

A new species of the pseudoscorpion genus *Megachernes* (Pseudoscorpiones: Chernetidae) associated with a threatened Sri Lankan rainforest rodent, with a review of host associations of *Megachernes*

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Most species of the Old World pseudoscorpion genus *Megachernes* are associated with mammals, either within their nests or in their pelage, whereas others are found in cave systems, usually in bat guano. The first Sri Lankan species of the genus, *Megachernes kanneliyensis*, is described from the fur of an endemic, threatened Sri Lankan mouse, *Mus mayori pococki* from the Kanneliya rainforest. The species is compared with other species of the genus. Host associations of all named and several unnamed species of *Megachernes* are reviewed, with two main habitat types, those found in mammal nests and in their pelage, and those found in bat guano. Based on similarities with *Megachernes*, *Chiridiochernes* is transferred to Lamprochernetinae as the spermathecae are T-shaped, the sole diagnostic feature of the subfamily.

Keywords: threatened species; *Mus mayori pococki*; rainforest; morphology; taxonomy

Introduction

Mayor's Mouse, *Mus mayori* (Thomas, 1915), is endemic to the rainforests of Sri Lanka, with *Mus mayori mayori* found in the montane zone and *Mus mayori pococki* Ellerman, 1947 found in the lowlands (Phillips 1980). It is listed as Vulnerable by the IUCN because of deforestation of its native habitat (Goonatilake et al. 2008). *Mus mayori pococki* is a medium-sized murid with a snout–vent length of approximately 90 mm (Phillips 1980; Ratnaweera et al. 2010). Previous studies on parasites occurring on *Mus mayori* found the laelapid mite *Laelaps atypicus* Turk, 1950 (Laelapidae) and the flea *Stivalius phoberus* Jordan and Rothschild, 1922 (Stivaliidae) (Turk 1950; Phillips 1980; Cruz 1984). Recent studies on populations of *Mus mayori pococki* from four rainforest reserves in Sri Lanka recorded several ectoparasitic or commensal

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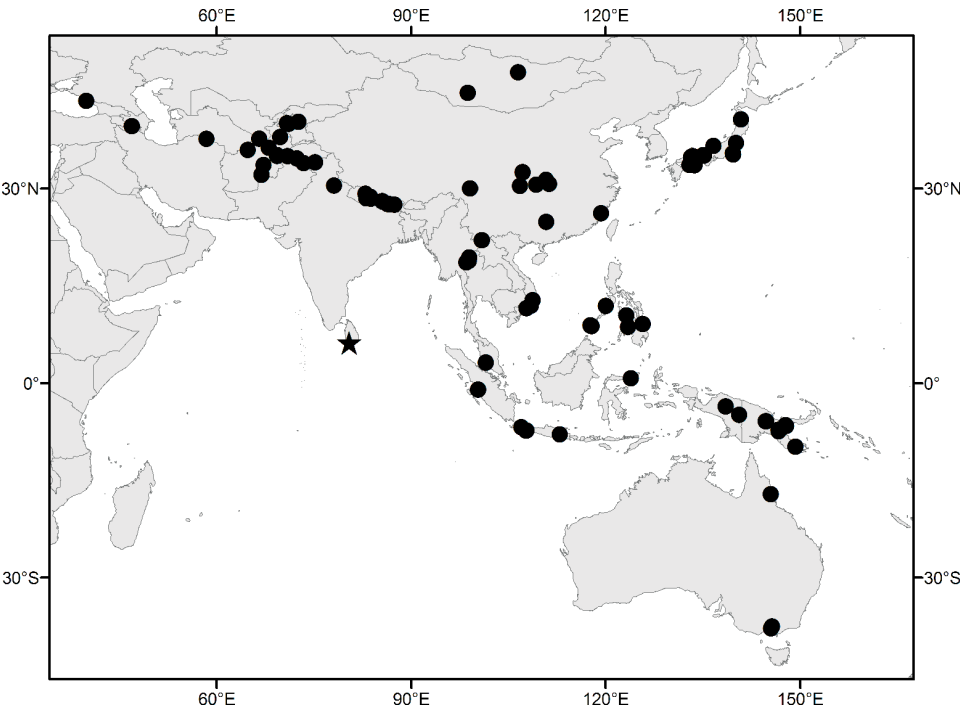


Figure 1. Map showing distribution of *Megachernes kanneliyensis* (★) and all other *Megachernes* species (●).

arthropods including mites of the genus *Echinolaelaps* Ewing, 1929 (Laelapidae), the louse *Polyplax serrata* (Burmeister, 1839) (Hoplopleuridae), a species of the tick genus *Ixodes* Latreille, 1795 (Ixodidae), and a pseudoscorpion of the genus *Megachernes* Beier, 1932 (Ratnaweera et al. 2010). The pseudoscorpion is now named and described in this paper.

Species of *Megachernes* occur widely throughout the eastern portion of the Old World, with the 22 named species ranging from the Black Sea in the west to Japan in the northeast and as far south as eastern Australia (Harvey 2011) (Figure 1). Members of the genus are unusual among pseudoscorpions in that many appear to be obligate commensals with mammals, occurring in their nests and living phoretically in their pelage (e.g. Beier 1948; Martens 1975; Durden 1991), or occurring in caves (e.g. Morikawa 1960). Despite records of *Megachernes* from other regions of Asia, and only two records from India, both of *Megachernes himalayensis* (Ellingsen, 1914) from the northern states of Uttarakhand (Ellingsen 1914) and Jammu and Kashmir (Beier 1978) there had been no records from Sri Lanka. The discovery of specimens of *Megachernes* in the fur of a Sri Lankan rodent allows us to record the genus from Sri Lanka for the first time.

Materials and methods

The material examined here is lodged in the collections of the Western Australian Museum, Perth (WAM). 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 1992) and chelicera (Judson 2007). The terminology for the mammalian hosts follows Wilson and Reeder (2005).

The terms antaxial and paraxial have been recently proposed to describe the lateral faces of pseudoscorpion appendages (Judson 2007) to replace the inadequate and ambiguous terms anterior and posterior. This change is welcome but we here use the terms prolateral and retrolateral as used in describing spider appendages (e.g. Forster 1967; Dondale and Redner 1978). When the appendage is (imaginarily) stretched at 90° to the longitudinal axis of the body, the anterior-facing surface is the prolateral face and the posterior-facing surface is the retrolateral face.

The specimens were collected and stored in 75% ethanol. They were studied using a Leica DM2500 compound microscope and Leica MZ16A and M205C stereo microscopes. The line drawings were prepared with the aid of a drawing tube attached to the Leica DM2500 microscope, and the digital images were taken with a Leica DFC 500 camera attached to the Leica MZ16A and M205C stereo microscopes. Measurements were taken at the highest possible magnification using an ocular graticule. The material was studied using temporary slide mounts prepared by the dissection of the pedipalps, one chelicera, leg I and leg IV from the body, immersion of the larger portions in concentrated lactic acid at room temperature for several days, and mounting them on microscope slides using 10-mm coverslips supported by small sections of nylon fishing line. After study the specimens were washed in distilled water and returned to 75% ethanol with the dissected portions placed in 12 × 3-mm glass genitalia microvials (BioQuip Products, Inc., Compton, CA, USA).

Family **CHERNETIDAE** Menge
Subfamily **LAMPROCHERNETINAE** Beier

Remarks

Harvey (1995) discussed the composition of the Lamprochernetinae, which was restricted to those chernetids with T-shaped spermathecae. Although the genera *Allochernes* Beier, 1932, *Lamprochernes* Tömösváry, 1882, *Lasiochernes* Beier, 1932, *Megachernes*, *Nudochernes* Beier, 1935, *Pselaphochernes* Beier, 1932 and *Wyochernes* Hoff, 1949 were included by Harvey (1995), it now appears that *Wyochernes* does not have T-shaped spermathecae (Muchmore 1996) and is better placed in the Chernetinae, despite the lack of a precise subfamilial definition (Harvey 1995).

The differences between *Megachernes* and *Lasiochernes* are slight and rest on the presence of a rounded protuberance on the posterolateral corner of coxa IV of *Megachernes*, which is absent in *Lasiochernes*. Beier (1932) claimed that the relative position of the tactile seta on legs III and IV differed between the genera, near the middle of the segment in *Megachernes* and more distally placed in *Lasiochernes*, but subsequent descriptions of other species of *Lasiochernes* suggest that a medial position typical of *Megachernes* species also occurs (Beier 1949, 1961, 1963), casting doubt on the utility of this feature. Other consistent differences may occur in the female genitalia, but too few species of either genus have been examined so far to establish whether this feature is reliable. The spermathecal arms of *Lasiochernes siculus* Beier, 1961, the only species described to date, are short (Callaini 1986), whereas those of *Megachernes* are extremely elongated and T-shaped as described for *Megachernes pavlovskyi* Redikorzev, 1949 (Vachon 1938, fig. 56k), *Megachernes ochotona* Krumpál

and Keifer, 1982 (Krumpál and Kiefer 1982, fig. 7) and *Megachernes tuberosus* Mahnert, 2009 (Mahnert 2009, fig. 25).

The southeast Asian chernetid genus *Chiridiochernes* Muchmore, 1972 is also associated with rodents and has posterolaterally enlarged fourth coxae characteristic of *Megachernes*. *Chiridiochernes* differs in numerous ways from *Megachernes* including the lack of a tactile seta on tarsi III and IV, the lack of trichobothrium *st*, a prominent rounded process on the proximal region of the prolateral face of the male pedipalpal femur, flattened pedipalpal segments and the junction between the femur and patella of legs I and II more like cheiridioids than cheliferoids (Muchmore 1972). The sole named species of the genus, *Chiridiochernes platypalpus* Muchmore, 1972 from Sulawesi, is only known from a single adult male (Muchmore 1972). Dr M. Judson (Muséum National d'Histoire Naturelle, Paris) kindly informed us (in litt., 16 March 2012) that females of an undescribed species of *Chiridiochernes* have T-shaped spermathecae and therefore conform to current diagnoses of Lamprochernetinae, to which it is here transferred.

Megachernes Beier

Megachernes Beier 1932: 128; Beier 1933: 518; Beier 1948: 476; Morikawa 1960: 144; Harvey 1991: 599; Harvey 2011, without pagination.

Type species

Chernes grandis Beier, 1930, by original designation.

Diagnosis

Megachernes differs from other chernetid genera by the following combination of character states: posterolateral corner of coxa IV enlarged and rounded (Figures 3, 4B); cheliceral rallum with three blades (Figure 4F); tarsus III and IV with long tactile seta situated in middle of segment (Figure 4G); and female spermathecae very long and T-shaped.

Megachernes kanneliyensis sp. nov. (Figures 2–4)

Material examined

Holotype. Male, Kanneliya rainforest, Southern Province, Sri Lanka, 6°09' to 6°18' N, 80°19' to 80°27' E, 9 November 2006, from dorsal fur of *Mus mayori pococki* Ellerman, P.B. Ratnaweera (WAM T121678).

Paratypes. One female (with attached brood-sac) (WAM T121679), two protonymphs (WAM T121680), collected with holotype.

Etymology

This species is named after the type locality, Kanneliya rainforest.

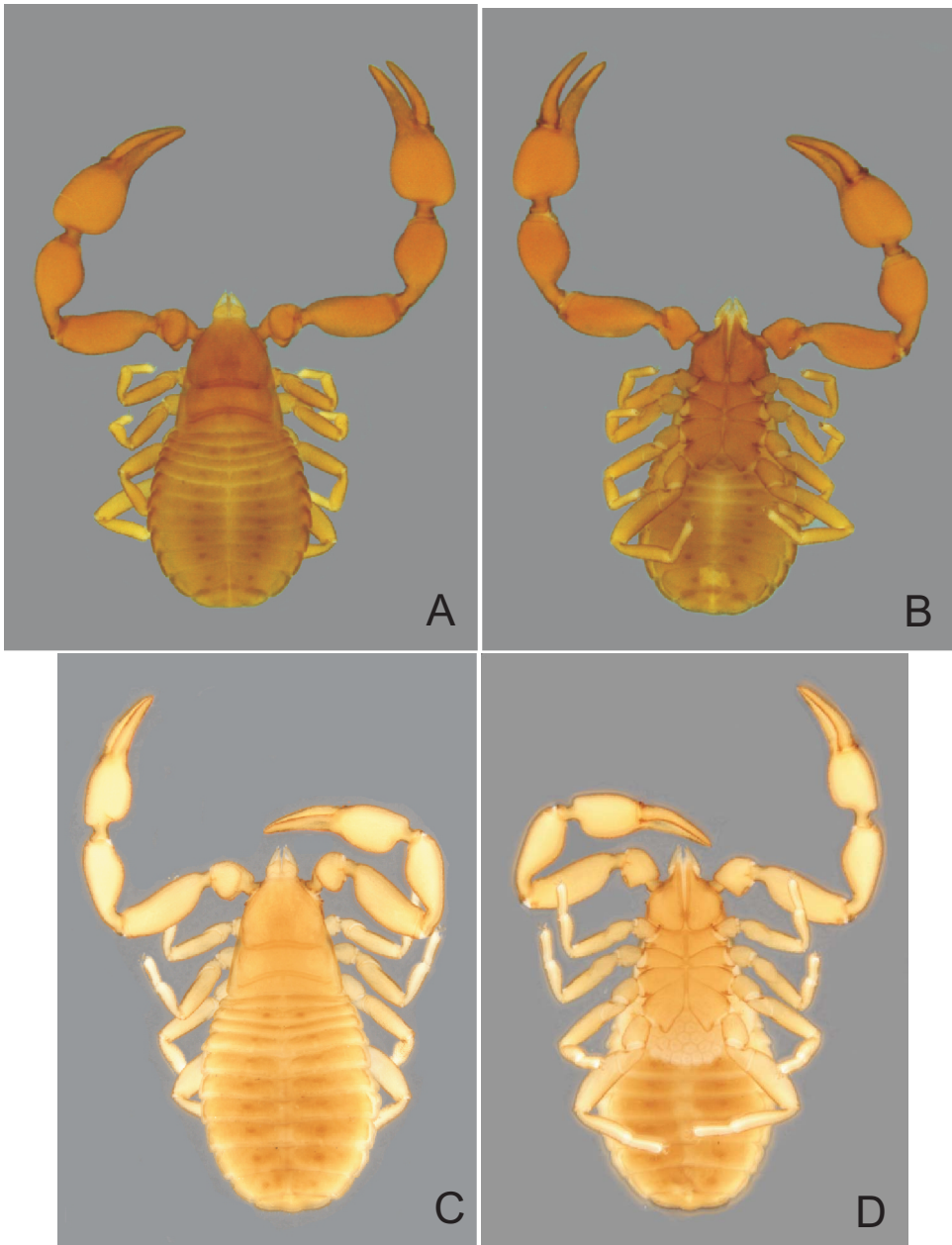


Figure 2. *Megachernes kanneliyensis* sp. nov. (A) Holotype male, dorsal; (B) holotype male, ventral; (C) paratype female, dorsal; (D) paratype female, ventral.

Diagnosis

Megachernes kanneliyensis is the only species of the genus in which males have been described with long setae on the pedipalpal patella and chela, particularly on the pro-lateral surfaces, but short setae on the femur (Figure 4C). Males of *Megachernes* with



Figure 3. *Megachernes kanneliyensis* sp. nov., paratype female, ventral showing detail of coxae and brood-sac.

long setae on the patella usually also have long setae on the femur as reported for *M. afghanicus* Beier, 1959, *M. barbatus* Beier, 1951, *M. glandulosus* Mahnert, 2009, *M. limatus* Hoff and Parrack, *M. loebli* Schawaller, 1991, *M. monstrosus* Beier, 1966, *M. trautneri* Schawaller, 1994 and *M. tuberosus* Mahnert, 2009 (Beier 1951, 1959, 1966, 1967; Hoff and Parrack 1958; Schawaller 1991, 1994; Mahnert 2009). Other species for which males have been described have short setae as in the majority of females. These include *M. grandis* (Beier, 1930), *M. mongolicus* (Redikorzev, 1934), *M. soriciola* Beier, 1974, *M. titanius* Beier, 1951 and *M. vietnamensis* Beier, 1967 (Beier 1930, 1951, 1967, 1974; Redikorzev 1934). Of the species for which males have not been fully described or illustrated, *M. kanneliyensis* is substantially larger than *M. crinitus* Beier 1948, *M. himalayensis* (Ellingsen 1914), *M. ochotonae* Krumpál and Kiefer 1982, *M. papuanus* Beier 1948, *M. pavlovskyi* Redikorzev 1949, *M. penicillatus* Beier 1948 and *M. queenslandicus* Beier 1948, which have a female pedipalpal femur length less than 1.30 mm (Beier 1932, 1948; Redikorzev 1949; Krumpál and Kiefer 1982; Dashdamirov 2005), compared with 1.44 mm for *M. kanneliyensis*. Of those species of a comparable size, *M. kanneliyensis* differs as follows: the pedipalpal segments are less slender than in *M. philippinus* Beier, 1966 (Beier 1966); and the prolateral face of the chelal hand is only slightly curved in *M. kanneliyensis*, but is noticeably curved in *M. ryugadensis* Morikawa, 1954 (Morikawa 1954).

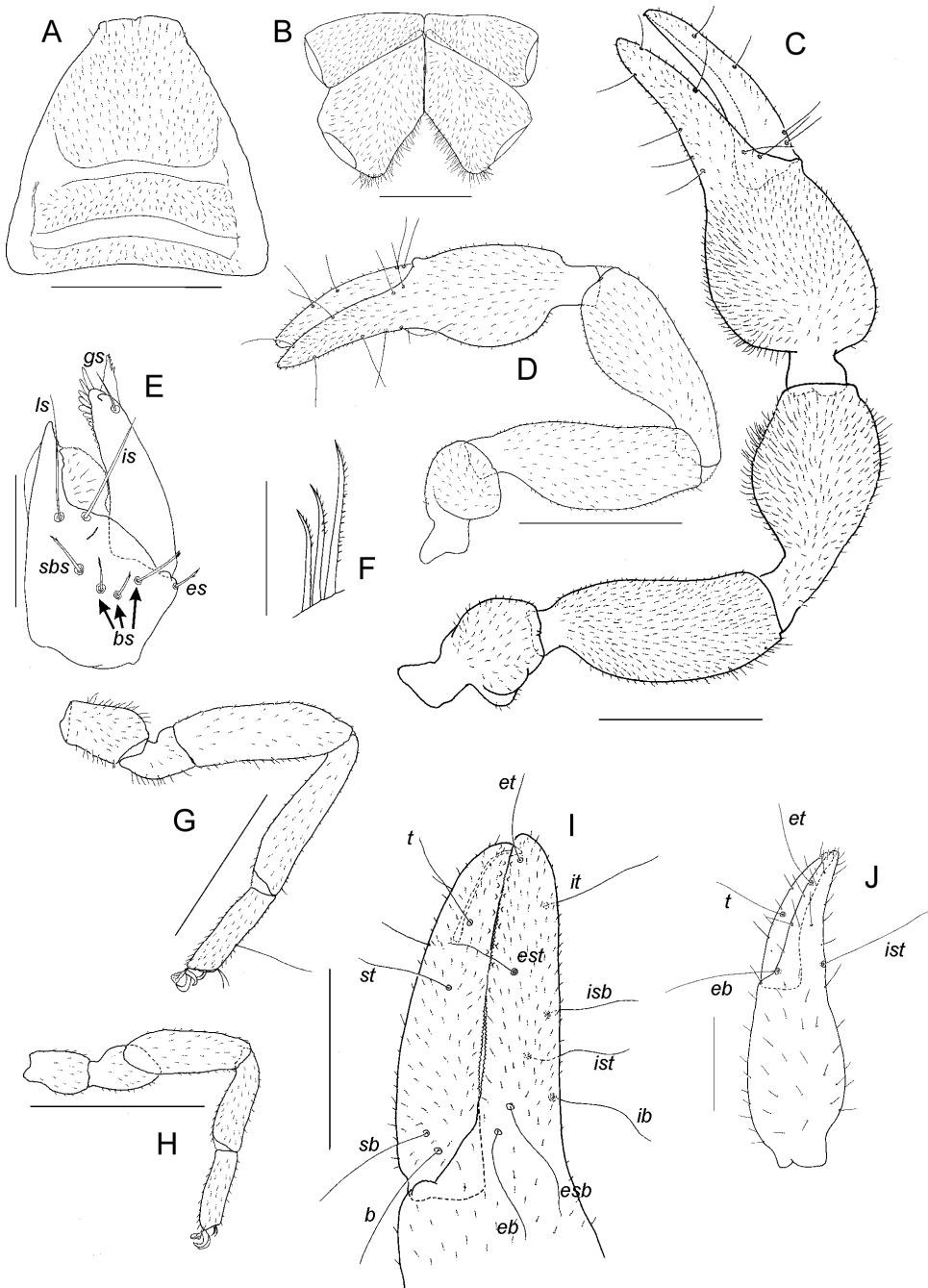


Figure 4. *Megachernes kanneliyensis* sp. nov., paratype female, unless stated otherwise. (A) Carapace, dorsal; (B) coxae III and IV, ventral; (C) right pedipalp, male holotype, dorsal; (D) right pedipalp, dorsal; (E) right chelicera, dorsal; (F) right rallum; (G) left leg IV, lateral; (H) left leg I, lateral; (I) left chela, lateral; (J) left chela, protonymph, dorsal. Scale bars = 1.0 mm (A, C, D, G, H), 0.5 mm (B, I), 0.2 mm (E, J), 0.1 mm (F).

Description – Adults

Pedipalps, cephalothorax, abdomen and legs uniformly pale yellow (Figures 2, 3). Vestitural setae generally short and inconspicuous, lightly dentate; most sternal setae acicular. Pleural membrane longitudinally wrinkled striate for entire length, without setae.

Pedipalps. Robust (Figures 2A–D, 4C,D), with trochanter 1.45 (♂), 1.55 (♀), femur 2.48 (♂), 2.62 (♀), patella 2.14 (♂), 2.56 (♀), chela (with pedicel) 2.78 (♂), 3.41 (♀), chela (without pedicel) 2.54 (♂), 3.08 (♀), hand (without pedicel) 1.26 (♂), 1.44 (♀) times longer than wide; movable finger 1.12 (♂), 1.14 (♀) times length of hand. All pedipalpal surfaces finely granulate. Fixed finger with *c.*60 (♂), *c.*64 (♀) marginal teeth, movable finger with *c.*64 (♂), *c.*70 (♀) marginal teeth; accessory teeth present in distal half of fingers, fixed finger with six (♂), eight (♀) retrolateral and 12 (♂), seven (♀) prolateral teeth; movable finger with six (♂), seven (♀) retrolateral and 10 (♂), 6 (♀) prolateral teeth; fingers not gaping when closed; chelal gland pores not observable. Pedipalpal setae: male with setae on trochanter and femur small and inconspicuous, on patella and chela long and slightly curved, especially on prolateral margin (Figure 4C); female with all setae small and inconspicuous (Figure 4D). Fixed finger with eight trichobothria, movable chelal finger with four trichobothria (Figure 4C,D,I); *eb* closer to *esb* than to *est*; *est* closer to *et* than to *esb*; *ib* and *ist* inserted basally; *isb* closer to *ist* than to *ib*; *sb* closer to *b* than to *st*; *st* closer to *t* than to *sb*. Venom apparatus only present in movable finger with nodus ramosus terminating between *t* and *st* (Figure 4I).

Chelicerae. Hand with seven (♂, ♀) setae, including the usual five setae and two additional *bs* setae, all except *ls* and *is* dentate; movable finger with one acuminate seta (Figure 4E). Galea long and stout with seven (♂), nine (♀) prominent distal rami (Figure 4E). Rallum (Figure 4F) composed of three blades; each dentate along anterior margin. Serrula exterior with 26 (♂), 20 (♀) lamellae. Lamina exterior present.

Cephalothorax. Carapace (Figures 2A,C, 4A) 1.09 (♂), 0.99 (♀) times longer than wide, broadest posteriorly; unicolored; eyes and eye-spots completely absent; setae small and inconspicuous, with numerous setae, including about six (♂), five (♀) setae near anterior margin, and *c.*59 (♂), *c.*62 (♀) setae on posterior disk; posterior half with two deeply incised transverse furrows, anterior furrow crosses the carapace at *c.*0.56 (♂), *c.*0.57 (♀) of carapace length, posterior furrow crosses at *c.*0.80 (♂), *c.*0.84 (♀) of carapace length; completely granulate with exception of transverse furrows. Manducatory process with one long distal and several other sub-distal setae, and with short, curved sub-oral seta; remainder of maxilla with numerous setae. Coxae (Figures 2B,D, 3, 4B) with numerous small setae over entire ventral surface, with longer setae on posterior margin of coxae IV; posterior corners of coxae IV rounded and slightly protruding but not particularly enlarged.

Abdomen. Tergites I–X and sternites V–X divided (Figure 2). Tergal chaetotaxy, ♂: 44: 49: 53: 66: 68: 64: 63: 65: 48: 39: 17: 2; ♀: 62: 60: 72: 76: 74: 72: 70: 68: 54: 52: 24: 2; setae usually restricted to posterior and lateral tergal margins. Sternal chaetotaxy, ♂: 70: (4)

61 (4): (2) 32 (2): 58: 66: 62: 60: 53: 45: 14: 2; ♀: 40: (2) 14 (2): (4) 42 (4): 66: 72: 82: 76: 72: 48: 14: 2.

Genital region. Male not studied in detail; female genitalia with anterior genital operculum with setae arranged in inverted-U, some long most short; spermathecae not observable. Brood-sac with *c.*24 embryos (Figure 3).

Legs. Legs I and II with a strongly oblique junction between femur and patella (Figure 4H). Leg IV (Figure 4G) with femur + patella 3.82 (♂), 3.72 (♀) times longer than broad. Tibiae of legs III and IV without tactile setae. Tarsi of legs III and IV with long tactile seta (Figure 4G), TS = 0.59 (♂), 0.54 (♀). Tarsi with slightly raised slit sensillum. Sub-terminal tarsal setae arcuate, not dentate. Tarsal claws simple; arolium shorter than claws.

Dimensions (mm). Male holotype: body length 4.2. Pedipalps: trochanter 0.94/0.65, femur 1.54/0.62, patella 1.56/0.73, chela (with pedicel) 2.47/0.89, chela (without pedicel) 2.26, hand length (without pedicel) 1.12, movable finger length 1.25. Chelicera 0.51/0.27, movable finger length 0.36. Carapace 1.72/1.58. Leg I: femur 0.48/0.30, patella 0.82/0.29, tibia 0.68/0.20, tarsus 0.53/0.16. Leg IV: femur + patella 1.45/0.38, tibia 1.16/0.23, tarsus 0.70/0.19.

Female paratype. Body length 4.2. Pedipalps: trochanter 0.79/0.51, femur 1.44/0.55, patella 1.36/0.53, chela (with pedicel) 2.08/0.61, chela (without pedicel) 1.88, hand length (without pedicel) 0.88, movable finger length 1.00. Chelicera 0.39/0.23, movable finger length 0.30. Carapace 1.52/1.54. Leg I: femur 0.42/0.27, patella 0.75/0.25, tibia 0.61/0.19, tarsus 0.48/0.14. Leg IV: femur + patella 1.34/0.36, tibia 1.04/0.22, tarsus 0.65/0.16.

Description – protonymph

Uniformly very pale yellow, nearly white. Vestitural setae generally short and inconspicuous, lightly dentate. Pleural membrane longitudinally striate for entire length, without setae.

Pedipalps. Robust, with trochanter 1.60, femur 2.44, patella 2.12, chela (with pedicel) 3.35, chela (without pedicel) 3.10, hand (without pedicel) 1.65 times longer than wide; movable finger 0.97 times the hand (with pedicel). All surfaces of pedipalps finely granulate with exception of fingers. Fixed finger with three trichobothria, movable chelal finger with one trichobothrium (Figure 4J); *eb* and *ist* situated basally; *et* situated subdistally; *t* medially. Venom apparatus only present in movable finger with nodus ramosus terminating slightly distal to *t*.

Chelicerae. With four setae on hand; movable finger without seta. Galea long and stout with seven prominent distal rami. Rallum composed of three blades.

Cephalothorax. Carapace: 0.91 times longer than wide, broadest posteriorly; eyes and eye-spots completely absent; setae small and inconspicuous, with five setae on anterior

margin, and six setae on posterior margin; shallow median furrow present, posterior furrow absent.

Abdomen. Tergites I–X and sternites II–X divided. Tergal chaetotaxy: 6: 6: 6: 6: 6: 6: 6: 6: 6: 6: T2T: 2. Sternal chaetotaxy: 0: (0) 2 (0): (1) 4 (1): 7: 6: 6: 6: 6: 6: 4: 2.

Legs. Tarsi of legs III and IV with long tactile seta, situated medially.

Dimensions (mm). Body length 1.56. Pedipalps: trochanter 0.24/0.15, femur 0.39/0.16, patella 0.36/0.17, chela (with pedicel) 0.67/0.20, chela (without pedicel) 0.62, hand length (without pedicel) 0.33, movable finger length 0.32. Carapace 0.56/0.61.

Remarks

Megachernes kanneliyensis is the first species of *Megachernes* recorded from Sri Lanka and the first pseudoscorpion recorded from the pelage of a Sri Lankan mammal. The occurrence of adult and nymphal specimens of *M. kanneliyensis* in the fur of *Mus mayori pococki* strongly suggests that the pseudoscorpions are either breeding in the pelage or in their nests and are being transported phoretically by the mouse. Species of *Megachernes* do not appear to be restricted to individual host species (Table 1).

Host associations of *Megachernes*

Species of *Megachernes* are closely associated with other animals, either in the nests or fur of small mammals, nests of birds and bumblebees, or in bat guano within caves (Tables 1, 2). The following species have been collected most frequently or exclusively in the nests or pelage of small mammals: *M. barbatus*, *M. crinitus*, *M. grandis*, *M. himalayensis*, *M. kanneliyensis*, *M. limatus*, *M. monstrosus*, *M. ochotona*, *M. penicillatus*, *M. philippinus*, *M. queenslandicus*, *M. soricicola*, *M. titanius*, *M. trautneri* and *M. vietnamensis*, as well as three undescribed species from Papua New Guinea and Australia (Table 1). This assemblage may also include *M. loebli*, specimens of which were sifted from leaf litter at the foot of a wall (Schawaller 1991), a habitat that Schawaller (1991) suggested is frequently occupied by murids and that a close association with a small mammal was likely.

Three other species, *M. afghanicus*, *M. pavlovskyi* and *M. ryugadensis*, have been collected from guano in caves (Table 1). Although the origin of the guano is rarely stated, deposits of bat faeces are the likely source in all cases. Two of these species have also been recorded from other habitats. *Megachernes pavlovskyi* has been taken from within a barn, under stones, in pigeon guano, forest litter, plant roots and rodent nests, and the subspecies *M. ryugadensis myophilus* differs from the other two subspecies (*M. ryugadensis ryugadensis* and *M. ryugadensis naikaiensis*) by its close association with other animals, having been collected on small mammals (*Rattus norvegicus* and *Mogera wogura*) and from nests of bumblebees. Of the remaining three species (Table 1), *M. glandulosus* and *M. tuberosus* have been collected in caves without any mention of whether they were taken in guano (Mahnert 2009), and *M. mongolicus* lacks any habitat data (Redikorzev 1934).

Table 1. Habitat data and hosts recorded for species of *Megachernes*

Taxon	Country	Host and habitat	References
<i>M. afghanicus</i> Beier, 1959	Afghanistan	from guano in cave	(Beier 1959, 1960)
<i>M. barbatus</i> Beier, 1951	Vietnam	from <i>Niviventer tenaster</i> (given as <i>Rattus niviventer champi</i>), <i>Maxomys surifer</i> (given as <i>R. rajah koratis</i>) and <i>R. sladeni</i>	(Beier 1967)
<i>M. crinitus</i> Beier, 1948	Vietnam	taken from fur of various species of rats	(Judson 1997)
<i>M. glandulosus</i> Mahnert, 2009	Indonesia	on <i>Maxomys bartelsii</i> (given as <i>Rattus bartelsi</i>); from <i>Hylomys suillus</i> ; from <i>Rattus lepturus</i>	(Beier 1948)
<i>M. grandis</i> (Beier, 1930)	China	in cave	(Mahnert 2009)
	Philippines	from <i>Apomys insignis</i> , <i>A. sp.</i> , <i>Bullinus bagobus</i> (given as <i>Apomys bagobus</i> and <i>Rattus bagobus</i>), <i>Cyanopterus brachyotis</i> , <i>Maxomys panglima</i> (given as <i>Rattus palawanensis</i>) and <i>Rattus sp.</i>	(Beier 1966)
	Indonesia	from <i>Maxomys muschenbroekii</i> and <i>Niviventer fulvescens</i> (given as <i>Rattus bukit treubi</i>)	(Beier 1948; Durden 1986)
<i>M. himalayensis</i> (Ellingsen, 1914)	Malaysia	from <i>Maxomys rajah</i> (given as <i>Rattus rajah</i>)	(Beier 1964)
	China	from <i>Niviventer confucianus</i> (given as <i>Echimys confucianus</i>)	(Beier 1948) (as <i>M. sinensis</i> Beier, 1932)
	India	from conifer leaf litter	(Beier 1978; Schwaller 1988)
	Nepal	from <i>Apodemus gorkha</i> , <i>Apodemus sylvaticus</i> , <i>Mus musculus</i> , <i>Niviventer fulvescens</i> (given as <i>Rattus fulvescens</i>) and <i>Rattus pectoris</i> (given as <i>Rattus rattoides</i>)	(Beier 1974; Martens 1975; Schwaller 1983)
<i>M. kameliyensis</i> sp. nov.	Sri Lanka	from pelage of <i>Mus mayori pococki</i>	this study
<i>M. limatus</i> Hoff and Parrack, 1958	Papua New Guinea	from <i>Melomys</i> sp., <i>Pogonomys</i> sp., <i>Rattus niobe</i> , <i>Rattus nitidus</i> (given as <i>Rattus ruber trimitius*</i>), and from rat	(Hoff and Parrack 1958; Beier 1965; Durden 1991)
<i>M. limatus crassus</i> Beier, 1965	Indonesia	from unidentified rodents [given as <i>Rattus</i> sp. by Beier (1965)] and from <i>Paramelomys</i> cf. <i>platyops</i> [given as <i>Pseudocheirus</i> sp. by Beier (1965)]	(Beier 1965; Tenorio and Muchmore 1982)

(Continued)

Table 1. (Continued)

Taxon	Country	Host and habitat	References
<i>M. leebli</i> Schawaller, 1991	Nepal	from forest litter	(Schawaller 1991)
<i>M. mongolicus</i> (Redikorzev, 1934)	Mongolia	habitat not stated	(Redikorzev 1934)
<i>M. monstrosus</i> Beier, 1966	Philippines	from nest of <i>Maxomys panglima</i> (given as <i>Rattus palawanensis</i> by Beier (1966))	(Beier 1966)
<i>M. ochotonae</i> Krumpál and Kiefer, 1982	Mongolia	under stones in hole of <i>Ochotona dauurica</i> ; in nest of <i>Passer</i> sp.	(Krumpál and Kiefer 1982)
<i>M. papuanus</i> Beier, 1948	Papua New Guinea	from <i>Paramelomys levipes</i> (given as <i>Melomys levipes</i>), <i>Melomys</i> sp., <i>Mus</i> sp., <i>Rattus niobe</i> , from unidentified rats and Rainbow Lory (<i>Trichoglossus haematodus</i>)	(Beier 1948, 1965; Hoff and Parrack 1958; Durden 1991; Judson 1997)
<i>M. pavlovskyi</i> Redikorzev, 1949	Afghanistan Azerbaijan	from guano in cave in cave; in bat guano (<i>Rhinolophus mehelyi</i> , <i>Myotis blythi</i> , <i>Miniopterus schreibersii</i>)	(Beier 1959) (Krumpál 1986; as <i>M. caucasicus</i> Krumpál 1986; Schawaller and Dashdamirov 1988) (Schawaller 1986) (Dashdamirov 2005)
	Kyrgyzstan Pakistan	in bat guano; and in pigeon guano roots of <i>Aesculus</i> and nest of rodent; and under stones at the edge of a stream	
	Russia	<i>Taxus</i> – <i>Buxus</i> woods with <i>Fagus</i>	(Schawaller and Dashdamirov 1988)
	Turkmenistan Turkmenistan	in cracks of a livestock barn in guano	(Redikorzev 1949) (Dashdamirov and Schawaller 1995)
<i>M. penicillatus</i> Beier, 1948	Australia	from <i>Phascogale</i> sp.	(Beier 1948; Judson 1997)
<i>M. philippinus</i> Beier, 1966	Philippines	from <i>Rattus</i> sp.	(Beier 1966; Tenorio and Muchmore 1982)

(Continued)

Table 1. (Continued)

<i>M. queenslandicus</i> Beier, 1948	Australia	from <i>Rattus fuscipes assimilis</i> , <i>R. fuscipes</i> and grey scrub rat	(Beier 1948; Judson 1997)
<i>M. ryugadensis</i> Morikawa, 1954	Japan	in bat guano in caves	(Morikawa 1954, 1960)
<i>M. ryugadensis myophilus</i> Morikawa, 1960	Japan	from nest of <i>Bombus diversus</i> and <i>B. ardens</i> ; on <i>Mogera wogura</i> ; on <i>Rattus norvegicus</i>	(Morikawa 1960)
<i>M. ryugadensis naikaiensis</i> Morikawa, 1957	Japan	from bat guano in caves	(Morikawa 1957, 1960)
<i>M. soricicola</i> Beier, 1974	Nepal	from <i>Soriculus nigrescens</i>	(Beier 1974; Martens 1975)
<i>M. titanius</i> Beier, 1951	Vietnam	from <i>Niviventer tenaster</i> (given as <i>Rattus niviventer champ</i>), <i>Maxomys surifer</i> (given as <i>R. rajah koratis</i>), <i>R. sladeni sladeni</i> ; and “from the fur of various species of rats”	(Beier 1967; Judson 1997)
<i>M. trautneri</i> Schawaller, 1994	Thailand	from small mammal nest	(Schawaller 1994)
<i>M. tuberosus</i> Mahnert, 2009	China	in cave	(Mahnert 2009)
<i>M. vietnamensis</i> Beier, 1967	Vietnam	from <i>Niviventer fulvescens</i> and <i>Rattus andamanensis</i> (originally reported as <i>Rattus niviventer</i> and <i>R. sladeni sladeni</i>)	(Beier 1967; Tenorio and Muchmore 1982)
<i>M. sp. indet.</i>	Papua New Guinea	from nests of <i>Micromurexia habbena</i> (given as <i>Antechinus habbena</i>) and <i>Phascomurexia naso</i> (given as <i>Antechinus naso</i>)	(Woolley 1989)
<i>M. sp. nov.</i> (Papua New Guinea)	Papua New Guinea	from <i>Rattus niobe</i> , <i>Melomys</i> sp. and <i>Murexechinus melanurus</i> (given as <i>Antechinus wilhelmina</i>)	(Durden 1991)
<i>M. sp. nov.</i> (Australia)	Australia	from <i>Vespadelus regulus</i> (given as <i>Eptesicus regulus</i>) and <i>Falsirellus tasmaniensis</i>	(Harvey and Parnaby 1993)
<i>M. sp. nov.</i> (Australia)	Australia	from nest box of Leadbeater's Possum (<i>Gymnobelideus leadbeateri</i>)	(Harvey and Parnaby 1993)

*The host name “*Rattus ruber trimitius*” recorded by Beier (1965) appears to be a lapsus. *Rattus ruber* is now a synonym of *R. nitidus* (Wilson and Reeder, 2005) and “trimitius” may refer to the trichoan blood parasite *Trimitus*.

Table 2. Host animals recorded for *Megachernes* species, excluding associations with mammal guano (see Table 1).**Phylum Chordata**

Class Mammalia

Order Dasyuromorpha

Micromurexia habbema (Tate and Archbold, 1941)*Murexechinus melanurus* (Thomas, 1899)*Phascomurexia naso* (Jentink, 1911)*Phascogale* sp.

Order Diprotodontia

Gymnobelideus leadbeateri McCoy, 1867

Order Soricomorpha

Mogera wogura (Temminck, 1842)*Soriculus nigrescens* (Gray, 1842)

Order Erinaceomorpha

Hylomys suillus Müller, 1840

Order Lagomorpha

Ochotona dauurica (Pallas, 1776)

Order Rodentia

Apodemus gorkha Thomas, 1924*Apodemus sylvaticus* (Linnaeus, 1758)*Apomys insignis* Mearns, 1905*Apomys* sp.*Bullimus bagobus* Mearns, 1905*Maxomys bartelsii* (Jentink, 1910)*Maxomys musschenbroekii* (Jentink, 1878)*Maxomys panglima* (Robinson, 1921)*Maxomys rajah* (Thomas, 1894)*Maxomys surifer* (Miller, 1900)*Melomys* sp.*Mus mayori pococki* Ellerman, 1947*Mus musculus* Linnaeus, 1758*Mus* sp.*Niviventer confucianus* (Milne-Edwards, 1871)*Niviventer fulvescens* (Gray, 1847)*Niviventer lepturus* (Jentink, 1879)*Niviventer tenaster* Thomas, 1916*Paramelomys levipes* (Thomas, 1897)*Paramelomys* cf. *platyops* (Thomas, 1906)*Pogonomys* sp.*Rattus andamanensis* (Blyth, 1860)*Rattus fuscipes* (Waterhouse, 1839)*Rattus fuscipes assimilis* Gould, 1858*Rattus niobe* (Thomas, 1906)*Rattus nitidus* (Hodgson, 1845)*Rattus norvegicus* (Berkenhout, 1769)*Rattus pyctoris* (Hodgson, 1845)*Rattus* sp.

(Continued)

Table 2. (Continued).

Order Chiroptera
<i>Cyanopterus brachyotis</i> (Müller, 1838)
<i>Vespadelus regulus</i> (Thomas, 1906)
<i>Falsistrellus tasmaniensis</i> (Gould, 1858)
Class Aves
Order Psittaciformes
<i>Trichoglossus haematododus</i> (Linnaeus, 1771)
Order Passeriformes
<i>Passer</i> sp.
Phylum Arthropoda
Class Hexapoda
Order Hymenoptera
<i>Bombus ardens</i> Smith, 1879
<i>Bombus diversus</i> Smith, 1869

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