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CHECKLIST

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Checklist of acanthocephalan parasites of South Africa

Ali Halajian[1], Lesley R. Smales[2], Sareh Tavakol[1], Nico J. Smit[3],
Wilmien J. Luus-Powell[1]

1 *DST-NRF SARChI Research Chair (Ecosystem Health), Department of Biodiversity, University of Limpopo, Sovenga, 0727, South Africa* **2** *Parasitology Section, South Australia Museum, North Terrace, Adelaide 5000 South Australia, Australia* **3** *Water Research Group, Unit for Environmental Sciences and Management, North-West University, Potchefstroom, South Africa*

Corresponding author: *Ali Halajian* (ali_hal572002@yahoo.com)

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Abstract

Twenty-one species of acanthocephalans, representative of thirteen genera from ten families of seven orders and three classes, are included in this updated checklist of acanthocephalans in South Africa. Although South Africa appears to have a less diverse acanthocephalan fauna compared to some other countries such as Iran in Asia, or Brazil in South America, this is probably an artefact of fewer parasitological surveys.

Keywords

Acanthocephala, helminths, diversity, wildlife, Africa

Introduction

South Africa's landscape is the third most biologically diverse in the world with 6% of the world's mammal species, 8% of bird species and 5% of reptile species of which many are endemic (da Silva and Willows-Munro 2016). In regard to invertebrates, only 36,803 species are listed for Africa, and 12,098 for South Africa (Hamer 2010). It is said that in South African habitats, there are many undiscovered and undescribed animal species, especially invertebrates. It is estimated that as many as 80,000 South

African animal species remain to be discovered or described, and most of these animals are invertebrates (Hamer 2013).

The most comprehensive checklist of helminth parasites of Africa was compiled for freshwater fishes by Khalil (1971) and updated by Khalil and Polling (1997). It included very few records of acanthocephalans considering the total number of freshwater fish species present in the continent. The updated list (Khalil and Polling 1997) comprised 568 adult helminth parasites of which only 21 species are acanthocephalans. These records were compiled from 359 species of African freshwater fishes (assigned to 89 genera belonging to 32 families) of an estimated 3000 existing inland fish species (Khalil and Polling 1997). These examples illustrate the lack of knowledge of the helminth fauna of the wildlife of the African continent in general and in South Africa in particular.

This is the first checklist of acanthocephalans of South Africa and the aim is to provide a comprehensive record of all the previously reported species of Acanthocephala occurring in South African hosts as well as new records from our on-going research on parasites of wildlife, while simultaneously demonstrating the need for more extensive parasitological surveys.

Materials and methods

Data were obtained from two sources, published records and our own ongoing studies on the Acanthocephala of South African wildlife. These data are presented in two parts. In the first part parasites are listed systematically, with families, genera, and species in alphabetical order. The scientific name, including any synonyms, followed by the scientific and common name of the host, the locality in which the parasite was reported and museum (location) of type specimens where known. In the second part, the hosts are listed systematically by their scientific names and parasite records from each host are given together with locality and reference. The records without references are those of our ongoing study that are being reported here for the first time.

Classification of the Acanthocephala follows Amin (2013). For the hosts, fish taxonomy is based on Skelton (2001, 2016) and Fishbase (Froese and Pauly 2016), bird taxonomy is based on Clements et al. (2016) and mammal taxonomy on Wilson and Reader (2005) and Apps (2012).

Abbreviations for museums are:

BMNH	Natural History Museum London, London, UK;
GNM	Gothenburg Natural History Museum, Gothenburg, Sweden;
SAMCTA	South African Museum at Cape Town, South Africa;
SAM	South Australian Museum, Adelaide, Australia;
USNM Helm. Coll.	United States National Museum Helminthological Collection
USNPC	United States National Parasite Collection now held in the Invertebrate Zoology collection of the Smithsonian Museum, Washington, USA.

Acanthocephalan specimens from our ongoing wildlife parasitology projects were mostly collected from roadkill animals, museum collections, hunting/culling surveys and other research permits received for a limited number of specimens through the Limpopo Department of Economic Development, Environment and Tourism (LEDET) (permit number CPM004961 and ZA/LP/HO/3370 for freshwater fish research, 001-CPM403-00012 and ZA/LP/HO/3448 for frogs, ZA/LP/HO/3432 for rodents and ZA/LP/87586 for roadkills).

Acanthocephalans from freshly dead animals were placed in tap water and refrigerated for a few hours to one day until the proboscis was everted and then fixed and stored in 70% ethanol until studied. Acanthocephalans from frozen hosts were fixed and stored in 70% ethanol. Some specimens were prepared for examination by staining in Mayer's acid carmine, destained in HCl in 70% ethanol, dehydrated through increasing concentrations of ethanol, cleared in xylene, and mounted as whole worms in Canada balsam. Other worms were examined as temporary mounts following clearing in lactophenol or beechwood creosote.

A total of 102 species of birds (151 individuals), 72 of mammals (420 individuals), 9 of reptiles (18 individuals) and 42 (1050 individuals) of fishes were examined for this study (details in Table 1).

Table 1. Total number of host taxa examined and those infected with acanthocephalans (i.e. number of taxa that harboured acanthocephalans, in parenthesis) during our ongoing study on wildlife parasites in South Africa.

Taxon Group	Order	Family	Genus	Species
Amphibians	1 (0)	8 (0)	13 (0)	19 (0)
Birds	21 (5)	50 (5)	87 (5)	102 (5)
Fishes (freshwater)	8 (1)	13 (1)	24 (1)	42 (1)
Mammals	10 (4)	26 (4)	59 (6)	72 (6)
Reptiles	3 (1)	6 (1)	7 (1)	9 (1)
Totals	43 (11)	103 (11)	190 (13)	244 (13)

Parasite-Host List

Acanthocephala
Class: Archiacanthocephala Meyer, 1931
Order: Gigantorhynchida Southwell & Macfie, 1925
Family: Gigantorhynchidae Hamann, 1892
Genus: *Mediorhynchus* Van Cleave, 1916

Mediorhynchus africanus Amin, Evans, Heckmann & El-Naggar, 2013

Empodius segmentatus (de Marval, 1902) Southwell & Mac-Fie, 1925
Mediorhynchus selengensis Harris, 1973
M. gallinarum (Bhalerao, 1937) Van Cleave, 1947 *sensu* Junker & Boomker, 2006

Notes. *M. gallinarum* is found only in Asia and the species in Africa is actually *M. africanus* (Amin et al. 2013; Amin 2013) and not *M. gallinarum* previously reported in South Africa (Junker and Boomker 2006).

Host. *Numida meleagris* (L. 1758) (Helmeted Guineafowl) (Numididae) (type host).

Localities. Kruger National Park, Mpumalanga Province, South Africa (type locality) (Junker and Boomker 2006); Vicinity of Petrus Steyn, Free State Province, South Africa (Davies et al. 2008); Musina, Limpopo Province, South Africa (Junker and Boomker 2007; Junker et al. 2008).

Mediorhynchus mokgalongi Smales & Halajian, 2018

Host. *Turdus smithi* Bonaparte, 1850 (Karoo Thrush) (Turdidae) (type host).

Locality. Polokwane, Limpopo Province, South Africa (type locality) (Smales et al. 2018).

Type specimens. Holotype male SAM AHC 48068, allotype female SAM AHC 48069, paratype SAM AHC 48070.

Mediorhynchus numidae (Baer, 1925) Meyer, 1932

Heteroplus numidae Baer, 1925; *Empodisma numidae* (Baer, 1925) Yamaguti, 1963

Host. *Numida meleagris* (L. 1758) (Helmeted Guineafowl) (Numididae)

Locality. Pretoria, Gauteng Province, South Africa (Oosthuizen and Markus 1967).

Mediorhynchus taeniatus (von Linstow, 1901) Dollfus, 1936

Echinorhynchus taeniatus von Linstow, 1901; *E. segmentatus* de Marval, 1902

Host. *Numida meleagris* (L. 1758) (Helmeted Guineafowl) (Numididae).

Locality. Rooipoort farm, Kimberley, Northern Cape Province, South Africa (Crowe 1977).

Host. *Tockus leucomelas* (Lichtenstein, 1842) (Southern Yellow-billed Hornbill) (Bucerotidae)

Locality. Limpopo Province, South Africa.

Order: Moniliformida Schmidt, 1972
Family: Moniliformidae Van Cleave, 1924
Genus: *Moniliformis* Travassos, 1915

Moniliformis kalahariensis Meyer, 1931

Host. *Atelerix frontalis* (Smith, 1831) (Southern African Hedgehog) (Erinaceidae)

Locality. Mohlonong village and University of Limpopo, Limpopo Province, South Africa (Amin et al. 2014).

Moniliformis moniliformis (Bremser, 1811) Travassos, 1915 (type species)

Echinorhynchus moniliformis Bremser, 1811
E. grassi Railliet, 1893
E. canis Porter, 1914
E. belgicus Railliet, 1919
Moniliformis moniliformis aegypticus Meyer in Petrochenko, 1958
M. dubius Meyer, 1932
M. travassosi Meyer, 1932 (*fide* Machado Filho 1946, Van Cleave 1952)

Host. *Atelerix frontalis* (Smith, 1831) (Southern African Hedgehog) (Erinaceidae).

Locality. Hammanskraal, Gauteng Province, South Africa (Le Roux 1930).

Notes. Host recorded as *Aethechinus frontalis* in Le Roux (1930).

Moniliformis acomysi Ward & Nelson, 1967

Host. *Gerbilliscus leucogaster* (Peters, 1852) (Bushveld Gerbil), *Mastomys natalensis* (Smith, 1834) (Natal Mastomys), *Mus minutoides* (Pygmy mouse) (Muridae).

Localities. Bloemhof, Free State Province; Vyeboom village, Limpopo Province; Hoopstad, Free State Province; South Africa.

Moniliformis sp.

Host. *Otolemur crassicaudatus* (É. Geoffroy Saint-Hilaire, 1812) (Thick-tailed Bushbaby) (Galagidae).

Locality. Venda, Limpopo Province, South Africa.

Remarks. One male and one female worm were found in the small intestine of an adult bushbaby.

Order: Oligacanthorhynchida Petrochenko, 1956
Family: Oligacanthorhynchidae Southwell & Macfie, 1925
Genus: *Heptamegacanthus* Spencer Jones, 1990

Heptamegacanthus niekerki Spencer Jones, 1990 (type species)

Host. *Chrysospalax trevelyani* (Günther, 1875) (Giant Golden Mole) (Chrysochloridae) (type host).

Locality. Nqadu Forest, Transkei, Eastern Cape Province, South Africa (type locality) (Spencer Jones 1990).

Type specimens. Holotype male BMNH 1988.2480; allotype female BMNH 1988.2481; paratypes BMNH 1988.2482-2491.

Oligacanthorhynchidae sp.

Host. *Varanus albigularis* Daudin, 1802 (Rock Monitor) (Varanidae).

Localities. Tzaneen; Tolwe, Limpopo Province, South Africa.

Class: Eoacanthocephala Van Cleave, 1936
Order: Gyracanthocephala Van Cleave, 1936
Family: Quadrigyridae Van Cleave, 1920
Genus: *Acanthogyrus* Thapar, 1927
Subgenus: *Acanthosentis* Verma & Datta, 1929

Acanthogyrus (*Acanthosentis*) *phillipi* (Mashego, 1988) Amin, 2005

Acanthosentis phillipi Mashego, 1988

Host. *Enteromius neefi* (Greenwood, 1962) (syn. *Barbus neefi*) (Sidespot Barb) (Cyprinidae) (type host).

Locality. Lingwe River, Venda, Limpopo Province, South Africa (type locality) (Mashego 1988).

Type specimens. Holotype in Transvaal Museum no. TM14659; Paratypes TM5 at University of Limpopo, Zoology, 5.

Acanthogyrus sp.

Host. *Oreochromis mossambicus* (Peters, 1852) (Mozambique Tilapia) (Cichlidae).

Locality. Molepo Dam, Limpopo Province, South Africa (Kunutu et al. 2013).

Order: Neoechinorhynchida Southwell & Macfie, 1925
Family: Neoechinorhynchidae (Ward, 1917) Van Cleave, 1928
Genus: *Neoechinorhynchus* Stiles & Hassall, 1905
Subgenus: *Neoechinorhynchus* Hamann, 1892

Neoechinorhynchus (*Neoechinorhynchus*) *dorsovaginatus* Amin & Christison, 2005

Host. *Argyrosomus japonicus* (Temminck & Schlegel, 1843) (Japanese Meagre, Dusky Kob) Sciaenidae) (type host).

Locality. Breede River Estuary, Western Cape Province, South Africa (type locality) (Amin and Christison 2005).

Type specimens. No. SAMCTA29536 (holotype male and allotype female; same slide), nos SAMCTA29537-29545 (paratypes), USNPC no. 94918 (paratypes).

Class: Palaeacanthocephala Meyer, 1931
Order: Echinorhynchida Southwell & Macfie, 1925
Family: Pomphorhynchidae Yamaguti, 1939
Genus: *Longicollum* Yamaguti, 1935

Longicollum chabanaudi Dollfus & Golvan, 1963

Host. *Barnardichthys fulvomarginata* (Gilchrist, 1904) (syn. *B. fulvomarginatus*) (Soleidae) (Sole).

Locality. False Bay, Western Cape Province, South Africa (Dollfus and Golvan 1963).

Longicollum sp. innom.

Host. *Pegusa nasuta* (Pallas, 1814) (syn. *Solea bleekeri*) (Blackhand Sole) (Soleidae).

Locality. Klein River estuary, Hermanus, Western Cape Province, South Africa (Bray 1974).

Remarks. Three contracted and immature specimens were found in one fish and one male in another fish. Thus it could not be identified to species level (Bray 1974).

Family: Rhadinorhynchidae Lühe, 1912
Genus: *Rhadinorhynchus* Lühe, 1911

Rhadinorhynchus cadenati (Golvan & Houin, 1964) Golvan, 1969

Nipporhynchus cadenati Golvan & Houin, 1964

Host. *Thyrsites atun* (Euphrasen, 1791) (Snoek) (Gempylidae).

Locality. South Africa's West and South coasts (Nunkoo et al. 2016).

Rhadinorhynchus capensis Bray, 1974

Host. *Pegusa nasuta* (Pallas, 1814) (syn. *Solea bleekeri*) (Blackhand Sole) (Soleidae) (type host)

Locality. Heuninges River estuary, near Cape Agulhas, Western Cape Province, South Africa (type locality) (Bray 1974).

Type specimens. British Museum, Registration number 1974.521-550.

Rhadinorhynchus sp.

Host. *Ruvettus pretiosus* Cocco, 1833 (Oilfish) (Gempylidae).

Locality. South Africa's West coast, Atlantic Ocean (Nunkoo et al. 2017).

Order: Polymorphida Petrochenko, 1956
Family: Centrorhynchidae Van Cleave, 1916 (Golvan, 1960)
Genus: *Centrorhynchus* Lühe, 1911

Centrorhynchus sarehae Smales & Halajian, 2017

Host. *Kaupifalco monogrammicus* (Temminck, 1824) (Lizard Buzzard) (Accipitridae) (type host).

Locality. Makhado (Louis Trichardt), Limpopo Province, South Africa (type locality) (Smales et al. 2017).

Type Specimens. Holotype male SAM AHC 47858; allotype female SAM AHC 47859; paratypes SAM AHC 47860.

Centrorhynchus clitorideus (Meyer, 1931) Golvan, 1958

Gordiorhynchus clitorideus Meyer, 1931 (*nec clitorideum*)

Host. *Bubo africanus*(Temminck, 1821) (Spotted Eagle Owl) (Strigidae).

Locality. Zandrivierspoort Farm, Polokwane, Limpopo Province, South Africa.

Centrorhynchus sp.

Host. *Felis catus* L., 1758 (Domestic Cat) (Felidae).
Locality. Pretoria, Gauteng Province, South Africa (Baker et al. 1989).

Centrorhynchus sp.

Host. *Mungos mungo* (Gmelin, 1788) (Banded Mongoose) (Herpestidae).
Locality. Polokwane, Limpopo Province, South Africa.

Family: Plagiorhynchidae Golvan, 1960
Genus: *Plagiorhynchus* Lühe, 1911
Subgenus: *Prosthorhynchus* Kostylew, 1915

Plagiorhynchus (*Prosthorhynchus*) *cylindraceus* (Goeze, 1782) Schmidt & Kuntz, 1966

Echinorhynchus cylindraceus Goeze, 1782
E. pici Gmelin, 1791 *fide* Florescu and Ienistea 1984
E. merulae Gmelin, 1791 *fide* Florescu and Ienistea 1984
E. transversus (Rudolphi, 1819) Travassos 1926
E. obliquus Dujardin, 1845 *fide* Florescu and Ienistea 1984
Centrorhynchus cylindraceus (Goeze 1782) Kostylew, 1914
C. fasciatus (Westrumb, 1821) Travassos, 1926 *fide* de Marval 1905
C. rostratus de Marval, 1902 *fide* Florescu and Ienistea 1984
Prosthorhynchus rosai (Porta, 1910) Meyer, 1932
Prosthorhynchus rostratus (de Marval, 1902) Meyer, 1932
Plagiorhynchus formosus Van Cleave, 1918 *fide* Amin et al. 1999
Plagiorhynchus taiwanensis Schmidt et Kuntz, 1966 *fide* Amin et al. 1999.

Host. *Calidris ferruginea* (Pontoppidan, 1763) (Curlew Sandpiper); *Charadrius pecuarius* Temminck, 1823 (Kittlitz's Plover); *Charadrius tricollaris* Vieillot, 1818 (Three-banded Plover) (Charadriidae).
Locality. Berg River, Western Cape Province, South Africa (Amin et al. 1999).
Host. *Crecopsis egregia* (Peters, 1854) (syn. *Crex egregia*) (African Crake) (Rallidae).
Locality. Blouberg, Limpopo Province, South Africa.
Host. *Vanellus armatus* (Burchell, 1822) (Blacksmith Lapwing) (Charadriidae).
Locality. Berg River, Western Cape Province, South Africa (Amin et al. 1999).

Unidentified plagiorhynchid

Host. *Charadrius marginatus* Vieillot, 1818 (White-fronted Plover), *Charadrius pallidus* Strickland, 1852 (Chestnut-banded Plover); *Charadrius pecuarius* Temminck, 1823 (Kittlitz's Plover); *Himantopus himantopus* (L., 1758) (Black-winged Stilt); *Vanellus armatus* (Burchell, 1822) (Blacksmith Lapwing)

Locality. Berg River, Western Cape Province, South Africa (Amin et al. 1999).

Family: Polymorphidae Meyer, 1931
Genus: *Andracantha* Schmidt, 1975

Andracantha tunitae (Weiss, 1914) Zdzitowiecki, 1989

Corynosoma tunitae Weiss, 1914

Host. *Microcarbo africanus* (Gmelin, 1789) (Long-tailed Cormorant) (Phalacrocoracidae).

Locality. Dyer Island, South Africa (Van Cleave 1937).

Notes. Van Cleave (1937) is mentioning that he looked at a large number of immature worms and he tentatively assigning them to *C. tunitae*.

Genus: *Arhythmorhynchus* Lühe, 1911

Skrjabinorhynchus Petrochenko, 1956

Arhythmorhynchus turbidus (Van Cleave, 1937) Golvan, 1994

Corynosoma turbidum Van Cleave, 1937

Host. *Phalacrocorax neglectus* (Wahlberg, 1855) (Bank Cormorant) (Phalacrocoracidae) (type host).

Locality. Dyer Island, South Africa (type locality) (Van Cleave 1937).

Type specimens. Holotype female (1737, 3) and one paratype female (1737, 1) in GNM. One paratype female (1737, 2) in the collection of H.J. Van Cleave, Urbana, Illinois, U.S.A.

Genus: *Bolbosoma* Porta, 1908

Bolbosoma capitatum (von Linstow, 1880) Porta, 1908

Echinorhynchus capitatum von Linstow, 1880
Bolbosoma physeteris Gubanov, 1952 (*fide* Amin & Margolis, 1998)

Host. *Ruvettus pretiosus* Cocco, 1833 (Oilfish) (Gempylidae).
Locality. South Africa's West coast, Atlantic Ocean (Nunkoo et al. 2017).

Bolbosoma vasculosum (Rudolphi, 1819) Porta, 1908

Echinorhynchus vasculosum Rudolphi, 1819
Bolbosoma annulatus Molin, 1858
B. aurantiacus Risso, 1826
B. pellucidus Leukart, 1828
B. serrani Linton, 1888
B. thunni Harada, 1935 (*fide* Petrochenko 1958)

Host. *Thyrsites atun* (Euphrasen, 1791) (Snoek) (Gempylidae).
Locality. South Africa's West and South coasts (Nunkoo et al. 2016).

Genus: *Corynosoma* Lühe, 1904 (*fide* Van Cleave, 1945)

Chentrosoma Monticelli, 1905
Centrosoma Lühe, 1912
Coryusoma Railliet & Henry, 1907 (misprint)
Echinosoma Porta, 1907

Corynosoma australe Johnston, 1937

Corynosoma otariae Morini & Boero, 1961

Host. *Thyrsites atun* (Euphrasen, 1791) (Snoek) (Gempylidae).
Locality. South Africa's West and South coasts (Nunkoo et al. 2016).

Host-Parasite List

Host	Parasite	Locality Country/ Reference
Class Aves		
Order Accipitriformes		
Family Accipitridae		
Kaupifalco monogrammicus (type host)	*Centrorhynchus sarehae* (Centrorhynchidae)	Makhado (Louis Trichardt), Limpopo Province, South Africa
Order Bucerotiformes		
Family Bucerotidae		
Tockus leucomelas	*Mediorhynchus taeniatus* (Gigantorhynchidae)	Limpopo Province, South Africa
Order Charadriiformes		
Family Charadriidae		
Calidris ferruginea	*Plagiorhynchus* (*Prosthorhynchus*) *cylindraceus* (Plagiorhynchidae)	Berg River, Western Cape Province, South Africa (Amin et al. 1999)
Charadrius marginatus	Unidentified plagiorhynchid acanthocephalan (Plagiorhynchidae)	Berg River, Western Cape Province, South Africa (Amin et al. 1999)
Charadrius pallidus	Unidentified plagiorhynchid acanthocephalan (Plagiorhynchidae)	Berg River, Western Cape Province, South Africa (Amin et al. 1999)
Charadrius pecuarius	*Plagiorhynchus* (*Prosthorhynchus*) *cylindraceus* (Plagiorhynchidae)	Berg River, Western Cape Province, South Africa (Amin et al. 1999)
	Unidentified plagiorhynchid acanthocephalan (Plagiorhynchidae)	Berg River, Western Cape Province, South Africa (Amin et al. 1999)
Charadrius tricollaris	*Plagiorhynchus* (*Prosthorhynchus*) *cylindraceus* (Plagiorhynchidae)	Berg River, Western Cape Province, South Africa (Amin et al. 1999)
Vanellus armatus	*Plagiorhynchus* (*Prosthorhynchus*) *cylindraceus* (Plagiorhynchidae)	Berg River, Western Cape Province, South Africa (Amin et al. 1999)
	Unidentified plagiorhynchid acanthocephalan (Plagiorhynchidae)	Berg River, Western Cape Province, South Africa (Amin et al. 1999)
Family Recurvirostridae		
Himantopus himantopus	Unidentified plagiorhynchid Acanthocephalan (Plagiorhynchidae)	Berg River, Western Cape Province, South Africa (Amin et al. 1999)
Order Galliformes		
Family Numididae		
Numida meleagris (type host)	*Mediorhynchus africanus* (previously identified as *Mediorhynchus gallinarum*) (Gigantorhynchidae)	Kruger National Park, Mpumalanga Province, South Africa (Junker and Boomker 2006); Vicinity of Petrus Steyn, Free State Province, South Africa (Davies et al. 2008); Musina, Limpopo Province, South Africa (Junker and Boomker 2007; Junker et al. 2008)
	Mediorhynchus numidae (Gigantorhynchidae)	Pretoria, Gauteng Province, South Africa (Oosthuizen and Markus 1967)
	Mediorhynchus taeniatus (Gigantorhynchidae)	Rooipoort farm, Kimberley, Northern Cape Province, South Africa (Crowe 1977)
Order Gruiformes		
Family Rallidae		
Crecopsis egregia	*Plagiorhynchus* (*Prosthorhynchus*) *cylindraceus* (Plagiorhynchidae)	Blouberg, Limpopo Province, South Africa
Order Passeriformes		
Family Turdidae		
Turdus smithi (type host)	*Mediorhynchus mokgalongi* (Gigantorhynchidae)	Polokwane, Limpopo Province, South Africa (type locality) (Smales et al. 2018)

Host	Parasite	Locality Country/ Reference
Order Strigiformes		
Family Strigidae		
Bubo africanus	*Centrorhynchus clitorideus* (Centrorhynchidae)	Zandrivierspoort Farm, Polokwane, Limpopo Province, South Africa
Order Suliformes		
Family Phalacrocoracidae		
Microcarbo africanus	*Andracantha tunitae* (Polymorphidae)	Dyer Island, South Africa (Van Cleave 1937)
Phalacrocorax neglectus (type host)	*Arhythmorhynchus turbidus* (Polymorphidae)	Dyer Island, South Africa (type locality) (Van Cleave 1937)
Class Actinopterygii		
Order Cypriniformes		
Family Cyprinidae		
Enteromius neefi	*Acanthogyrus* (*Acanthosentis*) *phillipi* (Quadrigyridae)	Lingwe River, Venda, Limpopo Province, South Africa (Mashego 1988)
Order Perciformes		
Family Cichlidae		
Oreochromis mossambicus	*Acanthogyrus* sp. (Quadrigyridae)	Molepo dam, Limpopo Province, South Africa (Kunutu et al. 2013)
Family Gempylidae		
Ruvettus pretiosus	*Bolbosoma capitatum* (Polymorphidae)	South Africa's West coast, Atlantic Ocean (Nunkoo et al. 2017)
	Rhadinorhynchus sp. (Rhadinorhynchidae)	South Africa's West coast, Atlantic Ocean (Nunkoo et al. 2017)
Thyrsites atun	*Bolbosoma vasculosum* (Polymorphidae)	South Africa's West and South coasts (Nunkoo et al. 2016)
	Corynosoma australe (Polymorphidae)	South Africa's West and South coasts (Nunkoo et al. 2016)
	Rhadinorhynchus cadenati (Rhadinorhynchidae)	South Africa's West and South coasts (Nunkoo et al. 2016)
Family Sciaenidae		
Argyrosomus japonicus (type host)	*Neoechinorhynchus* (*Neoechinorhynchus*) *dorsovaginatus* (Neoechinorhynchidae)	Breede River Estuary, Western Cape Province, South Africa (type locality) (Amin and Christison 2005)
Order Pleuronectiformes		
Family Soleidae		
Pegusa nasuta (*Solea bleekeri*) (type host)	*Rhadinorhynchus capensis* (Rhadinorhynchidae)	Heuninges River estuary (Bray 1974)
	Longicollum sp. innom. (Pomphorhynchidae)	Klein River estuary (Bray 1974)
Barnardichthys fulvomarginata (type host)	*Longicollum chabanaudi* (Pomphorhynchidae)	False Bay, Western Cape Province (Dollfus and Golvan 1963)
Class Mammalia		
Order Afrosoricida		
Family Chrysochloridae		
Chrysospalax trevelyani (type host)	*Heptamegacanthus niekerki* (Oligacanthorhynchidae)	Nqadu Forest, Transkai, Eastern Cape Province, South Africa (Spencer Jones 1990)
Order Carnivora		
Family Felidae		
Felis catus	*Centrorhynchus* sp. (Centrorhynchidae)	Pretoria, Gauteng Province, South Africa (Baker et al. 1989)

Host	Parasite	Locality Country/ Reference
Family Herpestidae		
Mungos mungo	*Centrorhynchus* sp. (Centrorhynchidae)	Polokwane, Limpopo Province, South Africa.
Order Eulipotyphla		
Family Erinaceidae		
Atelerix frontalis (*Aethechinus frontalis*)	*Moniliformis kalahariensis* (Moniliformidae)	Mohlonong village and University of Limpopo, Limpopo Province, South Africa (Amin et al. 2014)
	Moniliformis moniliformis (Moniliformidae)	Hammanskraal, Gauteng Province, South Africa (Le Roux 1930)
Order Primates		
Family Galagidae		
Otolemur crassicaudatus	*Moniliformis* sp. (Moniliformidae)	Venda, Limpopo Province, South Africa
Order Rodentia		
Family Muridae		
Gerbilliscus leucogaster	*Moniliformis acomysi* (Moniliformidae)	Vyeboom village, Limpopo Province, South Africa
Mastomys natalensis	*Moniliformis acomysi* (Moniliformidae)	Bloemhof, Free State Province
Mus minutoides	*Moniliformis acomysi* (Moniliformidae)	Hoopstad, Free State Province, South Africa
Class Reptilia		
Order Squamata		
Family Varanidae		
Varanus albigularis	Oligacanthorhynchidae sp. (Oligacanthorhynchidae)	Tzaneen; Tolwe, Limpopo Province, South Africa

Results and discussion

A total of twenty-one species of acanthocephalans, from thirteen genera from ten families of seven orders, comprise this updated checklist of acanthocephalans in South Africa. Representatives of three of the four classes of acanthocephalans (Amin 2013) have been reported in South Africa, with only the Polyacanthocephala Amin, 1987 not having been recorded yet. The composition of reported acanthocephalan fauna shows that the Polymorphidae is the most represented family with five named species parasitic in marine fish and wild birds.

In South Africa, birds have the highest species richness of acanthocephalans to this date with nine named species (from five genera) and five records only identified to group level, followed by fish with eight named species (from six genera) and two species only identified to genus level, mammals with four named species (from two genera) and three species only identified to genus level and finally reptiles with a single species only identified to group level. No acanthocephalans have been reported in amphibians to date. During the current study 110 frog specimens belonging to 19 species were examined but none harboured any acanthocephalans. However, this forms a small part of the entire amphibian fauna of the country which includes 128 described frog species (Frost 2018).

Only a small fraction of the vertebrate fauna of South Africa has been surveyed for acanthocephalans and we expect that in future additional acanthocephalan species will be discovered and described. For example it is estimated that many of South Africa's marine fish parasites have yet to be discovered (Smit and Hadfield 2015). South Africa has an extremely rich biodiversity (Huntley et al. 2005), with nearly 8% of the world's known species of birds, 6% of mammal species and 5% of reptile species (Driver et al. 2012). Therefore we might expect a more diverse acanthocephalan fauna compared to that of Brazil which has 23 genera and 34 species (from only 119 fish species) (Santos et al. 2008) or Iran with 30 described species (Tavakol et al. 2015). The lower species richness reported for South Africa probably reflects sampling effort rather than the true diversity of the acanthocephalan fauna. Until more data are available it will not be possible to determine the true species richness of the South African acanthocephalan assemblage.

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RESEARCH ARTICLE

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A new feather mite species of the genus *Trouessartia* Canestrini, 1899 (Acarina, Trouessartiidae) – an integrative description (morphology and DNA barcoding data)

Ioana Cristina Constantinescu[1], Oana Paula Popa[1], Luis Ovidiu Popa[1],
Ioana Cobzaru[2], Mukhim D. Khlur B.[3] , Costică Adam[1]

1 *"Grigore Antipa" National Museum of Natural History, Sos. Kiseleff no.1, 011341 Bucharest 1, Romania* **2** *Ecology, Taxonomy and Nature Conservation Department, Institute of Biology, Romanian Academy, Splaiul Independenței no. 296, 060031 Bucharest, Romania* **3** *Department of Zoology, Lady Keane College, 793001 Shillong, Meghalaya, India*

Corresponding author: *Ioana Cristina Constantinescu* (cristinactinescu@yahoo.com)

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Abstract

A new species of the feather mite genus *Trouessartia* (Trouessartiidae) is described from the Large Niltava *Niltava grandis* (Blyth) (Passeriformes, Muscicapidae) in Northeast India (Meghalaya, Jaintia Hills, Shnongrim village). *Trouessartia niltavae* Constantinescu, **sp. n.** is morphologically closely related (no phylogenetic meaning) to *T. bulligera* Gaud, 1968 from *Clytorhynchus hamlini* (Mayr) (Passeriformes: Monarchidae), sharing in males a unique character within the genus, by having setae *e* on legs IV hemispheroid, with spine-shaped apex. Males of the new species have the prodorsal shield without ornamentation, the prohysteronotal shield and lobar shield connected, and the terminal cleft parallel sided. Females have the posterior half of the hysteronotal shield ornamented with large ovate lacunae in central area and small elliptical lacunae marginally. To the morphological description of this new feather mite species we added sequence data on the mitochondrial cytochrome c oxidase subunit I gene fragment (COI). The phylogenetic relationships between *Trouessartia* species are briefly discussed.

Keywords

Feather mite, new species, taxonomy, *Trouessartia*

Introduction

The feather mite genus *Trouessartia* Canestrini, 1899 comprises about 120 described species associated predominantly with birds of the order Passeriformes. A world revision of this genus, including 71 species was performed by Santana (1976); other presently known species were described in the subsequent 40 years by various authors (Mauri and de Alzuet 1968, Černý and Lukoschus 1975, Gaud 1977, Černý 1979, Mironov 1983, Gaud and Atyeo 1986, 1987, Mironov and Kopij 1996, 2000, Mironov and Galloway 2002, O'Connor et al. 2005, Carleton and Proctor 2010, Constantinescu et al. 2013, 2016a, 2016b, 2017, 2018, Mironov and González-Acuña 2013, Hernandes 2014, 2017, Hernandes and Valim 2015, Mironov and Overstreet 2016, Mironov and Palma 2016, Mironov and Bermúdez 2017, Hernandes and OConnor 2017). A number of undetermined *Trouessartia* species were reported from the following areas of the world: 22 species from Colombia (Barreto et al. 2012), 15 species from Brazil (Silva et al. 2015) and 162 species from Southeast Asia (McClure and Ratanaworabhan 1973).

The bird genus *Niltava* Hodgson belongs to the family of Old World Flycatchers (Passeriformes: Muscicapidae) and currently includes six valid species distributed in the Indo-Malayan biogeographic region (Clements et al. 2016). Feather mites were previously recorded only on two of these species: *Analges* sp., *Anisodiscus* sp., *Mesalgoides* sp., *Proctophyllodes cotyledon* Trouessart, 1899, *Bicentralges distinctus* Orwig, 1968, *Proterothrix chachulae* Constantinescu, 2017 and *Trouessartia* sp. from *Niltava grandis* (Blyth); *Analges* sp., *Proctophyllodes elegans* Atyeo and Braasch, 1966, *Proterothrix* sp., *Therisalges* sp., *Trouessartia* sp., and *Xolalges* sp. from *Niltava sundara* Hodgson (Atyeo 1973, Atyeo and Braasch 1966, Constantinescu et al. 2017, Orwig 1968).

The main goals of this paper are to realise the description of a new species of *Trouessartia* and to analyse its relationships within the genus based on molecular data. This is the first species of *Trouessartia* described from a host of the genus *Niltava*, although, as mentioned above, two presumably new species of *Trouessartia* have been reported by Atyeo (McClure and Ratanaworabhan 1973) from *N. grandis* and *N. sundara*, but they have never been described.

The new species of *Trouessartia* described herein cannot be referred to any of the seven species groups previously established in the genus (Santana 1976, Mironov and Kopij 1996, 2000), because of having a specific combination of characters.

Materials and methods

The material used in the present paper was collected near Shnongrim (Meghalaya, India) in January 2014. The birds were captured using mist nets, identified and visually checked for the presence and collection of mites and released back to the wild. Mite specimens were collected manually with a needle and placed in tubes with 96% ethanol. Later, in laboratory conditions, mite specimens selected for morphological analysis were cleared in 90% lactic acid for 24 hours and mounted on microscope slides in Hoyer's medium. Some specimens preserved in ethanol were used for genetic analysis. Drawings were made using an Olympus CX21 microscope, with a camera lucida drawing device. The bird specimens were identified according to Rasmussen and Anderton (2012) and Grimmett et al. (2011), and the taxonomy of the birds follows Clements et al. (2016). The body setation of mites follows that of Griffiths et al. (1990) with the modifications by Norton (1998) concerning coxal setae, while the setation of legs follows Gaud and Atyeo (1996). Description of the new species of *Trouessartia* is given according to the standards proposed for mites of this genus and related genera (Orwig 1968, Santana 1976), and the measuring techniques of particular structures follow Mironov and González-Acuña (2013). We give the full set of measurements for a holotype (male) and a range of measurements for corresponding paratypes. All measurements are in micrometers (μm). The holotype and paratypes of the new species are deposited in the Acarological Collection of the "Grigore Antipa" National Museum of Natural History, Bucharest, Romania (MGAB). The inventory numbers are given in parentheses for all type specimens.

Three paratype specimens of *Trouessartia niltavae* sp. n. (one male ANA838 and two females ANA839, ANA840) were used to isolate DNA using DNAeasy Tissue Kit (Qiagen). All four specimens used for molecular analyses were mounted and kept as reference vouchers for morphological examination. The specimens preserved in ethanol 96% were transferred in 180 μl ATL Buffer with 20 μl of Proteinase K and incubated overnight at 56 °C on a shaking thermoblock. After 24 h, 5μl of Proteinase K were added and incubation was continued until 72 h. For the rest of the protocol we followed the manufacturer specifications and the modification suggested by Dabert et al. (2008).

As DNA barcode we used a region near the 5` terminus of the COI gene, amplified by PCR with the degenerate primers bcdF05 (5`- TTTTCTACHAAYCATAAAGATATTGC-3`) and bcdR04 (5`- TATAAACYTCDGGATGNCCAAAAAA-3`), according to Dabert et al. (2008). The PCR genotyping reaction was performed in a 50 μL total volume containing DNA template, 1X Green GoTaq Flexi Buffer, 2.5 mM MgCl2, each dNTP at 0.1 mM, each primer at 0.5 μM (the primers were M13 tailed) and 1.5 units of GoTaq DNA polymerase (5U/μl) (Promega, Madison, USA). The PCR products were isolated from samples containing visible bands and sent for sequencing to Macrogen (Seoul, South Korea).

Sequence chromatograms were edited and assembled with CodonCode Aligner version 3.7.1. For the phylogenetic analysis we used a dataset comprising three sequences obtained from the new species *Trouessartia niltavae* and 74 sequences belonging to 17 species of *Trouessartia* genus available in GenBank and BOLD data system and four sequences belonging to genus *Calcealges* (see Tabel 1), to be used as outgroup.

MEGA version 7 software (Kumar et al. 2016) was used to identify the most appropriate substitution model, which was subsequently used to generate phylogenetic trees using the Maximum Likelihood (ML) and Neighbor-Joining (NJ) methods. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (10000 replicates) was also computed. The same software was used to compute intraspecific pairwise distances between sequences using K2P distance model (Kimura 1980).

Results

Family Trouessartiidae Gaud, 1957
Genus *Trouessartia* Canestrini, 1899

Trouessartia niltavae Constantinescu, sp. n.

http://zoobank.org/4FB1A0C6-E767-4D46-AF88-B3BAB0E4ACD1
Figs 1–6

Type material. Male holotype (ANA663), 5 male (ANA661, ANA662, ANA664, ANA665, ANA838) and 8 female (ANA666, ANA667, ANA668, ANA669, ANA670, ANA839, ANA840) paratypes, 27.01.2014, from the Large Niltava *Niltava grandis grandis* (Blyth) (Passeriformes, Muscicapidae); **INDIA:** Meghalaya, Jaintia Hills, Shnongrim village, (25°21'12.36"N, 92°31'3.06"E); 1151 m; subtropical forest; collector D. K. B. Mukhim.

Description. Male (Figs 1; 2; 3A–E; holotype, range for four paratypes in parentheses): length of idiosoma from anterior end to bases of setae *h3* 384 (404–424), greatest width at level of humeral shields 182 (194–202). Length of hysterosoma from sejugal furrow to bases of setae *h3* 250 (260–272). Prodorsal shield: length along midline 130 (130–142), greatest width in posterior part 144 (142–148), lateral margins not fused with scapular shields, antero-lateral extensions almost extending to bases of epimerites Ia between legs I and II, surface without ornamentation (Fig. 1). Internal scapular setae *si* spiculiform, 32 (30–32) long, separated by 48 (42–46); external scapular setae *se* situated on prodorsal shield, separated by 80 (88–93). Vertical setae *ve* represented by alveoli. Humeral shield with setae *c2* spiculiform, 44 (42–46) long. Setae *c3* narrowly lanceolate with acute apex, 23 (20–25) long. Dorsal hysterosoma with prohysteronotal shield and lobar shield connected, delimited from each other by lateral incisions immediately posterior to setae *e2.* Prohysteronotal shield: length 162 (156–162), width at anterior margin 133 (126–132), lateral margins, each with two shallow incisions at level of trochanters III, dorsal hysterosomal apertures (DHA) absent. Dorsal setae *d1*, *d2* present, minute. Length of lobar shield excluding lamellae 90 (90–102). Opisthosomal lobes approximate, separated by narrow parallel-sided terminal cleft; length of this cleft from anterior end to apices of lamellae 42 (44–46), width in anterior part 6 (6–8). Lamellae smooth, slightly attenuate apically, length from bases of setae *h3* to lamellar apices 28 (30–32). Setae *h1* anterior to setae *h2*. Distance between dorsal setae: *c2-d2* 80 (80–82), *d2-e2* 82 (84–87), *e2-h2* 70 (70–76), *h2-h3* 22 (20–22), *h2-h2* 36 (34–38), *h3-h3* 29 (26–28), *d1-d2* 30 (24–30), *e1-e2* 38 (38–44).

Epimerites I free. Rudimentary sclerites rEpIIa present, roughly rounded. Genital apparatus situated between levels of trochanters III and IV, length excluding basal sclerite 38 (37–40), greatest width 14 (10–14) (Fig. 2). Epiandrum present, setae *g* long and filiform, contiguous at bases, postgenital plaque present. Adanal apodemes heavily sclerotised, with narrow lateral membrane and a pair of apophysis. Translobar apodeme present. Adanal shields very small, teardrop-shaped, bearing setae *ps3*. Anal

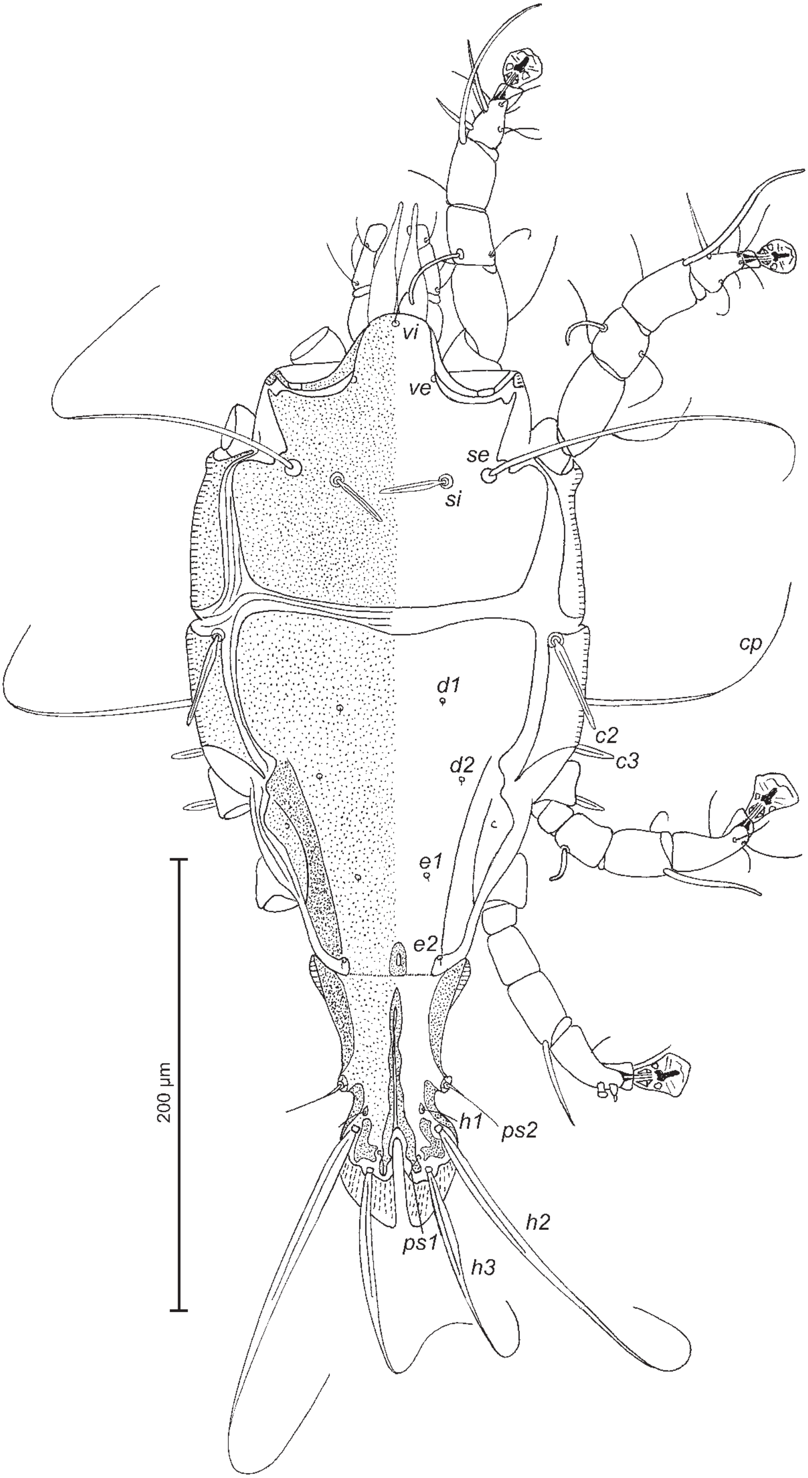

Figure 1. *Trouessartia niltavae* Constantinescu, sp. n., male holotype: dorsal view of idiosoma.

suckers 12 (12–13) in diameter. Anterior ends of epimerites IV extending beyond level of setae *4b*; epimerites IVa short, not extending to level of genital apparatus. Setae *4b* situated anterior to level of setae *3a*, setae *g* situated posterior to level of setae *4a*. Distance between ventral setae: *4b-3a* 31 (30–36), *4b-g* 72 (74–80), *g-ps3* 48 (44–50), *ps3-h3* 86 (86–94). Setae *sR* of trochanters III narrowly lanceolate, with acute apex 20 (19–24) long, setae *cG* and *mG* of genua I, II filiform, not thickened basally. Tarsus IV 36 (34–36) long; seta *d* barrel-shaped, with discoid cap; seta *e* with hemispheroid base and stick-shaped apical part, situated subapically (Fig. 3D). Legs IV with ambulacral disc extending to level of setae *h3*.

Female (Figs 4; 5; 6A–E; range for five paratypes): length of idiosoma from anterior end to apices of lamellar lobar processes 452–468, greatest width 148–200. Length of hysterosoma from sejugal furrow to apices of lamellar lobar processes 308–324. Prodorsal shield shaped as in male, 130–140 in length, 144–152 in width, surface without ornamentation. Setae *si* spiculiform, 29–34 long, separated by 44–48; external scapular setae *se* situated on prodorsal shield, separated by 90–94. Humeral shields with setae *c2* spiculiform, 42–44 long. Setae *c3* narrowly lanceolate, with acute apex, 22–24 in length. Hysteronotal shield: length from anterior margin to bases of setae *h3* 270–300, width at anterior margin 128–132, lateral margins with shallow concavity at level of trochanters III, bottom of these concavities with dark sclerotisation, DHA absent. Posterior half of hysteronotal shield with distinct ornamentation: with large ovate lacunae in median area and few small elliptical lacunae arranged marginally (Fig. 4). Dorsal setae *d1* and *d2* present. Setae *h1* thick, lanceolate, surrounded by small ovoid area of unsclerotised tegument, 24–28 long, situated antero-mesal to bases of setae *h2*, 20–24 from each lateral margin of hysteronotal shield. Setae *ps1* positioned dorsally on opisthosomal lobes, equidistant from outer and inner margins of lobe, close to bases of setae *h3*. Distance from bases of setae *h3* to membranous apices of lobes 29–32. Setae *f2* present. Supranal concavity open posteriorly into terminal cleft. Length of terminal cleft together with supranal concavity 102–120, width of cleft at level of setae *h3* 38–48. Interlobar membrane occupying anterior 1/3 of terminal cleft, distance from free margin of interlobar membrane to membranous lobar apices 78–88. External copulatory tube minute, 1-2 long, situated on free margin of interlobar membrane. Spermatheca with short collar, primary spermaduct without enlargements, secondary spermaducts with small verrucosities in distal half, length 26–30 (Fig. 6E). Distance between dorsal setae: *c2-d2* 76–80, *d2-e2* 82–92, *e2-h2* 50–56, *h2-h3* 58–64, *h2-h2* 68–80, *h3-h3* 50–60, *d1-d2* 29–34, *e1-e2* 45–52, *h1-h2* 18–21, *h1-h1* 38–46, *ps1-h3* 9–10.

Epimerites I free. Epigynum 36–38 in length, 76–80 in width (Fig. 5). Epimerites IVa present, short. Setae *sR* of trochanters III narrowly lanceolate, with acute apex, 18–21 long, setae *cG* and *mG* of genua I, II filiform, not thickened basally. Legs IV with ambulacral disc extending to midlevel between setae *h2* and *h3*.

Etymology. The specific name *niltavae* is derived from the generic name of the type host and is a noun in the genitive case.

Remarks. *Trouessartia niltavae* sp. n. is morphologically close to *T. bulligera* Gaud, 1968 from *Clytorhynchus hamlini* (Mayr) (Passeriformes: Monarchidae), shar-

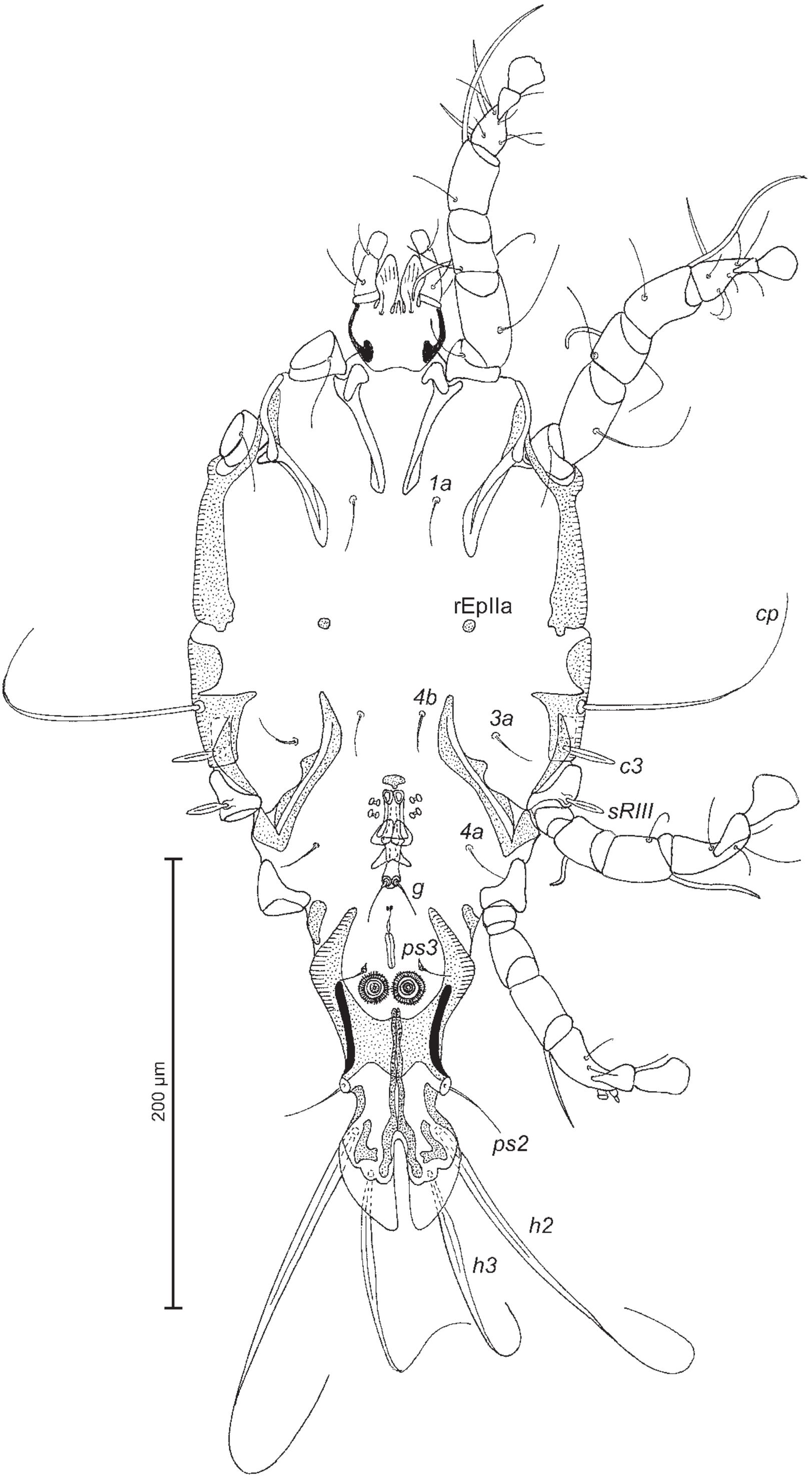

Figure 2. *Trouessartia niltavae* Constantinescu, sp. n., male holotype: ventral view of idiosoma.

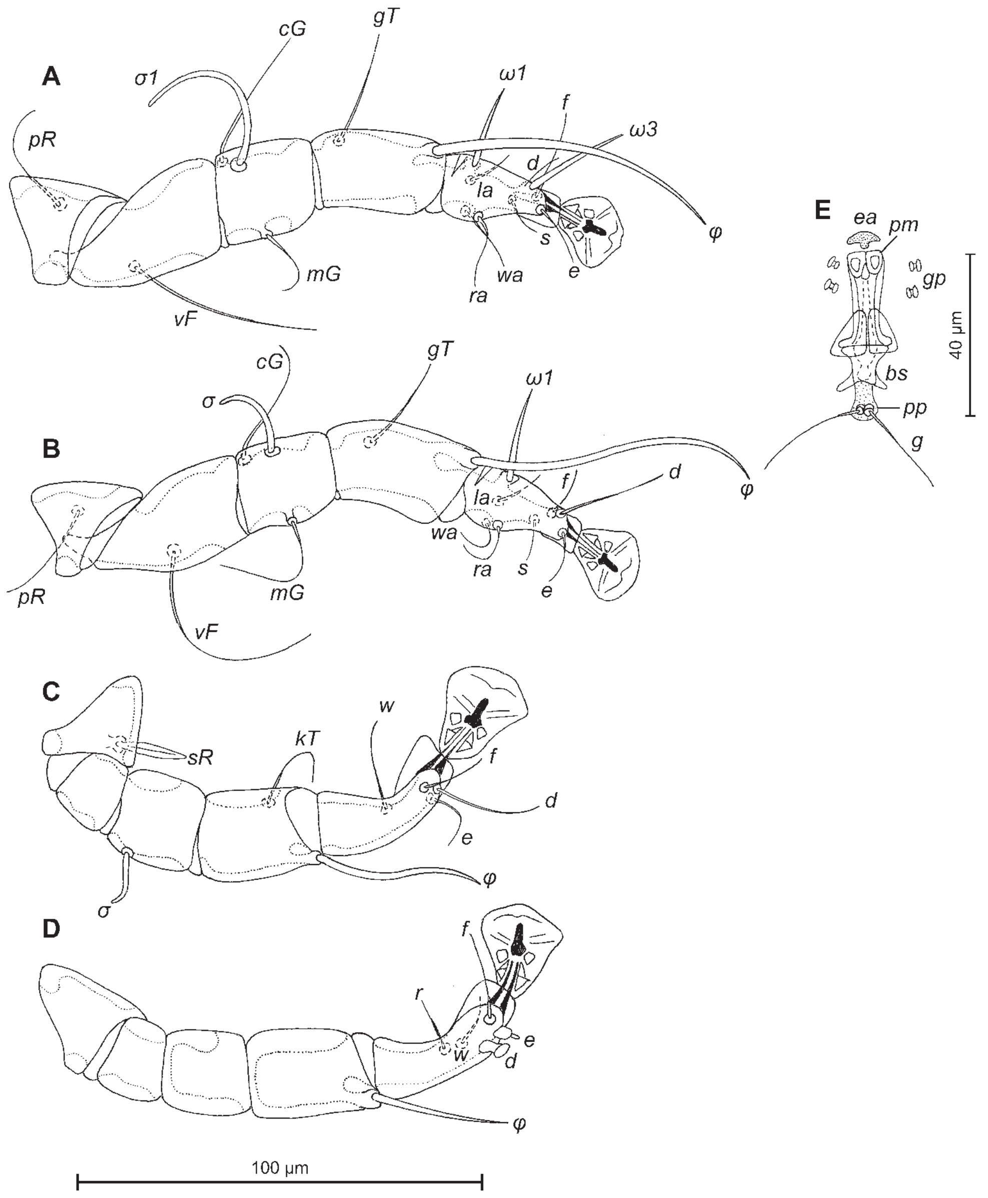

Figure 3. *Trouessartia niltavae* Constantinescu, sp. n., A–D details of male legs, dorsal view: A–leg I, B–leg II, C–leg III, D–leg IV; E–opisthosoma of male, ventral view. Abbreviations: bs – basal sclerite, ea – epiandrum, gp – genital papillae, pm – parameres, pp – postgenital plaque.

ing in males a unique character within the genus: setae *e* on tarsi IV are hemispheroid with stick-like apex. Additionally, in both sexes of these species, setae *d1* are present, setae *c2* and *sR*III are narrowly lanceolate, with acute apex and the dorsal hysterosomal apertures (DHA) is absent. Both sexes of *T. niltavae* differ from those of *T. bulligera* by the shape of setae *c2*, which are spiculiform in the first species ver-

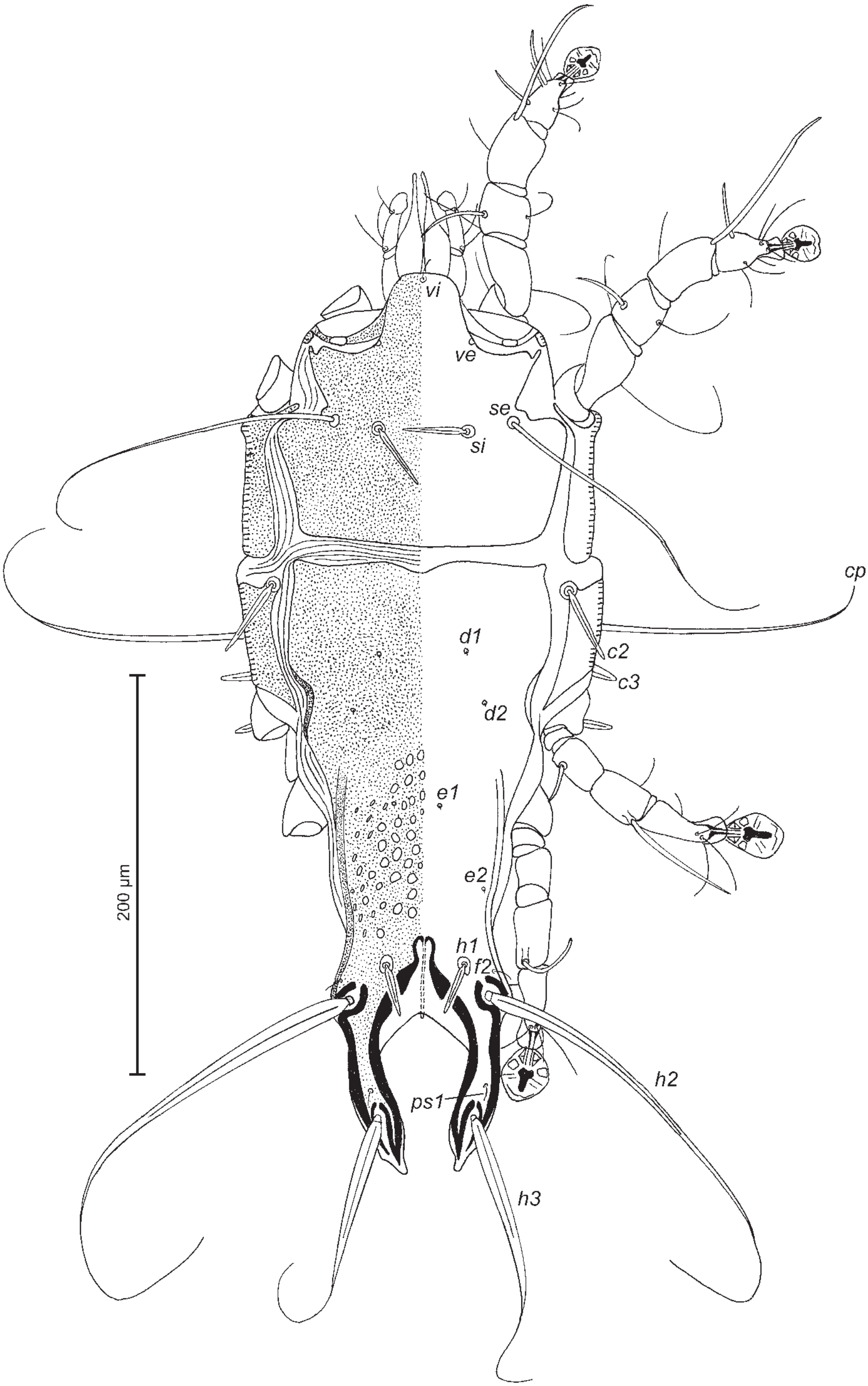

Figure 4. *Trouessartia niltavae* Constantinescu, sp. n., female paratype: dorsal view of idiosoma.

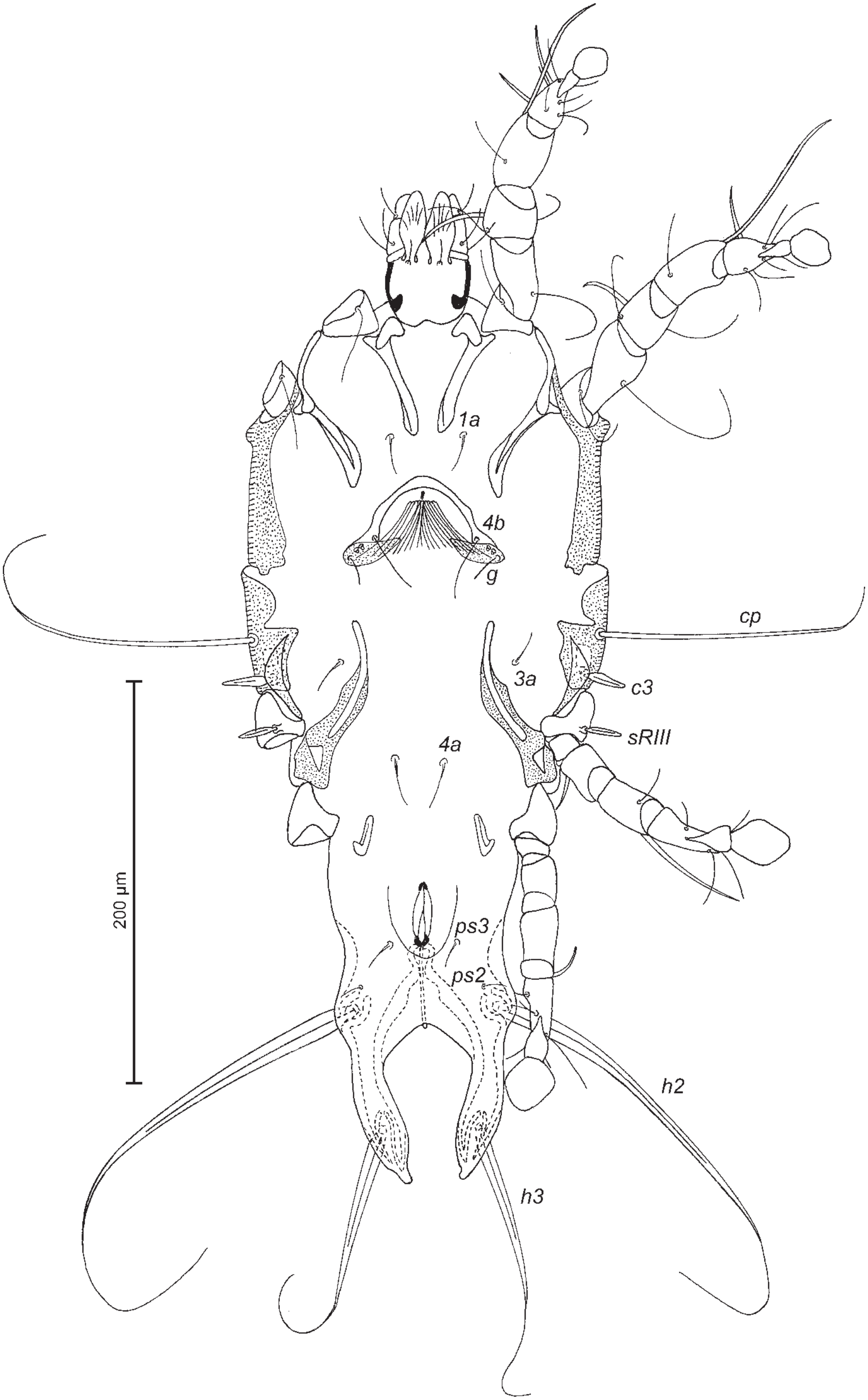

Figure 5. *Trouessartia niltavae* Constantinescu, sp. n., female paratype: ventral view of idiosoma.

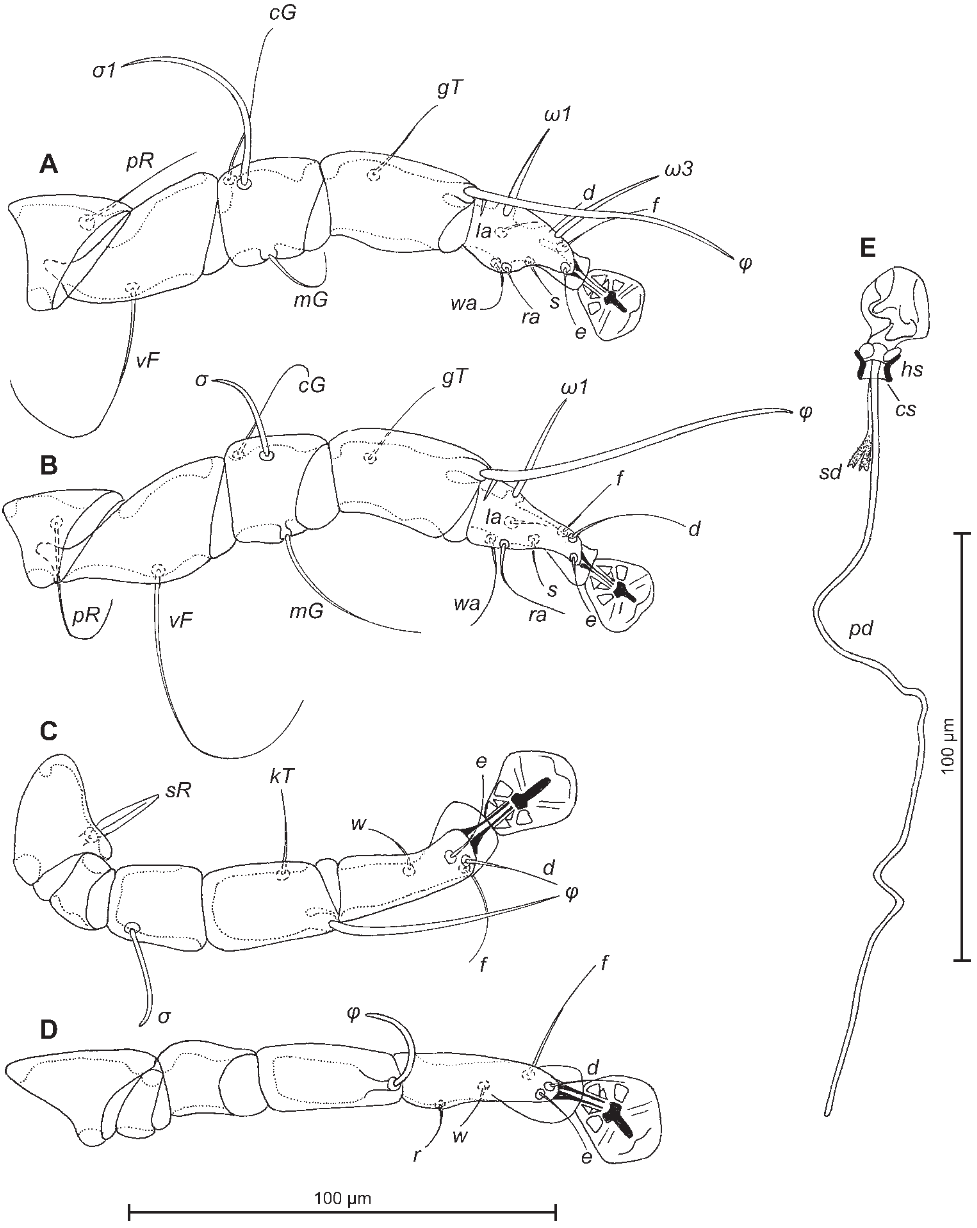

Figure 6. *Trouessartia niltavae* Constantinescu, sp. n., A–D details of female legs, dorsal view: A–leg I, B–leg II, C–leg III, D–leg IV; E–spermatheca and spermaducts of female; Abbreviations: hs – head of spermatheca; pd – primary spermaduct; sd – secondary spermaduct.

sus needle-like in the second. Males of both species have the prohysteronotal shield without ornamentation, the lamellae of opisthosomal lobes are attenuate apically and with entire margins, the translobar apodeme is present, setae *g* are contiguous at bases and situated on postgenital plaque. In males of *T. niltavae*, the prodorsal shield

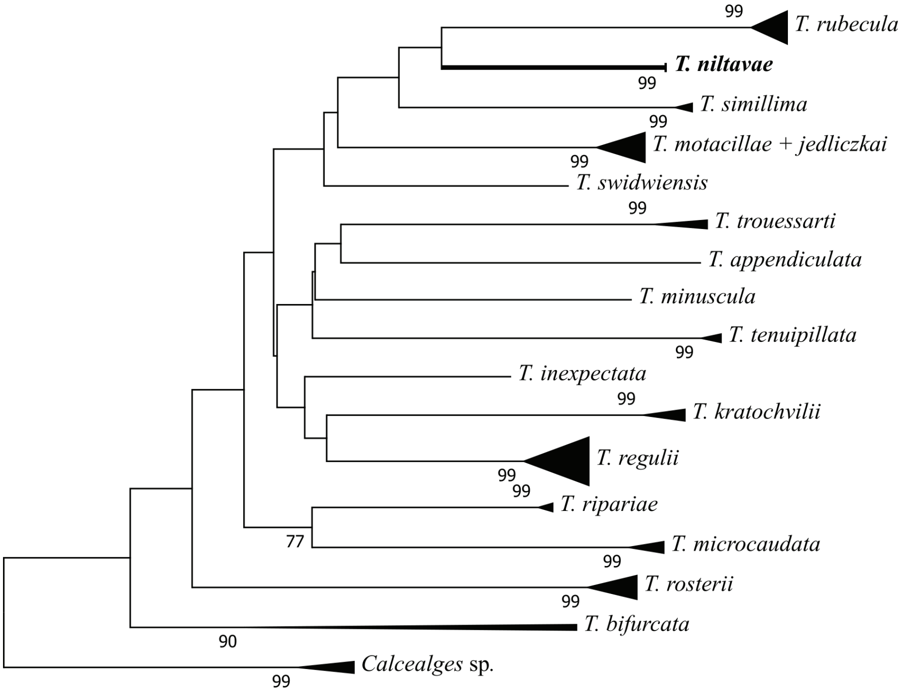

Figure 7. Evolutionary relationship between *Trouessartia* species inferred using the Neighbor-Joining method. The bootstrap test result (10000 replicates) is shown next to each branch.

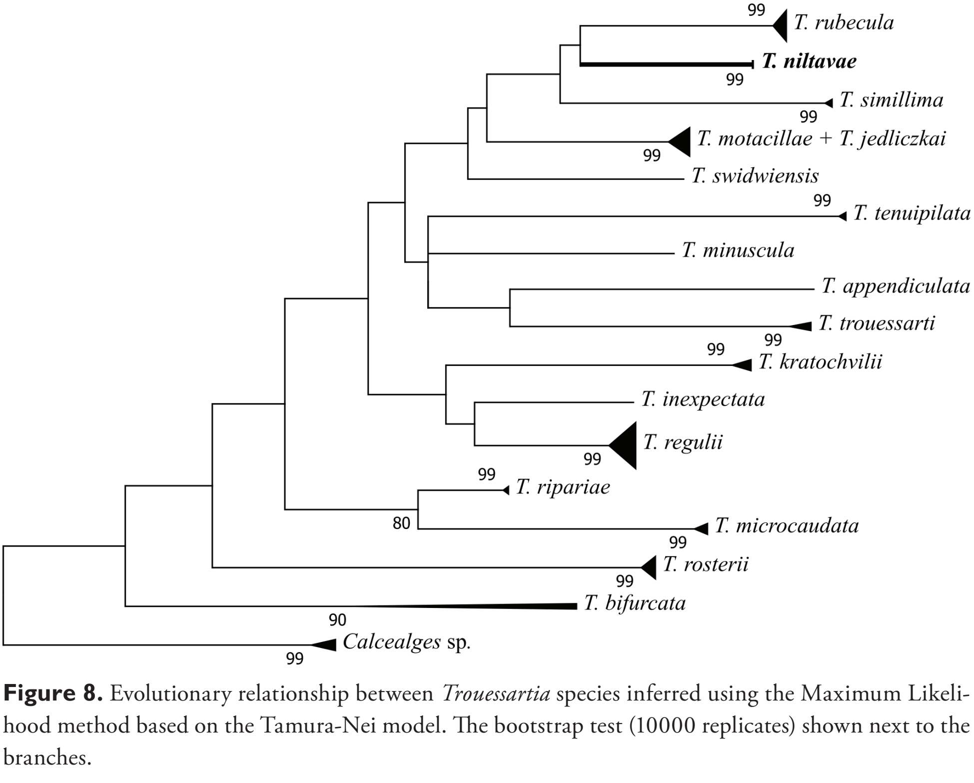

Figure 8. Evolutionary relationship between *Trouessartia* species inferred using the Maximum Likelihood method based on the Tamura-Nei model. The bootstrap test (10000 replicates) shown next to the branches.

Table 1. Analysed sequences of *Trouessartia* spp. from BOLD and GenBank databases.

Species	GenBank Accession Number	Species	GenBank Accession Number	Species	GenBank Accession Number
T. appendiculata	KP193765	*T. rubecula*	KP193799	*T. rosterii*	KP193796
T. bifurcata	KP193766	*T. rubecula*	KP193801	*T. rosterii*	KP193797
T. bifurcata	KP193767	*T. rubecula*	KP193802	*T. rosterii*	KP193798
T. inexpectata	KP193768	*T. rubecula*	KP193803	*T. reguli*	MG411516
T. jedliczkai	KP193769	*T. rubecula*	KP193804	*T. reguli*	MG409826
T. jedliczkai	KP193770	*T. rubecula*	KP193805	*T. reguli*	MG409631
T. jedliczkai	KP193771	*T. rubecula*	KP193806	*T. reguli*	MG414726
T. jedliczkai	KP193772	*T. rubecula*	KP193807	*T. reguli*	MG413144
T. jedliczkai	KP193773	*T. rubecula*	KP193808	*T. reguli*	MG410216
T. jedliczkai	KP193774	*T. rubecula*	KP193809	*T. reguli*	MG412618
T. kratochvili	KP193776	*T. rubecula*	KU203092	*T. reguli*	MG411130
T. kratochvili	KP193777	*T. simillima*	KP193810	*T. reguli*	MG416767
T. kratochvili	KP193778	*T. simillima*	KP193811	*T. reguli*	MG414272
T. kratochvili	KU203094	*T. simillima*	KP193812	*T. reguli*	KP193788
T. microcaudata	KP193779	*T. swidwiensis*	KP193813	*T. reguli*	KP193789
T. microcaudata	KP193780	*T. tenuipilata*	KP193814	*T. reguli*	KP193790
T. microcaudata	KP193781	*T. tenuipilata*	KP193815	*T. reguli*	KP193791
T. microcaudata	KP193782	*T. tenuipilata*	KP193816	*T. reguli*	KU203095
T. minuscula	KP193783	*T. trouessarti*	KP193817	*T. reguli*	KU203096
T. motacillae	KP193784	*T. trouessarti*	KP193818	*T. niltavae* sp. n.	MH094247*
T. motacillae	KP193785	*T. trouessarti*	KP193819	*T. niltavae* sp. n.	MH094248*
T. motacillae	KP193786	*T. rosterii*	KT025283	*T. niltavae* sp. n.	MH094249*
T. motacillae	KP193787	*T. rosterii*	KT025284	*Calcealges* sp.	MG410916
T. ripariae	KP193792	*T. rosterii*	KT025288	*Calcealges* sp.	MG412689
T. ripariae	KP193793	*T. rosterii*	KT025289	*Calcealges* sp.	KU203091
T. ripariae	KP193794	*T. rosterii*	KP193795	*Calcealges* sp.	MG409226

* sequences produced in the present study.

is without ornamentation, the prohysteronotal shield and lobar shield have wide median connection, the terminal cleft is parallel-sided and 44-46 μm long, and terminal lobes are separated by 6–8 μm. In males of *T. bulligera,* the prodorsal shield has ornamentation with faint, interconnecting network of irregular lines, the prohysteronotal shield is completely separated from the lobar shield, the terminal cleft is divergent in posterior half and 75 μm in length, and terminal lobes are separated by 12 μm. In females of both species, setae *h1* are lanceolate, the external copulatory tube is present, the supranal concavity is open posteriorly into terminal cleft, and the interlobar membrane occupies the anterior 1/3 of terminal cleft. In females of *T. niltavae* setae *f2* are present, the posterior half of the hysteronotal shield is ornamented with large ovate lacunae in the central area and small elliptical lacunae marginally arranged. In females of *T. bulligera* setae *f2* are absent, the posterior half of the hysteronotal shield has ornamentation with small elliptical lacunae in the central area and large ovate lacunae marginally arranged.

DNA barcode. Representative DNA sequences: molecular voucher specimens ANA838 male (GenBank accession number MH094247), ANA839 female (Gen-

Bank accession number MH094248), ANA840 female (GenBank accession number MH094249).

We sequenced a 586-pb fragment of the mitochondrial cytochrome c oxidase subunit I (COI) gene for two females and one male paratypes. All three sequences belong to a single haplotype. The calculated intra-specific genetic distances (K2P) for other species of *Trouessartia* was as follows: *Trouessartia rosterii* 0,8%, *T. reguli* 1,4%, *T. kratochvili* 1%, *T. rubecula* 0,5%, *T. simillima* 0.4%, *T. ripariae* 0,4%, *T. microcaudata* 0,7%, *T. tenuipillata* 0,6%, *T. jedliczkai* 1,6%, *T. trouessarti* 1.4%, *T. motacillae* 1.1%, *T. bifurcata* 11,5%.

The best-fit base substitution model for the analyzed data was determined to be TN93+G+I. The NJ and ML trees exhibited similar topologies and branching structures (see Figures 7 and 8). In both trees our new species was grouped with *Trouessartia rubecula* and *T. simillima*, also described from the Muscicapidae family. Our analysis resolved well the analysed *Trouessartia* species with the exception of *T. motacillae* and *T. jedliczkai*, which were poorly resolved in both analyses. Another noticeable feature of our analysis refers to the species *T. bifurcata*, identified on two avian families: Sylviidae and Acrocephalidae. The two sequences of *T. bifurcata* introduced in our analysis exhibit a high intraspecific diversity which can be a signal of two cryptic species presently identified as *T. bifurcata*.

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Three new species of the spider genus *Asceua* from Malaysia (Araneae, Zodariidae)

Bao-Shi Zhang[1,2], Feng Zhang[3]

[1] *College of Life Sciences, Hebei Normal University, Shijiazhuang, Hebei 050024, P. R. China* [2] *Department of Biochemistry, Baoding University, Baoding, Hebei 071051, P. R. China* [3] *The Key Laboratory of Invertebrate Systematics and Application, College of Life Sciences, Hebei University, Baoding, Hebei 071002, P. R. China*

Corresponding author: *Feng Zhang* (dudu06042001@163.com)

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Abstract

Three new species of the genus *Asceua* Thorell, 1887, from the natural forests of Malaysia, are described as *Asceua bifurca* **sp. n.** (♂♀), *A. curva* **sp. n.** (♂), and *A. trimaculata* **sp. n.** (♀). The genus *Asceua* is reported from Malaysia for the first time.

Keywords

description, distribution, Southeast Asia, taxonomy, Zodariid

Introduction

Members of the ant spider family Zodariidae Thorell, 1881 are small to medium-sized. It contains 85 genera and 1141 known species worldwide (World Spider Catalog 2018). Among them, 40 species are attributed to 5 genera (*Heliconilla* Dankittipakul, Jocqué & Singtripop, 2012, *Heradion* Dankittipakul & Jocqué, 2004, *Malayozodarion* Ono & Hashim, 2008, *Mallinella* Strand, 1906, and *Workmania* Dankittipakul, Jocqué & Singtripop, 2012) which have been reported from Malaysia. The genus *Asceua* was established by Thorell in 1887, with the type being *A. elegans* Thorell, 1887 from Myanmar. It was removed from synonymy with *Storena* Walckenaer, 1805 (Bosmans and van Hove 1986; Jocqué 1986). Jocqué (1991) later synonymized the genera *Suffucia* Simon, 1893 and *Doosia* Kishida, 1940 with *Asceua*. Members of this genus can be distinguished from other zodariids by their small size, laterally compressed bulb, developed cymbial fold, and the long and meandering copulatory ducts (Jocqué 1991).

At present, the genus includes 26 species worldwide (World Spider Catalog 2018). Among these, 22 are known from Southeast Asian countries that are close to Malaysia, including Japan, China (Southern part), Vietnam, Myanmar, Cambodia, Philippines and Indonesia; three are known from African countries and islands (Congo, Guinea-Bissau and the Comoros); and one is from Australia. Up until now, one described species is based on the specimen of unknown sex, eight are only known from female specimens and one only from male specimen. The species of this genus should be abundant, but are generally less well-known, and are worthy of further investigation in the future.

During the examination of spider collections from Malaysia, three new *Asceua* species were recognized and are described here as *Asceua bifurca* sp. n., *A. curva* sp. n., and *A. trimaculata* sp. n.

Materials and methods

All specimens have been kept in 75% ethanol and were examined, drawn, and measured under a Tech XTL-II stereomicroscope equipped with an Abbe drawing device. Photos were taken with a Leica M205A stereomicroscope fitted with a Leica DFC550 Camera and LAS software (Ver. 4.6). Carapace length was measured medially from the anterior margin to the rear margin of the carapace. Eye sizes were measured as the maximum diameter of the lens in dorsal or frontal view. The measurements of legs are shown as total length (femur, patella, tibia, metatarsus, tarsus). Only one specimen of paratypes was measured. The epigynes were cleared in a warm solution of potassium hydroxide, and transferred to 75% ethanol for drawing. All measurements are in millimeters. All specimens studied are deposited in the Museum of Hebei University (**MHBU**), Baoding, China.

The following abbreviations are used:

ALE	anterior lateral eyes;
AME	anterior median eyes;
C	conductor;
CD	copulatory ducts;
dRTA	dorsal apophysis of retrolateral tibial apophysis;
E	embolus;
MA	median apophysis;
MOA	median ocular area;
PLE	posterior lateral eyes;
PME	posterior median eyes;
RTA	retrolateral tibial apophysis;
S	spermatheca;
T	tegulum;
vRTA	ventral apophysis of retrolateral tibial apophysis.

Taxonomy

Family Zodariidae Thorell, 1881
Genus *Asceua* Thorell, 1887 (Type species: *Asceua elegans* Thorell, 1887)

***Asceua bifurca* sp. n.**
http://zoobank.org/20CC40AA-232A-4157-B9A5-F7508F1EB525
Figs 1–3

Type material. Holotype ♂, Malaysia, Sabah, Jalan Tambunan, Penampang, 05°48.739'N, 116°20.522'E, elev. 1583 m, 16 October 2015, Z.Z. Gao leg. **Paratypes:** 1 ♂ and 2 ♀, same data as holotype.

Diagnosis. The males of *A. bifurca* are very similar to those of *A. radiosa* Jocqué, 1986 (from the Comoro Islands) in having a large concavity on the basal embolus and a short conductor. The two species can be easily distinguished by the conductor being bifurcated in the new species, while it is not bifurcated in *A. radiosa*. The posterior part of the dorsal abdomen has three white median bands in the new species that are absent in *A. radiosa* (Figs 1A, B, 2A–C, 3A–C). The females of this new species resemble those of *A. piperata* Ono, 2004 (from Vietnam) in having a hillock between the two copulatory openings, but the two spermathecae are spaced by copulatory ducts in the new species while they are adjacent in *A. piperata* (Figs 2D, E, 3D, E).

Etymology. The specific name is taken from the Latin word *bifurca*, in reference to the bifurcated tip of the conductor; adjective.

Description. Male total length 2.11–2.18. Holotype total length 2.18; carapace 1.13 long, 0.86 wide; opisthosoma 1.00 long, 0.74 wide. Habitus shown as in Fig. 1A–B. Carapace shiny, brown, lateral margins dark brown, tegument smooth, median part with a wide V-shaped black patch in front of black fovea, posterior middle bright. Radial grooves dark brown. Clypeus 0.16 high, brown. Eye sizes and interdistances: AME 0.08, ALE 0.09, PME 0.09, PLE 0.09; AME–AME 0.04, AME–ALE 0.04, ALE–ALE 0.37, PME–PME 0.06, PME–PLE 0.08, PLE–PLE 0.47, ALE–PLE 0.02. MOA 0.22 long, frontal width 0.19, back width 0.24. Chelicerae brown, with 2 promarginal teeth and 1 retromarginal tooth, and terminal part armed with black hairs. Endites yellow brown, apices bright and furnished with dense black hairs. Labium triangular, 0.13 long, 0.12 wide, brown, median part with a semi-circular dark brown patch. Sternum 0.58 long, 0.50 wide, brown, lateral margin dark, median part bright and shiny, furnished with sparse black setae. Coxae of legs white, other sections brown, each femur with two dorsal spines, the distal part of tibia I bright. Measurements of legs: I 2.02 (0.40 + 0.20 + 0.61 + 0.38 + 0.43), II 1.84 (0.43 + 0.14 + 0.49 + 0.40 + 0.38), III 2.17 (0.62 + 0.21 + 0.51 + 0.46 + 0.37), IV 3.03 (0.61 + 0.33 + 0.72 + 0.95 + 0.42). Leg formula: 4312. Opisthosoma oval, covered with black short hairs, with a shiny and lanceolate dorsal scutum. Dorsum of opisthosoma black, with a pair of white median patches, followed by three transversal median bands, the first two bands wide and the third one narrow; anterior part of venter

Figure 1. *Asceua bifurca* sp. n., male holotype (**A–B**) and female paratype (**C–D**) Habitus (**A, C** dorsal view **B, D** ventral view).

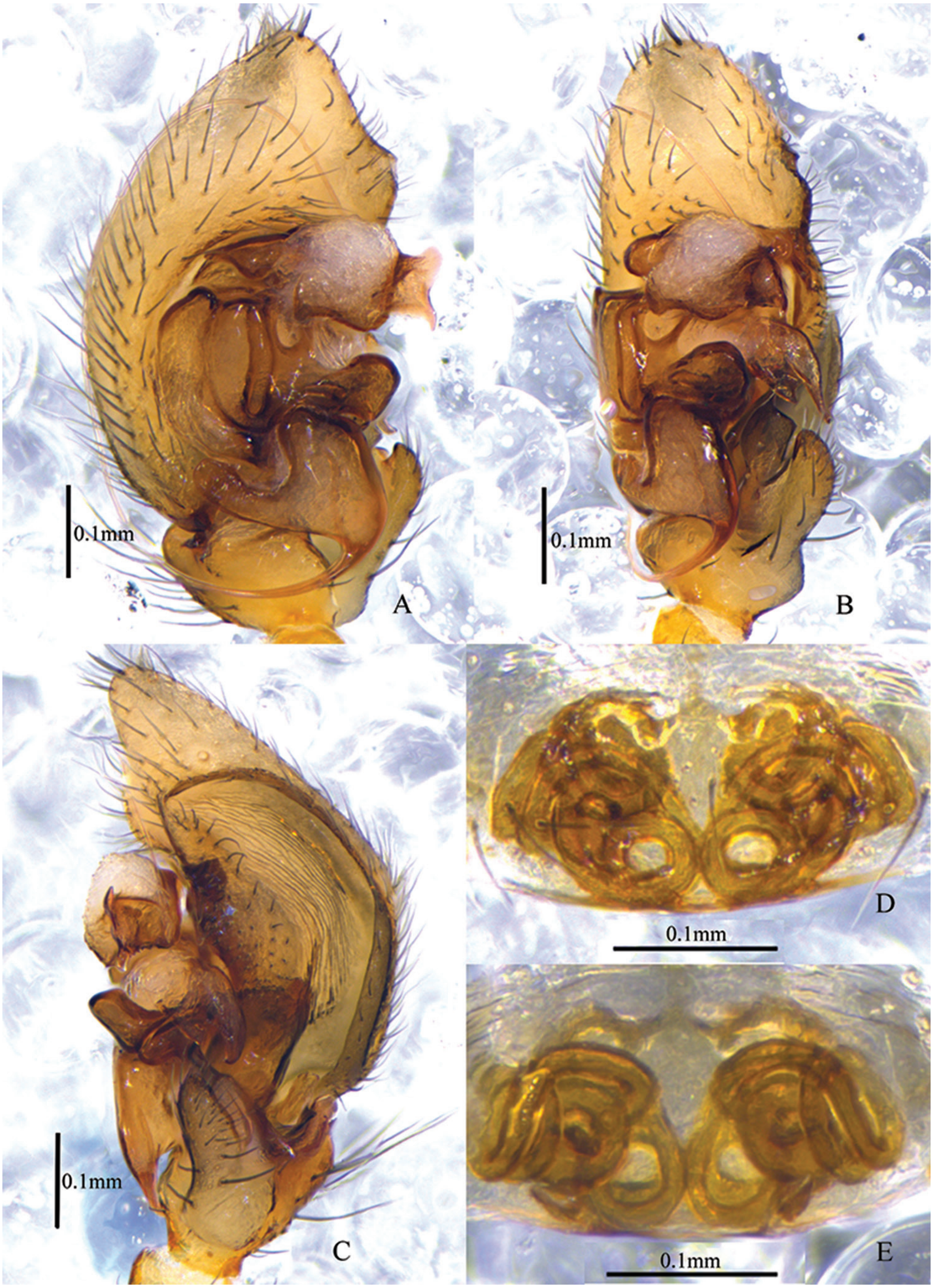

Figure 2. *Asceua bifurca* sp. n., male holotype (**A–C**) and female paratype (**D–E**) **A–C** Left male palp (**A** prolateral view **B** ventral view **C** retrolateral view) **D** Epigyne, ventral view **E** Epigyne, dorsal view.

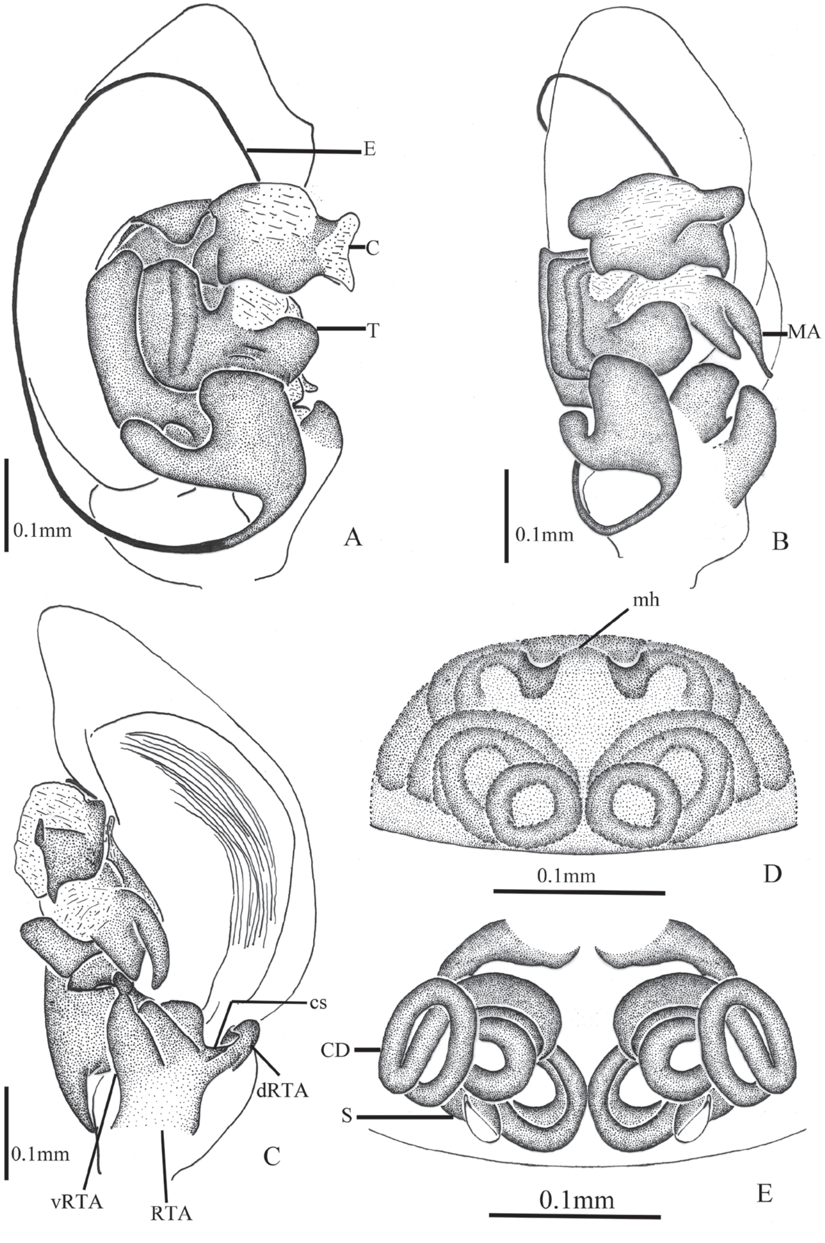

Figure 3. *Asceua bifurca* sp. n., male holotype (**A–C**) and female paratype (**D–E**) **A–C** Left male palp (**A** prolateral view **B** ventral view **C** retrolateral view) **D** Epigyne, ventral view **E** Epigyne, dorsal view. Abbreviations: cs, cuticularized sheet; mh, median hillock.

yellowish, posterior part white, and with a pair of lateral black patches, spinnerets brown, ringed with black.

Palp (Figs 2A–C, 3A–C). Coxae of palps white, other sections brown; length to width ratio of femur 2.6, length to width ratio of patella 1.2; RTA broad, ventral pointed apophysis broad and with trifurcate top, one of the forks longer than the other two forks, dorsal pointed apophysis thumb-like, with a cuticularized sheet situated between ventral and dorsal apophyses; cymbium with broad lateral fold which is wrinkly and with some hairs; conductor short, the tip bifurcated and sclerotized; distal median apophysis bifurcated; embolic base broad and almost an inverted triangle, with a large concavity on the apical margin.

Female total length 2.21–2.34. One of the paratypes total length 2.34; carapace 1.10 long, 0.84 wide; opisthosoma 1.25 long, 0.92 wide. Habitus as in Fig. 1C–D. Clypeus 0.15 high. Eye sizes and inter-distances: AME 0.07, ALE 0.09, PME 0.09, PLE 0.09; AME–AME 0.04, AME–ALE 0.03, ALE–ALE 0.37, PME–PME 0.05, PME–PLE 0.09, PLE–PLE 0.47, ALE–PLE 0.04. MOA 0.24 long, frontal width 0.17, back width 0.20. Labium 0.21 long, 0.24 wide. Sternum 0.53 long, 0.55 wide. Measurements of legs: I 2.07 (0.44 + 0.17+ 0.59 + 0.47 + 0.40), II 1.77 (0.44 + 0.11 + 0.41 + 0.47 + 0.34), III 1.99 (0.51 + 0.16 + 0.41 + 0.59 + 0.32), IV 2.53 (0.59 + 0.23 + 0.73 + 0.65 + 0.33). Leg formula: 4132. Dorsum of opisthosoma black, anterior median part dark brown and lacklustre, followed by a pair of white patches and three transversal bands, lateral parts with a pair of white oblique patches. Color of ventral opisthosoma and spinnerets as in male.

Epigyne (Figs 2D, E, 3D, E). Plate of epigyne approx. 1.9 times wider than long, the posterior margins of copulatory openings and the anterior margin of median hillock W-shaped; spermathecae small and oval, almost as wide as the copulatory ducts, situated posteriorly and well-spaced (approx. 6 times the spermathecal diameter).

Distribution. Malaysia (Sabah).

Asceua curva **sp. n.**

http://zoobank.org/280DE826-2A03-4081-87AC-EB17C530FCA2

Figs 4–5

Type material. Holotype ♂, Malaysia, Sabah, Pitas, 06°29.598'N, 117°18.499'E, elev. 45 m, 20 October 2015, Z.Z. Gao leg.

Diagnosis. The male of this species resembles *A. wallacei* Bosmans & Hillyard, 1990 (from Sulawesi, Indonesia) in having the very complicated copulatory organ. The two species can be easily distinguished by: the thinner and longer retrolateral pointed processes of the distal conductor in the new species, which is shorter and bifurcated in *A. wallacei*; the longer posterior projection of the cymbium in the new species, which is shorter in *A. wallacei*; and the hook-like median apophysis which is almost straight in *A. wallacei* (Figs 4C–F, 5A–C).

Etymology. The specific name is from the Latin word *curvus*, in reference to the shape of the posterior projection of the cymbium; adjective.

Description. Male (holotype): Total length 3.15; carapace 1.39 long, 1.12 wide; opisthosoma 1.49 long, 1.17 wide. Habitus as in Fig. 4A–B. Carapace shiny, brown, lateral margins dark brown, part of carapace swollen, radial grooves inconspicuous. Clypeus 0.30 high, brown. Eye sizes and inter-distances: AME 0.11, ALE 0.08, PME

Figure 4. *Asceua curva* sp. n., male holotype (**A–F**). **A–B** Habitus (**A** dorsal view **B** ventral view) **C–E** Left male palp (**C** prolateral view **D** ventral view **E** retrolateral view) **F** posterior projection of cymbium.

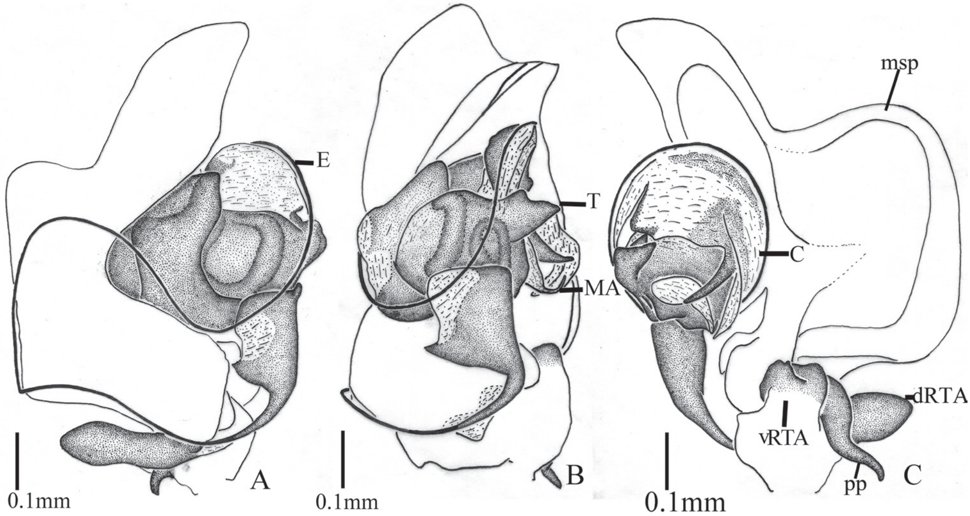

Figure 5. *Asceua curva* sp. n. (**A–C**). Left palp of the male holotype (**A** prolateral view **B** ventral view **C** retrolateral view). Abbreviations: pp, posterior projection; msp, median semi-circular projection.

0.08, PLE 0.13; AME–AME 0.05, AME–ALE 0.02, ALE–ALE 0.43, PME–PME 0.11, PME–PLE 0.10, PLE–PLE 0.59, ALE–PLE 0.02. MOA 0.27 long, frontal width 0.25, back width 0.27. Chelicerae brown, with two promarginal teeth and one retromarginal tooth, and terminal part armed with black hairs. Endites brown, apices bright and furnished with dense black hairs. Labium triangular, 0.20 long, 0.25 wide, brown, median part with a semicircular dark brown patch. Sternum 0.68 long, 0.66 wide, brown, lateral margin slightly dark brown, furnished with sparse black setae. Coxae of legs white, other sections brown, each femur with two dorsal spines, tibiae with long longitudinal dark stripes. Measurements of legs: I 3.74 (0.77 + 0.31 + 1.24 + 1.07 + 0.35), II 3.45 (0.89 + 0.36 + 0.94 + 0.88 + 0.38), III 3.46 (0.78 + 0.34 + 0.85 + 1.02 + 0.47), IV 3.80 (0.79 + 0.36 + 1.28 + 0.99 + 0.38). Leg formula: 4132. Opisthosoma covered with grey short hairs, dorsal scutum violin-like, dark brown. Dorsum of opisthosoma black, with a pair of white transversal chevrons, followed by three pairs of transversal stripes, the first two pairs being conjoint in the middle of the opisthosoma; anterior part of venter yellow, posterior part grey and lateral with two pairs of black oblique stripes, spinnerets brown.

Palp (Figs 4C–F, 5A–C). Tibia with two broad apophyses: dorsal apophysis and ventral apophysis, with a large concavity between them, in which fits a posterior projection of the cymbium; cymbium with a median semi-circular projection, which appears to be strongly excavated below in lateral view; tip of median apophysis hook-like; conductor large and semi-circular, with retrolateral and posterior pointed processes, not very chitinised except for the retrolateral processes; embolar base triangular; thread-like embolus very long, at first running to dorsal cymbium, then turning to ventral palp and following dorsal margin of conductor.

Female unknown.

Distribution. Malaysia (Sabah).

Remarks. Eight described *Asceua* species from nearby countries are only based on female specimens: *A. amabilis* Thorell, 1897 (from Myanmar), *A. anding* Zhang, Zhang & Jia, 2012 (from China), *A. daoxian* Yin, 2012 (from China), *A. elegans* Thorell, 1887 (from Myanmar), *A. kunming* Song & Kim, 1997 (from China), *A. longji* Barrion et al. 2013 (from China), *A. piperata* Ono, 2004 (from Vietnam), and *A. quinquestrigata* (Simon, 1905) (from Java). The patterns of the dorsal opisthosoma of these species are different by comparisons of illustrations and descriptions. The first pair of transversal chevrons are reniform in the new species, but are oval or long ovoid in all the other species, except for *A. quinquestrigata*. However, the new species can be distinguished from *A. quinquestrigata* by the broad bands on its posterior opisthosoma, which are only small in *A. quinquestrigata*. Also, the other white patches and transversal stripes on the opisthosoma of the new species contrasts with the lack of stripes in the other seven species except for *A. piperata*. However, the new species can be distinguished from *A. piperata* by its immaculate carapace. This new species is thus less likely to be conspecific with any of these 8 species that are only known from female specimens.

Asceua trimaculata sp. n.

http://zoobank.org/3212AFBA-61D7-439B-99C9-83E096C934BD
Fig. 6

Type material. Holotype ♀, Malaysia, Pahang, Cameron Highlands, Tanah Rata, 04°27.791'N, 101°22.091'E, elev. 1380 m, 22 October 2015, Z.Z. Gao leg. **Paratype:** 1 ♀, same data as holotype.

Diagnosis. The females of this new species resemble those of *A. lejeunei* Jocqué, 1991 (from Congo) in having widely spaced copulatory openings, but can be distinguished by the absence of the paired patches of dorsal opisthosoma which are present in *A. lejeunei* (Fig. 6A–F).

Etymology. The specific name is from the Latin words *tri-* and *maculata,* in reference to the three patches on the dorsal opisthosoma.

Description. Female total length 2.33–2.48. Holotype total length 2.48; carapace 1.21 long, 0.91 wide; opisthosoma 1.24 long, 0.95 wide. Habitus as in Figs 6A–B. Carapace, dark brown, median part with a black V-shaped patch and a longitudinal black thin band, radial grooves black. Clypeus 0.24 high, dark brown. Eye sizes and interdistances: AME 0.07, ALE 0.09, PME 0.08, PLE 0.09; AME–AME 0.02, AME–ALE 0.02, ALE–ALE 0.34, PME–PME 0.05, PME–PLE 0.12, PLE–PLE 0.46, ALE–PLE 0.05. MOA 0.26 long, frontal width 0.16, back width 0.21. Chelicerae dark brown, with two promarginal teeth and one retromarginal tooth, and terminal part armed with black hairs. Endites yellow brown, apices bright and furnished with dense black hairs. Labium triangular, 0.25 long, 0.28 wide, dark brown. Sternum 0.59 long,

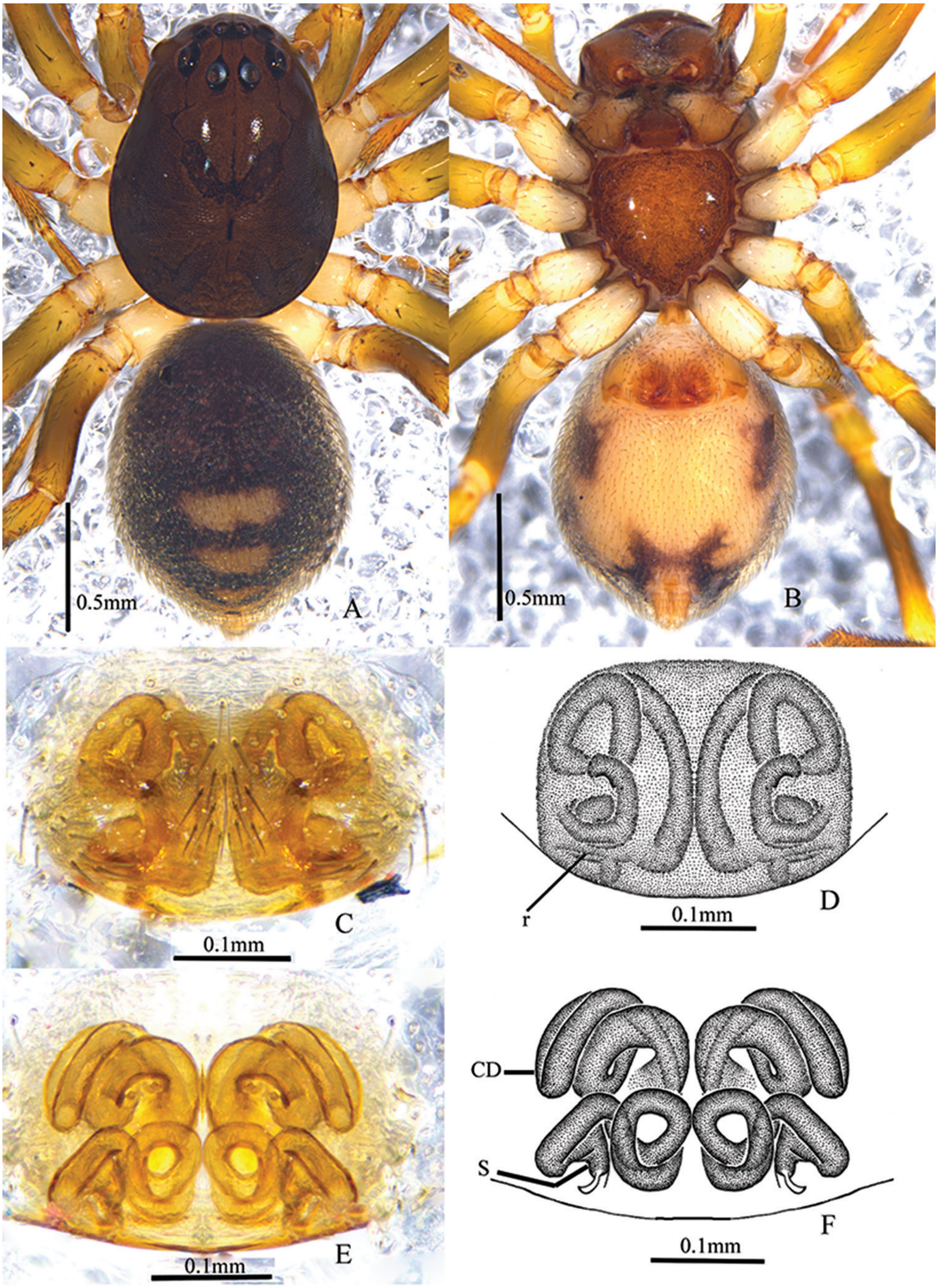

Figure 6. *Asceua trimaculata* sp. n., female holotype (**A–F**) **A–B** Habitus (**A** dorsal view **B** ventral view) **C–F** Epigyne (**C, D** ventral view **E, F** dorsal view). Abbreviation: r, ridge.

0.61 wide, dark brown, median part shiny, furnished with sparse black setae. Coxae of legs yellowish, other sections brown. Measurements of legs: leg I 2.82 (0.84 + 0.29 + 0.67 + 0.59 + 0.43), II 2.35 (0.68 + 0.23 + 0.49 + 0.58 + 0.37), III 2.06 (0.65 + 0.16 + 0.34 + 0.52 + 0.39), IV 2.93 (0.89 + 0.16 + 0.50 + 1.03 + 0.35). Leg formula: 4123. Opisthosoma covered with black short hairs, lanceolate dorsal scutum dark brown and with blunt edge. Dorsum of opisthosoma black, with three transverse white bands; anterior part of venter yellow brown, posterior part yellowish and with a pair of lateral black patches, spinnerets brown and ringed with black.

Epigyne (Fig. 6C–F). Plate of epigyne approx. 1.3 times wider than long, copulatory openings situated almost at the middle part of epigyne, posterior epigynum with a pair of ridges; long and winding copulatory ducts visible through integument; spermathecae small, situated posteriorly and well-spaced (approx. 8 times the spermathecal diameter).

Male unknown.

Distribution. Malaysia (Pahang).

Remarks. *Asceua septemmaculata* (Simon, 1893a) was described based only on a male specimen from Cambodia. The patterning of the dorsal opisthosoma differ, in that the pairs of white patches present in *A. septemmaculata* are absent in the new species, and it is unlikely that the latter is conspecific with *A. septemmaculata*.

Comments. There are five *Asceua* species in the adjacent region that are lacking illustrations: *A. bimaculata* (Simon, 1904) (from Vietnam), *A. heliophila* (Simon, 1893b) (from Philippines), *A. septemmaculata*, *A. amabilis* and *A. quinquestrigata*. The descriptions of the sexual organs were very simple. The three new species described here have to be distinguished by different patterns of the dorsal opisthosoma. *Asceua trimaculata* sp. n. lacks pairs of white patches that all the five known species above possess. *Asceua bifurca* sp. n. differs from the five species by the rectangular white bands on its dorsal opisthosoma. *Asceua curva* sp. n. differs from them by possessing the chevron patterning.

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RESEARCH ARTICLE

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The phylogeny of pholcid spiders: a critical evaluation of relationships suggested by molecular data (Araneae, Pholcidae)

Bernhard A. Huber[1], Jonas Eberle[1], Dimitar Dimitrov[2,3,4]

1 *Alexander Koenig Research Museum of Zoology, Adenauerallee 160, 53113 Bonn, Germany* **2** *Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark* **3** *Natural History Museum, University of Oslo, PO Box 1172 Blindern, NO-0318 Oslo, Norway* **4** *Current address: Department of Natural History, University Museum of Bergen, University of Bergen, PO Box 7800, NO-5020 Bergen, Norway*

Corresponding author: *Bernhard A. Huber* (b.huber@leibniz-zfmk.de)

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Abstract

With almost 600 species, the latest molecular phylogeny of pholcid spiders (Eberle et al. 2018, BMC Evolutionary Biology) more than triples the largest previously available molecular phylogeny of the family. At the level of genera, the coverage is high (86%, i.e., 75 of the 87 named genera), and at the level of subfamilies it is complete. The present paper is an effort to critically evaluate the implications of this phylogeny for pholcid systematics. The analyses largely support the division of Pholcidae into five subfamilies: Ninetinae, Arteminae, Modisiminae, Smeringopinae, and Pholcinae. Their compositions are largely unchanged except that *Chisosa* Huber, 2000 is moved from Ninetinae to Arteminae. The positions of *Artema* Walckenaer, 1837 and *Priscula* Simon, 1893 in this system remain dubious. Relationships among subfamilies remain weakly supported, except for the sister group relationship between Smeringopinae and Pholcinae. Several major clades within subfamilies are separated from each other along geographical boundaries; for example within Modisiminae a South American clade and a Central + North American + Caribbean clade, and within Smeringopinae a Sub-Saharan clade and a clade ranging from the Mediterranean to Central Asia. Central + North American + Caribbean clades in both Ninetinae and Modisiminae may originate from South American ancestors.

Many taxonomic changes are suggested by the data, some of which are formally implemented herein. Two new genera result from the splitting of *Calapnita* Simon, 1892 and *Panjange* Deeleman-Reinhold & Deeleman, 1983, respectively: *Nipisa* Huber, **gen. n.**; and *Apokayana* Huber, **gen. n.** Nine new genera result from splitting of *Pholcus*: *Cantikus* Huber, **gen. n.**; *Kelabita* Huber, **gen. n.**; *Kintaqa* Huber, **gen. n.**; *Muruta* Huber, **gen. n.**; *Meraha* Huber, **gen. n.**; *Paiwana* Huber, **gen. n.**; *Pribumia* Huber, **gen. n.**; *Teranga* Huber, **gen. n.**; and *Tissahamia* Huber, **gen. n.** Two genera are newly synonymized: *Platnicknia* Özdikmen & Demir, 2009 is synonymized with *Modisimus* Simon, 1893; *Sihala* Huber, 2011 is synonymized with *Pholcus* Walckenaer, 1805. *Pholcus agadir* Huber, 2011 is moved to *Micropholcus* Deeleman-Reinhold & Prinsen, 1987, resulting in the new combination *Micropholcus agadir* (Huber, 2011).

Keywords
Biogeography, phylogeny, systematics, taxonomy

Introduction

Pholcidae is among the most species-rich spider families (World Spider Catalog 2018) and includes some of the spiders best known to the general public due to their occurrence in houses all over the world. Large amounts of morphological, taxonomic, behavioural, and biogeographic data on pholcids have been gathered and published over the last decades (http://www.pholcidae.de). Pholcidae is emerging as an ecologically highly diverse family that includes representatives with exceptional morphology and behaviour (e.g., asymmetric genitalia, ocular area modifications; highly regular webs; wrapping of prey with sticky silk; Huber and Nuñeza 2015, Huber et al. 2016c, Deeleman-Reinhold 1986a, Huber 2005b, Japyassú and Macagnan 2004), and that in some parts of the world is either extremely abundant (e.g., in East African forests; Sørensen et al. 2002) or has extreme levels of endemism (e.g., in Brazil's Atlantic Forest; Huber and Rheims 2011, Huber 2015, 2016, 2018). However, convincing evolutionary interpretations are often impeded by insufficient phylogenetic resolution and by large gaps in the taxon sampling. The most recent molecular phylogeny of Pholcidae (Eberle et al. 2018) is undoubtedly a major step forward. Under the assumption that a good sample of taxa is possibly more important than an increase of characters/genes (cf. Graybeal 1998, Heath et al. 2008) we more than tripled the number of species as compared to the previous phylogeny of Dimitrov et al. (2013); many genera and major species groups were included for the first time. As far as the percentage of named genera included is concerned (86%), this is probably the most comprehensive molecular phylogeny of any major spider family so far. Despite this substantial increase in taxon sampling which has greatly improved our understanding of pholcid relationships, our tree remains a mosaic of 'good' and 'bad' parts: some nodes receive high support, others receive low or essentially no support. Revealingly, some support values changed dramatically among preliminary analyses of the present data. For example, unexpected clades with maximum support but contradicting any other evidence (e.g., morphology) suggested the existence of paralog sequences. In other cases, doubts persist but we were not able to identify problems with the molecular data. The idea of the present paper is thus to complement the primary phylogenetic data in Eberle et al. (2018) with a detailed account of arachnological implications and to look not only at but also beyond support values; we compare the molecular phylogeny with phylogenies derived from cladistic analysis of morphological characters and other information, and distinguish between clades that we consider a solid basis for further work and clades that we consider in need of further phylogenetic research.

Material and methods

The trees presented here are derived from mitochondrial and nuclear gene sequences (12S, 16S, 18S, 28S, CO1, H3) gathered from 597 species of Pholcidae plus 32 outgroup species representing nine entelegyne and ten non-entelegyne families. For detailed specimen data, primers, lab protocols, alignment and tree inference algorithms, see Eberle et al. (2018). The present evaluation is based on four trees resulting from maximum likelihood analyses of data sets with varying degrees of missing data and unstable taxa, using two algorithms (RAxML, Stamatakis 2014; IQ-TREE, Nguyen et al. 2015). For the complete set of taxa, RAxML found the tree with the highest likelihood while the tree inferred with IQ-TREE was in better concordance with the known morphological evidence as suggested by cladistic analyses of morphological data and by qualitative character assessment (detailed in the respective sections below). Further trees were inferred with RAxML based on a reduced data set without rogue taxa (RogueNaRok, Wilkinson 1996, Sanderson and Shaffer 2002, Aberer et al. 2013) and on a “4+ genes” data set, including only those taxa for which four or more of the six target genes were available.

We calculated three types of branch support values for all trees: standard bootstrapping (SBS), rapid bootstrapping (RBS; Stamatakis et al. 2008), and Shimodaira–Hasegawa-like approximate likelihood ratio test (SH-like aLRT; Guindon et al. 2010). Terminal taxa are composed of a consistent string of five variables: (1) unique specimen code; (2) genus name, either scientific name, unique code, or “Gen. n.” for putatively new genera; (3) species name, either scientific name or unique code; (4) code for vial containing the specimen; (5) x's and o's, to respectively clarify the presence or absence of loci in the following order: 12S, 16S, 18S, 28S, CO1, H3.

We chose the tree from the IQ-TREE analysis for illustration and annotation because it appears more congruent with morphology. For the sake of clarity, only the RBS support is shown here; it may reflect true support most accurately (Anisimova et al. 2011). The same tree with all support values but without additional annotations is available as Supplementary file, together with the trees derived from RAxML from the complete and the two reduced, i.e., RogueNaRok, and “4+ genes” data sets.

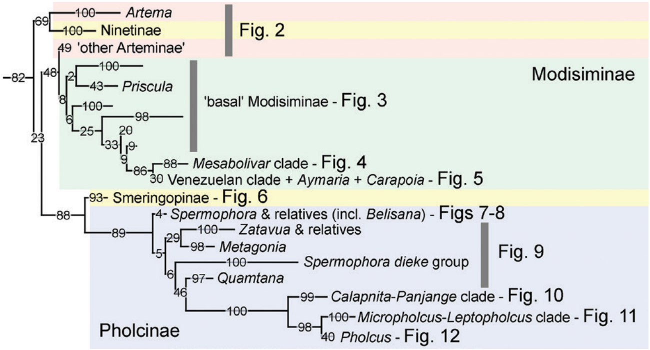

Figure 1. Backbone of the pholcid tree shown in Figs 2–12, derived from IQ-TREE analysis of the complete dataset.

To avoid overloading the text with numbers, we generally refer to the RBS support as follows: "low" (<70), "modest" (70–79), "reasonable" (80–94), "high" (95–99), or "full" (100) support. Even though the resolution of pholcid phylogeny has improved dramatically since 2011, the formal classification (Huber 2011b) into five subfamilies is not changed (Figure 1). Between the taxonomic levels of subfamilies and species we prefer to use informal names rather than tribes, subtribes, etc. Such unranked and formally unnamed taxa are less likely to burden future work as long as several major groups are still weakly supported and likely to change in composition or to be entirely rejected. The word "clade" is used like monophylum; thus, a clade can consist of subclades and those subclades are clades that again can consist of subclades. In general, colours in the phylogenies have no meaning beyond supporting the visual recognition of clades. The only exception is with *Belisana* Thorell, 1898, where litter and leaf-dwelling representatives are marked with different colours. Genus and species counts include the formal taxonomic changes herein. All measurements are in mm.

Systematic accounts

Subfamily Ninetinae Simon, 1890

Figure 2

Ninetinae Simon, 1890: 95. Type genus *Ninetis* Simon, 1890, by monotypy. Huber 2011b: 212.

Remarks. Ninetinae are small to tiny ground-dwelling spiders that are largely restricted to arid environments (Huber and Brescovit 2003; BA Huber, unpublished data). With only 31 described extant species, the subfamily is by far the smallest of the five currently recognized subfamilies in Pholcidae. Ninetinae seem to be diverse in the New World (ten named genera + about four unnamed genera; BA Huber,

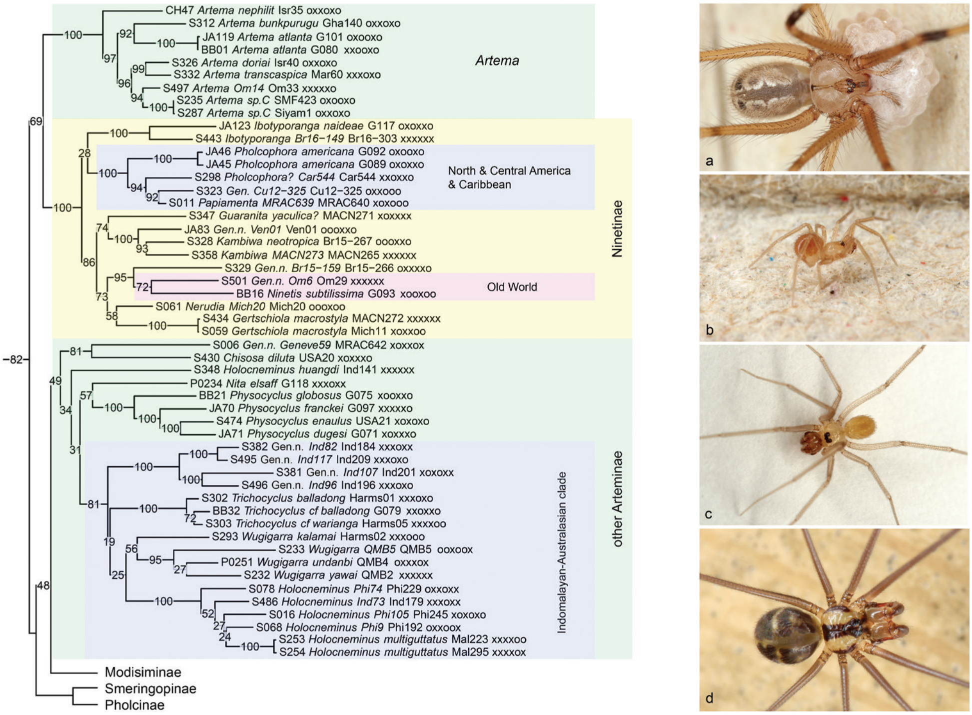

Figure 2. Ninetinae and Arteminae **a** *Artema* sp. n. "Om14" (Oman) **b** Gen. n. (Ninetinae) sp. n. "Om6" (Oman) **c** *Chisosa diluta* (USA) **d** Gen. n. (Arteminae) sp. n. "Ind82" (Sulawesi).

unpublished data) where they represent the most southern (Argentina) and most northern (Canada) autochthonous pholcid records worldwide. Only two genera (*Ninetis* Simon, 1890 and one unnamed; BA Huber, unpublished data) are known from the Old World.

Their short legs make them superficially strikingly different from 'typical' long-legged pholcids. This distinctness was recognized as early as 1893, when Eugène Simon classified the only ninetine species available to him in a separate subfamily "Ninetidinae", as opposed to all other pholcids classified in Pholcinae (Simon 1893). Subsequent morphological and molecular phylogenies have partly supported this view (Huber 2000, Dimitrov et al. 2013) but never convincingly with strong support.

Our present analyses include 15 species representing eight of the eleven described genera, originating from both the New World and the Old World (Figure 2). A sister-group relationship between Ninetinae and all other pholcids is not supported by our analyses. Instead, all four analyses put Ninetinae as sister to *Artema* Walckenaer, 1837, and this clade is in turn sister to all other pholcids. For reasons discussed below (under Arteminae), we consider this relationship between *Artema* and Ninetinae dubious. The conclusion here is that Ninetinae are 'basal', either with *Artema* or without, but in any case the external relationships of Ninetinae remain unsatisfactorily resolved and need further study.

The monophyly of the subfamily receives high to full support in all analyses but the composition is slightly different from previous concepts: the North American *Chisosa* Huber, 2000, originally thought to be a representative of Ninetinae (Huber 2000), is moved to Arteminae. This move is also supported by male genitalic characters (massive palpal femur; procursus with dorsal apophysis and ventral pocket) and by somatic characters (exposed tarsal organ; reduction of epiandrous spigots; Huber 2000). Another genus that was previously (Huber and El Hennawy 2007, Huber 2011b) thought to be a member of Ninetinae is *Nita* Huber & El Hennawy, 2007. As already suggested in a previous analysis (Dimitrov et al. 2013), *Nita* is not a member of Ninetinae but of Arteminae.

The internal relationships of Ninetinae suggested by the molecular data are difficult to evaluate: they are mostly neither supported nor contradicted by morphological data. Two details are remarkable because they suggest that South America may not only be the most diverse region as far as Ninetinae are concerned but also the ancestral region of the subfamily. First, the analyses fully support a monophyletic North and Central American/Caribbean clade (*Pholcophora* Banks, 1896; *Papiamenta* Huber, 2000; and unidentified taxa from Cuba and Puerto Rico; “clade 2e” in Huber 2011b) that is either nested among South American ancestors or is sister to the South American *Ibotyporanga* Mello-Leitão, 1944 (with reasonable support in the 4+ genes tree only). Based on its geographic distribution, we predict that the Mexican *Tolteca* is also a member of this clade. Second, the two Old World genera (*Ninetis* and an undescribed genus from Oman) are also sister taxa (with low to modest support) and in all analyses (except for the 4+ genes analysis where *Ninetis* is missing) nested among South American taxa.

Subfamily Arteminae Simon, 1893

Figure 2

Artemeae Simon, 1893: 463. Type genus *Artema* Walckenaer, 1837, by monotypy.
Arteminae Simon; Huber 2011b: 212.

Remarks. All our analyses exclude the name-giving genus *Artema* from the clade containing all other Arteminae and invariably place *Artema* as sister to Ninetinae (Figure 2), formally precluding the use of the name Arteminae for this clade. We do not propose a new subfamily name for this clade but treat it as ‘other Arteminae’ because we consider the position of *Artema* dubious. *Artema* shares with ‘other Arteminae’ a unique pair of structures on the procursus: a ventral pocket and a dorsal apophysis. These structures are associated with asymmetric palp insertion in both species studied with respect to this detail [*Physocyclus globosus* (Taczanowski, 1874), *Artema nephilit* Aharon et al., 2017: Huber and Eberhard 1997, Aharon et al. 2017]. The structures are present in all Arteminae, even in taxa that were previously thought to be representatives of other subfamilies, such as *Chisosa* and *Nita* (previously in Ninetinae; see above), and *Wugigarra* Huber, 2001 (previously in Modisiminae; see below) (Huber 2000, 2001, Huber and El Hennawy 2007). By contrast, these structures are apparently absent in all other Pholcidae. Curiously and unexplainable to us, previous molecular analyses have supported a position of *Artema* among 'other Arteminae' (Astrin et al. 2007: fig. 1, Dimitrov et al. 2013).

Some of the 99 currently known species of Arteminae are relatively large spiders with long, strong legs and high globose abdomens. The genus *Artema*, in particular, includes probably the largest pholcids in terms of body mass (Aharon et al. 2017). However, tiny species that were previously assigned to Ninetinae partly because of their size (*Chisosa*, *Nita*) are now included in Arteminae, and their 'basal' position in the cladogram suggests that ancestral Arteminae may in fact have been tiny. Just like Ninetinae, Arteminae often occur in rather dry regions, sometimes even in deserts like the Australian *Trichocyclus* Simon, 1908. They have a wide distribution, but are apparently absent from Sub-Saharan Africa and from South America (except for "Geneve59", a tiny undescribed species representing a new undescribed genus on Curaçao and Aruba).

The monophyly of 'other Arteminae' is supported in all our analysis, even though with low support (possibly because of the dubious position of *Artema*, see above). Similar to our previous analysis (i.e. except for the position of *Artema*; Dimitrov et al. 2013), 'other Arteminae' is sister to Modisiminae, with variable support (reasonable support only in the RogueNaRok tree; in other trees, bootstrap support is low but SH values range from 82 to 99). This sister group relationship is weakly supported by morphology: 'other Arteminae' and Modisiminae lack epiandrous spigots. However, epiandrous spigots have been lost several times convergently in Pholcidae (Huber 2000, BA Huber, unpubl. data).

Internal relationships in 'other Arteminae' are partly resolved with reasonable support. The data suggest a large Indomalayan-Australasian clade, including the genera *Trichocyclus* and *Wugigarra* (Australia), *Holocneminus* Berland, 1942 (SE Asia and Pacific; excluding the misplaced and highly isolated *H. huangdi* Tong & Li, 2009), and a new undescribed genus (without any described species; ranging from Eastern Indonesia to the Pacific). Sister to this clade is either the New World genus *Physocyclus* Simon, 1893 alone or *Physocyclus* together with the Middle-Eastern monotypic *Nita*. However, support values for any of these options are low and morphological data do not favour (nor contradict) any of them. Finally, the 'basal' branches, i.e., those leading to the taxa outside the Indomalayan-Australasian clade and *Physocyclus* (and *Nita* in the case of the IQ-TREE analysis) lead to a group of North American and Caribbean taxa (the North American genus *Chisosa* being sister to a tiny undescribed species representing a new undescribed genus on Curaçao and Aruba: "Geneve59"), and to the SE-Asian *Holocneminus huangdi*, an isolated species that appears misplaced also by morphological criteria (A Valdez-Mondragón, pers. comm., Nov. 2015).

Subfamily Modisiminae Simon, 1893

Figs 3–5

Modisimeae Simon, 1893: 484. Type genus *Modisimus* Simon, 1893, by subsequent designation (Huber 2011b).
Modisiminae Simon; Huber 2011b: 216.

Remarks. Modisiminae are the typical pholcids of the humid Neotropics, where they occupy a wide variety of microhabitats from leaf litter to high among the vegetation. This ecological variability is paralleled by a wide range of body forms, from tiny ground-dwelling forms (e.g., Gertsch 1982, Huber and Rheims 2011) to some of the largest pholcids with leg spans of over 15 cm (e.g., Huber and Astrin 2009, Huber 2015, 2018). With currently 480 species in 24 genera, Modisiminae is one of the two large subfamilies of Pholcidae, with several species-rich genera (e.g., *Anopsicus* Chamberlin & Ivie, 1938; *Psilochorus* Simon, 1893; *Modisimus* Simon, 1893; *Mesabolivar* González-Sponga, 1998; *Carapoia* González-Sponga, 1998) and many undescribed species.

All previous analyses have supported this group (Huber 2000, 2001, Bruvo Mađarić et al. 2005, Dimitrov et al. 2013), even though with minor differences in composition. The equivalent 'New World clade' in Huber (2001) still included the Australian *Wugigarra*, a genus that has since been moved to Arteminae (Dimitrov et al. 2013). As a result, Modisiminae is now considered to be restricted to the New World.

Our analyses all recover Modisiminae, but with very low support values. This is possibly due to the mysterious Andean genus *Priscula* Simon, 1893 (Figure 3) that is either included in Modisiminae (IQ-TREE) or not (RAxML). The position of *Priscula* has always been considered problematic. Simon (1893) created a separate taxon "Prisculeae" for this genus; Brignoli (1981) synonymized it with *Physocyclus*; the first morphological cladistic analysis (Huber 2000) supported the position of *Priscula* near *Physocyclus* but this result was explicitly doubted (Huber 2000: 129). In the molecular analysis of Dimitrov et al. (2013) *Priscula* was excluded because the positions of the included species varied dramatically among different types of analyses. Morphologically, *Priscula* differs from (other) Modisiminae by the presence of ALS piriform gland spigots and by the absence of a retrolateral apophysis on the male palpal coxa (Huber 2000), i.e., it has retained plesiomorphic characters. A sister-group relationship between *Priscula* and other Modisiminae appears thus plausible from a morphological point of view.

Despite the low support values, we thus consider Modisiminae (including *Priscula* or not) a likely monophyletic group. Several morphological characters support Modisiminae (incl. *Priscula*): an exposed tarsal organ; the reduction of epiandrous spigots (shared with 'other Arteminae'; see above); and a large distance between ALE and PME (Huber 2000). As indicated above (section Arteminae) our data weakly support a sister-group relationship between 'other Arteminae' and Modisiminae.

Within Modisiminae, many support values are extremely low, and the suggested relationships are thus unreliable (Figure 3). In addition, taxon sampling is very uneven,

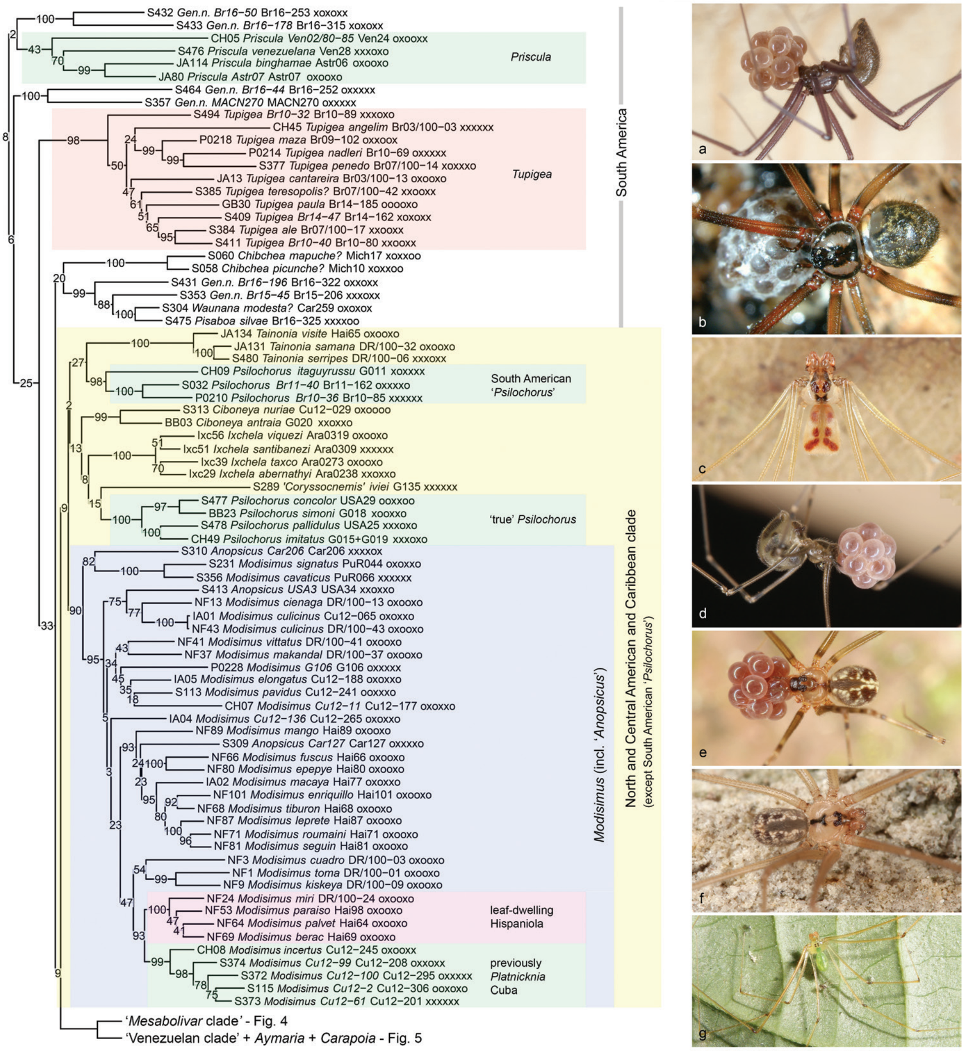

Figure 3. ‘Basal’ Modisiminae **a** Gen. n., sp. n. “Br16-50” (Brazil) **b** *Priscula andinensis*? (Venezuela) **c** Gen. n., sp. n. “Br16-196” (Brazil) **d** *Tupigea* sp. n. “Br14-47” (Brazil) **e** *Pisaboa silvae* (Brazil) **f** *Psilochorus imitatus* (USA) **g** *Modisimus incertus* (Cuba).

with some genera well represented (e.g., *Carapoia*, *Mesabolivar*, *Modisimus*), and others poorly represented or entirely missing (see below). However, several results are consistent among analyses and noteworthy for various reasons: they suggest groups that appear feasible in terms of biogeography; they suggest interesting evolutionary scenarios; and they suggest formal taxonomic changes, some of which have been suggested before based on morphology.

Apart from *Priscula*, the ‘basal’ branches within Modisiminae lead to small South American unnamed taxa (Figure 3). In particular, the two species “Br16-44” and

"MACN270" are both tiny, with body lengths of 0.9 and 1.3 mm, respectively. Other 'basal' branches lead to an unnamed Amazonian genus ("Br16-178" and "Br16-50"; body lengths: 1.5–1.8 mm) and the Atlantic Forest genus *Tupigea* Huber, 2000 (body lengths: 1.3–1.9 mm; Huber 2000, Huber and Rheims 2011). This suggests a similar evolutionary scenario as proposed for 'other Arteminae' above, i.e., that ancestral Modisiminae may have been small ground-dwelling species. *Priscula* is once again the disturbing factor in this scenario: all known representatives of *Priscula* are medium-size to large spiders (Huber 2000), possibly surpassed (as far as body mass is concerned) by *Artema* only. In both Arteminae and Modisiminae, the emerging picture is one of medium-sized forms missing or disappearing early, large forms experiencing little subsequent changes in body shape and poor subsequent speciation (*Artema*: currently eight species; *Priscula*: currently 17 species), and small forms diversifying dramatically in size, shape, and numbers ('other Arteminae': currently 91 species; Modisiminae without *Priscula*: currently 463 species).

The next branch (Figure 3; *Chibchea* Huber, 2000 to *Pisaboa* Huber, 2000) includes several South American genera, some of them diverse but poorly represented in our analyses (e.g., *Chibchea*). The close relationship between *Pisaboa* and *Waunana* Huber, 2000 was already suggested in the original descriptions of these genera (Huber 2000), even though based on highly homoplastic characters (vertical hairs on male leg tibiae in high density; shape of apophysis on male palpal femur). A close relationship of these two genera with *Chibchea* either receives very low support (IQ-TREE, RAxML) or is not recovered (RogueNaRok); it is neither supported nor contradicted by morphology. Clearly, this clade needs a much denser sampling and the addition of missing taxa that are possibly related (e.g., *Pomboa*).

The next clade (Figure 3) includes all North and Central American and Caribbean taxa, suggesting that the ancestor of this clade arrived in the region from South America. This scenario was explicitly rejected by Dimitrov et al. (2013) based on the supposed age of the group (~120–170 Ma). However, our upcoming analysis has not been able to confirm this age (Eberle et al. 2018; we were not able to calculate convincing absolute ages from the data). The clade is recovered in most analyses (it is paraphyletic in the 4+ genes tree) but always with low support (only SH values are reasonable to high). The only geographic outlier in this clade is South American '*Psilochorus*'. North American ('true') *Psilochorus* and South American '*Psilochorus*' each receive high to full support but are never resolved as sister taxa. Whether South American '*Psilochorus*' are ancestral within this large clade or represent a case of back-colonization is currently impossible to say; the internal nodes in this clade have partly too low support to favour a particular scenario. The inclusion of the Central American *Ixchela* Huber, 2000 in this clade fits the geographic pattern and contradicts a previous speculation (in Huber 2000) that *Ixchela* might be close to the South American genus *Aymaria* Huber, 2000. In much the same way, the only Central American representative of *Coryssocnemis* Simon, 1893 included in our analyses is placed in this group, far away from 'true' South American *Coryssocnemis* (the polyphyly of *Coryssocnemis* has long been suspected: Gertsch 1971, Brignoli 1981, Huber 1998, 2000). The Cuban endemic genus *Platnicknia* Özdikmen & Demir, 2009 is deeply nested within the large genus *Modisimus*. It is resolved as sister to a distinctive group of Hispaniolan leaf-dwelling representatives of *Modisimus* (the "leaf-dwelling species group" in Huber et al. 2010) and synonymized below. Finally, the large genus *Anopsicus* (63 described species) is poorly represented in our analyses. The three species included are all undescribed, do not group together, and are nested among *Modisimus*. Since neither the type species of *Anopsicus* is included nor is a potential close relative (or at least another species from Yucatán), the monophyly and position of *Anopsicus* both remain dubious.

Sister to the previous North and Central American and Caribbean clade is another large, entirely South American clade (Figure 3, bottom). The sister-group relationship is very poorly supported, but the monophyly of the South American clade has modest (4+ genes) to reasonable (RogueNaRok) support. It is divided into three subclades with reasonable to full support plus the genus *Aymaria* that is represented by a single species and whose position within this clade is not convincingly resolved. The first subclade included is here informally called the '*Mesabolivar* clade' (Figure 4); the second subclade is largely Venezuelan and thus called 'Venezuelan clade' (Figure 5); the third subclade is the genus *Carapoia* (Figure 5).

Within the '*Mesabolivar* clade' (Figure 4), our analyses suggest two specific relationships that are likely to have drastic taxonomic consequences. First, *Litoporus* Simon, 1893 is nested among 'true' northern South American *Mesabolivar*. This has been suggested before (Dimitrov et al. 2013), but that previous analysis included a single species of *Litoporus* whose generic identity was uncertain (Huber et al. 2013). The present analyses include several unambiguous (Amazonian) representatives of *Litoporus*. Our data support the monophyly of *Litoporus* (full support) but also its position within *Mesabolivar* (reasonable to high support). Second, *Mesabolivar* is composed of two sub-clades: 'true' northern South American *Mesabolivar*, and southern South American (largely Atlantic Forest) '*Mesabolivar*'. The southern sub-clade includes the monotypic genus *Teuia* Huber, 2000 (synonymized with *Mesabolivar* in Huber 2018; the type species of *Teuia* is not included but a putatively closely related species: *M. sepitus*). Potential formal taxonomic changes are discussed in the Taxonomy section below. The close relationship between *Otavaloa* Huber, 2000 and *Mesabolivar* is neither supported nor contradicted by morphological data.

The 'Venezuelan clade' (Figure 5) receives high to full support and is composed of several genera that are either known from Venezuela only (*Systenita* Simon, 1893, *Stenosfemuraia* González-Sponga, 1998), from Venezuela and Trinidad and Tobago (*Coryssocnemis*), or from Venezuela plus neighboring countries (*Mecolaesthus* Simon, 1893). A close relationship among these genera had been suspected before based on morphology (Huber 2000), and molecular data have always supported this (Bruvo-Mađarić et al. 2005: 28S data and combined analysis; Dimitrov et al. 2013). Our data suggest that *Coryssocnemis* may be nested within *Mecolaesthus*, but our taxon sampling is weak, the topology is unstable (*Systenita* is either nested within *Mecolaesthus* or not), and several internal nodes in the clade have low support. Formally, *Coryssocnemis* still includes several obviously misplaced species: several Central American species (see

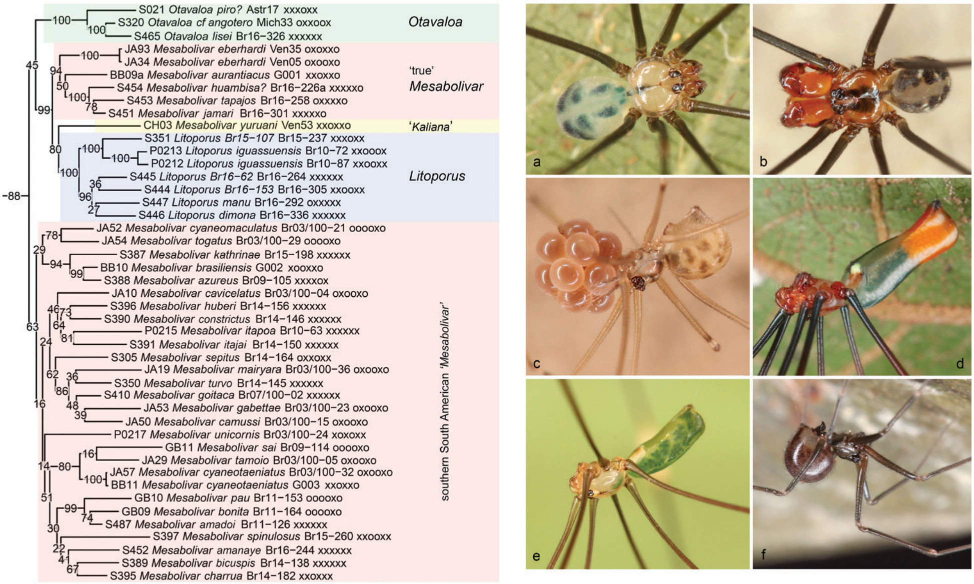

Figure 4. *Mesabolivar* clade **a** *Otavaloa lisei* (Brazil) **b** *Mesabolivar maraba* (Brazil) **c** *Litoporus* sp. n. "Br16-153" (Brazil) **d** *Mesabolivar cyaneotaeniatus* (Brazil) **e** *Mesabolivar kathrinae* (Brazil) **f** *Mesabolivar saci* (Brazil).

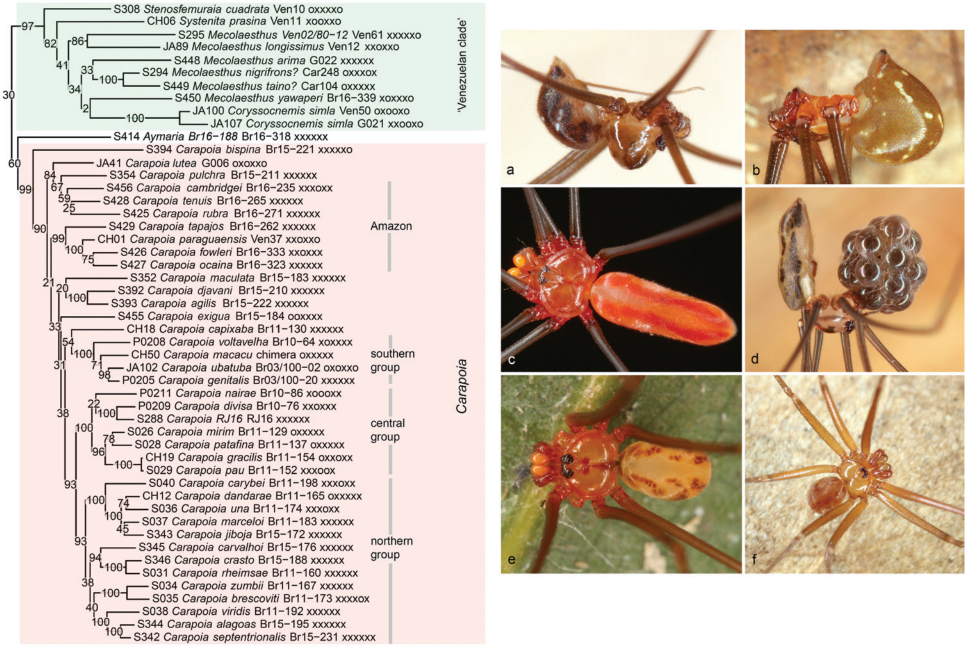

Figure 5. Venezuelan clade + *Aymaria* + *Carapoia* **a** *Mecolaesthus yawaperi* (Brazil) **b** *Aymaria* sp. n. "Br16-188" (Brazil) **c** *Carapoia rubra* (Brazil) **d** *Carapoia kaxinawa* (Brazil) **e** *Carapoia pulchra* (Brazil) **f** *Carapoia agilis* (Brazil).

above), and several Atlantic Forest (Brazilian) species whose identity is probably impossible to resolve (poor descriptions, lost types; see Huber 2000, 2018).

The third subclade in the South American clade is *Carapoia* (Figure 5). Unlike *Mesabolivar* it is monophyletic and apparently less problematic, but just as *Mesabolivar*, the genus has become very difficult to diagnose, mainly because of 'untypical' species added to the genus based in large part on the present molecular data (Huber 2018). Both for *Mesabolivar* and *Carapoia* our analyses suggest several species groups that are also supported by morphological data. For a detailed discussion of these groups, see Huber (2018).

Subfamily Smeringopinae Simon, 1893
Figure 6

Smeringopodeae Simon, 1893: 474. Type genus *Smeringopus* Simon, 1890, by subsequent designation (Huber 2011b).
Smeringopinae Simon; Huber 2011b: 217.

Remarks. Smeringopinae is a relatively homogeneous subfamily (with respect to body shapes, colour, webs, and microhabitats), and in this sense similar to Ninetinae and Arteminae but very unlike Modisiminae and Pholcinae. Most of the 125 known species of Smeringopinae are medium-size to large, have long legs, elongated to cylindrical abdomens, and all have eight eyes. Another similarity to Ninetinae and Arteminae is that Smeringopinae are often found in rather arid regions. The most obvious exception is the largely humid tropical genus *Smeringopina* Kraus, 1957, which is also the genus with the smallest and largest representatives in the subfamily (with body lengths ranging from 2.5–10 mm) and with the widest range of microhabitats used (leaf litter to large sheltered spaces) (Huber 2013). The original distribution of the subfamily is Africa, the Mediterranean, and the Middle East. Three species have attained much wider distributions, resulting from human-mediated dispersal (Huber 2011b).

As in previous molecular analyses (Bruvo-Mađarić et al. 2005, Astrin et al. 2007, Dimitrov et al. 2013), Smeringopinae is sister to Pholcinae (Figure 1) with reasonable to high support. This relationship is also supported by morphology: the two taxa share tarsus IV comb-hairs spread over the entire length of the tarsus (Huber and Fleckenstein 2008).

The monophyly of Smeringopinae receives reasonable to high support in all our analyses. Previous molecular analyses have partly supported Smeringopinae, but also suggested rather obscure relationships [e.g., the position of *Holocnemus pluchei* (Scopoli, 1763) among Ninetinae in Astrin et al. 2007]. *Holocnemus pluchei* was included in preliminary analyses of the present data but its position was drastically unstable, so we decided to exclude it from the final analyses. Smeringopinae monophyly is rather weakly supported by morphology, i.e., by the presence of a large thoracic pit on the carapace (rather than a narrow furrow or an evenly domed carapace; cf. Huber 2011b).

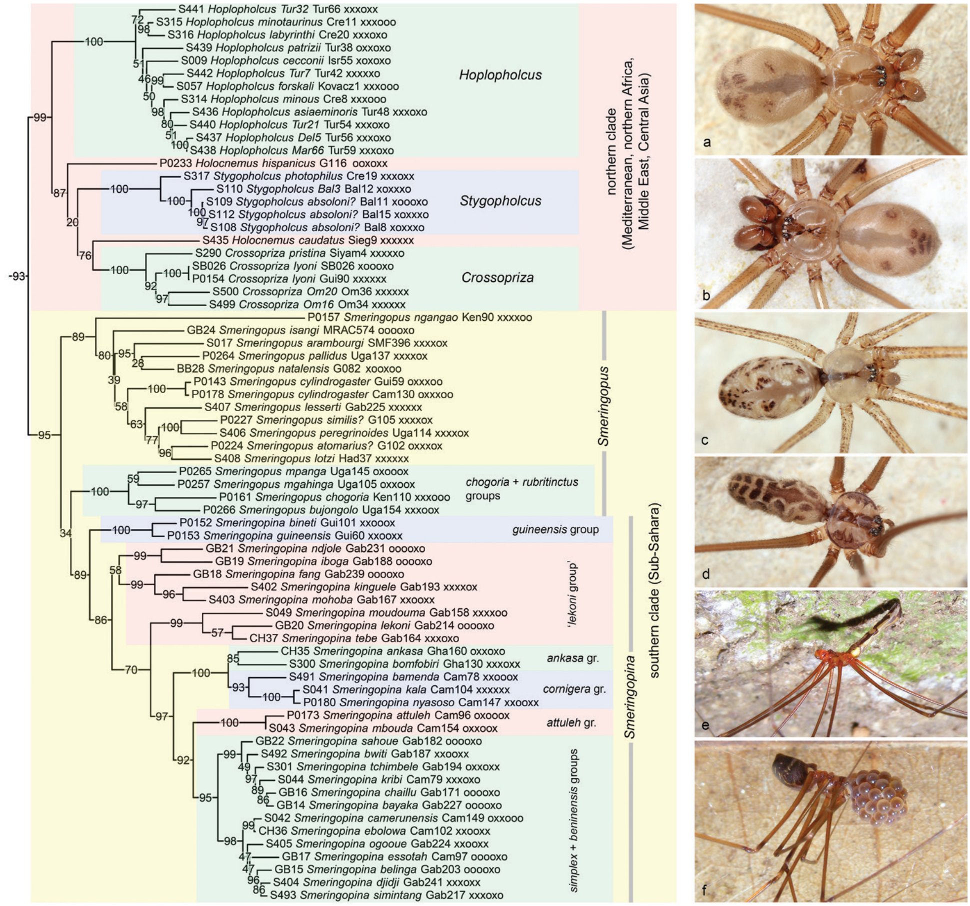

Figure 6. Smeringopinae **a** *Hoplopholcus* sp. n. "Mar66" (Turkey) **b** *Stygopholcus absoloni*? (Bosnia and Herzegovina) **c** *Crossopriza* sp. n. "Om11" (Oman) **d** *Smeringopus pallidus* (Philippines) **e** *Smeringopina pulchra* (Ghana) **f** *Smeringopina ankasa* (Ghana).

Within Smeringopinae, our data strongly support a basal split between a northern clade (Mediterranean, northern Africa, Middle East, Central Asia) and a southern clade (Sub-Sahara) (Figure 6). This basal split was also recovered in a morphological cladistic analysis (Huber 2012). Within the northern clade, *Hoplopholcus* Kulczynski, 1908 is sister to all other genera and not close to *Stygopholcus* Kratochvil, 1932 as repeatedly claimed by Brignoli (1971, 1976, 1979) but contested by Senglet (1971, 2001). The genera *Hoplopholcus*, *Stygopholcus*, and *Crossopriza* Simon, 1893 all receive full support, but the small Mediterranean genus *Holocnemus* Simon, 1873 (only three described species) continues to be problematic even after the exclusion of *H. pluchei*. The two species of *Holocnemus* included in our analyses never group together, and no morphological synapomorphy is known to suggest their sister-group relationship (in fact, *Holocnemus* has never been revised).

The southern (Sub-Saharan) clade includes *Smeringopus* Simon, 1890 and *Smeringopina*, and is also supported by a unique number of epiandrous spigots (two) (Huber 2012). The paraphyly of *Smeringopus* has been suggested before (Dimitrov et al. 2013), and our larger data set supports this view, but with low support values. Two of the species groups of *Smeringopus* proposed in Huber (2012) appear closer to *Smeringopina* than to other *Smeringopus*: the *chogoria* group and the *rubrotinctus* group. Morphological data do not support this view but they neither strongly contradict it: the two species groups lack the distinctive arrangement of pores on the pore plates (in groups or 'islands') and the retrolateral furrow on the male palpal femur present in all other species of *Smeringopus* (Huber 2012). Remarkably, *Smeringopus* and *Smeringopina* are largely separated geographically, with *Smeringopus* being most diverse in southern and eastern Africa, and *Smeringopina* in western and central Africa (Huber 2012, 2013). The *chogoria* and *rubrotinctus* groups are geographically restricted to an area where Central Africa (the Guineo-Congolian center of endemism) meets East Africa (Huber 2012). Other than that, our sampling in *Smeringopus* is not dense enough to test the species groups proposed in Huber (2012). Remarkably, though, the isolated 'basal' position of *S. ngangao* Huber, 2012 is supported by the present analyses.

Our analyses include 30 of the 44 described species of *Smeringopina* (68%), and all species groups proposed in Huber (2013) except two monotypic 'groups' (*S. fon* Huber, 2013; *S. ngungu* Huber, 2013). Even though for some species only one gene (CO1) was sequenced, our analyses support several species groups and deeper relationships proposed previously (Huber 2013), based on cladistic analysis of morphological characters. Morphology placed the West African *guineensis* group as sister to all other *Smeringopina*; all our analyses support both the monophyly of the *guineensis* group and its sister-group relationship with all other congeners. The next two branches are composed of representatives of the *lekoni* group, which is thus here considered paraphyletic rather than monophyletic. The *ankasa* and *cornigera* groups are both supported, as is their sister group relationship to each other. The *attuleh* group is supported, but not as sister to the *ankasa* + *cornigera* groups but as sister to the following group. The last clade is composed of representatives of the *simplex* and *beninensis* groups, but the clear dichotomy in the molecular trees is not equivalent to these groups. Instead, the *simplex* group includes all 'basal' representatives originally assigned to the *beninensis* group; the *beninensis* group includes only those species that have a light transversal element ventrally on the abdomen (character 9 in Huber 2013, which is thus less homoplastic than previously thought).

Subfamily Pholcinae C.L. Koch, 1850

Figs 7–12

Pholcidae CL Koch, 1850: 31. Type genus *Pholcus* Walckenaer, 1805, by monotypy.
Pholcinae CL Koch; Simon 1893: 461; Huber 2011b: 218.

Remarks. Pholcinae resemble Modisiminae in several respects. Their highest diversity is in the humid tropics and subtropics, and a large variety of body forms reflect adaptations to different microhabitats. With currently 922 species in 26 genera, Pholcinae is also similar to Modisiminae in diversity. In contrast to Modisiminae, Pholcinae is largely restricted to the Old World, with the notable exception of the New World endemic genus *Metagonia* Simon, 1893 and a few possibly relict species in *Pholcus* and *Micropholcus* (Huber 2011a, Huber et al. 2014). While only a single species of Modisiminae has followed humans around the globe [*Modisimus culicinus* (Simon, 1893)] and one further species has spread widely in Europe and neighboring regions [*Psilochorus simoni* (Berland, 1911)], several synanthropic species in Pholcinae have attained worldwide distributions or extended their ranges to another continent [most notably *Pholcus phalangioides* (Fuesslin, 1775); *Spermophora senoculata* (Dugès, 1836); *Micropholcus fauroti* (Simon, 1887); *Pholcus manueli* Gertsch, 1937].

The sister-group relationship between Pholcinae and Smeringopinae is well established (see above). The same is true for the monophyly of Pholcinae. All our analyses support this subfamily (reasonable to high support), and morphological data have also supported this group (presence of male lateral proximal cheliceral apophyses, Huber 1995, 2000; tarsus IV comb hairs in a single row, Huber and Fleckenstein 2008).

Even though Pholcinae are well represented in our analyses (317 of 597 species, i.e., 53%) internal relationships in this subfamily continue to be problematic. Several 'basal' nodes are poorly supported (Figure 1); in part the topology is highly sensitive to different algorithms of analysis; and some details appear dubious from the perspective of morphology. However, many details are strongly supported by morphology, including some deep nodes (e.g., the *Pholcus* group of genera); and some nodes, even though weakly supported or in conflict with morphology, provide reasonable and testable predictions for further research (e.g., the polyphyly of *Spermophora* Hentz, 1841; the close relationship of certain Sri Lankan taxa with African rather than Southeast Asian taxa; the monophyly of African *Pholcus*).

The subfamily is here divided into three operational groups, more for the sake of convenience than as a reflection of the support values they receive. Actually, support is low for all of them, but much of this division is consistent among different analyses and may well reflect real major groups. 'Group 1' (Figs 7, 8) is entirely composed of small six-eyed taxa, and is roughly equivalent to what was originally subsumed under the name *Spermophora*. 'Group 2' (Figure 9 part) is also entirely composed of six-eyed taxa and is remarkable because it places the exclusively New World genus *Metagonia* close to African and Madagascan taxa. 'Group 3' (Figure 9 part, Figs 10–12) includes the fully supported *Pholcus* group of genera as proposed previously (Huber 2011a) and its sister genus *Quamtana* Huber, 2003, a sister-group relationship that has also been proposed before (Huber 2003c). In the tree shown here (and in the RogueNaRok tree), the '*Spermophora*' *dieke* group has an isolated position outside of the three operational groups. In the other trees, it is part of 'group 1'.

Pholcinae 'group 1'
Figs 7, 8

Remarks. This group includes some genera named long ago, like *Spermophora*, *Belisana*, and *Paramicromerys* Millot, 1946. Most other genera were described relatively recently and resulted either from splitting of *Spermophora* (e.g., *Spermophorides* Wunderlich, 1992; *Buitinga* Huber, 2003; *Savarna* Huber, 2005; *Khorata* Huber, 2005) or from the discovery and description of new species (*Aetana* Huber, 2005; *Wanniyala* Huber & Benjamin, 2005; *Hantu* Huber, 2016).

A Southeast Asian clade that is consistently resolved with high to full support but variably placed either inside 'group 1' (IQ-TREE, RogueNaRok) or outside of the three operational groups as an isolated fourth group (4+ genes, RAxML) is composed of *Aetana*, Southeast Asian '*Spermophora*', and an undescribed new genus from Indonesia ("Ind206"). Morphological data have suggested a close relationship of *Aetana* with *Savarna*, *Khorata*, and *Hantu* (Huber et al. 2015). The positions of those three genera in our molecular trees are all unstable and problematic (see below). Thus, we consider it premature to conclude that the morphological data were misleading, and suggest that the positions of *Savarna*, *Khorata*, and *Hantu* need further analysis. A similar problem occurs with Southeast Asian '*Spermophora*'. The monophyly of the five species included receives reasonable to high support, but this group does not seem to be close to the type species *S. senoculata*. However, the position of *S. senoculata* varies strongly among analyses, and the idea that Southeast Asian taxa are in fact congeneric with *S. senoculata* (Huber 2005a) should not yet be discarded based on the present molecular data.

In *Aetana*, our analyses include 16 of 18 (89%) described species plus two undescribed species. The monophyly of the genus is highly to fully supported even though morphological support appeared weak (Huber et al. 2015). All four species groups proposed after cladistic analysis of morphological characters (Huber et al. 2015) are supported, but with different relationships among each other. Most of these relationships among species groups receive low support, but the *kiukoki* group is resolved as sister of the *omayan* group (with modest support) and this is in conflict with the results from morphology (Huber et al. 2015). The two unnamed subgroups within the *kinabalu* group and within the *omayan* group, respectively, proposed in Huber et al. (2015) are all recovered (with modest to full support).

The next clade within 'group 1' (Figure 7) includes three taxa whose position varies strongly among different analyses (see above): the type species of *Spermophora*, *S. senoculata*, and the Southeast Asian genera *Khorata* and *Savarna*. *Spermophora senoculata* is alternatively resolved as sister to the African '*Spermophora*' *akwamu* group (RAxML) or to the African '*Spermophora*' *kyambura* Huber & Warui, 2012 (4+ genes, RogueNaRok). Its sister group is essentially unknown. As indicated above, a close relationship with Southeast Asian '*Spermophora*', even though never recovered by our analyses, should not be definitely discarded. *Khorata* and *Savarna* are sister taxa in some analyses (low support; IQ-TREE, RogueNaRok), but wide apart in

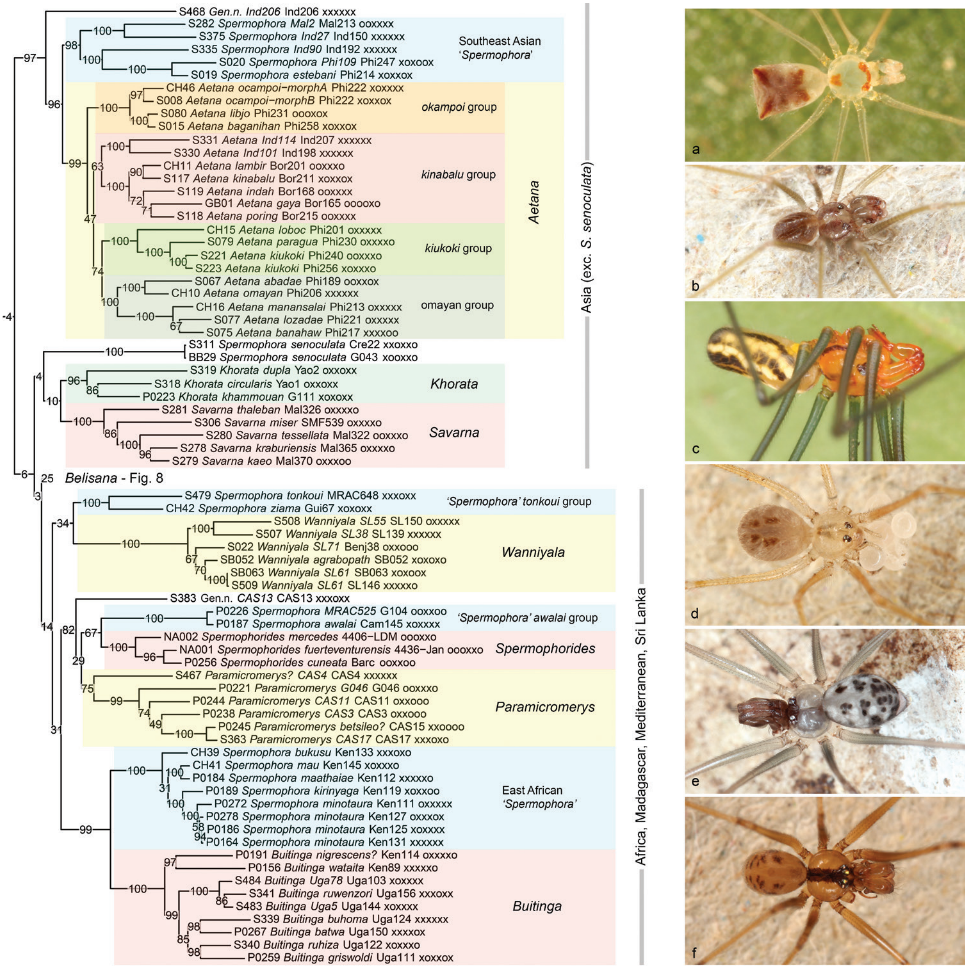

Figure 7. Pholcinae ‘group 1’ (*Spermophora* and relatives) **a** Gen. n., sp. n. “Ind206” (Halmahera); b, *Spermophora* sp. n. “Ind27” (Sumatra) **c** *Aetana baganihan* (Philippines) **d** *Spermophora senoculata* (Turkey) **e** *Savarna tessellata* (Thailand) **f** *Wanniyala agrabopath* (Sri Lanka).

others. The former result is considered more plausible for two reasons: (1) morphology supports a close relationship between *Khorata* and *Savarna* (Huber et al. 2015); (2) the alternative topology (4+ genes, RAxML) places the Southeast Asian *Savarna* as sister to an East African clade.

The large Asian genus *Belisana* (Figure 8) is well represented in our analyses (30 species) but seems to suffer from rogue taxa, paralogs, and/or other unidentified problems. Only the RogueNaRok tree resolves a monophyletic *Belisana*. In other analysis, either *Hantu* (RAxML) or *Hantu* and ‘*Spermophora*’ *kyambura* are nested within *Belisana* (IQ-TREE). A close relationship between *Belisana* and *Hantu* (that is also suggested in the RogueNaRok tree) is strongly contradicted by morphology: several characters support a close relationship between *Hantu*, *Khorata*, and *Savarna* (Huber et al. 2015). We have no explanation for the position of *Hantu* in our trees. Intriguingly, *H. niah* Huber, 2016 (but not *H. kapit* Huber, 2016) was placed in a clade together with *Khorata* and *Savarna* in preliminary analyses of the present data. On the other hand, the African '*Spermophora*' *kyambura* might indeed be close to *Belisana*. In fact, had it been collected in Southeast Asia, it would probably have been assigned to *Belisana*. It was tentatively assigned to *Spermophora* because African '*Spermophora*' were polyphyletic anyway and because the closest known record of *Belisana* was from India, more than 5000 km east. However, the position of '*Spermophora*' *kyambura* varies among analyses and should be considered unresolved.

Our sample of *Belisana* includes numerous representatives from different microhabitats (litter and leaves) and with different types of webs ('usual' pholcid domed sheets and highly regular 'curtain' webs; Figs 8e–f; see also Deeleman-Reinhold 1986a, Huber 2005b). The present data suggest multiple microhabitat shifts within *Belisana*, but note that many nodes within the genus have very low support values. These low values also impede a proper interpretation of the fact that the two species with a 'usual' domed web (marked with D in Figure 8) included in the analyses (*B.* "Mal77", *B. tambligan* Huber, 2005) are not 'basal' but nested among species with highly regular 'curtain' webs (marked with R in Figure 8) [confirmed for *B. bohorok* Huber, 2005; *B. leuser* Huber, 2005; *B.* "Bor85"; *B. junkoae* (Irie, 1997); *B. sabah* Huber, 2005; BA Huber, unpubl. data].

Except for the Sri Lankan genus *Wanniyala*, all remaining taxa of Pholcinae 'group 1' (Figure 7) are African, Madagascan, and Mediterranean. They are grouped together but with very low support. South African and Madagascan '*Spermophora*' were not available for sequencing and are thus not included in our analyses; we predict they are members of this clade. As mentioned above, some analyses (RAxML, 4+ genes) placed the East Asian genus *Savarna* within this clade; we consider this topology dubious.

A close relationship between the West African '*Spermophora*' *tonkoui* group and *Wanniyala* is suggested in all our analyses, even though with low support (only SH values are consistently at 96–97). This relationship is also supported by morphology: the two taxa share a hinged procursus with a membranous process arising from the proximal part (see Huber and Benjamin 2005: fig. 7, Huber 2003b: fig. 293, Huber and Kwapong 2013: fig. 101).

The following clade (Figure 7) places the Central African '*Spermophora*' *awalai* group as sister to the Macaronesian and Mediterranean genus *Spermophorides*, both together sister to the Madagascan genus *Paramicromerys*, and all together sister to an undescribed Madagascan genus ("CAS13"). Support for these relationships is modest, and the clade is different in composition in the 4+ genes tree (*Spermophorides* is missing from this analysis).

The last clade in Pholcinae 'group 1' is highly to fully supported in all analyses and includes the East African genus *Buitinga* and East African '*Spermophora*', each with full support in all analyses. The sister group relationship between these two taxa makes sense geographically but is not evident from morphology.

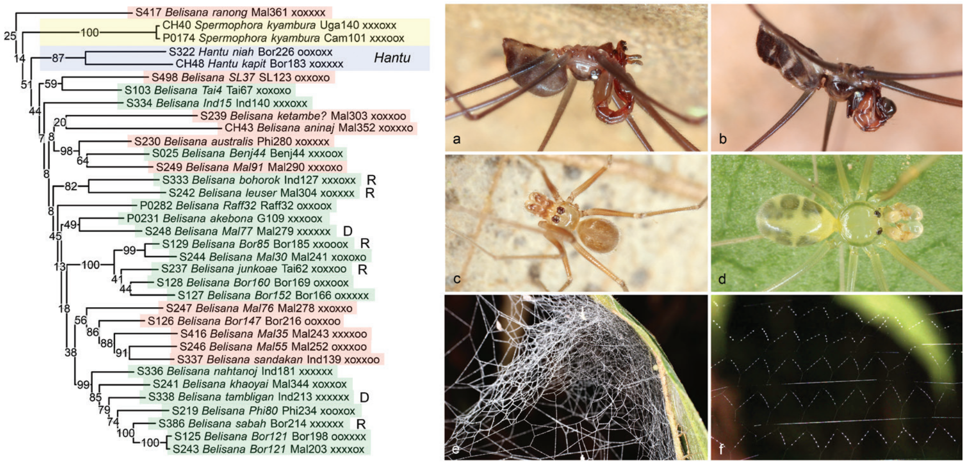

Figure 8. *Belisana* and *Hantu*. For *Belisana*, the background colours signify microhabitat: red = ground; green = leaf. D, domed web; R, highly regular 'curtain' web. Photos **a** *Hantu niah* (Sarawak) **b** *Hantu kapit* (Sarawak) **c** *Belisana sandakan* (Sumatra) **d** *Belisana sabah* (Sabah) **e** domed web of *Belisana* sp. n. "Mal77" (Malaysia) **f** regular 'curtain' web of *Belisana bohorok* (Sarawak).

Pholcinae 'group 2'

Figure 9

Remarks. This operational group (Figure 9 part, i.e., without the '*Spermophora*' *dieke* group and *Quamtana*) is similar to 'group 1' in that it is composed entirely of six-eyed species. It is weakly supported, indicating that the exact placement of its two clades among other Pholcinae remains dubious. The two clades, however, both receive high to full support in all analyses. The first clade unites the African genera *Anansus* Huber, 2007 and *Nyikoa* Huber, 2007 with the Madagascan genus *Zatavua* Huber, 2003. In a cladistic analysis of morphological characters (Huber 2007), the group was also recovered (even though as paraphyletic) when using successive character weighting (but not when using equal character weights). The character supporting this close relationship was the proximal cheliceral apophyses that point backwards in *Anansus* just as in *Nyikoa* and *Zatavua* (Huber 2007). The idea that these genera might be 'basal' in Pholcinae, i.e., sister to all other Pholcinae (Huber 2003a, 2007) is not supported by our analyses, but considering the low support values at deeper nodes within the subfamily it is neither strongly contradicted.

The second clade is the New World genus *Metagonia*. The genus is species-rich (currently 85 species) and ranges from Argentina to Mexico. The monophyly of the genus has never been seriously contested, and its position among the otherwise almost exclusively Old World Pholcinae has been strongly supported before, both using morphology (Huber 2000) and molecules (Bruvo-Mađarić et al. 2005, Dimitrov et al. 2013). Our analyses include 30 species of *Metagonia*, and provide for the first time a

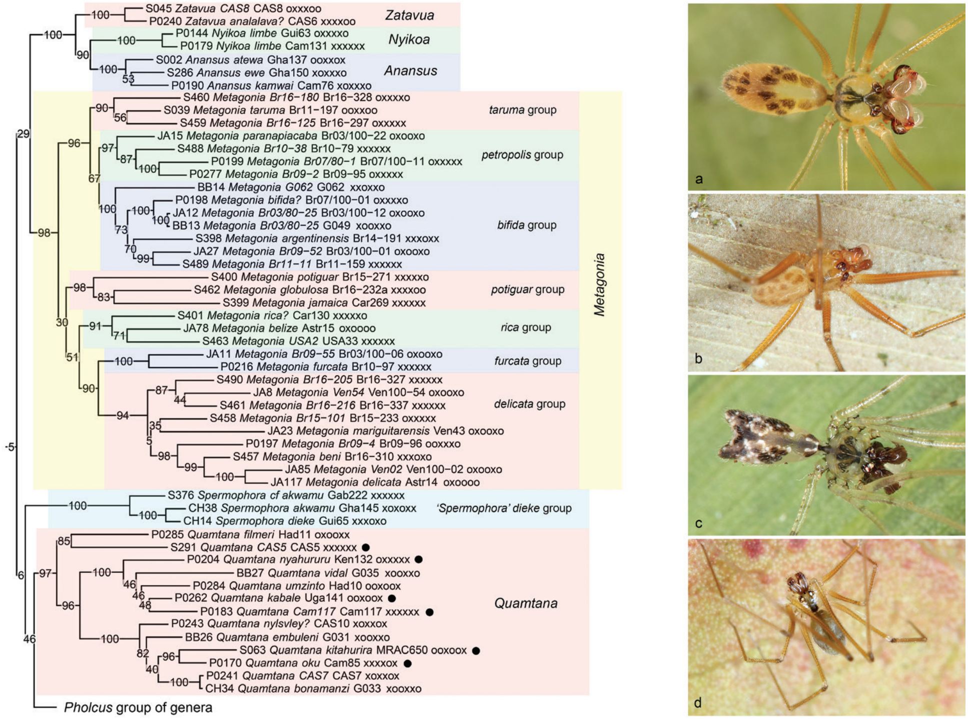

Figure 9. Pholcinae 'group 2' (*Zatavua* and relatives, *Metagonia*), and *Quamtana* (marked: non-South African species). Photos **a** *Metagonia taruma* (Brazil) **b** *Metagonia* sp. n. "Br07-1" (Brazil) **c** *Metagonia bifida*? (Brazil) **d** *Quamtana* sp. n. (cf. *mabusai*) (Germany).

test of the operational species groups proposed in Huber (2000: 54–55). Even though those groups were not based on formal cladistic analysis (such an analysis has not yet been performed for *Metagonia*) but on overall and specific similarities, all of them appear mostly or entirely congruent with the present analyses (the only exception is the single aberrant *M. globulosa*). They are listed here in the sequence in which they appear in Figure 9, with newly proposed informal names. (1) *taruma* group (group "3" in Huber 2000); a South American group that is here resolved as monophyletic and not as a paraphyletic 'basal' group as speculated before (Huber 2000); (2) *petropolis* group (no species was known in 2000); a group of litter-dwelling species restricted to the Brazilian Atlantic Forest (Huber et al. 2005b); (3) *bifida* group (group "1" in Huber 2000); this South American group includes the type species *M. bifida* Simon, 1893; all species included share a sclerotized epigynum and (except for the 'basal' undescribed species "G062") a distinctively bifid abdomen; (4) *potiguar* group (not recognized in Huber 2000); this group includes cave dwelling species in Brazil (*M. potiguar* Ferreira et al. 2011) and Jamaica (*M. jamaica* Gertsch, 1986) and the aberrant litter-dwelling *M. globulosa* Huber, 2000 (which was misplaced in group "5" in Huber 2000); *rica* group (group "4" in Huber 2000); a mainly North and Central American group, possibly ranging into South America, but not including all Caribbean and Central American species as speculated previously (Huber 2000; see previous group); (5) *furcata* group (group "5" in Huber 2000, together with *M. globulosa*); includes only *M. furcata* Huber, 2000 and the undescribed species "Br09-55"; as suspected previously (Huber 2000), it is close to (sister of) the next group; (6) *delicata* group (group "2" in Huber 2000); this group is composed of very small species and ranges from Mexico to northern Argentina.

Pholcinae 'group 3'

Figs 9–12

Remarks. A sister-group relationship between the African genus *Quamtana* and the *Pholcus* group of genera (Figure 9) is recovered in all our analyses. Support values are low, but a morphological cladistic analysis has partly suggested the same relationship (based on a distinct sclerite connecting the genital bulb to the palpal tarsus; Huber 2003c). The monophyly of *Quamtana* is highly supported in all analyses (except for the 4+ genes analysis). It was also supported by morphological data when using character weighting (but not in the equal weights analysis; Huber 2003c).

Within *Quamtana* (Figure 9), our data suggest that there is no simple geographic pattern with respect to South African species (the large majority) versus species from other parts of Africa (marked in Figure 9). By contrast, three species groups with reasonable to full support include species from both South Africa and other regions: the South African *Q. filmeri* Huber, 2003 is sister to the Madagascan undescribed species "CAS5"; the South African *Q. vidal* Huber, 2003 and *Q. umzinto* Huber, 2003 are placed in a group with species from East and Central Africa (*Q. kabale* Huber, 2003, "Cam117"); and the group including the South African *Q. embuleni* Huber, 2003 and *Q. bonamanzi* Huber, 2003 also includes species from East and Central Africa (*Q. kitahurira* Huber, 2003, *Q. oku* Huber, 2003). We suspect that *Quamtana* was once widely distributed throughout Africa but largely replaced by more modern taxa in humid regions and extinguished in northern Africa. The Paris amber fossil *Quamtana huberi* Penney, 2007 supports this view, but its generic assignment is uncertain (Penney 2007).

All remaining clades together (Figs 10–12) represent the *Pholcus* group of genera *sensu* Huber (2011a). This clade was first proposed in Huber & Fleckenstein (2009) based on the distinctive simplified shape of the tarsus IV comb-hairs, and later supported in a cladistic morphological analysis by an additional character (female epigynal 'knob') (Huber 2011a). All our analyses fully support this clade. The previous morphological analysis (Huber 2011a) identified two major problems within this clade: (1) relationships among genera were basically unresolved, resulting in large polytomies; and (2) several species groups assigned to *Pholcus* appeared more closely related to other genera. The present analysis strongly supports the polyphyly of *Pholcus* in its previous composition, and it provides for the first time a reasonable framework to redefine generic limits in this large group (currently 501 species).

The first major clade within the *Pholcus* group of genera (Figure 10) is composed of three Southeast Asian genera (*Calapnita*, *Panjange*, *Uthina* Simon, 1893) as well as several Southeast Asian and Sri Lankan species groups that were originally tentatively assigned to *Pholcus* (Huber 2011a; Huber et al. 2016a, 2016b, Huber and Dimitrov 2014). We informally call it the '*Calapnita-Panjange* clade' because many species in this group are leaf-dwellers, and representatives of *Calapnita* and *Panjange* are particularly strongly adapted to life on green leaves. Remarkably, even some of the species collected in the leaf litter (under large dead leaves on the ground) look like leaf-dwellers rather than litter dwellers (i.e., they have long abdomens, long legs, light colouration; e.g., *Kintaqa satun* (Huber, 2011) and *K. schwendingeri* (Huber, 2011); and Malaysian representatives of *Tissahamia*, previously the *Pholcus ethagala* group). Ancestral character state reconstruction suggests that the ancestor of the entire clade was leaf-dwelling (Eberle et al. 2018).

The present analyses reject the monophyly of *Calapnita* (Figure 10). A recent cladistic analysis of morphological data (Huber 2017) resolved *Calapnita* as monophyletic but with low support (< 50 using Jackknifing). On the other hand, support for the two subgroups, previously called *phyllicola* group and *vermiformis* group, is full in all analyses. The two species groups have been identified long ago (Deeleman-Reinhold 1986b), and have been supported by cladistic analysis (Huber 2017). Our analyses strongly suggest that the *vermiformis* group is closer to species previously in *Pholcus* than to the *phyllicola* group (see below). The *phyllicola* group is thus elevated to genus rank (*Nipisa*; see Taxonomy section below).

Within *Nipisa* (Figure 10), the internal relationships proposed previously (Huber 2017) are mostly supported even though data gaps are severe in this genus (several species with only two genes): (1) *N. lehi* (Huber, 2017) [but not *N. kubah* (Huber, 2017)] is a 'basal' species, i.e., sister to all other species (reasonable to high support); (2) a clade including the species with egg-sacs that have all eggs aligned in a single row (weak support, possibly because *N. kubah* is included, which is contradicted by morphology and egg-sac shape); (3) a clade including *N. semengoh* (Huber, 2011) and its sister group, characterized by the position of the tarsal organ on a turret, a serrate embolus, and the shape of the pore-plates (full support).

The relationships within 'true' *Calapnita* (previously *vermiformis* group) proposed in Huber (2017) are only partly supported: (1) a clade with a continuous connection between epigynal plate and 'knob' (all species in the present analysis except *C. bario* Huber, 2017 and *C. saluang* Huber, 2011; high support); (2) within the previous clade, a clade characterized by a prolateral process at the tip of the procursus (in the present analysis: *C. nunezae* Huber, 2017 and *C. dinagat* Huber, 2017; full support).

The present analyses also reject the monophyly of *Panjange* (Figure 10). They split the genus into two unrelated lineages, one of which is equivalent to what was previously called the *nigrifrons* group; the other is equivalent to the previous *vermiformis* + *cavicola* groups (Deeleman-Reinhold and Platnick 1986, Huber and Nuñeza 2015). Our analyses place each group with reasonable to full support in clades together with species previously assigned to *Pholcus*. A morphological cladistic analysis has recently supported the monophyly of *Panjange* based on the presence of parallel ridges ventrally on the procursus and on the reduction of the bulbal uncus (Huber and Nuñeza 2015). However, the monophyly was lost when using specific weighting parameters (implied weighting with K = 1 and K = 2), and some morphological characters do in fact support the split of *Panjange*: (1) the loss of distal cheliceral apophyses in 'true' *Panjange* and its closest relatives according to the present analyses; (2) the loss of an uncus in 'true' *Panjange* and its closest relatives according to the present analyses. The *nigrifrons* group is thus elevated to genus rank (*Apokayana*; see Taxonomy section below).

Apokayana is recovered with full support. This is remarkable considering the fact that in the morphological analysis its equivalent (the *Panjange nigrifrons* group) was supported by a single homoplastic character only (Huber and Nuñeza 2015). Within the genus, our analyses identify two subgroups with full support each. These groups do not correspond to the relationships suggested in Huber and Nuñeza (2015). In that analysis, each node was based on a single character, some of them not particularly convincing. We thus tend to prefer the present grouping even though our matrix is particularly incomplete in this genus (we did not manage to get 28S and CO1 sequences for any of the six species included).

The monophyly of 'true' *Panjange* (*vermiformis* + *cavicola* groups) is supported by several morphological characters (Huber and Nuñeza 2015), and receives high support in our present analyses (except for the 4+ genes analysis). The *cavicola* group (including also the two undescribed species "Ind103" and "Ind109") was recovered as paraphyletic in Huber and Nuñeza (2015) but is here resolved as monophyletic. By contrast, the *lanthana* group which was supported by two morphological characters, one of them considered particularly strong (the unique direction of the embolus, pointing in the opposite direction of the appendix) is resolved as monophyletic only in the RogueNaRok tree; in the IQ-TREE and RAxML trees it is paraphyletic with respect to the *cavicola* group (actually, these trees suggest a basal trichotomy). Within the *lanthana* group, three species (*P. malagos* Huber, 2015; *P. casaroro* Huber, 2015; *P. camiguin* Huber, 2015) share asymmetric male pedipalps, a character that is extremely rare in spiders (Huber et al. 2007, Huber and Nuñeza 2015). This group is not recovered in any of the present analyses, where it consistently includes the symmetric *P. lanthana* Deeleman-Reinhold & Deeleman, 1983 (requiring a regain of symmetry or two origins of asymmetry). Only the sister group relationship between *P. dinagat* Huber, 2015 and *P. marilog* Huber, 2015 is strongly supported by both morphology and molecules. In conclusion, alternative topologies within the *lanthana* group are supported by seemingly strong molecular and morphological data, respectively.

Ten species groups previously assigned to *Pholcus* (in Huber 2011a, Huber et al. 2016a, 2016b) are representatives of the '*Calapnita-Panjange* clade' (Figure 10). Of these, nine are entirely Southeast Asian; only the *ethagala* group (now *Tissahamia*) has representatives in Southeast Asia and Sri Lanka. For some of these species groups, our data provide strong evidence about the sister-group or close relatives. All of these groups are here transferred from *Pholcus* to new genera (see Taxonomy section below).

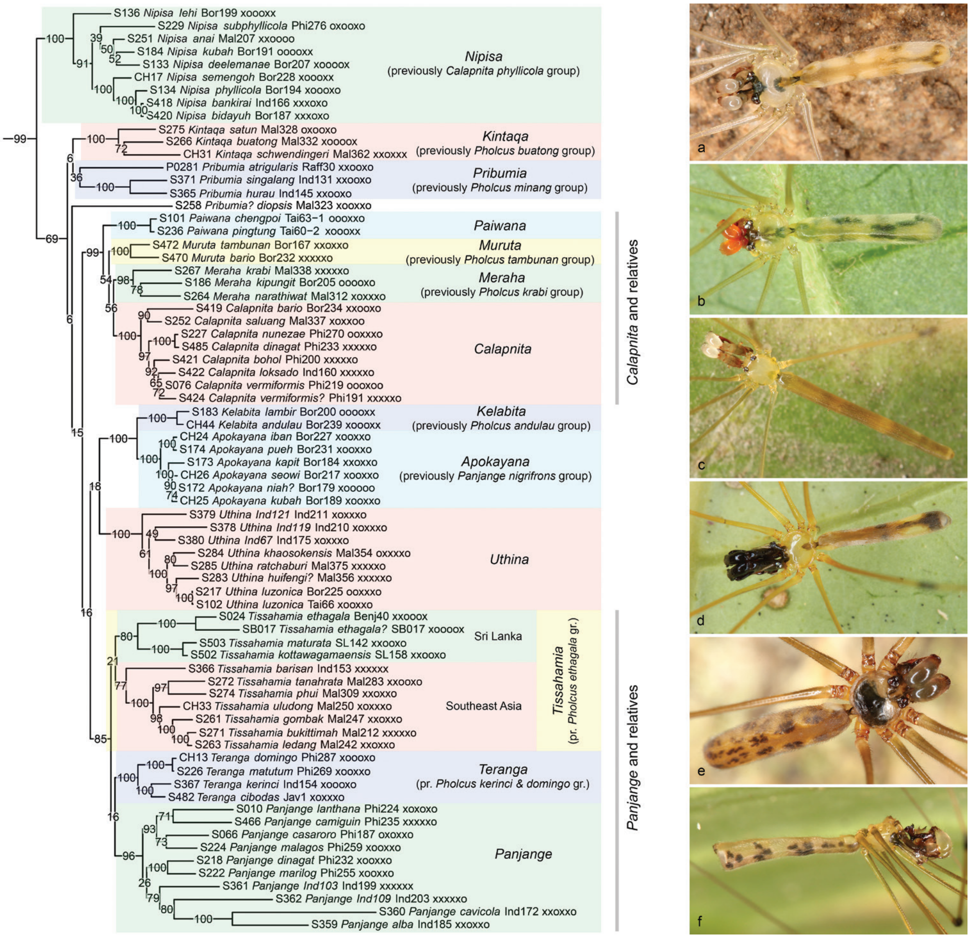

Figure 10. *Calapnita-Panjange* clade **a** *Kintaqa satun* (Malaysia) **b** *Meraha narathiwat* (Thailand) **c** *Calapnita vermiformis* (Philippines) **d** *Apokayana kapit* (Sarawak) **e** *Uthina* sp. n. "Ind121" (Indonesia) **f** *Panjange casaroro* (Philippines).

A sister-group relationship between *Kelabita* (previously the *Pholcus andulau* group) and *Apokayana* (previously the *Panjange nigrifrons* group) is fully supported in all our analyses (except for the 4+ genes tree where *Kelabita* is not represented). Both genera are restricted to Borneo and share habitus, colouration, web structure, and microhabitat (Huber and Leh Moi Ung 2016, Huber et al. 2016a).

The western Indonesian '*Pholcus kerinci* group' (Huber 2011a) and the Philippine '*Pholcus domingo* group' (Huber et al. 2016b) are both fully supported, as is their sister-group relationship (Figure 10). They are joined in the new genus *Teranga* (see Taxonomy section below). Together with *Tissahamia* (previously the *Pholcus ethagala* group) and with 'true' *Panjange* they form a clade that is recovered in all analyses with reasonable support. This clade was supported in almost exactly the same composition by morphological cladistic analysis (Huber 2011a) except that the '*Panjange*' *nigrifrons* group was also included (the '*Pholcus domingo* group' was not yet known in 2011). The clade is supported by the loss of the bulbal uncus and by the loss of distal male cheliceral apophyses [in Huber 2011a, the latter character supports a more inclusive taxon (including *Leptopholcus* Simon, 1893) that is strongly rejected by the present molecular data]. *Tissahamia* consists of two subgroups, a Sri Lankan subgroup and a Southeast Asian (Malaysian Peninsula, Sumatra) subgroup. The subgroups are consistently recovered in all our analyses with modest to reasonable support, but the monophyly of the entire group is only recovered in the IQ-TREE analysis (low support). Morphological analysis recovered the group, but with varying support depending on weighting regime (Huber 2011a).

Three genera composed of species that were previously assigned to *Pholcus* are consistently placed in a highly supported clade together with 'true' *Calapnita* (Figure 10): *Paiwana* (previously not assigned to a group), *Muruta* (previously the *Pholcus tambunan* group; Huber et al. 2016b), and *Meraha* (previously the *Pholcus krabi* group; Huber et al. 2016b). We know of no convincing morphological synapomorphy for this group but note two interesting similarities: representatives of 'true' *Calapnita* and of *Meraha* share the loss of piriform gland spigots on the anterior lateral spinnerets (Huber 2011a, 2017, Huber et al. 2016b); representatives of 'true' *Calapnita* and of *Muruta* and *Paiwana* share the distinctive shape of the epigynum (roughly triangular, with 'knob' directed towards anterior; Huber et al. 2016b, Huber 2017; Huber and Dimitrov 2014).

For two further genera composed of species previously assigned to *Pholcus* the present analysis supports the monophyly but gives not clear indication about their closest relatives within the '*Calapnita-Panjange* clade' (Figure 10): *Pribumia* (previously the *Pholcus minang* group; Huber 2011a) and *Kintaqa* (previously the *Pholcus buatong* group; Huber et al. 2016a). All analyses except the IQ-TREE analysis place *Kintaqa* as sister to *Uthina*, but with low support. We know of no potential morphological synapomorphy that links these two groups. *Pribumia* is in our analysis represented by four species. Of these, *P. diopsis* (Simon, 1901) is never placed within the group; together with *P. atrigularis* (Simon, 1901) it is detected as a rogue taxon and excluded in the RogueNaRok tree. External relationships of *Pribumia* remain dubious. The hypothesis that the genus might be close to *Tissahamia* (previously the '*Pholcus ethagala* group'; Huber 2011a) is supported by numerous distinctive morphological similarities but it is not supported by the present data. However, note that in our analysis *Pribumia* suffers seriously from missing data (we were not able to sequence 28S for any of the four species).

The second major clade within the *Pholcus* group of genera (Figure 11) is composed of four 'old' genera (*Micropholcus*; *Leptopholcus*; *Micromerys* Bradley, 1877; *Pehrforsskalia* Deeleman-Reinhold & van Harten, 2001) and *Cantikus* (previously the *Pholcus halabala* group; Huber 2011a, Huber et al. 2016a). Except for one clade of Neotropical *Micropholcus*, all representatives are Old World taxa. We informally call it the '*Micropholcus-Leptopholcus* clade'. This clade receives full support in all our analyses, and major internal relationships are also well resolved. Three subclades are

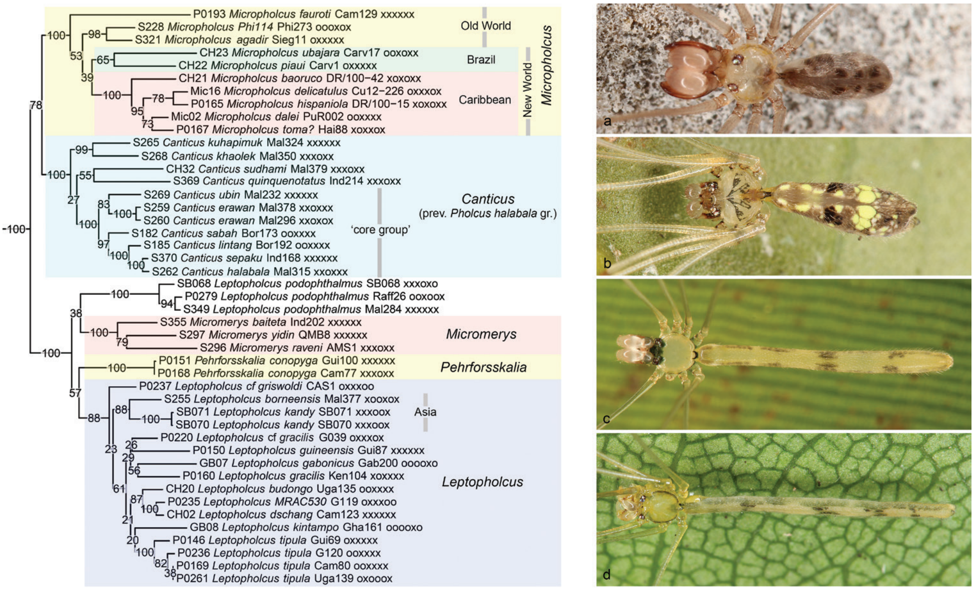

Figure 11. *Micropholcus-Leptopholcus* clade **a** *Micropholcus* sp. n. “Br15-152” (Brazil) **b** *Canticus sepaku* (East Kalimantan) **c** *Micromerys baiteta* (West Papua) **d** *Leptopholcus borneensis* (Singapore).

fully supported each: *Micropholcus*; *Cantikus*; and a subclade including *Leptopholcus*, *Micromerys*, and *Pehrforsskalia*. All analyses put *Micropholcus* as sister to *Cantikus*, but with modest support.

Micropholcus is ecologically diverse, including ground-dwelling as well as rock- and leaf-dwelling species, and together with *Pholcus* it is also the only genus with autochthonous species in both the New and Old World. Our analysis rejects the previous idea that *Micropholcus* is ‘basal’ in the *Pholcus* group of genera (i.e., in a basal trichotomy, with *Sihala* occupying the second branch and all other taxa the third branch; Huber 2011a). Within *Micropholcus*, our analyses all support a monophyletic New World clade, but with low support values (reasonable support in the 4+ genes analysis). Within the New World clade, a Caribbean clade is fully supported. A remarkable sister-group relationship that is highly supported by the present data is between the Moroccan ‘*Pholcus*’ *agadir* (now transferred to *Micropholcus*; see Taxonomy section below) and the undescribed Philippine species “Phi114”. Both have very limited distributions; only one further species of *Micropholcus* (other than the pantropical *M. fauroti*) is known from between Morocco and the Philippines: *M. jacominae* Deeleman-Reinhold & van Harten, 2001 from Yemen. We suspect that *Micropholcus* in the Old World has a relict distribution, just as it has been hypothesized for South American *Micropholcus* (Huber et al. 2005a, 2014).

Cantikus was recently revised (as ‘*Pholcus*’ *halabala* group; Huber et al. 2016a) and divided into a ‘core group’ that was supported by numerous morphological and behavioral similarities, and a group of species that were assigned to the group tentatively.

This tentative assignment was based mainly on preliminary results from the present molecular analysis; a putative morphological synapomorphy for the entire genus *Cantikus* was and is not known. The present analyses fully support both the entire genus and the core group; the genus includes *C. quinquenotatus* (Thorell, 1878), making the *quinquenotatus* group proposed in Huber (2011a) obsolete; and it highly to fully supports the sister group relationship between the two rock-dwelling species *C. kuhapimuk* Huber, 2016 and *C. khaolek* Huber, 2016.

The clade including *Leptopholcus*, *Micromerys*, and *Pehrforsskalia* (Figure 11) was only partly supported in a previous cladistic analysis of morphological data (Huber 2011a): while *Leptopholcus* and *Micromerys* were consistently seen as sister taxa (with a mono- or paraphyletic *Leptopholcus*), the position of *Pehrforsskalia* varied widely. The characters supporting a close relationship among the three genera are the distal position of the lateral apophyses on the male chelicerae, and the absence of frontal cheliceral apophyses (Huber 2011a). The present analyses fully support this clade. Within the clade, 'basal' relationships are unresolved, essentially resulting in a tetrachotomy: (1) '*Leptopholcus*' *podophthalmus* (Simon, 1893) is not clearly included in 'true' *Leptopholcus*. (2) The Australasian *Micromerys* receives full support in all analyses. (3) The African *Pehrforsskalia* is only represented by its type species. (4) 'True' *Leptopholcus* receives reasonable to full support and includes both African and Asian representatives but not the Asian *L. podophthalmus* (and its putative close relative *L. tanikawai* Irie, 1999 that is not included in our analyses). Within *Leptopholcus*, our data provide little resolution, but an Asian clade (represented by *L. borneensis* Deeleman-Reinhold, 1986 and *L. kandy* Huber, 2011) receives reasonable support. Among these four clades, *Pehrforsskalia* is the only one that does not share the distinctively serrated tip of the male palpal trochanter apophysis (Huber 2011b), suggesting that it may be sister to the other three clades.

The third and last major clade within the *Pholcus* group of genera is 'true' *Pholcus* (Figure 12). Support for this group is very low in the IQ-TREE analysis, which reflects the fact that one of the two basal subclades (including the *phungiformes* and *bidentatus* groups and *P. mentawir* Huber, 2011) is closer to the *Micropholcus-Leptopholcus* clade than to 'true' *Pholcus* in some analyses (RAxML, RogueNaRok). By contrast, the 4+ genes analysis recovers the monophyly of 'true' *Pholcus* with reasonable support, suggesting that the poor support or non-monophyly of 'true' *Pholcus* in some analyses may result from the many missing data in our full matrix.

Even after removing the eleven species groups that are here placed in the *Calapnita-Panjange* clade and in the *Micropholcus-Leptopholcus* clade, *Pholcus* continues to be the most species rich genus in Pholcidae. It now contains 321 species, most of which are distributed in tropical and subtropical Old World regions. The only exception is the *kingi* group with ten species in the southeastern USA (Huber 2011a). Most species of *Pholcus* resemble the synanthropic type species *P. phalangioides* in being relatively large, long-legged, brown, and in having a cylindrical abdomen; most or all of these species build their webs in large sheltered spaces. However, the genus is ecologically diverse and includes small litter dwellers with relatively short legs, rock- and ground dwellers with oval abdomens, and pale leaf-dwellers with worm-shaped abdomens.

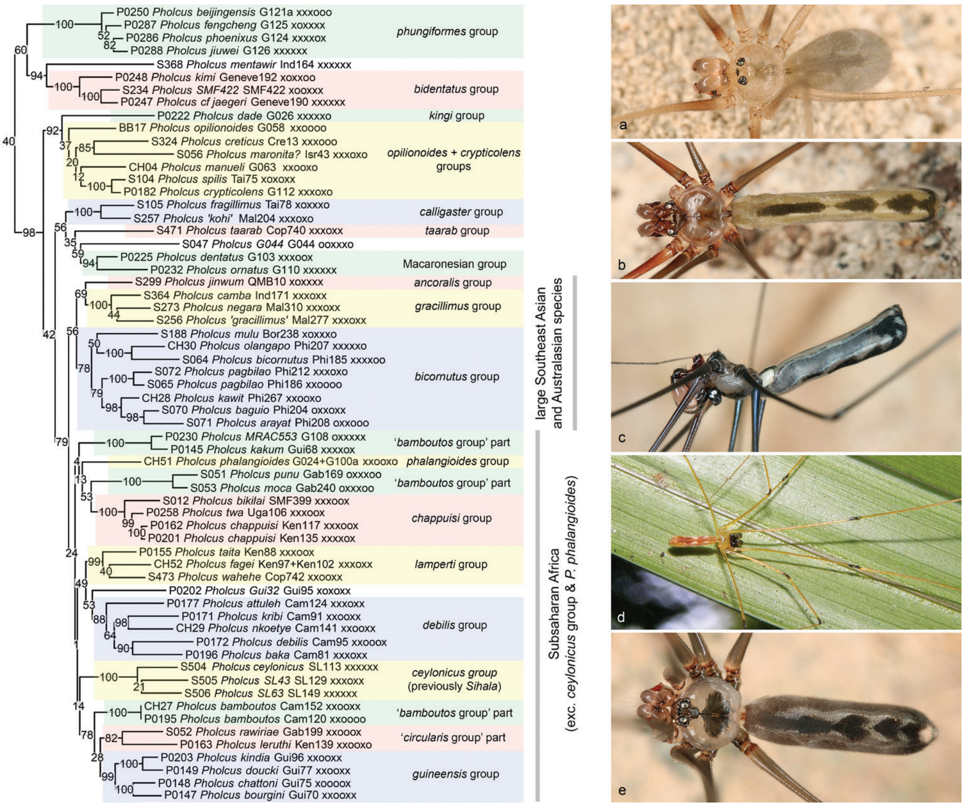

Figure 12. *Pholcus* **a** *P. creticus* (Crete) **b** *P. camba* (Sulawesi) **c** *P. mulu* (Sarawak) **d** *P. baka* (Gabon) **e** *P.* sp. n. "SL43" (Sri Lanka).

In a first effort to structure the known diversity of *Pholcus*, the genus was divided into 29 operational species groups (Huber 2011a), including 25 species groups in the 'core group', i.e., in 'true' *Pholcus*. Even though the aim was to identify monophyla, some groups were explicitly proposed as 'waste baskets groups' (e.g., the *bamboutos* group) or as "probably not monophyletic" (e.g., the *circularis* group). The present analysis clarifies a number of relationships, it supports several of the species groups and rejects others, and it confirms the non-monophyly of some groups as suspected. However, we acknowledge that internal relationships in *Pholcus* remain highly uncertain and need considerably more work. Our data seem to suffer from two main problems that result in variable topologies among different types of analyses: (1) Even though *Pholcus* is in our analyses represented by more species than any other genus (59), our sample is still highly incomplete, including only 18% of the described species and entirely missing seven of the previously suggested species groups (*alticeps*, *nenjukovi*, *ponticus*, *zham*, *yichengicus*, *taishan*, and *nagasakiensis* groups). (2) The percentage of missing sequences is high in *Pholcus*, partly due to the fact that we identified paralogs for 28S and 18S that we excluded, partly due to other unidentified problems.

Of the 25 operational species groups within 'true' *Pholcus* proposed previously (Huber 2011a), ten are supported by the present data: *phungiformes* group, *bidentatus* group, *calligaster* group, Macaronesian group, *gracillimus* group (excl. *P. mentawir*), *bicornutus* group, *chappuisi* group, *lamperti* group, *debilis* group (incl. *P. nkoetye* Huber, 2011 and *P. kribi* Huber, 2011), and *guineensis* group. Four groups are represented by single species (*taarab* group, *ancoralis* group, *phalangioides* group, *kingi* group). Seven groups are missing in the analyses (see above). For the remaining four groups, the present analyses reject the monophyly: (1) The *bamboutos* group is polyphyletic as expected and the six species in our analyses split into four parts; of these *P. kribi* is moved to the *debilis* group; *P. bamboutos* Huber, 2011 is close to the *guineensis* group; the affinities of the other four species are unclear. (2) The *circularis* group is represented by three species; of these, *P. nkoetye* is moved to the *debilis* group; *P. leruthi* Lessert, 1935 and *P. rawiriae* Huber, 2014 are sister species and close to the *guineensis* group. (3/4) The *opilionoides* and *crypticolens* groups are both rejected, but together with the North American *kingi* group they form a monophylum with reasonable to high support (except for the 4+ genes analysis) but with unknown affinities with other groups.

The present analysis identifies two major clades within 'true' *Pholcus* that are remarkable even though support values are low to modest. (1) A clade combining the *ancoralis*, *gracillimus*, and *bicornutus* groups is composed of large dark Southeast Asian and Australasian species; a close relationship between the *ancoralis* group and the *bicornutus* group has been suspected before, based on male ocular area modifications (Huber 2011a: 314). (2) A large clade including all Subsaharan African taxa. This clade has low bootstrap support but SH values range from 81 to 96, so we consider this a first tentative indication that tropical African *Pholcus* might form a large monophylum. The two species that disrupt this picture were both identified as rogue taxa: *P. taarab* Huber, 2011 (which is not included in the clade but is African), and *P. phalangioides* (which is included but is most probably not originally African). On the other hand, the inclusion of the Sri Lankan genus *Sihala* Huber, 2011 in this clade is plausible, even though weakly supported. Our data highly support the inclusion of *Sihala* in 'true' *Pholcus*, but neither morphology nor molecules seem to give an indication about its sister taxon.

Notes on genera not included in the present analyses

Aucana Huber, 2000. This Chilean genus (four species; formally including the mysterious New Caledonian *A. kaala* Huber, 2000) was previously thought to be a member of Ninetinae (Huber 2000, 2011b). However, the procursus (dorsal apophysis and corresponding ventral pocket) suggests a placement in Arteminae. Within Arteminae, it shares an exposed tarsal organ with *Chisosa* and *Nita* (Huber 2000, 2011b).

Blancoa Huber, 2000. A small Venezuelan genus (two species), probably member of Modisiminae (Huber 2000), but the sister group remains entirely obscure.

Canaima Huber, 2000. Also probably member of Modisiminae, with only two species restricted to Trinidad and Venezuela (Huber 2000). The shape of the ventral apophysis on the male palpal femur is reminiscent of the Venezuelan clade including *Mecolaesthus*, *Stenosfemuraia*, *Systenita*, and 'true' *Coryssocnemis*.

Cenemus Saaristo, 2001. A small Seychellois genus (three species), member of Smeringopinae; a morphological cladistic analysis (Huber 2012) suggested a placement in the 'northern clade' of Smeringopinae even though the Seychelles are geographically much closer to the 'southern clade'.

Enetea Huber, 2000. A monotypic Bolivian genus, member of Ninetinae (Huber 2000); the sister group remains entirely obscure.

Galapa Huber, 2000. A small genus (two species) restricted to the Galapagos Islands, member of Ninetinae (Huber 2000); the sister group remains entirely obscure.

Ossinissa Dimitrov & Ribera, 2005. A monotypic genus from the Canary Islands, member of the *Pholcus* group of genera (Huber 2011a); the sister group is dubious, but we suspect a close relationship with other Canary Island cavernicole species in 'true' *Pholcus* (*P. baldiosensis* Wunderlich, 1992; *P. corniger* Dimitrov & Ribera, 2006).

Pomboa Huber, 2000. Member of Modisiminae, with currently four species restricted to Colombia. The vertical hairs in high density on the leg tibiae suggest an affinity to *Pisaboa* and *Waunana* (Huber 2000).

Queliceria González-Sponga, 2003. A monotypic Venezuelan genus, probably member of Modisiminae; the sister group remains entirely obscure.

Tibetia Zhang, Zhu & Song, 2006. A monotypic Chinese (Tibetan) genus, probably member of Arteminae; the sister group remains entirely obscure.

Tolteca Huber, 2000. A small Mexican genus (two species), member of Ninetinae. We predict that *Tolteca* is member of the North and Central American & Caribbean clade (Figure 2), together with *Pholcophora* and *Papiamenta*. The frontal humps on the male sternum and the shape of the procursus are reminiscent of *Pholcophora* (Huber 2000).

Taxonomy

The present data suggest a large number of new undescribed genera. Twelve of them are composed entirely of undescribed new species; these will be described separately: three in Ninetinae (in our analyses: "Br15-159", "Om6", Ven01"); two in Arteminae ("Geneve59", "Ind82"–"Ind96"); five in Modisiminae ("Br16-44", MACN270", "Br16-178" + "Br16-50", "Br16-196", "Br15-45"); and two in Pholcinae ("CAS13", "Ind206").

Other new genera will result from splitting of known genera. Of these, several receive high support but taxonomic changes will not be implemented here for various reasons:

(1) taxonomic work on these taxa is currently in progress and the formal taxonomic changes will be published in that context ['*Holocneminus*' *huangdi*, South American '*Psilochorus*', *Holocnemus caudatus* (Dufour, 1820)].

(2) The included species need to be restudied in order to assess the scope of the new genera and to formulate diagnoses (Central American '*Coryssocnemis*').

Some potentially new genera are suggested by the present data but with low support values and/or without clear support from morphology. We suggest that these cases should be re-evaluated in detail in separate studies.

(1) For the southern clade of *Mesabolivar*, our analyses suggest two options: either to synonymize *Mesabolivar* and *Otavaloa* with *Litoporus* (resulting in a huge, very heterogeneous group), or to split *Mesabolivar*. The latter would preserve the names *Litoporus*, *Mesabolivar*, and *Otavaloa*, and possibly revalidate the name *Kaliana* Huber, 2000 (synonymized with *Mesabolivar* in Astrin et al. 2007), but possibly result in a morphologically non-diagnosable genus for the southern clade of *Mesabolivar*; *Teuia* would be an available name for this group.
(2) The *Smeringopus chogoria* and *rubrotinctus* groups together could either form a new genus, stay in *Smeringopus*, or be moved to *Smeringopina*.
(3) *Leptopholcus podophthalmus* (and its close relative *L. tanikawai*) may or may not represent a separate genus.

For *Spermophora*, our data strongly suggest the polyphyly of the genus and possibly five or more new genera: for four African taxa ('*S.*' *kyambura*, *tonkoui* group, *awalai* group, East African '*Spermophora*') and for East Asian '*Spermophora*'. However, several important species groups are missing in our analyses, such as South African, Madagascan, and Middle Eastern representatives. We strongly suggest including at least those groups before deciding on how to split *Spermophora*.

For *Calapnita* and *Panjange*, morphological cladistic analyses have weakly supported the monophyly of each genus, but also the existence of two distinctive subgroups in each (Huber and Nuñeza 2015, Huber 2017). The present analyses reject the monophyly of each of the two genera. Since the present analyses also strongly support the two subgroups in each genus, we feel that the pros of splitting (monophyletic genera in the most complete available analysis of Pholcidae relationships) outweighs the cons (weak morphological support of monophyly; the two subgroups of *Calapnita* are largely indistinguishable in the field).

Finally, our data strongly support the splitting of *Pholcus*, and this is largely in agreement with previous morphological cladistic analysis (Huber 2011a). The species groups that are here formally described as new genera have all been revised recently, and the diagnosis for *Pholcus* in Huber (2011a) that was explicitly valid for the 'core group' only, finally applies to the entire genus.

The present data also suggest a number of synonymies and new combinations, some of which are not formalized here.

(1) *Anopsicus* appears nested within *Modisimus*. However, neither the type species of *Anopsicus* is included in our analyses nor is a potential close relative; we conclude that the monophyly and position of *Anopsicus* both remain dubious.

(2) Our data suggest that *Coryssocnemis* and *Systenita* may both be synonyms of *Mecolaesthus*, but our taxon sampling is weak, the topology is unstable (see above), and several internal nodes in the clade have low support. The morphologically very diverse genus *Mecolaesthus* and its closest relatives clearly need more work.

(2) In most of our analyses, *Hantu* is nested within *Belisana*. For reasons detailed above we strongly doubt this result.

For other synonyms and transfers, we consider the available data strong enough to justify formal changes:

(1) The Cuban endemic genus *Platnicknia* Özdikmen & Demir, 2009 is newly synonymized with *Modisimus* Simon, 1893, syn. n. Our analyses do not include the type species *P. coxana* (Bryant, 1940) but two very similar undescribed species from near the type locality of *P. coxana* ("Cu12-99" and "Cu12-100"). Our analyses strongly support a sister group relationship of *Platnicknia* with a Hispaniolan group of leaf-dwelling *Modisimus*. Both together are deeply nested within other groups of *Modisimus* (Figure 3).

(2) The Moroccan *Pholcus agadir* is nested within *Micropholcus*. This placement receives high support in our analyses, while the previous assignment to *Pholcus* (Huber 2011a) was tentative; *Micropholcus agadir* (Huber, 2011), comb. n.

(3) The southern Indian/Sri Lankan genus *Sihala* Huber, 2011 is synonymized with *Pholcus* Walckenaer, 1805, syn. n. The position of *Pholcus ceylonicus* O. Pickard-Cambridge, 1869 (comb. re-established) in *Pholcus* had long been doubted (e.g., Brignoli 1972). The male genitalia of the two formally described species [*P. ceylonicus* and *P. alagarkoil* (Huber, 2011) comb. n.] are dramatically different from 'usual' *Pholcus* (shapes of trochanter apophysis and of femur; small and simple procursus without ventral 'knee'; bulb without uncus, with large massive appendix; Huber and Benjamin 2005, Huber 2011a). It was thus no surprise when a morphological cladistic analysis suggested a placement far away from the core group of *Pholcus* (Huber 2011a). However, our present analyses include three species of *Sihala*, two of them without missing genes, and *Sihala* was consistently placed in 'true' *Pholcus*.

Finally, the two changes at the level of subfamily suggested by all or some of our analyses are not implemented:

(1) All our analyses suggest that *Artema* is an isolated genus and single representative of Arteminae and that 'other Arteminae' should receive a new subfamily name. For reasons detailed above we consider the position of *Artema* in our analyses dubious and do not propose a new subfamily for 'other Arteminae'.

(2) Some of our analyses suggest an isolated position of the Andean genus *Priscula*: it may be either a 'basal' representative of Modisiminae or a separate subfamily. Since the relevant nodes in our analyses all receive low support values, we prefer to keep *Priscula* in Modisiminae until more convincing data become available.

Subfamily Pholcinae C.L. Koch, 1850

Nipisa Huber, gen. n.

http://zoobank.org/EB3A11CC-FE6C-4451-AA9A-8E582242C441

Calapnita phyllicola group: Deeleman-Reinhold 1986b: 212. Huber 2011a: 43. Huber 2017: 7.

Type species. *Calapnita phyllicola* Deeleman-Reinhold, 1986.

Etymology. The name is derived from the Malay word *nipis* (thin), and refers to the long and thin abdomen. Gender feminine.

Diagnosis (adapted from Huber 2017). Leaf-dwelling, pale whitish, long-legged pholcids with six eyes and long cylindrical abdomen (Huber 2017: figs 3-19). Distinguished from *Calapnita* by (1) tibia 2/ tibia 4 length >1.05 (*vs*. <0.95 in *Calapnita*); (2) ALS with eight spigots each (*vs.* two in *Calapnita*) (Huber 2017: figs 31, 41, 78); (3) proximal lateral processes on male chelicerae in 'usual' proximal position (*vs*. distal in *Calapnita*) (Huber 2017: figs 23, 35); (4) simple apophysis on male palpal trochanter (*vs*. hooked and sclerotized in *Calapnita*) (Huber 2017: figs 21, 34); (5) male palpal femur barely modified (*vs*. with series of three ventral sclerotized processes in *Calapnita*) (Huber 2017: figs 21, 34); (6) epigynum roughly rectangular or trapezoidal with folded cuticle and posterior 'knob' (*vs*. triangular with anterior 'knob' in *Calapnita*) (Huber 2017: figs 24, 32, 36, 43). For characters distinguishing *Nipisa* from similar species in other genera see Diagnosis of *Calapnita* in Huber (2017).

Distribution. Southeast Asia (Huber 2017: figs 281 and 282).

Composition. Ten species, all newly transferred from *Calapnita*: *N. anai* (Huber, 2017); *N. bankirai* (Huber, 2017); *N. bidayuh* (Huber, 2017); *N. deelemanae* (Huber, 2011); *N. kubah* (Huber, 2017); *N. lehi* (Huber, 2017); *N. phasmoides* (Deeleman-Reinhold, 1986); *N. phyllicola* (Deeleman-Reinhold, 1986); *N. semengoh* (Huber, 2017); *N. subphyllicola* (Deeleman-Reinhold, 1986).

Apokayana Huber, gen. n.

http://zoobank.org/3C3E969C-F000-4596-86B9-60F6C600C2FE

Panjange nigrifrons group: Deeleman-Reinhold and Platnick 1986: 561. Huber 2011a: 109. Huber and Leh Moi Ung 2016: 3.

Type species. *Panjange kapit* Huber, 2011.

Etymology. Named for the Apo Kayan people, one of the Dayak people groups that are spread throughout Sarawak, East Kalimantan, and North Kalimantan. Gender feminine.

Diagnosis (adapted from Huber and Leh Moi Ung 2016). Easily distinguished from *Panjange* by presence of distal male cheliceral apophyses (Huber and Leh Moi Ung 2016: fig. 18) and by ventral apophysis on male palpal femur (Huber and Leh Moi Ung 2016: fig. 30); also by absent or short epigynal scape. From representatives of *Pribumia* by ridges ventrally on procursus (Huber and Leh Moi Ung 2016: figs 17, 26, 34, 49; absent in *A. tahai*), by ventral apophysis on male palpal femur, and possibly by wide opening of palpal tarsal organ (Huber 2011a: figs 481, 686). From other similar genera on Borneo (*Calapnita*, *Leptopholcus*, *Kelabita*) by combination of: male colouration (Huber and Leh Moi Ung 2016: figs 8, 61; male ocular area and palps black; similar only in *Kelabita*), by bipartite distal apophyses on male chelicerae (Huber and Leh Moi Ung 2016: figs 35, 47; similar only in some *Calapnita*), by cylindrical rather than worm-shaped abdomen (Huber and Leh Moi Ung 2016: figs 8–15, 61–68; in contrast to *Calapnita* and *Leptopholcus*).

Distribution. Borneo (Huber and Leh Moi Ung 2016: fig. 1).

Composition. Ten species, all newly transferred from *Panjange*: *A. bako* (Huber, 2011); *A. iban* (Huber, 2011); *A. kapit* (Huber, 2016); *A. kubah* (Huber, 2016); *A. niah* (Huber, 2016); *A. nigrifrons* (Deeleman-Reinhold & Deeleman, 1983); *A. pueh* (Huber, 2016); *A. sedgwicki* (Deeleman-Reinhold & Platnick, 1986); *A. seowi* (Huber, 2016); *A. tahai* (Huber, 2011).

Pribumia Huber, gen. n.

http://zoobank.org/8BC96288-E983-4EAC-8015-7A6A26F5D729

Pholcus minang group: Huber 2011a: 144.

Type species. *Pholcus singalang* Huber, 2011.

Etymology. The name is derived from Pribumi, a name for native Indonesians. Gender feminine.

Diagnosis (adapted from Huber 2011a). Distinguished from other genera in Pholcinae by the combination of the following characters: elongate abdomen, six eyes, eye triads on stalks, male chelicerae with proximal and distal apophyses, distal apophyses 'divided' (consisting of two parts; Huber 2011a: figs. 640, 664), male palpal femur proximo-ventrally enlarged (Huber 2011a: figs. 628, 650), bulb with uncus, with complex sclerotized embolus, without appendix, epigynum weakly sclerotized, with small 'knob'.

Distribution. Malay Peninsula and Sumatra (Huber 2011a: fig. 626; note that *Pholcus tahai* in that figure is now in *Apokayana*).

Composition. The *Pholcus minang* group originally included seven species. Of these, *Pholcus tahai* is now in *Apokayana* (see above); the six others are newly transferred from *Pholcus*: *P. minang* (Huber, 2011); *P. singalang* (Huber, 2011); *P. hurau*

(Huber, 2011); *P. bohorok* (Huber, 2011); *P. atrigularis* (Simon, 1901); assigned tentatively: *P. diopsis* (Simon, 1901).

Tissahamia **Huber, gen. n.**

http://zoobank.org/14CB661D-B5F3-4DA8-B624-F02FF0AFC21E

Pholcus ethagala group: Huber 2011a: 171.

Type species. *Pholcus ethagala* Huber, 2011.

Etymology. Named for Wanniyalaeto chief Uru Warige Tissahami (1903–1996), who struggled (without success) against the government to keep the land of his ancestors. Gender feminine.

Diagnosis (adapted from Huber 2011a). Distinguished from other genera in Pholcinae by the combination of the following characters: elongate abdomen that is slightly pointed or elevated dorso-posteriorly, six eyes, eye triads on stalks, male chelicerae with proximal apophyses in frontal position, without distal apophyses (Huber 2011a: figs. 795, 811, 816), male palpal trochanter with short retrolateral and longer ventral apophyses, palpal tarsus with dorsal elongation (except *T. phui*), bulb with large and complex appendix and weakly sclerotized embolus, without uncus, procursus highly complex, epigynum weakly sclerotized, with 'knob'.

Distribution. Sri Lanka, Malay Peninsula, and Sumatra (Huber 2011a: fig. 718 – note that *Pholcus schwendingeri* in that figure is now in *Kintaqa*; Huber et al. 2016a: fig. 1).

Composition. The *Pholcus ethagala* group originally included seven species. Of these, *Pholcus schwendingeri* is now in *Kintaqa* (see below); five species have been added recently, resulting in eleven species, all newly transferred from *Pholcus*: *T. ethagala* (Huber, 2011); *T. kottawagamaensis* (Yao & Li, 2016); *T. maturata* (Huber, 2011). Assigned tentatively: *T. barisan* (Huber, 2016); *T. bukittimah* (Huber, 2016); *T. gombak* (Huber, 2011); *T. ledang* (Huber, 2011); *T. phui* (Huber, 2011); *T. tanahrata* (Huber, 2016); *T. uludong* (Huber, 2016); *T. vescula* (Simon, 1901).

Teranga **Huber, gen. n.**

http://zoobank.org/E67A0726-CF19-4CE3-ADFE-2D903D2778CB

Pholcus kerinci group: Huber 2011a: 166.
Pholcus domingo group: Huber et al. 2016b: 34.

Type species. *Pholcus kerinci* Huber, 2011.

Etymology. The name is derived from the Malay word *terang* (bright, light), and refers to the light colouration of the spiders. Gender feminine.

Diagnosis. Medium-sized, long-legged spiders (body length ~3.5–4.5, leg 1:~30–40) with slender elongate abdomen that is slightly elevated posteriorly (Huber 2011a: figs 606-609, Huber et al. 2016b: figs 131–139). Easily distinguished from similar relatives in other genera (*Panjange*, *Tissahamia*, *Apokayana*, *Paiwana*) by unmodified or barely modified male chelicerae Huber 2011a: fig. 722; Huber et al. 2016b: fig. 142); also by combination of: eight eyes, triads only slightly elevated; male palpal trochanter with long ventral apophysis (Huber 2011a: figs 720, 737; Huber et al. 2016b: figs 141, 158); male genital bulb without uncus but with massive appendix (Huber 2011a: figs 719, 736; Huber et al. 2016b: figs 140, 150, 157); epigynum weakly sclerotized, with numerous transversal folds, with 'knob' (Huber 2011a: figs 733, 739; Huber et al. 2016b: figs 143, 156, 159).

Distribution. Known from Indonesia (Sumatra, Java) and the Philippines (Mindanao) (Huber 2011a: fig. 718, Huber et al. 2016b: fig. 1).

Composition. The genus includes the four species originally described in the *Pholcus kerinci* and *domingo* groups. They are all newly transferred from *Pholcus*: *T. cibodas* (Huber, 2011); *T. domingo* (Huber, 2016), *T. kerinci* (Huber, 2011); *T. matutum* (Huber, 2016).

Paiwana Huber, gen. n.

http://zoobank.org/BAFDACD1-7142-4909-98E0-359BDC812698

Type species. *Pholcus pingtung* Huber & Dimitrov, 2014.

Etymology. Named for the Paiwan, an indigenous people of Taiwan. Gender feminine.

Diagnosis. Large, long-legged spiders with six eyes and cylindrical abdomen (Huber and Dimitrov 2014: figs 1–4). Easily distinguished from similar species in other genera (*Teranga*, *Pholcus*, *Muruta*) by unique modifications of male chelicerae (pair of weakly sclerotized lateral apophyses and two pairs of distinctive frontal apophyses: proximal pair flat and pointed, distal pair finger-shaped, both without modified hairs; Huber and Dimitrov 2014: fig. 19); from most genera (except *Muruta*, *Calapnita*) also by shape of epigynum (roughly triangular plate, 'knob' directed towards anterior) (Huber and Dimitrov 2014: fig. 20).

Distribution. Taiwan (Huber and Dimitrov 2014: fig. 34).

Composition. Only two species newly transferred from *Pholcus*: *P. chengpoi* (Huber & Dimitrov, 2014); *P. pingtung* (Huber & Dimitrov, 2014).

Muruta Huber, gen. n.

http://zoobank.org/E06DDC46-92E6-4740-BFCA-B2AD7807B9D5

Pholcus tambunan group: Huber et al. 2016b: 25.

Type species. *Pholcus tambunan* Huber, 2016.

Etymology. Named for the Murut, an indigenous ethnic group inhabiting northern inland regions of Borneo. Gender feminine.

Diagnosis (adapted from Huber et al. 2016b). The two species included in this genus are medium-sized, long-legged spiders (body length ~4, male leg 1 length: ~35–40), distinguished from other genera in Pholcinae by the combination of the following characters: elongate abdomen angular dorso-posteriorly (Huber et al. 2016b: figs 94, 98); six eyes; male chelicerae with distinctive distal apophyses (flat sclerites without modified hairs; Huber et al. 2016b: figs 103, 108, 120); most palpal structures unusually long (in particular genital bulb; Huber et al. 2016b: figs 101, 121); male bulb without uncus; epigynum weakly sclerotized, scape directed towards anterior with terminal 'knob' (Huber et al. 2016b: figs 104, 123); female internal genitalia with pair of highly distinctive three-layered telescopic tubes (Huber et al. 2016b: figs 105, 124).

Distribution. Northern Borneo (Huber et al. 2016b: fig. 1).

Composition. Only two species newly transferred from *Pholcus*: *M. tambunan* (Huber, 2016); *M. bario* (Huber, 2016).

***Meraha* Huber, gen. n.**

http://zoobank.org/14C88D64-C69D-4AB6-810B-45D93560B816

Pholcus krabi group: Huber et al. 2016a: 30.

Type species. *Pholcus krabi* Huber, 2016.

Etymology. The name is derived from the Malay word *merah* (red), and refers to the red or orange colour of the male pedipalps. Gender feminine.

Diagnosis. Medium size, light coloured pholcids with long legs and cylindrical abdomen (Huber et al. 2016a: figs 102-109); distinguished from similar species in other genera (*Kelabita*, *Apokayana*, *Teranga*, *Muruta*) by combination of: six eyes; absence of modified hairs on distal male cheliceral apophyses (Huber et al. 2016a: fig. 118); reduction of ALS spigots to two (Huber 2011a: fig. 566, Huber et al. 2016a: fig. 122); reddish to orange male palps (Huber et al. 2016a: figs 102, 106, 108). In the field they can be distinguished from most other genera (except *Kelabita*) by their domed webs relatively high among the vegetation (0.5–2 m above the ground), usually with the apex of the dome attached to the underside of a leaf.

Distribution. Mainland Southeast Asia and Borneo (Huber et al. 2016a: fig. 110).

Composition. Seven species newly transferred from *Pholcus*: *M. chiangdao* (Huber, 2011); *M. khene* (Huber, 2011); *M. kinabalu* (Huber, 2011); *M. kipungit* (Huber, 2016); *M. krabi* (Huber, 2016); *M. narathiwat* (Huber, 2016); *M. shuye* (Yao & Li, 2017).

Kelabita **Huber, gen. n.**

http://zoobank.org/D88513D8-B25E-4CE6-94D6-B7BF215B2AA7

Pholcus andulau group: Huber et al. 2016a: 47.

Type species. *Pholcus andulau* Huber, 2011.

Etymology. Named for the Kelabit, an indigenous Dayak people of the Sarawak/North Kalimantan highlands of Borneo with a minority in the neighboring state of Brunei. Gender feminine.

Diagnosis. Medium size, light coloured pholcids with long legs, six eyes, cylindrical abdomen (Huber et al. 2016a: figs 193–196). Distinguished from similar species in other genera (*Meraha*, *Apokayana*, *Teranga*, *Muruta*) by unique, partly sclerotized embolus with strong sclerotized pointed processes (Huber 2011a: fig. 570; Huber et al. 2016a: figs 200, 210); also by combination of: male chelicerae with pair of pointed apophyses close to median line and directed toward each other (Huber 2011a: fig. 572; Huber et al. 2016a: fig. 202); ALS with eight spigots each (Huber 2016a: figs 217, 218); male palps not reddish or orange; large unsclerotized 'knob' on posterior edge of female external genitalia, directed toward anterior (Huber 2011a: fig. 573; Huber et al. 2016a: figs 203, 213). In the field they can be distinguished from most other genera (except *Meraha*) by their domed webs among the vegetation (up to 2 m above the ground), usually with the apex of the dome attached to the underside of a leaf.

Distribution. Northern Borneo (Huber et al. 2016a: fig. 153).

Composition. Only two species newly transferred from *Pholcus*: *K. andulau* (Huber, 2011); *K. lambir* (Huber, 2016).

Kintaqa **Huber, gen. n.**

http://zoobank.org/F4C48066-1FEC-4E3B-958F-359242174F1B

Pholcus buatong group: Huber et al. 2016a: 38.

Type species. *Pholcus buatong* Huber, 2011.

Etymology. The name honours the Kintaq, a Mon-Khmer ethnic group in Thailand. Gender feminine.

Diagnosis. Medium size, light coloured pholcids with long legs, six or eight eyes, and cylindrical abdomen (Huber et al. 2016a: figs 143–152). Distinguished from similar species in other genera (*Tissahamia*, *Cantikus*, *Pribumia*) by distinctive dorsal bulging of male palpal patella (Huber 2011a: figs 581, 823; Huber et al. 2016a: fig. 155) and by epigynum with large, heavily sclerotized 'knob' (Huber et al. 2016a: figs 184, 187, 190); also by combination of: complete reduction of distal anterior apophyses on male chelicerae (Huber 2011a: figs 582, 825; Huber et al. 2016a: fig. 156); ALS with eight spigots each (Huber et al. 2016a: figs 166, 183); male palps not reddish or orange.

Distribution. Southern Thailand and northern mainland Malaysia (Huber et al. 2016a: fig. 153).

Composition. Five species, all newly transferred from *Pholcus*: *K. buatong* (Huber, 2016); *K. fuza* (Yao & Li, 2017); *K. mueangensis* (Yao & Li, 2017); *K. satun* (Huber, 2011); *K. schwendingeri* (Huber, 2011).

Cantikus Huber, gen. n.

http://zoobank.org/A71947B6-1279-4F84-8DB7-9B037D1BC70B

Pholcus halabala group: Huber 2011a: 126. Huber et al. 2016a: 3.
Pholcus quinquenotatus group: Huber 2011a: 290.

Type species. *Pholcus halabala* Huber, 2016.

Etymology. The name is derived from the Malay word *cantik* (beautiful), and refers to the colour patterns on the abdomen of several species. Gender masculine.

Diagnosis (adapted from Huber et al. 2016a): The core group of eight species (see below) includes medium-sized, long-legged spiders (body length ~3–4, male leg 1 length ~30–40); distinguished from other genera in Pholcinae by the combination of the following characters: elongate abdomen pointed dorso-posteriorly, with distinctive dorsal pattern of black and whitish or yellowish marks in life specimens (Huber et al. 2016a: figs 1–16); eight eyes; male ocular area with conspicuous modified hairs (setae), which may appear as stiff bristles or stout curved spines, or both (Huber et al. 2016a: figs 19, 23, 43); male chelicerae with proximal and distal apophyses, distal apophyses with two cone-shaped teeth (modified hairs) each (Huber et al. 2016a: fig. 28); male bulb with uncus and appendix; procursus with distinctive dorsal flap (Huber et al. 2016a: fig. 35; absent in *C. erawan*); epigynum weakly sclerotized, with 'knob'.

Distribution. Widely distributed in Southeast Asia, from Myanmar and southern China to Sumatra, Borneo, and Bali.

Composition. 27 species, all newly transferred from *Pholcus*: *C. anaiensis* (Yao & Li, 2016); *C. erawan* (Huber, 2011); *C. halabala* (Huber, 2011); *C. lintang* (Huber, 2016); *C. sabah* (Huber, 2011); *C. sepaku* (Huber, 2011); *C. ubin* (Huber, 2016); *C. zhuchuandiani* (Yao & Li, 2016).

Assigned tentatively. *C. ballarini* (Yao & Li, 2016); *C. cheni* (Yao & Li, 2017); *C. chiangmaiensis* (Yao & Li, 2016); *C. elongatus* (Yin & Wang, 1981); *C. exceptus* (Tong & Li, 2009); *C. gou* (Yao & Li, 2016); *C. khaolek* (Huber, 2016); *C. kuhapimuk* (Huber, 2016); *C. namou* (Huber, 2011); *C. pakse* (Huber, 2011); *C. phami* (Yao, Pham & Li, 2015); *C. pyu* (Huber, 2011); *C. quinquenotatus* (Thorell, 1878); *C. subwan* (Yao & Li, 2017); *C. sudhami* (Huber, 2011); *C. taptaoensis* (Yao & Li, 2016); *C. tharnlodensis* (Yao & Li, 2016); *C. wan* (Yao & Li, 2016); *C. youngae* (Huber, 2011).

Outlook

Even though the present tree of Pholcidae is a significant step forward in terms of comprehensiveness and resolution, we have identified above many weak points and aspects that need further study. Here we list a subjective 'top-ten' selection of projects that in our view might fill the most obvious gaps and provide the most valuable next steps.

1. Ninetinae external and internal relationships. The poorly known Ninetinae seem to differ from 'typical' pholcids in many respects, including body size and proportions, diversity, ecological requirements, and probably also biology. Ninetinae might be sister to all other pholcids and might have retained ancestral character states. Resolving external and internal relationships of Ninetinae is thus of particular interest but will probably require a genome-scale phylogenetic approach.
2. Position of *Artema*. Our analyses suggest an isolated position of *Artema*, not within or as sister to other Arteminae. We question this result but cannot explain it. Resolving the position of *Artema* will probably need a genome-scale phylogenetic approach.
3. Position of *Priscula*. The mysterious Andean genus *Priscula* is similar to *Artema* in including some of the largest pholcids and in defying placement in the phylogeny. As for *Artema*, a genome-scale phylogenetic approach will probably be necessary to resolve its position.
4. Andean Modisiminae. Most Pholcidae from anywhere in the world can now be quickly and reliably assigned to an existing genus. The only major exception is Modisiminae from northwestern South America, in particular Peru, Ecuador, Colombia, and Venezuela. Our analyses include a minimal sample of species from this megadiverse region that is still relatively poorly explored even at generic level.
5. Monophyly and position of *Anopsicus*. Our analyses suggest that *Anopsicus* might just be a group of dwarfed ground-dwelling *Modisimus*. However, our sample includes only three species of *Anopsicus* and none of them appears close to the type species. A much larger sample of this species-rich genus will thus be necessary to evaluate its monophyly and phylogenetic position.
6. *Holocnemus*. The type species of *Holocnemus*, *H. pluchei*, was excluded from our dataset because its position was drastically unstable in preliminary analyses. The two other species of *Holocnemus* are both included but do not group together. We suggest a genome-scale phylogenetic approach, including the three species of *Holocnemus* together with representatives of *Hoplopholcus*, *Stygopholcus*, and *Crossopriza* to solve this problem.
7. *Spermophora*. Even though many species originally described as *Spermophora* have been transferred to other or new genera, the genus continues to be polyphyletic. Our analyses suggest that five or more genera may need to be created to account for the relationships among the included species. A reanalysis of *Spermophora* should

focus on including South African and Madagascan taxa as well as Middle Eastern taxa that we predict are the closest relatives of the type species *S. senoculata*.

8. *Belisana*. *Belisana* is particularly interesting for including representatives in different microhabitats and with different types of webs. However, our sample of species is limited, web data are available for relatively few species, and several nodes in our tree have low support. Thus, a much denser sampling combined with field observations will be necessary to reconstruct microhabitat shifts and the evolution of web designs within *Belisana*.
9. *Pholcus*. Our sample includes only 18% of the described species of *Pholcus* and several species groups are entirely missing. As a result, internal relationships of this largest genus in the family remain highly uncertain and need considerably more study.
10. Missing genera. The eleven described genera that are missing from our analyses contain a total of only 24 known species, but some of them are of particular interest and should be added in future analyses. (1) *Aucana*, originally described as a Ninetinae genus, is predicted to be a member of Arteminae. (2) *Cenemus* is geographically closer to the 'southern clade' of Smeringopinae, but predicted to be a member of the 'northern clade'. (3) *Ossinissa*, possibly a close relative of cavernicole 'true' Macaronesian *Pholcus*, and thus a generic synonym. (4) *Tibetia*, probably member of Arteminae, possibly a dwarfed *Artema*. (5) *Tolteca*, predicted to be a member of the North and Central American and Caribbean clade of Ninetinae.

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Appendix 1. Summary of formal taxonomic acts, in alphabetical order.

Apokayana Huber, gen. n.; all species newly transferred from *Panjange*
Apokayana bako (Huber, 2011), comb. n.
Apokayana iban (Huber, 2011), comb. n.
Apokayana kapit (Huber, 2016), comb. n.
Apokayana kubah (Huber, 2016), comb. n.
Apokayana niah (Huber, 2016), comb. n.
Apokayana nigrifrons (Deeleman-Reinhold & Deeleman, 1983), comb. n.
Apokayana pueh (Huber, 2016), comb. n.
Apokayana sedgwicki (Deeleman-Reinhold & Platnick, 1986), comb. n.
Apokayana seowi (Huber, 2016), comb. n.
Apokayana tahai (Huber, 2011), comb. n.

Cantikus Huber, gen. n.; all species newly transferred from *Pholcus*

Cantikus anaiensis (Yao & Li, 2016), comb. n.
Cantikus ballarini (Yao & Li, 2016), comb. n.
Cantikus cheni (Yao & Li, 2017), comb. n.
Cantikus chiangmaiensis (Yao & Li, 2016), comb. n.
Cantikus elongatus (Yin & Wang, 1981), comb. n.
Cantikus erawan (Huber, 2011), comb. n.
Cantikus exceptus (Tong & Li, 2009), comb. n.
Cantikus gou (Yao & Li, 2016), comb. n.
Cantikus halabala (Huber, 2011), comb. n.
Cantikus khaolek (Huber, 2016), comb. n.
Cantikus kuhapimuk (Huber, 2016), comb. n.
Cantikus lintang (Huber, 2016), comb. n.
Cantikus namou (Huber, 2011), comb. n.
Cantikus pakse (Huber, 2011), comb. n.
Cantikus phami (Yao, Pham & Li, 2015), comb. n.
Cantikus pyu (Huber, 2011), comb. n.
Cantikus quinquenotatus (Thorell, 1878), comb. n.
Cantikus sabah (Huber, 2011), comb. n.
Cantikus sepaku (Huber, 2011), comb. n.
Cantikus subwan (Yao & Li, 2017), comb. n.
Cantikus sudhami (Huber, 2011), comb. n.
Cantikus taptaoensis (Yao & Li, 2016), comb. n.
Cantikus tharnlodensis (Yao & Li, 2016), comb. n.
Cantikus ubin (Huber, 2016), comb. n.
Cantikus wan (Yao & Li, 2016), comb. n.
Cantikus youngae (Huber, 2011), comb. n.
Cantikus zhuchuandiani (Yao & Li, 2016), comb. n.

Kelabita Huber, gen. n.; all species newly transferred from *Pholcus*
Kelabita andulau (Huber, 2011), comb. n.
Kelabita lambir (Huber, 2016), comb. n.

Kintaqa Huber, gen. n.; all species newly transferred from *Pholcus*
Kintaqa buatong (Huber, 2016), comb. n.
Kintaqa fuza (Yao & Li, 2017), comb. n.
Kintaqa mueangensis (Yao & Li, 2017), comb. n.
Kintaqa satun (Huber, 2011), comb. n.
Kintaqa schwendingeri (Huber, 2011), comb. n.

Meraha Huber, gen. n.; all species newly transferred from *Pholcus*
Meraha chiangdao (Huber, 2011), comb. n.
Meraha khene (Huber, 2011), comb. n.
Meraha kinabalu (Huber, 2011), comb. n.

Meraha kipungit (Huber, 2016), comb. n.
Meraha krabi (Huber, 2016), comb. n.
Meraha narathiwat (Huber, 2016), comb. n.
Meraha shuye (Yao & Li, 2017), comb. n.

Micropholcus agadir (Huber, 2011), comb. n., transferred from *Pholcus*

Modisimus coxanus (Bryant, 1940), comb. n., newly transferred from *Platnicknia*
Modisimus incertus (Bryant, 1940), comb. n., newly transferred from *Platnicknia*

Muruta Huber, gen. n.; all species newly transferred from *Pholcus*
Muruta bario (Huber, 2016), comb. n.
Muruta tambunan (Huber, 2016), comb. n.

Nipisa Huber, gen. n.; all species newly transferred from *Calapnita*
Nipisa anai (Huber, 2017), comb. n.
Nipisa bankirai (Huber, 2017), comb. n.
Nipisa bidayuh (Huber, 2017), comb. n.
Nipisa deelemanae (Huber, 2011), comb. n.
Nipisa kubah (Huber, 2017), comb. n.
Nipisa lehi (Huber, 2017), comb. n.
Nipisa phasmoides (Deeleman-Reinhold, 1986), comb. n.
Nipisa phyllicola (Deeleman-Reinhold, 1986), comb. n.
Nipisa semengoh (Huber, 2017), comb. n.
Nipisa subphyllicola (Deeleman-Reinhold, 1986), comb. n.

Paiwana Huber gen. n.; all species newly transferred from *Pholcus*
Paiwana chengpoi (Huber & Dimitrov, 2014), comb. n.
Paiwana pingtung (Huber & Dimitrov, 2014), comb. n.

Pholcus alagarkoil (Huber, 2011), comb. n., newly transferred from *Sihala*
Pholcus ceylonicus O. Pickard-Cambridge, 1869, comb. re-established, transferred from *Sihala*

Platnicknia Özdikmen & Demir, 2009 = *Modisimus* Simon, 1893, syn. n.

Pribumia Huber, gen. n.; all species newly transferred from *Pholcus*
Pribumia atrigularis (Simon, 1901), comb. n.
Pribumia bohorok (Huber, 2011), comb. n.
Pribumia diopsis (Simon, 1901), comb. n.
Pribumia hurau (Huber, 2011), comb. n.
Pribumia minang (Huber, 2011), comb. n.
Pribumia singalang (Huber, 2011), comb. n.

Sihala Huber, 2011 = *Pholcus* Walckenaer, 1805, syn. n.

Teranga Huber gen. n.; all species newly transferred from *Pholcus*
Teranga cibodas (Huber, 2011), comb. n.
Teranga domingo (Huber, 2016), comb. n.
Teranga kerinci (Huber, 2011), comb. n.
Teranga matutum (Huber, 2016), comb. n.

Tissahamia Huber gen. n.; all species newly transferred from *Pholcus*
Tissahamia barisan (Huber, 2016), comb. n.
Tissahamia bukittimah (Huber, 2016), comb. n.
Tissahamia ethagala (Huber, 2011), comb. n.
Tissahamia gombak (Huber, 2011), comb. n.
Tissahamia kottawagamaensis (Yao & Li, 2016), comb. n.
Tissahamia ledang (Huber, 2011), comb. n.
Tissahamia maturata (Huber, 2011), comb. n.
Tissahamia phui (Huber, 2011), comb. n.
Tissahamia tanahrata (Huber, 2016), comb. n.
Tissahamia uludong (Huber, 2016), comb. n.
Tissahamia vescula (Simon, 1901), comb. n.

Supplementary material 1

Figure S1. Maximum-likelihood tree of the complete set of taxa inferred with IQ-TREE

Authors: Bernhard A. Huber, Jonas Eberle, Dimitar Dimitrov
Data type: molecular data
Explanation note: This tree is identical to the one shown in Figs 2–12 except that it includes all outgroups and all support values are shown (in the sequence SBS / RBS / SH-like aLRT).

Link: https://doi.org/10.3897/zookeys.788.22781.suppl1

Supplementary material 2

Figure S2. Maximum-likelihood tree of the complete set of taxa inferred with RAxML

Authors: Bernhard A. Huber, Jonas Eberle, Dimitar Dimitrov

Data type: molecular data

Explanation note: Support values as in Figure S1.

Link: https://doi.org/10.3897/zookeys.788.22781.suppl2

Supplementary material 3

Figure S3. Maximum-likelihood tree (RAxML) of a reduced set of taxa (excluding rogue taxa with RogueNaRok)

Authors: Bernhard A. Huber, Jonas Eberle, Dimitar Dimitrov

Data type: molecular data

Explanation note: In the text we refer to this tree as 'RogueNaRok tree'. Support values: RBS.

Link: https://doi.org/10.3897/zookeys.788.22781.suppl3

Supplementary material 4

Figure S4. Maximum-likelihood tree (RAxML) of a reduced set of taxa (excluding taxa for which less than four genes were available)

Authors: Bernhard A. Huber, Jonas Eberle, Dimitar Dimitrov

Data type: molecular data

Explanation note: In the text we refer to this tree as '4+ genes tree'. Support values as in Figure S1.

Link: https://doi.org/10.3897/zookeys.788.22781.suppl4

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RESEARCH ARTICLE

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First record of *Scolopendrellopsis* from China with the description of a new species (Myriapoda, Symphyla)

Ya-Li Jin[1], Yun Bu[1]

1 *Natural History Research Center, Shanghai Natural History Museum, Shanghai Science & Technology Museum, Shanghai, 200041, China*

Corresponding author: *Yun Bu* (buy@sstm.org.cn)

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Abstract

The genus *Scolopendrellopsis* Bagnall, 1913 is recorded from China for the first time and *Scolopendrellopsis glabrus* **sp. n.** is described and illustrated. The new species is characterized by the short central rod on head, third tergite complete, four kinds of sensory organs present on antenna, and the cerci rather short and covered with a low number of straight setae.

Keywords

antennal sensory organ, chaetotaxy, taxonomy, tergal process, Tömösváry organ

Introduction

There are 204 symphylan species known in the world to date (Szucsich and Scheller 2011; Domínguez Camacho and Vandenspiegel 2012; Bu and Jin 2018); however, only few publications deal with those from Asia. Hansen firstly described five species of Symphyla from Southeast Asia (Hansen 1903). After that several species were described from India (Scheller 1971), Indonesia (Scheller 1988), USSR (Scheller and Golovatch 1982), Russian Far East (Scheller and Mikhaljova 2000) and Iran (Scheller et al. 2011). Symphyla is poorly studied in China with only *Hanseniella caldaria* from Zhejiang province and *Geophilella orientalis* from Hebei province recorded (Zhang and Wang 1992; Bu and Jin 2018). Three genera, *Scutigerella*, *Scolopendrelloides*, and *Symphylella*, were also mentioned for China, but without determined species recorded (Zhang and Wang 1992). During our ecological survey of soil animals of Zhejiang, Jiangsu, and Hainan provinces in recent years, many symphylans were obtained. Among them, one new species of *Scolopendrellopsis* was identified and is described in the present paper.

Materials and methods

Most specimens were collected during a project for soil animal survey of Gutian Mountain of Zhejiang Province during the years 2012 to 2013; others were collected in Jiangsu province and Hainan province recently. All were extracted by means of the Tullgren funnels from soil and humus samples and preserved in 75% ethanol. They were mounted under slides using Hoyer's solution and dried in an oven at 60 °C. Observations were made with a phase contrast microscope (Leica DM 2500). Photographs were taken by a digital camera installed on the microscope (Leica DMC 4500). Line drawings were drawn using a drawing tube. All specimens are deposited in the collections of Shanghai Natural History Museum (**SNHM**) and Shanghai Entomological Museum (**SEM**), Shanghai, China.

Taxonomy

Family Scolopendrellidae Bagnall, 1913

Genus *Scolopendrellopsis* Bagnall, 1913, new record

Diagnosis. Habitus slender. First pair of legs present, 3-segmented and with claws, not more than one-half length of the following pairs. Trunk with 16 or 17 tergites and most of tergites with a pair of posterior processes, without any striped band between each pair of processes on tergites, some tergites transversely divided.

Distribution. The genus *Scolopendrellopsis* includes fifteen species and is subcosmopolitan, widely distributed in Palaearctic, Nearctic, Neotropical, Ethiopian, Oriental, and Australian regions (Szucsich and Scheller 2011). It is newly recorded from China in this paper.

Scolopendrellopsis glabrus sp. n.

http://zoobank.org/95E5B444-5DEF-49CB-A699-E9730BD69528
Figs 1–3. Tables 1–3

Diagnosis. *Scolopendrellopsis glabrus* sp. n. is characterized by the short central rod on head, 3rd tergite not divided and with only weak middle indentation, rod-like sensory organs with setae surrounded on dorsal side of 3rd–17th antennal segments, cavity-shaped organs on dorsal side of subapical 5–6 antennal segments, mushroom-shaped organs at lateral side of subapical 4–7 segments and bladder-shaped organs on subapical 3–6 antennal segments, first pair of legs longer than the tarsus of the last pair of legs, cerci short and covered with a low number of straight setae.

Material examined. ***Holotype***, female (slide no. ZJ-GTS-SY2012017) (SNHM), China, Zhejiang Province, Gutian Mountain, extracted from soil samples in broad-leaved forest, Alt. 1000 m, 29°15'N, 118°06'E, 11-IV-2012, coll. Y. Bu et al. ***Paratypes***, 2 female (slides nos. ZJ-GTS-SY2012010, ZJ-GTS-SY2012016) (SNHM), same date as holotype; 1 female (slide no. ZJ-GTS-SY2012051) (SEM), ibidem, 14-X-2012; 2 females (slides nos. ZJ-GTS-SY2012055, ZJ-GTS-2012060) (SNHM), ibidem, 17-XI-2012; 1 female (slide no. ZJ-GTS-SY2013015) (SNHM), ibidem, 24-IV-2013; 1 male (slide no. JS-WX-SY2017001) (SNHM), China, Jiangsu Province, Wuxi, Daji Mountain, extracted from soil samples in bamboo forest, Alt. 5 m, 31°32'N, 120°12'E, 9-X-2017, coll. Y. Bu. ***Other material*** (SNHM): 8 juveniles with 8–10 pairs of legs (slides nos. ZJ-GTS-SY2012002, ZJ-GTS-SY2012004, ZJ-GTS-SY2012006, ZJ-GTS-SY2012012–ZJ-GTS-SY2012015, ZJ-GTS-SY2012019), same data as holotype; 1 juvenile with 10 pairs of legs (slide no. ZJ-GTS-SY2012023), ibidem, 19-VI-2012, coll. Y. Bu et al; 6 juveniles with 8–11 pairs of legs (slides nos. ZJ-GTS-SY2012028–ZJ-GTS-SY2012032, ZJ-GTS-SY2012039), ibidem, 15-VII-2012, coll. Y. Bu et al; 2 juveniles with 9 and 10 pairs of legs (slides nos. ZJ-GTS-SY2012046, ZJ-GTS-SY2012051), ibidem, 14-X-2012, coll. Y. Bu et al; 2 juveniles with 10 and 9 pairs of legs respectively (slides nos. ZJ-GTS-SY2012052, ZJ-GTS-SY2012055), ibidem, 17-XI-2012, coll. Y. Bu et al; 3 juveniles with 8–10 pairs of legs (slides nos. ZJ-GTS-SY2012064–ZJ-GTS-SY2012066), ibidem, 12-XII-2012, coll. Y. Bu et al; 1 juvenile with 8 pairs of legs (slide no. ZJ-GTS-SY2013004), ibidem, 23-II-2013, coll. Y. Bu et al; 6 juveniles with 8–10 pairs of legs (slides nos. ZJ-GTS-SY2013005, ZJ-GTS-SY2013009, ZJ-GTS-SY2013011, ZJ-GTS-SY2013013–ZJ-GTS-SY2013015), ibidem, 27-III-2013, coll. Y. Bu et al; 1 juvenile with 9 pairs of legs (slide no. HN-SY-SY2017001), China, Hainan Province, Sanya, Yalong bay tropical paradise forest park, extracted from soil samples in bamboo forest, Alt. 67 m, 18°15' N, 109°37'E, 22-III-2017, coll. Y. Bu.

Description. Adult body 1.57 mm long in average (1.45–1.65 mm, n = 8), holotype 1.65 mm (Figure 1A). *Head* longer than wide, length 145–175 µm, width 133–170 µm, with widest part a little behind the middle on a level with the points of articulation of mandibles. Central rod distinct and with anterior part absent, length 45–49 µm, approximately one-third of head. Dorsal side of head covered with sparse setae of different length, longest setae (12–17 µm) located at the anterior part of head, approx. 3.0 times as long as central ones (4–5 µm). Cuticle around Tömösváry organ and anterolateral part of head with rather coarse granulation. Central and posterior part of head with dense pubescence (Figs 1B, 3A).

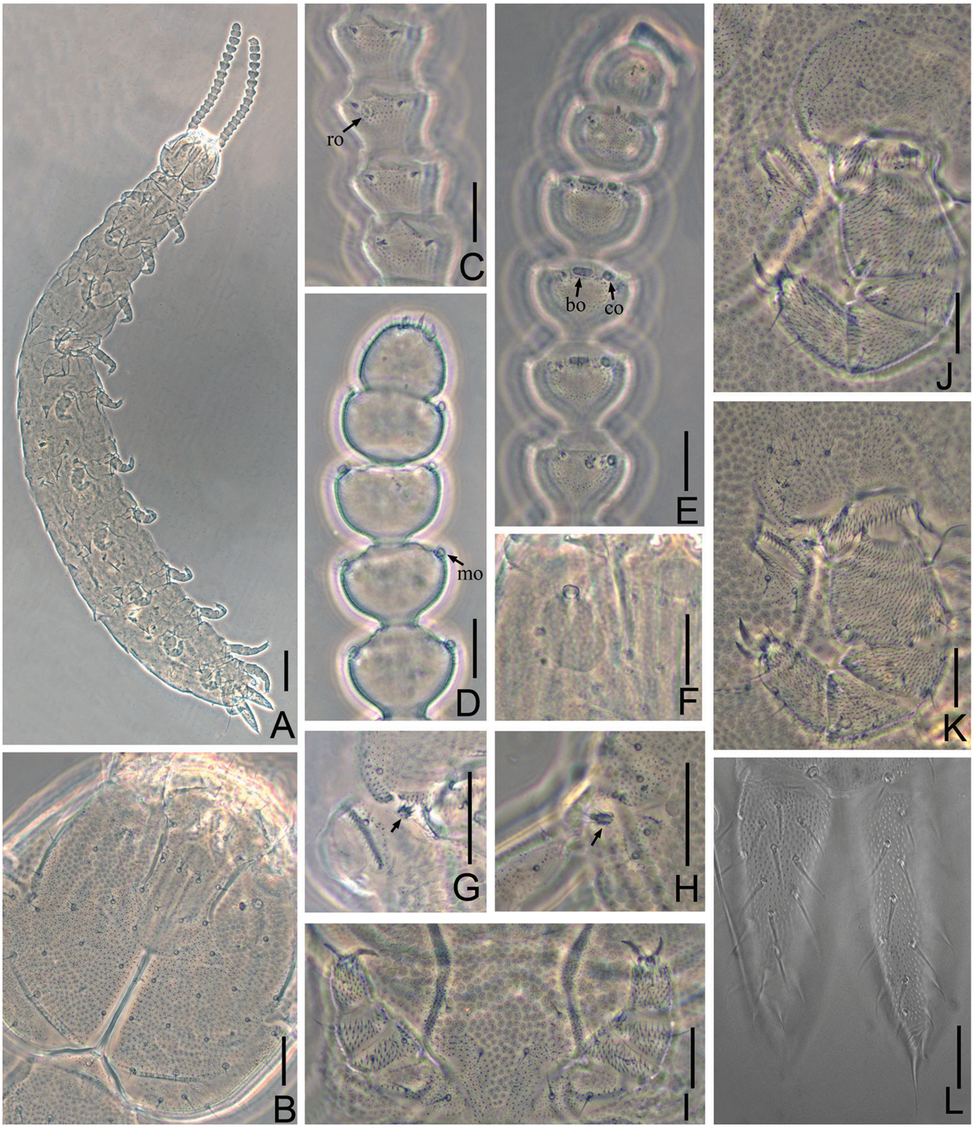

Figure 1. *Scolopendrellopsis glabrus* sp. n. (Holotype) **A** habitus **B** head, dorsal view **C** right antenna, 3th–6th segments, dorsal view **D** right antenna, 12th–16th segments, ventral view **E** right antenna, 11th–16th segments, dosal view **F** left Tömösváry organ **G** stylus on base of 6th leg (arrow indicated) **H** stylus on base of 11th leg (arrow indicated) **I** first pair of legs **J** 3rd leg and coxal sac **K** 9th leg and coxal sacs **L** cerci, dorsal view. ro-rod-like sensory organs with surrounded setae, co-cavity-shaped organ, mo-mushroom-shaped organ, bo-bladder-shaped organ. Scale bars: 100 µm (**A**), 20 µm (**B–L**).

Tömösváry organ oval, maximum diameter 17.0–22.5 µm, somewhat shorter than the greatest diameter of 3rd antennal segment (20–23 µm), opening at front position, with diameter (4–5 µm) approx. one-fourth of 3rd segment of antennae (Figs 1F, 3A).

Mandible with eleven teeth and divided into two parts by a gap, with five anterior and six posterior teeth respectively. First maxilla has two lobes, inner lobe with four

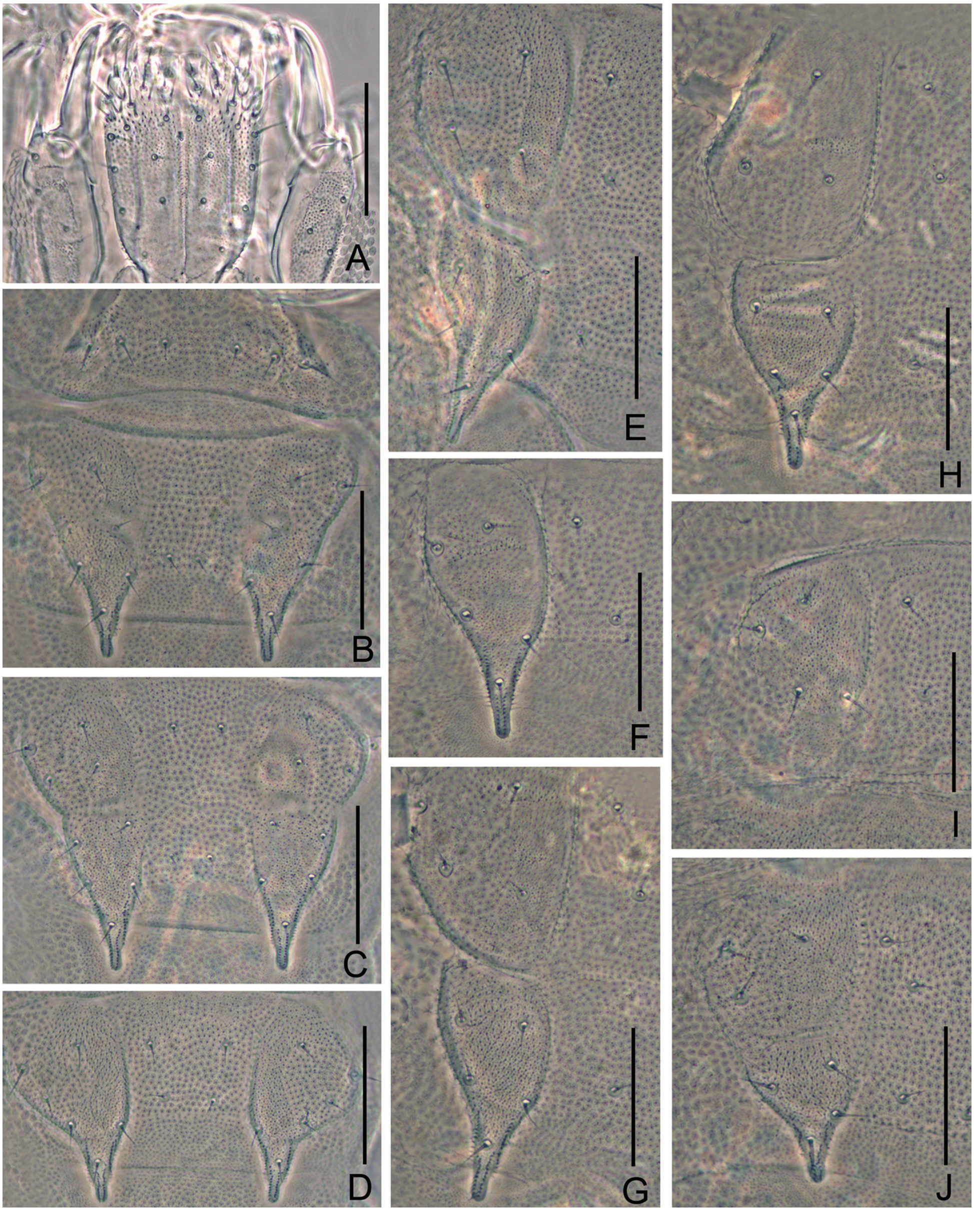

Figure 2. *Scolopendrellopsis glabrus* sp. n. (Holotype) **A** first and second maxilla **B** 1st and 2nd tergite **C** 3rd tergite **D** 4th tergite **E** 6th tergite, left side **F** 8th tergite, left side **G** 9th tergite, left side **H** 12th tergite, left side **I** 14th tergite, left side **J** 15th tergite, left side. Scale bars: 20 µm.

hook-shaped teeth, palp bud-like with two distal points close to outer lobe (Figure 3B). Anterior part of second maxilla with many small protuberances and posterior part with sparse setae. Cuticle of second maxilla covered with pubescence (Figure 2A).

Antennae 15–19 segments (16 in holotype), length 250–350 µm (320 µm in holotype), approx. 0.2 of the length of the body. First segment cylindrical, greatest diameter

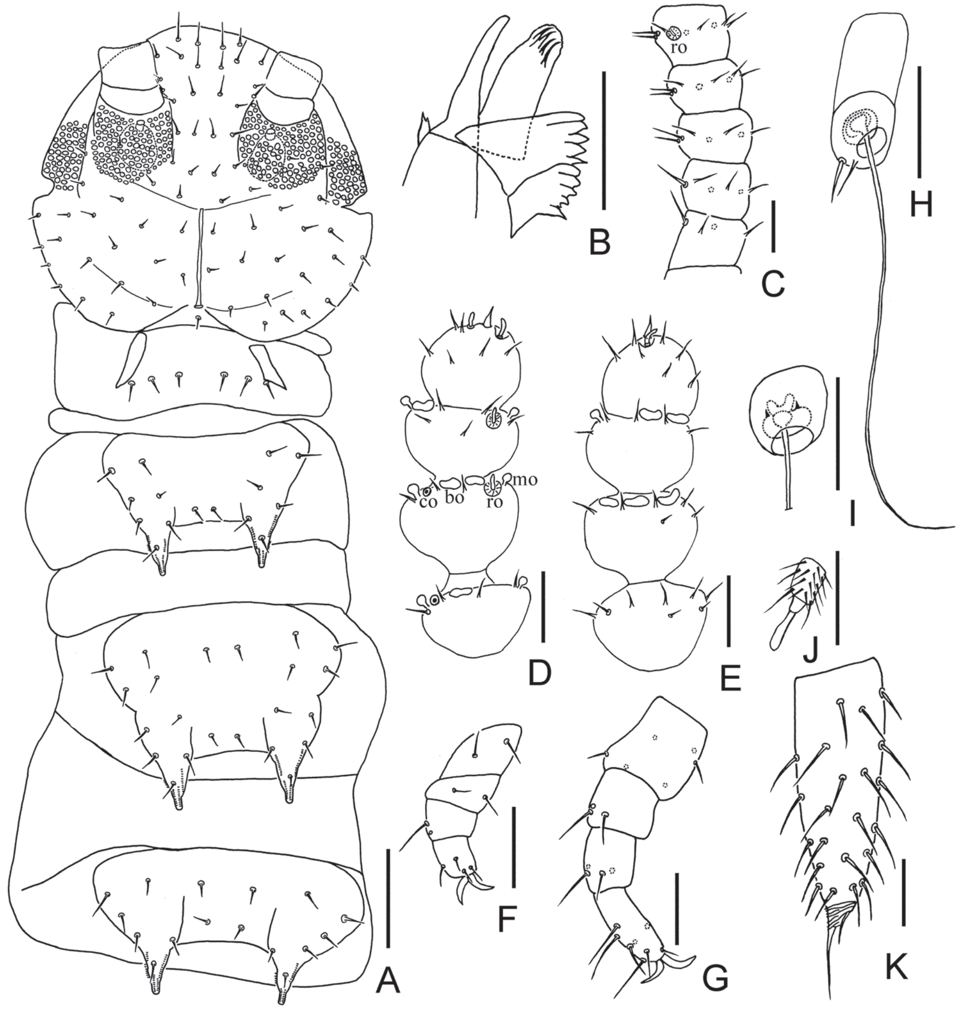

Figure 3. *Scolopendrellopsis glabrus* sp. n. (Holotype) **A** head and 1st–4th tergites **B** mandible and first maxilla **C** 1st–5th segments of right antenna **D–E** 13th–16th of right antenna **D** dorsal view **E** ventral view **F** first leg **G** 12th leg **H** left sense calicles, dorsal view **I** right sense calicles, dorsal view **J** stylus on base of 11th leg **K** right cercus, dorsal view. Scale bars: 50 μm (**A**), 20 μm (**B–I, K**), 5 μm (**J**).

a little wider than long (20–26 μm: 16–25 μm), with four setae in one whorl, the longest seta (6–11 μm) inserted at the inner side and distinctly longer than outer ones (5–8 μm). Second segment wider (20–30μm) than long (18–22 μm), with six or seven setae evenly inserted around the segment and inner setae (6–10 μm) a little longer than outer ones (5–7 μm). Chaetotaxy of 3rd segment similar to preceding ones (Figure 3C). Setae on the basal segments 1–3 are slender and on proximal and distal segments rather short. Basal and median parts of the antennae with only primary whorl of setae, in subapical

Table 1. Numbers of setae and sensory organs of antennae (holotype).

Segments	Nos. of primary whorl setae	Nos. of secondary whorl setae	Rod-like organ with setae surrounded	Cavity-shaped organs	Mushroom-shaped organs	Bladder-shaped organs	
						Dorsal	Ventral
1st	4						
2nd	6						
3rd	7						
4th	8						
5th	8		1				
6th	8						
7th	8						
8th	8						
9th	9						
10th	9	1	1	1	1		
11th	9	1	1	1	1		
12th	9	2		1	2	1	
13th	9	2		1	2	1	
14th	7	2	1	1	2	2	4
15th	8	2	1	1	2	1	3
16th	7	2					

segments one or two minute setae present in secondary whorl (Figure 3E). Four kinds of sensory organs present on antenna: rod-like sensory organs with setae surrounded present on dorsal side of 3rd–17th segments (Figs 1C, 3C, 3D); cavity-shaped organs present on dorsal side of subapical 5–6 segments (Figs 1E, 3D); mushroom-shaped organs present on lateral side of subapical 4–7 segments and bladder-shaped organs on subapical 3–6 segments (Figs 1D, 1E, 3D, 3E). Apical segment subspherical, width 21–22 μm, length 19–20 μm, with 10–12 short setae and wide connection to preceding segment and with two fire-shaped and three baculiform organs present on apex (Figs 1D, 3D, E). All segments covered with short pubescence. Chaetotaxy and sensory organs of antennae are given in Table 1.

Trunk: seventeen dorsal tergites present, with 6th, 9th, 12th, and 15th tergites transversely divided, longer than preceding ones (Figs 2E, 2G, 2H, 2J). Intertergal zones between former and later tergites present, except for 14th and 15th, 16th, and 17th tergites. Tergites 2th–13th and 15th each with one pair of slender chitinous processes, slightly finger-like. Basal distances between processes are approx. the same length as their length from base to tip, which is longer than its basal width. All tergites pubescent and the margins of apical part of processes ornamented with rowed coarse granules. Apical seta on processes slightly anteriorly located and anterolateral setae slightly longer than other setae. No seta between apical and inner basal setae (Figs 2B–2H).

Tergites: 1st tergite reduced to a narrow short plate with a pair of diagonal bands and with six short setae in a row (Figs 2B, 3A). Second tergite complete, broader than long, with two slender posterior processes, 1+1 axial setae and 7+6 lateral setae (asymmetrically lack one lateral seta in holotype, 7+7 lateral setae in all paratypes), with anterolateral setae slightly longer than others, processes approx. 1.5 times as long as broad, basal distance between processes approx. the same as long as their length (Figs 2B, 3A). Third tergite entire with weak middle indentation, broader and longer than preceding one with the ratios mentioned nearly 1.6 and 0.8 respectively, 2+2 axial setae and 9+9 lateral setae (Figs 2C, 3A). Fourth tergite broader than 3rd tergite, with the ratios approx. 1.2 and 0.9 respectively, 2+2 axial setae and 6+6 lateral setae (Figs 2D, 3A). The shape and chaetotaxy of 5th–7th, 8th–10th, and 11th–13th tergites similar as 2nd–4th tergites. 14th tergite without processes and relevant area replaced by two roundish tubercles with four setae inserted on (Figure 2I). 15th tergite shorter than 3rd, 6th, 9th, and 12th tergites, with smaller processes (Figs 2C, 2E, 2G, 2H, 2J). Chaetotaxy and measurements of tergites are given in Tables 2 and 3.

Legs: all twelve pairs of legs with claws.1st pair of legs short, 3-segmented, length 35–45 μm, not more than the length of 2th pair of legs, but longer than the tarsus (30–32 μm) of last pair of legs; femur at least 1.2 times wider than long (15–22 μm: 12–15 μm), with two setae at the outer side; tibia approx. 1.4 times wider than long (14–20 μm: 10–14 μm), with dorsal seta (8–10 μm) longer than ventral one (4–6 μm); tarsus longer than wide (12–19 μm: 10–17 μm), with four setae, three dorsal (5–7 μm) and one ventral (6–8 μm); claws simple and the anterior one a little larger and broader than posterior (Figs 1I, 3F). 12th pairs of legs approx. three-fourths as long as the length of the head. Trochanter longer than wide (30–40 μm: 23–31 μm), with 6 subequal setae; femur approx. as long as wide (19–25 μm: 19–25 μm), with three setae transversely, one (10–14 μm) distinctly longer than other two (6–9 μm); tibia longer than wide (19–25 μm: 15–21μm), with four dorsal setae, of which one (10–14 μm) distinctly longer than others (6–9 μm); tarsus not more than 3 times as long as wide (30–32 μm: 11–15 μm) with 8–9 setae, of which 3 are protruding and 2 depressed, longest setae (12 μm) approx. as long as the greatest width of the joint. Claws rather curved, anterior one a little longer and broader than posterior one (10 μm: 8 μm) (Figure 3G). All legs covered with dense pubescence (Figs 1I, J, K).

Coxal sacs present at bases of 3rd–9th pairs of legs, fully developed, each with 3 setae (Figs 1J, 1K).

Styli present at base of 3rd–12th pairs of legs, reduced into small knobs with tuft of setae, on 9th–12th legs larger than on former legs, especially on 11th legs (5–6 μm), distinctly longer than anterior ones (2–4 μm) (Figs 1G, 1H, 3J).

Sense calicles with smooth margin to pit, length nearly two times longer than outer diameter (25–35μm: 12–16μm). Sensory seta inserted in the center of cup, extremely long, length 100–120 μm, at least 8.5 times longer than other two lateral setae (11–14 μm, 7–10 μm respectively) that inserted at the edge of cup (Figs 3H, I).

Cerci subuliform, short, approx. half as long as head, somewhat shorter than 12th pairs of legs, length at least three times as long as its greatest width (80–95 μm: 25–30 μm), sparsely covered with long and straight setae, with the longest one (12.5–17 μm) approx. half of the greatest width of the cerci, terminal area (10–13 μm) short, with length at most half of the greatest width of the cerci and circled by 6–8 layers of curved ridges. Terminal setae length 18–20 μm, distinctly longer than terminal area (Figure 1L, 3K).

Table 2. Chaetotaxy of tergites (holotype).

Tergites	Axial setae	Lateral setae
1st	3+3	–
2nd	1+1[1]	7+6[8]
3rd	2+2[2]	9+9[9]
4th	2+2	6+6
5th	2+2	5+5
6th	3+3	9+9[10]
7th	2+2[3]	6+6
8th	2+2[4]	5+5
9th	3+3	9+9[11]
10th	2+2	6+6
11th	2+2[4]	5+5
12th	3+3[4]	9+9[12]
13th	2+2	6+6[13]
14th	3+3[5]	4+4[14]
15th	3+3[6]	7+7[15]
16th	1+1[7]	2+2[16]
17th		5+5[17]

Notes on chaetotaxy variations: [1] with single middle seta (in 5 specimens) or without setae (1); [2] asymmetrically lack one seta (3) or lack one pair of seta (1). [3] with 1+1 setae (1); [4] asymmetrically present of one additional seta (1); [5] with 2+2 setae (5); [6] with 1+1 or 2+2 setae (4); [7] asymmetrically present of one additional setae (1); [8] with 7+7 setae in all paratypes (7); [9] asymmetrically lack 1 or 2 setae (2); [10] with 7+7 setae (1); [11] asymmetrically present of one additional setae (1); [12] asymmetrically lack one or present of one additional seta (2), or with 10+10 setae (1); [13] with 4+4 setae (2); [14-16] asymmetrically present of one additional seta (2); [17] asymmetrically lack one or two seta (2).

Table 3. Measurements of tergites and processes (holotype in brackets) (in μm).

No. of tergites	Length	Width	Length of processes	Width of processes	Basal distance between processes
1st	30–40 (40)	75–100 (80)	–	–	–
2nd	45–55 (55)	78–100 (100)	25–45 (31)	15–35 (20)	25–35 (30)
3rd	50–85 (82)	95–130 (112)	30–48 (40)	23–30 (25)	28–35 (33)
4th	45–61 (61)	100–125 (122)	30–50 (50)	30–40 (40)	35–45 (45)
5th	41–59 (59)	103–125 (107)	50–55 (50)	25–30 (30)	40–50 (40)
6th	55–123 (116)	130–150 (140)	40–58 (55)	25–35 (35)	40–55 (55)
7th	60–71 (71)	140–160 (160)	50–65 (50)	40–50 (50)	40–66 (66)
8th	55–75 (75)	110–135 (110)	50–65 (55)	25–35 (33)	58–68 (68)
9th	100–110 (110)	150–170 (160)	60–70 (60)	25–40 (30)	70–80 (80)
10th	67–71 (71)	150–187 (166)	40–70 (70)	30–50 (50)	45–74 (74)
11th	60–75 (68)	130–138 (138)	30–65 (50)	33–40 (33)	55–70 (60)
12th	75–120 (120)	150–165 (160)	54–60 (55)	25–40 (33)	55–65 (64)
13th	45–69 (69)	110–180 (156)	30–50 (50)	25–50 (50)	50–60 (60)
14th	55–80 (65)	95-140 (140)	–	–	–
15th	70–98 (85)	110–150 (140)	38–45 (40)	25–30 (30)	35–50 (42)
16th	35–43 (38)	95–130 (115)	–	–	–
17th	58–65 (65)	75–125 (90)	–	–	–

Etymology. The species name *glabrus*, meaning bald, to indicate the lower number of setae on cerci.

Distribution. China (Zhejiang, Jiangsu, Hainan).

Remarks. *Scolopendrellopsis glabrus* sp. n. is similar to *S. hirta* (Scheller, 1971) and *S. spinosa* (Sheller, 1979) in the shape of 3rd tergite which is not divided, shape of processes on tergites, shape of sensory organs on antennae. It differs from the latter two species in the absence of anterior part of central rod (anterior part present but indistinct in *S. hirta*, distinct in *S. spinosa*), chaetotaxy of the 2nd and 3rd tergites (with four and five lateromarginal setae in *S. glabrus* respectively, five and six in the other two species), cerci with lower number of setae (more setae in *S. hirta* and *S. spinosa*), all setae on cerci long and straight (setae on inner side of cerci slightly curved in *S. hirta*, most setae on cerci short and curved in *S. spinosa*). It is also similar to the worldwide species *S. subnuda* in the shape of the first three tergites, number of lateromarginal setae of the 3rd tergite, shape and number of setae of the cerci, but differs in the absence of anterior part of central rod (anterior part present in *S. subnuda*), apical seta on processes slightly anteriorly located (rather close to the apex in *S. subnuda*).

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The Oriental flat bug genus *Libiocoris* Kormilev, 1957 revisited: re-examination, synonymy, and description of a new genus (Heteroptera, Aradidae)

Xiaoshuan Bai[1], Ernst Heiss[2], Wanzhi Cai[3]

1 *Institute of Life Science and Technology, Inner Mongolia Normal University, Zhaowuda Road 81, Huhhot, 010022, Inner Mongolia, China* **2** *Entomological Research Associate, Tiroler Landesmuseum, 2a Josef Schraffl Strasse, A-6020 Innsbruck, Austria* **3** *Department of Entomology, China Agricultural University, Yuanmingyuan West Road, Beijing, 100094, China*

Corresponding author: *Ernst Heiss* (aradus@aon.at)

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Abstract

Re-examination of type specimens of *Libiocoris* Kormilev 1957, *L. poecilus* from New Guinea and other taxa assigned to this genus, the Chinese *Libiocoris heissi* Bai, Yang & Cai, 2006 and *Libiocoris sinensis* Bai, Yang & Cai, 2006 proved to be synonyms, thus *L. heissi* = *L. sinensis* syn. n. They are, however, different from *Libiocoris* Kormilev, 1957 to which they were originally assigned and a new genus *Paralibiocoris* **gen. n.** is proposed for them. Therefore *Paralibiocoris heissi* comb. n. = *Libiocoris heissi* Bai et al., 2006 = *Libiocoris sinensis* Bai et al., 2006, syn. n. From Hainan Island, China, the following new species, *P. roundangulus* **sp. n.**, *P. hainanensis* **sp. n.**, and *P. limuensis* **sp. n.**, are described and figured and a key to species is provided.

Keywords

Aradidae, Carventinae, China, Heteroptera, *Libiocoris*, new combination, new genus, new species, new synonymy, *Paralibiocoris*

Introduction

The genus *Libiocoris* was erected by Kormilev, 1957 for the species *poecilus* from New Guinea. Usinger & Matsuda, 1959 improved the generic description based on the new species *L. antennatus* from Papua (New Guinea) and added *L. angulatus*, also from New Guinea to this genus. Later, *L. lobatus* Kormilev, 1968 and *L. pilicornis* Kormilev, 1972 were described again from New Guinea. Heiss (1982) described the species *L. indicus* from north India and two more species, *L. heissi* and *L. sinensis,* were described by Bai et al. (2006) from Hainan Island in south sast China.

The distribution pattern of these eight species within the Indo-Pacific region seems restricted to two biogeographically different areas: the Indo-China region (*L. indicus*, *L. heissi*, and *L. sinensis*) and the Papuasian region (*L. poecilus*, *L. antennatus, L. angulatus*, *L. lobatus*, and *L. pilicornis*), which raises questions about their assignment to the same genus of apterous Carventinae, all having very limited distribution ranges.

As a result of the re-examination of the genus-type species *L. poecilus* (holotype male, allotype female, HMHN), of *L. angulatus* (holotype female, MCSM), and of *L. antennatus* (paratype female, CEHI ex. coll. Kormilev), the original descriptions of *L. lobatus* and *L. pilosus* as well as the types of other species assigned to this genus, we can now confirm the following results:

1 After removal of the waxy incrustation obscuring the dorsal structures and examination of the female holotypes of *heissi* and *sinensis* it was evident that both belong to the same taxon and are synonyms.
2 The Chinese species *heissi* and *sinensis* differ in essential morphological characters from *Libiocoris* sensu Kormilev, 1957, for which a new genus *Paralibiocoris* gen. n. is proposed. A further three new species from China belonging to this genus are recognized and described herein.
3 The single species *L. indicus* Heiss, 1982 described from north India, tentatively assigned to *Libiocoris*, is not congeneric with *Libiocoris* sensu Kormilev, 1957 nor to *Paralibiocoris* gen. n. erected for the Chinese species.
4 Inconsistencies and remarkable differences in the descriptions of *angulatus*, *antennatus*, *lobatus,* and *pilosus* raise questions about their congeneric assignment when compared with *poecilus*.

Materials and methods

Depositories of type material examined:

MNHUK	Museum of Natural History, London, Great Britain
CAU	China Agricultural University, Beijing, China
CEHI	Collection Ernst Heiss, Tiroler Landesmuseum Innsbruck, Austria

EMIH	Entomological Museum of Inner Mongolia Normal University, Huhhot, China
HNHM	Hungarian Natural History Museum, Budapest Hungary
MCSM	Museo Civico di Storia Naturale "Giacomo Doria", Genoa, Italy
MHNG	Muséum d' Histoire Naturelle, Geneva, Switzerland

Photographs were taken through Keyence VHX-1000 equipment. Measurements were made using a calibrated micrometre; all measurements are given in millimetres. Abbreviations used as follows:

deltg	dorsal external laterotergite (connexivum);
mtg	mediotergite;
ptg	paratergite;
vltg	ventral laterotergite.

Taxonomy

Synonymy

Type specimens of *L. heissi* and *L. sinensis* are conspecific, thus the following synonymy *Libiocoris heissi* Bai, Yang & Cai, 2006: 41 = *Libiocoris sinensis* Bai, Yang & Cai, 2006: 43 syn. n. is here established, *heissi* having priority.

Paralibiocoris **gen. n.**

http://zoobank.org/BE3C5C3E-DE96-418B-A434-A60EBC5E0FB8

Type species. *Libiocoris heissi* Bai, Yang & Cai, 2006.

Diagnosis. General aspect similar to *Libiocoris* Kormilev, 1957 but is distinguished from the type species *Libiocoris poecilus* (characters in brackets) by the following set of morphological characters:

- position of spiracles: II ventral, III–VII lateral and visible from above (II–III ventral IV–V sublateral not visible from above, VI–VII lateral and visible);
- fused deltg II+III shorter, reaching only posterior border of metanotum (Figs 1, 3) (extending forward to half-length of mesonotum which is not shown in Fig. 1 of Kormilev's (1957) description but mentioned by Usinger and Matsuda's (1959) redescription, and verified at types (Figs 81, 82);
- presence of a smooth oblique callus on vltg VII of male which is independent of spiracle VII (Figure 12) (lacking and not developed, fig. 4 of Kormilev 1957);
- fused median longitudinal sclerite reaching from pronotum to tergal plate bottle-shaped along meso- and metanotum, then restricted along mtg I+II and carinate,

the fusion line between metanotum – mtg I+II marked by a suture (Figs 5, 7) (narrow and subparallel along meso-metanotum with a longitudinal sulcus, fused to but without a suture between metanotum – mtg I+II) (Figs 81, 82);

- median ridge of abdomen distinctly elevated along midline (flat, not developed), dorsally reflexed vltg VII subrectangular (produced posteriorly, long and acute in male, shorter and acute in female);
- shape of male pygophore pyriform, produced posteriorly (wide and short).

Paralibiocoris gen. n. is very similar to *Bruneiaptera* Heiss, 2011 from Borneo, sharing basic habitus and dorsal thoracic structures; however, in *Brunneiaptera* all spiracles (II–VII) are lateral and visible from above.

Description. Apterous, of small size 4.4–5.8 mm; habitus elongate-oval; legs and antennae beset with small setigerous granules; coloration yellowish to reddish or blackish brown.

Head. Subquadrangular, longer or as wide as distance across eyes; clypeus short, genae slightly produced; antenniferous tubercles short with acute apices; antennae long and slender, first and third and second and fourth segments subequal in length, first stout, incrassate, second and third cylindrical, fourth fusiform; eyes small, granulate; postocular tubercles distinct; rostrum arising from a slit-like atrium, not reaching limits of rostral groove.

Thorax. Pronotum short and wide; anterolateral angles produced forward beyond collar forming large blunt or rounded lobes; disc with a median sulcus; separated from mesonotum by a transverse intersegmental furrow; meso- and metanotum separated only laterally, the elevated median ridge smooth without sulcus; lateral sclerites with longitudinal elevations; metanotum separated from fused mtg I+II by a narrow transverse sulcus;

Abdomen. Mtg I and II fused together; mtg III to VI fused into a subquadrangular tergal plate, elevated along midline with usual pattern of large and small callous spots and dots; mtg VII strongly elevated posteriorly in male and slightly elevated in female; pygophore cordate; paratergites VIII clavate or lobiform.

Venter. Prosternum raised and with Y-shaped median carina; meso- and metasternum and sternum II+III fused and flattened medially. Spiracles II ventral, III-VII lateral on dorsally reflexed vltg III-VII and visible from above; spiracle VIII terminal on ptg VIII.

Legs. long and slender, without spine, preapical comb on fore tibia present, femora subcylindrical, claws with fine pulvilli.

Etymology. From "para-" close to (Greek) and *Libiocoris*.

Key to species *Paralibiocoris* gen. n. from China.

1 Antennal segment I as long as III **2**

– Antennal segment I longer than III **3**

2 Antennae longer, 2.1 times as long as width of head, anterolateral lobes of pronotum narrow and produced (Figs 1, 3), abdomen of female egg shaped, widely rounded (Figs 1, 2); abdomen of male more slender, ratio length of body / width of abdomen 2.15 (Figure 3) and deltg VII angularly produced posterolaterally (Figs 11, 12) .... ***heissi*** **(Bai et al., 2006), comb. n.**

– Antennae shorter, approx. 1.9 times as long as width of head, anterolateral lobes of pronotum wider and less produced (Figs 39, 41), abdomen of female evenly rounded (Figs 40, 41), abdomen of male wider, ratio length of body / width of abdomen 2.0 and deltg VII less produced and rounded (Figs 47, 48) .... ***hainanensis*** **sp. n.**

3 Pronotum narrower 2.86 times wider than long, anterolateral lobes widely rounded (Figs 18, 20, 22, 24), median thoracic plate of meso- metanotum wider and lateral borders subparallel basally and at conical anterior part (Figs 18, 20, 22, 24) .... ***roundangulus*** **sp. n.**

– Pronotum wider, more than three times as wide as long, anterolateral lobes narrower (Figs 60, 62, 64, 66), median thoracic plate of meso- metanotum narrower and distinctly leaf- shaped, diverging posteriorly, apical part attenuated anteriorly (Figs 60, 62, 64, 66) .... ***limuensis*** **sp. n.**

Paralibiocoris heissi **(Bai, Yang & Cai, 2006), comb. n.**

Figs 1–17

Libiocoris heissi Bai, Yang & Cai 2006: 41, figs 1, 3–7 (CAU).
Libiocoris sinensis Bai, Yang & Cai 2006: 43, figs 2, 8–12 (CAU) syn. n.

Type material. Holotype (♀): China, Hainan, Baisha, Yinggeling, 1050 m, 10.IX.2005, L. S. Chen leg. (EMIH). **Additional material examined.** ♂, China, Hainan, Baisha,Yinggeling, 950 m, 2.VIII.2007, Bai X.S.; ♂, China, Hainan, Wuzhi mountain, 8.V.2008, Bai X.S.; ♀, China, Hainan, Baisha,Yinggeling, 950m, 2.VIII.2007, Bai X.S.; 2♀, China, Hainan, Ledong, Jianfengling, 900 m, 21.VII.2004, Wu Jie (EMIH, CAU); ♂,♀ China, Baisha, / Yinggeling 1200 m / 19°03'16"N, 109°33'53"E /2.VIII.2007, Bai X.S. (CEHI ex CAU).

As both taxa were described on single females and males are now available, the holotype of *heissi* is redescribed and additional features of the male added.

Diagnosis. As generic description.

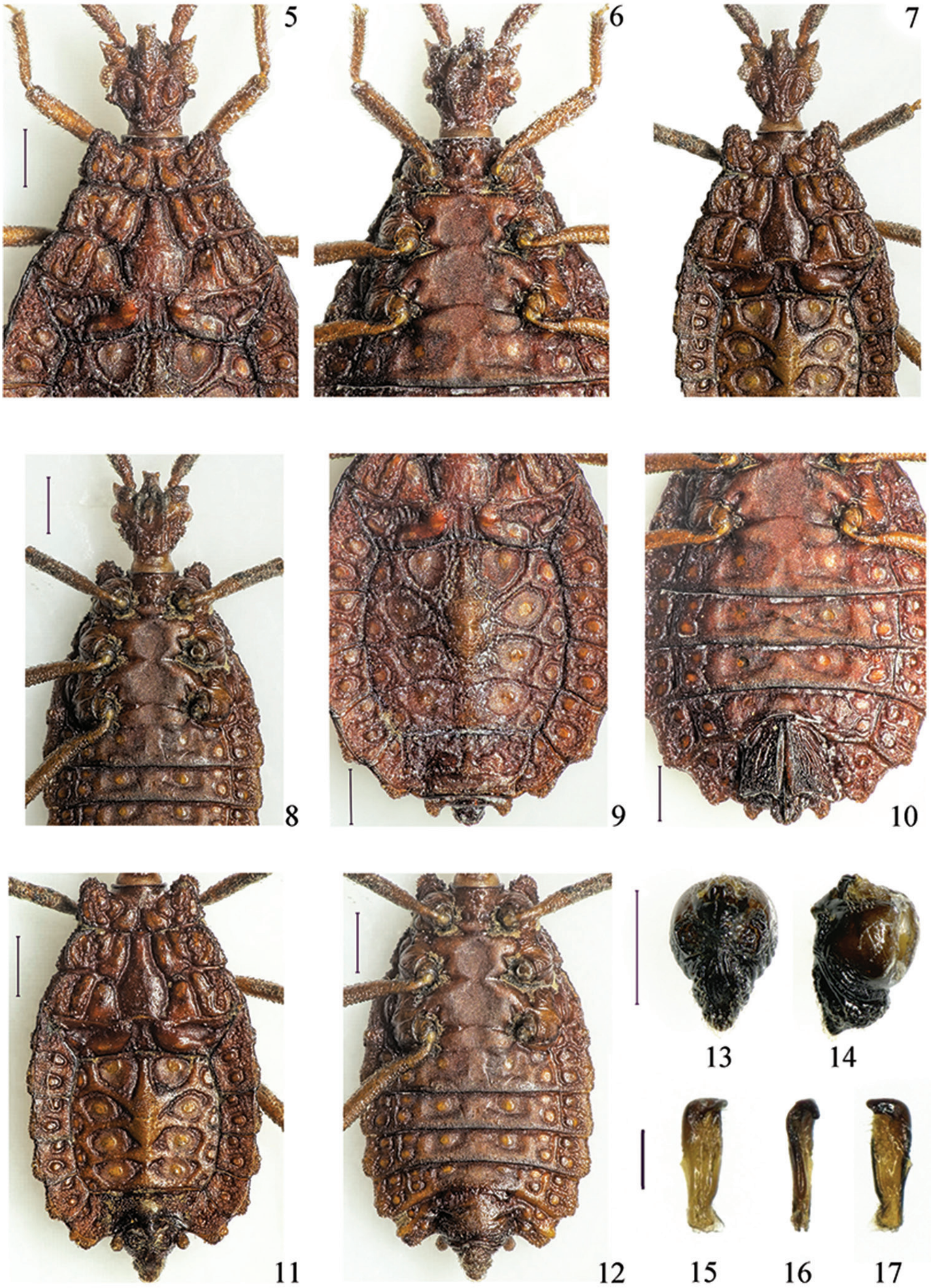
Redescription. Apterous female, incrustation removed to recognise dorsal structures.

Head. Slightly longer than wide across eyes (1.0/0.9); clypeus short reaching basal one-third of first antennal segment, strongly raised anteriorly, with tubercle near apex; genae slightly produced over clypeus; antenniferous tubercles short, dilated, apices acute, diverging anteriorly; antennae 2.1 times as long as width of head across eyes, length of antennal segments I to IV = 0.65, 0.30, 0.65, 0.30; eyes small, not protruding; postocular tubercles small but distinct, not reaching outer margin of eyes; pos-

Figures 1–4. *Paralibiocoris heissi*. Holotype female (**1, 2**) dorsal and ventral view; male (**3, 4**) dorsal and ventral view. Scale bar: 1 mm.

tocular borders behind tubercles straight and converging to constricted collar; vertex with Y-shaped granulate carina flanked by two(1+1) large, ovate infraocular callosities; rostrum short, rostral groove wide and deep, closed posteriorly.

Pronotum. 2.8 times as wide as long (1.4/0.5); collar narrow, anterolateral angles produced forward beyond collar as two (1+1) large, blunt, granulate lobes; disc with a longitudinal median furrow flanked by ovate callosities; posterior margin of pronotum slightly convex posteriorly, separated from mesonotum by a deep furrow.



Figures 5–17. *Paralibiocoris heissi*. Holotype female (**5, 6, 9, 10**) dorsal and ventral thorax and abdomen; male (**7, 8, 11, 12**) dorsal and ventral thorax and abdomen; pygophore dorsal and lateral view (**13, 14**); right paramere in three positions (**15, 16, 17**). Scale bars: 0.5 mm (**5–14**), 0.1 mm (**15–17**).

Mesonotum. Wider than pronotum, separated from metanotum by two (1+1) deep furrows laterally; across meso- and metanota medially with an elongate, subpentagonal bottle-shaped ridge, 1.53 times as long as wide (0.87/0.57), subrounded anteriorly and truncate posteriorly, smooth and without longitudinal sulcus; lateral of median ridge disc with four (2+2) longitudinal sclerites, lateral margins granulate.

Metanotum. Wider than mesonotum; separated from fused mtg I+II by a slightly sinuate thin sulcus; lateral of median ridge with two (1+1) large subtriangular callosities, 2 (1+1) longitudinal ridges lateral of callosity discs, lateral margins granulate, similar to those of mesonotum.

*Abdomen***.** Mtg I and II completely fused, depressed at middle, there with a median longitudinal ridge laterally separated by deep furrows from wide oblique lateral plates, sloping posteriorly and sideways, further laterally with two (1+1) large subtriangular depressions; tergal plate with a slightly raised median ridge on mtg III, a pentagonal elevation on mtg IV then tapering posteriorly.

Venter. Sterna III to VI raised along posterior border, depressed along anterior border, and with triangular, smooth spots medially, flanked by two (1+1) large, transversely ovate depressions, these bearing two (1+1) round callous spots; laterally four (2+2) smaller round callous spots present; spiracles II ventral, III–VIII lateral and visible from above.

Legs. Long and slender, without spines, preapical comb on fore tibia present, femora subcylindrical, claws with fine pulvilli.

Male. Morphological features similar to female but of smaller size. Head as long as wide across eyes; median plate of meso- metanotum more elongate 1.82 times as long as wide (0.73/0.40); mtg VII strongly elevated posteriorly; reflexed vltg VII forming triangular lobes posterolaterally, ventral side with a distinct oblique smooth callus, reaching lateral margin; ptg VIII short and clavate much shorter than cordate pyriform pygophore (Figs 13, 14); parameres slender (Figs 15–17).

Measurements [in mm, ♂(n = 2)/♀ (n = 3), holotype in parentheses]. Body length 4.4-4.45/5.1-5.8 (5.6); maximal width of abdomen 2.05-2.2/2.65-3.05 (3.05). Head length 0.8-0.85/0.9-1.05 (1.0), width 0.8/0.8-0.95 (0.9). Pronotum length 0.4/ 0.45-0.5 (0.5), width 1.15-1.2/1.3-1.45 (1.4). Mesonotum width 1.5-1.6/1.7-1.95 (1.8). Metanotum width 1.8-1.9/2.05-2.3 (2.25). Length of antennal segments I–IV = 0.60, 0.25, 0.60, 0.30/0.6-0.7, 0.3-0.35, 0.6-0.7, 0.3-0.35 (0.65, 0.30, 0.65, 0.30).

Distribution. China (Hainan).

Comments. As the generic characters and diagnosis are valid for all hereafter described new congeneric taxa, common features are not repeated except those differing in structure of thoracic median plate, size, and measurements distinctive for the specific taxa.

Paralibiocoris roundangulus **sp. n.**

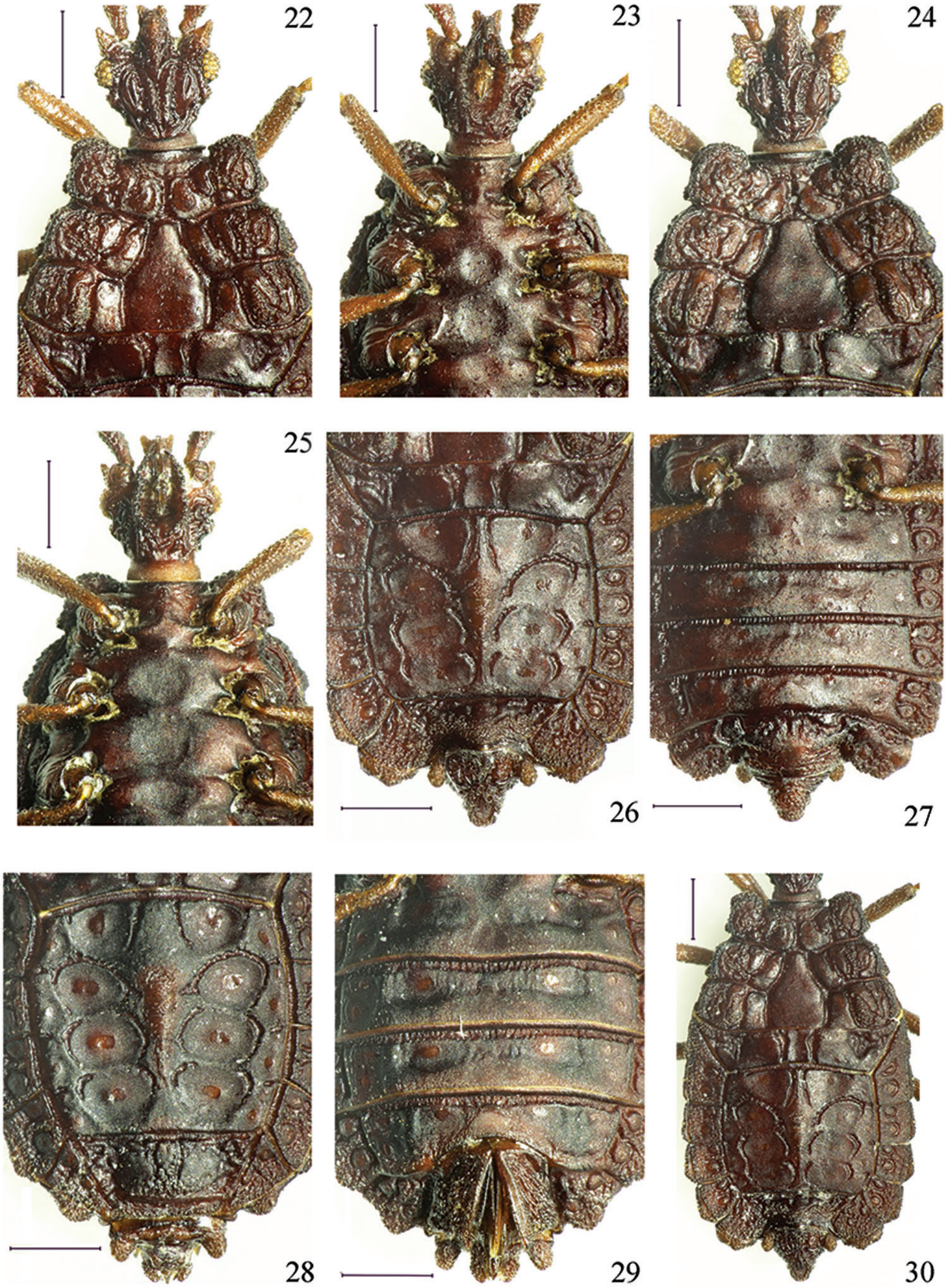
http://zoobank.org/7B6A48C4-B46F-49A5-BE47-635F083B0DFA
Figs 18–38

Type material. Holotype: ♂, China, Hainan, Jianfeng, Tianchi, 810 m, 16.VIII.2007, Zhang & Bai (EMIH). **Paratypes.** 2♂, China, Hainan, Jianfeng, Tianchi, 810 m,

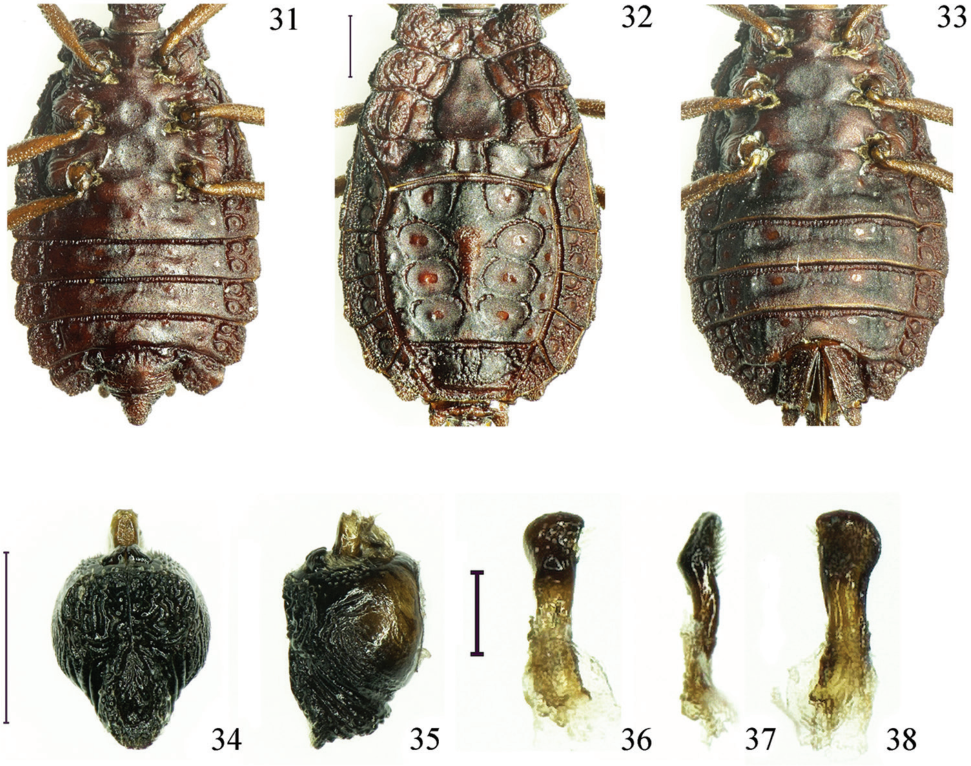
Figures 18–21. *Paralibiocoris roundangulus* sp. n. Holotype male (**18, 19**) dorsal and ventral view; female (**20, 21**) dorsal and ventral view. Scale bar: 1 mm.

16.VIII.2007, Zhang & Bai; ♂, China, Hainan, Tongzha, Wuzhishan, 6.V.2009, Zhang & Yang; 2♀, China, Hainan, Jianfeng, Beiganxian, 820 m, 9.VIII.2007, Bai, X. S. (EMIH); 3♂, 3♀ collected with holotype (CEHI ex CAU).

Diagnosis. General aspect similar to *Paralibiocoris heissi*, but distinguished from it by a wider pronotum, 2.86 times as wide as long (2.80 in *P. heissi*), anterolateral lobes



Figures 22–30. *Paralibiocoris roundangulus* sp. n. Holotype male (**22, 23, 26, 27, 30**) dorsal and ventral thorax and abdomen; female (**24, 25, 28, 29**) dorsal and ventral thorax and abdomen. Scale bars: 0.5 mm (**22–30**).



Figures 31–38. *Paralibiocoris roundangulus* sp. n. Holotype male (**31**) ventral thorax and abdomen; female (**32, 33**) dorsal and ventral thorax and abdomen; pygophore dorsal and lateral view (**34, 35**); right paramere in three positions (**36, 37, 38**). Scale bars: 0.5 mm (**31–35**), 0.1 mm(**36–38**).

widely rounded (narrow and more produced), shorter antennae 1.79 times as long as width of head (2.1). *Paralibiocoris roundangulus* sp. n. differs from *P. hainanensis* sp. n. and *P. limuensis* sp. n. by a different shape of the median ridge of meso- and metanotum (Figs 22, 24) and shorter antennae which are 1.79 times as long as width of head (1.89 and 1.82 respectively).

Description. Male. Basic morphological structures as of *P. heissi*. *Head.* As long as wide across eyes (0.82/0.82); antennae 1.79 times as long as width of head across eyes, length of antennal segments I to IV = 0.48, 0.24, 0.44, 0.31.

Pronotum. 2.86 times as wide as long (1.23/0.43); collar narrow; anterolateral angles produced forward beyond collar as two (1+1) widely rounded granulate lobes; disc with a longitudinal median furrow flanked by 2 (1+1) large, subtriangular and smaller callosities; lateral margin granulate.

Mesonotum. Wider than pronotum (1.60/1.23); separated from metanotum by two (1+1) deep furrows laterally; across meso- and metanota medially with an elongate, smooth bottle-shaped plate similar to *P. heissi*, 1.56 times as long as wide (0.67/0.43).

Metanotum. Wider than mesonotum (1.83/1.60); separated from mtg I by a slightly sinuate thin sulcus.

Abdomen. Mtg I and II completely fused, disc with a wide, smooth rectangular plate at middle flanked by two (1+1) large oblique plates, sloping posteriorly and sideways, laterally with two (1+1) small subtriangular depressions; deltg II and III fused, the following separated by fine sulci; posterolateral angles of deltg V to VII progressively angularly protruding; paratergites clavate, short, not reaching beyond posterolateral angles of deltg VII; pygophore elongate cordate, surface rugose (Figs 34, 35); parameres slender (Figs 36–38).

Venter. Sterna III to VI raised along posterior border, depressed along anterior border, and with triangular, smooth spots medially, flanked by 2 (1+1) shallow, transversely ovate depressions, these bearing 2 (1+1) round callous spots; 4 (2+2) smaller round callous spots present laterally; vltg VII with a small callus near spiracle VII; spiracles II ventral, III–VIII lateral and visible from above.

Female. Morphological features similar to male but of larger size; head slightly longer than wide across eyes (0.93/0.87); length of antennal segments I to IV = 0.48, 0.24, 0.44, 0.31; pronotum wider than long (1.47/0.43); width of mesonotum 1.90; width of metanotum 2.16, anterior lobe of median plate across meso- and metanota truncate, 1.2 times as long as wide (0.78/0.65); mtg VII moderately elevated posteriorly, the posterolateral angles forming triangular lobes; ptg VIII lobiform, reaching basal half of segment IX.

Measurements. [in mm, ♂(n = 4)/♀ (n = 2), holotype in parentheses]. Body length 4.1-4.15/4.9-5.1 (4.1); maximal width of abdomen 2.05-2.1/2.55-2.75 (2.1). Head length 0.82/0.9-0.93 (0.82), width 0.82/0.8-0.87 (0.82). Pronotum length 0.43/0.43 (0.43), width 1.23/1.4-1.47 (1.23). Mesonotum width 1.55-1.6/1.85-1.90 (1.60). Metanotum width 1.83-1.9/2.1-2.16 (1.83). Length of antennal segments I–IV = 0.48, 0.24, 0.44, 0.31/0.48, 0.24, 0.44, 0.31 (0.48, 0.24, 0.44, 0.31).

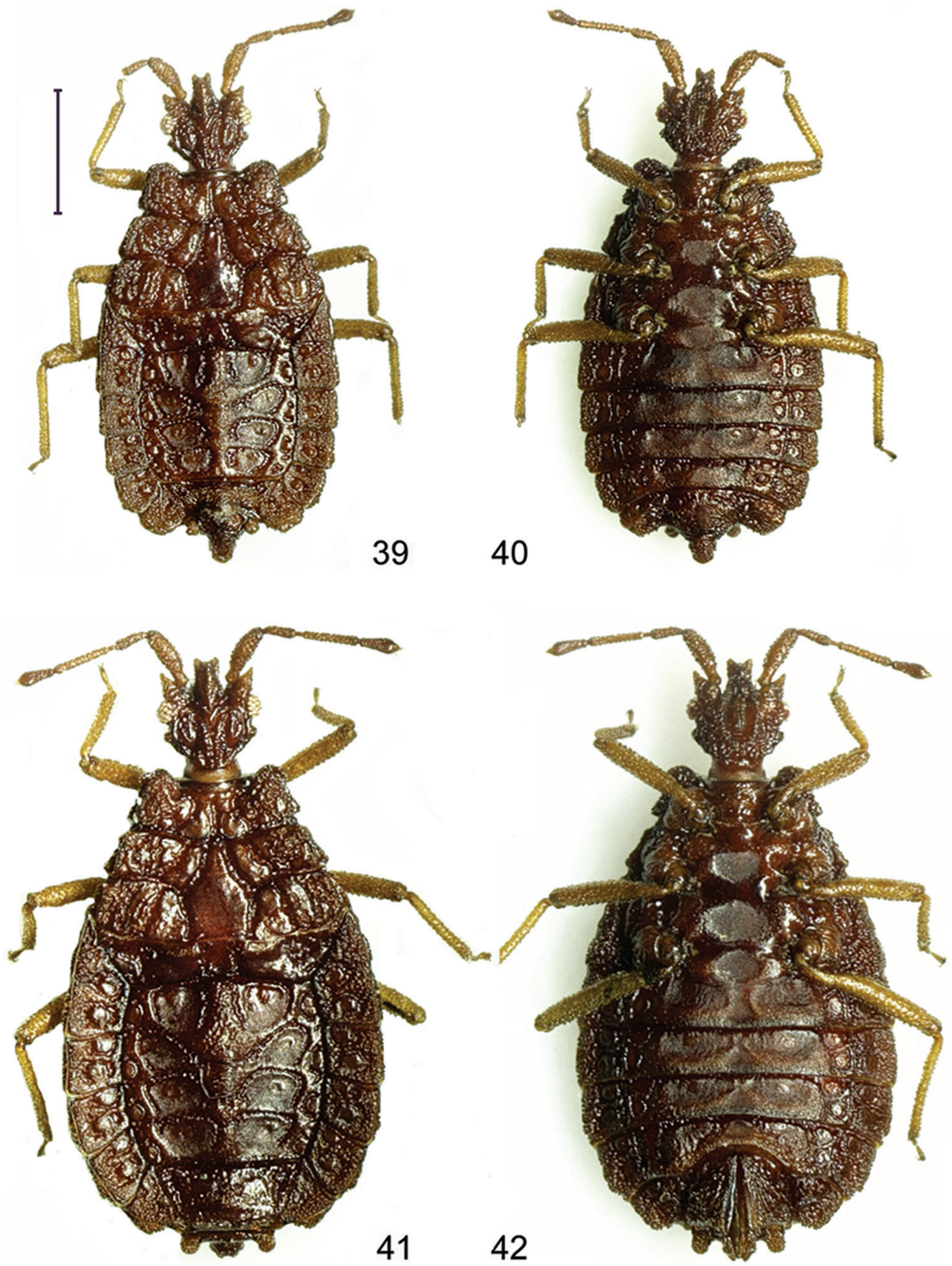
Etymology. The name of species refers to the widely rounded anterolateral angles of pronotum.

Distribution. China (Hainan).

***Paralibiocoris hainanensis* sp. n.**

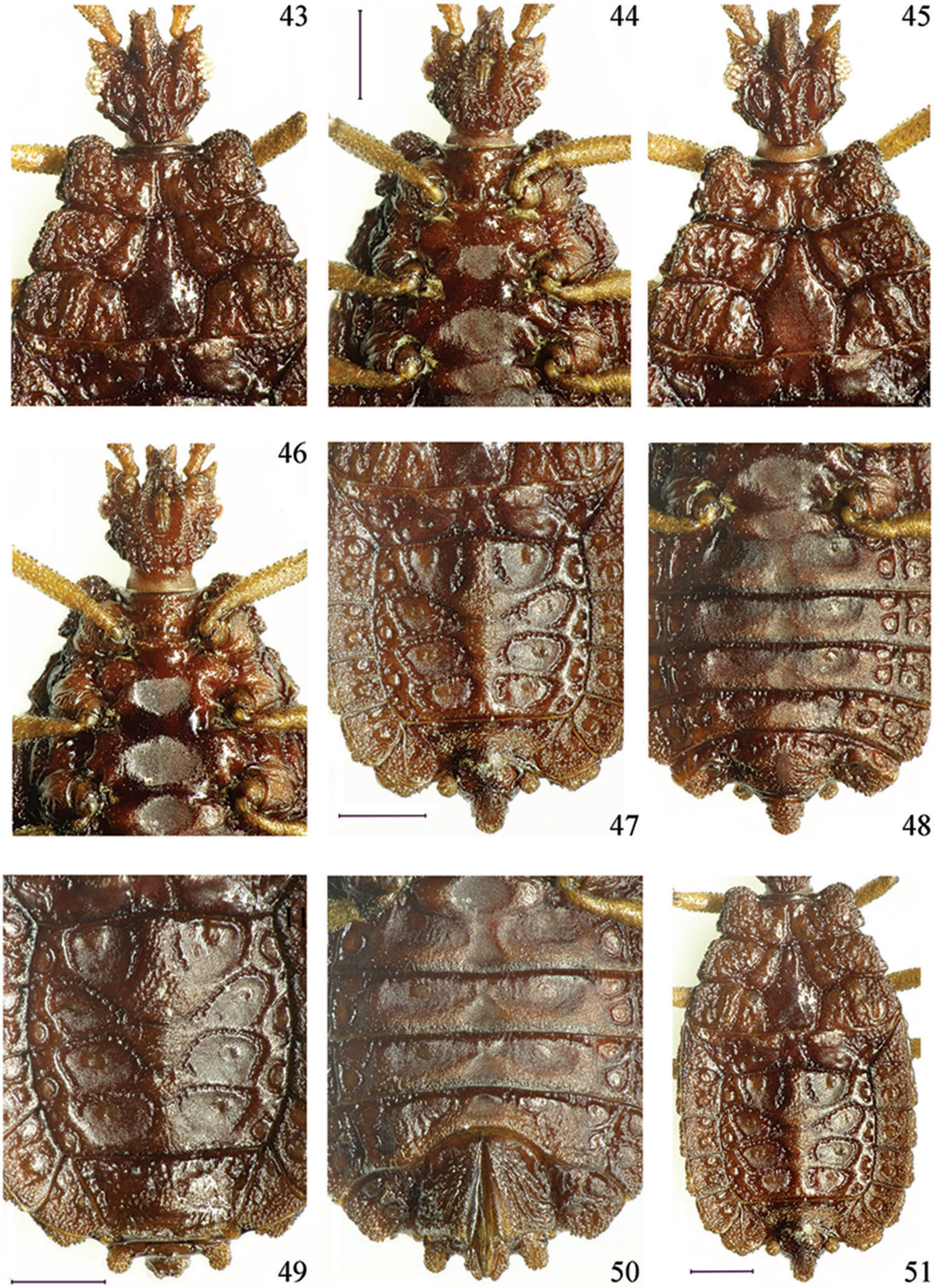
http://zoobank.org/0E59DCF2-1EE8-4D07-90FF-9F14731E277F
Figs 39–59

Type material. Holotype (♂): China, Hainan, Jianfeng, Tianchi, 810 m, 16.VIII.2007, Zhang & Bai; (EMIH). Paratypes**:** 2♂, China, Hainan, Changjiang, Bawangling, 13.IX.2008, Zhang W. J.; 2♂, 3♀ China, Hainan, Jianfeng, Tianchi, 810 m, 16.VIII.2007, Zhang & Bai; 3♂, China, Hainan, Tongzha, Wuzhishan, 6.V.2009, Zhang & Yang; ♂, China, Hainan, Wanning, Shimeiwan, 12.VIII.2007, Bai, X. S.; ♀, China, Hainan, Jianfeng, Nanya, 644 m, 22.VIII.2007, Bai, X. S. (EMIH); 2♂,2♀ collected with holotype (CEHI ex CAU).

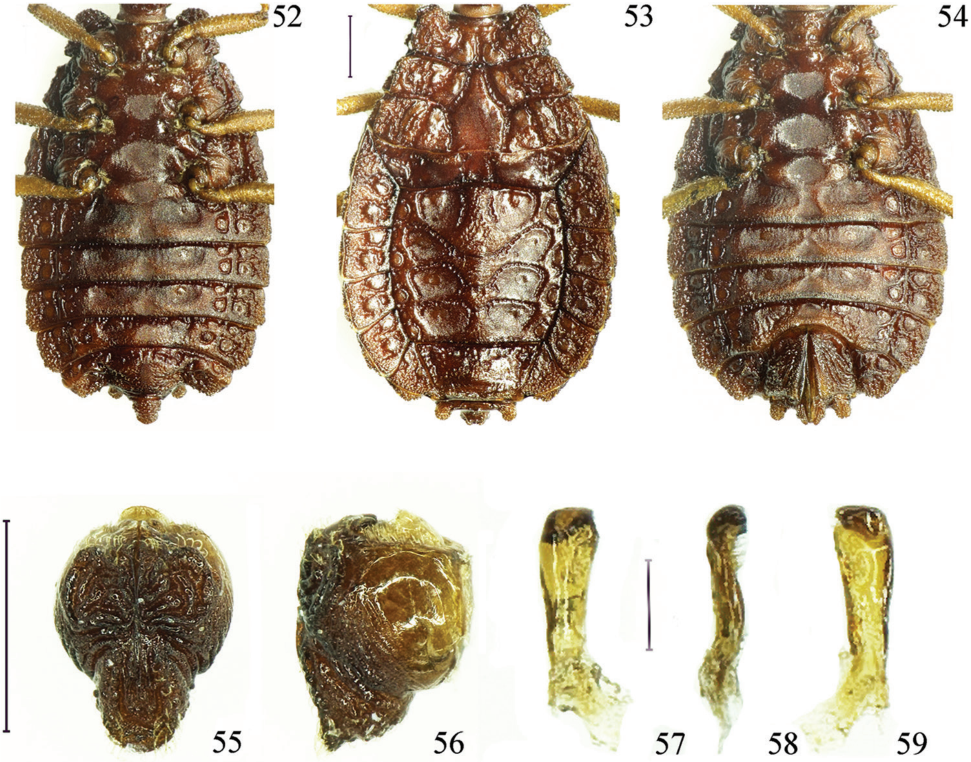


Figures 39–42. *Paralibiocoris hainanensis* sp. n. Holotype male (**39, 40**) dorsal and ventral view; female (**41, 42**) dorsal and ventral view. Scale bar: 1 mm.

Diagnosis. General aspect similar to *Paralibiocoris heissi*, but distinguished from the latter by the wider pronotum, 2.91 times as wide as long (2.80 in *P. heissi*) and more rounded less produced anterolateral lobes (produced and blunt), shorter anten-



Figures 43–51. *Paralibiocoris hainanensis* sp. n. Holotype male (**43, 44, 47, 48, 51**) dorsal and ventral thorax and abdomen; female (**45, 46, 49, 50**) dorsal and ventral thorax and abdomen. Scale bars: 0.5 mm.



Figures 52–59. *Paralibiocoris hainanensis* sp. n. Holotype male (**52**) ventral thorax and abdomen; female (**53, 54**) dorsal and ventral thorax and abdomen; pygophore dorsal and lateral view (**55, 56**); right paramere in three positions (**57, 58, 59**). Scale bars: 0.5 mm (**52–56**), 0.1 mm (**57–59**).

nae 1.89 times as long as width of head (2.1) and by posterolateral angles of deltg V to VII slightly protruding and rounded in female. *Paralibiocoris hainanensis* sp. n. differs from *P. roundangulus* sp. n. and *P. limuensis* sp. n. by a different shape of the median ridge of meso- and metanotum (Figs 43, 45 vs. Figs 22, 24 and Figs 64, 66, respectively) and antennal segment I as long as III (III shorter than I).

Description. Male. Basic morphological structures as of *P. heissi* and other congeners. *Head.* Slightly longer than wide across eyes (0.8/0.78); antennae 1.89 times as long as width of head across eyes, length of antennal segments I to IV = 0.47, 0.24, 0.47, 0.30.

Pronotum. 2.91 times as wide as long (1.25/0.43); collar narrow; anterolateral lobes produced forward beyond collar as two (1+1) widely rounded granulate lobes; disc with a longitudinal median furrow flanked by 2 (1+1) large, subtriangular and smaller callosities, lateral margin granulate, converging anteriorly.

Mesonotum. Wider than pronotum (1.60/1.25); separated from metanotum by two (1+1) deep furrows laterally; across meso- and metanota medially with an elongate, smooth bottle - shaped plate as *P. heissi,* 1.63 times as long as wide (0.70/0.43).

Metanotum. Wider than mesonotum (1.80/1.60); separated from mtg I by a slightly sinuate thin sulcus.

Abdomen. Mtg I and II completely fused, disc depressed at middle with a flat rectangular sclerite separated from lateral ovate plates by deep furrows; tergal plate with a slightly elevated granulate ridge which is widest on mtg III, sloping posteriorly; pygophore elongate cordate, surface rugose (Figs 55, 56); parameres slender (Figs 57–59).

Venter. Vltg VII with a small shiny callus, near spiracle VII; spiracles II ventral, III–VIII lateral and visible from above.

Female. Morphological features similar to male but of larger size. Head slightly longer than wide across eyes (0.80/0.78); length of antennal segments I to IV = 0.46, 0.27, 0.46, 0.33; pronotum wider than long (1.27/0.43); width of mesonotum 1.60; bottle-shaped median thoracic plate 1.56 times as wide as long (0.67/0.43); width of metanotum 1.93.

Measurements [in mm, ♂ (n = 9)/♀ (n = 4), holotype in parentheses]. Body length 3.65-4.2/4.2-4.55 (4.2); maximal width of abdomen 1.75-2.1/2.2-2.4 (2.1). Head length 0.7-0.8/0.75-0.8 (0.8), width 0.65-0.78/0.7-0.78 (0.78). Pronotum length 0.35-0.43/0.4-0.45 (0.43), width 1.05-1.25/1.2-1.3 (1.25). Mesonotum width 1.4-1.6/1.45-1.6 (1.6). Metanotum width 1.5-1.8/1.65-1.9 (1.8). Length of antennal segments I–IV = 0.44-0.47, 0.24, 0.44-0.47, 0.3/0.47, 0.24-0.27, 0.47, 0.3-0.34 (0.47, 0.24, 0.47, 0.3).

Etymology. The name refers to the Island of Hainan, the type locality.

Distribution. China (Hainan).

Paralibiocoris limuensis **sp. n.**

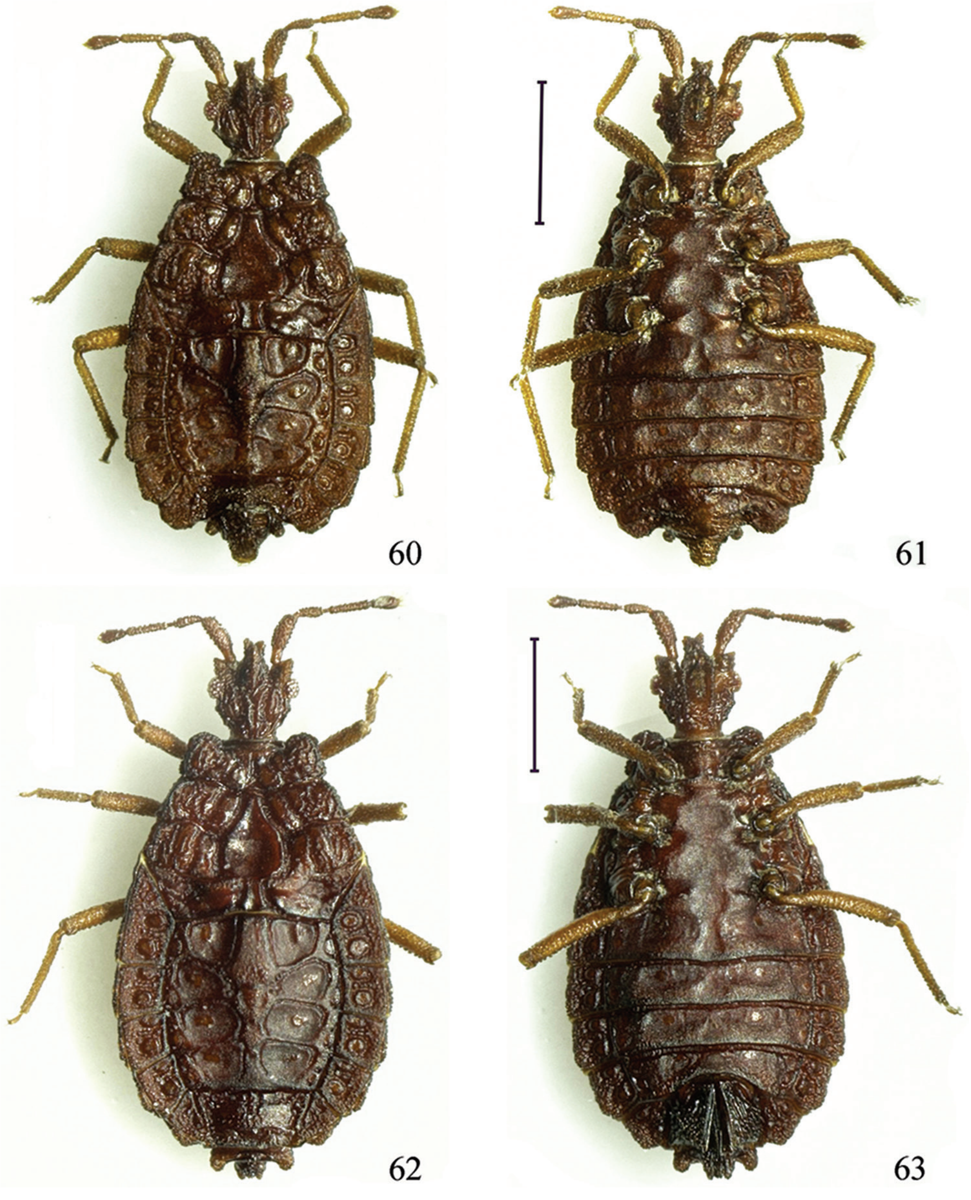
http://zoobank.org/10341EE3-0E54-4128-880D-304F8D2CD496

Figs 60–80

Type material. Holotype (♂): China, Hainan, Limu, Montain, 6.V.2008, Bai, X. S.; (EMIH). **Paratypes.** 2 ♂, China, Hainan, Limu, Montain, 6.V.2008, Bai, X. S.; 2♀, China, Hainan, Limu, Montain, 6.V.2008, Bai, X. S. (EMIH).

Diagnosis. General aspect similar to *Paralibiocoris heissi*, but distinguished from the latter by wider pronotum 3.06 times as wide as long (2.80) and more rounded less produced anterolateral lobes (produced and blunt), shorter antennae 1.82 times as long as width of head (2.1) and by antennal segment I longer than III (of same lengths in *heissi*). *Paralibiocoris limuensis* sp. n. differs from *P. roundangulus* sp. n. and *P.hainanensis* sp. n. by a wider pronotum (3.06 vs. 2.86 and 2.91 respectively) and a leaf-like shape of the median ridge of meso- and metanotum (Figs 60, 62) and smaller size.

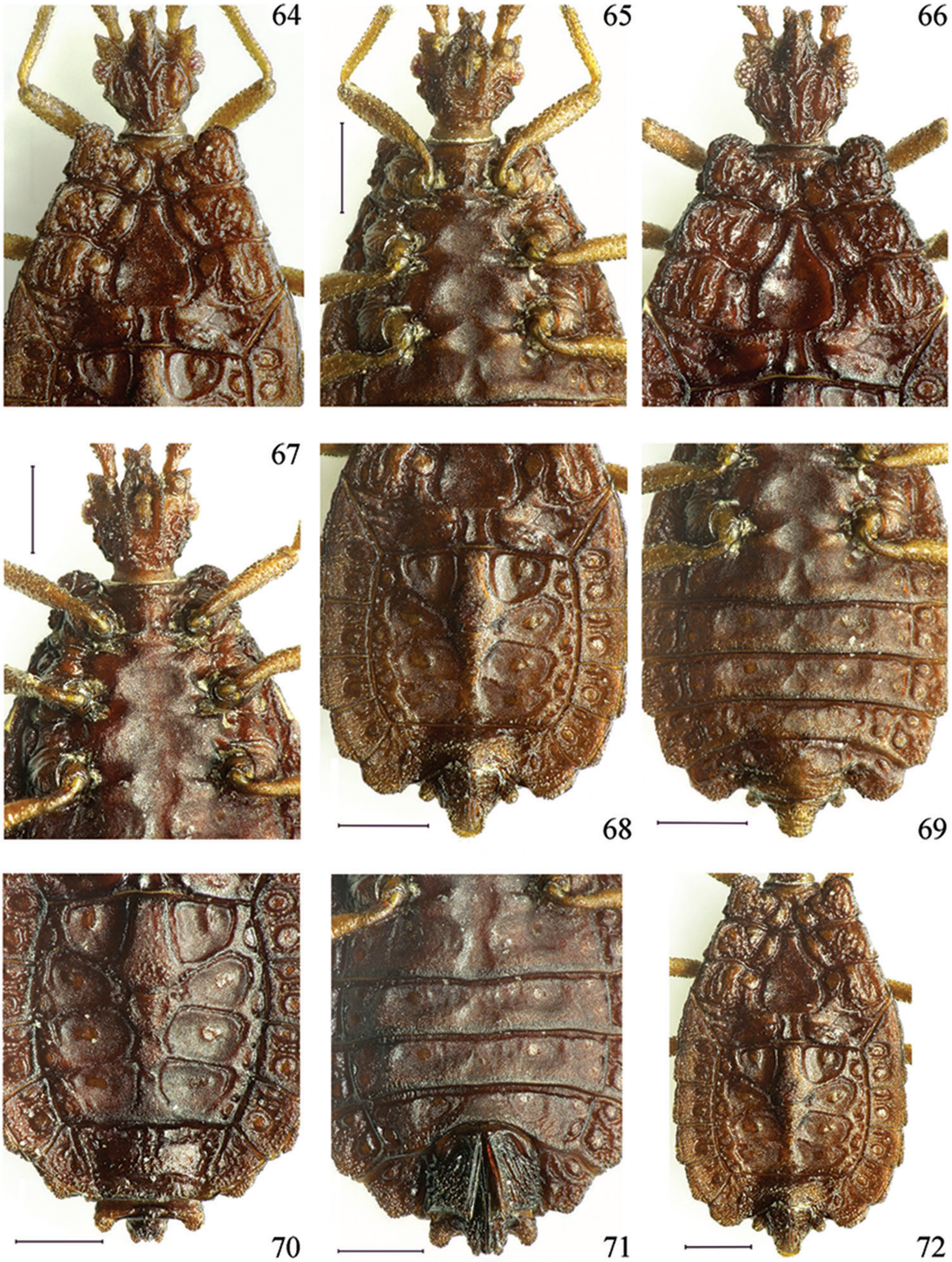
Description. Male. Basic morphological structures as of *P. heissi* and other congeners. *Head.* Slightly longer than wide across eyes (0.75/0.68); antennae 1.82 times as long as width of head across eyes, length of antennal segments I to IV = 0.40, 0.20, 0.37, 0.27.



Figures 60–63. *Paralibiocoris limuensis* sp. n. Holotype male (**60, 61**) dorsal and ventral view; female (**62, 63**) dorsal and ventral view. Scale bars: 1 mm.

Pronotum. 3.06 times as wide as long (1.13/0.37); collar narrow; anterolateral lobes produced forward beyond collar as two (1+1) widely rounded granulate lobes, lateral margins converging anteriorly; structure of disc as in other congeners.

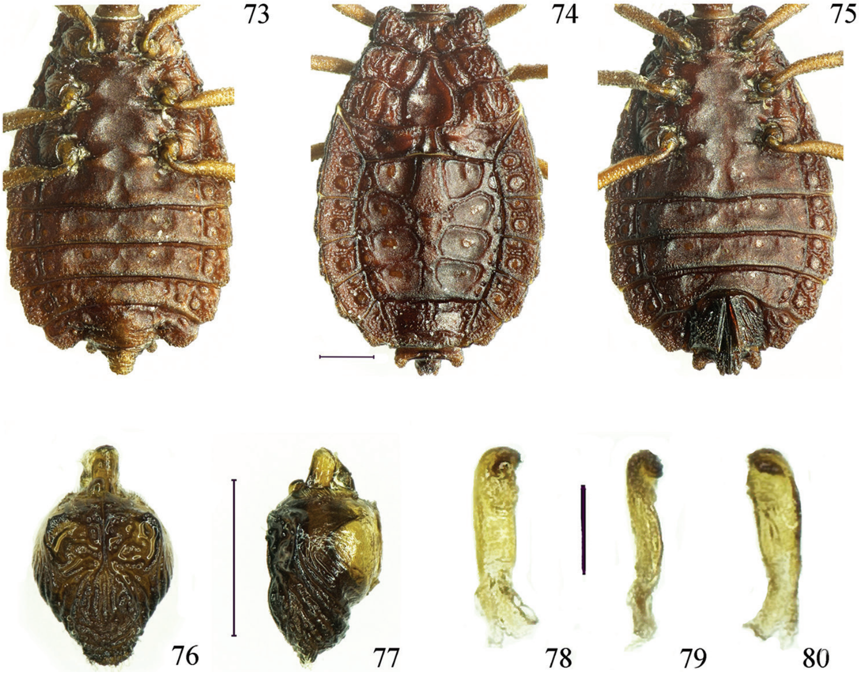
Mesonotum. Wider than pronotum (1.40/1.13); separated from metanotum by two (1+1) deep furrow laterally; across meso- and metanota medially with an elongate, anteriorly tapering leaf-like shaped plate, its surface slightly concave, 1.34 times as long as wide (0.63/0.47).



Figures 64–72. *Paralibiocoris limuensis* sp. n. Holotype male (**64, 65, 68, 69, 72**) dorsal and ventral thorax and abdomen; female (**66, 67, 70, 71**) dorsal and ventral thorax and abdomen. Scale bars: 0.5 mm.

Metanotum. Wider than mesonotum (1.6/1.40); separated from mtg I by a slightly sinuate thin sulcus.

Abdomen. Mtg I and II completely fused, disc medially with a barrel-shaped sclerite resembling the leaf-stalk of the leaf - shaped ridge, separated from lateral ovate plates



Figures 73–80. *Paralibiocoris limuensis* sp. n. Holotype male (**73**) ventral thorax and abdomen; female (**74, 75**) dorsal and ventral thorax and abdomen; pygophore dorsal and lateral view (**76, 77**); right paramere in three positions (**78, 79, 80**). Scale bars: 0.5 mm (**73–77**), 0.1 mm (**78–80**).

by deep furrows; tergal plate with a slightly elevated granulate ridge which is widest on mtg III, sloping posteriorly; pygophore elongate cordate, surface rugose (Figs 76, 77); parameres slender (Figs 78–80).

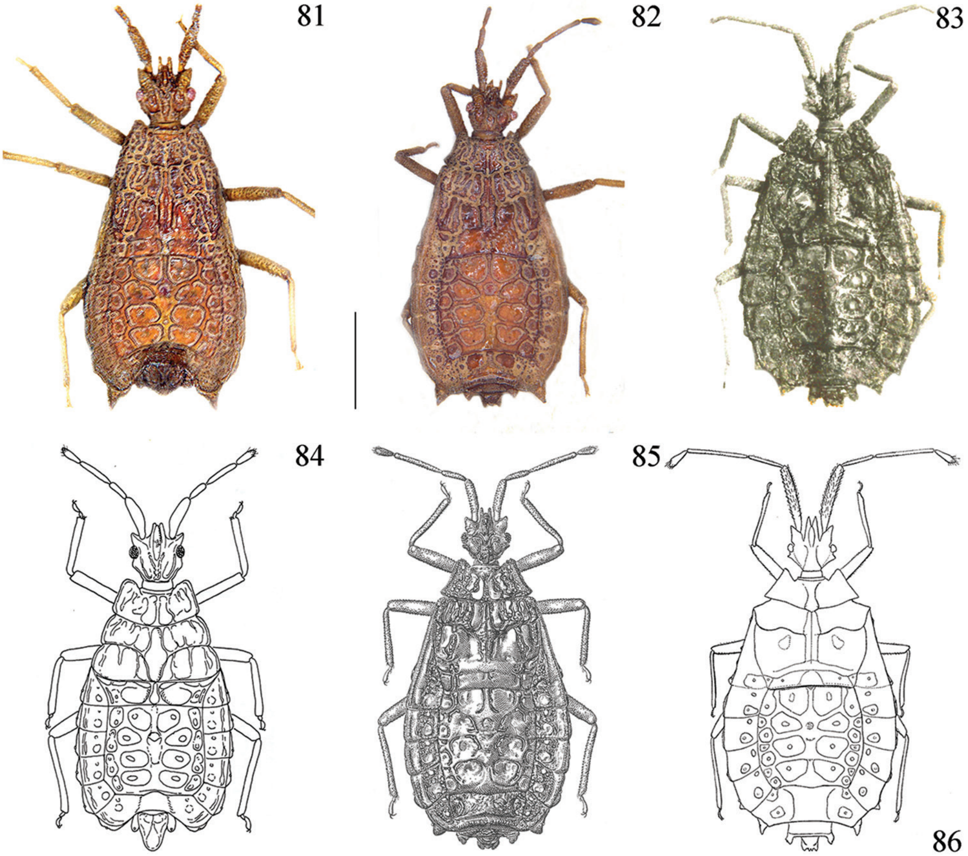
Venter. Vltg VII with a glabrous callus near spiracle VII; spiracles II ventral, spiracles III–VIII lateral and visible from above.

Female. Morphological features similar to male but of larger size; head slightly longer than wide across eyes (0.80/0.75); length of antennal segments I to IV = 0.44, 0.24, 0.37, 0.27; pronotum wider than long (1.17/0.40); width of mesonotum 1.6; width of metanotum 1.73; lateral margins of leaf-like median plate across meso- and metanota bisinuous, converging anteriorly to narrow apex, ratio length/width as of male (Figure 66); mtg VII moderately elevated posteriorly, surface rugose, posterolateral angles truncate.

Measurements. [in mm, ♂(n = 3)/♀ (n = 2), holotype in parentheses]. Body length 3.7-3.8/4.2-4.4 (3.8); maximal width of abdomen 1.76-1.9/2.2-2.3 (1.9). Head length 0.7-0.75/0.8 (0.75), width 0.65-0.68/0.7-0.75 (0.68). Pronotum length 0.35-0.37/0.4-0.45 (0.37), width 1.02-1.13/1.17-1.2 (1.13). Mesonotum width 1.3-1.4/1.5-1.6 (1.4). Metanotum width 1.5-1.6/1.73-1.8 (1.6). Length of antennal segments I–IV = 0.40, 0.20, 0.37, 0.27/0.4-0.44, 0.20-0.24, 0.37, 0.27 (0.40, 0.20, 0.37, 0.27).

Etymology. The name of species reflects the locality of this new taxon.

Distribution. China (Hainan).



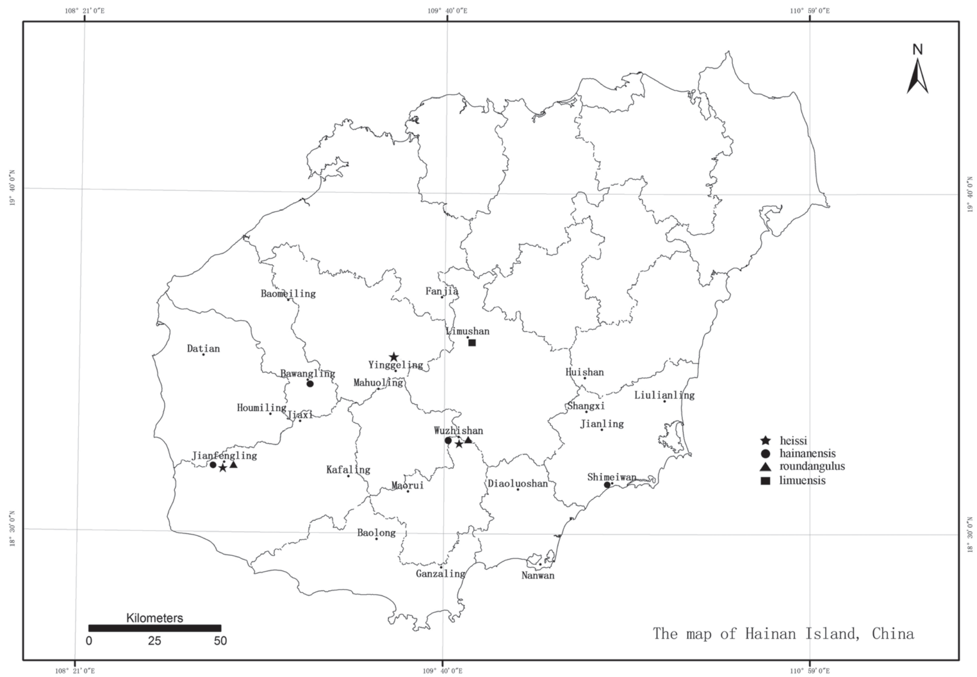
Figures 81–86. *Libiocoris*, habitus dorsal view. *L. poecilus* holotype male (**81**); ditto paratype female (**82**); *L. angulatus* holotype female (**83**); *L. indicus* holotype male (**84**)(after Heiss, 1982); *L. antennatus* holotype female (85) (after Usinger & Matsuda, 1959); *L. angulatus* holotype female, illustration in Usinger & Matsuda, 1959 with incorrect scale for antennae (**86**). Scale bar: 1 mm.

The case of *Libiocoris indicus* Heiss, 1982
Figure 84

Libiocoris indicus Heiss 1982: 248 (description), figs 3–5 (HNHM, CEHI).

The species was described upon two males and a female from Meghalaya State in the north of India, and shares several morphological characters with *Libiocoris* (habitus, head and antennae, fusion of thoracic segments) and according to the (misleading) redescription of *Libiocoris* (based on their new species *L. antennatus* Usinger & Matsuda, 1959) also the position of spiracles II-VII placed laterally and visible from above. Due to this similarity it was "tentatively" assigned to *Libiocoris*.

Re-examination of the paratype male of *indicus* has shown that it belongs neither to *Libiocoris* sensu Kormilev, 1957 (abbreviated L below) nor to *Paralibiocoris* gen. n. (abbreviated P below) showing following set of characters:



Map 1. Distribution of *Paralibiocoris* in China, Hainan Island.

- position of spiracles: II-VII lateral and visible from above (not L, not P);
- fused deltg I+II shorter, reaching laterally only to metanotum (as P, not L);
- distinct glabrous oblique callus on vltg VII of male is lacking (as L, not P);
- fused median thoracic ridge of different shape (not L, not P);
- median thoracic ridge is elevated to sulcus of border metanotum, mtg I+II then sloping posteriorly (as P, not L);
- median ridge of abdomen raised along midline (as P, not L);
- dorsally reflexed vltg VII is subrectangular and not produced (as P, not L);
- shape of pygophore pyriform and produced posteriorly (as P, not L).

The position of spiracles, different from both *Libiocoris* and *Paralibiocoris,* is recognized as a diagnostic character used in Aradidae taxonomy for distinguishing genera [e.g., *Acaricoris* from *Kolpodaptera*; *Parapictinus* from *Mezira* (Usinger & Matsuda, 1959)] which supports a separate generic category for *indicus*. As other similar specimens from Vietnam and Japan present in our collections need to be included in a separate study, we refrain here from describing a new genus, but this species should be removed from *Libiocoris* sensu Kormilev, 1957. Inconsistencies and remarkable differences in the descriptions and illustrations of *angulatus*, *antennatus*, *lobatus,* and *pilosus* compared with *poecilus* raise questions about their generic assignment.

Libiocoris Kormilev, 1957

Libiocoris Kormilev, 1957 (1956): 390 (original description).
Type species *poecilus* by original designation, 391: figs 1–5 male HT, female AT, New Guinea (LP) HNHM (Figs 81, 82).

Libiocoris antennatus Usinger & Matsuda, 1958: 181, fig. 53 female HT, New Guinea (LA) MNHUK, PT in CEHI ex. coll. Kormilev (Figure 85).

Libiocoris angulatus Usinger & Matsuda, 1959: 84, fig. 84 female HT, New Guinea (LG) MCSM.

Libiocoris angulatus Heiss, 1989: 349, figs 12a, b (redescription, correction antennae) (Figs 83, 86).

Libiocoris lobatus Kormilev 1968: 593 (description, no figure), New Guinea (LL); not seen.

Libiocoris pilicornis Kormilev, 1972: 568, figs 9, 9A, New Guinea (LPC); not seen.

Comparison of essential morphological characters and their differences

Anterior extension of fused deltg II+III reaching pronotum.

In LP present in types, not shown in Figure 1 of description; figured in LA, LG, LL?, figured only reaching mesonotum in LPC.

Position of spiracles denoted as + for visible from above and - for not visible. In LP II-III, VI-VII lateral +, IV ventral -, V sublateral -; LA II-VII lateral +; LG II-III lateral +, IV-V sublateral -; LL II-III, V-VIII lateral +, IV-V sublateral -; LPC II-VII lateral +.

Shape of median longitudinal ridge: in LP narrow with furrow; LA narrow with furrow; LG narrow, furrow figured; LL?; LPC posteriorly wider, without furrow.

As none of those female type specimens described after Kormilev's definition of *Libiocoris* shares all these characters, it is questionable as to what might be a valid character state and what is due to variability, and whether they belong to the same generic category. This question can be resolved when further material will be available for study and barcoding.

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We sincerely thank Tamás Vásárhelyi and David Redei (HNHM) and Roberto Poggi (MCSM) for the loan of types and the reviewers of the manuscript for their comments. This research is supported the National Natural Science Foundation of China (Nos. 31460573) to XB.

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RESEARCH ARTICLE

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A new species of the ant genus *Lasius* Fabricius, 1804 from Crete (Hymenoptera, Formicidae)

Sebastian Salata[1], Lech Borowiec[1]

[1] *Department of Biodiversity and Evolutionary Taxonomy, University of Wrocław, Przybyszewskiego 65, 51-148 Wrocław, Poland*

Corresponding author: *Sebastian Salata* (sdsalata@gmail.com)

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Abstract

Lasius tapinomoides **sp. n.** from Crete, Greece, is described and illustrated. It belongs to *L. turcicus* complex and is well characterized by very small body, extremely shallow metanotal groove and presence of suberect to erect setae on the apical part of scape. New records of Cretan members of the genus *Lasius* Fabricius, 1804 are provided, their checklist is updated, and the key to their determination is presented.

Keywords

Endemic species, Greece, *Lasius*, Mediterranean

Introduction

The genus *Lasius* Fabricius, 1804 is widely distributed throughout the Holarctic. Within its range, it is one of the most abundant of all Formicidae genera and its species are very often dominants of local myrmecofauna (Janda et al. 2004). Forty-three *Lasius* species are known from Europe and Mediterranean area (Borowiec 2014, Talavera et al. 2015, Seifert and Galkowski 2016), divided in five subgenera (Maruyama et al. 2008). The most numerous is the nominotypical subgenus *Lasius* s. str. Ruzsky, 1913 – 23 species, followed by *Chthonolasius* Ruzsky, 1913-13 species, *Cautolasius* Wilson, 1955 – 3 species, *Dendrolasius* Ruzsky, 1913 – 2 species, and *Austrolasius* Faber, 1967 - 2 species (Borowiec 2014, Talavera et al. 2015, Seifert and Galkowski 2016). Most of these species are characterised by possessing a wide geographical range. Only a few representatives of the subgenus *Lasius* s. str. are known from narrow area and could be considered as endemic species. Among these are *Lasius karpinisi* Seifert, 1992, known from Mt. Timfristos in the Greek mainland, *Lasius balearicus* Talavera, Espadaler & Vila, 2015 described from Mallorca and *Lasius casevitzi* Seifert & Galkowski, 2016 inhabiting Corsica.

Crete, as one of the largest Mediterranean islands, with very diverse, mountainous landscape (Grove and Rackham 1993), has poorly known myrmecofauna and requires more detailed study. Based on the literature, seven *Lasius* species are known from this island (Forel 1886, 1889, 1910, Neuenschwander et al. 1983, Legakis 2011, Borowiec and Salata 2012). However, presence of some of them requires confirmation. During our fieldwork, performed in different parts of Crete, new ant material was collected. Together with material deposited in the Natural History Museum of Crete it was used to review Cretan *Lasius* species. As results of this research a new species has been discovered and few other species have been recognised as new records for Crete. Below we describe *Lasius tapinomoides*, a new Cretan endemic, provide detailed occurrence data of other Cretan *Lasius* species, and present an identification key.

Materials and methods

Ants were sampled between 2007 and 2014 from sites in different parts of Crete. The method was direct sampling (hand collecting). Individual specimens and nests were collected on the ground, in leaf litter and rock rubble, under stones and tree trunks. All specimens were preserved in 75% EtOH. Study was supported with material deposited in the Natural History Museum of Crete (Iraklion, Greece).

Examined specimens are housed in the following collections:

BMNH	Natural History Museum, London;
DBET	Department of Biodiversity and Evolutionary Taxonomy, University of Wrocław, Poland;
HNHM	Hungarian National History Museum, Budapest, Hungary;
MSNG	Museo Civico di Storia Naturale, Genova, Italy;
NHMB	Naturhistorisches Museum Basel, Switzerland;
NHMC	Natural History Museum of Crete, Iraklion;
SMNG	Senckenberg Museum für Naturkunde Görlitz, Görlitz, Germany.

Specimens were compared using standard methods of comparative morphology. Photos were taken using a Nikon SMZ 1500 stereomicroscope, Nikon D5200 photo camera, and Helicon Focus software.

All given label data are in original spelling, presented in quotation marks; a slash (/) separates data on different rows and double slash (//) separate labels.

Specimens of *Lasius tapinomoides* sp. n. were compared with all other known Cretan species of the genus *Lasius* and type material of members of the *Lasius alienus* group listed below. Type specimens photographs of the *Lasius alienus* group members are available online on AntWeb (www.AntWeb.org) and are accessible using the unique CASENT or FOCOL identifying specimen code. Moreover, we compared them with samples of members of the *Lasius alienus* group from other Greek regions. Data concerning distribution of Greek *Lasius* samples used in the comparison is provided in series of regional checklists (Borowiec and Salata 2012, 2013, 2014, 2017a,b, 2018, Bračko et al. 2016). Therefore, we see no reason to repeat this information. The list of Cretan *Lasius* species, together with their occurrence data on the island is provided below. This study was also supported by data published in recent revisions of *Lasius* s. str. (Seifert 1992, Talavera et al. 2015, Seifert and Galkowski 2016).

We decided to list all other ant species collected from the same localities where the new species has been found. In our opinion it provides valuable information about ecosystem structure and species diversity characteristic for habitats preferred by this species. Distribution maps of all recorded *Lasius* species were created in DivaGis 7.5 (Hijmans et al. 2011).

Measurements:

EL	eye length; measured along the maximum vertical diameter of eye;
EW	eye width; measured along the maximum horizontal diameter of eye;
HL	head length; measured in straight line from mid-point of anterior clypeal margin to mid-point of posterior margin; the head must be carefully tilted to the position with the true maximum; excavations of posterior margin reduce HL;
HTL	hind tibia length; maximum length of hind tibia;
HW	head width; measured in full-face view directly above the eyes;
ML	mesosoma length; measured as diagonal length from the anterior end of the neck shield to the posterior margin of the propodeal lobe;
PNW	pronotum width; maximum width of pronotum in dorsal view;
SL	maximum straight-line scape length excluding the articular condyle.

Indices:

HI	HW/HL * 100;
SI1	SL/HL * 100;
SI2	SL/HW * 100;
MI	HTL/ML * 100;
EI1	EW/EL * 100;
EI2	EW/HL * 100;
TI	HW/HTL * 100.

Abbreviations:

q.	gyne;
w.	worker.

Pilosity inclination degree applies to this used in Hölldobler and Wilson (1990). The adpressed (0–5°) hairs run parallel, or nearly parallel to the body surface. Decumbent hairs stand 10–15°, subdecumbent hair stands 30°, suberect hairs stand 35–45°, the erect hairs stand more than 45° from the body surface.

Type material of taxa compared with *Lasius tapinomoides* sp. n.

Lasius alienus (Foerster, 1850), neotype (w.) (FOCOL0754): "GER: Eifel, 7.9.1991 / 37km SE Aachen / Schleiden / leg. Seifert // *Formica aliena* / Förtser 1850 / Neotype / des B. Seifert 1992" (SMNG);

L. austriacus Schlick-Steiner, Steiner, Schödl & Seifert, 2003, paratype (w.) (CASENT0916646): "#11055: Feldberg near / Pulkau, Austria (15°51'E/ / 48°40'N), 360 m / a.s.l., 06.08.2002. // leg. B.C. Schlick-Steiner & / F.M Steiner // *Lasius austriacus* / Schlick-Steiner / 2003 / PARATYPE" (HNHM); paratype (q.) (CASENT0916647): "#11055: Feldberg near / Pulkau, Austria (15°51'E/ / 48°40'N), 360 m / a.s.l., 06.08.2002. // PARATYPE / *Lasius austriacus* / design. Schlick-Steiner, Steiner / Schödl & Seifert 2003" (HNHM);

L. neglectus Van Loon, Boomsma & Andrasfalvy, 1990, paratype (w.) (CASENT0903220): "*Lasius neglectus* // HUNGARY / Budapest / 1.VII.88 / JJ. Boomsma // ANTWEB / CASENT / 0903220 // BMNH(E) / 1016243 // PARA- / TYPE" (BMNH);

Lasius paralienus Seifert, 1992, paratype (w.) (FOCOL0751): "Germania: Kr. Bautzen / 2 km S Weißenberg; N066 / 11.7.1991, leg. Seifert // *Lasius paralienus* / Seifert / Holotypus" (SMNG);

Lasius psammophilus Seifert, 1992, holotype (w.) (FOCOL0752): "GER: Kr Weißwasser / 4 km N Steinbach: N 135 / 30.7.1991 leg. Seifert // *Lasius psammophilus* / Seifert / Holotype" (SMNG);

Lasius turcicus Santschi, 1921, lectotype (w.) (CASENT0912297): "*Lasius* / turcicus / Santschi / Type / SANTSCHI det. 1920 // lectotype / desig. by / E. O. Wilson // Asie min. / Angora / G. d. Kerville // Sammlung / Dr. F. Santschi / Kairouan // ANTWEB / CASENT / 0912297" (NHMB).

Results

Lasius tapinomoides sp. n.

http://zoobank.org/412DD1F4-21DA-4A85-B4CB-5031FC049560
Figs 1–7

Type material. Holotype (w.): "*Lasius* / *tapinomoides* sp. nov. / HOLOTYPE // Collection L. Borowiec / Formicidae / LBC-GR00976 // GREECE, Crete, Rethymno Pr. / Antonios Spilia Gorge / 35°15.245 N,24°34.220 E / 11 V 2013, 342 m /

Table 1. Measurements and indices: *L. tapinomoides* and *L. turcicus*.

Measurements and indices	***L. tapinomoides* N = 10**	***L. turcicus* N = 10**
HL	0.707 ± 0.02 (0.679–0.749)	0.891 ± 0.06 (0.782–0.983)
HW	0.578 ± 0.03 (0.525–0.637)	0.798 ± 0.06 (0.682–0.905)
SL	0.668 ± 0.02 (0.625–0.715)	0.836 ± 0.04 (0.743–0.95)
EL	0.179 ± 0.008 (0.167–0.19)	0.214 ± 0.012 (0.201–0.235)
EW	0.132 ± 0.004 (0.123–0.136)	0.157 ± 0.015 (0.123–0.184)
ML	0.791 ± 0.04 (0.726–0.827)	1.06 ± 0.08 (0.935–1.18)
HTL	0.709 ± 0.02 (0.682–0.76)	0.892 ± 0.05 (0.799–0.961)
PNW	0.417 ± 0.018 (0.38–0.447)	0.558 ± 0.04 (0.48–0.631)
HI	81.8 ± 3.3 (73.4–85.0)	90.2 ± 1.8 (87.2–92.8)
SI1	94.5 ± 1.5 (91.4–96.3)	93.9 ± 2.9 (87.8–98.7)
SI2	115.7 ± 4.4 (112.2–127.6)	104.7 ± 3.6 (97.3–109.3)
MI	89.0 ± 3.1 (84.8–95.5)	84.5 ± 3.0 (81.1–91.9)
EI1	74.0 ± 3.6 (68.7–80.2)	73.3 ± 4.6 (61.2–78.3)
EI2	18.9 ± 0.9 (17.0–19.9)	17.8 ± 1.3 (15.0–19.8)
TI	82.0 ± 2.6 (75.8–85.2)	89.2 ± 2.2 (85.4–93.8)

L.Borowiec // CASENT0845075" (DBET); paratypes (6w.,1q.): data same as holotype, CASENT0845076 to CASENT0845082 (DBET, NHMC, NHMB); paratypes (15w.), CASENT0845460 to CASENT0845474: "GREECE, Crete, Rethymno Pr. / Kato Malaki / 35.28333 N,24.4 E / 15 V 2013, 235 m / L. Borowiec" (DBET, NHMC, BMNH).

Non-type material. 2w. (pin): "Collection L. Borowiec / Formicidae / LBC-GR00467 // GREECE, W Crete, 339 m / Plemeniana n. Kandanos / 35.31666 N,23.71666 E / 2 V 2011, L. Borowiec (DBET); 1w. (pin): Collection L. Borowiec / Formicidae / LBC-GR01420 // GREECE, Crete, Rethymno / Orthes Gorge, 318 m / 35.3336 N,24.6848 E / 28 IV 2014, S. Salata" (DBET); 2w. (pin): "Collection L. Borowiec / Formicidae / LBC-GR00993 // GREECE, Crete, Rethymno / n. Argioupolis / 35.28333 N,24.33333 E / 13 V 2013, 197 m / L. Borowiec" (DBET); 1w. (pin): "GREECE, Crete, Rethymno Pr. / Preveli Beach / 35.16666 N,24.46666 E / 7 V 2013, 10 m / L. Borowiec" (DBET); 7w. (pin): "GREECE, Crete, Rethymno Pr. / Road to Preveli Beach loc. 1 / 35.16666 N,24.45 E / 7 V 2013, 58 m / L. Borowiec" (DBET; 12w. (EtOH), Crete, Lasithi Prov., Gorge of Richtis, 35.16667N, 25.98333E, 245m, 08.iv.2014, leg. S. Salata (DBET); 2w. (EtOH), Orthes Gorge, 35.3336N,24.6848E, 318 m, 28.iv.2014, leg. S. Salata (DBET); 3w. (EtOH), Antonios Spilia Gorge, 35°15.245 N,24°34.220, 342m, 11.v.2013, leg. S. Salata (DBET); 5w. (EtOH), road to Preveli Beach loc. 1, 35.16666N,24.45E, 58m, 7.v.2013, leg. S. Salata (DBET).

Etymology. The name refers to the similarity of this species to species of the *Tapinoma* genus, caused by a very shallow metanotal groove.

Description. Worker.

Measurements: see Table 1.

Head, mesosoma, petiole and gaster uniformly coloured, brown to dark brown. Antennae, tibiae and tarsi bright brown to orange (Figs 1–4).

Figures 1–2. *Lasius tapinomoides* sp. n., holotype. **1** Lateral view **2** Dorsal view. Scale bar: 0.5 mm.

Head oval, 1.2 times as wide as long, lateral surfaces above eyes convex, occipital margin of head slightly convex (Figs 3–4). Clypeus shiny and smooth, its anterior margin convex, lacking median anterior notch, covered with sparse, decumbent to erect pubescence, average distance between setae longer than three fourths of their length.

Figures 3–5. *Lasius tapinomoides* sp. n. **3** Holotype, head with antennae **4** Holotype, head **5** Gyne, head. Scale bar: 0.5 mm.

Masticatory border of mandibles with 7–8 teeth. Eyes medium-sized, oval, 0.25 times as long as length of the head. Antennal scape long, straight or slightly curved on its anterior part, 0.9 times as long as length of the head, exceeding beyond occipital margin of head, in apex gradually widened. Pedicel more than 2.0 times longer than wide, average 2.5 times longer than second segment of funiculus. Other funicular segments from 1.5 to 2.0 times longer than wide (Figs 3–4). Surface of scape with very fine microreticulation, shiny. Its surface covered with thin, dense, adpressed setae, on its apical part several suberect setae also occur.

Genae with few adpressed to suberect setae (Figure 3). Underside of head with thin, dense, adpressed setae and a few long, suberect to erect setae (Figure 1). Whole frontal head surface covered with short, adpressed and dense pubescence and sparse, long, thick suberect to erect setae, the distance between setae at least as long as three fourths of their length (Figs 3–4).

Figures 6–7. *Lasius tapinomoides* sp. n., gyne. **6** Lateral view **7** Dorsal view. Scale bar: 0.5 mm

Mesosoma short, 1.9 times as long as wide. In lateral view, promesonotum low and flattened, metanotal groove very shallow, propodeum very low, propodeal dorsum slightly convex, propodeal declivity convex, less than twice length of propodeal dorsum (Figure 1). Whole mesosoma surface shiny with sparse microreticulation, covered with short, adpressed and dense pubescence, and sparse, long, thick suberect to erect setae, the distance between setae at least as long as half of their length, metapleuron below the level of the propodeal spiracle with more than 5 setae (Figs 1–2).

Petiole scale low, in lateral view with slightly convex sides, its dorsal crest thick and arched (Figure 1). Gaster with very rare and fine microreticulation, shiny, bearing pilosity similar to this covering mesosoma. Legs long, shiny, with fine microreticulation. Surface of tibia and femora with thin, dense, adpressed to subdecumbent setae, extensor profile without erect setae (Figs 1–2).

Description. Gyne.

Measurements and Indices (n=1): HL: 1.03; HW: 1.2; SL: 0.9; EL: 0.3; EW: 0.24; ML: 2.3; HTL: 1.3; PNW: 1.4; HI: 116.5; SI1: 87.4; SI2: 75; MI: 56.5; EI1: 80; EI2:23; TI: 92.

Head, mesosoma, petiole and gaster dark brown. Antennae, tibiae and tarsi bright brown to orange (Figs 5–7).

Head trapezoidal, 1.1 times as wide as long, lateral surfaces above eyes convex, sides of occipital margin of head slightly convex, its central part concave (Figure 5). Clypeus shiny and smooth, its anterior margin convex, lacking median anterior notch, covered with decumbent to erect setae, average distance between setae longer than one third of their length. Masticatory border of mandibles with seven teeth. Eyes medium-sized, oval, 0.3 times as long as length of the head. Antennal scape short, curved on its anterior part, 0.9 times as long as length of the head, slightly exceeding beyond occipital margin of head, in apex gradually widened. Pedicel more than 2.0 times longer than wide, 2.0 times longer than second segment of funiculus. Other funicular segments from 1.5 to 2.0 times longer than wide (Figure 5). Surface of scape with very fine microreticulation, shiny. Its surface covered with thin, dense, adpressed to decumbent pubescence, on its apical part a few short, suberect setae also occur. Genae with thin, dense adpressed pubescence and a few suberect setae (Figure 5). Underside of head with thin, dense, adpressed pubescence and a few long, suberect setae (Figure 6). Whole frontal head surface covered with short, adpressed and dense pubescence and sparse, long, thick suberect to erect setae, the distance between setae at least as long as three fourths of their length (Figs 5–6).

Mesosoma long, 1.6 times as long as wide. In lateral view moderately high, its dorsum slightly convex, propodeal dorsum slightly convex, propodeal declivity convex (Figure 6). Whole mesosoma surface shiny with very sparse microreticulation, covered with short, adpressed and dense pubescence, and sparse, long, thick suberect to erect setae, the distance between setae at least as long as half of their length (Figs 6–7).

Petiole scale low and wide, in lateral view with slightly convex sides, its dorsal crest wide and deeply concave in central part. Gaster with moderately thick and fine microreticulation, shiny, bearing pilosity denser than this covering mesosoma. Legs long, shiny, with fine microreticulation. Surface of tibia and femora with thin, dense, adpressed to subdecumbent setae, extensor profile of tibia with erect setae (Figs 6–7).

Differential diagnosis. Worker. As a member of the *L. alienus* group it is characterized by dorsal plane of scape, genae, and extensor profile of hind tibiae lacking or having very few erect or suberect setae and, in all species known from Crete, presence of >15 erect setae on the occipital edge of the head. Within the *L. alienus* group it can be classified to the *L. turcicus* complex. This complex can be characterized by small number of mandibular teeth (6–8), usually lack of suberect setae on hind tibia, very sparse clypeal pubescence, and more or less shallow metanotal groove. There are three known species of this complex: *L. turcicus*, *L. neglectus* and *L. austriacus*. *Lasius tapinomoides* sp. n. differs from all of them in presence of suberect to erect setae on antennal scape covering its apical part (ca. 1/3 upper part of the scape). Additionally from first two relatives it differs also in very shallow metanotal groove and from *L. austriacus* it differs in more flattened promesonotum, antennal sockets set not very close to posterior clypeal margin and habitat preferences. *Lasius austriacus* is related with xerothermous sites (Schlick-Steiner et al. 2003, Steiner et al. 2004) while *L. tapinomoides* inhabits moist, closed canopy forests.

There are two other species of the *L. alienus* group known from Crete: *L. bombycina* Seifert & Galkowski, 2016 and *L. turcicus* Santschi, 1921. *Lasius tapinomoides* differs from all of them in very small body size. Nevertheless, at the first glance it can be confused with small workers of *L. turcicus*, from which it differs in the following measurements (*L. tapinomoides* sp. n. vs *L. turcicus*): HI: 81.8 ± 3.3 (73.4–85.0) vs 90.2 ± 1.8 (87.2–92.8), SI2: 115.7 ± 4.4 (112.2–127.6) vs 104.7 ± 3.6 (97.3–109.3), TI: 82.0 ± 2.6 (75.8–85.2) vs TI: 89.2 ± 2.2 (85.4–93.8). For more measurements data see Table 1.

Gyne. During our fieldwork we could observe several gynes of *L. tapinomoides* and all detected nests were monogynous. Unfortunately, we were able to collect only a single specimen, therefore we provide very scarce data. As a coherent differential diagnosis is impeded, we decided to limit it to the most visible difference. Based on the morphology, *L. tapinomoides* differs from *L. turcicus*, *L. austriacus* and *L. neglectus* in presence of erect setae on tibiae.

General distribution. Greece: Crete – endemic species.

Biology. Species inhabiting moist, closed canopy forests, which are most often located in stream valleys. Nesting in wet soil, under shallow and small rocks. Nests, most often, located in the vicinity of water sources. Workers were found in the litter or on the rocks surrounding the nest entrance. Colonies monogynous.

The following ant species were recorded in the same areas as *L. tapinomoides*:

Antonios Spilia Gorge: *Aphaenogaster cecconii* Emery, *A. rugosoferruginea* Forel, *A. simonellii* Emery, *Camponotus candiotes* Emery, *C. lateralis* (Olivier), *Crematogaster ionia* Forel, *Messor wasmanni* Krausse, *Pheidole* cf. *pallidula*, *Stigmatomma denticulatum* Roger, *Temnothorax ariadnae* Csősz, Heinze & Mikó, *T.* cf. *graecus*, *T.* cf. *exilis*, *T.* cf. *luteus*, *Tetramorium caespitum* (Linnaeus), *T. diomedeum* Emery;

Plemeniana n. Kandanos: *Aphaenogaster rugosoferruginea*, *A. simonellii*, *Camponotus candiotes*, *C. gestroi* Emery, *C. lateralis*, *Colobopsis truncata* (Spinola), *Crematogaster* cf. *ionia*, *Lasius lasioides* (Emery), *Messor ibericus* Santschi, *Tetramorium caespitum*;

Orthes Gorge: *Aphaenogaster cecconii*, *A.* cf. *subterranea*, *A. simonellii*, *Camponotus baldaccii* Emery, *C. candiotes*, *C. jaliensis* Dalla Torre, *C. kiesenwetteri* (Roger), *C. rebeccae* Forel, *Crematogaster sordidula* (Nylander), *Lasius lasioides*, *Lepisiota nigra* Dalla Torre, *Messor* cf. *muticus*, *M. wasmanni*, *Tetramorium* cf. *caespitum*, *T. kephalosi* Salata & Borowiec

n. Argioupolis: *Aphaenogaster cecconii*, *A. rugosoferruginea*, *A. simonellii*, *Camponotus candiotes*, *C. lateralis*, *Crematogaster* cf. *ionia*, *Lepisiota nigra*, *Messor* cf. *muticus*, *M. wasmanni*, *Pheidole* cf. *pallidula*, *Plagiolepis pallescens* sensu Radchenko, *Temnothorax* cf. *luteus*, *T. ariadnae*, *T.* cf. *exilis*, *T.* cf. *graecus*, *Tetramorium* cf. *caespitum*;

Preveli Beach: *Aphaenogaster cecconii*, *Crematogaster ionia*, *Lasius psammophilus* Seifert, *Lepisiota melas* (Emery), *Pheidole* cf. *pallidula*, *Tapinoma festae* Emery, *Tetramorium kephalosi*;

road to Preveli Beach loc. 1: *Aphaenogaster rugosoferruginea*, *A. simonellii*, *Camponotus baldaccii*, *C. candiotes*, *C. gestroi*, *C. kiesenwetteri*, *C. lateralis*, *Cardiocondyla mauritanica* Forel, *Crematogaster* cf. *ionia*, *Cryptopone ochracea* (Mayr), *Lasius lasioides*, *L. bombycina* Seifert & Galkowski, *L. psammophilus*, *Lepisiota nigra*, *Messor ibericus*, *M. wasmanni*, *Pheidole* cf. *pallidula*, *Plagiolepis pallescens* sensu Radchenko, *Temnothorax* cf. *luteus*, *T.* cf. *graecus*, *T. recedens* (Nylander), *Tetramorium* cf. *caespitum*;

Kato Malaki: *Aphaenogaster simonellii*, *Camponotus baldaccii*, *C. gestroi*, *C. jaliensis*, *Crematogaster* cf. *ionia*, *Crematogaster sordidula*, *Messor ibericus*, *M. wasmanni*, *Pheidole* cf. *pallidula*, *Plagiolepis pallescens* sensu Radchenko, *Temnothorax ariadnae*, *T. recedens*, *Tetramorium diomedeum*, *Tetramorium punctatum* Santschi;

Gorge of Richtis: *Aphaenogaster rugosoferruginea*, *Camponotus candiotes*, *C. gestroi*, *C. lateralis*, *Crematogaster sordidula*, *Lasius lasioides*, *Messor wasmanni*, *Temnothorax* cf. *exilis*, *T.* cf. *graecus*, *Tetramorium* cf. *caespitum*.

Comments. We examined several hundred specimens of *Lasius turcicus* from 76 samples across Greece and western Turkey (including initial nest samples), also numerous samples from Crete (see new material listed below). In none of these samples did we find specimens with such a shallow metanotal groove like in *L. tapinomoides*. This character is constant in all examined specimens and is always correlated with very small body size of workers and preference to humid habitats. Across all the sampled area within Greece and Turkey, where we collected species of the *L. turcicus* complex, we have not found workers or nests with workers similar to *L. tapinomoides*. Moreover, *L. tapinomoides* is the only known member of the *L. turcicus* complex that have suberect to erect setae on the apical 1/3 part of the antennal scape. This has prompted us to hypothesize that Cretan samples represent a new species.

New records of Cretan members of the genus *Lasius*

Lasius bombycina Seifert & Galkowski, 2016

GREECE, **Crete**: 2w (EtOH), Omalos, 35.31667N,23.9E, 1122 m, 03.v.2014, leg. S. Salata (DBET); 4w. (pin), 03.v.2011, Omalos Plateau, 35.33333N,23.88333E, 1034 m, leg. L. Borowiec (DBET); 1w. (EtOH), Potamida n. Mythimna, 35.46666N,23.68333E, 37 m, 02.v.2011, leg. L. Borowiec (DBET); 1w. (pin), W of Georgioupoli, 35.36666N,24.25E, 17 m, 02.v.2007, leg. L. Borowiec (DBET); 8w. (EtOH), Zaros Lake, 35.13333N,24.9E, 409 m, 26.iv.2014, leg. S. Salata

(DBET); 3w. (EtOH), Kato Symi loc. 3, 35.05N,25.48333E, 818 m, 16.iv.2014, leg. S. Salata (DBET); 4w. (EtOH), Lasithi Platou – Plati, 35.16667N,25.43333E, 831 m, 01.v.2014, leg. S. Salata (DBET); 2w. (EtOH), Orino, 35.06667N,25.9E, 523 m, 12.iv.2014, leg. S. Salata (DBET); 2w. (pin), Ag. Joannis Forest loc. 1, 35.23333N,24.4E, 448 m, 06.v.2013, leg. L. Borowiec (DBET); 1w. (pin), Ampelakiou, 35.26666N,24.46666E, 464 m, 10.v.2013, leg. L. Borowiec (DBET); 1w. (EtOH), Fourfouras, 35.21666N,24.71666E, 578 m, 14.v.2013, leg. S. Salata (DBET); 5w. (EtOH), n. Velonado, 35.25N,24.36667E, 373 m, 13.v.2013, leg. S. Salata (DBET); 2w. (EtOH), n. Vilandredo, 35.25N,24.31667E, 354 m, 13.v.2013, leg. S. Salata (DBET); 2w. (EtOH), road to Preveli Beach loc. 1, 35.16666N,24.45E, 58 m, 7.v.2013, leg. S. Salata (DBET); 3w. (EtOH), Selli-Oros rd., 35.28333N,24.5E, 473 m, 11.v.2013, leg. S. Salata, (DBET); 1w. (pin), Spili-Gerakari rd. loc. 2, 35.21987N,24.57144E, 804 m, 09.v.2013, leg. L. Borowiec (DBET); 1w. (EtOH), Asi Gonia, 35.25N,24.26667E, 716 m, 29.v.2001, leg. S. Salata (DBET); 1w. (EtOH), Niato plateau, 35.28333N,24.13333E, 1200 m, 19.vii.2013, leg. S. Salata (DBET); 1w. (EtOH), Therisso to Kaloros Mt., 35.35N,23.95E, 1130 m., 31.xii.2013, leg. Simaiakis (NHMC); 1w. (EtOH), Therisso to Kaloros Mt., 35.3667N,23.9833E, 1134 m., 19.Vii.2013, leg. Simaiakis (NHMC); 1w. (EtOH), Diplori, 35.1667N,24.9333E, 1350 m., 19.x.1999, leg. Nikolakakis (NHMC); 1w. (EtOH), Dikti Mt., 35.11667N,25.4667E, 1450 m., 9.i.2001, leg. Simaiakis (NHMC); 1w. (EtOH), Tigania, 35.28333N,24.7333E, 1100 m., 7.iv.2000, leg. Nikolakakis (NHMC).

Lasius myops Forel, 1894

GREECE, **Crete**: 3w. (pin), 3w. (EtOH), Anopoli, 35.26667N,24.06667E, 1780 m, 22.vii.2006, leg. Chatzaki M. (NHMC, DBET).

Lasius illyricus Zimmermann, 1935

GREECE, **Crete**: 6w. (pin), Limnakarou platou, 35.13333N,25.46667E, 1130 m, 26.iv.2014, leg. S. Salata (DBET); 6w. (EtOH), Limnakarou platou, 35.13333N,25.46667E, 1130 m, 10.iv.2014, leg. S. Salata (DBET); 2w. (EtOH), Dikti mt., 35.1N,25.46667E, 1750 m, 05.viii.2000, leg. M. Chatzaki (NHMC).

Lasius lasioides (Emery, 1869)

GREECE, **Crete**: 1w. (pin), Agia, 6 km SW Chania, 35.46666N,23.91666E, 22 m, 03.v.2011, leg. L. Borowiec (DBET); 5w. (pin), Askifou, 35.26666N,24.16666E, 730 m, 01.v.2007, leg. L. Borowiec & M.L. Borowiec (DBET); 7w. (EtOH), Diktamos Gorge n. Stilos, 35.43333N,24.1E, 160 m, 04.v.2011, leg. L. Borowiec (DBET); 3w. (EtOH), Kalives river, 35.45N,24.13333E, 26 m, 01.v.2014, leg. S. Salata (DBET); 1w. (pin), Kourna Lake, 35.31666N,24.28333E, 95 m, 03.v.2007, leg. L. Borowiec & M.L. Borowiec (DBET); 1w. (pin), Koutsomatados-Mili rd., 35.38333N,23.66666E, 308 m, 02.v.2011, leg. L. Borowiec (DBET); 2w. (EtOH), Omalos, 35.31667N,23.9E, 1122 m, 03.v.2014, leg. S. Salata (DBET); 1w. (pin), Plemeniana n. Kandanos, 35.31666N,23.71666E, 339 m, 02.v.2011, leg. L. Borowiec (DBET); 4w. (EtOH), Potamida n. Mythimna, 35.46666N,23.68333E, 37 m, 02.v.2011, leg. L. Borowiec (DBET); 17w. (EtOH), Therisso Gorge, 35.43333N,23.98333E, 320 m, 01.v.2011, leg. L. Borowiec (DBET); 3w. (EtOH), Ganies–Kalamaki road, 35.28333N,24.93333E, 439 m, 16.iv.2014, leg. S. Salata (DBET); 3w. (EtOH), Iraklion city-walls, 35.31667N,25.11667N, 46 m, 03.iv.2014, leg. S. Salata (DBET); 3w. (EtOH), Kastelli 1 km E, 35.2N,25,33333E, 363 m, 15.iv.2014, leg. S. Salata (DBET); 6w. (EtOH), Katofigi, 35.08333N,25.4E, 560 m, 12.iv.2014, leg. S. Salata (DBET); 2w. (EtOH), Miamou, 34.96667N,24.93333E, 494 m, 24.iv.2014, leg. S. Salata (DBET); 2w. (EtOH), Rouvas Forest loc. 1, 35.15N,24.93333, 1316 m, 10.iv.2014, leg. S. Salata (DBET); 3w. (EtOH), Rouvas Gorge, 35.13333N,24.9E, 455 m, 26.iv.2014, leg. S. Salata (DBET); 5w. (EtOH), Xanias–Miliarades road, 35.08333N,25.38333E, 504 m, 13.iv.2014, leg. S. Salata (DBET); 3w. (EtOH), Dead's Gorge, 35.08333N,26.25E, 15 m, 09.iv.2014, leg. S. Salata (DBET); 3w. (EtOH), Gorge of Richtis, 35.16667N,25.98333E, 245 m, 08.iv.2014, leg. S. Salata (DBET); 4w. (EtOH), Hristos–Mathokotsana road, 35.08333N,25.56667E, 703 m, 11.iv.2014, leg. S. Salata (DBET); 3w. (EtOH), Kalami–Psari Forada road, 35.016667N,25.48333, 419 m, 12.iv.2014, leg. S. Salata (DBET); 5w. (EtOH), Kato Symi loc. 1, 35.05N,25.48333E, 1206 m, 12.iv.2014, leg. S. Salata (DBET); 5w. (EtOH), Lasithi Platou – Pinakiano, 35.18333N,25.45E, 806 m, 23.iv.2014, leg. S. Salata (DBET); 3w. (EtOH), Lastros, 35.13333N,25.88333E, 336 m, 06.iv.2014, leg. S. Salata (DBET); 10w. (EtOH), Limnakarou plato, 35.13333N,25.46667E, 1130 m, 26.iv.2014, leg. S. Salata (DBET); 1w. (EtOH), Merisini, 35.16667N,25.9333E, 309 m, 06.iv.2014, leg. S. Salata (DBET); 3w. (EtOH), Mesa Lasithi, 35.16667N,25.5E, 838 m, 28.iv.2014, leg. S. Salata (DBET); 2w. (EtOH), Moni Kapsa, 35.01667N,26.05E, 1 m, 10.iv.2014, leg. S. Salata (DBET); 3w. (EtOH), Neapoli–Vrisses road, 35.2333N,25.6E, 443 m, 05.iv.2014, leg. S. Salata (DBET); 2w. (EtOH), Perma–Koutounari road, 35.01667N,25.83333E, 0 m, 11.iv.2014, S. Salata (DBET); 2w. (EtOH), Schinokapsala–Agios Ioannis road, 35.05N,25.85, 452 m, 10.iv.2014, leg. S. Salata (DBET); 3w. (EtOH), Tourloti–Mirsini road, 35.15N,25.93333E, 266 m, 06.iv.2014, leg. S. Salata (DBET); 2w. (EtOH), Voila, 35.08333N,26.1E, 578 m, 10.iv.2014, leg. S. Salata (DBET); 12w. (EtOH), Ag. Joannis Forest loc. 2, 35.23333N,24.4E, 480 m, 06.v.2013, leg. S. Salata (DBET); 2w. (EtOH), Chromonastiri, 35.326944N,24.510278E, 262 m, 10.v.2013, leg. S. Salata (DBET); 1w. (EtOH), Katsifou Gorge, 35.2N,24.38333E, 57 m, 05.v.2013, leg. S. Salata (DBET); 5w. (EtOH), Kissos, 35.18333N,24.56667E, 623 m, 09.v.2013, leg. L. Borowiec (DBET); 1w. (pin), Klisidi, 35.26666N,24.63333E, 642 m, 06.v.2013, leg. L. Borowiec (DBET); 4w. (EtOH), n. Velonado, 35.25N,24.36667E, 373 m, 13.v.2013, leg. S. Salata (DBET); 1w. (EtOH), n. Vilandredo, 35.25N,24.31667E, 354 m, 13.v.2013, leg. S. Salata (DBET); 3w. (EtOH), Orthes Gorge, 35.33333N,24.68333, 318 m, 28.iv.2014, leg. S. Salata (DBET); 2w. (EtOH), Plakias, 35.191389N,24.395E,

4 m, 05.v.2013, leg. S. Salata (DBET); 41w. (EtOH), Plakias; Akrotiri Kakomouri, 35.16667N,24.398055E, 28 m, 05.v.2013, leg. S. Salata (DBET); 1w. (pin), road to Preveli Beach loc. 1, 35.16666N,24.45E, 58 m, 07.v.2013, leg. L. Borowiec (DBET); 1w. (pin), Spili, 35.21666N,24.53333E, 537 m, 09.v.2013, leg. L. Borowiec (DBET); 1w. (pin), Vistagi, 35.23333N,24.68333E, 563 m, 06.v.2013, leg. L. Borowiec (DBET); 1w. (pin), Xirokambos, 35.110556N,24.558889E, 24 m, 12.v.2013, leg. L. Borowiec (DBET); 3w. (EtOH), Kournas lake, 35.31667N,24.26667E, 30 m, 10.vii.1997, leg. P. Lymberakis (NHMC); 1w. (EtOH), Kardaki, 650 m, 35.2N,24.61667E, 21.vii.1999, leg. E. Nikolakakis (NHMC).

Lasius psammophilus Seifert, 1992

GREECE, **Crete**: 4w. (EtOH), Agia Triada n. Kalamaki, 35.0508N,25.7542E, 1 m, 28.iv.2014, leg. S. Salata (DBET); 3w. (EtOH), Moni Kapsa, 35.01667N,26.05E, 1 m, 24.iv.2014, leg. S. Salata (DBET); 2w. (EtOH), Episkopi beach, 35.35N,24.35E, 0 m, 09.iv.2014, leg. S. Salata (DBET); 1w. (pin), Gerakari, 35.21666N,24.58333E, 751 m, 09.v.2013, leg. L. Borowiec (DBET); 1w. (pin), Plakias, 35.191389N,24.395E, 4 m, 05.v.2013, leg. L. Borowiec (DBET); 4w. (pin), Preveli Beach, 35.154444N,24.472778E, 10 m, 07.v.2013, leg. L. Borowiec (DBET); 1w. (EtOH), Irakleio, 35.33333N,25.13333E, 10 m, 18.ix.2010, leg. E. Panagiotou (NHMC); 2w. (EtOH), Chamaitoulo, 35.03333N,26.2E, 06.v.2001, 180 m, leg. E. Nikolakakis (NHMC).

Lasius turcicus Santschi, 1921

GREECE, **Crete**: 3w. (EtOH), Kalives river, 35.45N,24.13333E, 26 m, 03.v.2014, leg. S. Salata (DBET); 13w. (EtOH), Kato Daratso n. Chania, 35.5N,23.983333E, 35–40 m, 07.v.2011, leg. L. Borowiec (DBET); 4w. (pin), Koutsomatados–Mili rd., 35.38333N,23.66666E, 308 m, 02.v.2011, leg. L. Borowiec (DBET); 1w. (pin), Potamida n. Mythimna, 35.46666N,23.68333E, 37 m, 02.v.2011, leg. L. Borowiec (DBET); 1w. (pin), Agia Triada n. Kalamaki, 35.0508N,25.7542E, 1 m, 24.iv.2014, leg. S. Salata (DBET); 2w. (EtOH), Agios Eirini, 35.26667N,25.15E, 130 m, 02.iv.2014, leg. S. Salata (DBET); 4w. (EtOH), Avgeniki, 35.18333N,25.01667E, 227 m, 03.v.2014, leg. S. Salata (DBET); 3w. (EtOH), Kastelli 1 km E, 35.2N,25.33333E, 363 m, 16.iv.2014, leg. S. Salata (DBET); 5w. (EtOH), Katofigi, 35.08333N,25.4E, 560 m, 13.iv.2014, leg. S. Salata (DBET); 2w. (EtOH), Panastros, 35.11667N,24.98333E, 545 m, 03.v.2014, leg. S. Salata (DBET); 5w. (EtOH), Sfendili, 35.25N,25.38333E, 151 m, 06.iv.2014, leg. S. Salata (DBET); 2w. (EtOH), Stoli–Louves road, 35.03333N,25.01667E, 197 m, 30.iii.2014, leg. S. Salata (DBET); 2w. (EtOH), Xanias–Miliarades road, 35.08333N,25.38333E, 504 m, 25.iv.2014, leg. S. Salata (DBET); 3w. (EtOH), Dead's Gorge, 35.08333N,26.25E, 15 m, 09.iv.2014, leg. S. Salata (DBET); 3w. (EtOH), Hametoulo, 35.05N,26.18333E, 520 m, 12.iv.2014, leg. S. Salata (DBET); 3w. (EtOH), Kalamafka, 35.06667N,25.65E, 472 m, 12.iv.2014, leg. S. Salata (DBET); 6w. (EtOH), Lasithi Platou – Pinakiano, 8

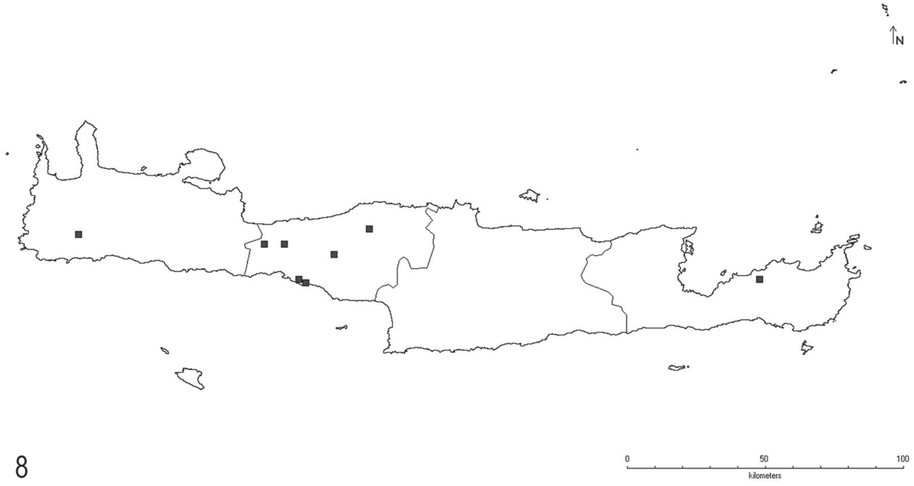
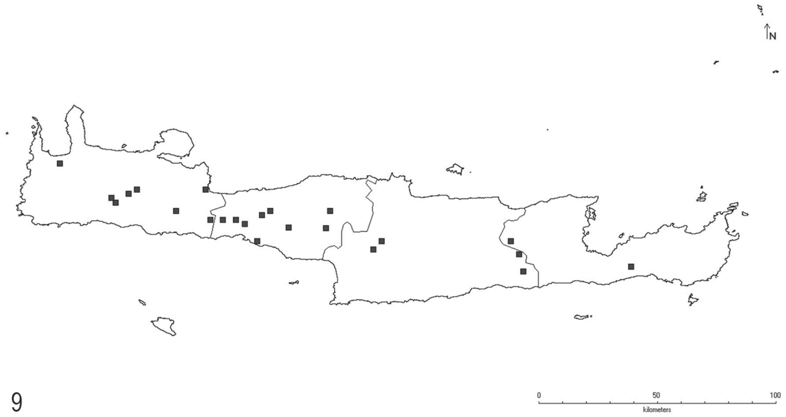


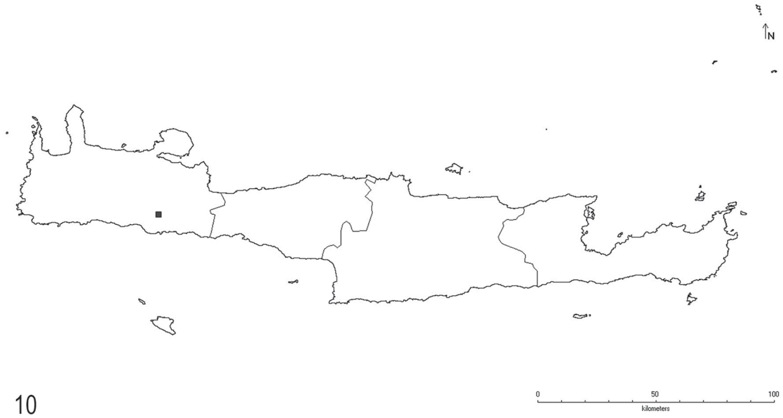
Figure 8. Distribution of *L. tapinomoides* sp. n. on Crete.

35.18333N,25.45E, 806 m, 28.iv.2014, leg. S. Salata (DBET); 2w. (EtOH), Praisos, 35.11667N,26.06667E, 193 m, 11.iv.2014, leg. S. Salata (DBET); 6w. (EtOH), Ag. Joannis forest loc. 1, 35.23333N,24.4E, 448 m, 06.v.2013, leg. S. Salata (DBET); 2w. (EtOH), Chromonastiri, 35.326944N,24.510278E, 262 m, 10.v.2013, leg. S. Salata (DBET); 3w. (EtOH), Frati, 35.2N,24.46666E, 297 m, 7.v.2013, leg. S. Salata (DBET); 2w. (EtOH), Kissos, 35.18333N,24.56667E, 623 m, 09.v.2013, leg. S. Salata (DBET); 1w. (EtOH), Kissou Kambros, 35.16666N,24.55E, 514 m, 14.v.2013, leg. S. Salata (DBET); 3w. (EtOH), Palelimnos, 35.3N,24.41666E, 262 m, 15.v.2013, leg. S. Salata (DBET); 4w. (EtOH), Plakias, 35.191389N,24.395E, 4 m, 05.v.2013, leg. S. Salata (DBET); 5w. (EtOH), road to Nida platou, 35.25N,24.88333E, 1166 m, 01.iv.2014, leg. S. Salata (DBET); 3w. (EtOH), Setoures, 35.26667N,24.38333E, 305 m, 15.v.2013, leg. S. Salata (DBET); 2w. (EtOH), Vistagi, 35.23333N,24.68333E, 563 m, 16.v.2013, leg. S. Salata (DBET); 1w. (EtOH), Agia lake, 35.46667N,23.93333E, 40 m, 08.vii.1997, leg. P. Lymberakis (NHMC); 2w. (EtOH), Almyros river, 35.33469N,25.05441E, 297 m, 03.vi.2012, leg. E. Aspradaki (NHMC); 1w. (EtOH), Aposelemis, 35.33333N,25.33333E, 7 m, 02.viii.2000, leg. A. Trichas (NHMC); 1w. (EtOH), Dikti mt., 35.11667N,25.46667, 1450 m, 05.viii.2000, leg. S. Simaiakis (NHMC); 2w. (EtOH), Dikti mt., 35.1N,25.46667E, 1750 m, 10.v.2001, leg. M. Chatzaki (NHMC); 2w. (EtOH), Before Amygdali after Neapoli, 35.2N,25.58333E, 561 m, 06.viii.1997, leg. I. Stathi (NHMC); 1w. (EtOH), Agios Titos, 35.18333N,24.75E, 1000 m, 14.iv.2000, leg. M. Papadimitrakis (NHMC); 1w. (EtOH), Ano Meros, 35.16667N,24.65E, 750 m, 15.iv.2000, leg. I. Stathi (NHMC); 3w. (EtOH), Garazo, 35.33333N,24.78333E, 100 m, 07.iv.2000, leg. E. Nikolakakis (NHMC); 1w. (EtOH), Tigania, 35.28333N,24.73333, 1100 m, 07.iv.2000, leg. E. Nikolakakis (NHMC).



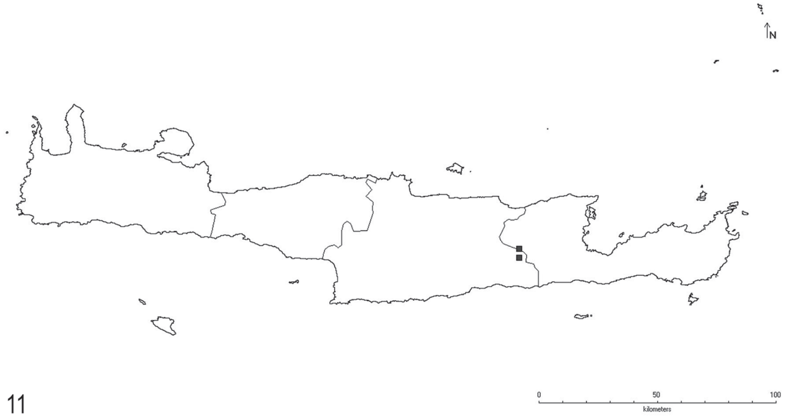
9

Figure 9. Distribution of *L. bombycina* Seifert & Galkowski on Crete.



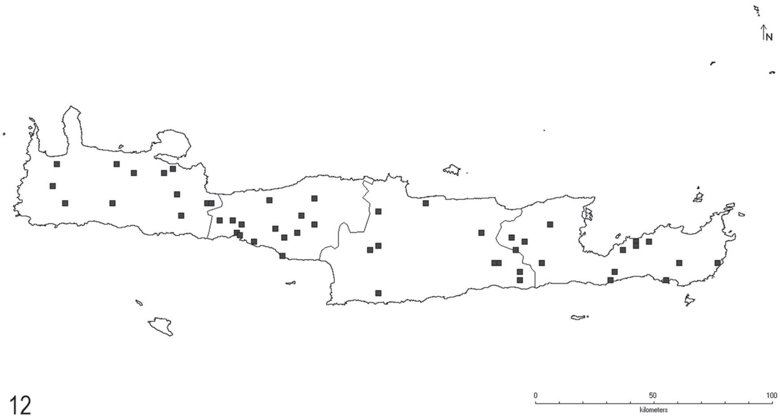
10

Figure 10. Distribution of *L. myops* Forel on Crete.



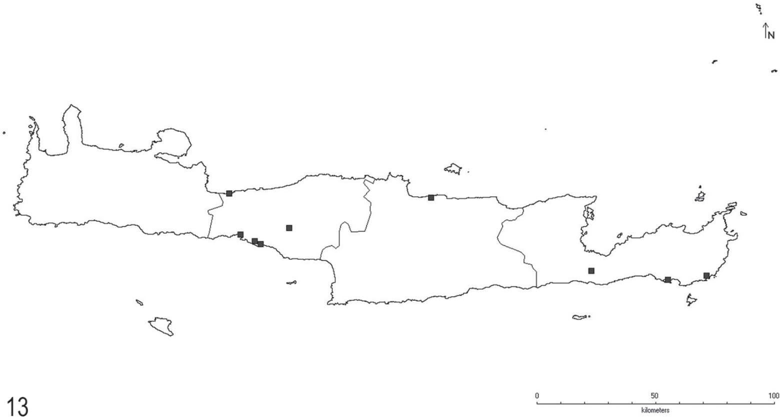
11

Figure 11. Distribution of *L. illyricus* Zimmerman on Crete.



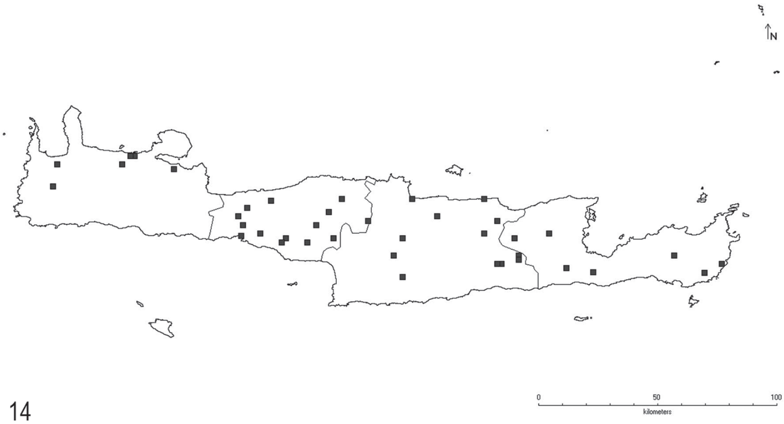
12

Figure 12. Distribution of *L. lasioides* (Emery) on Crete.



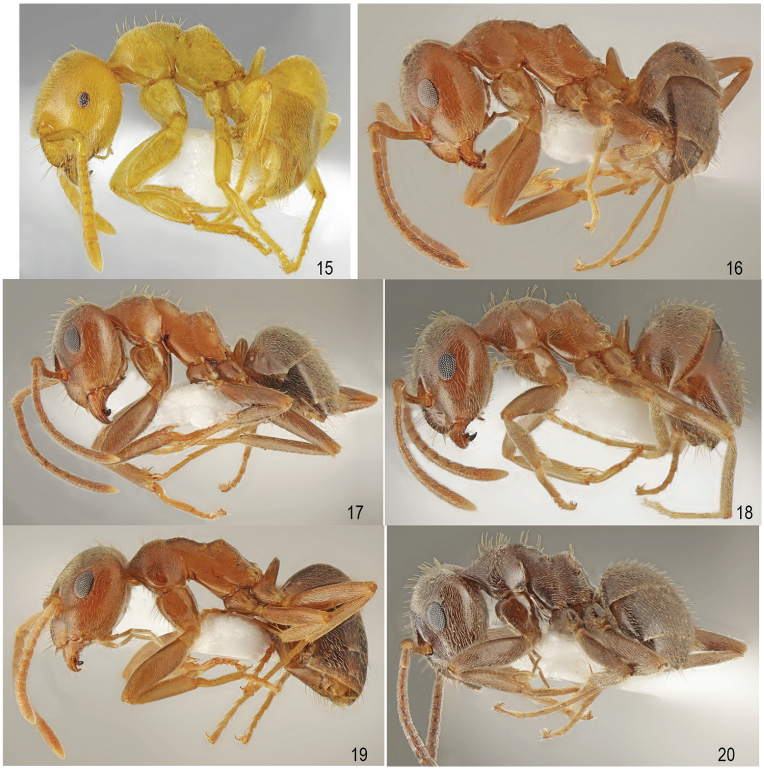
13

Figure 13. Distribution of *L. psammophilus* Seifert on Crete.



14

Figure 14. Distribution of *L. turcicus* Santschi on Crete.



Figures 15–20. Lateral view. **15** *Lasius myops* Forel **16** *L. lasioides* (Emery) **17** *L. illyricus* Zimmerman **18** *L. psammophilus* Santschi **19** *L. turcicus* Santschi **20** *L. bombycina* Seifert & Galkowski.

Figures 21–25. Head and scapus. **21** *L. lasioides* (Emery) **22** *L. illyricus* Zimmerman **23** *L. turcicus* Santschi **24** *L. bombycina* Seifert & Galkowski **25** *L. psammophilus* Santschi.

Key to Cretan *Lasius* species (based on the worker caste)

1. Maxillary palps short, not reaching midpoint between mouth and occipital foramen, body yellow to orange (Fig. 15)............................. ***L. myops*** **Forel**

– Maxillary palps long, distinctly reaching beyond midpoint between mouth and occipital foramen, body brown to black or bicoloured (Figs 1, 16–20) **2**

2. Scape, genae and hind tibiae only with perfectly adpressed pubescence, without setae, occipital margin of head usually with 8 erect setae at most (Fig. 21)... ***L. lasioides*** **(Emery)**

– Scape, genae and hind tibiae often with occasional setae, pubescence not perfectly adpressed, occipital margin of head with more than 8 erect setae (Figs 22–25) **3**

3. Scape with few (>5) erect setae, body bicoloured, hind tibiae with numerous erect setae, mesosoma brighter than head and gaster (Figs 17, 22) .... ***L. illyricus*** **Zimmerman**

– Scape without or with maximum 5 erect setae, hind tibiae without or with a few erect setae, body uniformly coloured or head and mesosoma uniformly coloured, brighter than gaster (Figs 18–20, 23–25)...................................**4**

4. Clypeus with dense pubescence, average distance between setae 3.5 times shorter than their length (Fig. 24).........***L. bombycina*** **Seifert & Galkowski**

– Clypeus with sparse pubescence, average distance between setae equal or longer than a half of their length (Figs 3–4, 23, 25) **5**

5 Workers small, ML 0.726–0.827 mm, mesosoma with very shallow metanotal groove, apical part of scape with >5 suberect to erect setae (Figs 1–4) ....***L. tapinomoides*** **sp. n.**

– Workers larger, ML 0.935–1.18 mm, metanotal groove distinct, apical part of scape without or with <5 suberect to erect setae (Figs 18–19, 23, 25) **6**

6 Metanotal groove relatively shallow, propodeal dorsum flattened, hind tibia usually without suberect setae, number of mandibular dents < 7.7 (Fig. 19) . ... ***L. turcicus*** **Santschi**

– Metanotal groove deeper and sharp, propodeal dorsum convex, hind tibia with few suberect setae, number of mandibular dents >7.7 (Fig. 18) ....***L. psammophilus*** **Santschi**

Discussion

Based on the literature (Forel 1886, 1889, 1910, Neuenschwander et al.1983, Legakis 2011, Borowiec and Salata 2012) there are 7 *Lasius* species reported from Crete: *L. alienus*, *L. brunneus* (Latreille), *L. niger* (Linnaeus), *L. paralienus* Seifert, *L. lasioides*, *L. psammophilus*, and *L. turcicus*, all members of the subgenus *Lasius* s. str. Our study confirmed the presence of the last 3 listed species and shown 4 species new for Cretan fauna: *L. bombycina*, *L. myops*, *L. illyricus* and *L. tapinomoides*, the latter being endemic to Crete and new to science. The first records of *L. alienus* and *L. niger* come from literature published in the 19th century (Forel 1886, 1889). Seifert (1992) proved that Crete is beyond the range of occurrence of these species, thus those records probably refer to *L. bombycina* or *L. psammophilus*. Based on most recent revisions (Seifert 1992, Seifert and Galkowski 2016) *Lasius brunneus* and *L. paralienus* should be also excluded from the list of Cretan species. On Crete they are replaced by *L. lasioides* and *L. bombycina* respectively. *Lasius myops* and *L. illyricus* were recorded on Crete only from high mountains (above 1000 m a.s.l.). These two species are common on Greek mainland, and most often were recorded from lower altitudes. Cretan record of *L. illyricus* is so far the southernmost known place of occurrence of this species. It is worth noting that all *Lasius* species known from Crete manifest independent colony foundation. The updated list of Cretan *Lasius* is as follows: *L. bombycina*, *L. myops*, *L. illyricus*, *L. lasioides*, *L. psammophilus*, *L. tapinomoides*, and *L. turcicus*, six members of *Lasius* s. str. and one representative of *Cautolasius*.

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