

A review of the taxonomy and biology of pseudoscorpions of *Nannowithius* and *Termitowithius* (Pseudoscorpiones, Withiidae), inquilines of social insects

Mark S. Harvey: Department of Terrestrial Zoology, Western Australian Museum, Locked Bag 49, Welshpool DC, Western Australia 6986, Australia; Research Associate: Division of Invertebrate Zoology, American Museum of Natural History, 79th Street @ Central Park West, New York, New York 10024-5192, USA; Research Associate: Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94103–3009 USA; Adjunct: School of Animal Biology, University of Western Australia, Crawley, Western Australia 6009, Australia; Adjunct: School of Natural Sciences, Edith Cowan University, Western Australia 6027, Australia. E-mail: mark.harvey@museum.wa.gov.au

Abstract. The *Nannowithius* group of the pseudoscorpion family Withiidae is newly defined, consisting of *Nannowithius* Beier, 1932 from northern Africa and the Middle East, and *Termitowithius* Muchmore, 1990 from east Africa. The group is characterized by the lack of a tactile seta on the posterior tarsi, and they are the only withiids to possess this character state. Both genera are associated as inquilines with social insects, *Nannowithius* with ants and *Termitowithius* with termites. *Withius caecus* Beier, 1929 and *Plesiowithius dekeyseri* Vachon, 1954 are redescribed and transferred to the genus *Nannowithius*, forming the new combinations *N. caecus* (Beier) and *N. dekeyseri* (Vachon). *Plesiowithius* is treated as a new synonym of *Nannowithius*. A revised description and new illustrations of *Termitowithius kistneri* Muchmore, 1990 are presented.

Keywords: Taxonomy, morphology, new synonymy

Many different pseudoscorpions have been recorded in the nests of social insects, termites, bees and ants. However, many of these records are rather circumstantial and based on collecting records, rather than any detailed examination of the biology of the pseudoscorpion and its association with its host. In most cases, the pseudoscorpions are species that occur in other habitats, and their association with insects is fortuitous or, at best, temporary.

Perhaps the best documented example is the association between species of the cheliferid genus *Ellingsenius* Chamberlin, 1932 and bees in Africa, Asia and southern Europe; there are virtually no records of *Ellingsenius* being collected anywhere other than bee nests. Likewise, species of the chernetid genus *Dasychernes* Chamberlin, 1929 are known from bee nests in Central America (Chamberlin 1929; Gonzalez et al. 2008). The Australian genus *Marachernes* Harvey, 1992 is associated with ants of the genus *Anonychomyrma* Donisthorpe (Harvey 1992a; Cole et al. 1995). The sole species of *Myrmochernes* Tullgren, 1907, *M. africanus* Tullgren, 1907 occurs with *Camponotus maculatus* (Fabricius, 1782) in South Africa (Tullgren 1907). The three species of *Sphenochernes* Turk, 1953 have been found in ants' nests, with *S. bruchi* Mello-Leitão, 1925 and *S. schulzi* Turk, 1953 from Argentina associated with *Acromyrmex lundii* Guérin-Méneville, 1838 (Mello-Leitão 1925; Turk 1953), and *S. camponoti* (Beier, 1970) with *C. rufipes* (Fabricius, 1775) in southern Brazil (Beier 1970). Another genus that is strongly associated with social insects is the African chernetid genus *Pilanus* Beier, 1930, with *P. pilatus* Beier, 1930 from Senegal and *P. pilifer* Beier, 1930 from Eritrea found in termite nests (Beier 1930), and *P. proximus* Beier, 1955 from a nest of the ant *Messor cephalotes* (Emery, 1895) in Kenya (Beier 1955a). Other species associated with termites are relatively rare, but the best known association is the bizarre African termitophile *Termitowithius kistneri* Muchmore, 1990 of the family Withiidae (Muchmore 1990), although other pseudoscorpions are known to inhabit the abandoned nests of termites (e.g., Girard & Lamotte 1990; Heurtault 1994; Martius et al. 1994).

While examining specimens of the family Withiidae, major similarities between the genera *Termitowithius* and *Nannowithius* Beier, 1932 were noted, which were also shared with the genus *Plesiowithius* Vachon, 1954. These resemblances may indicate a common ancestry. The purposes of this paper are to provide a redescription of some species of *Nannowithius* and *Termitowithius*, to transfer *Withius caecus* Beier, 1929 to *Nannowithius*, and to examine the relationship of *Plesiowithius* with *Nannowithius*.

METHODS

The material mentioned in this study is lodged in the Florida State Collection of Arthropods, Gainesville (FSCA), Hungarian Natural History Museum, Budapest (HNHM), Hebrew University of Jerusalem (HUJ), Museo Civico di Storia Naturale di Genova (MCSNG), Muséum d'histoire naturelle de la Ville de Genève (MHNG), Museum National d'histoire Naturelle, Paris (MNHN), Museo Zoologico di Università degli Studi di Napoli, Portici, Italy (MZUN), Naturhistorisches Museum Basel (NMB), and Naturhistorisches Museum Wien (NHMW). The specimens stored in ethanol were examined by preparing temporary slide mounts by immersing the specimen in 75% lactic acid at room temperature for several days, and mounting them on microscope slides with 10 mm coverslips supported by small sections of 0.25 mm diameter nylon fishing line. Specimens were observed with a Leica DM2500 compound microscope and illustrated with the aid of a drawing tube. Measurements were taken at the highest possible magnification using an ocular graticule. After study, the specimens were rinsed in water and returned to 75% ethanol with the dissected portions placed in 12 x 3 mm glass genitalia microvials (BioQuip Products, Inc.).

Terminology and mensuration mostly follow Chamberlin (1931), with the exception of the nomenclature of the pedipalps and legs, and with some minor modifications to the terminology of the trichobothria (Harvey 1992b), cheliceral setation (Harvey & Edward 2007), cheliceral rallum (Judson 2007)

and faces of the appendages (Harvey et al. 2012). The ratio TS is the distance from the base of tarsus IV to the tactile seta, divided by the length of the entire tarsus. The abbreviation gls refers to the abdominal glandular setae found on the sternites of many withiids. The following abbreviations are used for the male genitalia: ca, chitinized arch; ejca, ejaculatory canal atrium; la, lateral apodeme; pvd, postero-ventral diverticulum; vd, ventral diverticulum.

Only the original description is given in the synonymy of each taxon; other citations can be found in Harvey (2013).

SYSTEMATICS

Family Withiidae Chamberlin, 1930

Genus *Nannowithius* Beier, 1932

Nannowithius Beier 1932:57.

Plesiowithius Vachon 1954:1029. **Syn. nov.**

Myrmecowithius Beier 1963: 195–196 (synonymized by Mahnert 1988:68).

Type species.—*Nannowithius*: *Chelififer aethiopicus* Simon, 1900, by original designation.

Plesiowithius: *Plesiowithius dekeyseri* Vachon, 1954, by original designation.

Myrmecowithius: *Myrmecowithius wahrmani* Beier, 1963, by original designation.

Diagnosis.—Species of *Nannowithius* differ from all other withiids, except *Termitowithius kistneri*, by the lack of a tactile seta on the tarsi of legs III and IV. *Nannowithius* differs from *Termitowithius* by the presence of a venom apparatus in both chelal fingers (vestigial in *Termitowithius*), the presence of abdominal glandular setae (absent in *Termitowithius*), the lack of numerous sense spots on the chelal fingers (present in *Termitowithius*), and the presence of paired spermathecae (spermathecae absent in *Termitowithius*).

Description.—*Adults*: Chelicera: with 5 setae on hand and 1 subdistal seta on movable finger; seta *bs* and *sbs* dentate, remaining setae acuminate; seta *bs*, *sbs* and *es* shorter than others; rallum of 4 blades, the most distal blade with several serrations on leading edge, other blades smooth.

Pedipalp: Chelal fingers elongated. Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria: *est* situated closer to *et* than to *esb* or midway between *esb* and *et*; *it* situated subdistally; *st* situated closer to *t* than to *sb*; *sb* situated much closer to *b* than to *st*. Retrolateral margin of chelal fingers without numerous sensilla. Venom apparatus present in both chelal fingers, nodus ramosus slightly inflated.

Carapace: Eyes present (as vestigial eye-spots) or absent; with 2 furrows, posterior furrow situated closer to posterior carapace margin than to anterior furrow.

Legs: junction between femora and patellae I and II slightly oblique to long axis; tarsus IV without tactile seta; subterminal tarsal setae arcuate and acute; claws of legs unmodified.

Abdomen: Most tergites and sternites with medial suture. Male tergites without lateral keels. Males without paired sac-like invaginations on anterior margins of sternites; males with patches of glandular setae on sternites V–IX, V–VIII, V–X, VII–VIII or IV–IX, females with glandular setae on segments V–IX or VI–X; glandular setae short and conical.

Spiracular helix present. Pleural membrane longitudinally striate and somewhat wrinkled.

Genitalia: Male: lateral apodemes extending laterally, with obvious dorsal branches forming chitinized arch; rams horn organs absent; lateral apodemes paired, extending posteriorly. Female: with 1 pair of small lateral cribriform plates and 1 large, median cribriform plate; with a pair of distinct spermathecae.

Remarks.—Species of *Nannowithius* are unusual amongst the Withiidae, as they lack a tactile seta on tarsi III and IV. The only other withiids that lack this seta are *Plesiowithius dekeyseri* and *Termitowithius kistneri*, the sole representatives of *Plesiowithius* and *Termitowithius*, respectively (Vachon 1954; Muchmore 1990). All other withiids possess a tactile seta in the medial or distal section of the tarsus. Eyes are lacking in both species of *Plesiowithius* and *Termitowithius*, and in the majority of *Nannowithius* species; a single pair of eye-spots or corneate eyes is present in all other withiids. The only exceptions appear to be *N. aethiopicus* and *N. paradoxus* (Mahnert, 1980) which are described as having rudimentary eye-spots (Mahnert 1980, 1988).

Vachon (1954) distinguished *Plesiowithius* from *Nannowithius* by the presence of multiple setal rows on the tergites (compared with a single row in *Nannowithius*), and the slightly larger size (e.g., pedipalpal femur 0.93 mm in length, compared with 0.41–0.64 mm in *Nannowithius*). He also listed the presence of glandular setae on sternites V–IX in *Plesiowithius*, but the type species of *Nannowithius*, *N. aethiopicus*, only has glandular setae on sternites VI and VII (Mahnert 1988), and the other species have them on sternites V–IX [*N. buettikeri* (Mahnert, 1980) and *N. pakistanicus* (Beier, 1978)], IV–IX (*N. paradoxus*), IV–VIII (*N. wahrmani*) or V–VII (*N. caecus*, see below). Therefore, the main criteria used by Vachon (1954) to separate *Plesiowithius* from *Nannowithius* no longer apply, and *Plesiowithius* is relegated to the synonymy of *Nannowithius*. Incidentally, four of the five species of *Nannowithius* were originally placed in the aptly named *Myrmecowithius*, which was synonymized with *Nannowithius* by Mahnert (1988).

With the inclusion of *P. dekeyseri* and *W. caecus* in *Nannowithius* (see below), the distribution of the genus now extends from Pakistan through the Middle East to eastern and northern Africa (Fig. 1).

Nannowithius aethiopicus (Simon, 1900)

Chelififer aethiopicus Simon 1900:596.

Type specimens.—ERITREA: *Gash-Barka*: lectotype male, Agordat [15°33'N, 37°53'E], 1896, F. Derchi (MCSNG, not examined). Paralectotype: 1 specimen, collected with lectotype (MNHN, no. 20732) (not examined).

Description.—See Mahnert (1988).

Remarks.—*Nannowithius aethiopicus* is only known from the type locality in Eritrea.

Nannowithius buettikeri (Mahnert, 1980)

Myrmecowithius buettikeri Mahnert 1980:40–42, figs 23–28.

Type specimens.—SAUDI ARABIA: *Ar Riyād*: holotype male, Khushūm al Buwaybiyah (as Kushm al Buwaybiyat) [25°10'N, 46°52'E] (NMB, not examined). Paratypes (NMB,

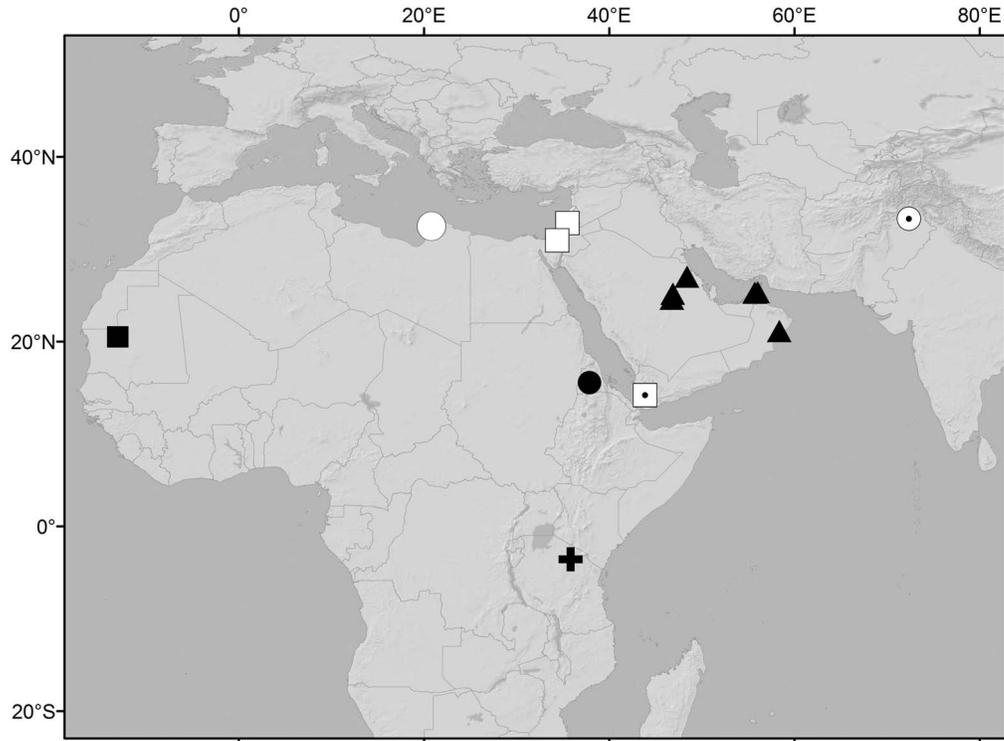


Figure 1.—Map showing distribution of species of the *Nannowithius* group: *Nannowithius aethiopicus* (●); *N. buettikeri* (▲); *N. caecus* (○); *N. dekeyseri* (■); *N. pakistanicus* (⊙); *N. paradoxus* (□); *N. wahrmani* (◻); *Termitowithius kistneri* (+).

MNHG, not examined): 3 females, collected with holotype; 1 female, Al Khubra [27°01'N, 48°24'E], 29 May 1978, W. Bütiker; 1 female, Riyadh [27°01'N, 48°24'E], 3 March 1978, A. M. Talhouk.

Description.—See Mahnert (1980).

Remarks.—*Nannowithius buettikeri* is known from Saudi Arabia (Mahnert 1980), Oman (Mahnert 1991) and the United Arab Emirates (Mahnert 2009).

Nannowithius caecus (Beier, 1929), comb. nov.

Figs. 2, 3

Withius caecus Beier 1929:78–79, figs 1a–b.

Material examined.—LIBYA: *Banghazi*: holotype male, Marj (as El Merg) [32°29'N, 20°50'E], Cyrenaica, 14 April (year not stated), F. Silvestri (MZUN).

Diagnosis.—*Nannowithius caecus* differs from *N. aethiopicus* and *N. paradoxus* by the lack of eyes or eye-spots, from *N. buettikeri* by the less sharply defined pedicel on the pedipalpal femur, from *N. wahrmani* by the longer chelal fingers, and from *N. dekeyseri* and *N. pakistanicus* by the position of trichobothrium *est* which is situated only slightly distal to *ist* (*est* strongly distal to *ist* in *N. dekeyseri*, and basal to *ist* in *N. pakistanicus*).

Description.—*Adult male*: color: with sclerotized portions generally pale red-brown, legs and sternites paler than remainder of body.

Chelicera: With 5 setae on hand, all acuminate; movable finger with 1 subdistal seta; galea small, with 1–2 small terminal rami; rallum of 4 blades; serrula exterior with 20 blades; lamina exterior present.

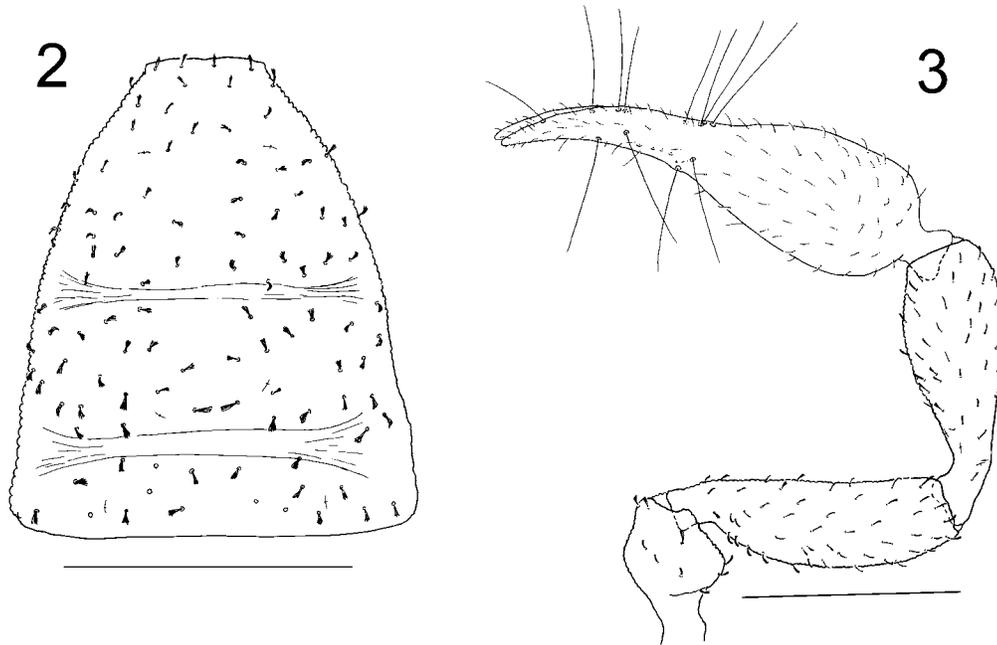
Pedipalp: Trochanter, femur and patella granulate, chela smooth; trochanter 1.76, femur 3.52, patella 2.80, chela (with pedicel) 3.51, chela (without pedicel) 3.24, hand 1.54 x longer than broad, movable finger 1.14 x longer than hand (without pedicel). Femur of male with basal region not expanded (Fig. 3). Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Fig. 3): *eb*, *esb*, *ib* and *ist* situated basally; *isb* and *it* situated sub-medially; *b* and *sb* situated sub-basally near one another; *st* much closer to *t* than to *sb*. Venom apparatus not visible.

Carapace (Fig. 2): 1.18 x longer than broad; posteriorly widened; eyes absent; with 99 setae, including 4 near anterior margin, 42 additional setae in anterior zone, 37 in medial zone and 16 in posterior zone; with 2 distinct furrows; posterior furrow slightly closer to posterior carapaceal margin than to median furrow.

Coxal region: Maxilla with 2 apical setae and 1 very small internal, sub-oral seta, maxilla without rugose area; chaetotaxy of coxae I–IV: 7: 7: 9: 16.

Legs: Junction between femora and patellae I and II only slightly oblique; posterior tarsi without tactile seta; subterminal tarsal setae arcuate and acute; arolium slightly longer than claws.

Abdomen: Tergites and sternites with faint medial suture. Tergal chaetotaxy: 14: 13: 13: 19: 19: 22: 21: 22: 20: 20: 8: 2; mostly uniseriate but some tergites with a few setae placed anteriorly; all setae strongly foliate. Sternal chaetotaxy: 12: (3) 8 (3): (2) 10 (2): 17 + 10/11 gls: 17 + 7/8 gls: 16 + 6/6 gls: 14 + 3/3 gls: 14: 14: 8: 2; sternites V–VII of ♂ with patches of glandular setae; setae uniseriate and acuminate; glandular setae of ♂ stout and conical; ♂ without paired invaginations on anterior margins of sternites.



Figures 2–3.—*Nannowithius caecus* (Beier), holotype male: 2. Carapace, dorsal; 3. Right pedipalp, dorsal. Scale lines = 0.5 mm.

Genitalia: Male with lateral apodemes short, other details not visible in specimens.

Dimensions (mm): Male holotype: Body length 1.94. Pedipalps: trochanter 0.413/0.234, femur 0.686/0.195, patella 0.642/0.229, chela (with pedicel) 1.056/0.301, chela (without pedicel) 0.976, hand length 0.464, movable finger length 0.531. Carapace 0.832/0.706.

Remarks.—Beier (1929) described *Withius caecus* from a single male collected at El Merg, Cyrenaica. This locality is nowadays known as Barce and located in the Libyan district of Benghazi. Beier's choice of name reflected the lack of eyes in the holotype, and he also clearly stated that the posterior tarsi lacks a tactile seta. As all other species currently attributed to *Withius* have eyes which are either rounded, corneate eyes or flat eye-spots, and have a tactile seta on the posterior tarsi, the position of *W. caecus* seems anomalous. The holotype male of *W. caecus* is in good condition and clearly does not belong to *Withius*, and is readily identified as a species of *Nannowithius* by the lack of a tactile seta, the position of the chelal trichobothria and the lack of eyes (Mahnert 1988). Therefore, *W. caecus* is here transferred to *Nannowithius*.

Nannowithius dekeyseri (Vachon, 1954), comb. nov.

Figs. 4–10

Plesiowithius dekeyseri Vachon 1954:1026–1029, figs 6–11.

Material examined.—Syntypes: MAURITANIA: *Adrar*: 1 male, Atar [20°31'N, 13°03'W], May 1949, A. Villiers (MNHN; 3 slides); 1 male, same locality, 26 November 1951, P. Dekeyser and A. Villiers (MNHN; 1 slide consisting only of chelicerae).

Diagnosis.—*Nannowithius dekeyseri* differs from all other species of the genus by the position of trichobothrium *est* which is situated distal to *ist*, but is either basal to *ist* or is opposite *ist* in the other species (Beier 1963, 1978; Mahnert 1980, 1988).

Description.—*Adult male*: color: pedipalps, legs and carapace deep red-brown, other body portions yellow-brown.

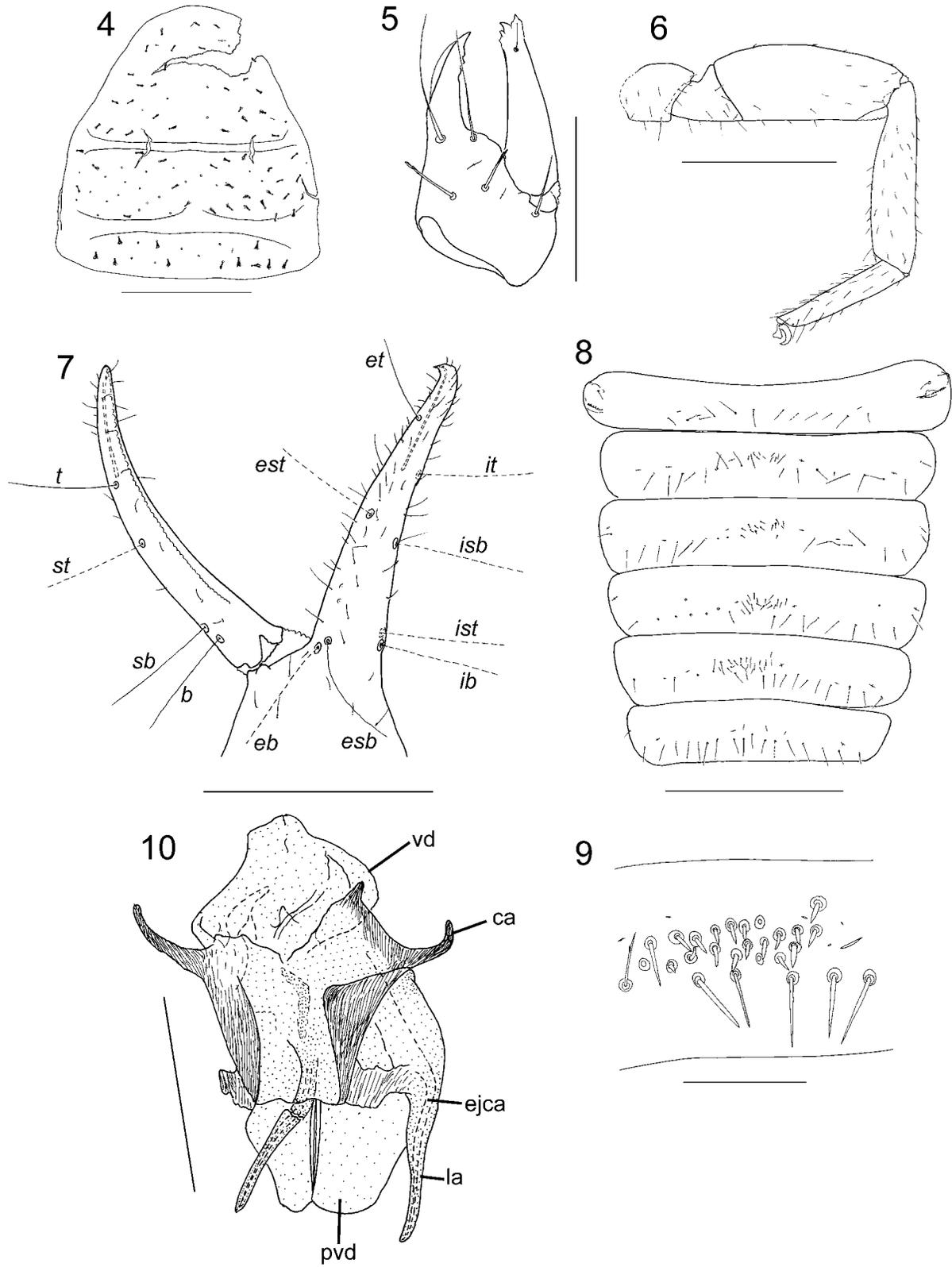
Chelicera (Fig. 5): With 5 setae on hand, *bs* and *sbs* dentate, all others acuminate; movable finger with 1 subdistal seta; galea with 2 small terminal rami; rallum of 4 blades; serrula exterior with 18 blades; lamina exterior present.

Pedipalp: Trochanter, femur and patella coarsely granulate, chela slightly granulate, and fingers smooth; setae generally clavate and denticulate; femur 3.89 x longer than broad. Femur of male with basal region not expanded. Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Fig. 7): *eb*, *esb*, *ib* and *ist* situated basally; *est* and *isb* sub-medial, with *est* situated slightly distal to *isb*; *it* situated sub-distally; *b* and *sb* situated sub-basally near one another; *st* closer to *t* than to *sb*. Venom apparatus present in both chelal fingers, venom ducts long, terminating in nodus ramosus between near *it* in fixed finger and near *t* in movable finger. Retrolateral margin of fixed finger with 2 sense-spots, prolateral margin with 14 sense-spots; retrolateral margin of movable finger with 2 sense-spots, prolateral margin with 3 sense-spots. Chelal teeth small; fixed finger with 46 teeth; movable finger with 48 teeth; accessory teeth absent.

Carapace (Fig. 4): ca. 1.05 x longer than broad; posteriorly widened; eyes absent; with 97 strongly foliate setae, including 32 in anterior zone, 48 in medial zone and 17 in posterior zone; with 2 distinct furrows; posterior furrow slightly closer to posterior carapaceal margin than to median furrow.

Coxal region: Maxilla with 2 apical setae and 1 very small internal, sub-oral seta, plus 16 additional setae, maxilla without rugose area; chaetotaxy of coxae I–IV: 9: 8: 9: ca. 20.

Legs: Junction between femora and patellae I and II slightly oblique to long axis; junction between femora and patellae III and IV very angulate; femora III and IV much smaller than patellae III and IV (Fig. 6); femur + patella of leg IV 3.12 x longer than broad; tarsi III and IV without tactile seta;



Figures 4–10.—*Nannowithius dekeyersi* (Vachon), syntype male: 4. Carapace, dorsal; 5. Left chela, lateral; 6. Right chelicera; 7. Left leg IV; 8. Sternites IV–IX, ventral; 9. Sternite VIII, detail of setae; 10. Genitalia, ventral. Scale lines = 0.5 mm (Figs. 4, 5, 7, 8), 0.2 mm (Figs. 6, 9, 10).

subterminal tarsal setae arcuate and acute; claws of legs unmodified; arolium shorter than claws (Fig. 6).

Abdomen. Tergites I–X with suture line; sternites V–VII with faint medial suture. Tergal chaetotaxy: 15: 15: 13: 16: 20: 19: 20: 23: 21: 20: 16: 2; tergites I–III and X uniseriate, IV uniseriate but with pair of discal setae, and V–IX biseriate; all setae strongly foliate. Sternal chaetotaxy: 15: (2) 10 (2): (2) 13 [0+0] (2): 19 + 12 gls: 21 + 17 gls: 18 + 15 gls: 15 + 21 gls: 20 + 2 gls: 11: 12: 2; sternites V–VIII of ♂ with patches of glandular setae (Fig. 9); sternites V–VI uniseriate but with pair of discal setae, and VIII–X uniseriate; glandular setae of ♂ stout and conical; ♂ without paired invaginations on anterior margins of sternites.

Genitalia (Fig. 10): Lateral apodemes extending laterally, with obvious dorsal branches forming chitinized arch; rams horn organs absent; lateral apodemes paired, extending posteriorly.

Dimensions (mm): Male syntype: body length ca. 2.9. Pedipalps: not measurable. Chelicera 0.272/0.170, movable finger length 0.207. Carapace ca. 1.06/1.008. Leg I: femur 0.187/0.195, patella 0.429/0.169, tibia 0.461/0.129, tarsus 0.378/0.080. Leg IV: femur + patella 0.755/0.242, tibia 0.619/0.142, tarsus 0.435/0.088.

Remarks.—Vachon (1954) described this species from two males collected in north-western Mauritania. One of these males, collected during March 1949, is mounted on three microscope slides and in fair condition. The chelae are crushed and immeasurable, and the carapace is slightly flattened and cracked (Fig. 4). The other specimen, collected during September 1951, is only represented by the chelicerae, which are also slide-mounted.

Nannowithius pakistanicus (Beier, 1978)

Myrmecowithius pakistanicus Beier 1978:233–234, fig 2.

Type specimens.—PAKISTAN: *Punjab*: holotype male, Kohala, Kashmir [33°17'N, 72°22'E], 3,000 feet, in nest von *Messor* sp., 13 June 1974, C. Baroni Urbani (NMB, not examined). Paratypes: 3 males, collected with holotype (NMB, NHMW, not examined)

Description.—See Beier (1978).

Remarks.—*Nannowithius pakistanicus* is only known from the type locality in Pakistan.

Nannowithius paradoxus (Mahnert, 1980)

Myrmecowithius paradoxus Mahnert 1980:38–40, figs 17–22.

Type specimens.—YEMEN: *Ibb*: holotype male, Wadi Zabib [14°11'N, 43°53'E], November 1971, A. Szalai-Marzso (HNHM, not examined). Paratype: 1 female, collected with holotype (MNHG, not examined).

Description.—See Mahnert (1980).

Remarks.—*Nannowithius paradoxus* is only known from the type locality in Yemen.

Nannowithius wahrmani (Beier, 1963)

Myrmecowithius wahrmani Beier 1963:196–197, fig 8

Type specimens.—Syntypes: ISRAEL: *HaDarom* (*Southern*): 3 males, 1 female, 2 tritonymphs, Wadi Abyad

[30°57'N, 34°23'E], aus einem Nest van *Messor semirufus*, 27 March 1952, J. Wahrman (HUJ, not examined).

Description.—See (Beier 1963). Mahnert (1975) provided an illustration of the female genitalia.

Remarks.—*Nannowithius wahrmani* is only known from the type locality, Wadi Abyad Beier (1963) and Mt. Arbel (Mahnert 1974), both located in Israel.

Genus *Termitowithius* Muchmore, 1990

Termitowithius Muchmore 1990:125.

Type species.—*Termitowithius kistneri* Muchmore, 1990, by original designation.

Diagnosis.—*Termitowithius* is the only withiid genus that lacks a fully developed venom apparatus in the chelal fingers (Figs. 17, 18). It also is the only genus that lacks abdominal glandular setae that also lacks a tactile seta on tarsi III and IV (Fig. 21).

Description.—*Adults*: Chelicera (Fig. 12): with 5 setae on hand and 1 subdistal seta on movable finger; seta *bs* and *sbs* dentate, remaining setae acuminate; seta *bs* and *sbs* much shorter than others; rallum of 4 blades, the most distal blade with several serrations on leading edge, other blades smooth (Fig. 13).

Pedipalp (Figs. 15, 16): Chelal fingers greatly elongated, movable finger much longer than hand (without pedicel). Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Fig. 16): *est* situated closer to *et* than to *esb*; *it* situated subdistally; *st* situated closer to *t* than to *sb*; *sb* situated much closer to *b* than to *st*. Retrolateral margin of chelal fingers with numerous sensilla, more numerous on fixed chelal finger. Venom apparatus absent in both chelal fingers, nodus ramosus absent.

Carapace (Fig. 11): Eyes absent; with 2 furrows, posterior furrow situated closer to posterior carapace margin than to anterior furrow.

Legs (Figs. 20, 21): Junction between femora and patellae I and II slightly oblique to long axis; tarsus IV without tactile seta; subterminal tarsal setae arcuate and acute; claws of legs unmodified.

Abdomen: Male tergites without lateral keels; all setae thickened and strongly dentate (Fig. 22); glandular setae absent.

Genitalia: Male (Fig. 24): lateral apodemes extending laterally, with obvious dorsal branches forming chitinized arch; rams horn organs absent; lateral apodemes paired, extending posteriorly, very slender. Female (Fig. 25): with 1 pair of small lateral cribriform plates and 1 large, median cribriform plate with small protrusions; spermathecae not visible.

Remarks.—Muchmore (1990) suggested that *Termitowithius* should be included in the Withiidae, despite the lack of glandular setae on the sternites, a feature that is found in most other withiids apart from *Protowithius* Beier, 1955 from Juan Fernandez Islands and *Juxtachelifer* Hoff, 1956 from southwestern U.S.A. (Beier 1955b; Hoff 1956; Harvey 1992b). He reasoned that the morphology of the anterior pairs of legs in which the junction between the femora and patellae was perpendicular or only slightly oblique was characteristic of all Withiidae, including *Termitowithius*.

The affinities of *Termitowithius* within the family Withiidae are difficult to discern. While it resembles *Protowithius* and *Juxtachelifer* in the lack of glandular setae on the sternites, it

seems to be most similar to *Nannowithius* which is the only other withiid that lack a tactile seta on tarsi III and IV, and which lack eyes or have the eyes reduced to rudimentary eye-spots. All other withiids have a strongly developed tarsal tactile setae, and eyes in the form of distinct eye-spots or rounded, corneate eyes.

Termitowithius kistneri Muchmore, 1990
Figs. 11–25

Termitowithius kistneri Muchmore 1990:126–127, figs 1–7.

Material examined.—TANZANIA: *Arusha*: holotype male, Lake Manyara National Park [3°35'S, 35°50'E], from fungus gardens in nest (T-374) of *Macrotermes subhyalinus* (Blattodea: Termitidae), 19 June 1970, D.H. Kistner (FSCA WM2662.01001). Paratypes: TANZANIA: *Arusha*: 1 female (allotype), collected with holotype (FSCA WM2662.01003); 1 male, 1 female, collected with holotype (FSCA WM2662.01002, 4).

Diagnosis.—As for genus.

Description.—*Adults*: color: sclerotized portions generally light red-brown, coxae and legs lighter. Pedipalps, carapace, and to a lesser extent, tergites and legs, with an obvious pseudo-derm layer.

Chelicera (Fig. 12): With 5 setae on hand and 1 subdistal seta on movable finger; seta *bs* and *sbs* dentate, remaining setae acuminate; seta *bs* and *sbs* much shorter than others; with 2 dorsal lyrifissures and 1 ventral lyrifissure; galea of ♂ and ♀ with ca. 10 small terminal rami (Fig. 14); rallum of 4 blades, the most distal blade with several serrations on leading edge, other blades smooth (Fig. 13); serrula exterior 19 (♂, ♀) blades; lamina exterior present.

Pedipalp (Fig. 15): Surfaces of trochanter, femur and patella granulate, chela smooth; patella with 2 small sub-basal lyrifissures; trochanter 1.62–1.76 (♂), 1.58–1.64 (♀), femur 3.86–4.30 (♂), 4.00–4.18 (♀), patella 3.53–3.88 (♂), 3.45–3.50 (♀), chela (with pedicel) 6.11–6.24 (♂), 5.68–5.88 (♀), chela (without pedicel) 5.91–5.96 (♂), 5.46–5.69 (♀), hand 2.17 (♂), 2.02 (♀) x longer than broad, movable finger much longer than hand (without pedicel), 1.74–1.76 (♂), 1.74–1.85 (♀) x longer than hand (without pedicel). Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Fig. 16): *eb* and *esb* situated basally, *ib* and *ist* subbasally, *est* and *isb* submedially, *et* and *it* subdistally, *est* situated distal to *isb*; *t* situated subdistally, *st* slightly closer to *t* than *sb*, and *sb* situated much closer to *b* than to *st*. Diploid sensillum situated slightly basal to *st*. Venom apparatus absent from both chelal fingers, but vestigial venom ducts present in distal tooth (Figs. 17, 18). Retrolateral margin of chelal fingers with numerous sensilla, more numerous on fixed chelal finger. Chelal teeth rounded; fixed finger with 48 (♂, ♀) teeth; movable finger with 52 (♂, ♀) teeth; accessory teeth absent.

Carapace (Fig. 11): Coarsely granulate; 0.89–0.95 (♂), 0.99–1.01 (♀) x longer than broad; eyes absent; with ca. 169 (♂), 181 (♀) setae, arranged with ca. 68 (♂), 70 (♀) (including 4 (♂), 5 (♀) near anterior margin) in anterior zone, ca. 65 (♂), 70 (♀) in median zone, and ca. 36 (♂), 41 (♀) in posterior zone; with few lyrifissures; with 2 furrows, posterior furrow situated closer to posterior carapace margin than to anterior furrow; posterior margin with median indentation.

Coxal region: Maxillae lightly granulate near anterior and lateral margins, remainder smooth; coxae smooth; manducatory process with 2 apical and subapical acuminate setae, plus 1 small sub-oral seta, and 21 (♂), 23 (♀) additional setae; median maxillary lyrifissure rounded and situated submedially; posterior maxillary lyrifissure rounded. Coxa IV of male not modified; coxal sac absent. Chaetotaxy of coxae I–IV: ♂, 10: 14: 14: 22; ♀, 10: 17: 19: 24.

Legs (Figs. 20, 21): Junction between femora and patellae I and II slightly oblique to long axis; junction between femora and patellae III and IV very angulate; femora III and IV much smaller than patellae III and IV; femur + patella of leg IV 2.90–3.13 (♂), 2.92–3.06 (♀) x longer than broad; tarsi III and IV without tactile seta; subterminal tarsal setae arcuate and acute; claws of legs unmodified; arolium shorter than claws.

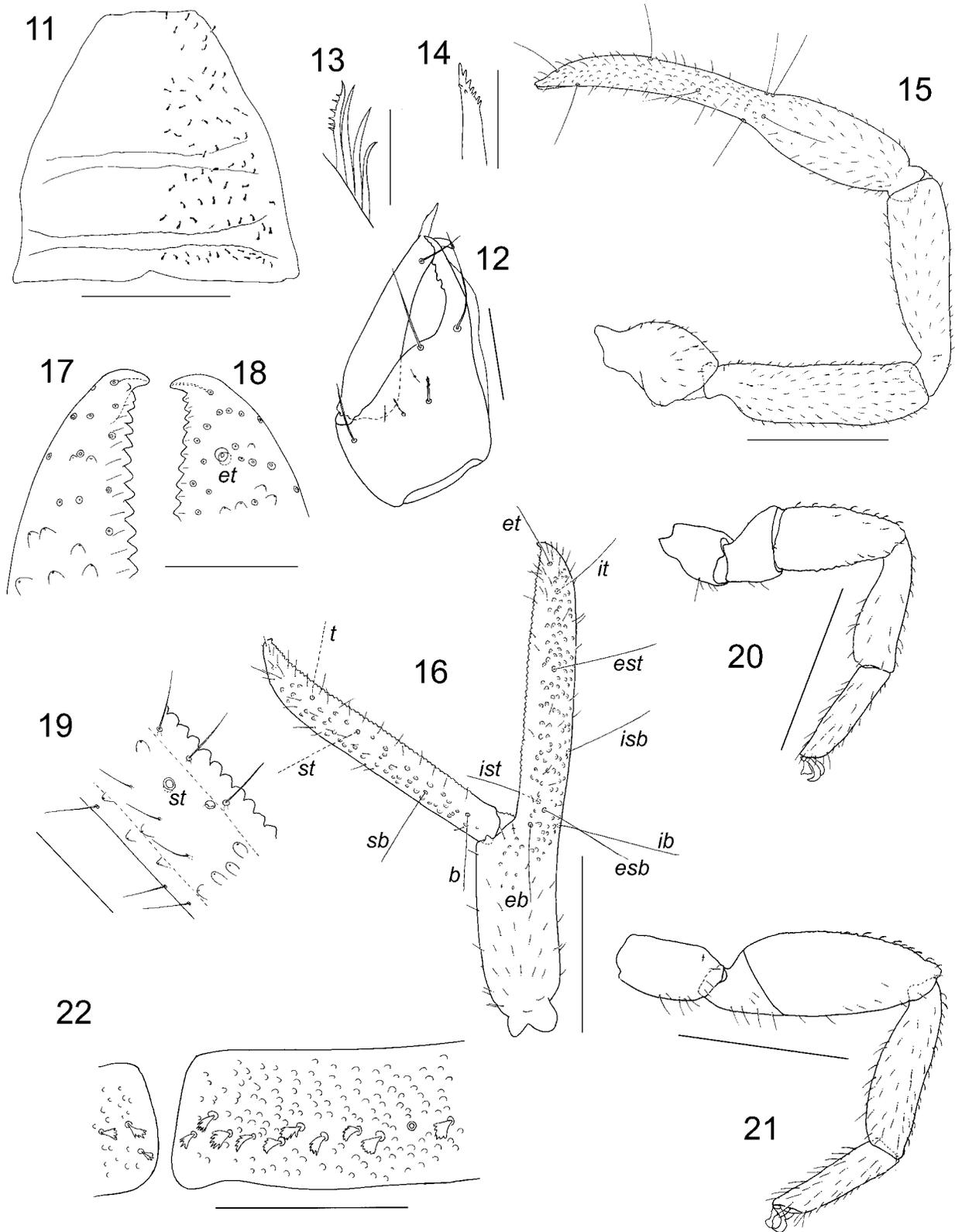
Abdomen: Tergites I–X and sternites V–X with median suture line (Fig. 22). Tergal chaetotaxy: ♂, 35: 35: 41: 43: 46: 44: 46: 46: 49: 41: 30: 2; ♀, 44: 43: 45: 49: 53: 50: 59: 55: 55: 49: 25: 2; tergites irregularly uniseriate except for multiple discal seta on the posterior tergites; all setae thickened and strongly dentate (Fig. 22); ♂ tergites without lateral keels. Sternal chaetotaxy: ♂, 19: (1) 15 [0+0] (1): (1) 16 (1): 21: 20: 21: 20: 21: 19: 14: 2; ♀, 19: (1) 22 (2): (1) 18 (1): 23: 24: 24: 21: 20: 15: 12: 2; sternites irregularly uniseriate, except for lateral discal seta on sternites IX–XI; all setae acicular; ♂ sternite II with scattered setae (Fig. 23); glandular setae absent. Spiracles with helix. Anal plates (tergite XII and sternite XII) situated between tergite XI and sternite XI. Pleural membrane finely wrinkled-plicate; without any setae.

Genitalia: Male (Fig. 24): lateral apodemes extending laterally, with obvious dorsal branches forming chitinized arch; rams horn organs absent; lateral apodemes paired, extending posteriorly, very slender. Female (Fig. 25): with 1 pair of small lateral cribriform plates and 1 large, median cribriform plate with small protrusions; spermathecae not visible.

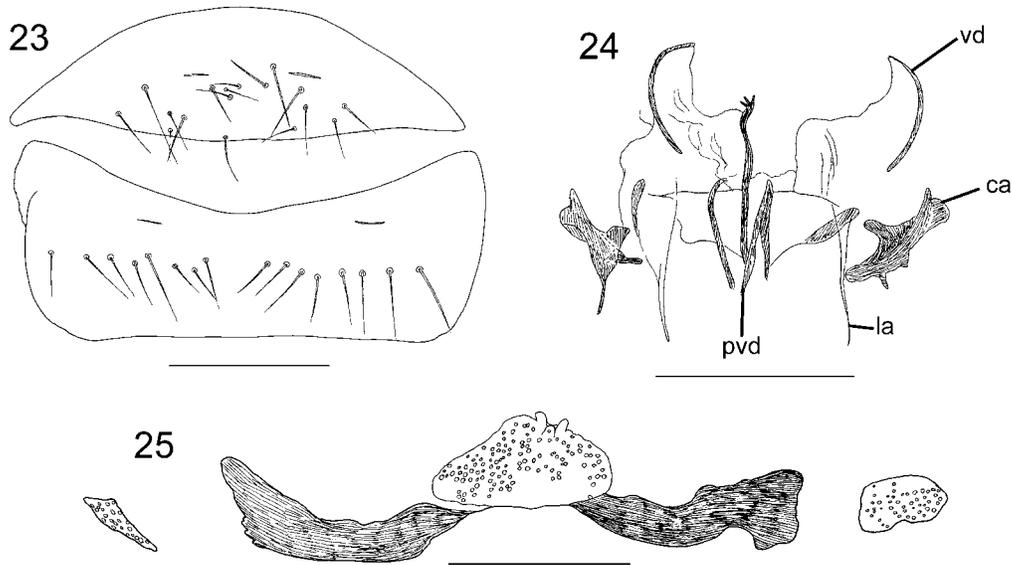
Dimensions (mm): Male holotype followed by male paratype (where applicable): Body length 2.45 (2.79). Pedipalps: trochanter 0.445/0.275 (0.475/0.27), femur 0.81/0.21 (0.86/0.20), patella 0.76/0.215 (0.795/0.205), chela (with pedicel) 1.405/0.23 (1.435/0.23), chela (without pedicel) 1.36 (1.37), hand length 0.50 (0.50), movable finger length 0.87 (0.88). Chelicera 0.29/0.165, movable finger length 0.22. Carapace 0.91/1.025 (0.89/0.94). Leg I: femur 0.18/0.18, patella 0.375/0.185, tibia 0.40/0.13, tarsus 0.35/0.09. Leg IV: femur + patella 0.695/0.24 (0.72/0.23), tibia 0.535/0.145, tarsus 0.38/0.095.

Female allotype followed by female paratype (where applicable): Body length 3.54 (3.38). Pedipalps: trochanter 0.46/0.29 (0.46/0.28), femur 0.84/0.21 (0.835/0.20), patella 0.76/0.22 (0.77/0.22), chela (with pedicel) 1.42/0.25 (1.41/0.24), chela (without pedicel) 1.365 (1.365), hand length 0.505 (0.485), movable finger length 0.88 (0.895). Chelicera 0.29/0.17, movable finger length 0.19. Carapace 0.985/0.975 (0.97/0.975). Leg I: femur 0.20/0.175, patella 0.41/0.185, tibia 0.405/0.135, tarsus 0.355/0.075. Leg IV: femur + patella 0.745/0.255 (0.735/0.24), tibia 0.55/0.145, tarsus 0.41/0.10.

Remarks.—Muchmore (1990) examined 11 adult specimens, of which the four slide-mounted specimens (the holotype, allotype and two paratypes) were examined for this study.



Figures 11–22.—*Termitowithius kistneri* Muchmore, holotype male, unless stated otherwise: 11. Carapace, dorsal; 12. Left chelicera; 13. Right rallum, female allotype; 14. Galea; 15. Right pedipalp, dorsal; 16. Left chela, lateral; 17. Tip of chelal finger; 18. Tip of movable chelal finger; 19. Teeth of movable chelal finger; 20. Leg I; 21. Leg IV; 22. Right tergite III. Scale lines = 0.5 mm (Figs. 11, 15, 16, 20, 21), 0.2 mm (Fig. 22), 0.1 mm (Figs. 12, 17–19), 0.05 mm (Figs. 13, 14).



Figures 23–25.—*Termitowithius kistneri* Muchmore: 23. Genital sternites, male paratype; 24. Genitalia, ventral, male paratype; 25. Genitalia, female allotype. Scale lines = 0.2 mm (Figs. 23, 24), 0.1 mm (Fig. 25).

As explained by Muchmore (1990), *Termitowithius kistneri* is a highly modified inquiline that is found within the fungus gardens in the nests of the African termite *Macrotermes subhyalinus* (Rambur, 1842). The fungus gardens of macrotermite nests are composed of the fungus *Termitomyces* which is cultivated by the termites, presumably to provide nutrition through the breakdown of grasses brought into the nest by the termites. The apparent modifications for an inquiline existence of *T. kistneri* include the lack of eyes, and the highly modified chelae of the pedipalps. The chelal fingers are greatly enlarged, and are nearly twice as long as the chelal hand (Fig. 16), and the retro-lateral margins of the fingers bear numerous sensilla that are more numerous on the fixed finger (Fig. 16). The venom apparatus of *T. kistneri* appears to be completely absent, as the venom tooth of both fingers is reduced in size, and the venom duct is restricted to a small channel within the venom tooth (Figs. 17, 18), but does not lead into a long venom duct and associated nodus ramosus found with the chelal fingers of all other species assigned to the suborder Iocheirata (e.g. Chamberlin

1931; Harvey 1992b; Muriene et al. 2008). It is not known whether the pseudoscorpion feeds on termites or some other inquiline in the nest, but it seems apparent that they have foregone using venom to subdue their prey and instead use their massive chelal fingers to grasp and probably crush their prey.

The termite host *Macrotermes subhyalinus* is widely distributed across much of tropical Africa (Ruelle 1970), where they build mounds with extensive subterranean galleries (Tilahun et al. 2012).

BIOLOGY

Some species of the genus *Nannowithius* and *Termitowithius kistneri*, which are the only withiids that lack a tactile seta on the posterior tarsi (see above), have strong affinities with social insects (Table 1). The original specimens of *N. wahrmanni* were collected from a nest of the ant *Messor semirufus* (André, 1883) in southern Israel (Beier 1963), whereas other specimens were found under stones but with no recorded association with ants (Mahnert 1974). Specimens of *N. pakistanicus* were also found

Table 1.—Locality and habitat data for species of *Nannowithius* and *Termitowithius*.

Species	Locality	Habitat	Reference
<i>Nannowithius aethiopicus</i>	ERITREA: Agordat	not stated	Simon (1900)
<i>Nannowithius buettikeri</i>	SAUDI ARABIA: Khushūm al Buwaybyah; Al Khubra; Riyadh	not stated	Mahnert (1980)
	OMAN: Shaqq	not stated	Mahnert (1991)
	UNITED ARAB EMIRATES: Sharjah Desert Park	light trap	Mahnert (2009)
	UNITED ARAB EMIRATES: Wadi Madaq	in leaf litter	Mahnert (2009)
<i>Nannowithius caecus</i>	LIBYA: Barce	not stated	Beier (1929)
<i>Nannowithius dekeyseri</i>	MAURITANIA: Atar	not stated	Vachon (1954)
<i>Nannowithius pakistanicus</i>	PAKISTAN: Kohala	in nest of <i>Messor</i> sp.	Beier (1978)
<i>Nannowithius paradoxus</i>	YEMEN: Wadi Zabib	not stated	Mahnert (1980)
<i>Nannowithius wahrmani</i>	ISRAEL: Wadi Abyad	in nest of <i>Messor semirufus</i>	Beier (1963)
	ISRAEL: Mt Arbel	under stones	Mahnert (1974)
<i>Termitowithius kistneri</i>	TANZANIA: Lake Manyara National Park	from fungus gardens in nest of <i>Macrotermes subhyalinus</i>	Muchmore (1990)

in the nests of ants (*Messor* sp.) (Beier 1978), and although the original description of *N. buettikeri* (Mahnert, 1980) contained no mention of habitat data (Mahnert 1980), specimens collected a few years later were recovered from light traps and leaf litter (Mahnert 2009), with at least the light trap records suggesting they were attached to flying insects. The termitophile *T. kistneri* has only been collected from the nest of the termite *Macrotermes subhyalinus* (Muchmore 1990). All other collections of the remaining four species of *Nannowithius*, *N. aethiopicus*, *N. caecus*, *N. dekeyseri* and *N. paradoxus*, lack any mention of habitat data (Table 1). While the evidence is not particularly overwhelming, it is likely that all species of these two withiid genera are associated with social insects, *Nannowithius* with ants and *Termitowithius* with termites. Further evidence of an obligate existence with social insects may lie with the lack of eyes in *Termitowithius* and in most species of *Nannowithius*. Only *N. aethiopicus* and *N. paradoxus* have eye-spots which are reported to be rudimentary (Mahnert 1980, 1988).

The only other withiids that are known to be associated with social insects are *Girardwithius pumilus* Heurtaut, 1994 and *Rexwithius girardi* Heurtaut, 1994 which occur in the defunct galleries of *Macrotermes* termites in west Africa (Heurtaut 1994). The presence of tarsal setae in both species (Heurtaut 1994) does not suggest a particularly close relationship with either *Nannowithius* or *Termitowithius*.

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