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***Caenonychus*, a senior synonym of *Speleorchestes* (Acariformes: Nanorchestidae)**

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Abstract

The single known specimen of the monotypic genus *Caenonychus* Oudemans, 1902 was examined. No distinguishing characters could be found to justify the retention of *Speleorchestes* Trägårdh, 1909 as a separate genus from *Caenonychus*. Grandjean (1939) suspected these genera were synonymous but retained *Speleorchestes* as valid because of a difference between the two genera in opisthosomal shape. An artifactual explanation for the difference in opisthosomal shape is herein accepted based on the effects of applying different pressures to the coverslip over the same specimen. Therefore, *Speleorchestes* is treated as a junior synonym of *Caenonychus*.

Keywords: Endeostigmata, Nanorchestidae, *Caenonychus*, *Speleorchestes*

Introduction

Nanorchestidae, which predominantly live in soils, sands, mosses and lichens, can be readily distinguished from other Acariformes by the presence of an epistomal plate (Bolton *et al.* 2017). This family comprises five genera, described in the following order: *Nanorchestes* Topsent & Trouessart, 1890; *Caenonychus* Oudemans, 1902; *Speleorchestes* Trägårdh, 1909; *Protospeleorchestes* Dubinin, 1962; *Neonanorchestes* McDaniel & Bolen, 1981.

Protospeleorchestes is known from a single fossil from the Devonian (Dubinin 1962), but the morphology of this mite is too poorly preserved to provide reliable diagnostic characters. Moreover, the placement of this mite within Nanorchestidae is doubtful because it was only based on the shared possession of wedge (fan) shaped opisthosomal setae with *Speleorchestes*. This single character is unreliable for family-level placement because it is also present in Oehserchestidae and Grandjeanicidae (Theron 1974; Walter 2001).

Neonanorchestes can be distinguished from *Nanorchestes* by the clavate shape of the posterior pair of trichobothria (McDaniel & Bolen 1981), but otherwise these genera appear identical, and so a case has been made for synonymy (Booth 1984). However, the discovery of alternating calyptostasy in *Neonanorchestes* but not *Nanorchestes* has resulted in the retention, for the time being, of the former as a valid genus (Kethley 1991).

Both *Nanorchestes* and *Neonanorchestes* are clearly very distinct from *Caenonychus* and *Speleorchestes* (Table 1). However, Trägårdh (1909) hypothesized two potentially significant differences between *Nanorchestes* and *Speleorchestes* in error because of mistakes from the first description of *Nanorchestes* by Topsent & Trouessart (1890). *Nanorchestes* was described as having chelicerae that are like those of *Ereynetes*, which are not chelate due to the reduction of the fixed

chela. But both *Speleorchestes* and *Nanorchestes* have chelate chelicerae (SJB pers. obs.). *Nanorchestes* was also described as having four-segmented palps (excluding coxae). But *Nanorchestes* shares the state of five-segmented palps with *Speleorchestes* (Theron 1975; SJB pers. obs.). The error in the original description of *Nanorchestes* can be attributed to the difficulty of discerning the palpal trochanters.

Caenonychus was first described from the Netherlands by Oudemans (1902). This was shortly followed by a much more detailed description by the same author (Oudemans 1903). When Trägårdh (1909) described *Speleorchestes*, he noted the similarities and differences of this genus from *Nanorchestes* but made no mention of *Caenonychus*, presumably because he was unaware of it. Robust characters have not been found to distinguish *Speleorchestes* (13 species) from *Caenonychus* (monotypic until herein). Grandjean (1939) very cautiously refrained from synonymizing *Caenonychus* with *Speleorchestes* due to a single difference that he suspected was an artifact (see Results & Discussion).

This paper only addresses characters that are diagnostic at the genus level in order to justify a taxonomic amendment concerning *Caenonychus*. The determination of diagnostic characters for species, which was not attempted because of the lack of available specimens and the relatively poor quality of early descriptions, will require a much larger amount of study, including the collection of fresh specimens.

Materials and methods

Only a single specimen of *Caenonychus fallax* Oudemans, the type species of *Caenonychus*, appears to have been retained from its only known collection event: Rotterdam, April, 1901 (Oudemans 1902). This specimen, which is considered to be the holotype, was borrowed from the Naturalis Biodiversity Center, Leiden, Netherlands. Type material of *Speleorchestes*, thought to have been deposited at either the Swedish Museum of Natural History or the Swedish University of Agricultural Sciences, could not be found (Gunvi Lindberg, pers. comm.). However, the descriptions by Trägårdh provide a detailed set of diagnostic characters that are sufficient for synonymizing *Caenonychus* with *Speleorchestes*. Examinations were also undertaken of recently collected specimens of *Caenonychus* (identified as *Speleorchestes* before the realization of synonymy), *Nanorchestes* and *Neonanorchestes*.

Most specimens were examined and imaged using a Leica DM 2500 compound microscope equipped with differential interference contrast (DIC) and a digital single lens reflex camera (Canon EOS 80D). Focus stacking was carried out with Zerene Stacker (version 1.04). Low-temperature scanning electron microscopy (LT-SEM) was undertaken on *Caenonychus* sp. A (Fig. 7, 17) and *Nanorchestes* sp. B (Fig. 8) in accordance with Bolton *et al.* (2014) but with a single modification: specimens were dead (stored in 95% ethanol) before being frozen.

Relevant drawings from the descriptions by Oudemans (1903) and Trägårdh (1909) are herein republished (their copyright has expired). New drawings were generated in Adobe Illustrator (version 15.0.0) based on DIC images of *Nanorchestes* (Fig. 3, 11) and the holotype of *Caenonychus fallax* (Fig. 9). Information on life stage and sex of imaged and drawn specimens is in the appendix. Supplementary images of the holotype of *Caenonychus fallax* are available at the following URL: <https://zenodo.org/record/4774294#.YKWNtr5KhaQ>. Specimens mentioned or figured herein are deposited at the following institutions: Ohio State Acarology Laboratory (OSAL), Ohio, USA; Florida State Collection of Arthropods (FSCA), Florida, USA; Naturalis Biodiversity Center, formerly the Rijksmuseum van Natuurlijke Historie (RMNH), Netherlands (see Appendix for more detailed information on specimens and their repositories).

Results and discussion

Caenonychus Oudemans, 1902.

Type species *Caenonychus fallax* Oudemans, 1902 by monotypy

Speleorchestes Trägårdh, **syn. nov.**

Type species *Speleorchestes formicorum* Trägårdh, 1909.

Diagnosis: *Caenonychus* is readily distinguished from the other extant genera of Nanorchestidae by the possession of opisthosomal setae that are not fractal in form, i.e. all setules (terminal branches) project from the stem (Fig. 5–7). Additional diagnostic characters listed in Table 1.

Caenonychus elongatus (Berlese), **com. nov.**

Alichus elongatus Berlese, 1904.

Caenonychus fallax Oudemans, 1902

Caenonychus formicorum (Trägårdh), **com. nov.**

Speleorchestes formicorum Trägårdh, 1909.

Caenonychus globulus (Theron), **com. nov.**

Speleorchestes globulus Theron, 1975.

Caenonychus latus (Halbert), **com. nov.**

Alichus latus Halbert, 1920.

Caenonychus meyeræ (Theron & Ryke), **com. nov.**

Speleorchestes meyeræ Theron & Ryke, 1969.

Caenonychus natulus (Theron & Ryke), **com. nov.**

Speleorchestes natulus Theron & Ryke, 1969.

Caenonychus nylsvleyensis (Olivier & Theron), **com. nov.**

Speleorchestes nylsvleyensis Olivier & Theron, 1989.

Caenonychus paolii (Berlese), **com. nov.**

Alichus paoli Berlese, 1910.

Caenonychus poduroides (Hirst), **com. nov.**

Speleorchestes poduroides Hirst, 1917.

Caenonychus potchefstroomensis (Theron & Ryke), **com. nov.**

Speleorchestes potchefstroomensis Theron & Ryke, 1969.

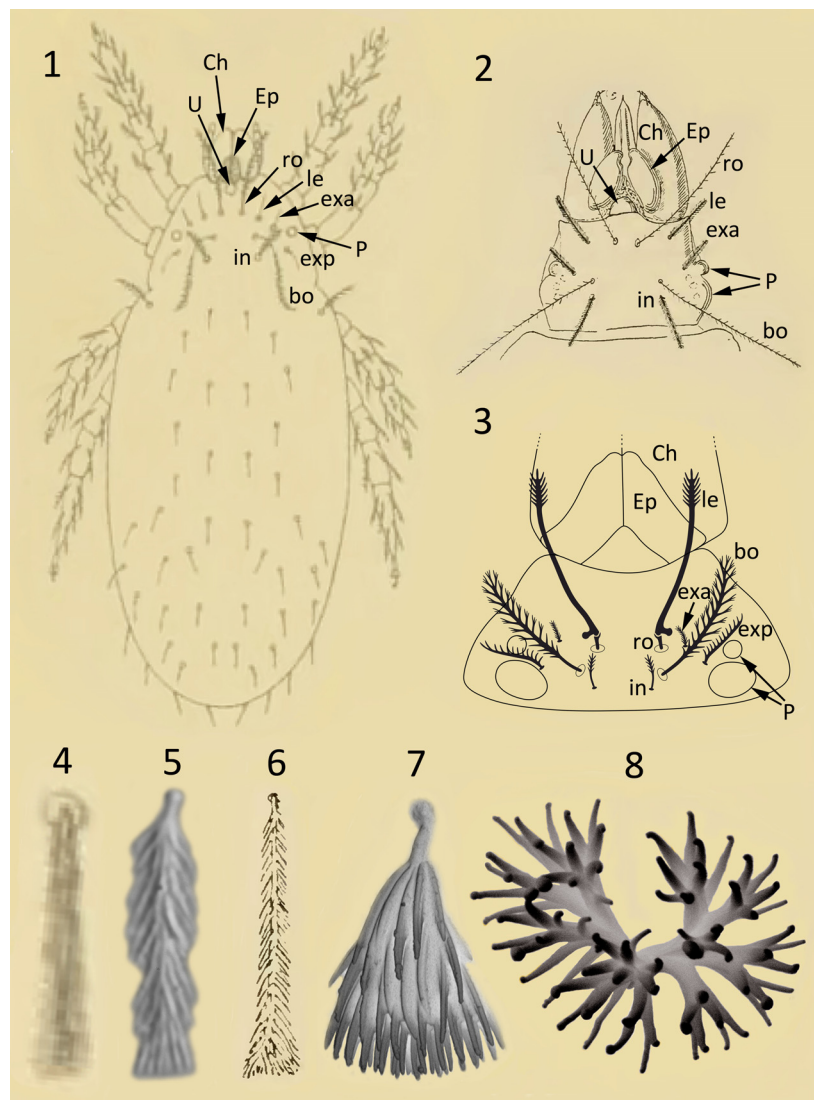
Caenonychus pratensis (Willmann), **com. nov.**

Speleorchestes pratensis Willmann, 1936.

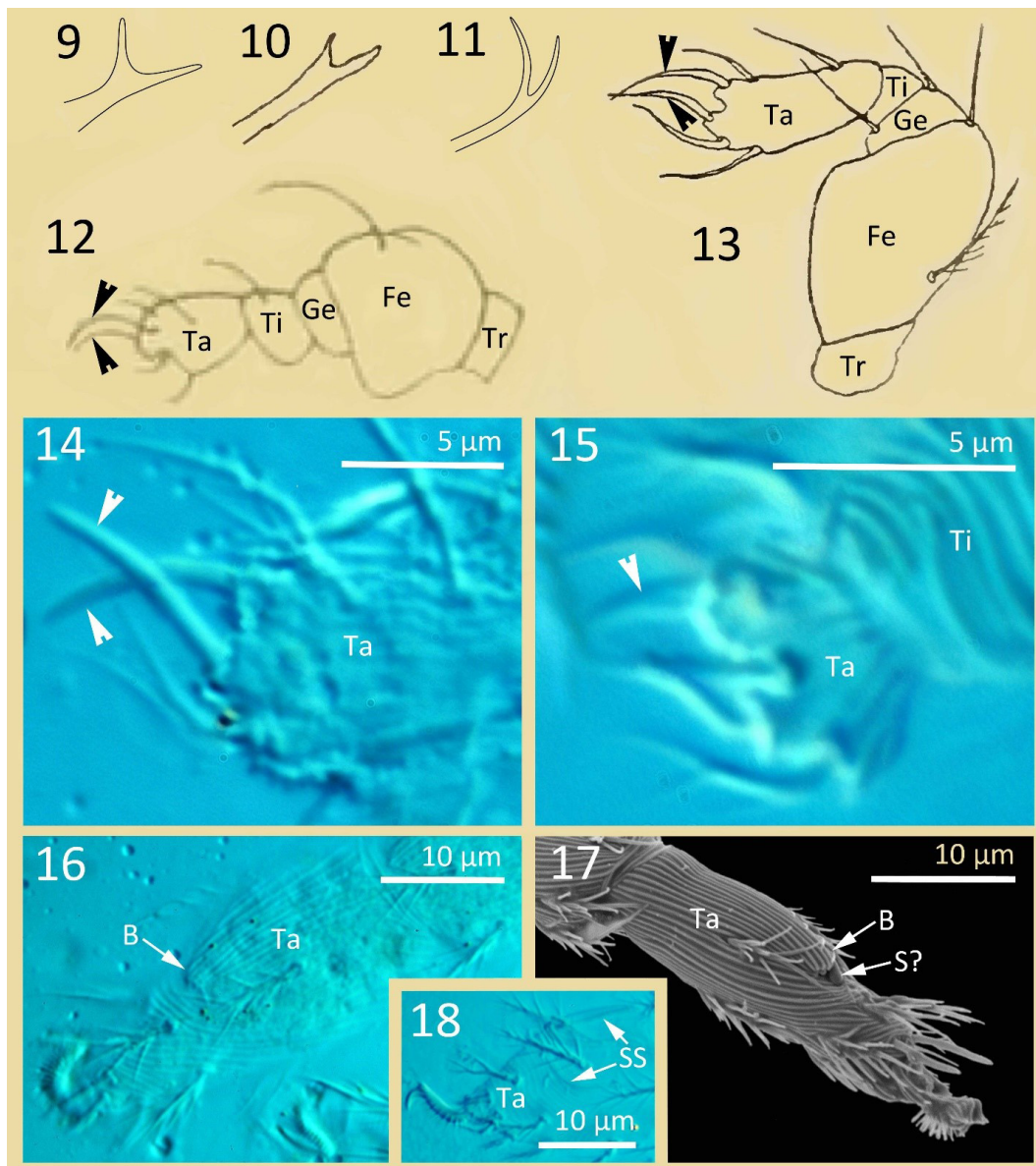
Caenonychus termitophilus (Trägårdh), **com. nov.**
Speleorchestes termitophilus Trägårdh, 1909.

Caenonychus ventriosus (Hirst), **com. nov.**
Speleorchestes ventriosus Hirst, 1921.

Caenonychus and *Speleorchestes* share all eight characters that distinguish them from the other extant genera of Nanorchestidae (*Nanorchestes* and *Neonanorchestes*) (Table 1; Fig. 1–19). No characters have been found to support the retention of *Speleorchestes* (referred to as *Caenonychus* in the figure captions) as a valid genus.



FIGURES 1–8. Body (dorsal): 1, *Caenonychus fallax* Oudemans (type species of *Caenonychus*) (from Oudemans, 1903). Prodorsum: 2, *C. formicorum* (Trägårdh) (type species of *Speleorchestes*) (from Trägårdh, 1909); 3, *Nanorchestes* sp. A. Opisthosomal setae: 4, *C. fallax* (from Oudemans, 1903); 5, *C. fallax* (DIC); 6, *C. formicorum* (from Trägårdh, 1909); 7, *Caenonychus* sp. A (LT-SEM); 8, *Nanorchestes* sp. B (LT-SEM). Ch=chelicera; Ep=epistomal plate; U=unpaired eye; P=paired eye; ro=rostral seta; le=lamellar seta; exa=anterior exobothridial seta; exp=posterior exobothridial seta; bo=bothridial seta; in=interlamellar seta.



FIGURES 9–18. Rutellum: 9, *C. fallax*; 10, *C. formicorum* (from Trägårdh, 1909); 11, *Nanorchestes* sp. C. Palp: 12, *C. fallax* (from Oudemans, 1903); 13, *C. termitophilus* (Trägårdh) (from Trägårdh, 1909). Palp tarsus: 14 *C. fallax* (DIC); 15, *Nanorchestes* sp. D (DIC). Tarsus I: 16, *C. fallax* (DIC); 17, *Caenonychus* sp. A (LT-SEM); 18, *Nanorchestes* sp. C (DIC). Ta=tarsus; Ti=tibia; Ge=genu; Fe=femur, Tr=trochanter; B=bulge; S?=possible solenidion; SS=swollen stria; tailless arrow (black or white)=palpal solenidion.

The narrow opisthosomal setae of *Caenonychus fallax* (Figs. 4, 5) readily distinguish this mite from species of *Caenonychus* with globose or wedge-shaped setae (Fig. 7), which were all formerly designated *Speleorchestes*. But note that the type species of *Speleorchestes* has narrow opisthosomal setae (Fig. 6), like those of *C. fallax*, and so these differences in setal shape do not provide a basis for retaining *Speleorchestes* as a valid genus.

Perhaps the strongest character in support of synonymy is the dorsal bulge on tarsus I, which appears identical in shape and position between *Caenonychus fallax* (Fig. 16) and a mite that was originally identified as *Speleorchestes* (Fig. 17). This character is also visible in the descriptions of other species that were originally placed in *Speleorchestes* (Theron & Ryke 1969; Olivier & Theron 1989).

TABLE 1. Characters used to treat *Caenonychus* as a senior synonym of *Speleorchestes*.

Character	<i>Caenonychus</i> (= <i>Speleorchestes</i> *)	<i>Nanorchestes</i> and <i>Neonanorchestes</i>
Anterior, unpaired eye†	Present (Figs. 1–2)	Absent (Fig. 3)
Setae <i>ro</i> and <i>le</i>	Separate (Figs. 1–2)	Attached together (Fig. 3)
Genital papillae (adult)	Three pairs ^{1,2}	Two pairs ^{3,4}
Shape of opisthosomal setae	Non-fractal: setules (terminal branches) project from stem (Figs. 5–7)	Fractal: setules project from branches (Fig. 8)
Rutella	Thick, rigid and either toothed ⁵ or Y-shaped (Figs. 9–10)	Thin and seta-like (Fig. 11)
Solenidia on palpal tarsi	Two per tarsus (Figs. 12–14) ^{3,4,6}	One per tarsus (Fig. 15) ^{3,4}
Dorsal bulge on tarsus I	Present and distinct (Figs. 16–17) ^{3,6}	Absent (Fig. 18)
Striae on leg segments	Striae never swollen (Figs. 16–17)	Some leg segments, including tarsi and tibiae of legs I and II, with swollen striae (Fig. 18)

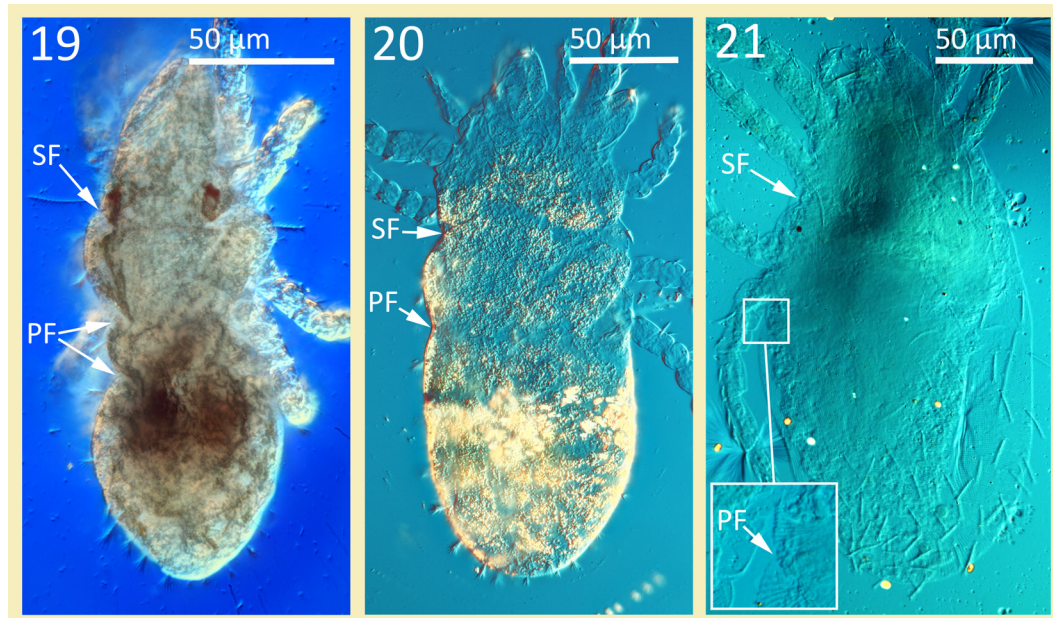
*Although no figures are labelled as *Speleorchestes* in the captions, all *Caenonychus* that are not *C. fallax* were treated as *Speleorchestes* prior to this publication. †Homology of the median protuberance with an unpaired eye is in accordance with Walter, 2009. Supporting citations: ¹Oudemans, 1903; ²Trägårdh, 1909; ³Theron & Ryke, 1969; ⁴Theron, 1975; ⁵Hirst, 1917; ⁶Olivier & Theron, 1989.

Whereas setae *exp* are present on the prodorsum of *Caenonychus fallax* (Fig. 1), these setae appear absent from the type species of *Speleorchestes* (Fig. 2) (Trägårdh 1909). However, *exp* are clearly present on species of *Caenonychus* that were formerly designated *Speleorchestes* (Hirst 1917; Halbert 1920; Willmann 1936; Theron & Ryke 1969; Theron 1975; Olivier & Theron 1989). Therefore, this difference, assuming it is real and not an omission by Trägårdh, does not justify the retention of *Speleorchestes* as a valid genus.

Structures that have been termed ‘post-ocular bodies’ (e.g. Theron & Ryke 1969) are herein homologized with a posterior pair of eyes (Figs. 2, 3) in accordance with Uusitalo (2010). Given the difficulty of discerning the posterior paired eyes, especially before the invention of phase-contrast and DIC microscopy, their absence from the drawing of the dorsum of *Caenonychus fallax* (Fig. 1) is considered to be an omission rather than a distinguishing feature. Unfortunately, none of the eyes are visible from the single available specimen of this species because they have faded out of view.

Grandjean (1939), who makes no mention of setae *exp* or the eyes, suggested a single possible difference between *Caenonychus* and *Speleorchestes*, which is that in the former the opisthosoma is oval whereas in the latter the opisthosoma has an hourglass shape due to two post-pedal furrows. Although Grandjean (1939) cautiously decided against synonymizing the two genera, he indicated that the oval shape observed for the opisthosoma of *Caenonychus* was probably an artifact. An artifactual explanation for the difference in opisthosomal shape is herein accepted based on the effects of applying different pressures to the coverslip over the same specimen. A high degree of compression causes the opisthosoma to convert from a natural hourglass shape (Fig. 19) to a much more oval shape (Fig. 20). Oudemans appears to have applied a high degree of compression to his specimen of *Caenonychus* (Figs. 1, 21). However, even the holotype of *Caenonychus fallax* retains a slight post-pedal furrow (Fig. 21).

For the aforementioned reasons, *Caenonychus* is herein treated as a senior synonym of *Speleorchestes*. *Caenonychus* is seldom mentioned in the biological literature because mites that belong to this genus have almost always been identified as *Speleorchestes* (e.g. Theron & Ryke 1969; Steinberger & Whitford 1985; Silva *et al.* 1989; Russell & Alberti 2009).



FIGURES 19–21. Opisthosomal shapes (dorsal): 19, *Caenonychus* sp. B. immediately before any compression under a coverslip (DIC); 20, *Caenonychus* sp. B. immediately after a large degree of compression under a coverslip (same specimen as Fig. 19) (DIC); 21, *C. fallax* (DIC). SF=sejugal furrow; PF=Post-pedal furrow.

Author contributions

SJB undertook DIC, drawings, character examination, plate production and writing. GRB undertook LT-SEM.

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Appendix: material examined.

Caenonychus fallax Oudemans, Rotterdam, Netherlands, moss; collector: H. Schütz, April, 1901. Adult/tritonymph, holotype (RMNH. ACA.P 5645). Used for rutellum (Fig. 9), palp tarsus (Fig. 14), tarsus I (Fig. 16) and body shape (Fig. 21).

Caenonychus sp. A. U.S.A., Indiana, Lake County, Marquette Park, 41.6156 N 87.2743 W, top of sand dune (10 cm deep); collector: Samuel Bolton, April, 2013. Nymph/adult. Used for seta (Fig. 7) and tarsus I (Fig. 17). Specimen lost.

Caenonychus sp. B. U.S.A., Maryland, Prince George’s Co., Entomology Rd., 39.0417 N 78.8642 W, lichen over soil; collector: Samuel Bolton, August, 2013; Deutonymph (FSCA 00030192). Used for opisthosomal shape (Fig. 19–20).

Nanorchestes sp. A. U.S.A., Indiana, Porter Co., Indiana Dunes State Park, 41.6872 N 86.9944 W, sand dune near Lake Michigan shoreline (10 cm deep); collector: Samuel Bolton, 17 May, 2013. Female (OSAL 0114062). Used for prodorsum (Fig. 3).

Nanorchestes sp. B. U.S.A., Maryland, Prince George’s Co., Entomology Rd., 39.0417 N 78.8642 W, lichen over soil; collector: Samuel Bolton, August, 2013; Nymph/adult. Used for seta (Fig. 8). Specimen lost.

Nanorchestes sp. C. U.S.A., Ohio, Athens Co., Burr Oak Rd., Wayne National Forest, 39.5482 N 82.0563 W, loam soil (10 cm deep); collector: Samuel Bolton, 1 June, 2012. Female (OSAL 0114229). Used for rutellum (Fig. 11) and tarsus I (Fig. 18).

Nanorchestes sp. D. U.S.A., Indiana, Porter Co., Indiana Dunes State Park, 41.6872 N 86.9944 W, sand dunes near lake Michigan shoreline (10 cm deep); collector: Samuel Bolton, 17 May, 2013. Female (OSAL 0114263). Used for palp tarsus (Fig. 15).

Neonanorchestes sp. U.S.A., Maryland, Worcester Co., Assateague National Park, 38.1845 N 75.1633 W, sand dune next to inlet (10 cm deep); collector: Samuel Bolton, April, 2013. Female (FSCA 00030191).