



TEXAS TECH UNIVERSITY

Natural Science Research Laboratory

SPECIAL PUBLICATIONS

Museum of Texas Tech University

Number 67

17 July 2018

HARVESTMEN OF THE FAMILY PHALANGIIDAE (ARACHNIDA, OPILIONES) IN THE AMERICAS



JAMES C. COKENDOLPHER AND ROBERT G. HOLMBERG

Front cover: *Opilio parietinus* in copula (male on left with thicker legs and more spines) from Baptiste Lake, Athabasca County, Alberta. Photograph by Robert G. Holmberg.

SPECIAL PUBLICATIONS

Museum of Texas Tech University

Number 67

Harvestmen of the Family Phalangiidae (Arachnida, Opiliones) in the Americas

JAMES C. COKENDOLPHER AND ROBERT G. HOLMBERG

Layout and Design: Lisa Bradley
Cover Design: Photograph by Robert G. Holmberg
Production Editor: Lisa Bradley

Copyright 2018, Museum of Texas Tech University

This publication is available free of charge in PDF format from the website of the Natural Sciences Research Laboratory, Museum of Texas Tech University (nsrl.ttu.edu). The authors and the Museum of Texas Tech University hereby grant permission to interested parties to download or print this publication for personal or educational (not for profit) use. Re-publication of any part of this paper in other works is not permitted without prior written permission of the Museum of Texas Tech University.

This book was set in Times New Roman and printed on acid-free paper that meets the guidelines for permanence and durability of the Committee on Production Guidelines for Book Longevity of the Council on Library Resources.

Printed: 17 July 2018

Library of Congress Cataloging-in-Publication Data

Special Publications of the Museum of Texas Tech University, Number 67
Series Editor: Robert D. Bradley

Harvestmen of the Family Phalangiidae (Arachnida, Opiliones) in the Americas

James C. Cokendolpher and Robert G. Holmberg

ISSN 0149-1768
ISBN 1-929330-34-0
ISBN13 978-1-929330-34-8

Museum of Texas Tech University
Lubbock, TX 79409-3191 USA
(806)742-2442

HARVESTMEN OF THE FAMILY PHALANGIIDAE (ARACHNIDA, OPILIONES) IN THE AMERICAS

JAMES C. COKENDOLPHER AND ROBERT G. HOLMBERG

ABSTRACT

This paper reviews 68 scientific names of species of Phalangiidae reported from North, Central, and South America. We found that: 1) 16 species of Phalangiidae distributed across 10 genera (*Leptobunus*, *Liopilio*, *Lophopilio*, *Mitopus*, *Odiellus*, *Oligolophus*, *Opilio*, *Paroligolophus*, *Phalangium*, and *Rilaena*) are still valid; 2) up to 38% of these species have been introduced into North America from Europe and possibly Asia; and 3) no members of this family are native to Mexico, Central and South America, or the Caribbean. An additional genus and species (i.e., *Megabunus diadema*) is recorded from Iceland and is to be watched for in North America. We recognize four new synonyms, one change in family status, and two other changes in status. We confirm both the statement by Levi and Levi (1955) that *Opilio angulatichelis* Roewer 1952 = *Phalangium opilio* Linnaeus 1758 and Bishop's (1949) conclusion that *Lacinius ohioensis* (Weed 1889a) = *Odiellus pictus* (Wood 1868). *Egaenus* and *Lacinius* do not occur anywhere in the Americas. Range extensions (i.e., new provinces or states) are given for *Liopilio glaber* (1 new extension), *Lophopilio palpinalis* (1, introduced; new record for North America), *Mitopus morio* (2 new provinces), *Odiellus pictus* (3 new provinces; 1 new USA county), *Rilaena triangularis* (1, introduced), *Opilio parietinus* (2, possibly introduced), and *Phalangium opilio* (18, possibly introduced). Taxonomic changes are: lectotypes and paralectotypes are designated for *Mitopus californicus* Banks 1895, *Odiellus pictus argentus* Edgar 1966, and *Oligolophus montanus* Banks 1893c; *Lacinius texanus* Banks 1893a = *Odiellus pictus* (Wood 1868), new synonym; *Mitopus californicus* Banks 1895 = *Opilio parietinus* (De Geer 1778), new synonym; *Mitopus dorsalis* Banks 1900 = *Mitopus morio* Fabricius (1779), new synonym; *Parodiellus projectus* Goodnight and Goodnight 1942a (Phalangiidae) = *Protolophus niger* Goodnight and Goodnight 1942b (Protolophidae), new synonym, new family rank; *Opilio chickeringi* = *Lanthanopilio chickeringi* is placed in the "Metopilio group", new status; and *Phalangium rudipalpe* Gervais 1849 = Genus and species *inquirenda* (Sclerosomatidae: Gagrellinae), new status. A new subgeneric name, *Slimlepto*, is given for the *parvulus* group of *Leptobunus*. A taxonomic key to the valid Phalangiidae of the Americas is provided.

Key words: *Leptobunus*, *Liopilio*, *Lophopilio*, *Megabunus*, *Mitopus*, *Odiellus*, *Oligolophus*, *Opilio*, *Paroligolophus*, *Phalangium*, *Rilaena*, *Slimlepto*

INTRODUCTION

The Opiliones (formerly, also referred to as the Phalangida) are the third largest order of the class Arachnida. Colloquially they are known in the Americas as the daddy-long-legs or the more acceptable name of harvestmen. With slightly over 6,650 species worldwide, the Opiliones are split unequally among four suborders (Kury 2017). Almost all long-legged

harvestmen observed walking or resting in/on open situations like leaves, bark, walls, etc. (both during the daytime and night) will be members of the suborder Eupnoi. The most common and conspicuous members of this suborder will be the species of the Phalangiidae and Sclerosomatidae.

The Phalangiidae (with over 380 species) occur throughout most of the cold temperate parts of the Northern Hemisphere. In these areas, they are the most likely family of harvestmen encountered by humans in disturbed areas such as croplands, gardens, and urban areas. However, some species, and most other Opiliones families, are found only in undisturbed habitats of forests and mountains. Phalangiids are moderately sized, with globular bodies and thin legs, not heavily sclerotized, and drab colored.

For this study, we include all the Nearctic and Neotropical Realms of the Americas, including the Caribbean islands, as well as Kalaallit Nunaat (Greenland) and Iceland. There are three or four Phalangiidae species on Iceland. Henriksen (1932), Stol (2007), and Bezděčka et al. (2017) recorded *Megabunus diadema* (Fabricius 1779), *Mitopus morio* (Fabricius 1779), and *Oligolophus tridens* (C. L. Koch 1836) (as well as *Nemastoma bimaculatum* (Fabricius 1775, Family Nemastomatidae). However, Spoek (1963) also mentions *Opilio parietinus* (De Geer 1778) as being present in Iceland but gave no further information. All these species occur further to the west in North America except *Megabunus*. Iceland is part of the mid-Atlantic ridge which is the boundary between the North American and Eurasian plates. As it originated volcanically from the collision of the two plates, is far from other land masses, and phalangiids have poor dispersal capabilities, the Opiliones of Iceland probably resulted from human activities and we predict that *Megabunus* will eventually populate more of North America. Thus, it is included in this paper.

Shear (2016) reviewed the known Eurasian Opiliones species that have been recorded as being

introduced into North America: *Nemastoma bimaculatum* (Fabricius 1775) (Nemastomatidae from Europe) and *Trogulus tricarinatus* (Linnaeus 1767) (Trogulidae from Europe). He also recorded three European members of the Phalangiidae that have been introduced: *Oligolophus tridens* (C. L. Koch 1836), *Paroligolophus agrestis* (Meade 1855), and *Rilaena triangularis* (Herbst 1799). He also briefly mentioned that three other species might have been introduced but might otherwise be of a natural Holarctic distribution: *Mitopus morio* (Fabricius 1779), *Opilio parietinus* (De Geer 1778), and *Phalangium opilio* (Linnaeus 1758). It is clear that the former three phalangiid species are recent introductions to the New World from Europe. In this publication, we also add another species of Phalangiidae introduced from Europe into North America: *Lophopilio palpinalis* (Herbst 1799).

The purpose of this study was to document the identity and distributions of, and provide a means to identify, members of the Phalangiidae in the Americas. Where possible we have included data on the juvenile life stage as well as the adults. *Phalangium* Linnaeus 1758 (originally Greek) and *Opilio* Herbst 1798 (originally Latin) have appeared in the taxonomic literature many times and in combinations with what are now understood not to be closely related species (some even in separate families). All of these combinations based on species reported from the Americas are reviewed and updated where needed. The member species of the genera *Odiellus* Roewer 1923 and *Mitopus* Thorell 1876 are distributed throughout the Holarctic region and both are in need of modern taxonomic studies. The last times they were reviewed on a world basis was by Roewer 1956 and 1957. At that time, the morphology of the genitalia and genetics were not studied.

SYSTEMATICS

ORDER OPILIONES Sundevall 1833
 Suborder Eupnoi Hansen and Sørensen 1904
 Superfamily Phalangioidea Latreille 1802
 Family Phalangiidae Latreille 1802

Because *Phalangium* was the first genus of Opiliones to be named by Linnaeus in 1758, its definitions

have changed remarkably over the centuries. Likewise, the family based upon that genus has shown great taxonomic changes over time. For this reason there are numerous species that were named early-on in combination with *Phalangium* that are no longer even recognized in the same families or, occasionally, the same suborders. The current use of the Phalangiidae

has been fairly constant since about the middle 1970's, but there is some disagreement regarding the number and position of the subfamilies (Hedin et al. 2012; JCC personal observation).

Kury (2013) estimated 55 extant genera with 394 extant species in the Phalangiidae. The family is characterized by a combination of characters recorded below, but only that of the male genitalia is uniquely diagnostic: palp, leg-like but may be armed ventrally with spines or spine-tipped tubercles; palpal tarsus longer than the palpal tibia; palpal claw single, well developed, curved, simple (smooth, without bumps, denticulation/pectination); palps and chelicerae clearly visible from above, not covered by a hood; eyes raised above the prosoma on an ocularium, spination variable; leg coxae without denticles (especially on lateral margins); single, undivided claw on terminus of each leg; second leg (leg II) usually longest; no nodules or pseudosegments in any leg femora; genitalia covered with a ventral operculum that extends backwards from the posterior edge of the second leg coxae to beyond the fourth leg coxae, operculum flexible, not heavily sclerotized; penis, in lateral view, strongly bent between the long corpus and shorter glans; stylus simple and not twisted; ovipositor long, many segmented, and flexible. It is not clear what characters best separate the subfamilies (Martens 1978; Crawford 1992). For the 11 genera considered valid for the Americas, we placed them according to Crawford 1992 and will discuss them in this order:

Phalangiinae Latreille 1802: *Leptobunus*, *Liopilio*, *Phalangium*

Opilioninae C. L. Koch 1839a: *Opilio*

Oligolophinae Banks 1893b: *Mitopus*, *Odiellus*, *Oligolophus*, *Paroligolophus*

Platybuninae Starega 1976: *Lophopilio*, *Megabunus*, *Rilaena*

Misplaced species: *Parodiellus*

Subfamily Phalangiinae Latreille 1802

***Leptobunus* Banks 1893b**

(Figs. 1–13)

Cokendolpher (1985) revised the taxonomy of this genus. He recognized two parts: the *californicus* group and the *parvulus* group. We propose here to recognize and formalize the naming of the *californicus* group in the nominal subgenus *Leptobunus* (*Leptobunus*) because the type species of the genus is included in this group. The second group we propose to call *Leptobunus* (*Slimlepto*). ***Slimlepto*, new subgenus**, is fitting as the first part of the new name is “slim”, in English to be slender, and the second part, “lepto” is a shortened form of the genus *Leptobunus*. In this case, we are not using “lepto” as a Greek adjective meaning thin. *Slimlepto* is considered masculine and therefore the endings of the existing species names remain the same: *Leptobunus* (*Slimlepto*) *parvulus*, type species, **new combination**, and *Leptobunus* (*Slimlepto*) *aureus*, **new combination**. The subgenera can be distinguished by the differences noted in the key and illustrations.

Leptobunus aureus Cokendolpher 1985 was reported only from California. *Leptobunus borealis* Banks 1898a has been collected from Bering and Copper Islands of Russia as well as coastal Alaska. *Leptobunus californicus* Banks 1893b was reported from California and Nevada. Schenkel (1951) named *Liomitopus laevis*; however, Cokendolpher (1980a) synonymized it under *L. californicus*. *Leptobunus parvulus* (Banks 1894) (= *Liobunum parvulum*, *Leuronychus parvulus*) is distributed from Alaska to California (Cokendolpher 1985; Bragg and Holmberg 2009).

A fossil harvestman described from the USA (Colorado) as *Leptobunus atavus* Cockerell 1907 has been transferred to the genus *Amauropilio* Mello-Leitão 1937 by Cokendolpher and Cokendolpher 1982. Similarly, the Mexican (Michoacán) species described as *Leptobunus mexicanus* Goodnight and Goodnight 1942c was moved to the genus *Paranelima* Caporiacco 1938 by Cokendolpher (1985). Both of these species are now placed in the Sclerosomatidae: Leiobuninae (Cokendolpher and Lee 1993). *Leptobunus spinulatus* Banks 1898b, described from México (Nayarit, Guanajuato, Jalisco, México, and Michoacán), has



Figure 1. *Leptobunus californicus* dorsal view of male palpal tibia and tarsus that are noticeably expanded on mesal margins, setae not illustrated. Illustration from Cokendolpher 1985.

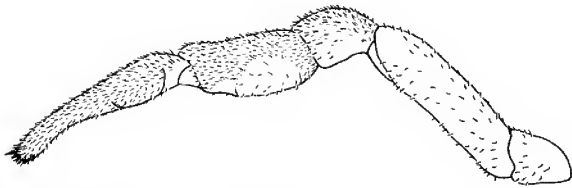


Figure 2. *Leptobunus californicus* male palp, mesal view. Illustration from Cokendolpher 1985; flipped horizontally so palp faces left.

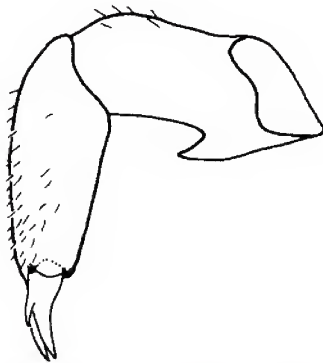


Figure 3. *Leptobunus parvulus* mesal view of male chelicera. Illustration from Cokendolpher 1985.

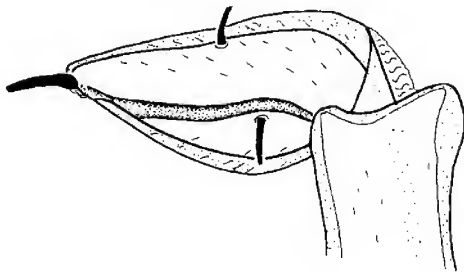


Figure 4. *Leptobunus aureus* lateral view of distal end of penis. Illustration from Cokendolpher 1985.

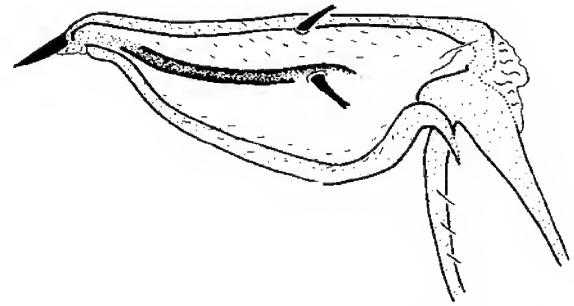


Figure 5. *Leptobunus parvulus* lateral view of distal end of penis. Illustration from Cokendolpher 1985.

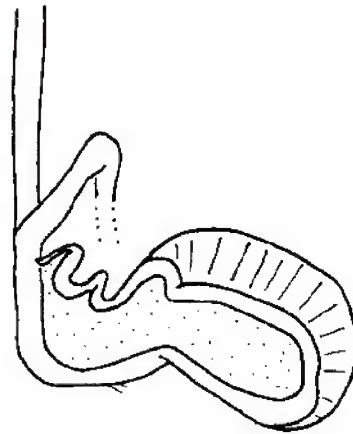


Figure 6. *Leptobunus parvulus* lateral view of seminal receptacle. Illustration from Cokendolpher 1985.

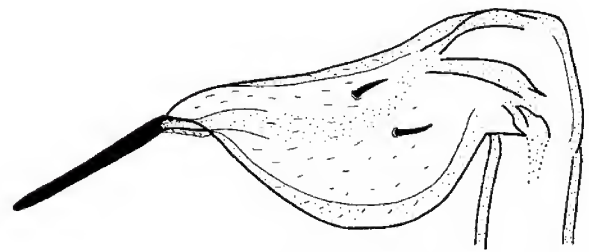


Figure 7. *Leptobunus californicus* lateral view of distal end of penis. Illustration from Cokendolpher 1985.

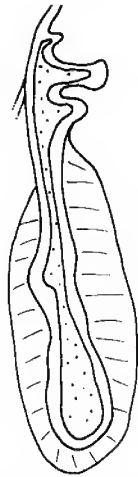


Figure 8. *Leptobunus californicus* lateral view of seminal receptacle. Illustration from Cokendolpher 1985.

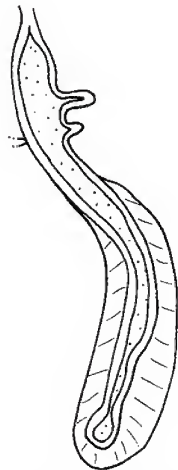


Figure 9. *Leptobunus borealis* lateral view of seminal receptacle. Illustration from Cokendolpher 1985.



Figure 10. Preserved *Leptobunus parvulus* female from Vancouver Island, British Columbia. Photograph by Don J. Buckle.



Figure 11. *Leptobunus borealis* dorsal view of male palpal tibia and tarsus; setae not illustrated. Illustration from Cokendolpher 1985.

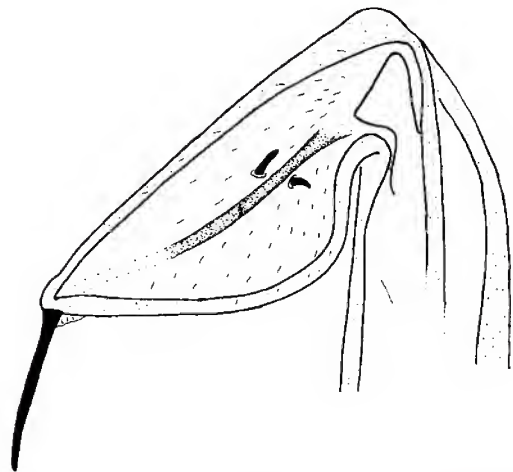


Figure 12. *Leptobunus borealis* lateral view of distal end of penis. Illustration from Cokendolpher 1985.



Figure 13. Preserved *Leptobunus borealis*, sex not determined, from Kenai National Wildlife Refuge, Alaska. Photograph by Matt Bowser.

been transferred to *Metopilio* Roewer 1911 by Cokendolpher (1985). This genus currently is placed in an undescribed assemblage (new family) that is informally referred to as the “*Metopilio* group” (Cokendolpher and Lee 1993; Hedin et al. 2012). This group provisionally has been treated in the Sclerosomatidae (Tourinho 2007), but because of the striking differences in penial morphology (JCC personal observations) and molecular studies of Opiliones (Giribet et al. 2002; Hedin et al. 2012), it appears to be distinct from both Sclerosomatidae and Phalangiidae.

***Liopilio* Schenkel 1951**
(Figs. 14–21)

Cokendolpher and Lee (1993) reported that *Liopilio glaber* Schenkel 1951 occurred in the mountains of Alberta, British Columbia, and Washington. A new state record is: USA: MONTANA: Park County: Grasshopper Glacier, 24 km North of Cooke City, 21 August 1959, D. C. Lowerie, 1 female (AMNH); Stillwater County: “W. Rosebud Plat.” [Plateau?], 21 July 1966, B. and C. Durden, 1 female (AMNH). Both of these records are from 3,050–3,200 m elevation.

Cokendolpher (1981a) described *Liopilio yukon* from Yukon Territory and Alaska. We have no new distribution records of this species.

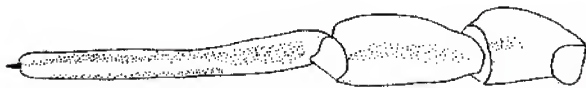


Figure 14. *Liopilio yukon* ventral view of distal end of male palp; setae not illustrated. Illustration from Cokendolpher 1981a.



Figure 15. *Liopilio yukon* dorsal view of distal end of female palp. Illustration from Cokendolpher 1981a.

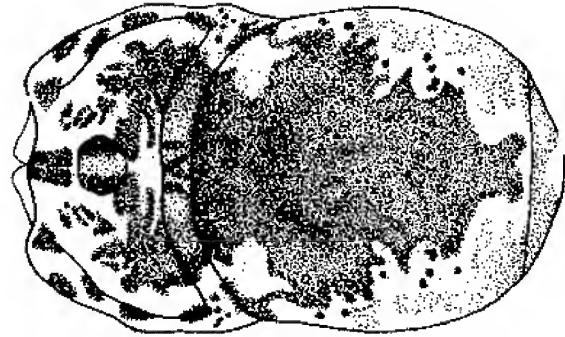


Figure 16. *Liopilio yukon* dorsal view of male body. Illustration from Cokendolpher 1981a.

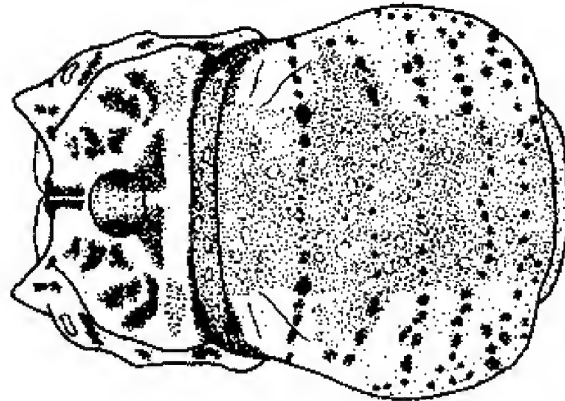


Figure 17. *Liopilio glaber* dorsal view of male body. Illustration from Cokendolpher 1981a.



Figure 18. Live *Liopilio glaber* male from Lemming Lake, Kakwa Wildlife Park, Alberta. Photograph by Robert G. Holmberg; enlargement of Fig. 20.



Figure 19. Live *Liopilio glaber* female from Lemming Lake, Kakwa Wildlife Park, Alberta. Photograph by Robert G. Holmberg; rotated enlargement of Fig. 21.



Figure 20. Live *Liopilio glaber* male from Lemming Lake, Kakwa Wildlife Park, Alberta. Photograph by Robert G. Holmberg.



Figure 21. Live *Liopilio glaber* female from Lemming Lake, Kakwa Wildlife Park, Alberta. Photograph by Robert G. Holmberg.

Phalangium Linnaeus 1758

(Figs. 22–26)

Because of the antiquity of the name, some of the older specific names to New World harvestmen have been associated incorrectly with *Phalangium* and the Phalangiidae, namely those of Say (1821), Gervais (1849), and Wood (1868, 1869). The named *Phalangium* from the New World are arranged alphabetically below. Only a few references are recorded for each species (the original and usually one or two more relevant ones).

Phalangium acanthipes Pickard-Cambridge 1905, from Guerrero, México, in *Metopilio* by Roewer (1911) (new family, “*Metopilio* group”).

Phalangium armigerum Pickard-Cambridge 1905 from Guerrero and Morelos, México, in *Metopilio* by Roewer (1911) (new family, “*Metopilio* group”).

Phalangium bicolor Wood 1868 (\neq *Phalangium bicolor* Fabricius 1793; Wood’s name is a primary homonym of that named by Fabricius and as such it was replaced by the oldest available synonym, *Leiobunum elegans* Weed 1889b; see Cokendolpher 1984) = *Nelima elegans* (Weed 1889b); Cokendolpher and Zeiders (2004) in Sclerosomatidae: Leiobuninae.

Phalangium calcar = *Leiobunum calcar* (Wood 1868), Davis (1934), Ingiani et al. (2011) in Sclerosomatidae.

Phalangium cinereum Wood 1868 = *Opilio parietinus* (De Geer 1778)—see below under *Opilio*.

Phalangium dorsatum = *Leiobunum vittatum* (Say 1821); Davis (1934) in Sclerosomatidae.

Phalangium exilipes = *Leiobunum exilipes* (Wood 1868); Davis (1934) in Sclerosomatidae. Hallan (2005) recorded in his internet biology catalog the species name spelled with two l’s and incorrectly recorded the year of description as 1878. Unfortunately, this has been followed generally by internet related catalogs and other resources. It is incorrect and a misspelling. Wood (1868; page 23) clearly spelled the name with a single l.



Figure 22. *Phalangium opilio* prosoma including ocularium and eyes, ventral arrow points to left ozopore, center arrow points to spine-tipped spur on left suprachelical laminae, sex not determined. SEM photograph by Robert G. Holmberg.

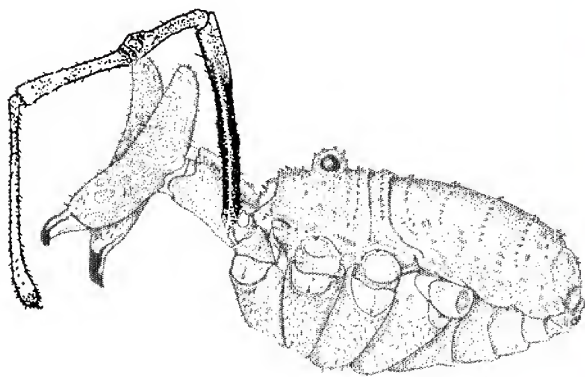


Figure 23. *Phalangium opilio* lateral view of male. Illustration traced and modified from Bishop 1949; flipped horizontally so body faces left.

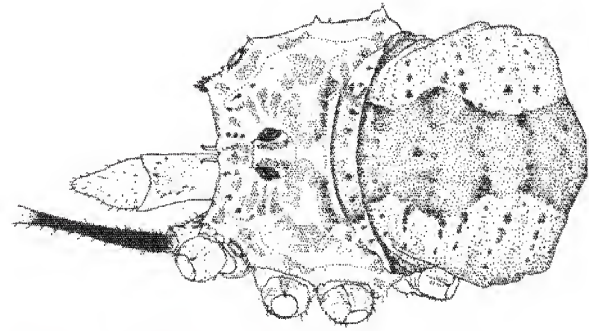


Figure 24. *Phalangium opilio* dorsal body view, chelicera, and palp of male. Illustration traced from Bishop 1949.



Figure 25. Live *Phalangium opilio* male from Saskatoon, Saskatchewan. Photograph by Don J Buckle.



Figure 26. Live *Phalangium opilio* female from Ottawa, Ontario. Photograph by Robert G. Holmberg, modified; flipped horizontally so body faces left.

Phalangium favosum Wood 1868 = *Trachyrhinus favosus* (Wood 1868); Cokendolpher (1981b) in Sclerosomatidae.

Phalangium formosum = *Leiobunum formosum* (Wood 1868); Davis (1934) in Sclerosomatidae. Shultz (2012) noted that this species was “soon to be transferred to *Hadrobunus*.”

Phalangium grande = *Hadrobunus grandis* (Say 1821); Shultz (2010, 2012) in Sclerosomatidae.

Phalangium horridum Pickard-Cambridge 1905 from Guerrero and Michoacán, México, is a secondary homonym of the Old World species *P. horridum* Panzer 1794 (now used in the combination *Lacinius horridus*, Phalangiidae). Pickard-Cambridge's *P. horridum* was placed in *Metopilio* by Roewer (1911) (new family, “*Metopilio* group”). Because it is a homonym, *Metopilio cambridgei* Mello-Leitão 1944 was supplied as the replacement name.

Phalangium longipalpis—see below under *Phalangium opilio*.

Phalangium maculatipes Pickard-Cambridge 1905, from Guerrero, Hidalgo, and Puebla, México, was placed in *Metopilio* by Roewer (1911) (new family, “*Metopilio* group”).

Phalangium maculosum = *Hadrobunus maculosus* (Wood 1868); Shultz (2010) in Sclerosomatidae.

Phalangium nigropalpi = *Leiobunum nigropalpi* (Wood 1868); Davis (1934), Ingianni (2010) in Sclerosomatidae.

Phalangium nigrum = *Eumesosoma nigrum* (Say 1821); Cokendolpher (1980b) in Sclerosomatidae.

Phalangium opilio Linnaeus 1758 was the first harvestman officially named, with types from Europe and, later (as synonyms), North America (Crawford 1992; Cokendolpher and Lee 1993). It is the only member of the genus currently recorded from North America. *Phalangium opilio* is found throughout much of the Holarctic region as well as New Zealand (Martens 1978; Butcher et al. 1988) and Japan (Suzuki

and Tsurusaki 1983; Tsurusaki and Takenaka 2010). *Phalangium opilio* is now the most widely distributed species of harvestmen in the world (Novak et al. 2009). It was first recorded in North America as *Phalangium longipalpus* Weed 1890 and later as *P. opilio* and *Opilio angulatichelis* Roewer 1952 (see below under *Opilio*). As human activities are suspected for its transport to Newfoundland (Lindroth 1957; p. 190), New Zealand (Gruber and Hunt 1973), and Japan (Tsurusaki and Takenaka 2010), and this species usually is found in areas disturbed by humans but very seldom in undisturbed habitats, we support the conclusion that this common and very wide spread species is not native to the Americas (Bragg and Holmberg 2009). Cokendolpher and Lee (1993) recorded *P. opilio* from five provinces of Canada (Alberta, British Columbia, both Newfoundland and Labrador, Ontario, and Saskatchewan) and 17 states of the USA (Alaska, Arkansas, Idaho, Illinois, Maine, Massachusetts, Michigan, Minnesota, Montana, New York, North Dakota, Ohio, Oklahoma, Pennsylvania, Texas, Washington, and Wisconsin). Koponen (1995) recorded it from Quebec, Newton and Yeargan (2002) from Kentucky, and Clark et al. (1994) from Virginia.

Six new provincial/territorial and 13 new state/district records are: CANADA: MANITOBA: Birch River campground, Primrose Wayside Park, 25 July 1997, RGH, 1 male (RGH); Blue Lake campground, Duck Mountain Provincial Park, 15 August 1969, ROM Field Party, 1 male (ROM); 4 km west of Clear Lake, Riding Mountain National Park, 21–30 August 1979, R. B. Sample, 3 males, 9 females (CNC); Delta Marsh, University of Manitoba Field Station, summer 1970, L. Hlynka, 2 males (RGH); 18 km north on Highway 10 of Forrest, 5 September 1970, ROM Field Party, 1 male (ROM); Glen Lea Research Station, 16 km south of Winnipeg, 8–15 September 1972, R. G. Sample, many males and females (CNC); Grandview Beach, 11–12 August 1970, ROM Field Party, 2 males, 1 female (ROM); Lake Audy, Riding Mountain National Park, 21–28 August 1979, J. and M. Redner, 3 males, 5 females (CNC); Lake of the Prairies, 24 July 1997, RGH, 1 male (RGH); 59 km north of Mafeking, 16 August 1969, ROM Field Party, 1 female (ROM); 20 km south of Melita, 23 July 1997, RGH, 1 female (RGH); Moon Lake, Riding Mountain National Park, 9 September 1987, CWA, 1 female (CWA); Swanson

Spring, Riding Mountain National Park, several collections 29–30 August 1979, D. B. Lyons and S. J. Miller, 8 males, 24 females (CNC); 15 km southwest of Swan River, 25 July 1997, RGH, 1 male (RGH); Viriden and 40 km southwest, 23–24 July 1997, RGH, 2 males, 2 females (RGH). NEW BRUNSWICK: Fredericton, 11–16 July 1978, C. D. Dondale, 1 male (CNC); Kouchibouquac National Park, several collections 12 July–12 September 1977, several collectors, many males and females (CNC); St Andrews, 17 July 1978, S. A. Marshall, 1 male (CNC); Saint John, 20 July 1968, E. E. Linqvist, 2 males (CNC); St-Léonard, 23 September 1974, C. D. Dondale, 1 female (CNC). NORTHWEST TERRITORIES: campsite at NWT-Alberta border (60°00'N, 116°59'W), 13–14 August 1998, RGH, 1 male (RGH); Fort Liard, summer 2000, R. Smith, 3 males, 4 females (RGH); Fort Smith, 16 August 1998, RGH, 1 male, 1 female (RGH); Hay River, 15–19 August 1998, RGH, 1 male (RGH); Yellowknife, 18–30 July 2009, summer 2010, and 15 July–6 August 2011, Brian Latham, 28 males, 8 females (RGH). NOVA SCOTIA: Barton, 23 July 1959, C. D. Dondale, 1 male, 1 female (CNC); Brair Island, 20 September 1996, DJB, 3 males (DJB); Canard, various dates between 1956 and 1959, C. D. Dondale, 8 males, 7 females (CNC); Coldbrook, 10–11 July 1957 and 1959, C. D. Dondale, 2 females (CNC); Cow Bay, 28 September 1956, C. D. Dondale, 1 male, 1 female (CNC); Digby, 29 July–23 August 1960, Fox and Sawler, many males and females (CNC); Graywood, 1–12 July 1957, unknown collector, many males and females (CNC); Gulliver's Cove, 20 September 1996, DJB, 1 male (DJB); Halls Harbour, 27 July–31 August 1960, unknown collector, many males and females (CNC); Kentville, 29 August and 3 September 1966, C. D. Dondale, 4 males, 3 females (CNC); Lakeview, 4 October 1956, unknown collector, 5 males, 1 female (CNC); Lily Lake, 27 September 1960, C. D. Dondale, 1 female (CNC); Marshalltown, 14 September–5 October 1960, unknown collector, many males and females (CNC); Martins River, 27 July 1956, C. D. Dondale, 1 male (CNC); Sable Island, several collections between 13 July–15 September 1967, J. E. H. Martin, several males and females (CNC); Sable Island, 8–12 September 1977, B. Wright, 1 male (CNC); Sweets Corner, 14 August 1956, C. D. Dondale, 1 female (CNC); White Rock, 14 September 1956, C. D. Dondale, 8 males (CNC). PRINCE EDWARD ISLAND: Malpeque Bay, Green Park, 5–8 September 1972, C. Starr, 1 male, 1 female (CNC). YUKON: Carcross, 14 August 1987, RGH, 3 males, 1 female (RGH); Takhini Hot Springs, 20 km northwest of Whitehorse, 16 August 1987, RGH, 3 males, 3 females (RGH); 5 km northwest of Watson Lake, 17 August 1987, RGH, 1 male (RGH); Whitehorse, 25 August 1969, J. Belicek, 1 male, 1 female (RGH); Whitehorse, 9 August 1982, J. J. Robinson, 1 male (UBC); Whitehorse, 10 August 1987, RGH, 3 males, 1 female (RGH). USA: ALASKA: Municipality of Anchorage: Anchorage, 100 m, August 1974, N. L. H. Krauss, 2 females (AMNH). Yukon-Koyukuk: Circle Hot Springs, 65.29°N, 144.40°W, 14 August 1968, W. Ivie, 1 female (AMNH). CALIFORNIA: Contra Costa County: Richmond, 15 January–15 March 1987, S. Stockwell, J. Steele, 2 males, 1 female (JCC); Monterey County, Monterey, 5 June 1982, R. Johnson, Jr., 4 males, 4 females (JCC); Riverside County: Riverside, 22 May, 10 June 1977, D. Carroll, 2 females (UCR); Riverside, 12 May 1979, G. Cavender, 1 female (UCR); San Mateo County: San Francisco, 16 July 1963, J. and W. Ivie, 1 female (AMNH). COLORADO: Boulder County: Boulder, 1 August 1945, R. E. Gregg, 1 female (AMNH); Nederland, 16 August 1952, B. Malkin, 1 female (JCC); Denver County: Denver, 21 June 1952, R. A. Stirton, 1 female (JCC); Gilpin County: Golden Gate Canyon State Park, 28 July 2004, unknown collector, 1 male (RGH); Larimer County: Glen Haven, 27 August 1961, J. and W. Ivie, 1 male, 1 female (AMNH); Pitken County: between Aspen and Glenwood Springs along the Roaring Fork River, 12 September 1981, T. Wood, 2 males (JCC). DELAWARE: New Castle County: Wilmington, 30 June 1941, A. L. Bacon, 1 female (AMNH). DISTRICT OF COLUMBIA: Washington, September 1975, RGH, 3 males, 2 females (RGH). IOWA: Johnson County: 3 km N. Iowa City, 9 August 1984, D. K. Hoffmaster, 1 female (JCC). NEBRASKA: Scotts Bluff County: Minatare, 19 July 1978, W. F. Rapp, 2 females (JCC). NEW HAMPSHIRE: Hillsboro County: Hollis, 19 June 1987, C. D. Dondale, 1 female (CNC). NEW JERSEY: Monmouth County: Fair Haven, 30 May 1982, S. Sickerman, 1 male (JCC). NEW MEXICO: Bernalillo County: Albuquerque, 28 September 1980, J. W. Jennings, 1 male (JCC), 15 October 1982, J. W. Jennings, 1 male (JCC); Taos County: 3 km east of Taos, 6 October 1965, J. and W. Ivie, 1 female (AMNH). OREGON: numerous records of males and females from Benton

County (UCR, ROM, OSU, TTU-Z); Douglas County (AMNH, ROM, RGH) and Lincoln County (OSU, TTU-Z); Coos County: Charleston, 3 September 1947, I. Newell, 1 female (AMNH); Curry County: Denmark, 3 August 1985, B. T. Finnamore and T. W. Thormin, 1 female (RGH); Lane County, Eugene, March 1947, B. Malkin, 2 males, 1 female (JCC); Washington County, Portland, 12 July 1971, D. J. Starkey, 1 female (JCC); Yamhill County, McMinnville, 1 June–10 July 1946, K. M. Fender, 1 female (JCC). UTAH: Cache County: Logan, 21 June 1983, 1 male (JCC); Daggett County: Red Canyon, 19 July 1949, W. J. and J. W. Gertsch, 2 males (JCC); Utah County: Provo, 3 July 1946, L. R. Allen, 1 female (AMNH). WYOMING: Park County: Bechler Ranger Station, 29 August 1982, R. Kral, 1 female (JCC).

Phalangium ortonii Wood 1869 from Ecuador is a *species inquirenda* (Sclerosomatidae) according to Cokendolpher and Peek (1991).

Phalangium pictum—see *Odiellus pictus* (Wood 1868).

Phalangium rudipalpe Gervais 1849 is still recorded in combination with *Phalangium* from South America (Cekalovic 1985). Because the description and illustrations (Gervais 1849) do not resemble *Phalangium* and because this is the only record of the family Phalangiidae south of New Mexico in the New World, it is misidentified and represents a member of some other family. From the locality (central Chile), description of the body coloration, and the illustration of the palps, this species could be a member of *Thrasychirus* Simon 1884. However, the presence of the leg femora spines/tubercles is unlike that of any member of the Neopilionidae: Enantiobuninae from South America. The only other possibility is that it could be a member of the Sclerosomatidae: Gagrellinae; however, the description of *P. rudipalpe* is insufficient in detail to currently permit generic recognition. From a biogeographic standpoint it is best treated as a *genus* and *species inquirenda* under the Sclerosomatidae: Gagrellinae.

Phalangium spinigerum Pickard-Cambridge 1905, from Guerrero, México, was placed in *Metopilio* by Roewer (1911) (new family, “*Metopilio* group”).

Phalangium ventricosum = *Leiobunum ventricosum* (Wood 1868); Davis (1934) in Sclerosomatidae.

Phalangium ventricosum hiemale = *Leiobunum ventricosum hiemale* (Weed 1890); Davis (1934) in Sclerosomatidae.

Phalangium ventricosum ventricosum = *Leiobunum ventricosum ventricosum* (Wood 1868); Davis (1934) in Sclerosomatidae.

Phalangium verrucosum = *Leiobunum verrucosum* (Wood 1868); Davis (1934) in Sclerosomatidae.

Phalangium vittatum = *Leiobunum vittatum* (Say 1821); Davis (1934) in Sclerosomatidae.

Subfamily Oligolophinae Banks 1893b

***Lacinius* Thorell 1876**

Two *Lacinius* species have been described from North America, namely *Lacinius texanus* Banks 1893a and *Lacinius (Oligolophus) ohioensis* (Weed 1889a). Banks (1893a) described *L. texanus* from Brazos County, Texas. JCC examined the holotype (MCZ) and found it to be a penultimate female. Banks' description is accurate but it can be added that metatarsi of leg II have 4–5 bands of setae and tibiae of leg II have no pseudosegments. There is nothing remarkable about the specimen and we conclude that it is an immature *Odiellus pictus*. **New synonymy:** *Lacinius texanus* Banks 1893a = *Odiellus pictus* (Wood 1868). We were unable to locate any other published records or collections of *Lacinius* (or *Odiellus*) from Texas, or the surrounding states of Louisiana, Arkansas, Oklahoma, or New Mexico. This especially is noteworthy as one of the oldest and largest entomological collections for Texas is located at Texas A&M University in Brazos County. Thus, we conclude that Banks' specimen of *L. texanus* was probably not from Texas.

Crosby and Bishop (1924) recorded “1 specimen” of an unsexed *L. texanus* from Summerville, Georgia. In the same paper, they recorded both males and females and two other immatures as *Odiellus* species. As Bishop (1949) also recorded specimens of *O. pictus* from Summerville, Georgia, we conclude that Crosby' and Bishop's earlier report of *L. texanus* was an immature *O. pictus*.

Weed (1889a) described *Oligolophus ohioensis* from a single “female” (later reported as a juvenile by Weed 1893) from Warren County, Ohio. Cokendolpher and Zeiders (2004) reported that this specimen apparently was lost or destroyed. Banks (1893b) transferred the species to *Lacinius*. In 1957, Roewer reported that he had a male (SNMF number RI/6/708) from Ohio that Banks had identified as *Lacinius ohioensis*, but no one has reported on the genitalia of that specimen. Walker (1928) recorded several new records of both *Lacinius ohioensis* and *Odiellus pictus* for Ohio. In her key, Walker recorded the body length of *L. ohioensis* as being 4–5 mm with the ocularium (= ocular tubercle) close to the margins and *O. pictus* as 5–6 mm long with the ocular “tubercle farther removed from the margin.” Unfortunately, she did not record the ages or sexes of the specimens examined. The specimens studied by Walker for her 1928 paper are now lost, according to one of the anonymous manuscript reviewers. Richard Bradley of the Ohio State University Chelicerates Collection (OSAL) kindly checked in their collection in April 2017 for these specimens without success.

As Roewer (1923) and Bishop (1949) reported the body lengths of *O. pictus* as 5–6 mm, it is likely that Walker’s *L. ohioensis* were actually immature *O. pictus*. Bishop (1949) synonymized *L. ohioensis* with *Odiellus pictus*. We concur with Bishop’s synonymy. *Lacinius* can no longer be considered as occurring in the New World. Therefore, *Lacinius* species are known only from the western Palearctic (Martens 1978).

***Mitopus* Thorell 1876** (Figs. 27–31)

Mitopus morio (Fabricius 1779) (including synonyms *Oligolophus montanus* Banks 1893c and *Opilio scabripes* Walker 1860 from the New World) is patchily found throughout the northern Holarctic region (all north of about 40°N latitude) and probably has the second largest distribution of any harvestman (cf. *Phalangium opilio* as having the widest distribution—although aided by humans) (Fig. 27). In North America it has been reported from northeastern areas [Kalaallit Nunaat (Greenland), Newfoundland, Nova Scotia, Quebec, Maine, New Hampshire, New York] as well as northwestern areas (Alaska, Montana/Wyoming) (Cokendolpher and Lee 1993). The most northern records (only two above 75°N latitude) of this

species are Fort Conger, Nunavut, in North America and slightly more southern on Spitsbergen Island, Norway.

The Montana or Wyoming record (Savory 1933) is very unlikely as many Opiliones collections have been made from around that area without another record of this species. The color patterns of *M. morio* are extremely variable (see Meinertz 1973 and Martens 1978) and based solely on color it is easily confused with *Phalangium opilio*, which has been recorded from the region. This sample may have been incorrectly identified or labeled.

This species is characterized by extreme variability in body size, leg lengths, and body coloration and patterns. Arthofer et al. (2013) looked at *Mitopus “morio”* from a single location at Tyrol, Austria, and found what they cautiously interpreted as three sympatric cryptic species. The differences were detected with whole-genome scans, mitochondrial sequences, and morphometric characters. We agree with Arthofer et al. that much greater genetic sampling should be undertaken and hopefully will help better differentiate the various species/populations. Within North America, some western individuals have a distinct, light-colored, line running the length of the opisthosoma behind the ocularium (Fig. 28). Individuals that we have studied from eastern areas are without this pattern (Figs. 29, 30).

JCC examined (in 1980) the cotypes of *Oligolophus montanus* Banks 1893c, and here we designate a male placed in a separate vial as the lectotype and the contents of a second vial with 2 males, 12 females, 14 immatures as paralectotypes. All of them were collected from Mount Washington, New Hampshire (Nathan Banks Collection, MCZ). The lectotype matches the original description of the species. The synonym *Oligolophus montanus* was first used in combination with *Mitopus* by Banks (1901).

The record of *M. morio* as *Mitopus californicus* Banks 1895 from California is incorrect (see under *Opilio parietinus*). *Mitopus morio* otherwise has not been reported from California.

Except for two records that are between one and one and a half centuries old, *M. morio* has not been collected from the northern territories of Canada.

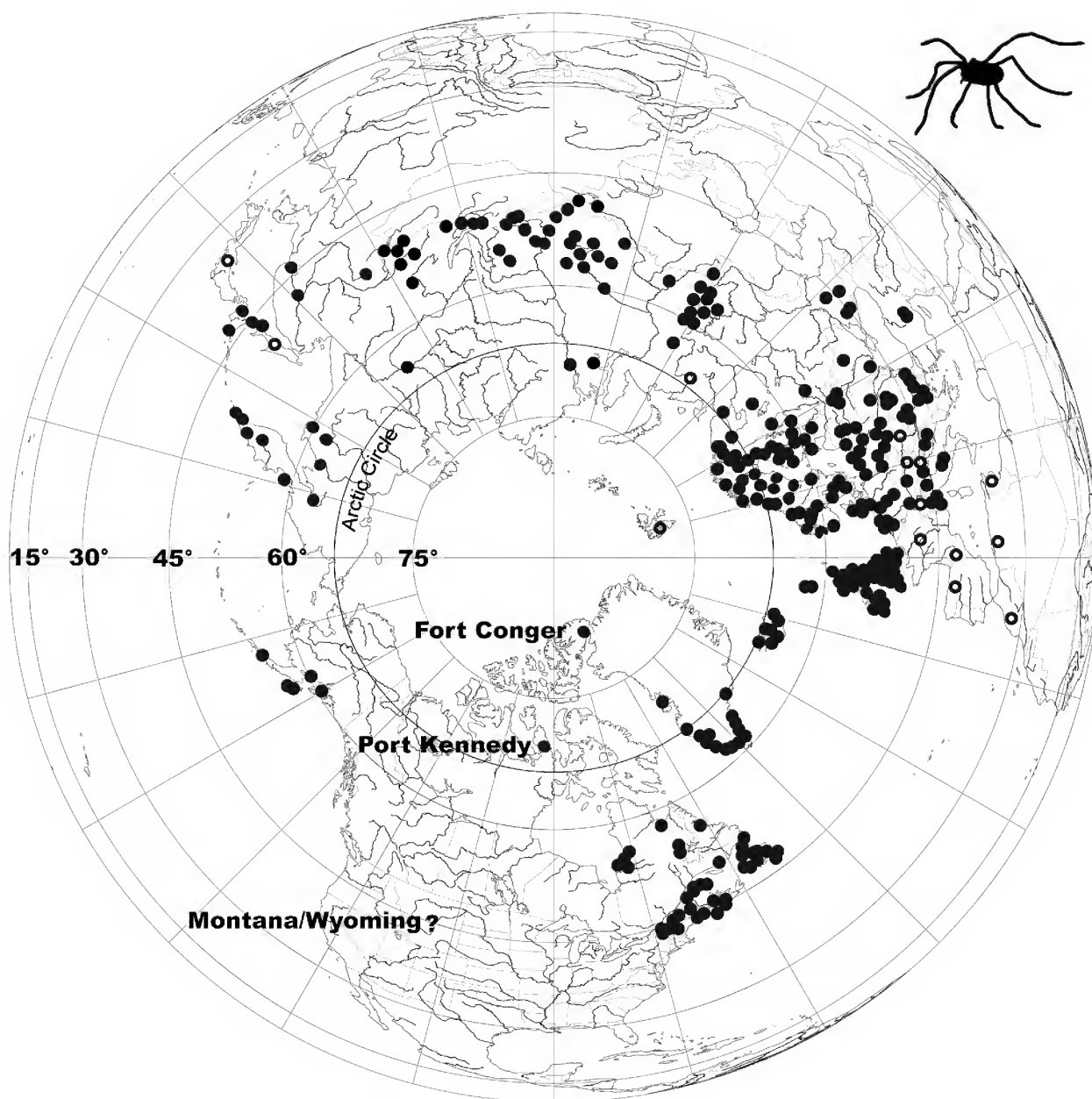


Figure 27. *Mitopus morio* world distribution. Solid circles indicate precise locations; open circles indicate approximate locations (e.g., country records). Complete North American records from: Banks (1893c, 1900, 1902); Bishop (1949); Crosby et al. (1928); Drummond et al. (2010); Hackman (1956); Koponen (1995); Lindroth and Ball (1969); Marx (1892); Meinertz (1973); Savory (1933); Walker (1860); and our collections. See text for discussion regarding Fort Conger, Port Kennedy, and Montana/Wyoming collections. Selected Eurasian and questionable African records from: Crawford and Marusik (2006); Farzalieva and Esyunin (2000); Heinäjoki (1944); Hillyard and Sankey (1989); Kauri (1980); Kurt et al. (2008); Leirikh et al. (2009); Lengyel and Páll-Gergely (2010); Martens (1978); Marusik (2005); Marusik and Khrulyova (2011); Marusik and Koponen (2015); Meinertz (1973); Novak (2005); Novak et al. (2006); Roewer (1912, 1924); Šilhavý (1965); Slagsvold (1979); Stol (2003); Spoek (1963); Starega (1975, 1976, 1978, 1984); Suzuki and Tsurusaki (1983); Tchemeris et al. (1999); and references therein.



Figure 28. Preserved *Mitopus morio*, sex not determined, from Kenai National Wildlife Refuge, Alaska. Photograph by Matt Bowser.

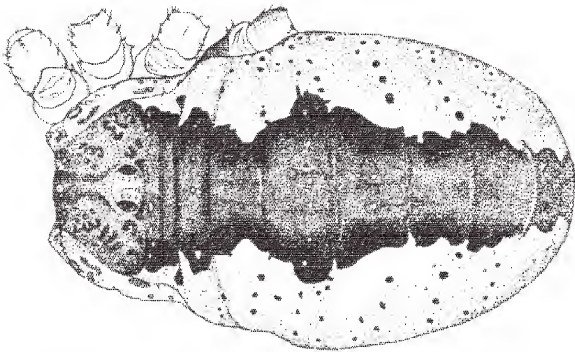


Figure 29. *Mitopus morio* dorsal view of female body, from New York. Illustration traced and modified from Bishop 1949.



Figure 30. *Mitopus morio*, sex not determined, from Mont Écho, Quebec. Photograph by Pierre-Marc Brousseau.

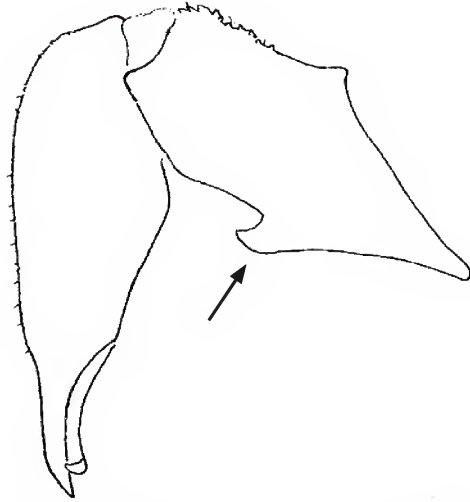


Figure 31. *Mitopus morio*, sex not determined, lateral view of chelicera, arrow points to ventral spur. Illustration traced and modified from Martens 1978.

There is one record described as a new species, *Opilio scabripes*, by Walker (1860) from Port Kennedy, 72°N, 94°W, which would now be in the territory of Nunavut. Port Kennedy is not mentioned in any of the Canadian gazetteers or atlases that we examined. However, it is mentioned in some historical documents. William Kennedy assisted Captain Francis Leopold McClintock, and McClintock later named a harbor after Kennedy when McClintock was looking for the lost Franklin expedition (Barr 1986). There is a tidal station, near the east end of Bellot Strait, named Port Kennedy at 72°01'N, 94°12'W. Also Fort Ross is located at 72°00'N, 94°14'W. Thus, the location recorded by Walker in 1860 is correct. The second record is from further north (Marx 1892). Marx reported that Lieutenant Greely of the Lady Franklin Bay expedition related that Opiliones “were frequently found in the immediate neighborhood of our camp” at Fort Conger. The Fort Conger locality (now located in Quttinirpaaq National Park on Ellesmere Island of Nunavut, 81°45'N, 64°45'W) is about 1,200 km northwest from the nearest collection sites in Kalaallit Nunaat and represents the most northern record for the Order Opiliones (Fig. 27). The specimens from Marx have been destroyed or lost but from the location they can only be *M. morio*. Although it is true that Marx is notorious for his geographic mislabeling of both specimens he collected and those that came into his hands from others (Hamilton et al. 2016),

Strand (1906) thought that this species was probably *Mitopus morio*; whereas Roewer (1923) did not offer an opinion because the specimens could not be found. Cokendolpher and Lee (1993) recorded the synonymy with *M. morio* and we agree. Even without examining the type material, the specimens could only be *M. morio* based on the original description as “blackish dingy whitish beneath; mandibles with black teeth; legs piceous, thick, comparatively short, minutely serrated,” and being collected from an inland locality at 72°N in the territory of Nunavut.

As many spider collections, but no harvestmen, have been made in the far north of Canada, we are uncertain about these two old records. Port Kennedy is about 1,400 km from the closest known collection locality in Kalaallit Nunaat, 2,500 km from the closest in Labrador, and 3,200 km from the closest in Alaska. As mentioned above, the Fort Conger record is about 1,200 km from other *M. morio* collection sites. It is possible that individuals of this species could have been transported by the explorers to these remote locations with lumber (the sites are beyond the tree line) or vegetable garden supplies (including soil) (see Lindroth 1957), or other goods. If harvestmen were transported there, they may have established local populations that by now may or may not be extinct. From the studies on cold hardiness of *M. morio* by Leirikh et al. (2009), cold temperature is not the limiting factor. It is also possible that some *M. morio* populations in eastern North America came from or were modified by early introductions by humans.

New records of *Mitopus morio*: CANADA: NEW BRUNSWICK: St. John, 20 July 1960, E. E. Linquest, 2 females (CNC). LABRADOR: Carol Lake, n[orth] end, 13 September 1953, F. Harper, 1 female (AMNH), 12 September 1958, F. Harpen (= Harper?), 2 females (AMNH).

Mitopus dorsalis Banks 1900 = *Mitopus morio* Fabricius (1779), **new synonym**.

Mitopus dorsalis Banks 1900:484, plate 29, Fig. 2; Banks 1901:674; Comstock 1940:70.

Nitopus dorsalis Banks 1911:420 (sic).

Oligolophus dorsalis Strand 1906:474.

Strandibunus dorsalis Roewer 1912:57.

Parodiellus dorsalis Roewer 1923:724.

“*Parodiellus*” *dorsalis* Cokendolpher and Lee 1993:22.

Originally, Banks (1900) described *Mitopus dorsalis* based on one adult and one immature specimens collected at Popof Island during the Harriman Alaska Expedition (1899). The type specimen was deposited in the U. S. National Museum, Cat. no. 5272. The late Ralph E. Crabill (personal communication) informed JCC that the type was never deposited but more recent (2017) efforts by staff at the USNM discovered the tube with both specimens. The vial containing the two specimens had a label indicating it was “44” from the “Harriman Expedition ’99 T. Kincaid, collector” “Popoff Is 1899”. We did not separate or dissect the specimens. They are represented by two immatures, the larger (total body length 4.77 mm; femur I 3.56 mm long) we accept as the holotype and the smaller (total body length 3.73 mm; femur I 3.01 mm long) the “paratype.” The specimens now are light tan to amber colored with a very faint “clear” area where Banks indicated in his drawing of the light stripe on the opisthosoma. JCC examined a series [2 males, 1 female, 5 immatures (BMM); 1 male, 1 female, 1 immature (NMW # 6084)] of this species that was collected at Karlýuk, Kodiak Island, Alaska, by T. Kincaid. A handwritten label in one vial indicated the collection date to be 19 July 1897, whereas other labels (typed) in the vials indicated 19 August 1897. Kincaid (1900) was in charge of the entomological collections on the Harriman Alaska Expedition. He made no mention of an 1897 collection, but did state that collections were made at Kodiak on 20 July 1899 and at Popof Island 7–17 July 1899. It appears these collection dates were mislabeled and were collected on the Harriman Alaska Expedition. The reason this series was never transmitted to Banks is unknown.

The specimens from Karlýuk agree with *Mitopus morio* and as such are regarded as this species. These specimens are different in appearance from those from

eastern North America and those from Kamkatcha. Their shorter legs and color pattern most resemble those reported from Japan by Suzuki (1939).

***Odiellus* Roewer 1923**

(Figs. 32–37)

Oligolophus ohioensis = *Lacinius ohioensis* = *Odiellus pictus*. See under *Lacinius* for discussion of synonymy.

Cokendolpher and Lee (1993) summarized the distribution of *Odiellus pictus* (= *Phalangium pictum*) (Wood 1868) as occurring in six provinces (Manitoba, New Brunswick, both Newfoundland and Labrador, Ontario, Quebec, and Saskatchewan) and 16 states (Connecticut, Georgia, Illinois, Indiana, Maine, Massachusetts, Michigan, New Hampshire, New York, North Carolina, Ohio, Pennsylvania, Tennessee, Vermont, Virginia, and Wisconsin). Bragg and Holmberg (2009) recorded one locality from British Columbia. Shoemaker et al. (2017) gave the first records of this species from two counties in Minnesota and we add a third county below.

New records of *Odiellus pictus*: CANADA: ALBERTA: Baptiste Lake, 23 August–7 October 1988, RGH, 3 males (RGH); 11 km northeast of Clyde, 10–17 August 1988, T. W. Thormin, 2 males, 1 female (RGH); George Lake, 53°57'N, 114°06'W, 1 July 1973, J. Belicek, 1 female (JCC); Wagner Natural Area, west of Edmonton, 13–17 August 1985, A. T. Finnermore and T. W. Thormin, 1 male, 1 female (RGH). NOVA SCOTIA: Black River, 17 July 1956, C. D. Dondale, 1 female (CNC); Bridgewater, winter 1964–spring 1965, B. Wright, 1 male, 1 female (CNC); Coldbrook, 27 August 1958, C. D. Dondale, 1 female (CNC); Cow Bay, 28 September 1956, C. D. Dondale, 2 females (CNC); Halls Harbour, 22 August 1960 and 30 October 1956, 1 male and 1 female (CNC); New Grafton, 26 August 1960, C. D. Dondale, 1 male, 1 female (CNC); Prospect Bay Road, 8 October 1966, J. Gilhen, 1 male (CNC); Upper Canard, 5 September 1956, C. D. Dondale, 1 male, 2 females (CNC); Wellington, 12 October 1950, unknown collector, 2 males, 1 female (CNC). PRINCE EDWARD ISLAND: Malpaque Bay, Green Provincial Park, 5–8 September 1972, C. Starr, 2 males, 3 females (CNC). USA: MINNESOTA: Clearwater County: Lake

Itasca Biological Station, Itasca State Park, August 1970, G. B. Wiggins, 4 females (ROM).

Crosby and Bishop (1924) described *Odiellus nubivagus* from the tallest mountain peak of eastern North America in North Carolina. The type locality is Mount Mitchell at 2,037 m elevation. Nearby at the 3rd highest peak, a new collection of what is likely this species was photographed and preserved (Fig. 32) at Clingmans Dome (2,025 m). The new specimen was not as darkly pigmented on the sides of the opisthosoma as illustrated in the original description but is considered here to represent the same species. In the original publication of the species, Crosby and Bishop (1924) reported the holotype and numerous paratypes were housed in the Cornell University and New York State Museum collections. There is now one pair of the original paratypes housed at MSU. There is a second sample of this species at MSU (from Grandfather Mountain) that apparently was identified by Arlan Edgar and is not a type and detailed below. The peak of Grandfather Mountain is lower at about 1,812 m. Crosby and Bishop (1924) recorded a female from Grandfather Mountain at 1,219 m elevation as being *Odiellus pictus*.

New records of *Odiellus nubivagus*: USA: NORTH CAROLINA, Great Smoky Mountains National Park, Swain County, Clingmans Dome just south of parking lot, 31 July 2000, J. C. Cokendolpher, M. Hedin (1 male, GRSM 164165). Avery County, Grandfather Mountain, 4 Oct. 1960, Gertsch and Ivie, 1 male (MSU).

In his dissertation, Arlan Edgar (1960) recognized *Odiellus pictus* as a “typical form” and as “var. I.” He presented a map (Fig. 33 on p. 58) where he showed seven counties (Chippewa, Huron, Iron, Livingston, Ontonagon, Newaygo, Tuscola) with variety 1. In 1966, Edgar described (a male and female) of his variety 1 as *Odiellus pictus argentus* from Michigan, without a type specimen or locality (other than state) mentioned. Later in 1971, he raised this taxon to full species and again had no types but recorded nine counties in Michigan: adding Alger and Marquette counties. Because Edgar did not list locations in his 1966 description, we are considering all of the specimens from the nine counties that still exist to be “syntypes” if they do



Figure 32. Live *Odiellus nubivagus* male from Clingman's Dome, Great Smoky Mountains National Park, Tennessee. Photograph by James C. Cokendolpher, modified; flipped horizontally so body faces left.

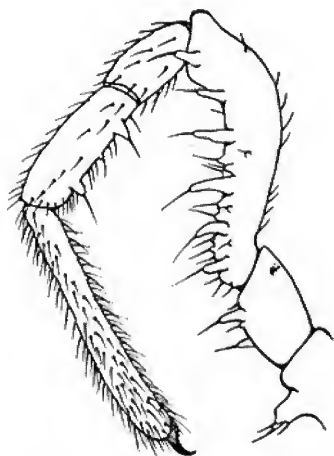


Figure 33. *Odiellus pictus* male palp, ectal view. Illustration traced and modified; flipped horizontally so palp faces left, from Crosby and Bishop 1924.

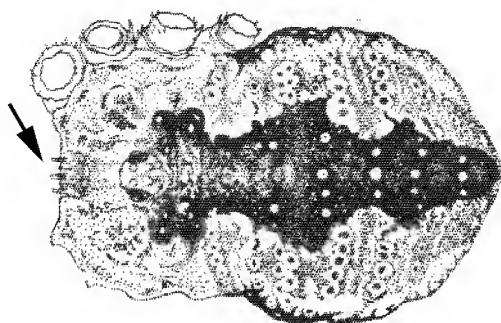


Figure 34. *Odiellus pictus* dorsal view of female body; arrow points to prosomal spine-tipped tubercles. Illustration traced and modified from Bishop 1949.

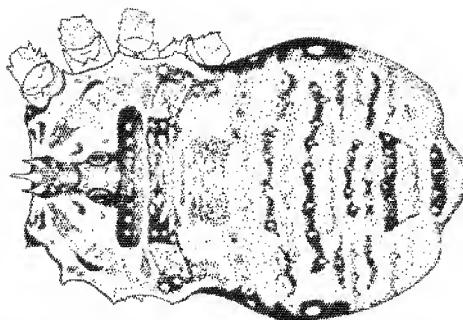


Figure 35. *Odiellus pictus* dorsal view of male body (atypical central figure). Illustration traced and modified from Bishop 1949.



Figure 36. Live *Odiellus pictus* male from Indian Gap, Great Smoky Mountains National Park, Tennessee. Photograph by James C. Cokendolpher.



Figure 37. Live *Odiellus pictus* female from Athabasca, Alberta. Photograph by Robert G. Holmberg.

not bear a label stating that they were collected after the date of publication in April of 1966.

We have located two vials of specimens at MSU that are labeled as “*Odiellus pictus argentus*” but they are not here considered to be syntypes because one vial contains specimens from outside of Michigan (and possibly misidentified) and the other vial is not from one of the nine published counties. The non-type specimens are: 1 male, 1 female, and 1 juvenile and typewritten label “*Odiellus pictus argentus* Mill Creek, P.C.334 Cheb[oigan] Co. Mich. among leaves along stream Coll. A. L. Edgar.” This sample has no date label.

We did find two vials at MSU which appear to contain specimens that are “syntypes.” They are: “*Odiellus pictus* variant Probably 7th mo., Probably Huron Co.”, 9 males, 1 female (MSU) and two specimens and two labels in the second vial: “*Odiellus pictus*—variant 1, Newaygo Co., Col. 7/20/57. F.R. 45.” and “Larger of 2 specimens from Livingston Co., 7/26/57 F.R. 66.” A typewritten label from the 1960’s recorded both sets of data but is written “larger of two species” rather than “larger of two specimens.” Therefore, we are considering the smaller sized male to belong with the Newaygo County label and the female to be the Livingston County specimen. The dates correspond to dates Edgar was collecting for his dissertation so he presumably was the collector of these samples. F.R. probably means Farm Road. There are county roads running east-west through Newaygo County numbered 40, 44, and 48; but none can be located in Livingston County. With the development of these areas over the last 60 years, these farm/dirt roads may no longer exist. These latter two specimens are here designated the lectotype (male Newaygo County) and paralectotype (female Livingston County). We have separated the two specimens and re-labeled the vials so no confusion will exist in future studies. We also designate the Huron County specimens all as paralectotypes. The lectotype male and paralectotype female (from Livingston County) match the original description of the species (except much faded in color—white to silver, tinged with pink is now creamy to light tan in color), including the measurements. The “white spines” on the abdomen are little more than granules that are spine-tipped, not very noticeable. The total length of the lectotype was taken from the anterior-most point of the prosoma to

the end of the opisthosoma. This anterior point is not in the center in front of the trident, but an imaginary line drawn from the forward pointing sides of the prosoma in front of each ozopore. The paralectotypes from Huron County match the description, but are slightly smaller in measurements.

Neither *O. argentus* nor *O. nubivagus* has been recorded outside the states in which they were originally described. As *O. pictus* is such a widespread and variable species and *O. argentus* and *O. nubivagus* seem to be restricted to very local areas, it appears that this genus needs a thorough taxonomic study of North American specimens to determine the relationships. The penis has only been illustrated by Bishop (1949: Figs. 27, 28); *O. pictus* specimen presumably from New York. We have used a very conservative approach by identifying many collections as *O. pictus*.

***Oligolophus* C. L. Koch 1871**

(Figs. 38, 39)

Oligolophus tridens (C. L. Koch 1836) is known from Iceland, northern through central Europe, and was first reported in America as being introduced into Vermont prior to 1974 (Bell 1975). However, Hackman (1956) speculated that his immature *Oligolophus* sp. from Newfoundland was this species. Bragg and Holmberg (2009) gave their earliest collection dates for British Columbia, New Brunswick, Newfoundland, Nova Scotia, Ontario, Prince Edward Island, Quebec, and Maine. Our work indicates that this species was present in Newfoundland as early as 1947 [i.e., St



Figure 38. Live *Oligolophus tridens*, sex not determined, from the Netherlands. Photograph by Jan van Duinen.

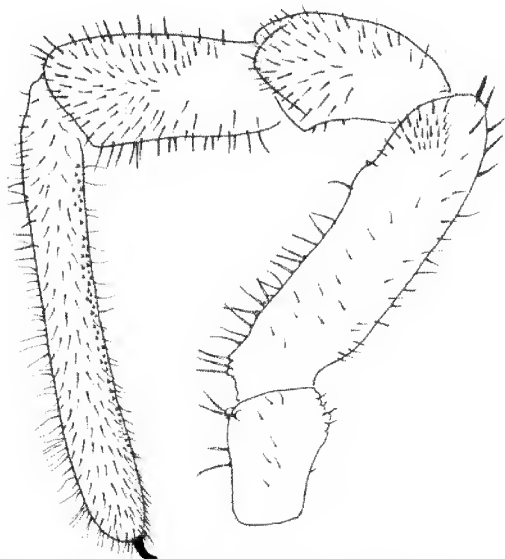


Figure 39. *Oligolophus tridens* male palp, ectal view. Illustration traced and modified; flipped horizontally so palp faces left, from Martens 1978.

John's, 27 October 1947, R. Traub, 1 male, 2 females (JCC)]. All records are from introductions into eastern and western North America.

Oligolophus ohioensis = *Odiellus pictus*; see *Lacinius* for details.

Oligolophus montanus = *Mitopus morio*; see *Mitopus* for details.

***Paroligolophus* Lohmander 1945**
(Figs. 40–43)

Bragg and Holmberg (1975) reported that *Paroligolophus agrestis* (Meade 1855) was introduced into British Columbia and Washington. The species is otherwise known from Europe. Bragg and Holmberg (2009) recorded new records from British Columbia as well as noting collections from Alberta and Nova Scotia. The earliest east coast record [Nova Scotia: Halifax, 29 September 1950, unknown collector, 1 female (CNC)] coincides with the earliest west coast record that we have found [i.e., British Columbia: Vancouver Island, Wellington, 20–24 August 1950, R. Guppy, 1 female (JCC)].

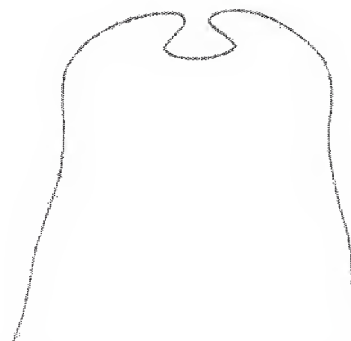


Figure 40. *Paroligolophus agrestis* female genital operculum with a large notch on anterior border. Illustration traced from Martens 1978.

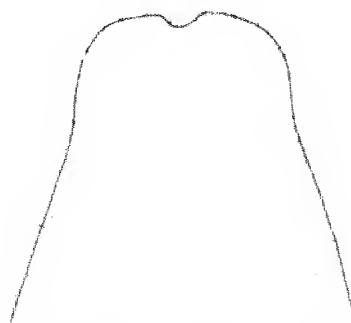


Figure 41. *Paroligolophus agrestis* male genital operculum with a small notch on anterior border. Illustration traced from Martens 1978.



Figure 42. *Paroligolophus agrestis* penis. Illustration traced from Martens 1978.



Figure 43. Live *Paroligolophus agrestis*, sex not determined, from Spanaway, Pierce County, Washington. Photograph by Joseph V. Higbee.

Subfamily Opilioninae C. L. Koch 1839a
***Egaenus* Koch, in Hahn and Koch 1839b**

The only species from the New World described in this otherwise Eurasian genus is *Egaenus mexicanus* Becker 1886. No specific locality in Mexico was recorded by Becker. Currently, the species is considered a synonym of *Opilio ischionotatus* Dugès 1884 (= *Leiobunum ischionotatum*), see below under *Opilio*. *Egaenus* is not known from the Americas.

***Opilio* Herbst 1798**
 (Figs. 44, 45)

Because of the antiquity of the name, some of the older specific names for New World harvestmen have been associated incorrectly with *Opilio*. Roewer (1952, 1956) described three new species from the New World under *Opilio*. All have been moved to other genera or synonymized.

In 1955, Levi and Levi indicated (in a footnote) that *Opilio angulaticHELIS* Roewer 1952 from “Glacial” (Glacier) National Park, Montana, was an immature male *Phalangium opilio*. JCC examined the holotype (SNMF, vial RII/11048/328 with body and legs; microscope slide number 16107 with left palp and chelicera) and found it to be as Levi and Levi suggested (Cokendolpher and Lee 1993). The smooth supracheliceral laminae and reduced spur on the chelicerae are normal for immature male *P. opilio*.

Opilio bolivianus Roewer 1956 was synonymized under *Cristina bispinifrons* Roewer 1917 (subfamily Phalangiinae) by Cokendolpher and Rylander (1986). However, they concluded that the collection locality of Bolivia was incorrect and suggested that it originated from the Cameroon region of western Africa.

Opilio chickeringi Roewer 1956, from Costa Rica, became the type species for the genus *Lanthanopilio* Cokendolpher and Cokendolpher 1984. This species was first placed in the Phalangiinae by Cokendolpher and Cokendolpher (1984) but provisionally was transferred to the *Dicranopalpus* genus group (family *incertae sedis*) by Crawford (1992). Both *Opilio gertschi* and *Opilio mexicanus* Roewer 1956, from Mexico (Tamaulipas), were transferred to the



Figure 44. Live *Opilio parietinus* male from Baptiste Lake, Athabasca County, Alberta. Photograph by Robert G. Holmberg.



Figure 45. Live *Opilio parietinus* female from Baptiste Lake, Athabasca County, Alberta. Photograph by Robert G. Holmberg.

genus *Metopilio* Roewer 1911 (new family, “*Metopilio* group”) by Cokendolpher and Cokendolpher (1984). We also recognize *Lanthanopilio* as being a member of that same new family. The reason this genus was first placed in the Phalangiidae was based on the morphology of the penis: bent junction of the glans and shaft. This derived condition apparently was developed independently a second time in the “*Metopilio* group.” The biogeography and other morphological characters place this species in the “*Metopilio* group.”

Opilio scabripes Walker 1860 = *Mitopus morio*; see *Mitopus* for details.

Mitopus californicus Banks 1895 = *Opilio parietinus* (De Geer 1778), **new synonym**.

Mitopus californicus Banks 1895:66, 1901:674, 1904:362; Myers 1921:19; Comstock 1940:69.

Nitopus californicus Banks 1911:420 (*lapsus calami*).

There are two cotypes of *Mitopus californicus* in the Nathan Banks collection (MCZ). The male is hereby designated the lectotype, the female a paralectotype. Examination of the types reveals that they are both specimens of *Opilio parietinus* (De Geer 1778) and not *Mitopus morio* as indicated by Roewer (1912) and subsequent authors. The type specimens of *M. californicus* were reported (Banks 1895) to have been from Los Angeles, California. Like so many other harvestmen described by Banks from southern California, the type locality data appear to be in error. In the USA, *Opilio parietinus* is only encountered in the more northern regions; no valid records from southern California are known.

The above discussion leaves *Opilio parietinus* (De Geer 1778) as the only *Opilio* in the New World. It is widely distributed in the western Palearctic and introduced into Tasmania (Martens 1978). It was first described from North America from New York as *Phalangium cinereum* Wood 1868. Human transport was possibly responsible for aiding the movement of this species around the globe (Gruber and Hunt 1973) and it was likely introduced into North America from Europe (Bragg and Holmberg 2009). It is uncommon in collections from the Nearctic and seldom occurs in great numbers as *Phalangium opilio*, with which it is often collected and sometimes confused. Cokendolpher and Lee (1993) recorded this species from three Canadian provinces (Ontario, Quebec, and Saskatchewan) and 18, mostly northern, states (Colorado, Idaho, Illinois, Iowa, Maine, Massachusetts, Michigan, Montana, Nebraska, New Hampshire, New Mexico, New York, North Dakota, Ohio, Pennsylvania, South Dakota, Texas, Vermont, and Wisconsin). Bragg and Holmberg (2009) noted records from British Columbia as well as Alberta and Manitoba.

Additional state records are: USA: UTAH: Box Elder County: Raft River Mountains, Lynn, "9-8-32",

R. V. Chamberlin and W. Ivie, 3 males, 4 females (AMNH); Carbon County: Price, November 1942, H. and M. Higgins, 2 males, 3 females (AMNH); Daggett County: Red Canyon, 19 July 1949, W. J. and J. W. Gertsch, 1 male (JCC); Garfield County: Henry Mountains, Horse Valley, "9-6-29", R. V. Chamberlin, 1 female (AMNH); Salt Lake County: Mill Creek Canyon, no date, R. V. Chamberlin, 1 female (AMNH); Salt Lake City, 18 October 1930, W. Ivie, 2 males, 1 female (AMNH); Salt Lake City, 30 October 1956, R. Rosella, 2 females (AMNH); west of Salt Lake City, no date, H. Fowler, 1 female (AMNH); unknown county: specific locality?, 14 May 1931, Yu-hsi M. Wang, 4 males, 9 females (AMNH); WYOMING: unknown county: "So. Mountainea", "8-6-46", collector unknown, 1 female (AMNH).

Opilio ischionotatus Dugès 1884 (= *Egaenus mexicanus* Becker 1886) from Guanajuato and Michoacán, México, is now known (Kury and Cokendolpher 2000) in the combination *Leiobunum ischionotatum* (Sclerosomatidae: Leiobuninae).

Platybuninae Staręga 1976

***Lophopilio* Hadži 1931**

(Fig. 46)

The single species of the genus recorded from the region is *Lophopilio palpinalis* (Herbst 1799) from Canada. This species is otherwise known from across Central and Northern Europe (Martens 1978) and Latvia, Lithuania, Byelorussia, Ukraine, Russia:



Figure 46. Live *Lophopilio palpinalis*, sex not determined, from the Netherlands. Photograph by Jan van Duinen.

Kaliningrad, Leningrad and Moscow areas, Karelia (Farzalieva and Eshunin 2000). Although this introduced species resembles the native *Odiellus pictus*, they are easily told apart by the absence of a hook on the ventral surface of the basal cheliceral segment in *Lophopilio*. This is a good character as it can be seen on adults as well as immatures.

New record of *Lophopilio palpinalis*: CANADA: NEW BRUNSWICK: Fundy, Laverty Falls, 11 August 2009, J. Cossey, J. Fernandez, R. Labbee, J. Smith, M. Zhang Mixed forest, N45.6570015, W65.01499939, 404 m. elev., 1 male (Biodiversity Institute of Ontario, University of Guelph).

Megabunus Meade 1855

(Fig. 47)

Megabunus diadema (Fabricius 1779) is a species of harvestman widely distributed in Europe, where it has been found in Iceland, Faroe Islands, western Norway, Great Britain, western France, Belgium, and northern Spain (Stol 2005). It presumably was introduced into Iceland and possibly will be introduced to other areas west with shipping and commerce in the Americas. This species was reported as being mainly parthenogenetic by Stol (2005), which would greatly increase the odds in establishing a population with only a single specimen. More recently populations that are not parthenogenetic have been discovered (D'Amico



Figure 47. Preserved *Megabunus diadema* female from England. Photograph by Robert G. Holmberg.

and Danflous 2015) but they are in the warmer/southern reaches of the distribution in Spain.

Rilaena Šilhavý 1965

(Figs. 48–51)

Martens (1978) discussed European species of *Rilaena*. Bragg and Holmberg (1975) reported that *Rilaena triangularis* (Herbst 1799) was introduced into British Columbia and Washington. Bragg and Holmberg (2009) noted that the earliest North American record was 1951 (Washington) but there also were collections from Maine (see also Drummond et al. 2010), Massachusetts, and New York. The first record from Quebec was photographs by Pierre-Marc Brousseau



Figure 48. Live *Rilaena triangularis* subadult male from Kentville, Nova Scotia. Photograph by Robert G. Holmberg, modified; flipped horizontally so body faces left.



Figure 49. *Rilaena triangularis* male from Mont St-Bruno, Quebec. Photograph by Pierre-Marc Brousseau.



Figure 50. *Rilaena triangularis* anterior view of prosoma and chelicerae (2nd segment with large distal spur) of male from Mont St-Bruno, Quebec. Photograph by Pierre-Marc Brousseau.

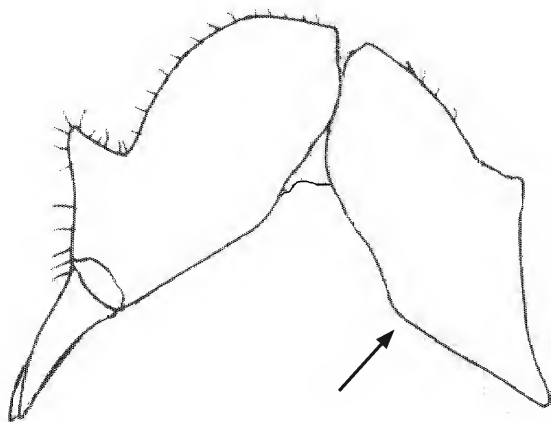


Figure 51. *Rilaena triangularis* lateral view of chelicera, arrow points to region where ventral spur is missing, sex not determined. Illustration traced and modified from Martens 1978.

(Figs. 49, 50 herein) on the internet (<https://bugguide.net/node/view/897539/bgimage>). Some other authors have reported *triangularis* in combination with *Parapltybunus* Dumitrescu 1970 and *Platybunus* C. L. Koch 1839a, but, most recent authors do not. We

herein report *R. triangularis* for the first time from Nova Scotia (Fig. 48).

New records of *Rilaena triangularis*: CANADA: NOVA SCOTIA: Cape Breton Island, St. Anns, 22 June 2005, RGH, 1 subadult male (RGH); Kentville, 24 June 2005, RGH, 15 subadults, 3 of which have the cheliceral spurs typical of males (RGH).

Misplaced Species
Protolophidae Banks 1893b
***Parodiellus* Roewer 1923**

The single species from the Americas recorded in *Parodiellus* is misplaced in that genus. Cokendolpher and Lee (1993) indicated that this species may have been placed in the wrong family. The species correctly is placed in *Protolophus* Banks 1893b of the Protolophidae Banks 1893b.

Parodiellus projectus Goodnight and Goodnight 1942b (Phalangiidae) = *Protolophus niger* Goodnight and Goodnight 1942a (Protolophidae), **new synonym**.

Goodnight and Goodnight (1942b) described *Parodiellus projectus* from Oregon. Examination of the male (penultimate) holotype (by JCC) revealed that it is conspecific with *Protolophus niger* Goodnight and Goodnight 1942a. As the name *P. niger* was published 22 January 1942a, and *P. projectus* was published 13 February 1942b, the later name is the junior synonym. The holotype of *P. projectus* apparently was collected with part of the type series of *P. niger* at Rogue River Valley, Oregon (April 1934, Lawrence). It presumably was considered different due to the fact that it was in the process of the final molt when it was preserved and therefore the external morphology was different. Adult members of the genus *Protolophus* Banks show considerable sexual dimorphism (Goodnight and Goodnight 1942a; JCC personal observation); whereas penultimate males show characteristics of both sexes. Fortunately, the holotype of *P. projectus* has a well-formed penis making identification certain. The holotype of *P. projectus* and the type series of *P. niger* are deposited in AMNH.

TAXONOMIC KEY TO THE PHALANGIIDAE OF THE AMERICAS

The following key primarily is based on Edgar's publication (1990). The key is applicable for adults, most subadults, and older immatures. For positive identifications, mature males are best. Females, subadults, and older immatures often need to be associated with mature males for positive identification. Most immatures cannot be identified to more than family level unless one already knows what species occur in a specific area and has an extensive knowledge about their variability.

Any key only provides tentative identification, therefore, one must also check other characteristics provided in Table 1 and the text as well as in the literature cited. To confirm identification of European species, see Hillyard and Sankey (1989), Martens (1978), Spoek (1963), and Uddström and Rinne (2016). The latter has excellent color photographs of most European species covered here. For *Leptobunus* species, see Cokendolpher (1985). For *Liopilio* species, see Cokendolpher (1981a). Bishop (1949) still has the best illustrations for most eastern species.

The best morphological and anatomical characteristics (in descending order) are on the: penis [consisting of a long, basal shaft (corpus) topped with a bulbous glans that has a long, terminal spine-like stylus; in lateral view, the glans is bent about 90 degrees from the corpus]; palp (= pedipalp, palpus); spine-tipped tubercles on the anterior dorsal prosoma (= cephalothorax); chelicera; ocularium (= ocular tubercle, eye turret); genital operculum; coloration; other characteristics. The segments of the palp, from the base, are as follows:

coxa [sometimes with an apophysis (= lobe; distal end expanded on inner/mesal margins) and/or spine-tipped tubercles], trochanter (sometimes with ventral spine-tipped tubercles), femur (longest segment; sometimes with ventral, elongate spine-tipped tubercles), patella (usually with a small to large mesal apophysis), tibia (usually with a small to large mesal apophysis), and tarsus (males may have a ventral series of denticles; ensure the claw is smooth, not toothed). The sizes of bodies and body parts are variable.

For specimens preserved in alcohol, one can determine maturity by examining the anterior edge of the genital operculum. In adult specimens, the anterior edge is open and can be lifted slightly with fine-tipped forceps or a needle. With forceps, the genital operculum can be pulled/ripped backwards to reveal the penis or ovipositor. In immatures, the anterior edge of the operculum is fused to the body and the penis or ovipositor is absent or only partially developed.

Phalangiids are drably colored (shades of brown, grey, black, tan, yellowish and white). The pigmentation patterns can be useful for identification but are inconstant because of genetic variability as well as sex, age, and stage within the molting cycle. Generally, adult males are more darkly pigmented, more armored and smaller, than females. Methods of preservation and lengths of time of preservation also affect color. Colors referred to in the key apply to specimens preserved in alcohol. To observe the seminal receptacles, the tip of the ovipositor must be cleared (clove oil or lactophenol work well; see Acosta et al. 2007).

Key

1. Anterior median border of prosoma with one to three conspicuous spine-tipped tubercles much longer than any other tubercles in the anterior area (area in front of the eyes); the tubercles usually form a trident with the central tubercle the longest (Figs. 34, 35, 46, 47).....2
- 1'. Anterior median border of prosoma smooth, granulated, or with one to several small spines/tubercles of near equal length (Figs. 10, 16, 17, 22, 38) 8
2. Ocularium spines/tubercles not exceedingly prominent, shorter than the eye diameter3
- 2'. Ocularium spines/tubercles longer than the eye diameter and nearly the height of the ocularium (Fig. 47) (in Europe and Iceland, not yet found in mainland North America) *Megabunus diadema*
3. Genital operculum with a smooth, rounded anterior margin; ocularium with two longitudinal rows of small tubercles 4
- 3'. Genital operculum with a medial notch on the anterior border (Figs. 40, 41); ocularium nearly smooth with a few setae only (Fig. 43). See also Fig. 42 *Paroligolophus agrestis*
4. Palpal femur with several large spine-tipped tubercles ventrally (Fig. 33).....5
- 4'. Palpal femur with only spines or a few short spine-tipped tubercles (Fig. 39). See also Fig. 39.....
..... *Oligolophus tridens*
5. Basal segment of the chelicera with a ventral hook (spur) (like in Fig. 31)..... *Odiellus*.....6
- 5'. Basal segment of chelicerae smooth, without a ventral hook (like in Fig. 51). See also Fig. 46
..... *Lophopilio palpinalis*
6. Central figure (dorsal, bilaterally symmetrical, pigmented pattern on body; also called a saddle) distinct or not, generally more obscure in females, mottled with brown, remaining dorsum silvery with brown wisps (Figs. 34–37); femur of leg II tan but blotched with dark brown and ringed with brown distally; ocularium generally lighter except beneath the eyes. *Odiellus pictus*
- 6'. Central figure of dorsum not conspicuously mottled but uniform dark brown or black, except for a few small white spots (Fig. 32); femur of leg II tan to black with little or no distal dark ring; ocularium dark, not contrasting with the central figure 7
7. Lateral borders of central figure distinct, nearly parallel on opisthosoma (abdomen), dark brown, remaining dorsum silvery white, female with tan and pink tinge, diverging anteriolaterally on prosoma; femur of leg II tan with little or no distal dark ring; ocularium a bit lighter than central figure; from Michigan.....
..... *Odiellus argentus*
- 7'. Legs, sides of opisthosoma and much of prosoma including ocularium dark brown to black; from high mountains of North Carolina and Tennessee (Fig. 32) *Odiellus nubivagus*
8. Ocularium with spine-tipped tubercles 14
- 8'. Ocularium smooth or, at most, small setae 9
9. Palpal femur and patella expanded mesally (Figs. 14, 15); Male: palpal tarsus ventrally with denticles (Fig. 14) *Liopilio*.....13
- 9'. Palpal tibia and tarsus may be expanded mesally (Figs. 1, 11), femur and patella not expanded mesally (Fig. 2); Male: palpal tarsus ventrally without denticles *Leptobunus*.....10

10. Male: distal segment of chelicera with distinct lateral spur (apophysis) on movable finger (Fig. 3); stylus of penis nearly equal to or shorter than setae of glans (Figs. 4, 5); Female: primary loop of seminal receptacle short, less than three times as long as wide (Fig. 6) *Slimlepto* **new subgenus**.....11
- 10'. Male: distal segment of chelicera without lateral spur on movable finger; stylus of penis much longer than setae of glans (Figs. 7, 12); Female: primary loop of seminal receptacle long, more than four times as long as wide (Figs. 8, 9)..... *Leptobunus* subgenus.....12
11. Body color usually golden; legs speckled; Male: setae of glans separated by more than the length of the stylus (Fig. 4); only known from California *Leptobunus aureus*
- 11'. Body color brown, gray, or bronze; legs banded; Male: setae of glans closely spaced (Fig. 5). Distributed from Alaska to California. See also Fig. 10 *Leptobunus parvulus*
12. Male: palpal tibiae and tarsi expanded on mesal side (Fig. 1); dorsum of penis glans slightly depressed (Fig. 7); Female: basal loops of seminal receptacles consisting of three coils or loops (Fig. 8) *Leptobunus californicus*
- 12'. Male: palpal tibiae and tarsi only slightly expanded (Fig. 11); dorsum of penis glans straight (Fig. 12); Female: basal loops of seminal receptacles consisting of two coils or loops (Fig. 9). See also Fig. 13..... *Leptobunus borealis*
13. Central figure on opisthosoma distinct and not cross-shaped (Fig. 16); body sometimes yellowish; Male: palpal patella and tibia armed ventrally with small spines as well as denticles (Fig. 14). See also Fig. 15..... *Liopilio yukon*
- 13'. Central figure on opisthosoma obscured, with light and dark spotting, or absent (Figs. 17–19); body often yellowish green; Male: palpal patella and tibia without small spines but with denticles. See also Figs. 20–21..... *Liopilio glaber*
14. Basal segment of chelicera ventrally with a sharp, forward-pointed hook (spur) (Fig. 31). See also Figs. 28–30..... *Mitopus morio*
- 14'. Basal segment of chelicera ventrally smooth, without a hook (like in Fig. 51) 15
15. Supracheliceral laminae smooth; Male: chelicerae and palps normal 16
- 15'. Supracheliceral laminae, of adults and subadults, with two anteriorly directed spines visible below anterior margin of prosoma (Figs. 22, 24); Male: distal segment of chelicera elongated dorsally as a spur (length is variable) and palps very slender and elongate, extending considerably above the prosoma (Figs. 23, 25); Female: see Fig. 26..... *Phalangium opilio*
16. Ocularium strongly canaliculate (grooved) and about one-third the width of the prosoma (Figs. 49, 50). Palp with a distinct apophysis on the inner side of the patella and a much smaller one on the tibia (Figs. 48, 49). Male with large spur on 2nd segment of chelicera (Figs. 50, 51) *Rilaena triangularis*
- 16'. Ocularium not canaliculate and about one-fifth the width of the prosoma (Figs. 44–45). Palpal segments nearly cylindrical with only slight apophyses. Male femur I thicker than that of other legs and all female legs (Figs. 44, 45)..... *Opilio parietinus*

Table 1. Summary of diagnostic features of adult and subadult Phalangiidae of North America. See text for details and references.

Species	Penis	Palp	Prosoma	Chelicera	Ocularium	Genital Operculum	Coloration	Comments
Oligolophinae								
<i>Mitopus morio</i>	Corpus stout, tapering distally. Glans longer than stylus; with a retractable bladder.	Trochanter and femur with a few small spine-tipped tubercles. Femur with a small apophysis. Male: ventral denticles on tarsus.	Anterior with small, scattered tubercles; no obvious trident. Figs. 28-30.	Basal segment with ventral hook. Fig. 31	2 rows of 3 to 7 small spine-tipped tubercles. Generally pale between the eyes. Figs. 28-30.	Typical with smooth distal margin.	Extremely variable. Dark brown to black central figure may be outlined with white. Figs. 28-30.	East coast and Alaska but not found in much of northern Canada. Possibly introduced to parts of the range. Fig. 27.
<i>Odiellus argentinus</i>	Not published, see <i>Odiellus pictus</i> .	See <i>Odiellus pictus</i> .	See <i>Odiellus pictus</i> .	Basal segment with ventral hook.	See <i>Odiellus pictus</i> ; a bit lighter than central figure.	See <i>Odiellus pictus</i> .	Central figure uniform dark brown or black not mottled; sides nearly parallel on opisthosoma. Leg II femur without distal dark ring.	Reported only from Michigan.
<i>Odiellus bivagus</i>	Not published, see <i>Odiellus pictus</i> .	See <i>Odiellus pictus</i> .	See <i>Odiellus pictus</i> . Figs. 34-37; compare Fig. 32.	Basal segment with ventral hook.	See <i>Odiellus pictus</i> . Figs. 34, 37; compare Fig. 32.	See <i>Odiellus pictus</i> .	Sides of opisthosoma and much of prosoma including ocularium dark brown to black. Leg II femur without distal dark ring. Fig. 32.	Reported only from high mountains of North Carolina and Tennessee.

Table 1. (cont.)

Species	Penis	Palp	Prosoma	Chelicera	Ocularium	Genital Operculum	Coloration	Comments
<i>Odiellus pictus</i>	Corpus long and slender with a single, dorsal, concave, oval area distally and a small dorsal indentation at the base. Glans longer than stylus. Stylus short and curved.	Trochanter and femur with a few long spine-tipped tubercles. Femur, patella, and tibia with apophyses; most prominent on patella. Male: ventral denticles on tarsus. Fig. 33.	Anterior edge with trident of 3 spine-tipped tubercles backed with a few smaller ones. Figs. 34-37.	Basal segment with ventral hook.	2 rows of about 7 small spine-tipped tubercles; generally paler than central figure. Figs. 34, 35.	Typical with smooth distal margin.	Central figure light to dark mottled brown; widest on tergite 3; extends to posterior of opisthosoma. Leg II femur with distal dark ring. Figs. 34-37.	Distributed across North America but near Michigan, North Carolina and Tennessee, also consider <i>Odiellus argentus</i> and <i>O. nubivagus</i> .
<i>Oligolophus tridens</i>	Corpus long and slender; slightly tapering distally. Glans longer than stylus. Glans with 2 setae near tip.	Trochanter and femur with only spines or a few short spine-tipped tubercles. Femur, patella, and tibia with small apophyses. Fig. 39. Male: denticles ventrally on tarsus.	Anterior edge with small, nearly vertical trident of 3 spine-tipped tubercles. Only a few small accessory tubercles to sides and rear of trident. Fig. 38.	Basal segment with ventral hook.	2 rows of 4 to 7 small spine-tipped tubercles. Mostly pale. Fig. 38.	Typical with smooth distal margin.	Central figure dark brown and abruptly truncated on tergite 5. Female central figure usually straight-sided. Fig. 38.	Small species; may morphologically appear as immatures of other species. Found in disturbed areas. Introduced to North America.
<i>Paroligolophus agrestis</i>	Corpus long and slender but with a broad base. Glans shorter than stylus. Glans with 2 setae near tip. Fig. 42.	Only a few short spine-tipped tubercles on the trochanter and femur. Coxa, femur, patella, and tibia with small apophyses. Male: denticles ventrally on tarsus.	Anterior edge with an obscure trident of 3 spine-tipped tubercles. Trident surrounded with slightly shorter tubercles.	Basal segment with small ventral hook.	Very small spines; mostly smooth. Wider than long. Mostly pale. Fig. 43.	Female: definite notch at distal margin. Male: indentation at distal margin (Figs. 40, 41); black corpus of the penis visible through the operculum. Female: slight darkened indentation at distal margin. Fig. 41.	Variable and diffuse. Usually a central pale stripe from operculum to tergite 5. Fig. 43.	Now found in the east and west of North America, especially in disturbed areas. Introduced.

Table 1. (cont.)

Species	Penis	Palp	Prosoma	Chelicera	Ocularium	Genital Operculum	Coloration	Comments
Opilioninae								
<i>Opilio parietinus</i>	Corpus stout with a pair of dorsal, concave, oval, areas distally. Glans longer than stylus,	Short spine-tipped tubercles, especially on femur. Coxa, femur, patella, and tibia with small apophyses. Male: denticles ventrally on tarsus.	Scattered small spine-tipped tubercles. Brown stripe in front of ocularium bordered by small tubercles. Figs. 44, 45.	Basal segment without ventral hook.	2 rows of 5 to 7 moderate spine-tipped tubercles. Eyes angled distinctly upwards from prosoma. Ocularium close to anterior edge of prosoma, about width of ocularium. Pale between the eyes. Figs. 44, 45.	Distal end enlarged laterally with a smooth edge.	Central figure indistinct. Dorsum brown with tan spots. Venter light colored with dark brown spots. Figs. 44, 45.	Often collected with <i>Phalangium opilio</i> but in fewer numbers. Possibly introduced to parts of the range.
Phalangiinae								
<i>Leptobunus aureus</i>	Stylus of penis nearly equal to or shorter than setae of glans. Setae separated by more than the length of the stylus. Fig. 4.	Femur, patella, tibia and tarsus without prominent expanded areas.	Prosoma smooth, devoid of spines.	Basal segment with ventral hook. Lateral spur on movable finger.	2 rows of small tubercles with setae.	Typical with smooth distal margin.	Body color usually golden brown; legs speckled. Central figure forms a broad cross-pattern but less distinct near the prosoma.	Reported only from California.
<i>Leptobunus borealis</i>	Stylus of penis much longer than setae of glans. Dorsum of penis glans straight. Fig. 12.	Femur, patella, tibia and tarsus without prominent expanded areas. Fig. 11.	Prosoma smooth, devoid of spines. Fig. 13.	Basal segment with ventral hook. No lateral spur on movable finger.	2 rows of small tubercles with setae. Fig. 13.	Typical with smooth distal margin.	Central figure dark brown; forms a broad cross-pattern. Fig. 13.	Reported from Alaska and Aleutian Islands. See also Fig. 9 for drawing of seminal receptacle.

Table 1. (cont.)

Species	Penis	Palp	Prosoma	Chelicera	Ocularium	Genital Operculum	Coloration	Comments
<i>Leptobunus californicus</i>	Stylus of penis much longer than setae of glans. Dorsum of glans slightly depressed. Fig. 7.	Tibiae and tarsi with prominent apophyses. Femur and patella without prominent expanded areas. Figs. 1, 2.	Prosoma smooth, devoid of spines.	Basal segment with ventral hook. No lateral spur on movable finger.	2 rows of small tubercles with setae. Concolorous with dorsum.	Typical with smooth distal margin.	Central figure brown; forms a broad cross-pattern but less distinct near the prosoma.	Reported from California and Nevada. See also Fig. 8 for drawing of seminal receptacle.
<i>Leptobunus parvulus</i>	Stylus of penis nearly equal to or shorter than setae of glans. Setae closely spaced, less than length of stylus. Fig. 5.	Patella with prominent apophysis. Femur, tibia and tarsus without prominent expanded areas.	Prosoma smooth, devoid of spines. Fig. 10.	Basal segment with ventral hook. Lateral spur on movable finger.	2 rows of small tubercles with setae. Slightly paler between the eyes. Fig. 10.	Typical with smooth distal margin.	Central figure dark brown, gray or bronze extending to sides of opisthosoma on tergites 1 to 3 and terminating on tergite 5, making more of a broad T-rather than a cross-pattern. Most leg segments darkly banded apically. Fig. 10.	Distributed from Alaska to California. See also Fig. 6 for drawing of seminal receptacle.
<i>Liopilio glaber</i>	Corpus moderate, tapering distally with a single, dorsal, concave area adjacent to the glans. Glans longer than stylus. Glans with 2 setae about 1/3 back from stylus.	Femur and patella with prominent expanded areas. Male: denticles ventrally on tarsus.	Prosoma smooth, devoid of spines. Figs. 17-19.	Basal segment with (especially immatures) or without (especially adults) ventral hook.	2 rows of small tubercles with setae. Dark between the eyes. Figs. 17-19.	Typical with smooth distal margin.	Central figure indistinct. Yellowish green opisthosoma often fades in alcohol to brown or gray. Figs. 17-21.	Reported from Alberta, British Columbia, Montana, and Washington. Legs relatively long (Figs. 20, 21).

Table 1. (cont.)

Species	Penis	Palp	Prosoma	Chelicera	Ocularium	Genital Operculum	Coloration	Comments
<i>Liopilio yukon</i>	Corpus moderate, tapering distally with a single, dorsal, concave area adjacent to the glans. Glans longer than stylus. Glans with 2 setae about 1/3 back from stylus.	Femur and patella with prominent expanded areas. Male: denticles ventrally on tarsus. Patella and tibia with more denticles and spines than <i>L. glaber</i> . Figs. 14, 15.	Prosoma smooth, devoid of spines. Fig. 16.	Basal segment with or without ventral hook.	Nearly smooth. Dark between the eyes. Fig. 16.	Typical with smooth distal margin.	Central figure distinct, widest at tergite 3 and terminates on tergite 6. Yellowish opisthosoma. Fig. 16.	Reported from Alaska and Yukon.
<i>Phalangium opilio</i>	Corpus narrows and then widens distally (lateral view). Glans, nearly as deep as long; longer than stylus. Glans with 2 setae near stylus.	Short spine-tipped tubercles, especially on femur. Femur, patella, and tibia with small apophyses. Male: very elongate (nearly half length of body) with wide, dark band on femur. Figs. 23-25. Female: Fig. 26. Immatures: large apophyses on patella and tibia.	Anterior edge with several small spine-tipped tubercles. supracheliceral laminae with spine-tipped spurs. Figs. 22-26.	Basal segment without ventral hook. Male: distal segment with a dorsal spur (length variable). Figs. 23-25.	2 rows of 6 to 10 moderate spine-tipped tubercles. Eyes angled slightly upwards but close to parallel to prosoma. Figs. 22-26.	Typical with smooth distal margin.	Brown above, yellowish to white below. Central figure often obscure in males. Figs. 24-26.	Very common in disturbed areas throughout much of North America. Possibly introduced to parts of the range.

Table 1. (cont.)

Species	Penis	Palp	Prosoma	Chelicera	Ocularium	Genital Operculum	Coloration	Comments
Platybuninae								
<i>Lophopilio palpinalis</i>	Corpus slender but with a bulbous base. Glans longer than stylus. Glans with 2 setae near stylus.	Elongate spine-tipped tubercles, especially on trochanter, femur and tibia. Femur, patella and sometimes tibia with apophyses. Fig. 46.	Anterior edge with conspicuous trident of 3 spine-tipped tubercles. Fig. 46.	Basal segment without ventral hook. Relatively robust.	2 rows of 3 to 5 rather blunt tubercles. Fig. 46.	Typical with smooth distal margin.	Central figure of paired dark brown patches to tergite 6; also on prosoma. Fig. 46.	Reported only from New Brunswick, Nova Scotia and Quebec. Introduced.
<i>Megabunus diadema</i>	Corpus slender but with a broad base. Glans longer than stylus. Glans with 2 setae near stylus.	Elongate spine-tipped tubercles on all segments except patella. A dorsal spine-tipped tubercle on the distal end of the femur. Femur, patella, and tibia with apophyses. Fig. 47.	Anterior area with only 1 large spine-tipped tubercle but lateral edges each with 3 prominent tubercles. Fig. 47.	Basal segment without ventral hook. Relatively small.	2 rows of about 5 conspicuous, long spines; crown-like. Each spine longer than the eye diameter. Fig. 47.	Typical with smooth distal margin.	Central figure dark brown in double diamond shape. Spine-tipped tubercles on Leg I coxa.	Reported in our study area only from Iceland but also much of Europe.

Table 1. (cont.)

Species	Penis	Palp	Prosoma	Chelicera	Ocularium	Genital Operculum	Coloration	Comments
<i>Rhlaena triangularis</i>	Corpus slender but with a broad base. Glans longer than stylus, with 2 setae near stylus.	Moderately large spine-tipped tubercles on coxa, trochanter and femur; tibia with at least 1 tubercle midway. Prominent apophyses on coxa and patella and smaller ones on femur and tibia. Figs. 48, 49. Male: denticles ventrally on tarsus.	Anterior area only with a few small spine-tipped tubercles. Usually 1 medial tubercle on the anterior margin in a dark band extending anteriorly from the ocularium. Figs. 49, 50.	Basal segment without ventral hook. Male: lateral spur on distal segment pointing outwards. Figs. 50, 51.	2 rows of 7 to 11 small spine-tipped tubercles. Ocularium very wide, about one-third the width of the prosoma; close to anterior edge of prosoma, less than the width of the ocularium.	Typical with smooth distal margin.	Central figure variable; usually brown, spotted with white, darker towards rear and truncated on tergite 5. Figs. 48-50.	Now found in eastern and western North America. Introduced.

SUMMARY

The conclusions of this study are summarized in Table 2. Of the 68 scientific names considered, only 16 species of Phalangiidae in 10 genera are still valid for the Americas. No Phalangiidae are known to occur in Mexico, the Caribbean, Central or South America. *Egaenus* and *Lacinius* do not occur in the Americas. The single species of each of the genera *Lophopilio*, *Oligolophus*, *Opilio*, *Paroligolophus*, *Phalangium*, and

Rilaena were introduced accidentally by humans from Europe to more northern locations of North America. It is unclear if *Mitopus morio* is native to parts of North America and introduced to others; it is now found in the northeastern and northwestern areas of the continent. A taxonomic key to the members proper of the Phalangiidae is presented.

Table 2. Summary of the Family Phalangiidae in North America, listed alphabetically. There are no true Phalangiidae species in Mexico, Central and South America, or the Caribbean.

Species	Taxonomic Status	Distribution in North America	Native / Introduced	Comments
<i>Egaenus mexicanus</i>	= <i>Leiobunum ischionotatum</i>	—	—	Sclerosomatidae: Leiobuninae
<i>Lacinius ohioensis</i>	= <i>Odiellus pictus</i>	—	—	Phalangiidae: Oligolophinae
<i>Lacinius texanus</i>	= <i>Odiellus pictus</i>	—	—	Phalangiidae: Oligolophinae, new synonymy
<i>Leptobunus atavus</i>	= <i>Amauropilio atavus</i>	Fossil - Colorado	—	Sclerosomatidae: Leiobuninae
<i>Leptobunus aureus</i>	Valid	California	Native	Phalangiidae: Phalangiinae
<i>Leptobunus borealis</i>	Valid	Alaska and nearby Russian islands	Native	Phalangiidae: Phalangiinae
<i>Leptobunus californicus</i>	Valid	California and Nevada	Native	Phalangiidae: Phalangiinae
<i>Leptobunus mexicanus</i>	= <i>Paranelima mexicana</i>	—	—	Sclerosomatidae: Leiobuninae
<i>Leptobunus parvulus</i>	Valid	West coast, Alaska to California	Native	Phalangiidae: Phalangiinae
<i>Leptobunus spinulatus</i>	= <i>Metopilio spinulatus</i>	—	—	“ <i>Metopilio</i> group”, not Phalangiidae
<i>Leuronychus parvulus</i>	= <i>Leptobunus parvulus</i>	—	—	Phalangiidae: Phalangiinae
<i>Liobunum parvulum</i>	= <i>Leptobunus parvulus</i>	—	—	Phalangiidae: Phalangiinae
<i>Liomitopus laevis</i>	= <i>Leptobunus californicus</i>	—	—	Phalangiidae: Phalangiinae
<i>Liopilio glaber</i>	Valid	Rocky Mountains, south of <i>L. yukon</i>	Native	Phalangiidae: Phalangiinae, new record from 1 state
<i>Liopilio yukon</i>	Valid	Alaska, Yukon	Native	Phalangiidae: Phalangiinae
<i>Lophopilio palpinalis</i>	Valid	New Brunswick	Introduced from Europe by 2009	Phalangiidae: Platybuninae, new record from 1 province

Table 2. (cont.)

Species	Taxonomic Status	Distribution in North America	Native / Introduced	Comments
<i>Megabunus diadema</i>	Valid	—	European species introduced to Iceland and not yet found in North America	Phalangiidae: Platybuninae
<i>Mitopus californicus</i>	= <i>Opilio parietinus</i>	—	—	Phalangiidae: Opilioninae, new synonymy
<i>Mitopus dorsalis</i>	= <i>Mitopus morio</i>	—	—	Phalangiidae: Oligolophinae, new synonymy
<i>Mitopus morio</i>	Valid	Northwest and northeast North America, including Kalaallit Nunaat	Native but possibly introduced in some areas in the northeast and Alaska	Phalangiidae: Oligolophinae, new records for 2 provinces
<i>Nitopus dorsalis</i>	= <i>Mitopus morio</i>	—	—	Phalangiidae: Oligolophinae, <i>lapsus</i> , misspelling of genus
<i>Odiellus argentus</i>	Valid	Michigan	Native	Phalangiidae: Oligolophinae
<i>Odiellus nubivagus</i>	Valid	North Carolina, Tennessee	Native	Phalangiidae: Oligolophinae
<i>Odiellus pictus</i>	Valid	Cool, wet forests across southeastern and northern North America	Native	Phalangiidae: Oligolophinae, new records from 3 provinces and 1 county
<i>Oligolophus dorsalis</i>	= <i>Mitopus morio</i>	—	—	Phalangiidae: Oligolophinae
<i>Oligolophus montanus</i>	= <i>Mitopus morio</i>	—	—	Phalangiidae: Oligolophinae
<i>Oligolophus ohioensis</i>	= <i>Odiellus pictus</i>	—	—	Phalangiidae: Oligolophinae
<i>Oligolophus tridens</i>	Valid	Eastern North America and British Columbia	Introduced from Europe by 1947	Phalangiidae: Oligolophinae
<i>Opilio angulatichelis</i>	= <i>Phalangium opilio</i>	—	—	Phalangiidae: Phalangiinae
<i>Opilio bolivianus</i>	= <i>Cristina bispinifrons</i>	West Africa, not South America	—	Phalangiidae: Phalangiinae
<i>Opilio chickeringi</i>	= <i>Lanthanopilio chickeringi</i>	—	—	“ <i>Metopilio</i> group”, new status
<i>Opilio gertschi</i>	= <i>Metopilio gertschi</i>	—	—	“ <i>Metopilio</i> group”
<i>Opilio ischionotatus</i>	= <i>Leiobunum ischionotatum</i>	—	—	Sclerosomatidae: Leiobuninae
<i>Opilio mexicanus</i>	= <i>Metopilio mexicanus</i>	—	—	“ <i>Metopilio</i> group”

Table 2. (cont.)

Species	Taxonomic Status	Distribution in North America	Native / Introduced	Comments
<i>Opilio parietinus</i>	Valid	Northern U.S.A. and southern Canada	Possibly introduced from Europe by 1868	Phalangiidae: Opilioninae, new records from 2 states
<i>Opilio scabripes</i>	= <i>Mitopus morio</i>	—	—	Phalangiidae: Oligolophinae
<i>Paraplatybunus triangularis</i>	= <i>Rilaena triangularis</i>	—	—	Phalangiidae: Platybuninae
<i>Parodiellus dorsalis</i>	= <i>Mitopus morio</i>	—	—	Phalangiidae: Oligolophinae
<i>Parodiellus projectus</i>	= <i>Protolophus niger</i>	—	—	Protolophidae, Protolophinae, new synonymy, new family status
" <i>Parodiellus</i> " <i>dorsalis</i>	= <i>Mitopus morio</i>	—	—	Phalangiidae: Oligolophinae
<i>Paroligolophus agrestis</i>	Valid	Eastern and western North America	Introduced from Europe by 1950	Phalangiidae: Oligolophinae
<i>Phalangium acanthipes</i>	= <i>Metopilio acanthipes</i>	—	—	" <i>Metopilio</i> group"
<i>Phalangium armigerum</i>	= <i>Metopilio armigerum</i>	—	—	" <i>Metopilio</i> group"
<i>Phalangium bicolor</i>	= <i>Nelima elegans</i>	—	—	Sclerosomatidae: Leiobuninae
<i>Phalangium calcar</i>	= <i>Leiobunum calcar</i>	—	—	Sclerosomatidae: Leiobuninae
<i>Phalangium cinereum</i>	= <i>Opilio parietinus</i>	—	—	Phalangiidae: Opilioninae
<i>Phalangium dorsatum</i>	= <i>Leiobunum vittatum</i>	—	—	Sclerosomatidae: Leiobuninae
<i>Phalangium exilipes</i>	= <i>Leiobunum exilipes</i>	—	—	Sclerosomatidae: Leiobuninae
<i>Phalangium favosum</i>	= <i>Trachyrhinus favosus</i>	—	—	Sclerosomatidae: Gagrellinae
<i>Phalangium formosum</i>	= <i>Leiobunum formosum</i>	—	—	Sclerosomatidae: Leiobuninae
<i>Phalangium grande</i>	= <i>Hadrobunus grandis</i>	—	—	Sclerosomatidae: Leiobuninae
<i>Phalangium horridum</i>	= <i>Metopilio cambridgei</i>	—	—	" <i>Metopilio</i> group"
<i>Phalangium longipalpus</i>	= <i>Phalangium opilio</i>	—	—	Phalangiidae: Phalangiinae
<i>Phalangium maculatipes</i>	= <i>Metopilio maculatipes</i>	—	—	" <i>Metopilio</i> group"
<i>Phalangium maculosum</i>	= <i>Hadrobunus maculosus</i>	—	—	Sclerosomatidae: Leiobuninae
<i>Phalangium nigropalpi</i>	= <i>Leiobunum nigropalpi</i>	—	—	Sclerosomatidae: Leiobuninae

Table 2. (cont.)

Species	Taxonomic Status	Distribution in North America	Native / Introduced	Comments
<i>Phalangium nigrum</i>	= <i>Eumesosoma nigrum</i>	—	—	Sclerosomatidae: Leiobuninae
<i>Phalangium opilio</i>	Valid	Southern Canada and northern U.S.A.	Possibly introduced from Europe by 1890	Phalangiidae: Phalangiinae, new records from 19 provinces/states
<i>Phalangium ortonii</i>	species <i>inquirenda</i>	—	—	Sclerosomatidae: Gagrellinae
<i>Phalangium pictum</i>	= <i>Odiellus pictus</i>	—	—	Phalangiidae: Oligolophinae
<i>Phalangium rudipalpe</i>	Genus and species <i>inquirenda</i>	—	—	Sclerosomatidae: Gagrellinae, new status ; described from central Chile
<i>Phalangium spinigerum</i>	= <i>Metopilio spinigerus</i>	—	—	“ <i>Metopilio</i> group”
<i>Phalangium ventricosum hiemale</i>	= <i>Leiobunum ventricosum hiemale</i>	—	—	Sclerosomatidae: Leiobuninae
<i>Phalangium ventricosum ventricosum</i>	= <i>Leiobunum ventricosum ventricosum</i>	—	—	Sclerosomatidae: Leiobuninae
<i>Phalangium verrucosum</i>	= <i>Leiobunum verrucosum</i>	—	—	Sclerosomatidae: Leiobuninae
<i>Phalangium vittatum</i>	= <i>Leiobunum vittatum</i>	—	—	Sclerosomatidae: Leiobuninae
<i>Platybunus triangularis</i>	= <i>Rilaena triangularis</i>	—	—	Phalangiidae: Platybuninae
<i>Rilaena triangularis</i>	Valid	Eastern and western North America	Introduced from Europe by 1951	Phalangiidae: Platybuninae, new records from 1 province
<i>Strandibunus dorsalis</i>	= <i>Mitopus morio</i>	—	—	Phalangiidae: Oligolophinae
Totals	16 valid North American species in 10 genera and 4 subfamilies; 1 species in Iceland and Europe	Canada, northern and central U.S.A., Kalaallit Nunaat, Iceland	10 native, 6 introduced or possibly introduced from 4 subfamilies	30 new province/ state records, 4 new synonyms, 1 family change, 2 new status, 1 new subgenus

ACKNOWLEDGMENTS

We are grateful to many people for their help. The following curators kindly loaned material from their respective museums: David Barr, Royal Ontario Museum (ROM); Gergin A. Blagoev and Allison Brown, Biodiversity Institute of Ontario, University of Guelph; David Blades and Robert Cannings (retired), Royal British Columbia Museum; Jonathan A. Coddington, Ralph E. Crabill, Jr. (deceased), Patricia Gentili-Poole, and Hannah Wood, Smithsonian Institution, United

States National Museum (USNM); Rod Crawford (retired), Burke Memorial Washington State Museum (BMM); C. D. Dondale (retired), Canadian National Collection of Insects, Arachnids and Nematodes (CNC); Bert Finnermore and Terry Thormin (retired), Royal Alberta Museum; Saul Frommer (retired), University of California Riverside (UCR); Manfred Grasshoff (retired), Senckenberg Natur-Museum und Forschungsinstitut (SNMF); Jürgen Gruber (retired),

Naturhistorisches Museum, Wien (NMW); Erling Hauge (deceased), Universitetsmuseet i Bergen; Torbjörn Kronestedt (retired), Naturhistoriska Riksmuseet, Stockholm (NRS); Herbert Levi (deceased), Museum of Comparative Zoology, Cambridge (MCZ); Andrew Moldenke, Oregon State University (OSU); Gary L. Parsons, Michigan State University, East Lansing (MSU); Norman Platnick (retired), American Museum of Natural History (AMNH); and Geoff Scudder (retired), Spencer Museum, University of British Columbia (UBC). GRSM = Great Smoky Mountains National Wildlife Refuge collection at Twin Creeks Science and Education Center. Phil Bragg, Cassie Aitchison (CWA), Dave Blades, Don J. Buckle (DJB), Laurent Lesage, and Seppo Koponen also loaned us specimens from their personal collections or provided other help. The collections recorded in this paper as JCC will be transferred to the AMNH; several of these specimens appear (based on data labels) to have started there in the first place. RGH stands for Robert G. Holmberg as

the collector and the personal collection. Gifts of specimens were appreciated from: Matthew Bowser, Kenai National Wildlife Refuge, Alaska; Maria L. Goodnight (deceased); Daniel T. Jennings (retired), University of Maine at Orono, Maine; Yuri M. Marusik, Institute for Biological Problems of the North, Magadan, Russia; and Nobuo Tsurusaki, Tottori University, Japan. Richard Bradley (retired) of The Ohio State University Chelicerates Collection (OSAL) kindly checked for specimens that Mary Walker recorded in 1928. Finally, Gary L. Parsons (MSU) was of considerable help in understanding the specimens and labels of *Odiellus* housed at that collection. We also thank the following for the use of their photographs to help illustrate our fauna: Matthew Bowser (Kenai National Wildlife Refuge, Alaska), Pierre-Marc Brousseau (Montreal, Quebec), Don J. Buckle (Saskatoon, Saskatchewan), Jan van Duinen (Odoorn, Netherlands), and Joseph V. Higbee (Spanaway, Washington). Finally, we thank the many collectors.

LITERATURE CITED

- Acosta, L. E., A. Perez González, and A. L. Tourinho. 2007. Methods for taxonomic study. Pp. 494–505 in *The Harvestmen: The Biology of Opiliones* (R. Pinto da Rocha, G. Machado, and G. Giribet, eds.). Harvard University Press, Cambridge, Massachusetts.
- Arthofer, W., H. Rauch, B. Thaler-Knoflach, K. Moder, K. Muster, B. C. Schlick-Steiner, and F. M. Steiner. 2013. How diverse is *Mitopus morio*? Integrative taxonomy detects cryptic species in a small-scale sample of a widespread harvestman. *Molecular Ecology* 22:3850–3863.
- Banks, N. 1893a. A new American *Lacinius*. *Psyche* 6:402–403.
- Banks, N. 1893b. The Phalanginae of the United States. *Canadian Entomologist* 25:205–211.
- Banks, N. 1893c. A new species of *Oligolophus*. *Canadian Entomologist* 25:252–253.
- Banks, N. 1894. Washington Phalangida, with description of a new southern *Liobunum*. *Canadian Entomologist* 26:160–164.
- Banks, N. 1895. Two California phalangids. *Journal of the New York Entomological Society* 3(2):66.
- Banks, N. 1898a. Arachnida. Pp. 347–350, plate A in *Reports upon the insects, spiders, mites, and myriapods collected by Dr. L. Stejneger and Mr. G. E. H. Barrett-Hamilton on the Commander Islands* (W. H. Ashmead, ed.). Pp. 328–351 in *The fur seal and fur-seal islands of the North Pacific Ocean. Part 4. The Asiatic fur-seal islands and fur-seal industry*. United States Government Printing Office, Washington, D.C.
- Banks, N. 1898b. Some Mexican Phalangida. *Journal of the New York Entomological Society* 6:181–182.
- Banks, N. 1900. Papers from the Harriman Alaska Expedition. XI. Entomological results (5): Arachnida. *Proceedings of the Washington Academy of Sciences* 2:477–486, plate 29.
- Banks, N. 1901. Synopses of North American invertebrates. XVI. The Phalangida. *American Naturalist* 35:669–679.
- Banks, N. 1902. Daddy-long-legs from Mt. Katahdin, Maine. *Entomological News* 13:308–309.
- Banks, N. 1904. Some Arachnida from California. *Proceedings of the California Academy of Science, Zoology* 3:331–377.
- Banks, N. 1911. The Phalangida of California. *Pomona College Journal of Entomology* 3:412–421.
- Barr, W. 1986. William Robert Hobson (1831–1880). *Arctic* 39:184–185.
- Becker, L. 1886. Diagnoses de quelques Arachnides nouveaux. *Annales de la Société Entomologique de Belgique* 30:23–27.
- Bell, R. T. 1975. A European harvestman in North America (Phalangida, Phalangiidae). *Entomological News* 85:154.

- Bezděčka, P., K. Bezděčková, and T. Kvamme. 2017. Revised checklist of Nordic harvestmen (Opiliones) with five species new to Norway. *Arachnologische Mitteilungen / Arachnology Letters* 54:59–62.
- Bishop, S. C. 1949. The Phalangida (Opiliones) of New York with special reference to the species of The Edmund Niles Huyck Preserve, Rensselaerville, New York. *Proceedings of the Rochester Academy of Science* 9:159–235.
- Bragg, P. D., and R. G. Holmberg. 1975. *Platybunus triangularis* and *Paroligolophus agrestis*: two phalangids introduced to North America (Arachnida, Opiliones). *Journal of Arachnology* 2:127.
- Bragg, P. D., and R. G. Holmberg. 2009. The harvestmen (Arachnida, Opiliones) of British Columbia. *Proceedings of the Entomological Society of British Columbia* 106:29–37.
- Butcher, M. R., D. R. Penman, and R. R. Scott. 1988. Field predation of two spotted spider mites in a New Zealand strawberry crop. *Entomophaga* 33:173–185.
- Caporiacco, L. di 1938. Aracnidi del Messico, di Guatemala e Honduras Britannico. *Atti della Societa Italiana Scienze Naturalie del Museo Civico di Storia Naturale di Milano* 77:251–282.
- Cekalovic, T. 1985. Catálogo de los Opiliones de Chile (Arachnida). *Boletín de la Sociedad Biologica de Concepción* 56:7–29.
- Clark, M. S., J. M. Luna, N. D. Stone, and R. R. Youngman. 1994. Generalist predator consumption of armyworm (Lepidoptera: Noctuidae) and effect of predator removal on damage in no-till corn. *Environmental Entomology* 23:617–622.
- Cockerell, T. D. A. 1907. Some Coleoptera and Arachnida from Florissant, Colorado. *Bulletin of the American Museum of Natural History* 23:617–621.
- Cokendolpher, J. C. 1980a. Comments on Opiliones described from western North America by Schenkel. *Entomological News* 91:133–135.
- Cokendolpher, J. C. 1980b. Replacement name for *Mesosoma* Weed with a revision of the genus (Opiliones, Phalangidae, Leiobuninae). *Occasional Papers of the Museum, Texas Tech University*, 66:1–19.
- Cokendolpher, J. C. 1981a. The harvestman genus *Liopilio* Schenkel (Opiliones, Phalangidae). *Journal of Arachnology* 9:309–316.
- Cokendolpher, J. C. 1981b. Revision of the genus *Trachyrhinus* Weed (Opiliones, Phalangioidea). *Journal of Arachnology* 9:1–18.
- Cokendolpher, J. C. 1984. Homonyms of American and European *Leiobunum* (Opiliones, Palpatores, Leiobuninae). *Journal of Arachnology* 12:118–119.
- Cokendolpher, J. C. 1985. Revision of the harvestman genus *Leptobunus* and dismantlement of the Leptobunidae (Arachnida: Opiliones: Palpatores). *Journal of the New York Entomological Society* 93:371–402.
- Cokendolpher, J. C., and J. E. Cokendolpher. 1982. Reexamination of the Tertiary harvestmen from the Florissant Formation, Colorado (Arachnida: Opiliones: Palpatores). *Journal of Paleontology* 56:1213–1217.
- Cokendolpher, J. C., and J. E. Cokendolpher. 1984. A new genus of harvestmen from Costa Rica with comments on the status of the Neotropical Phalanginae (Opiliones, Phalangidae). *Bulletin of the British Arachnological Society* 6:167–172.
- Cokendolpher, J. C., and V. F. Lee. 1993. Catalogue of the Cyphopalpatores and bibliography of the harvestmen (Arachnida, Opiliones) of Greenland, Canada, U.S.A., and Mexico. Privately Printed, Lubbock, Texas, 82 pp.
- Cokendolpher, J. C., and M. L. Peek. 1991. Horatio C Wood (1841–1920) and his contributions to arachnology. *Revue Arachnologique* 9(8):89–101.
- Cokendolpher, J. C., and M. K. Rylander. 1986. *Opilio bolivianus* Roewer 1956: junior synonym of *Cristina bispinifrons* Roewer 1917 (Arachnida: Opiliones: Phalangidae). *Senckenbergiana Biologica* 66:339–343.
- Cokendolpher, J. C., and K. R. Zeiders. 2004. Clarence Moores Weed (1864–1947) and notes on his species of Opiliones (Arachnida). *Occasional Papers, Museum of Texas Tech University* 237:1–14.
- Comstock, J. H. 1940. *The spider book*. (W. J. Gertsch, rev. and ed.). Doubleday, Doran and Co., Inc., New York xi + 729 pp. [reissued 1948, Cornell University Press, Ithaca, New York; 1965, Comstock Publishing Co., Inc., New York].
- Crawford, R. L. 1992. Catalog of the genera and type species of the harvestman superfamily Phalangioidea (Arachnida). *Burke Museum Contributions in Anthropology and Natural History* 8:1–60.
- Crawford, R. L., and Yu. M. Marusik. 2006. Harvestmen (Arachnida Phalangida or Opiliones) of Moneron Island. (Materials of International Sakhalin Island Project). Part 2, pp. 196–201 in *Flora and Fauna of Moneron Island* (S. Yu. Storozhenko, ed.). Dal'nauka, Vladivostok, Russia, 324 pp.
- Crosby, C. R., and S. C. Bishop. 1924. Notes on the Opiliones of the southeastern United States with descriptions of new species. *Journal of the Elisha Mitchell Scientific Society* 40:8–26.
- Crosby, C. R., A. Wolf, and S. C. Bishop. 1928. Order Opiliones. Pp. 1074–1076 in *A List of Insects of New York with a List of the Spiders and Certain Other Allied Groups*. Cornell University Agricultural Experiment Station, Memoir 101. (Leonard, M. D., ed.) Cornell University, Ithaca, New York.

- Davis, N. W. 1934. A revision of the genus *Leiobunum* (Opiliones) of the United States. *American Midland Naturalist* 15:662–705.
- De Geer, C. 1778. Mémoires pour servir à l'histoire des insectes. Stockholm, Sweden 7:i–vi + 1–950, 1–49 plates.
- D'Amico, F., and S. Danflous. 2015. North Pyrenean populations of *Megabunus diadema* (Fabricius, 1779) (Arachnida: Opiliones) are characterized by highly male-biased sex ratios. *Pirineos. Revista de Ecología de Montaña*, 170:1–12 [Pirineos, 170, e016. doi: <http://dx.doi.org/10.3989/Pirineos.2015.170009>].
- Drummond, F. A., J. A. Collins, B. Choate, D. Woodman, D. T. Jennings, H. Y. Forsythe, and J. C. Cokendolpher. 2010. Harvestman (Opiliones) fauna associated with Maine lowbush blueberry fields in the major production areas of Washington and Hancock Counties. *Environmental Entomology* 39:1428–1440.
- Dugès, A. 1884. A la note rectificative de M. le Dr A. Dugès insérée dans le dernier Compte-rendu (p. CXXXVI) je puis ajouter les renseignements suivants. *Annales de la Société Entomologique de Belgique* 30:CXXXII.
- Dumitrescu, D. 1970. Contributions à l'étude de la morphologie des organes génitaux externes chez quelques Opilions de la famille Phalangidae de Roumanie. *Travaux du Muséum d'Historie Naturelle "Grigore Antipa," București* 10:79–90.
- Edgar, A. L. 1966. Phalangida of the Great Lakes region. *American Midland Naturalist* 75:347–366.
- Edgar, A. L. 1971. Studies on the biology and ecology of Michigan Phalangida (Opiliones). *Miscellaneous Publications of the Museum of Zoology, University of Michigan* 144:1–64.
- Edgar, A. L. 1990. Chapter 19. Opiliones (Phalangida). Pp. 529–581 in *Soil Biology Guide* (D. L. Dindal, ed.). John Wiley and Sons, New York.
- Fabricius, J. C. 1775. *Systema entomologiae: sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus*. Flensbvirgi et Lipsiae: In Officina Libraria Kortii, 832 pp.
- Fabricius, J. C. 1779. *Reise nach Norwegen mit Bemerkungen aus der Naturhistorie und Oekonomie*. Carl Ernst Bohn, Hamburg, Germany lxiv + 388 + [12] pp.
- Fabricius, J. C. 1793. *Entomologia systematica emendata et aucta. Secundum classes, ordines, genera, species adjectis synonymis, locis, observationibus, descriptionibus*. Tome 2, Impensis Christian Gottlob Proft, Hafniae-Copenhagen, Denmark, VIII + 519 pp.
- Farzalieva, G. Sh., and S. L. Esyunin. 2000. The harvestman fauna of the Urals, Russia, with a key to the Ural species (Arachnida: Opiliones). *Arthropoda Selecta* (1999) 8(3):183–199.
- Gervais, P. 1849. Falángidos. Pp. 18–28 in C. Gay, *Historia física y política de Chile segun documentos adquiridos en esta republica durante doce años de residencia en ella y publicada bajo los auspicios del supremo gobierno*. *Zoologia* 4, Atlas Zoologie, plate 1.
- Giribet, G., G. D. Edgecombe, W. C. Wheeler, and C. Babbitt. 2002. Phylogeny and systematic position of Opiliones: A combined analysis of chelicerate relationships using morphological and molecular data. *Cladistics* 18:5–70.
- Goodnight, C. J., and M. L. Goodnight. 1942a. The genus *Protolophus* (Phalangida). *American Museum Novitates* 1157:1–7.
- Goodnight, C. J., and M. L. Goodnight. 1942b. New American Phalangida. *American Museum Novitates* 1164:1–4.
- Goodnight, C. J., and M. L. Goodnight. 1942c. Phalangida from Mexico. *American Museum Novitates* 1211:1–18.
- Gruber, J., and G. S. Hunt. 1973. *Nelima doriae* (Canestrini), a south European harvestman in Australia and New Zealand (Arachnida, Opiliones, Phalangidae). *Records of the Australian Museum* 28(16):383–392.
- Hackman, W. 1956. Phalangida (Opiliones) from Newfoundland. *Societas Scientiarum Fennica Commentationes Biologicae* 15(17):1–19.
- Hadži, J. 1931. Opilioni Triglavskoga masiva [Die Opilionen des Triglavmassivs]. *Prirodoslovne Razprave, Muzejsko Društvo za Slovenijo, Ljubljana* 1:107–154.
- Hahn, C. W., and C. L. Koch 1839b. see Koch, C. L. 1839b.
- Hallan, J. 2005. Synopsis of the described Opiliones of the world (3/7/2005). Formerly online at: <http://insects.tamu.edu/research/collection/hallan/Acari/Family/Opiliones1.htm>. [Last accessed August 2011 by Kury (2012); currently Dec. 2017 not online].
- Hansen, H. J., and W. Sørensen. 1904. On two orders of Arachnida: Opiliones, especially the suborder Cyphophthalmi, and Ricinulei, namely the family Cryptostemmatidae. Cambridge University Press XI + 182 pp.
- Hamilton, C. A., B. E. Hendrixson, J. E. Bond. 2016. Taxonomic revision of the tarantula genus *Aphonopelma* Pocock, 1901 (Araneae, Mygalomorphae, Theraphosidae) within the United States. *ZooKeys* 560:1–340.
- Hedin, M., N. Tsurusaki, R. Macias-Ordóñez, and J. W. Shultz. 2012. Molecular systematics of sclerosomatid harvestmen (Opiliones, Phalangioidea, Sclerosomatidae): Geography is better than taxonomy in predicting phylogeny. *Molecular Phylogenetics and Evolution* 62:224–236.
- Heinäjoki, M. 1944. Die Opilionenfauna Finnlands. *Acta Zoologica Fennica* 42:1–26.
- Henriksen, K. L. 1932. 1. Opiliones. Pp. 4–6 in Henriksen, K. L., C. H. Lindroth, and C. H. Braendegaard. *Isländische Spinnentiere. I. Opiliones, Chernetes, Araneae*. Göteborgs

- Kungliga Vetenskaps- och Vitterhets-Samhälles handlingar. Series B 2(7):1–36.
- Herbst, J. F. W. 1798. Naturgeschichte der Insecten-gattung *Opilio*. In J. F. W. Herbst, Natursystem der Ungeflügelten Insekten, Volume 2. Gottlieb August Lange, Berlin, Germany iv + 26 pp., 5 plates.
- Herbst, J. F. W. 1799. Fortsetzung der Naturgeschichte der Insectengattung *Opilio*. In J. F. W. Herbst, Natursystem der Ungeflügelten Insekten, Volume 3. Gottlieb August Lange, Berlin, Germany iv + 30 pp., plates 6–10.
- Hillyard, P. D., and J. H. P. Sankey. 1989. Harvestmen: Keys and notes for the identification of the species. Synopses of the British Fauna (New Series) Number 4, 2nd edition. E. J. Brill, New York, for The Linnean Society of London and The Estuarine and Brackish-water Sciences Association.
- Ingianni, E. A. 2010. Taxonomy of the *Leiobunum nigropalpi* species group (Opiliones: Sclerosomatidae). Unpublished M. S. thesis, University of Maryland, College Park v + 81 pp.
- Ingianni, E. A., C. R. McGhee, and J. W. Shultz. 2011. Taxonomy of the *Leiobunum calcar* species-group (Opiliones: Sclerosomatidae: Leiobuninae). *Journal of Arachnology* 39:454–481.
- Kauri, H. 1980. Terrestrial invertebrates of the Faroe Islands: II. Harvest-spiders (Opiliones). *Fauna Norvegica, Serie B* 27:72–75.
- Kincaid, T. 1900. Papers from the Harriman Alaska Expedition. VII. Entomological Results (1): The Tenthredinoidea. *Proceedings of the Washington Academy of Sciences* 2:341–365.
- Koch, C. L. 1836. Die Arachniden. C. H. Zeh'schen Buchhandlung, Nürnberg, Germany vol. 3, 120 pp., plates LXIII–CVIII.
- Koch, C. L. 1839a. Übersicht des Arachnidensystems. Zweites Heft. C. H. Zeh'schen Buchhandlung, Nürnberg, Germany, 38 pp., 6 plates.
- Koch, C. L. 1839b. Die Arachniden. Getreu nach der Natur abgebildet und beschrieben. (C. W. Hahn and C. L. Koch, eds.). C. H. Zeh'schen Buchhandlung, Nürnberg, Germany 5:1–158.
- Koch, C. L. 1871. Beiträge zur Kenntniss der Opilioniden des Mittel-Rhein-Gebietes. Bericht über die Tätigkeit des Offenbacher Vereins für Naturkunde 12:52–91.
- Koponen, S. 1995. Quelques opilions (Arachnida) de la Province de Québec. *Fabriques* 20:1–5.
- Kurt, K., A. Babaşoğlu, O. Seyyar, H. Demir, and A. Topçu. 2008. New faunistic records for the Turkish harvestmen fauna (Arachnida: Opiliones). *Munis Entomology & Zoology* 3:654–660.
- Kury, A. B. 2012. A synopsis of catalogs and checklists of harvestmen (Arachnida, Opiliones). *Zootaxa* 3184:35–58.
- Kury, A. B. 2013. Order Opiliones Sundevall, 1833. Pp. 27–33. In Zhang, Z.-Q., ed. *Animal Biodiversity: An Outline of Higher-level Classification and Survey of Taxonomic Richness* (Addenda 2013). *Zootaxa* 3703:1–82.
- Kury, A. B. 2017. Classification of Opiliones. Museu Nacional/UFRJ website. Online at: <http://www.museunacional.ufrj.br/mndi/Aracnologia/opiliones.html> [Last accessed 21 Feb. 2018].
- Kury, A. B., and J. C. Cokendolpher. 2000. Opiliones. Pp. 137–157 in *Biodiversidad, Taxonomía y Biogeografía de Artrópodos de México: Hacia una síntesis de su conocimiento* (J. E. Llorente Bousquets, E. González Soriano, and N. Papavero, eds.). Volumen II. Universidad Nacional Autónoma de México, México, D.F., México.
- Latreille, P. A. 1802. Histoire naturelle, générale et particulière des crustacés et des insectes. Ouvrage faisant suite à d'Histoire Naturelle générale et particulière, composée par Leclerc de Buffon, et rédigé par C. S. Sonnini, membre de plusieurs Sociétés savantes. Familles naturelles des genres. Tome 3, F. Dufart, Paris, France, 468 pp.
- Leirikh, A. N., E. N. Meshcheryakova, G. V. Kuzminykh, and D. K. Kurenshchikov. 2009. Cold hardiness and development rate as elements of adaptive strategies of phalangiid harvestmen (Opiliones, Phalangiiidae) in northeastern Asia. *Entomological Review* 89(3):323–331 [Original Russian text published (2009), *Zoologicheskii Zhurnal* 88(4):419–428].
- Lengyel, G. D., and B. Páll-Gergely. 2010. Notes on the landsnail (Gastropoda) and harvestman (Opiliones) fauna of Bihor and Vlădeasa mountains, Romania. *Satu Mare-Studii și Comunicări Seria Științele Naturii X–XI* (2009–2010):91–111.
- Levi, L. R., and H. W. Levi. 1955. Spiders and harvestmen from Waterton and Glacier National Parks. *Canadian Field-Naturalist* 69(2):32–40.
- Lindroth, C. H., and G. E. Ball. 1969. An annotated list of invertebrates of the Kodiak Island refugium. Pp. 122–155 in *The Kodiak Island refugium. Its geology, flora, and history* (T. N. V. Karlstrom and G. E. Ball, eds.). Boreal Institute, University of Alberta, Edmonton, Canada.
- Lindroth, C. L. 1957. *The Faunal Connections between Europe and North America*. John Wiley and Sons, New York and Almqvist and Wiksell, Stockholm, Sweden, 344 pp.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. 10th Ed., revised. Vol. 1 (1–4):824 pp. Laurentius Salvius, Stockholm, Sweden.
- Linnaeus, C. 1767. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis locis*. 12th Ed., revised. Vol. 1 (2):533–1327 + [37 pp]. Laurentius Salvius, Stockholm, Sweden.

- Lohmander, H. 1945. Arachnologische Fragmente 1–3. Göteborgs Kungliga Vetenskaps Vitterhets-Samhälles Handlingar (6-B) 3(9):15–30.
- Martens, J. 1978. Die Tierwelt Deutschlands, Teil 64. Spinnentiere, Arachnida. Weberknechte, Opiliones. Gustav Fischer, Jena, Germany, 464 pp.
- Marusik, Yu. M. 2005. Паукообразные (Arachnida: Aranei, Opiliones) Северного Охотоморья [Arachnids (Arachnida: Aranei, Opiliones) of northern Cisokhotia]. Евразийский энтомолог. журнал [Euroasian Entomological Journal] 4:187–208 [in Russian, English abstract].
- Marusik, Yu. M. and O. A. Khrulyova. 2011. First data on spiders and harvestmen (Arachnida: Aranei, Opiliones) from Karaginski Island, Eastern Koryakia, Kamchatka Peninsula. *Arthropoda Selecta* 20(4):323–329.
- Marusik, Yu. M. and S. Koponen. 2015. New biogeographical records of spiders and harvestmen (Arachnida: Araneae & Opiliones) from West Siberia, including an annotated list of species. *Entomological Fennica* 26:165–170.
- Marx, G. 1892. A contribution to the study of the spider fauna of the Arctic regions. *Proceedings of the Entomological Society of Washington* (1891) 2:186–200.
- Meinertz, T. 1973. The occurrence of *Mitopus morio* (Fabr.) Phalangidae, Opiliones in Greenland and in other northern regions. *Meddelelser om Grønland* 191(7):1–16, plates 1–5.
- Meade, R. H. 1855. Monograph on the British species of Phalangidae or harvestmen. *Annals and Magazine of Natural History, Series 2* 15(90):393–416 + plates 10, 11.
- Mello-Leitão, C. F. de 1937. Distribution et phylogénie des faucheurs Sud-Américains. *Proceedings 12th Congress International Zoology, Lisbon, Portugal* 2(5):1217–1228.
- Mello-Leitão, C. F. de 1944. Descripción de *Barbiellinia hirsuta* g.n., sp.n., y notas de nomenclatura aracnológica. *Comunicaciones Zoológicas del Museo Historia Natural de Montevideo* 1(21):1–4.
- Myers, L. 1921. A list of California Arachnida. V. Phalangida or harvestmen. *Journal of Entomology and Zoology, Pomona College* 13(3):19–22.
- Newton, B. L., and K. V. Yeagan. 2002. Population characteristics of *Phalangium opilio* (Opiliones: Phalangidae) in Kentucky agroecosystems. *Environmental Entomology* 31:92–98.
- Novak, T. 2005. An overview of harvestmen (Arachnida: Opiliones) in Bosnia and Herzegovina. *Natura Croatica* 14:301–350.
- Novak, T., S. L. Delakorda, and L. S. Novak. 2006. A review of harvestmen (Arachnida: Opiliones) in Slovenia. *Zootaxa* 1325:267–276.
- Novak, T., V. Klokočovník, S. Lipovšek Delakorda, D. Devetak, and F. Janželpvoč. 2009. Preferences for different substrates in *Phalangium opilio* (Opiliones: Phalangidae) in natural environment. *Acta Biologica Slovenica* 52:29–35.
- Panzer, G. W. F. 1794. Fauna Insectorum Germanicae initia oder Deutschlands Insecten. Zweyter Jahrgang. XIII–XXIV Heft. Felseckersche Buchhandlung, Nürnberg 284 pp. + 284 plates.
- Pickard-Cambridge, F. O. 1904–1905. [Order Opiliones, pp. 546–585 + plates 52–54]. Arachnida. Araneidea and Opiliones. *Biologia Centrali-Americana* 2, ix + 610 pp. + 54 plates [1904, pp. 545–560, plate 52; 1905 pp. 561–610, plates 53, 54; all Palpatores sections printed January 1905].
- Roewer, C. F. 1911. Übersicht der Genera der Subfamilie der Phalangini der Opiliones Palpatores nebst Beschreibung einiger neuer Gattungen und Arten. *Archiv für Naturgeschichte, Berlin, Germany* 77(Band 1, Supplementheft 2):1–106, plates 1–3.
- Roewer, C. F. 1912. Revision der Opiliones Palpatores (= Opiliones Plagiostethi). II. Teil: Familie der Phalangidae. (Subfamilien: Sclerosomini, Oligolophini, Phalangini). *Abhandlungen aus dem Gebiete der Naturwissenschaften, herausgegeben vom Naturwissenschaftlichen Verein in Hamburg* 20:1–295, plates 1–4.
- Roewer, C. F. 1917. 52 neue Opilioniden. *Archiv für Naturgeschichte, Berlin, Germany* 82A (2):90–158, 47 figures.
- Roewer, C. F. 1923. Die Weberknechte der Erde. Systematische Bearbeitung der bisher bekannten Opiliones. Gustav Fischer, Jena, Germany, 1,116 pp.
- Roewer, C. F. 1924. Opilioniden von der Insel Rhodos, Italien und Sardinien, sowie der Cyrenaica. *Bollettino dei Musei di Zoologia ed Anatomia comparata della R. Università di Torino, nuova serie* 39(19):1–7.
- Roewer, C. F. 1952. Einige Phalangiden aus den Vereinigten Staaten von Nord-Amerika. *Zoologischer Anzeiger* 149:267–273.
- Roewer, C. F. 1956. Über Phalanginae (Phalangidae, Opiliones Palpatores). (Weitere Weberknechte XIX). *Senckenbergiana Biologica* 37:247–318.
- Roewer, C. F. 1957. Über Oligolophinae, Caddoinae, Sclerosomatinae, Leiobuninae, Neopilioninae und Leptobuninae (Phalangidae, Opiliones Palpatores). (Weitere Weberknechte XX). *Senckenbergiana Biologica* 38:323–358.
- Savory, T. 1933. Hot spring spiders. *Nature* 132(3340):712.
- Say, T. 1821. An account of the Arachnides of the United States. *Journal of the Academy of Natural Sciences of Philadelphia* 2:59–82.
- Schenkel, E. 1951. Spinnentiere aus dem westlichen Nordamerika, gesammelt von Dr. Hans Schenkel-Rudin. Zweiter Teil. *Verhandlungen der Naturforschenden Gesellschaft in Basel* 62:24–62.

- Shear, W. A. 2016. New Canadian records of *Nemastoma bimaculatum* (Fabricius), and a brief summary of introduced Eurasian harvestmen in North America (Arachnida, Opiliones). *Zootaxa* 4088:139–140.
- Shoemaker, A. K., M. Burns, and S. L. Boyer. 2017. New records of harvestmen (Arachnida, Opiliones) from Minnesota, USA. *Zootaxa* 4273:279–286.
- Shultz, J. W. 2010. A new species of *Hadrobunus* (Opiliones, Sclerosomatidae, Leiobuninae) from the southeastern United States. *Journal of Arachnology* 38:572–580.
- Shultz, J. W. 2012. The identity of *Hadrobunus grandis*: Reassignment of *Leiobunum aurugineum* to *H. grandis* and *H. nonsacculatus* new species (Opiliones: Sclerosomatidae: Leiobuninae). *Journal of Arachnology* 40:296–303.
- Šilhavý, V. 1965. Die Weberknechte der Unterordnung Eupnoi aus Bulgarien; zugleich eine Revision Europäischer Gattungen der Unterfamilien Oligolophinae und Phalangiinae (Arachnoidea, Opilionea). *Acta Entomologica Bohemoslovaca* 62:369–406.
- Simon, E. 1884. Arachnides recueillis par la mission du Cap Horn en 1882–1883. *Bulletin de la Société Zoologique de France* 9:117–144, plate 3.
- Slagsvold, T. 1979. Environment and morphological variation of *Mitopus morio* (Fabr.) (Opiliones) in Norway. *Journal of Biogeography* 6:267–276.
- Spoeck, G. L. 1963. The Opilionida (Arachnida) of the Netherlands. *Zoologische Verhandelingen, Leiden* 63:1–70.
- Staręga, W. 1975. Opiliones Kosarze (Arachnoidea). *Fauna Polski, Polska Akademia Nauk Instytut Zoologii* 5:1–197.
- Staręga, W. 1976. Die Weberknechte (Opiliones, excl. Sironidae) Bulgariens. *Annales Zoologici* 33(18):1–147.
- Staręga, W. 1978. Katalog der Weberknechte (Opiliones) der Sowjetunion. *Fragmenta Faunistica, Warszawa* 23:197–241.
- Staręga, W. 1984. Revision der Phalangiidae (Opiliones), III. Die afrikanischen Gattungen der Phalangiinae, nebst Katalog aller afrikanischen Arten der Familie. *Annales Zoologici* 38:1–79.
- Stol, I. 2003. Distribution and ecology of harvestmen (Opiliones) in the Nordic countries. *Norwegian Journal of Entomology* 50:33–41.
- Stol, I. 2005. Ecology and body size of the parthenogenetic *Megabunus diadema* (Fabricius, 1779) (Opiliones: Phalangiidae) at Karmøy, Western Norway. *Fauna Norvegica* 25:39–44.
- Stol, I. 2007. Checklist of Nordic Opiliones. *Norwegian Journal of Entomology* 54:23–26.
- Strand, E. 1906. Die arktischen Araneae, Opiliones und Chernetes. *Fauna Arctica* 4:431–478.
- Sundevall, C. J. 1833. *Conspectus arachnidum*. C. F. Berling: Londini Gothorum, 39 pp.
- Suzuki, S. 1939. [Opiliones from the Japanese Alps]. *Dobutsugaku zasshi [Zoological Magazine]* 51:734–743. [in Japanese].
- Suzuki, S., and N. Tsurusaki. 1983. Opilionid fauna of Hokkaido and its adjacent areas. *Journal of the Faculty of Science Hokkaido University, Series VI, Zoology* 23(2):195–243.
- Tchemeris, A. N., D. V. Logunov, and N. Tsurusaki. 1999. A contribution to the knowledge of the harvestman fauna of Siberia (Arachnida: Opiliones). *Arthropoda Selecta* 7(3):189–199.
- Thorell, T. 1876. Sopra alcuni Opilioni (Phalangides) d'Europa e dell'Asia occidentale, con un quadro dei generi europei de quest'Ordine. *Annali del Museo Civico di Storia Naturale, Genova* (1)8:452–508.
- Tourinho, A. L. 2007. Sclerosomatidae. Pp. 128–131 in *The Harvestmen: The Biology of Opiliones* (R. Pinto da Rocha, G. Machado, and G. Giribet, eds.). Harvard University Press, Cambridge, Massachusetts.
- Tsurusaki, N., and K. Takenaka. 2010. Recent expansion of distribution range of *Phalangium opilio*, a presumably introduced harvestman, in Hokkaido, Japan, with notes on the chromosomes and male dimorphism. Pp. 445–446 in *Book of Abstracts, 18th International Congress of Arachnology* (M. Žabka, ed.). 2010, Siedlce, Poland.
- Uddström, A., and V. Rinne. 2016. Suomen lukit ja valeskorpionit [Harvestmen (Opiliones) and Pseudoscorpions (Pseudoscorpiones) of Finland]. *Tibiale, Helsinki, Finland*, 223 pp.
- Walker, D. 1860. Notes on the zoology of the last Arctic Expedition under Captain Sir F. L. McClintock, R. N. *Journal of the Royal Dublin Society* 3(18):61–77.
- Walker, M. E. 1928. A revision of the order Phalangida of Ohio. *Ohio State University Studies* 4(4), *Ohio Biological Survey Bulletin* no. 19:149–175.
- Weed, C. M. 1889a. A new harvest-spider. *American Naturalist* 23:1102–1104, plate 42.
- Weed, C. M. 1889b. A partial bibliography of the Phalangiinae of North America. *Bulletin of the Illinois State Laboratory of Natural History* 3:99–106.
- Weed, C. M. 1890. A new *Phalangium*. *American Naturalist* 24:783–785, plate 27.
- Weed, C. M. 1893. A descriptive catalogue of the harvest-spiders (Phalangiidae) of Ohio. *Proceedings of the United States National Museum* 16:543–563, plates 57–69.
- Wood, H. C., Jr. 1868. On the Phalangeae of the United States of America. *Communications of the Essex Institute, Salem, Massachusetts* 6:10–40.

Wood, H. C., Jr. 1869. On the Phalangia and Pedipalpi collected by Professor Orton in western South America, with the description of new African species, accompanied with a

plate. Transactions of the American Philosophical Society, new series 13:435–442, plate 24.

Addresses of authors:

JAMES C. COKENDOLPHER

*Natural Science Research Laboratory
Museum of Texas Tech University
Lubbock, Texas 79409, USA
james.cokendolpher@ttu.edu*

ROBERT G. HOLMBERG

*Centre for Science
Athabasca University
Athabasca, Alberta, T9S 3A3, Canada
robert@athabascau.ca*

