & van Bronswijk, 1973, after Brennan and van Bronswijk (1973); 28. *Blix cabassoi* Brenann & Yunker, 1966, after Brenann and Yunker (1966).

The same concerns the difference between the sinuous and the bilobate posterior scutal margin. The term “bilobate” can be applied to a projected margin, whereas “sinuous” means that the margin

is situated almost in line with PL setae. I see no way to distinguish between these cases other than a comparison with the figures of most characteristic examples.

By the ratio of the lengths of AL and AM setae, the taxa considered here are divided by those having AM definitely shorter than ALs, which situated in the projected anterior corners of the scutum (*Guntheria* and *Helenicula*), and those with ALs shorter, about equal, or only slightly longer than AM (in the last case, all scutal setae are usually short, as compared with the size of the scutum). Only in *Pseudoschoengastia* Lipovsky, 1951 both variants are observed. The presence of greatly elongated ALs correlates also with the presence of globose sensilla, whereas the taxa having ALs shorter than AM possess sensilla of various shapes, from globose to fusiform.

The femora of all legs divided by two segments, basifemur and telofemur (and, consequently, fsp = 7.7.7), are considered a common trait of the subfamily Trombiculinae, contrary to Leeuwenhoekiinae and Gahrliepiinae (Kudryashova 1998; Stekolnikov 2018). At the same time, many species and genera of Trombiculinae were described as possessing undivided femora of legs III (fsp = 7.7.6), III and II (7.6.6), and rarely I–III (6.6.6) (Vercammen-Grandjean 1965a; Nadchatram and Dohany 1974; Brennan and Goff 1977). However, as Geest and Loomis (1968) showed for *Pseudoschoengastia* Lipovsky, 1951, the degree of the fusion of basi- and telofemur varied among different species. Thus, this character can be indistinct and should be applied with care in the taxonomy of Trombiculinae.

RESULTS

Genus *Guntheria* Womersley, 1939

Guntheria Womersley, 1939; Domrow 1971; Goff 1980c; Domrow and Lester 1985; Stekolnikov 2021
Guntherana Womersley & Heaslip, 1943 (*nomen novum*); Womersley 1944; Domrow 1960; Vercammen-Grandjean and Langston 1971

Type species: *Neoschoengastia kallipygos* Gunther, 1939, by monotypy and original designation.

Diagnosis

SIF = 5B(5BS)-N(B)-3-(1–3)111.0000; fsp = 7.7.7; fCx = 1.1.1; fSt = 2.2(4). Eyes 2 + 2; two humeral setae and usually by six setae in anterior post-humeral rows (fD = 2H-6-6-6-…), sometimes fD = 2H-8-6-6-…, other variants rare; two (rarely three) pairs of sternal setae; NDV usually 46–80 and only in four species > 100. Cheliceral blade with tricuspid cap; galeal seta nude (in *Domrowana* and *Domrowella* rarely branched); palpal claw three-pronged; fPp mostly B/B/NNN or B/B/NNB; palpal tarsus with five branched setae and basal tarsala (*ω*), in *Domrowella* also with subterminala (*ζ*). Scutum (Figs. 1–3 and 14) trapezoidal, not telostigmal, with slightly projected, sinuous or bilobate, rarely rounded posterior margin; setae AL and PL situated in more or less projected scutal corners; usually AL ≫ AM, rarely ALs and AM subequal; sensilla globose or subglobose (clavate in *G. alpina*); sensillary bases situated anterior, at level of PLs or slightly posterior. Legs seven-segmented; mostly 1–2 genualae on leg I (3 in six species); famulus (*ε*) proximal, distal or at level of tarsala (*ω*) on leg I and proximal to tarsala on leg II; other setation standard for Trombiculinae (but see remarks on variation below).

Subgenus *Guntheria* (*Guntheria*) Womersley, 1939

Diagnosis

Guntheria with two separate or fused pygosomal plates bearing 2–4 pairs of modified, branched or nude setae; NDV < 70; palpal tarsus 5B (without subterminala); fPp mostly B/B/NNN (B/B/NNB

in three species); sensilla globose; sensillary bases anterior to level of PLs; one genuala I.

Species included
Guntheria (*Guntheria*) *bisetosa* Goff, 1981d
Guntheria (*Guntheria*) *cowanensis* (Vercammen-Grandjean & Langston, 1971) (syn. of *G. kallipygos*: Domrow and Lester 1985)
Guntheria (*Guntheria*) *ditrichia* (Vercammen-Grandjean & Langston, 1971) (syn. of *G. kallipygos*: Domrow and Lester 1985)
Guntheria (*Guntheria*) *forbesi* Goff, 1983
Guntheria (*Guntheria*) *heterotrichia* (Vercammen-Grandjean & Langston, 1971) (syn. of *G. kallipygos*: Domrow and Lester 1985)
Guntheria (*Guntheria*) *hoxieae* Goff, 1978
Guntheria (*Guntheria*) *inflata* Goff, 1978
Guntheria (*Guntheria*) *kallipygos* (Gunther, 1939)
Syn.: *Neoschoengastia callipygea* Gunther, 1938 (*nomen nudum*)
Syn.: *Neoschoengastia bipygalis* Gunther, 1939
Guntheria (*Guntheria*) *margaretae* Goff, 1981e
Guntheria (*Guntheria*) *melomys* Goff, 1981e
Guntheria (*Guntheria*) *mirzai* Goff, 1979
Guntheria (*Guntheria*) *ornamentata* (Nadchatram & Traub, 1969)
Guntheria (*Guntheria*) *pannosa* (Domrow, 1960)
Guntheria (*Guntheria*) *parana* (Womersley, 1944)
Guntheria (*Guntheria*) *scrobiculata* Goff, 1979

Subgenus *Guntheria* (*Domrowana*) Vercammen-Grandjean & Langston, 1971

Guntherana (*Domrowana*) Vercammen-Grandjean & Langston, 1971
Guntheria (*Domrowana*) Goff, 1980c

Type species: *Neoschoengastia womersleyi* Gunther, 1940, by original designation.

Diagnosis
Guntheria without pygosomal plates; NDV = 48–152; palpal tarsus 5B (without subterminala); fPp variable; sensilla globose or subglobose (clavate in *G. alpina*); sensillary bases anterior, slightly posterior or at level of PLs; 1–3 genualae I.

Species included
Guntheria (*Domrowana*) *alpina* (Domrow, 1964)
Guntheria (*Domrowana*) *bosaviensis* Goff, 1981c
Guntheria (*Domrowana*) *buelowi* Goff, 1981b
Guntheria (*Domrowana*) *bushlandi* (Philip, 1947) (syn. of *G. innisfailensis*: Womersley 1952)
Guntheria (*Domrowana*) *cassiope* (Womersley, 1952)
Guntheria (*Domrowana*) *chawiensis* Stekolnikov, 2024
Guntheria (*Domrowana*) *chingae* (Goff, 1982b)
Guntheria (*Domrowana*) *daniae* Domrow, 1971
Guntheria (*Domrowana*) *domrowi* (Brennan, 1965)
Guntheria (*Domrowana*) *emphyla* (Domrow, 1960), **comb. nov.**
Guntheria (*Domrowana*) *empusa* (Domrow, 1984), **comb. nov.**
Guntheria (*Domrowana*) *failensis* (Vercammen-Grandjean & Langston, 1971) (syn. of *G. innisfailensis*: Domrow and Lester 1985)

Guntheria (*Domrowana*) *foliata* (Gunther, 1940)
Guntheria (*Domrowana*) *japonica* (Vercammen-Grandjean & Langston, 1971)
Guntheria (*Domrowana*) *joannae* Goff, 1981c
Guntheria (*Domrowana*) *innisfailensis* (Womersley & Heaslip, 1943)
Syn.: *Neoschoengastia melomys* Womersley & Heaslip, 1943
Guntheria (*Domrowana*) *kethleyi* Goff, 1979
Guntheria (*Domrowana*) *lappacea* (Womersley, 1952)
Guntheria (*Domrowana*) *lavaniensis* Goff, 1977b
Guntheria (*Domrowana*) *mccullochi* (Womersley, 1944)
Syn.: *Ascoschoengastia uromys* Womersley & Kohls, 1947
Guntheria (*Domrowana*) *mena* (Vercammen-Grandjean & Langston, 1971) (syn. of *G. lappacea*: Domrow and Lester 1985)
Guntheria (*Domrowana*) *mimema* (Domrow, 1984), **comb. nov.**
Guntheria (*Domrowana*) *minima* (Nadchatram & Traub, 1969)
Guntheria (*Domrowana*) *niobensis* Goff, 1977b
Guntheria (*Domrowana*) *parva* (Womersley, 1954)
Guntheria (*Domrowana*) *pectinata* Goff, 1981b
Guntheria (*Domrowana*) *philippensis* (Philip & Woodward, 1946)
Guntheria (*Domrowana*) *sabinae* Goff, 1981b
Guntheria (*Domrowana*) *salmleni* Domrow, 1984
Guntheria (*Domrowana*) *serrata* Goff, 1980a
Guntheria (*Domrowana*) *sphinx* Domrow, 1972
Guntheria (*Domrowana*) *squamosa* Goff, 1981a
Guntheria (*Domrowana*) *strandtmanni* (Nadchatram & Traub, 1969)
Guntheria (*Domrowana*) *wrenni* Goff, 1981d
Guntheria (*Domrowana*) *wauensis* Goff, 1980c
Guntheria (*Domrowana*) *womersleyi* (Gunther, 1940)

Remarks

ALs, PLs, and dorsal idiosomal setae are expanded (foliate or lanceolate) in *G. foliata*, *G. mccullochi*, and *G. squamosa*; expanded and serrate (covered by strong upstanding spikes, in addition or instead of usual barbs) in *G. chingae* and *G. serrata*; ALs and AM are subequal in *G. alpina*, *G. chingae*, *G. daniae*, and *G. salmleni*. Leg I subterminala (ζ) is absent in *G. parva*, *G. philippensis*, and *G. salmleni*; subterminala is forked in *G. sphinx*; companion seta (*z*) is branched in *G. sphinx* and *G. alpina*. Genualae II and III are absent in *G. sphinx* and *G. salmleni*; tibiala III is absent in *G. emphyla*, *G. empusa*, and *G. mimema*. *Guntheria salmleni* is unique by a very small size of scutum, presence of only 20 setae on tarsus I (vs. usual 22), and presence of a dorsal tooth on the cheliceral blade.

Domrow (1984) described *Schoutedenichia empusa* and *S. mimema* from Australia and transferred one more Australian species, *Guntherana emphyla*, to *Schoutedenichia*. These three species, however, differ from *Schoutedenichia* in the presence of more or less omorostigmal scutum vs. telostigmal. They also have five branched setae on palpal tarsus (5B) vs. four (4B or 4BS) in almost all *Schoutedenichia*. At the same time, the only three known *Schoutedenichia* species with 5B (members of the subgenus *Pentachia* Vercammen-Grandjean, 1958) possess in addition a cheliceral blade with a row of dorsal teeth, fusiform sensilla, and AM > AL, unlike the aforementioned three Australian species, which have a cheliceral blade with the tricuspid cap only, globose sensilla, and AL ≫ AM. Here I include them in *Guntheria* (*Domrowana*).

Subgenus *Guntheria* (*Domrowella*) Vercammen-Grandjean, 1960

Pseudoschoengastia (*Domrowella*) Vercammen-Grandjean, 1960a

Type species: *Schoengastia antipodianum* Hirst, 1929, by original designation.

Diagnosis

Guntheria without pygosomal plates; NDV = 74–106; palpal tarsus 5BS (with subterminala); fPp variable; sensilla globose or subglobose; sensillary bases anterior to level of PLs; two or three genualae I.

Species included

Guntheria (*Domrowella*) *antipodiana* (Hirst, 1929)
Guntheria (*Domrowella*) *echymipera* (Womersley & Kohls, 1947)
Guntheria (*Domrowella*) *platalea* Domrow, 1984
Guntheria (*Domrowella*) *podiana* (Vercammen-Grandjean & Langston, 1971) (syn. of *G. queenslandica*: Domrow and Lester 1985)
Guntheria (*Domrowella*) *quatuor* Domrow, 1972
Guntheria (*Domrowella*) *queenslandica* (Womersley, 1939)
Guntheria (*Domrowella*) *shareli* Domrow, 1984
Guntheria (*Domrowella*) *tessares* Domrow, 1971
Guntheria (*Domrowella*) *weedunnarti* (Goff, 1980b) (syn. of *G. quatuor*: Domrow and Lester 1985)

Remarks

Three pairs of sternal setae (fSt = 2.4) and subequal ALs and AM are present in *G. quatuor*, *G. tessares*, and *G. weedunnarti*.

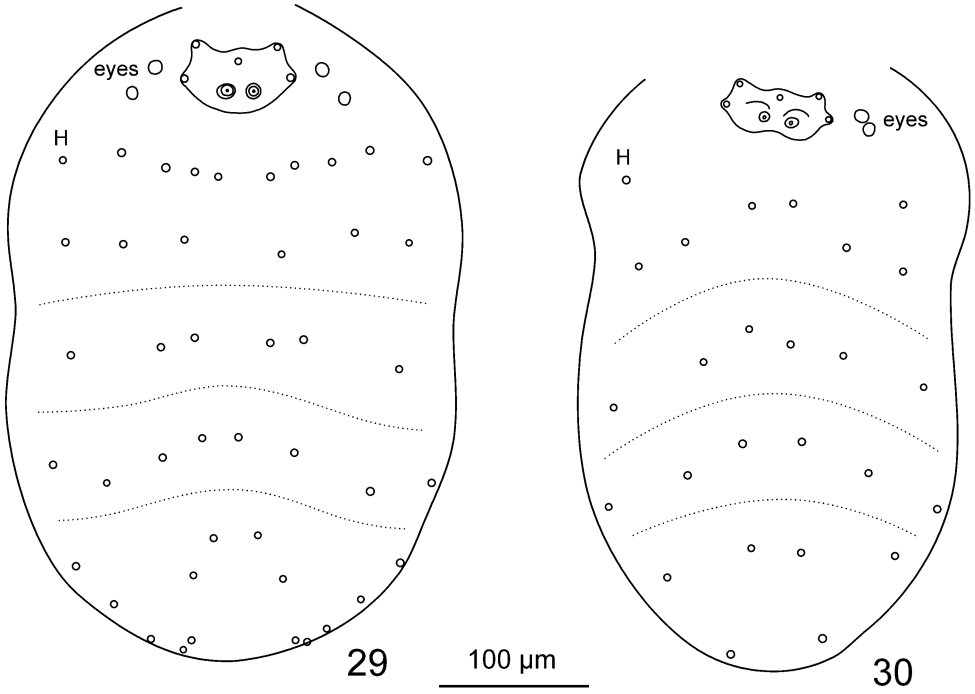
Genus *Helenicula* Audy, 1954

Euschoengastia (*Helenicula*) Audy, 1954
Helenicula: Womersley and Audy 1957; Vercammen-Grandjean 1960a, 1968; Nadchatram and Traub 1971
Globularoschoengastia Chen & Hsu, 1955

Type species: *Neoschoengastia lanius* Radford, 1946, by original designation.

Diagnosis

SIF = 4B(5B)-N(B)-3-1(2)111.0000; fsp = 7.7.7; fCx = 1.1(2).(1–6); fSt = 2.(2–6). Eyes 2 + 2 or 1 + 1, not in ocular plate; at least first row of dorsal idiosomal setae double (Fig. 29), 2–6 humeral setae in line with anterior sub-row; two, rarely three or four pairs of sternal setae; NDV from ca. 70 to 200. Cheliceral blade with tricuspid cap; galeal seta nude or branched; palpal claw three-pronged; fPp = B/B/BBB or B/B/BNB, rarely B/B/NNB; palpal tarsus with four or five branched setae and basal tarsala (*ω*). Scutum (Fig. 4) trapezoidal, with more or less projected, rounded, rarely angulate posterior margin; AL > AM, ALs situated in projected anterior corners of scutum; PLs either situated in extended posterior corners of scutum, or these corners rounded; sensilla globose; sensillary bases situated very close to each other (distance between them not exceeds diameter of base), anterior, posterior or at level of PLs. Legs seven-segmented; number of setae on coxa III frequently more than one (up to seven); one or two genualae on leg I; tarsala (*ω*) on leg I usually occupies terminal position — distal, slightly proximal or in line with subterminala (*ζ*) — only in three species definitely proximal; famulus (*ε*) proximal to tarsala (*ω*) on leg I and proximal or at level of tarsala on leg II; other setation standard for Trombiculinae.



Figures 29–30. Arrangement of dorsal idiosomal setae – 29. *Helenicula lanius* (Radford, 1946), after Nadchatram and Traub (1971); 30. *Guntheria* (*Domrowana*) *sphinx* Domrow, 1972, after Domrow (1972), with changes. Abbreviation: H, humeral setae.

Species included
Helenicula abaensis Wang, Zhai & Chen, 1984
Helenicula amicula Nadchatram & Traub, 1971
Helenicula aulacochaeta Sun, Wang & Wang, 1997 (in Li *et al.* 1997)
Helenicula baylissi (Asanuma, 1959)
Helenicula caucasica Muljarskaja, 1971
Helenicula comata (Womersley, 1952)
Helenicula consonensis Hadi & Carney, 1977
Helenicula dipodilli Taufflieb, 1958
Helenicula discalis Nadchatram & Traub, 1971
Helenicula edibakeri Nadchatram & Traub, 1971
Helenicula globulare (Walch, 1927)
Helenicula goodorziani Kudryashova, 1973 (in Kudryashova *et al.* 1973)
Helenicula hirtipectoralis Nadchatram & Traub, 1971
Helenicula hsui Zhao, 1990
Helenicula kohlsi (Philip & Woodward, 1946)
Syn.: *Helenicula hongkongensis* Womersley, 1957
Helenicula lanius (Radford, 1946b)
Syn.: *Neoschoengastia covelli* Radford, 1953
Helenicula litchia Liu, Wen & Hsu, 1965
Helenicula longipoda Nadchatram & Traub, 1971
Helenicula lukshumiae Nadchatram & Traub, 1971
Syn.: *Helenicula lanius caspica* Muljarskaja, 1971
Helenicula mattei Fernandes & Kulkarni, 2003
Helenicula miyagawai (Sasa, Kumada & Miura, 1951)

Helenicula mutabilis (Gater, 1932)
Helenicula myospalacis Huang, 1986
Helenicula nadchatrami Fernandes & Kulkarni, 2003
Helenicula naresuani Stekolnikov, 2016 (in Chaisiri *et al.* 2016)
Helenicula nepalensis Nadchatram & Traub, 1971
Helenicula oculicola (Womersley, 1952)
Helenicula olsufjevi (Schluger, 1955)
Helenicula pilosa (Abonnenc & Taufflieb, 1957a)
Helenicula pulchella Schluger & Amanguliev, 1975
Helenicula rattihaikonga (Hsu & Chen, 1957)
Helenicula rectangia Liu, Wen & Hsu, 1965
Helenicula rossolimae Kudryashova & Rybin, 1974
Helenicula saihsuensis Hsu & Chen, 1964
Helenicula scanloni Domrow & Nadchatram, 1964
Helenicula selvana Schluger, Grochovskaja, Ngu, Hoe & Tung, 1960
Helenicula signata (Womersley, 1952)
Helenicula simena (Hsu & Chen, 1957)
Helenicula sparsa (Schluger, 1955)
Helenicula thomasi (Jadin & Vercammen-Grandjean, 1954)
Helenicula ungkomari Nadchatram & Traub, 1971
Helenicula vercammengrandjeani (Abonnenc & Taufflieb, 1957b)
Helenicula wagamiya Nadchatram & Traub, 1971
Helenicula yunnanensis Wen & Xiang, 1984

Remarks

I transfer *Euschoengastia euryphylla* Brennan & Jones, 1961, *E. frondosa* Brennan & Jones, 1961, and *E. wenzeli* Brennan & Jones, 1961, which were previously included in *Helenicula,* to the genus *Euryphylla* Vercammen-Grandjean, 1967 (see Remarks under this genus below).

Vercammen-Grandjean (1965b) followed by Nielsen *et al.* (2021) included *Euschoengastia bigenuala* Farrell, 1956, *E. loomisi* Crossley & Lipovsky, 1954, and *Neoschoengastia strongi* Wharton & Hardcastle, 1946 in *Helenicula*. However, *E. bigenuala* has AM ≥ AL and simple rows of dorsal idiosomal setae (fD = 2H-6-6-6-6-4); *E. loomisi* possess three genualae I, AM ≥ AL, tarsala I situated far proximal to subterminala, and the distance between sensillary bases exceeds their diameter. The proper generic placement of these species is unclear. In general, the presence of *Helenicula* in the Americas is dubious. *Neoschoengastia strongi* differs from *Helenicula* in the presence of cuticular striations on the scutum, two humeral setae clearly separated from the 1st row of dorsal idiosomal setae, nude palpal genual seta (vs. always branched), mastitarsala on leg III, and tarsala I situated far proximal to subterminala. It can belong to *Neoschoengastia* or *Ornithogastia*. Nielsen *et al.* (2021) included *Euschoengastia cynomyicola* Crossley & Lipovsky, 1954 in *Helenicula* with a wrong reference to Vercammen-Grandjean (1965b). Actually, this author included *E. cynomyicola* in the *cordiremus* species group of *Euschoengastia* (not in the *loomisi* group of *Helenicula*).

Genus *Derrickiella* Audy & Domrow, 1957

Euschoengastia (*Derrickiella*) Audy & Domrow, 1957
Pseudoschoengastia (*Derrickiella*): Vercammen-Grandjean 1960a
Guntherana (*Derrickiella*): Domrow 1960; Vercammen-Grandjean and Langston 1971
Derrickiella: Kudryashova, Neronov and Farhang-Azad 1978

Guntheria (*Derrickiella*): Goff 1980c; Domrow and Lester 1985

Type species: *Neoschoengastia smithi* Womersley, 1939, by original designation.

Diagnosis

SIF = 5BS(5B)-N(B)-3(2)-(1–3)111.0000; fsp = 7.7.7; fCx = 1.1(2).1(2); fSt = 2.2(4). Eyes 2 + 2 (1 + 1 in *D. trichosuri*); 2–4 humeral setae, fD variable; two or three (in *D. vorax*) pairs of sternal setae; NDV from 66 to more than 300. Cheliceral blade with tricuspid cap; galeal seta nude or branched; palpal claw three-pronged (two-pronged in *D. newmani*); fPp variable, but palpal femoral and genual seta always branched; palpal tarsus with five branched setae and basal tarsala (*ω*), with or without subterminala (*ζ*). Scutum (Figs. 5–7) trapezoidal, not omorostigmal, with bilobate posterior margin; AM > AL (sometimes AL ≥ AM); sensilla clavate or fusiform; sensillary bases situated anterior to level of PLs (rarely at level or slightly posterior). Legs seven-segmented; mostly 2–3 genualae on leg I (1 in *D. expansus*); famulus (*ε*) proximal, at level or distal to tarsala (*ω*) on leg I and proximal to tarsala on leg II; other setation standard for Trombiculinae (but see remarks on variation below).

Subgenus *Derrickiella* (*Derrickiella*) Audy & Domrow, 1957

Diagnosis

Derrickiella with palpal tarsus 5BS (with subterminala).

Species included (all combinations are new)
Derrickiella (*Derrickiella*) *apteryxi* (Loomis & Goff, 1983)
Derrickiella (*Derrickiella*) *cairnsensis* (Womersley & Heaslip, 1943) (syn. of *D. coorongensis*: Domrow 1960)
Syn.: *Neoschoengastia cairnsensis* var. *gateri* Womersley & Heaslip, 1943
Derrickiella (*Derrickiella*) *coorongensis* (Hirst, 1929)
Derrickiella (*Derrickiella*) *popei* (Womersley, 1954) (syn. of *D. coorongensis*: Domrow 1960)
Derrickiella (*Derrickiella*) *heaslipi* (Womersley & Heaslip, 1943)
Derrickiella (*Derrickiella*) *lawrencei* (Womersley, 1952) (syn. of *D. smithi*: Domrow 1960)
Derrickiella (*Derrickiella*) *miles* (Domrow, 1978)
Derrickiella (*Derrickiella*) *newmani* (Womersley, 1952)
Syn.: *Schoengastia westraliense* Womersley, 1934
Derrickiella (*Derrickiella*) *peregrina* (Womersley, 1952)
Derrickiella (*Derrickiella*) *phascogale* (Womersley & Heaslip, 1943) (syn. of *D. smithi*: Domrow 1960)
Derrickiella (*Derrickiella*) *smithi* (Womersley, 1939)
Derrickiella (*Derrickiella*) *waterhousei* (Vercammen-Grandjean & Langston, 1971) (syn. of *D. coorongensis*: Domrow and Lester 1985)

Subgenus *Derrickiella* (*Argentinacarus*) Goff & Gettinger, 1995

Argentinacarus Goff & Gettinger, 1995; Nielsen *et al.* 2021

Type species: *Argentinacarus expansus* Goff & Gettinger, 1995, by monotypy and original designation.

Diagnosis

Derrickiella with palpal tarsus 5B (without subterminala).

Species included (all combinations are new, except *D. kolebinovae*)
Derrickiella (*Argentinacarus*) *agnewi* (Domrow, 1964)
Syn.: *Euschoengastia procana* Womersley, 1954
Derrickiella (*Argentinacarus*) *andromeda* (Womersley, 1954)
Derrickiella (*Argentinacarus*) *dogieli* (Muljarskaja, 1971)
Derrickiella (*Argentinacarus*) *dumosa* (Womersley, 1952)
Derrickiella (*Argentinacarus*) *expansus* (Goff & Gettinger, 1995)
Derrickiella (*Argentinacarus*) *kolebinovae* Kudryashova, Neronov & Farhang-Azad, 1978
Derrickiella (*Argentinacarus*) *kowanyama* (Domrow, 1978)
Derrickiella (*Argentinacarus*) *petrogale* (Womersley, 1934)
Derrickiella (*Argentinacarus*) *trichosuri* (Womersley, 1939)
Derrickiella (*Argentinacarus*) *vegrandis* (Domrow, 1974)
Derrickiella (*Argentinacarus*) *vorax* (Schluger & Amanguliev, 1975)
Syn.: *Derrickiella danieli* Kudryashova, Neronov & Farhang-Azad, 1978

Remarks

Three close species from Iran, Turkmenistan, and Azerbaijan — *D. dogieli*, *D. kolebinovae*, and *D. vorax* — differ from all other species of *Derrickiella* by fCx = 1.2.1 and fPp = B/B/BBB. They also share the presence of four humeral setae (vs. two) and tibialae (*φ*) inserted apically on tibia I with *D. expansus*. Eyes 1 + 1 in *D. trichosuri*; fCx = 1.1.2 in *D. agnewi*, *D. petrogale*, *D. vegrandis*, and *D. andromeda*; fSt = 2.4 in *D. vorax*. Tarsala (*ω*) occupies terminal position on leg I of *D. expansus*, slightly posterior to subterminala (*ζ*) and parasubterminala (*z*).

The legs of *D. expansus* were described as six-segmented (Goff and Gettinger 1995); however, in the new material of this species collected in Chile (Silva de la Fuente *et al.* 2023) the furrow between the basifemur and telofemur is clearly visible both on the dorsal and ventral side of all legs. According to the original description, the type specimens of *D. expansus* were deposited at the National Museum of Natural History (USNM, Washington, D.C., US), the Bernice Pauahi Bishop Museum (BPBM, Honolulu, Hawaii, US), and in the Sam Noble Oklahoma Museum of Natural History (OMNH, Norman, Oklahoma, US). However, none of the *D. expansus* type specimens were included in the catalogue of chigger types housed at the U.S. National Entomology collection, which currently includes chigger collections of USNM and BPBM (Bassini-Silva *et al.* 2021a). I have not received a reply to my request sent to the collection curator of OMNH about two years ago; my repeated attempts to make contact with the collection curator of the U.S. National Entomology collection were also unsuccessful. Thus, I had to be content with the examination of the aforementioned new material.

Genus *Cordiseta* Hoffmann, 1954

Walchiella (*Cordiseta*) Hoffmann, 1954
Helenicula (*Cordiseta*): Vercammen-Grandjean 1960a
Cordiseta: Geest and Loomis 1968; Loomis 1969; Brennan and Goff 1977

Type species: *Walchiella* (*Cordiseta*) *mexicana* Hoffmann 1954, by monotypy and original designation.

Diagnosis

SIF = 5B-N-3-1001.0000; fsp = 7.7.7; fCx = 1.1.1; fSt = 2.2. Eyes 1 + 1; two pairs of humeral setae; 1st posthumeral row with four marginal foliate (cordiform) setae and four central setiform setae; 2nd posthumeral row with two central long setiform setae and six foliate setae; next rows with foliate

setae; two pairs of sternal setae; two pairs of humeroventral setae between coxae II and III; NDV ca. 73. Cheliceral blade with tricuspid cap; galeal seta nude; fPp = B/N/NNB; palpal tarsus with five branched setae and basal tarsala (*ω*). Scutum (Fig. 8) nearly rectangular, not omorostigmal, with posterior margin slightly bilobate; PLs foliate; AM > AL; sensilla clavate; sensillary bases situated anterior to level of PLs. Legs seven-segmented; one genuala (*σ*) on leg I, genualae on leg II and III absent; famulus (*ε*) proximal to tarsala (*ω*) on leg I and slightly proximal to tarsala on leg II; pretarsala II (*ζ*) absent; other setation standard for Trombiculinae.

Species included

Cordiseta mexicana (Hoffmann, 1954)

Remarks

I do not support inclusion of the species *Pseudoschoengastia aberrans* Brennan & Jones, 1959 and *P. hoffmannae* Brennan, 1960 in *Cordiseta* proposed by Hoffmann (1990). See remarks on these species under *Kayella* and *Pseudoschoengastia*.

Cordiseta is similar to *Argentinacarus*, but differs in the presence of foliate PLs and dorsal idiosomal setae, presence of humeroventral setae, absence of genualae II and III (*σ*), and absence of pretarsala II (*ζ*).

Genus *Susa* Audy & Nadchatram, 1960

Susa Audy & Nadchatram, 1960; Vercammen-Grandjean 1960a; Kudryashova 1998; Stekolnikov 2018, 2021
Guntherana (*Susa*): Vercammen-Grandjean 1968
Cheladonta (*Susa*): Lakshana 1969; Nadchatram and Dohany 1974

Type species: *Neoschoengastia debilis* Gater, 1932, by original designation.

Diagnosis

SIF = 5B-B(N)-3-2(3)111.0000; fsp = 7.7.7; fCx = 1.1.1; fSt = 2.2(4). Eyes not in ocular plates, small, 1 + 1 or absent (2 + 2 in *Susa scaevola* **comb. nov.**); 2–6 humeral setae; two pairs of sternal setae (three in *S. chiropteraphilus*); NDV = 72–160. Cheliceral blade with tricuspid cap and one dorsal tooth (in *S. scaevola* **comb. nov.**); galeal seta branched or nude; palpal claw three-pronged; fPp variable, but femoral and genual setae usually nude (both nude in four species, only genual seta branched in two species, only femoral seta branched in *S. chiropteraphilus* and with one branch in *S. debilis*); palpal tarsus with five branched setae and basal tarsala (*ω*). Scutum (Figs. 9 and 10) trapezoidal, telostigmal, posterior scutal margin almost straight, lightly sinuous or concave; ALs and PLs situated in more or less projected scutal corners; AM > AL; sensilla broadly clavate or subglobose; sensillary bases far anterior to level of PLs. Legs seven-segmented; two genualae on leg I (three in *S. chiropteraphilus* and *S. scaevola* **comb. nov.**); famulus (*ε*) proximal to tarsala (*ω*) on leg I (distal in *S. chiropteraphilus*) and slightly proximal to tarsala on leg II; other setation standard for Trombiculinae.

Subgenus *Susa* (*Susa*) Audy & Nadchatram, 1960

Diagnosis

Susa with eyes 1 + 1 or absent; at least one seta on palpal femur, genu, and tibia branched; nude setae on palps tend to decrease in size; cheliceral blade with tricuspid cap; 2–6 humeral setae; NDV usually > 100 (ca. 84 in *S. debilis* and ca. 72 in *S. chiropteraphilus*).

Species included
Susa (*Susa*) *chiropteraphilus* (Brown, 1997)
Susa (*Susa*) *debilis* (Gater, 1932)
Susa (*Susa*) *labuanensis* (Womersley, 1952)
Susa (*Susa*) *macdonaldi* Audy & Nadchatram, 1960
Susa (*Susa*) *reidi* Audy & Nadchatram, 1960
Susa (*Susa*) *traubi* Nadchatram & Lakshana, 1965
Susa (*Susa*) *masawanensis* (Brown, 1998)
Susa (*Susa*) *palawanensis* (Brown & Goff, 1998)

Subgenus *Susa* (*Ophthalmophila*) Vercammen-Grandjean & Langston, 1971

Guntherana (*Ophthalmophila*) Vercammen-Grandjean & Langston, 1971

Type species: *Ascoschoengastia* (*Oculicola*) *scaevola* Domrow, 1960, by monotypy and original designation.

Diagnosis
Susa with eyes 2 + 2, small, not in ocular plate; all setae on palpal femur, genu, and tibia nude (fPp = N/N/NNN), nearly equal in length; cheliceral blade with tricuspid cap and pointed dorsal tooth; two humeral setae and by six setae in thirst three post-humeral rows (fD = 2H-6-6-6-4-2); NDV = 64.

Species included
Susa (*Ophthalmophila*) *scaevola* (Domrow, 1960), **comb. nov.**

Remarks
Kudryashova (1998) included *Schoutedenichia dogieli*, *Guntherana vorax*, and *Derrickiella kolebinovae* in *Susa*. However, these species are characterized by the presence of two pairs of normally developed eyes set in an ocular plate and both femoral and genual palpal setae branched vs. both nude or only one seta branched. Here I include them in *Derrickiella* (*Argentinacarus*). *Susa bauchani* Jacinavicius & Bassini-Silva, 2020 is here excluded from *Susa* based on the same morphological evidence and transferred to *Pseudoschoengastia*. *Cheladonta* (*Susa*) *prachongae* Lakshana, 1969 cannot be included in *Susa*, since this species has four setae on palpal tarsus (4B vs. 5B), and both femoral and genual palpal setae branched. Its taxonomic position is unclear. The systematic position of *Guntherana* (*Hexasternalaea*) *hexasternalaea* Vercammen-Grandjean, 1960b, which was previously included in *Susa* (Stekolnikov 2018), is discussed in a separate paper (Stekolnikov 2024).

Genus *Kayella* Vercammen-Grandjean, 1960

Helenicula (*Kayella*) Vercammen-Grandjean, 1960a
Cordiseta (*Kayella*): Vercammen-Grandjean 1968
Kayella: Nadchatram and Dohany 1974; Kudryashova 1998; Stekolnikov 2021; Nielsen *et al.* 2021; Stekolnikov and Matthee 2022

Type species: *Euschoengastia lacerta* Brennan, 1948, by original designation.

Diagnosis
SIF = 5B(4B)-N(B)-3-2(1)001.0000; fsp = 7.7.7; fCx = 1.1.1(2); fSt = 2.2. Eyes 2 + 2 or 1 + 1; two humeral setae; dorsal idiosomal setae arranged in simple, non-double rows (Fig. 30); two pairs

of sternal setae; NDV from ca. 46 to 94. Cheliceral blade with tricuspid cap; galeal seta nude (branched in *K. lacerta*); palpal claw three-pronged; fPp usually B/B/BBB (lateral tibial seta nude in *K. parumsetosa* and forked in *K. utahensis*; fPp = N/N/bNN(b) in *K. novita*); palpal tarsus with five or four branched setae and basal tarsala (*ω*). Scutum (Fig. 11) trapezoidal, telostigmal; posterior scutal margin almost straight, sinuous, or bilobate; peniscutum (with PLs extrascutal) is present in *K. novita*; AM ≥ AL; sensilla globose or clavate; sensillary bases anterior to level of PLs. Legs seven-segmented; pretarsalae I and II (*ζ*) present; subterminala (*ζ*) and nude parasubterminala (*z*) absent in *K. lacerta*; famulus (*ε*) proximal, distal or at level of tarsala (*ω*) on leg I and at level or proximal to tarsala on leg II; 2 tibialae I and II, 1 tibiala III (*φ*); 1–2 genualae (*σ*) on leg I, genualae II and III absent; microtibiala I and microgenuala I (*κ*) present.

Species included
Kayella bobaci (Hushcha, 1966)
Kayella bothmai Stekolnikov & Matthee, 2022
Kayella lacerta (Brennan, 1948)
Kayella novita (Audy & Womersley, 1957)
Kayella pannonica Kaluz, 2008
Kayella parumsetosa Schluger & Amanguliev, 1975
Kayella utahensis (Brennan & Beck, 1955)
Kayella xerothermobia (Willmann, 1942)

Remarks

Nielsen *et al.* (2021) listed 12 species of *Kayella*. Later Stekolnikov and Matthee (2022) described one more species. Here, I transfer two species previously included in *Kayella* to *Schoutedenichia* and thus propose the new combinations *Schoutedenichia masta* (Traub & Sundermeyer, 1950), **comb. nov.** (originally described in *Ascoschoengastia*) and *Schoutedenichia nakayamai* (Suzuki, 1976), **comb. nov.** [originally described in *Cordiseta* (*Kayella*)]. Both species differ from *Kayella* in the absence of tibiala III and presence of double rows of dorsal setae (at least 1st row is double). They are similar to *Schoutedenichia turkmenica* (Schluger & Amanguliev, 1975) and *S. lucida* (Schluger & Sosnina, 1956) by the extrascutal PLs (peniscutum), palpal tarsus 4B, two or three setae on coxa III, and the absence of genuala III (tibiala III is absent in all *Schoutedenichia*).

This group of four species (*S. lucida, S. masta* **comb. nov.**, *S. nakayamai* **comb. nov.**, and *S. turkmenica*) differs from other *Schoutedenichia*, including those with peniscutum, by the absence of a concavity of the posterior scutal margin. This group is also characterized by the position of tibialae I at one level close to the end of the segment (not examined in *S. lucida*). Probably, after a revision of *Schoutedenichia*, they will constitute a separate genus or a subgenus.

I do not support the inclusion of *Pseudoschoengastia aberrans* Brennan & Jones, 1959, *P. hoffmannae* Brennan, 1960, and *P. hypopsia* Brennan & Jones, 1959 in *Kayella* proposed by Vercammen-Grandjean (1965b) and accepted by Nielsen *et al.* (2021). All three species have ventrohumeral setae and *P. aberrans* and *P. hoffmannae* have fPp = 7.6.6 or 7.7.6 (undivided femur of legs II and/or III). Thus, they fit the diagnosis of *Pseudoschoengastia*. I should note that the reduction of genualae II and III could arise independently; for example, it occurs rarely in *Guntheria* and *Euryphylla*.

In the original description of *K. utahensis* (Brennan and Beck 1955), the figure captions are wrong. In fact, drawings of this species are present in Figure 1E–H, but their captions were placed under Figure 4.

Genus *Phyllacarus* Vercammen-Grandjean, 1967, stat. nov.

Derrickiella (*Phyllacarus*) Vercammen-Grandjean, 1967

Guntheria (*Phyllacarus*): Domrow and Lester 1985
Zyzomyacarus Goff, 1979

Type species: *Schoengastia* (*Ascoschoengastia*) *pseudomys* Womersley, 1952, by monotypy and original designation.

Diagnosis

SIF = 5B(5BS)-B(N)-3-(1–3)11(0)1(0).0000; fsp = 7.7.7; fCx = 1.1.1; fSt = 2.(2–16). Eyes 2 + 2 (1 + 1 in *P. davidleei* and *P. megale*, absent in *P. ornithorhynchi*); 2–4 humeral setae; fD variable; two or more pairs of sternal setae; NDV from 50 to more than 300. Cheliceral blade with tricuspid cap; galeal seta branched or nude; palpal claw three-pronged; fPp variable; palpal tarsus with five branched setae, basal tarsala (*ω*), and rarely with subterminala (*ζ*). Scutum not omorostigmal, with greatly projected posterior margin, almost straight in center and deeply rounded at edges (Figs. 12, 13, and 15) or evenly rounded (Fig. 16); AM > AL; ALs and PLs frequently situated close to each other; sensilla clavate or fusiform, sometimes narrow fusiform, rarely subglobose; sensillary bases posterior to, at level or anterior to PLs. Legs seven-segmented; 2–3 genualae on leg I (1 in *P. ornithorhynchi*); famulus (*ε*) distal, at level or proximal of tarsala (*ω*) on leg I and proximal to tarsala on leg II; other setation standard for Trombiculinae (but see remarks on variation below).

Subgenus *Phyllacarus* (*Phyllacarus*) Vercammen-Grandjean, 1967

Diagnosis

Phyllacarus without palpal subterminala (palpal tarsus 5B); galeal seta branched in 16 species and nude in seven; fPp variable, but palpal femoral and genual setae always branched; sensillary bases posterior to or at level of PLs (slightly anterior in *P. raui* and *P. megale*); famulus (*ε*) usually distal or at level of tarsala (*ω*) on leg I (proximal in four species).

Species included (all combinations are new)
Phyllacarus (*Phyllacarus*) *arguri* (Goff, 1979)
Phyllacarus (*Phyllacarus*) *bamaga* (Domrow, 1978)
Phyllacarus (*Phyllacarus*) *crinita* (Womersley, 1952) (syn. of *P. perameles*: Domrow 1960)
Phyllacarus (*Phyllacarus*) *dasycerci* (Hirst, 1929)
Phyllacarus (*Phyllacarus*) *davidleei* (Vercammen-Grandjean & Langston, 1971) (syn. of *P. shieldsi*: Domrow and Lester 1985)
Phyllacarus (*Phyllacarus*) *derricki* (Womersley, 1939)
Phyllacarus (*Phyllacarus*) *falx* (Domrow, 1971)
Phyllacarus (*Phyllacarus*) *heterosetosa* (Goff, 1982b)
Phyllacarus (*Phyllacarus*) *hirsti* (Womersley & Heaslip, 1943) (syn. of *P. shieldsi*: Domrow 1960)
Phyllacarus (*Phyllacarus*) *mackerrasae* (Womersley, 1952)
Phyllacarus (*Phyllacarus*) *megale* (Domrow, 1972)
Phyllacarus (*Phyllacarus*) *mohri* (Womersley, 1952) (syn. of *P. perameles*: Domrow 1960)
Syn.: *Neoschoengastia isoodon* Derrick, Smith, Brown & Freeman, 1939
Phyllacarus (*Phyllacarus*) *napierensis* (Goff, 1979)
Phyllacarus (*Phyllacarus*) *omega* (Goff, 1977a)
Phyllacarus (*Phyllacarus*) *perameles* (Womersley, 1939)
Phyllacarus (*Phyllacarus*) *pertinax* (Domrow, 1972)
Phyllacarus (*Phyllacarus*) *pseudomys* (Womersley, 1952)
Phyllacarus (*Phyllacarus*) *raui* (Womersley, 1952)
Phyllacarus (*Phyllacarus*) *rex* (Domrow, 1960) (syn. of *P. derricki*: Domrow and Lester 1985)
Phyllacarus (*Phyllacarus*) *shieldsi* (Gunther, 1941) (syn. of *D. trichosuri*: Womersley 1952)

Phyllacarus (*Phyllacarus*) *similis* (Womersley & Heaslip, 1943) (syn. of *P. derricki*: Domrow and Lester 1985)
Phyllacarus (*Phyllacarus*) *syllogisma* (Goff, 1982b)
Phyllacarus (*Phyllacarus*) *taylorae* (Domrow, 1962)

Subgenus *Phyllacarus* (*Platypacarus*) subgen. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:455B3408-3F09-4414-864B-8CDF7398C4CA

Type species: *Guntheria* (*Phyllacarus*) *ornithorhynchi* Fain & Stekolnikov, 2004, designated here.

Diagnosis

Phyllacarus with palpal subterminala (palpal tarsus 5BS) in three species and without palpal subterminala (palpal tarsus 5B) in *P. ornithorhynchi*; galeal seta nude; fPp variable, but all tibial setae nude in three of four species, palpal genual seta nude in one species and with one branch in one species; scutum (Figs. 12, 13) almost quadrate, telostigmal; PLs not situated in projected corners of scutum; sensillary bases far anterior to level of PLs; famulus (*ε*) proximal to tarsala (*ω*) on leg I.

Etymology

The name of the new subgenus is combined from the word *platypus*, the common name of *Ornithorhynchus anatinus* (Shaw), which is the host of the type species, *P. ornithorhynchi*, and the new Latin word *acarus* meaning “mite”.

Species included (all combinations are new)
Phyllacarus (*Platypacarus*) *athertoni* (Vercammen-Grandjean & Langston, 1971) (syn. of *P. wongabelensis*: Domrow and Lester 1985)
Phyllacarus (*Platypacarus*) *ornithorhynchi* (Fain & Stekolnikov, 2004)
Phyllacarus (*Platypacarus*) *petulans* (Domrow, 1960)
Phyllacarus (*Platypacarus*) *wongabelensis* (Womersley, 1952)

Remarks

In *P. mackerrasae* parasubterminala (*z*) branched, tarsala I (*ω*) occupies terminal position, in line with subterminala (*ζ*). ALs, PLs, and dorsal idiosomal setae are expanded and lanceolate in *P. pseudomys*, expanded and serrate in *P. falx*, *P. mackerrasae*, and *P. taylorae*. *Phyllacarus ornithorhynchi* differs from all other species of the genus by the absence of eyes, palpal subterminala (*ζ*), pretarsala II (*ζ*), tibiala and genuala III, presence of only one genuala I (vs. 2–3), terminal position of tarsala (*ω*) on leg I (slightly posterior to subterminala and parasubterminala). *Phyllacarus petulans* is unique in its greatly shortened scutal setae (14–19 µm).

Genus *Pseudoschoengastia* Lipovsky, 1951

Pseudoschoengastia Lipovsky, 1951; Vercammen-Grandjean 1960a; Brennan 1960; Geest and Loomis 1968

Type species: *Pseudoschoengastia hungerfordi* Lipovsky, 1951, by original designation.

Diagnosis

SIF = 5B-N(B)-3-(1–3)111.0000; fsp = 7.7.7, 7.7.6, 7.6.6; fCx = 1.1.1; fSt = 2.2(4). Eyes 2 + 2 or 1 + 1; 4–6 humeral setae, anterior post-humeral rows (at least 1st) double (Fig. 29); two (rarely three) pairs of sternal setae; 2–3 pairs of humeroventral setae between coxae II and III (1 pair in *P. bauchani* **comb. nov.**); NDV = 78–166. Cheliceral blade with tricuspid cap and frequently with one

dorsal tooth (one dorsal and one ventral tooth described in some species); galeal seta nude or branched; fPp variable; palpal tarsus with five branched setae and basal tarsala (*ω*). Scutum (Figs. 17 and 18) not omorostigmal, with posterior margin of variable shape, but usually concave; PLs frequently extrascutal (peniscutum); ratio of ALs and AM lengths variable, from AL ≫ AM to AM > AL; in first case, ALs situated in projected scutal corners; sensilla from globose to fusiform; sensillary bases situated anterior to level of PLs. Leg I seven-segmented; in legs II and III basifemur and telofemur can be fused to different extent; 1–3 genualae on leg I; famulus (*ε*) proximal, distal or at level of tarsala (*ω*) on leg I and proximal or at level of tarsala on leg II; other setation standard for Trombiculinae (but see remarks on variation below).

Subgenus *Pseudoschoengastia* (*Pseudoschoengastia*) Lipovsky, 1951

Diagnosis

Pseudoschoengastia with PLs extrascutal (peniscutum).

Species included

Pseudoschoengastia (*Pseudoschoengastia*) *abditiva* Brennan, 1960
Pseudoschoengastia (*Pseudoschoengastia*) *aberrans* Brennan & Jones, 1959
Pseudoschoengastia (*Pseudoschoengastia*) *aeci* Brennan, 1965
Pseudoschoengastia (*Pseudoschoengastia*) *anomala* (Hoffmann, 1951)
Pseudoschoengastia (*Pseudoschoengastia*) *apista* Brennan & Yunker, 1966
Pseudoschoengastia (*Pseudoschoengastia*) *audyi* Brennan & Jones, 1959
Pseudoschoengastia (*Pseudoschoengastia*) *bisetosa* Loomis, 1976
Pseudoschoengastia (*Pseudoschoengastia*) *brennani* Hoffmann, 1960
Pseudoschoengastia (*Pseudoschoengastia*) *bulbifera* Brennan, 1960
Pseudoschoengastia (*Pseudoschoengastia*) *dasypi* Brennan & Yunker, 1966
Pseudoschoengastia (*Pseudoschoengastia*) *diazi* (Hoffmann, 1948)
Pseudoschoengastia (*Pseudoschoengastia*) *disparunguis* Goff, 1982a
Pseudoschoengastia (*Pseudoschoengastia*) *extrinseca* Brennan, 1960
Pseudoschoengastia (*Pseudoschoengastia*) *farneri* Lipovsky, 1951
Pseudoschoengastia (*Pseudoschoengastia*) *finitima* Brennan & Yunker, 1966
Pseudoschoengastia (*Pseudoschoengastia*) *guatemalensis* Brennan, 1952
Pseudoschoengastia (*Pseudoschoengastia*) *hoguei* Geest & Loomis, 1968
Pseudoschoengastia (*Pseudoschoengastia*) *hooperi* Geest & Loomis, 1968
Pseudoschoengastia (*Pseudoschoengastia*) *hungerfordi* Lipovsky, 1951
Pseudoschoengastia (*Pseudoschoengastia*) *hypopsia* Brennan & Jones, 1959
Pseudoschoengastia (*Pseudoschoengastia*) *intermedia* Geest & Loomis, 1968
Pseudoschoengastia (*Pseudoschoengastia*) *matudai* Suzuki & Kamiya, 1982
Pseudoschoengastia (*Pseudoschoengastia*) *mexicoensis* Suzuki & Kamiya, 1982
Pseudoschoengastia (*Pseudoschoengastia*) *montana* Geest & Loomis, 1968
Pseudoschoengastia (*Pseudoschoengastia*) *occidentalis* Brennan, 1952
Pseudoschoengastia (*Pseudoschoengastia*) *pedregalensis* (Hoffmann, 1951)
Pseudoschoengastia (*Pseudoschoengastia*) *peromysci* Geest & Loomis, 1968
Pseudoschoengastia (*Pseudoschoengastia*) *rheomys* Geest & Loomis, 1968
Pseudoschoengastia (*Pseudoschoengastia*) *scitula* Brennan & Jones, 1959
Pseudoschoengastia (*Pseudoschoengastia*) *smithi* Loomis, 1976
Pseudoschoengastia (*Pseudoschoengastia*) *zona* Brennan, 1960

Subgenus *Pseudoschoengastia* (*Walchioides*) Vercammen-Grandjean, 1960

Susa (*Walchioides*) Vercammen-Grandjean, 1960a

Pseudoschoengastia (*Walchioides*): Geest and Loomis 1968
Walchioides: Brennan and Goff 1977; Bassini-Silva *et al.* 2021b; Nielsen *et al.* 2021
Guntherana (*Pseudosusa*) Vercammen-Grandjean, 1960a, **syn. nov.**
Pseudosusa: Brennan and Goff 1977

Type species: *Walchia gouldi* Hoffmann 1954, by original designation.

Diagnosis

Pseudoschoengastia with PLs on scutum.

Species included

Pseudoschoengastia (*Walchioides*) *bauchani* (Jacinavicius & Bassini-Silva, 2020, in Jacinavicius *et al.* 2020), **comb. nov.**
Pseudoschoengastia (*Walchioides*) *costaricensis* Geest & Loomis, 1968
Pseudoschoengastia (*Walchioides*) *finleyi* (Crossley, 1955)
Pseudoschoengastia (*Walchioides*) *gouldi* (Hoffmann, 1954)
Pseudoschoengastia (*Walchioides*) *guanacastensis* Geest & Loomis, 1968
Pseudoschoengastia (*Walchioides*) *hoffmannae* Brennan, 1960
Pseudoschoengastia (*Walchioides*) *inevicta* Brennan, 1960
Pseudoschoengastia (*Walchioides*) *intrinseca* Brennan, 1960
Pseudoschoengastia (*Walchioides*) *mermeriza* Brennan & Yunker, 1966
Pseudoschoengastia (*Walchioides*) *verdensis* Geest & Loomis, 1968
Pseudoschoengastia (*Walchioides*) *whartoni* Brennan, 1960

Remarks

I found no evidence that any species was ever included in *Pseudosusa* in addition to its type, *Euschoengastia finleyi*. Vercammen-Grandjean (1965b), followed by Nielsen *et al.* (2021), included this species in *Pseudoschoengastia*. The reduction of subterminala (ζ) and parasubterminala (*z*) on leg I, which is a characteristic of this species, undoubtedly does not support its separation as a taxon of the generic rank. Since nobody yet performed a formal synonymization of *Pseudosusa*, I designate it above as a new synonym. The name *Pseudosusa* was created in the same publication as *Walchioides* (Vercammen-Grandjean 1960a). Both these taxa were of the same rank (subgenus). Thus, none of them can be treated as having a precedence objectively. However, *Walchioides* is in prevailing usage. Therefore, I hereby fix the precedence of *Walchioides* over *Pseudosusa* on the base of the Principle of the First Reviser (ICZN Code, Art. 24.2.1).

Euschoengastia eadsi Loomis & Crossley, 1963, *E. gagarini* Brennan, 1962, *E. lipoglena* Brennan & Jones, 1960, and *Schoengastia trouessarti* Oudemans, 1910 were included in *Pseudoschoengastia* by Vercammen-Grandjean (1965b), followed by Nielsen *et al.* (2021). However, none of these species fits the diagnosis of this genus: *E. eadsi* has four setae on the palpal tarsus (Loomis and Crossley 1963), *E. gagarini* has six (Brennan 1962), and the setation of palpal tarsus in *S. trouessarti* is probably other than 5B (Oudemans 1912; Fuller 1952). These three species also have no humeroventral setae and the shape of their scuta are different from those of *Pseudoschoengastia*. *Euschoengastia lipoglena* has two humeral setae, simple post-humeral rows and has no humeroventral setae. I do not discuss a possible generic placement of these species in the present paper.

Pseudoschoengastia petrolinensis Jacinavicius, Bassini-Silva & Barros-Battesti, 2019, according to the original description, has two humeral setae, simple rows of dorsal idiosomal setae (2H-8-6-6-6-…), and has no humeroventral setae. Therefore, I here transfer it to the genus *Vanidicus* Brennan & Jones, 1961.

Variation within the genus, as follows: AM is absent in *P*. (*W*.) *gouldi*. Genualae II and III (*σ*) are absent in *P*. (*P*.) *aberrans*, *P*. (*P*.) *hypopsia*, *P*. (*P*.) *mexicoensis*, *P*. (*W*.) *hoffmannae*, and *P*. (*W*.) *verdensis*. Ventrofemorala (short ventral nude seta on the fused femur III, which was recorded in many Gahrliepiinae) is present in *P*. (*P*.) *finitima* and *P*. (*P*.) *hooperi*, according to the figures in the original descriptions (Brennan and Yunker 1966, Fig. 26; Geest and Loomis 1968, Fig. 11).

Genus *Vanidicus* Brennan & Jones, 1961

Vanidicus Brennan & Jones, 1961b; Brennan 1973; Brennan and Goff 1977; Nielsen *et al.* 2021

Type species: *Vanidicus tricosus* Brennan & Jones, 1961, by monotypy and original designation.

Diagnosis

SIF = 5B-N(B)-3-3111.0000; fsp = 7.6.6 or 7.7.7; fCx = 1.1.1; fSt = 2.2. Eyes 2 + 2; two humeral setae, anterior post-humeral rows simple, with six or eight setae; two pairs of sternal setae; NDV = 48–91. Cheliceral blade with tricuspid cap; galeal seta nude or branched (in *V. petrolinensis* **comb. nov.**); fPp = B/B/BBB in *V. petrolinensis* **comb. nov.** and B/N/NNN in other three species; palpal tarsus with five branched setae and basal tarsala (*ω*). Scutum (Fig. 19) with extrascutal PLs (peniscutum), with posterior margin almost straight or slightly concave; AL ≥ AM; sensilla globose or clavate. Leg I seven-segmented; in legs II and III basifemur and telofemur can be fused or separate (in *V. petrolinensis* **comb. nov.**); 3 genualae on leg I; famulus (*ε*) proximal or distal (in *V. tricosus*) to tarsala (*ω*) on leg I and proximal or at level of tarsala on leg II; other setation standard for Trombiculinae.

Species included

Vanidicus chalepis Brennan, 1973
Vanidicus jojosti Brennan, 1973
Vanidicus petrolinensis (Jacinavicius, Bassini-Silva & Barros-Battesti, 2019, in Jacinavicius *et al.* 2019), **comb. nov.**
Vanidicus tricosus Brennan & Jones, 1961b

Remarks

Tarsala (*ω*) occupies terminal position on leg I, tibialae (*φ*) I are situated at one level, with microtibiala (*κ*) inserted between them, and tibialae II are situated at one level in *V. petrolinensis*.

Genus *Fauranius* Brennan & Lukoschus, 1971

Fauranius Brennan & Lukoschus, 1971; Brennan and Goff 1977

Type species: *Fauranius atecmartus* Brennan & Lukoschus, 1971, by original designation.

Diagnosis

SIF = 5B-N-3-2001.0000; fsp = 6.6.6; fCx = 1.1.1; fSt = 2.2. Eyes 2 + 2 or absent; two humeral setae, anterior three post-humeral rows with six setae; two pairs of sternal setae; NDV ca. 64. Cheliceral blade with tricuspid cap; galeal seta nude; fPp = B/B/BNB; palpal tarsus with five branched setae and basal tarsala (*ω*). Scutum (Fig. 20) wide, telostigmal, with slightly concave posterior margin; PLs extrascutal (peniscutum); AM > AL; shape of sensilla unknown. Legs six-segmented (with undivided femur); two genualae (*σ*) on leg I, genualae II and III absent; famulus (*ε*) proximal to level of tarsala (*ω*) on leg I and at level of tarsala on leg II; other setation standard for Trombiculinae.

Species included

Fauranius atecmartus Brennan & Lukoschus, 1971
Fauranius myoproctae (Fauran, 1960)

Remarks

The genus is similar to *Pseudoschoengastia* and *Vanidicus* and differs from these genera in fsp = 6.6.6 vs. 7.7.7, 7.7.6 or 7.6.6. Examination of additional materials is required to establish its taxonomic position more definitely.

Genus *Ornithogastia* Vercammen-Grandjean, 1960

Pseudoschoengastia (*Ornithogastia*) Vercammen-Grandjean, 1960a
Guntherana (*Ornithogastia*): Vercammen-Grandjean *et al.* 1970; Vercammen-Grandjean and Langston 1971
Ornithogastia: Goff 1980c; Hushcha 1982; Kudryashova 1998; Stekolnikov 2018

Type species: *Neoschoengastia paenitens* Brennan, 1952, by original designation.

Diagnosis

SIF = 5B-N-3-2111.3(4)2(3)00; fsp = 7.7.7; fCx = 1.1.1; fSt = 2.2(4).2. Eyes 2 + 2, large; two humeral setae, first post-humeral row usually double (Fig. 29) or triple; 3–4 pairs of sternal setae; NDV = 77–175. Cheliceral blade with tricuspid cap; galeal seta nude; palpal claw three-pronged; fPp = B/B/NNB; palpal tarsus with five branched setae and basal tarsala (ω). Scutum (Fig. 21) trapezoidal, with cuticular striations (epiostracal pleats) around sensillary bases, with bilobate posterior margin; AL > PL > AM (PL > AL in *O. ornata*); sensilla clavate; sensillary bases situated far anterior to level of PLs. Legs seven-segmented; two genualae on leg I; famulus (ε) distal to tarsala (ω) on leg I and slightly proximal to tarsala on leg II; 3–4 dorsal setae on tibia III and 2–3 on tarsus III extended into long thin whip distally, but branched basally (not true mastisetae); other setation standard for Trombiculinae.

Species included

Ornithogastia ariadnae Hushcha, 1982
Ornithogastia barskauniensis Kharadov, 1996
Ornithogastia erythrinae Yang, 1992
Ornithogastia merops (Vercammen-Grandjean, Rohde & Mesghali, 1970)
Ornithogastia ningxiaensis Li, Wang & Chattopadhyay, 1997 (in Li *et al.* 1997)
Ornithogastia oenanthe (Vercammen-Grandjean, Rohde & Mesghali, 1970)
Ornithogastia ornata (Schluger, 1961)
Ornithogastia paenitens (Brennan, 1952)
Syn.: *Neoschoengastia kohlsi* Brennan, 1951 (rejected as a junior homonym of *Neoschoengastia kohlsi* Philip & Woodward, 1946)
Ornithogastia pastoriana (Taufflieb, 1958)
Ornithogastia ripariae (Schluger & Zhmajeva, 1961)
Ornithogastia riversi (Wharton & Hardcastle, 1946)
Ornithogastia wangi (Chen & Hsu, 1955), **comb. nov.**

Remarks

Neoschoengastia wangi Chen & Hsu, 1955 was placed in *G.* (*Guntherana*) by Vercammen-Grandjean (1968) followed by Nielsen *et al.* (2021), but the original description of this species (Chen and Hsu 1955) fits the diagnosis of *Ornithogastia*.

Genus *Colicus* Brennan, 1970

Colicus Brennan, 1970b; Brennan and Goff 1977; Goff and Brennan 1978
Type species: *Colicus icomi* Brennan, 1970, by original designation.

Diagnosis

SIF = 5BS-N(b)-3-3(2)111.0000; fsp = 7.7.7; fCx = 1.1.1; fSt = 2.2 or 2.2.2. Eyes 2 + 2; two humeral setae; two or three pairs of sternal setae; NDV from ca. 72 to ca. 230. Cheliceral blade with tricuspid cap; galeal seta nude; palpal claw three-pronged; fPp variable, but most frequently B/B/BBB or B/B/NBB; palpal tarsus with five branched setae, basal tarsala (ω) and subterminala (ζ). Scutum (Fig. 22) slightly wider than long, rectangular or trapezoidal, frequently telostigmal, posterior scutal margin almost straight or lightly sinuous; AM > AL, rarely AL > AM; sensilla clavate or subglobose; sensillary bases anterior to level of PLs. Legs seven-segmented; 2–3 genualae on leg I; famulus (ε) proximal or at level of tarsala (ω) on leg I (rarely distal) and proximal to tarsala on leg II; other setation standard for Trombiculinae.

Species included
Colicus barrosbattestiae Bassini-Silva, Welbourn & Ochoa, 2021c
Colicus brasiliensis Goff, Whitaker & Dietz, 1983
Colicus colombiae (Boshell & Kerr, 1942)
Colicus dasyproctae (Ewing, 1937)
Syn.: *Colicus downsi* (Brennan & Jones, 1960)
Colicus dyscrita (Brennan & Jones, 1961b)
Colicus exhumatus Brennan, 1970b
Colicus icomi Brennan, 1970b
Colicus inexcitus Goff & Brennan, 1978
Colicus johnsoni (Yunker & Brennan, 1964)
Colicus kunsi (Yunker & Brennan, 1964)
Colicus liomys (Brennan & Jones, 1961b)
Colicus minicolus Brennan, 1970b
Colicus nesudatus Goff & Brennan, 1978
Colicus oblongus (Fauran, 1959)
Colicus oopsi (Brennan, 1968)
Colicus pichindensis (Brennan, 1968)
Colicus sinpretarsus Goff & Gettinger, 1995
Colicus spinosus Goff & Gettinger, 1989
Colicus vesudor Goff & Brennan, 1978

Remarks

Peniscutum (with PLs extrascutal) is present in *C. dyscrita* and *C. oopsi*. Galeal seta with one branch in *C. brasiliensis* and *C. nesudatus* and nude in all other species. Pretarsala II (ζ) is absent in *C. sinpretarsus*.

Genus *Boshellia* Ewing, 1950

Boshellia Ewing, 1950; Brennan and Vercammen-Grandjean 1970; Brennan and Goff 1977

Type species: *Neoschoengastia hirsuta* Boshell & Kerr, 1942, by monotypy and original designation.

Diagnosis

SIF = 5BS-N-3-3111.0000; fsp = 7.6.6; fCx = 1.1.1; fSt = 2.2. Eyes 2 + 2; humeral setae not

separated from dorsal idiosomal setae; two pairs of sternal setae; NDV > 300. Cheliceral blade with tricuspid cap; galeal seta nude; palpal claw three-pronged; fPp = B/B/BBB; palpal tarsus with five branched setae, basal tarsala (*ω*) and subterminala (*ζ*). Scutum (Fig. 23) slightly wider than long, rectangular, posterior scutal margin widely rounded; PL > AL > AM; sensilla clavate; sensillary bases anterior to level of PLs. Leg I seven-segmented, legs II and III six-segmented (with undivided femur); three genualae on leg I; famulus (*ε*) proximal to tarsala (*ω*) on leg I and II; other setation standard for Trombiculinae.

Species included

Boshellia hirsuta (Boshell & Kerr, 1942)

Remarks

This genus does not differ from *Colicus*, except for the leg segmentation 7.6.6 vs. 7.7.7. Brennan and Vercammen-Grandjean (1970) also included coxa III with angular posteromedial projection in the diagnosis of *Boshellia*, but taxonomic significance of this trait is unclear.

Genus *Perissopalla* Brennan & White, 1960

Perissopalla Brennan & White, 1960; Goff and Brennan 1982
Pseudoschoengastia (*Perissopalla*): Vercammen-Grandjean 1964

Type species: *Perissopalla flagellisetula* Brennan & White, 1960, by monotypy and original designation.

Diagnosis

SIF = 5BS-N-3-3(2)1(0)1(0)1.0000; fsp = 7.7.7; fCx = 1.1.1; fSt = 2.2. Eyes 2 + 2; two humeral setae, first three post-humeral rows usually with six setae (sometimes 8 or 4 setae in 3rd row; fD = 2H-8-10-12-… in *P. pogoi*); two pairs of sternal setae; NDV from ca. 80 to 148. Cheliceral blade with tricuspid cap; galeal seta nude; palpal claw three-pronged; fPp variable; palpal tarsus with five branched setae, subterminala (*ζ*), and basal tarsala (*ω*). Scutum (Fig. 24) nearly quadrate, with posterior margin not projected, lightly sinuous; PL > AM ≥ AL; sensilla fusiform, with long filiform setules; sensillary bases situated far anterior to level of PLs, at about midway from level of ALs to level of PLs. Legs seven-segmented; three genualae on leg I (two in *P. famulidistalis* **comb. nov.**); famulus (*ε*) at level, distal or proximal to tarsala (*ω*) on leg I and proximal or at level of tarsala on leg II; genuala III and, sometimes, II (*σ*) absent in *P. famulidistalis* **comb. nov.**; other setation standard for Trombiculinae.

Species included

Perissopalla barticonycteris Brennan, 1969
Perissopalla calculata Goff & Brennan, 1982
Perissopalla deopertus (Brennan, 1970b)
Perissopalla famulidistalis (Daniel & Stekolnikov, 2006), **comb. nov.**
Perissopalla flagellisetula Brennan & White, 1960
Perissopalla ipeani Brennan, 1969
Perissopalla irwingi (Vercammen-Grandjean, 1964)
Perissopalla pogoi Goff & Brennan, 1982
Perissopalla precaria (Brennan & Dalmat, 1960)
Perissopalla rationalis Goff & Brennan, 1982
Perissopalla tanycera Brennan, 1969

Remarks

Nielsen *et al.* (2021) erroneously designated *P. irwingi* as a new combination; in fact, this combination was proposed by Goff and Brennan (1982). They also mentioned *P. deopertus* as a species of *Colicus*, according to its original description, although this species was placed in *Perissopalla* by Webb and Loomis (1977) followed by Goff and Brennan (1982). Daniel and Stekolnikov (2006) described *Colicus famulidistalis* from specimens lacking sensilla; however, the shape of scutum in this species is typical for *Perissopalla*.

Genus *Schoutedenichia* Jadin & Vercammen-Grandjean, 1954
Subgenus *Schoutedenichia* (*Pentachia*) Vercammen-Grandjean, 1958

Schoutedenichia (*Pentachia*) Vercammen-Grandjean, 1958; Zumpt 1961; Stekolnikov 2018; Nielsen *et al.* 2021

Type species: *Euschoengastia rouchoni* Abonnenc, 1955, by original designation.

Diagnosis

SIF = 5B-B-3-2111.0000; fsp = 7.7.7; fCx = 1.1.1; fSt = 2.2. Eyes 2 + 2; two humeral setae, first three post-humeral rows with six setae in *S.* (*P.*) *rouchoni* and *S.* (*P.*) *xeri* and double, with at least 20 setae in *S.* (*P.*) *lorgei*; two pairs of sternal setae; NDV = 90, 78, and 224, respectively. Cheliceral blade with tricuspid cap and row of dorsal teeth; galeal seta branched; palpal claw three-pronged; fPp = B/B/BBB; palpal tarsus with five branched setae and basal tarsala (ω). Scutum (Fig. 25) trapezoidal, telostigmal, with slightly concave posterior margin; PL > AM ≥ AL; sensilla fusiform; sensillary bases situated far anterior to level of PLs. Legs seven-segmented; two genualae on leg I; famulus (ε) at level of tarsala (ω) or proximal on leg I and at level of tarsala or slightly proximal on leg II; tibiala III (φ) absent; other setation standard for Trombiculinae.

Species included

Schoutedenichia (*Pentachia*) *lorgei* Vercammen-Grandjean, 1958
Schoutedenichia (*Pentachia*) *rouchoni* (Abonnenc, 1955)
Schoutedenichia (*Pentachia*) *xeri* Taufflieb, 1966

Remarks

Vercammen-Grandjean (1965b) abolished the subgenus *Pentachia* and included *S. lorgei* and *S. rouchoni* in the nominative subgenus of *Schoutedenichia*. Stekolnikov (2018) accepted the new placement of these species, but erroneously retained the subgenus *Pentachia* with the only remained species *S. xeri*. Thus, the subgenus lost its type species, *S. rouchoni*. Nielsen *et al.* (2021) reproduced this mistake. Hereby I restore this subgenus, which differs from all other *Schoutedenichia* by the presence of five branched setae on the palpal tarsus vs. four and the row of dorsal teeth on the cheliceral blade vs. at most three teeth (in *S. major* Vercammen-Grandjean, 1958).

Here I transferred three species from *Schoutedenichia* to *Guntheria* (see Remarks under the subgenus *Domrowana*) and two species from *Kayella* to *Schoutedenichia* (see Remarks under the genus *Kayella*).

Genus *Euryphylla* Vercammen-Grandjean, 1967, stat. nov.

Helenicula (*Euryphylla*) Vercammen-Grandjean, 1967
Eusaperium Brennan, 1970a, **syn. nov.**; Brennan and Goff 1977; Goff 1992

Type species: *Euschoengastia euryphylla* Brennan & Jones, 1961, by original designation.

Diagnosis

SIF = 6B-N-3-21(0)1(0)1.0000; fsp = 7.7.7; fCx = 1.1.1; fSt = 2.2. Eyes 2 + 2; 2–6 humeral setae; two pairs of sternal setae (in two species sternal setae cannot be separated from ventral); NDV from 70 to more than 300. Cheliceral blade with tricuspid cap; galeal seta nude; palpal claw three-pronged; fPp = B/B/BBB; palpal tarsus with six branched setae and basal tarsala (*ω*). Scutum trapezoidal, omorostigmal; posterior scutal margin lightly sinuous or rounded; AL > PL > AM; sensilla globose; sensillary bases anterior to level of PLs. Legs seven-segmented; two genualae on leg I; famulus (*ε*) proximal, distal or at level of tarsala (*ω*) on leg I and proximal to tarsala on leg II; other setation standard for Trombiculinae (but see remarks on variation below).

Species included

Euryphylla colombiana (Brennan, 1968), **comb. nov.**
Euryphylla euryphylla (Brennan & Jones, 1961a)
Euryphylla frondosa (Brennan & Jones, 1961a)
Euryphylla pamelae (Brennan, 1968), **comb. nov.**
Euryphylla phylloti (Wharton, 1948), **comb. nov.**
Euryphylla reversa (Brennan & Jones, 1961a), **comb. nov.**
Euryphylla spinicoxa (Goff, 1992), **comb. nov.**
Euryphylla vangelderi (Brennan, 1970a), **comb. nov.**
Euryphylla wenzeli (Brennan & Jones, 1961a), **comb. nov.**

Remarks

Vercammen-Grandjean (1967) created the subgenus *Helenicula* (*Euryphylla*) to accommodate two species, *Euschoengastia euryphylla* Brennan & Jones, 1961 and *Euschoengastia frondosa* Brennan & Jones, 1961, characterized by having foliate PL and dorsal idiosomal setae. However, these species have no such characteristic trait of *Helenicula* as the terminal position of tarsala (*ω*) on leg I. In addition, *E. euryphylla* has six setae on palpal tarsus vs. 4–5 in *Helenicula* and *E. frondosa* has "5, possibly 6" setae (Brennan and Jones 1961a). At the same time, both these species fit the diagnosis of the genus *Eusaperium* Brennan, 1970a, except for the presence of foliate setae. Therefore, I raise *Euryphylla* to the genus level and synonymize *Eusaperium* with it.

Eusaperium originally included three species – *E. vangelderi* (type species), *E. colombiana*, and *E. pamelae*; later Goff (1992) described one more species, *E. spinicoxum*.

The name *Euryphylla* Duchassaing & Michelotti, 1864 that can be found in the lists of synonyms of the sponge genus *Cliona* Grant, 1826 (Rützler 2002) is a *lapsus calami* in the explanation of the plates included in the original description (Duchassang and Michelotti 1864) instead of *Euryphylle* Duchassaing & Michelotti, 1864 (Pang 1973). Therefore, this name is unavailable and cannot be regarded a senior homonym of *Euryphylla* Vercammen-Grandjean, 1967, according to the ICZN Code, Art. 32.4.

Vercammen-Grandjean (1965b) followed by Nielsen *et al.* (2021) included *Euschoengastia wenzeli* Brennan & Jones, 1961 in *Helenicula*. However, tarsala I in this species does not occupy the terminal position (although it is situated on the distal part of the segment). The exact number of setae on the palpal tarsus of this species is unknown ("more than 4", according to the original description), but its similarity with other species of *Euryphylla* is undoubted.

Vercammen-Grandjean (1965b) followed by Nielsen *et al.* (2021) placed *Euschoengastia reversa* Brennan & Jones, 1961 in *G.* (*Guntherana*), but this species has six palpal tarsal setae, according to the original description, vs. five in *Guntheria*. Vercammen-Grandjean (1965b) followed by Nielsen *et al.* (2021) included *Euschoengastia phylloti* Wharton, 1948 in *Guntherana* (*Susa*), but this species has six palpal tarsal setae, according to the original description, vs. five in *Susa*. Brennan (1970a) did not include *E. phylloti* in *Eusaperium* because it has microtarsala (famulus, *ε*) situated distal to tarsala (*ω*) on leg I and the two genualae I are not in tandem, contrary to the three species

originally included in *Eusaperium*. However, *E. spinicoxa* and *E. wenzeli* have famulus I situated at the level of the tarsala; and genualae I are not arranged in tandem in *E. spinicoxa* and *E. frondosa*.

Variation within the genus: PLs and dorsal idiosomal setae are foliate in *E. euryphylla* and *E. frondosa*; bear strong spikes in *E. pamelae* and *E. spinicoxa*. *Euryphylla euryphylla* has no genualae II and III (*σ*).

Genus *Proschoengastia* Vercammen-Grandjean, 1967

Schoengastia (*Proschoengastia*) Vercammen-Grandjean, 1967
Proschoengastia: Brennan and Goff 1977; Stekolnikov and Gonzalez-Acuña 2015

Type species: *Euschoengastia herniosa* Brennan & Jones, 1961, by original designation.

Diagnosis

SIF = 7B-N-3-(1–3)111.0000; fsp = 7.7.7; fCx = 1.1.1; fSt = 2.2. Eyes 2 + 2, on ocular plate; 2 humeral setae; two pairs of sternal setae; NDV from ca. 60 (*P. insolita*) to more than 200. Cheliceral blade with tricuspid cap; galeal seta nude; palpal claw three-pronged; fPp = B/B/BNB or B/B/BBB (in *P. insolita*); palpal tarsus with seven branched setae and basal tarsala (*ω*). Scutum trapezoidal, omorostigmal, posterior scutal margin slightly projected, lightly sinuous or rounded; AL ≫ AM; sensilla globose or subglobose; sensillary bases slightly anterior, posterior or at level of PLs. Legs seven-segmented; 1–3 genualae on leg I; famulus (*ε*) distal, proximal or at level of tarsala (*ω*) on leg I and slightly proximal or at level of tarsala on leg II; other setation standard for Trombiculinae.

Species included

Proschoengastia eloisae (Stekolnikov & Silva-de la Fuente, 2020, in Silva-de la Fuente *et al.* 2020), **comb. nov.**
Proschoengastia herniosa (Brennan & Jones, 1961a)
Proschoengastia insolita (Brennan & Jones, 1961a)
Proschoengastia macrochaeta (Brennan & Jones, 1961a)
Proschoengastia antarctica Stekolnikov & Gonzalez-Acuña, 2015

Remarks

Silva-de la Fuente *et al.* (2020) synonymized *Proschoengastia* with *Herpetacarus* (*Abonnencia*) Vercammen-Grandjean, 1960 and described a new species *H.* (*A.*) *eloisae*. However, *Proschoengastia* possess an omorostigmal scutum vs. telostigmal in *Herpetacarus*. Here I restore it as a valid genus and place *H.* (*A.*) *eloisae* in *Proschoengastia*.

Vercammen-Grandjean (1965b) placed *Trombicula macrochaeta* in the species group *kallipygos* of the genus *Guntherana*. However, Vercammen-Grandjean and Langston (1971) did not mention this species in their revision of this genus. Stekolnikov and González-Acuña (2015) transferred *T. macrochaeta* to *Proschoengastia*.

Incertae sedis

Guntheria insueta Lester, 1984

Guntheria insueta Lester, 1984
Guntheria (*Derrickiella*) *insueta*: Domrow and Lester 1985

Remarks

This species has non-expanded, flagelliform sensilla and the shape of scutum characteristic of the generic complex *Leptotrombidium* from the tribe Trombiculini — widely rectangular, with

bilobate posterior margin. Lester (1984) regarded this species as an argument against maintaining the tribe Schoengastiini, which differs from Trombiculini by the presence of expanded sensilla vs. flagelliform. I, however, believe that it could rather constitute a monotypic genus of Trombiculini. Re-examination of the type material is desirable to come to the final conclusion.

***Guntheria tindalei* (Womersley, 1936)**
Trombicula tindalei Womersley, 1936
Guntherana tindalei: Womersley 1952; Domrow 1960
Guntheria (*Guntheria*) *tindalei*: Nielsen *et al.* 2021

Remarks
This species is known only from the nymph.

***Guntheria translucens* (Womersley, 1944)**
Trombicula translucens Womersley, 1944
Guntherana translucens: Womersley 1952; Domrow 1960
Guntheria (*Guntheria*) *translucens*: Nielsen *et al.* 2021

Remarks
This species is known only from two females.

Key to genera and subgenera of Trombiculinae with expanded sensilla and five non-specialized setae on palpal tarsus (5B or 5BS)

1. Idiosoma dorsally with 7–26 sclerite plates (platelets) posterior to scutum; scutum (Fig. 26) trapezoidal, telostigmal, sensillary bases far anterior to level of PLs ..... *Polylopadium* Brennan & Jones, 1961b
– Idiosoma with at most two sclerite plates in caudal part, in addition to scutum 2
2. Scutum (Figs. 27, 28) small, telostigmal, with AM situated far anterior to short nude ALs; cheliceral blade with at least one large dorsal hook. Intranasal parasites of mammals 3
– AM situated nearly at level or posterior to ALs 4
3. Scutum as in Fig. 27, PLs extrascutal (peniscutum); coxae II and III multisetose ..... *Kymocta* Yunker & Brennan, 1962
– PLs on scutum; scutum longer than wide, with sensillary bases situated on lateral scutal margins, directly above PLs and near to reduced spine-like ALs (Fig. 28); coxae II and III with one seta ..... *Blix* Brennan & Yunker, 1966
4. Scutum with cuticular striations around sensillary bases (Fig. 21); 3–4 pairs of sternal setae; famulus (ε) distal to tarsala (ω) on leg I; tibia and tarsus III with dorsal setae extended into long thin whip distally ..... *Ornithogastia*
– Scutum without cuticular striations around sensillary bases; all setae on tibia and tarsus III uniformly branched 5
5. Humeroventral setae present between coxae II and III 6
– Humeroventral setae absent 8
6. PLs (Fig. 8) and part of dorsal idiosomal setae foliate (cordiform) ..... *Cordiseta*
– Foliate setae absent 7
7. PLs extrascutal (Fig. 17) ..... *Pseudoschoengastia* (*Pseudoschoengastia*)
– PLs on scutum (Fig. 18) ..... *Pseudoschoengastia* (*Walchioides*)
8. ALs definitely longer than AM (Figs. 1–4) and situated in projected anterior corners of scutum; sensilla globose or subglobose 9
– ALs shorter, equal in length, rarely slightly longer than AM 12

9. Distance between sensillary bases lesser or at most equal to diameter of each base (Fig. 4); tarsala I (*ω*) usually occupies terminal position — distal, slightly proximal or in line with subterminala (*ζ*); number of setae on coxa III frequently more than one (up to seven) ..... *Helenicula* (species with 5B)
– If sensillary bases situated close to each other, then tarsala I doesn't occupy terminal position 10
10. Pygosomal plates present ..... *Guntheria* (*Guntheria*)
– Pygosomal plates absent 11
11. Palpal tarsus with subterminala (5BS) ..... *Guntheria* (*Domrowella*) (part)
– Palpal tarsus without subterminala (5B) ..... *Guntheria* (*Domrowana*) (part)
12. Scutum omorostigmal, with slightly projected and sinuous (Fig. 14) or widely rounded posterior margin 13
– Scutum not omorostigmal 14
13. Palpal tarsus with subterminala (5BS) ..... *Guntheria* (*Domrowella*) (part)
– Palpal tarsus without subterminala (5B) ..... *Guntheria* (*Domrowana*) (part)
14. Scutum almost quadrate, telostigmal, with greatly projected posterior margin, almost straight or slightly rounded in center and deeply rounded at edges (Figs. 12, 13); PLs not situated in projected corners of scutum; sensillary bases far anterior to level of PLs ..... *Phyllacarus* (*Platypacarus*) **subgen. nov.**
– Scutum of another shape 15
15. Palpal tarsus with subterminala (5BS) 16
– Palpal tarsus without subterminala (5B) 19
16. Scutum nearly quadrate; sensilla fusiform, with long filiform setules; sensillary bases situated far anterior to level of PLs, at about midway from level of ALs to level of PLs (Fig. 24). Parasites of bats ..... *Perissopalla*
– Scutum wider than long, rectangular or trapezoidal; sensilla clavate or subglobose 17
17. Anterior legs seven-segmented, medial and posterior six-segmented (with undivided femur); NDV > 300; dorsal idiosomal setae on small platelets ..... *Boshellia*
– All legs seven-segmented (all femora divided), NDV < 250 18
18. Scutum trapezoidal, clearly wider than long, with bilobate posterior margin (Fig. 5); palp tibia with none or one branched seta ..... *Derrickiella* (*Derrickiella*)
– Scutum only slightly wider than long (Figs. 22 and 23), posterior scutal margin almost straight, widely rounded or lightly sinuous; palp tibia usually with two or three branched setae ..... *Colicus*
19. Cheliceral blade with tricuspid cap and row of dorsal teeth; scutum trapezoidal, telostigmal, with slightly concave posterior margin (Fig. 25) ..... *Schoutedenichia* (*Pentachia*)
– Cheliceral blade without row of dorsal teeth 20
20. PLs extrascutal (Figs. 19, 20); palpal femoral seta branched 21
– PLs on scutum (extrascutal in *K. novita*, but palpal femoral seta nude in this species) 22
21. Anterior legs seven-segmented, medial and posterior seven- or six-segmented (with undivided femur) ..... *Vanidicus*
– All legs six-segmented ..... *Fauranius*
22. Scutum with greatly projected posterior margin, almost straight in center and deeply rounded at edges or evenly rounded, not bilobate (Figs. 15, 16); sensillary bases posterior to or at level of PLs (rarely slightly anterior) ..... *Phyllacarus* (*Phyllacarus*)
– Posterior scutal margin concave, lightly sinuous or bilobate; sensillary bases anterior to level of PLs (rarely at level or slightly posterior) 23
23. Genualae II and III (*σ*) absent ..... *Kayella* (species with 5B)
– Genualae II and III present 24
24. Palpal femoral and genual setae branched; posterior scutal margin bilobate (Figs. 6, 7) ..... *Derrickiella* (*Argentinacarus*)

– At least one of palpal femoral and genual setae nude; posterior scutal margin almost straight, lightly sinuous or concave (Figs. 9, 10) 25

25. Eyes 1 + 1 or absent; at least one seta on palpal femur, genu, and tibia branched ..... *Susa* (*Susa*)

– Eyes 2 + 2; all setae on palpal femur, genu, and tibia nude (fPp = N/N/NNN) .... *Susa* (*Ophthalmophila*)

DISCUSSION

In the new system here proposed, *Guntheria* in the sense of the latest revisions (Goff 1980c; Domrow and Lester 1985) is divided into three genera — *Guntheria*, *Derrickiella*, and *Phyllacarus*. All their species are endemics of Australia and New Guinea, except for four species or *Guntheria* (*Domrowana*) described from Japan, the Philippines, the islands of North Pacific Ocean, and one from Africa (*G. chawiensis*), three species of *Derrickiella* (*Argentinacarus*) (known from Iran, Turkmenistan, and Azerbaijan), and *D.* (*A.*) *expansus* (Argentina and Chile). One species, *Derrickiella apteryxi*, was described from New Zealand.

Helenicula seems the most similar genus to *Guntheria*; their common characters are AL ≫ AM, the presence of globose or subglobose sensilla, sensillary bases situated rather close to each other (especially in *Helenicula*), and 1–2 genuala I (3 in four species of *Guntheria*). At the same time, *Helenicula* is mainly an Asian genus and only one its species (*H. kohlsi*) is known in Australia (Domrow and Lester 1985). Two South American genera, *Euryphylla* and *Proschoengastia*, possess the same complex of characters, but they have six and seven setae on palpal tarsus, respectively, whereas *Guntheria* has five and *Helenicula* has 4–5.

The South American genera of Schoengastiini with the formula of palpal tarsus 5B or 5BS (*Cordiseta*, *Pseudoschoengastia*, *Vanidicus*, *Fauranius*, *Colicus*, *Boshellia*, *Perissopalla*, *Polylopadium*, *Kymocta*, and *Blix*) are clearly different from the aforementioned Australian genera and can be easily discriminated from any of them, as evident from the proposed identification key. The Asian genus *Susa*, in the sense of present work (with only one Australian species, *S. scaevola*), has a rather peculiar appearance, but its main characters, such as the reduction of eyes and the presence of nude setae on palpal femur and/or genu, seems taxonomically weak. The same is true for *Kayella*: its main distinctive feature is the reduction of genualae II and III; at the same time, such reduction is rarely observed in other genera, for example, in *Guntheria* and *Pseudoschoengastia*.

Ornithogastia occurs mainly in Asia (nine species). One of its species was described from Africa, one from North America, and one is known from the Philippines and Solomon Islands. This genus is morphologically similar to *Neoschoengastia* and both these genera are specific to bird hosts.

After our transfer of three Australian species from *Schoutedenichia* to *Guntheria*, I can conclude that *Schoutedenichia* does not occur in the Australasian realm. This genus is mainly distributed in Africa (Vercammen-Grandjean 1958; Stekolnikov 2018) and to a lesser extent in Asia (Kudryashova 1998; Fernandes and Kulkarni 2003; Stekolnikov 2021).

ACKNOWLEDGEMENTS

I am grateful to Owen Seeman (Queensland Museum, South Brisbane, Queensland, Australia) and Stanislav Kalúz (Institute of Zoology, Slovak Academy of Sciences, Bratislava, Slovakia) for a careful review of the manuscript and useful suggestions. This research was supported by the cooperative agreement No. 122031100263-1 from the Ministry of Science and Higher Education of the Russian Federation.

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رده‌بندی *Guntheria* Womersley, 1939 و جنس‌های مربوط به هرناهای چیگر (Acariformes: Trombiculidae)

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چکیده

هرناهای چیگر از قبیلهٔ Schoengastiini Vercammen-Grandjean, 1960، که دارای پنج موی معمولی روی پنجهٔ پرماسه هستند و برخی از جنس‌های دیگر مرتبط با *Guntheria* Womersley, 1939، بر اساس منابع منتشر شده بررسی شدند. توصیف اصلی و بازتوصیف ۲۸۳ گونه مورد بررسی قرار گرفت. طبقه‌بندی جدیدی از *Guntheria* با بازتعریف زیرجنس‌های *G.* (*Domrowana*) Vercammen-Grandjean & Langston, 1971، و *G.* (*Domrowella*) Vercammen-Grandjean, 1960، و جنس مرتبط *Derrickiella* Domrow & Audy ارایه شد. زیرجنس *G.* (*Phyllacarus*) Vercammen-Grandjean, 1967 بازتعریف شد و به سطح جنس ارتقا یافت. زیرجنسی جدید، *Phyllacarus* (*Platypacarus*) **subgen. nov.** تعریف شد. یکی از جنس‌های تک گونهٔ پیشین *Argentinacarus* Goff & Gettinger, 1995 گسترش داده شد و زیرجنس *Derrickiella* به آن اضافه شد. جنس *Proschoengastia* Vercammen-Grandjean, 1967 که پیش‌تر با *Herpetacarus* (*Abonnencia*) Vercammen-Grandjean, 1960 مترادف شده بود، معتبر شناخته شد. دو مترادف جدید ایجاد شد: [*Guntherana* (*Pseudosusa*) **مترادف جدید**] *Pseudoschoengastia* (*Walchioides*) Vercammen-Grandjean 1960، و Vercammen-Grandjean, 1960 [*Eusaperium* **مترادف جدید**] *Euryphylla* Vercammen-Grandjean, 1967 **stat. nov.**]. شصت و شش ترکیب جدید در جنس‌های *Guntheria* (3)، *Derrickiella* (22)، *Susa* Audy & Nadchatram, 1960 (1)، *Schoutedenichia* Jadin & Vercammen-Grandjean, 1954 (2)، *Phyllacarus* (26)، *Pseudoschoengastia* Lipovsky, 1951 (1)، *Vanidicus* Brennan & Jones, 1961 (1)، *Ornithogastia* Vercammen-Grandjean, 1960 (1)، *Perissopalla* Brennan & White, 1960 (1)، *Euryphylla* (7) و *Proschoengastia* (1) در نظر گرفته شد. کلیدی برای جنس‌ها و زیرجنس‌های Schoengastiini با پنج مو روی پنجهٔ پرماسه نوشته شد.

واژگان کلیدی: استرالیا، چیگرها، طبقه‌بندی، گینه نو، قبیلهٔ Schoengastiini.

اطلاعات مقاله: تاریخ دریافت: ۱٤۰۲/۹/۲۵، تاریخ پذیرش توسط ع. صبوری: ۱٤۰۲/۱۱/۵، تاریخ چاپ: ۱٤۰۳/۱/۲۷