

Phoretic chernetid species newly recorded from Slovakia and Austria (Pseudoscorpiones: Chernetidae)

Authors: Červená, Martina, Kirchmair, Gabriel, and Christophoryová, Jana

Source: Arachnologische Mitteilungen: Arachnology Letters, 57(1) : 65-68

Published By: Arachnologische Gesellschaft e.V.

URL: <https://doi.org/10.30963/aramit5712>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Phoretic chernetid species newly recorded from Slovakia and Austria (Pseudoscorpiones: Chernetidae)

Martina Červená, Gabriel Kirchmair & Jana Christophoryová



doi: 10.30963/aramit5712

Abstract. New cases of phoresy by chernetids (Pseudoscorpiones: Chernetidae) are documented from Slovakia and Austria. Pseudoscorpion phoresy involving Heteroptera as a host is documented for the first time in Slovakia, as well as a case of phoresy by the genus *Pselaphochnes* Beier, 1932. Three chernetid species were observed for the first time as phoretic in Austria on Mecoptera, Diptera and Hymenoptera.

Keywords: Central Europe, host, phoretic association, phoront, pseudoscorpion

Zusammenfassung. Phoretische Chernetiden-Arten neu für die Slowakei und für Österreich (Pseudoscorpiones: Chernetidae). Neue Fälle von Phoresie durch (Pseudoscorpiones: Chernetidae) werden aus der Slowakei und aus Österreich dokumentiert. Phoresie von Pseudoskorpionen an Wanzen (Heteroptera) wird aus der Slowakei berichtet sowie ein Fall von Phoresie durch die Gattung *Pselaphochnes* Beier, 1932. Drei Chernetiden-Arten wurden das erste Mal in Österreich phoretisch an Mecoptera, Diptera und Hymenoptera beobachtet.

Phoresy is the most common method of passive dispersal among arachnids. Pseudoscorpions have the ability to attach themselves to a wide variety of other, more mobile, arthropods and after that disperse into new habitats (White et al. 2017). Many authors consider that phoresy in pseudoscorpions evolved from predatory behaviour towards the host (Beier 1948, Cuthbertson 1984), or that it is behaviour functioning specifically for dispersal (Weygoldt 1969, Zeh & Zeh 1992). Generally, pseudoscorpions do not reduce the viability of their hosts. However, this depends on many factors such as: frequency of phoretic episodes, phoront and host specificity, number of individuals on the host and distance that hosts travel with their phoronts. These factors play a major role in the evolution of phoresy and might have some costs for the hosts. Pseudoscorpions can cause additional load and movement blocking (Athias-Binche 1994, Szymkowiak et al. 2007). Carl (1994) observed that pressure from the palpal teeth can cause low damage to the exoskeleton of the host. Pseudoscorpions have developed two strategies to avoid being dislodged by the host's movement, flight or being brushed off (Jones 1978, Carl 1994). In the first strategy, species typically hide under the elytra, or among the feathers or fur, where they can feed on mites or where even mating takes place during dispersal (Zeh & Zeh 1992). In the second strategy, pseudoscorpions grasp the extremities, sternites or other body parts of the hosts (Jones 1978, Carl 1994).

Phoretic associations in Europe were documented by Poinar et al. (1998) between three families of Pseudoscorpiones and 21 families of Insecta, as well as two families of Opiliones. In Europe, the most frequent phoretic pseudoscorpions are known from the families Chernetidae and Cheliferidae (e.g. Beier 1948, Legg & Jones 1988, Poinar et al. 1998). Poinar et al. (1998) observed just one case of phoresy from the family Neobisiidae, between *Neobisium sylvaticum* (C. L. Koch, 1835) and *Musca domestica* Linnaeus, 1758 (Diptera, Muscidae). Beyond Europe, phoresy was also recorded from

many other families such as Chthoniidae, Geogarypidae, Atemnidae, Cheiridiidae and Withiidae in Brazilian Amazonia (Aguiar & Bührnheim 1998).

In Slovakia, ten cases of phoretic associations have been observed. Three chernetid and one cheliferid species were phoretic on four dipteran and one lepidopteran species. All recorded phoretic associations in Slovakia were summarised by Christophoryová et al. (2018).

In Austria, most records of phoresy are represented by the species *Lamprochernes nodosus* (Schrank, 1803). Beier (1948) summarised previously published data about phoresy between *L. nodosus* and dipteran species *Physiphora alceae* (Preysler, 1791) (as *Chloria demandata*) (Diptera, Ulidiidae) and *M. domestica*. Multiple phoresy was observed by Ressler (1965), where 124 specimens of *L. nodosus* were phoretic on 32 house-flies (*M. domestica*). At most, 11 pseudoscorpions were attached to one single house-fly. In addition, Ressler (1965) mentioned phoresy between one female of *L. nodosus* and *Physiphora demandata* (Fabricius, 1798) (Diptera, Ulidiidae) and between one female of *Dinocheirus panzeri* (C. L. Koch, 1837) and *M. domestica*. Later, Ressler (1970) documented another phoresy between three specimens of *L. nodosus* and *P. demandata*. New records of phoresy near a compost heap were added by Ressler (1983), in which 268 specimens of *L. nodosus* were phoretic on 111 Muscidae flies. The first record of phoresy by *Mesochelifer reslii* Mahnert, 1981 was noticed by Hauser (1990); one female was found phoretic on tactile seta of the leg of a nun moth *Lymantria monacha* (Linnaeus, 1758) (Lepidoptera, Erebiidae).

Summarizing all published data, four pseudoscorpion species in Slovakia and three species in Austria have been recorded as phoretic, mainly on dipterans. In the present study, new records of phoresy in chernetids are documented from both of the studied countries.

Material and methods

All pseudoscorpions were studied as temporary slide mounts using lactic acid and then rinsed in the water and returned to 70 % alcohol. The pseudoscorpion specimens were identified using the key in Christophoryová et al. (2011). Details about collecting the specimens are given in the results. Hosts were identified by specialists, also mentioned in the results. When

MARTINA ČERVENÁ, JANA CHRISTOPHORYOVÁ, Department of Zoology, Faculty of Natural Sciences, Comenius University in Bratislava, Mlynská dolina, Ilkovičova 6, SK 842 15 Bratislava, Slovakia; E-mail: martinacervena.lr@gmail.com, E-mail: jana.christophoryova@gmail.com
GABRIEL KIRCHMAIR, Institute of Biology, Karl-Franzens-Universität Graz, Universitätsplatz 2, AT 8010 Graz, Austria; E-mail: gabriel.kirchmair@uni-graz.at

submitted 24.1.2019, accepted 21.2.2019, online 25.3.2019

the attachment mode of the pseudoscorpion to the host body had not been registered by the observer, this data is omitted. The Austrian material is deposited in the collection of the second author at the Institute of Biology, Karl-Franzens-Universität Graz and the Slovakian material in the collection of the third author at the Department of Zoology, Comenius University in Bratislava.

Results

Slovakia

14. Jun. 2017: One female of *Pselaphochernes scorpoides* (Hermann, 1804) attached to an empidid fly (Diptera, Empididae; det. M. Kozánek) was found in the centre of Trenčín (48.89469°N, 18.04295°E; 230 m a.s.l.; leg. M. Dolinský). Specimens were individually collected in a family house. During the observation, the female was attached to the host's leg (unspecified which one). After putting the host into the tube with alcohol, the pseudoscorpion immediately detached from the fly.

22. May–30. May 2018: One phoretic female of *L. nodosus* was attached to the antenna of *Polymerus unifasciatus* (Fabricius, 1794) (Heteroptera, Miridae; det. P. Kment; Fig. 1) and one female of the same species to the base of the third leg of *P. alceae* (Diptera, Ulidiidae; det. M. Semelbauer; Fig. 2). Specimens were collected using a Malaise trap situated in the garden of a farm in Podunajská nížina Lowland, at the locality of Virt belonging to cadastre Radván nad Dunajom (47.76217°N, 18.33997°E; 125 m a.s.l.; leg. J. Kodada and M. Kozánek).

Austria

30. May 2017: One female of *Chernes habnii* (C. L. Koch, 1839) was phoretic on a species from the *Chrysis ignita* group (Linnaeus, 1758) (Hymenoptera, Chrysididae; det. D. Fröhlich). Specimens were individually collected at the lakeside of Lange Lacke in Apetlon (47.75924°N, 16.86513°E; 118 m a.s.l.; leg. D. Fröhlich).

31. May 2017: One female of *C. habnii* phoretic on a scorpion fly *Panorpa communis* Linnaeus, 1758 (Mecoptera, Panorpidae; det. S. Koblmüller) was individually collected at the locality of Andau between a group of trees (47.70750°N, 17.07622°E; 114 m a.s.l.; leg. S. Koblmüller).

9. Jun. 2017: One female of *P. scorpoides* was phoretic on *Leptopeza flavipes* (Meigen, 1820) (Diptera, Hybotidae; det. A. Stark) and individually collected in an alluvial forest at the locality of Alland (48.05944°N, 16.05750°E; 356 m a.s.l.; leg. G. Kirchmair). The pseudoscorpion was attached to the proximal part of the host's leg (unspecified which one).

11. Jul. 2017: One female of *Dendrochernes cyrneus* (L. Koch, 1873) was found attached to the antenna of the parasitoid wasp *Rhyssa persuasoria* (Linnaeus, 1758) (Hymenoptera, Ichneumonidae; det. G. Kirchmair, Fig. 3), while the wasp was ovipositing. This phoretic association was observed in a forest near the locality Pürgg bei Trautenfels (47.52861°N, 14.06194°E; 860 m a.s.l.; leg. G. Kunz). Specimens were collected by individual sampling.

29. Apr. 2018: One female of *C. habnii* was attached to *Brachyopa bicolor* (Fallén, 1817) (Diptera, Syrphidae; det. H. Heimbürg). Specimens were individually collected in an alluvial forest near the locality of Schönau an der Donau (48.13917°N, 16.61444°E; 150 m a.s.l.; leg. H. Heimbürg).



Fig. 1: *Lamprochernes nodosus* attached to the antenna of *Polymerus unifasciatus* from Slovakia (Photo: J. Christophoryová and K. Krajčovičová)

28. May 2018: One female of *P. scorpoides* was attached to the proximal part of the leg (unspecified which one) of *L. flavipes* (Diptera, Hybotidae; det. A. Stark) and was individually collected in a garden at the locality Pollham (48.25806°N, 13.88111°E; 346 m a.s.l.; leg. G. Kirchmair).



Fig. 2: *Lamprochernes nodosus* attached to the third leg of *Physiphora alceae* from Slovakia (Photo: J. Christophoryová and K. Krajčovičová)



Fig. 3: *Dendrochernes cyrneus* attached to the antenna of *Rhyssa persuasoria* from Austria (Photo: G. Kunz)

Discussion

The most common way for phoront and host to make contact is the fact that they occupy the same habitat and have the same activity and breeding season (Jones 1970, 1978, Poinar et al. 1998). *Lamprochernes nodosus* and *P. scorpioides* are frequently found in compost heaps and most of the dipterans are regular visitors to this habitat type (Jones 1978, Christophoryová et al. 2017). Jones (1978) mentioned that gravid pseudoscorpion females are more often phoretic than males or nymphs. These observations correspond with the presence of phoretic females in the present study. One of the reasons why phoresy is much more frequent in chernetid and cheliferid species (as compared to neobisiid or chthoniid species) is that some species are found in less stable habitats such as compost heaps or bird nests. In these habitat types, they have more possibility to attach themselves to mobile phoronts belonging to Insecta or Arachnida. Furthermore, Cheliferidae and in particular Chernetidae have evolved to be phoretic expert species that have developed morphologies adapted to this behaviour, i.e. additional chelal teeth in Chernetidae. Pseudoscorpions use phoresy for dispersion from less stable habitats towards more stable ones (Beier 1948, Jones 1978, Carl 1994).

In Central Europe, phoretic associations were recorded mainly in chernetid species, such as *P. scorpioides*, *D. panzeri*, *D. cyrneus*, *L. nodosus* and *Anthrenochernes stellae* Lohmander, 1939 (e.g. von Helvesen 1966, Droglá & Lippold 2004, Ssymank & Muster 2010, Christophoryová et al. 2017, 2018, Karpiński et al. 2017). Phoresy of the genus *Pselaphochernes* Beier, 1932 was most recently documented from the Iberian Peninsula (e.g. Ricarte et al. 2016, Mederos & Zaragoza 2017, Ruiz de la Cuesta Santiago & Zaragoza 2017, Zaragoza & Ruiz de la Cuesta Santiago 2017). Only few records exist from Central Europe: von Helvesen (1966) recorded three females of *P. scorpioides* phoretic on *Musca* Linnaeus, 1758. Droglá & Lippold (2004) found one adult of *P. scorpioides* phoretic on an unspecified dipteran species. Three cases of phoresy between *P. scorpioides* and dipteran species in the present study are documented for the first time in both of the studied countries.

One case of phoresy in the genus *Chernes* Menge, 1855 in Europe was mentioned by Poinar et al. (1998), in which *Chernes cimicoides* (Fabricius, 1793) was phoretic on *Dolichomitus mesocentrus* (Gravenhorst, 1829) (as *Ephialtes m.*). In Central Europe, phoresy records of *Chernes* species are rare. Opatová & Štáhlavský (2018) suggest phoretic dispersal for *C. habnii* but confirmed phoresy records of this species were missing in their paper. During the present study, three new cases of phoresy by *C. habnii* were documented from Austria. The phoretic association between *C. habnii* and *Panorpa communis* from Austria in the present paper represents the second known case. The first worldwide known phoresy between a pseudoscorpion and the common scorpionfly (Mecoptera) was presented by Christophoryová et al. (2017) from the Czech Republic. One female of *D. panzeri* was attached to the second leg of *P. communis* (Christophoryová et al. 2017). Phoresy on Syrphidae is known from *L. nodosus* on different host species and from *Pselaphochernes lacertosus* (L. Koch, 1873) (Jones 1978, Ricarte et al. 2016), but phoretic association between *C. habnii* and a host from Syrphidae represents the first such case in Austria in this study. No published data are yet available for a phoretic relationship between a pseudoscorpion and a cuckoo wasp (Chrysididae). Therefore, the phoresy of *C. habnii* on an individual of the *Chrysis ignita* group is treated as a first record for this host's family.

Pseudoscorpion phoresy on ichneumonid hosts is only documented by a few records (Jones 1978, Legg 2015, Ruiz de la Cuesta Santiago & Zaragoza 2017). Legg (2015) recorded *D. cyrneus* on *Ephialtes manifestor* (Linnaeus, 1758) from Britain. In the present paper, a phoretic association between *D. cyrneus* and *Rhyssa persuasoria* is recorded for the first time in Austria.

The most frequently recorded phoresy in Central Europe is between *L. nodosus* and dipteran species, which has been demonstrated in many publications (e.g. Beier 1948, Ressler 1983, Mašán & Krištofik 1992, Droglá & Lippold 2004, Christophoryová et al. 2018). Poinar et al. (1998) mentioned phoresy of *L. nodosus* on five species of Opiliones, one species of Coleoptera and 28 species of Diptera. In Slovakia, *L. no-*

dosus has been found phoretic until now only on three dipteran species (Mašán & Křišťofík 1992, Christophoryová et al. 2018). Phoresy of *L. nodosus* and *P. alceae* was already observed in the past by Christophoryová et al. (2018). On the contrary, present data of phoresy of *L. nodosus* and *P. unifasciatus* documented the first known record of a phoretic association of pseudoscorpions with true bug in Slovakia.

Summarising the newly obtained data, phoresy of a pseudoscorpion on a host from Heteroptera and phoresy of the genus *Pselaphochernes* were observed for the first time in Slovakia. In Austria, phoretic associations of *C. habnii*, *D. cyrneus* and *P. scorpioides* with their hosts were recorded for the first time.

Acknowledgements

We are very thankful to all collectors for providing the material of phoretic pseudoscorpions and to all specialists for identification of the hosts. We would like to thank Katarína Krajčovičová (Comenius University in Bratislava) for the technical assistance with the figures and Gernot Kunz (Karl-Franzens-Universität Graz) for the provided photo. We are grateful to Juan A. Zaragoza and one anonymous reviewer for all their suggestions and corrections which improved the quality of the paper. The work was supported by the Slovak Research and Development Agency under the contract no. APVV-15-0147.

References

- Aguiar NO & Bührnheim PF 1998 Phoretic pseudoscorpions associated with flying insects in Brazilian Amazônia. – *Journal of Arachnology* 26: 452–459
- Athias-Binche F 1994 La phorésie chez les acariens, aspects adaptatifs et évolutifs. Editions du Castillet, Perpignan. 178 pp.
- Beier M 1948 Phoresie und Phagophilie bei Pseudoscorpionen. – *Österreichische Zoologische Zeitschrift* 1: 441–451
- Carl M 1994 Injurious effects on the exoskeleton of *Musca domestica* L. (Diptera) of phoresy by *Lamprochernes nodosus* (Schrank) (Pseudoscorpiones, Chernetidae) and the possible functional significance of accessory teeth on the chelal fingers. – *Bulletin of the British Arachnology Society* 9: 246–248
- Christophoryová J, Gruľa D & Krajčovičová K 2017 New records of pseudoscorpions (Arachnida: Pseudoscorpiones) associated with animals and human habitats in Slovakia and Czech Republic. – *Arachnologische Mitteilungen* 53: 67–76 – doi: [10.5431/aramit5311](https://doi.org/10.5431/aramit5311)
- Christophoryová J, Štáhlavský F & Fedor P 2011 An update identification key to the pseudoscorpions (Arachnida: Pseudoscorpiones) of the Czech Republic and Slovakia. – *Zootaxa* 2876: 35–48 – doi: [10.11646/zootaxa.2876.1.4](https://doi.org/10.11646/zootaxa.2876.1.4)
- Christophoryová J, Vidlička L & Krajčovičová K 2018 New cases of phoresy of *Lamprochernes nodosus* (Pseudoscorpiones: Chernetidae) on Diptera observed in Slovakia. – *Biharean Biologist* 12: 114–115
- Cuthbertson DR 1984 Catalepsy and phoresy in pseudoscorpions. – *Newsletter of the British Arachnological Society* 39: 3
- Drogla R & Lippold K 2004 Zur Kenntnis der Pseudoscorpion-Fauna von Ostdeutschland (Arachnida, Pseudoscorpiones). – *Arachnologische Mitteilungen* 27/28: 1–54 – doi: [10.5431/aramit2701](https://doi.org/10.5431/aramit2701)
- Hauser E 1990 Ein Phoresie-Nachweis beim Pseudoskorpion *Mesochelifer resli* Mahnert (Cheliferidae) mit der “Nonne” *Lymantria monacha* L. (Lep., Lymantridae) im Bezirk Steyr (Oberösterreich). – *Steyrer Entomologenrunde* 24: 62–66
- Helversen O von 1966 Pseudoskorpione aus dem Rhein-Main-Gebiet. – *Senckenbergiana Biologica* 47: 131–150
- Jones PE 1970 *Lamprochernes nodosus* (Schrank) – an example of phoresy in Pseudoscorpions. – *Bulletin of the British Arachnological Society* 1: 118–119
- Jones PE 1978 Phoresy and commensalism in British pseudoscorpions. – *Proceedings and Transactions of the British Entomological and Natural History Society* 11: 90–96
- Karpiński L, Rutkowski T & Szczepański WT 2017 First record of phoresy of *Dendrochernes cyrneus* (L. Koch, 1873) (Pseudoscorpiones, Chernetidae) on *Cerambyx cerdo* Linnaeus, 1758 (Coleoptera, Cerambycidae) and their potential value as bioindicators. – *Animal Biodiversity and Conservation* 40: 187–192 – doi: [10.32800/abc.2017.40.0187](https://doi.org/10.32800/abc.2017.40.0187)
- Legg G 2015 *Dendrochernes cyrneus* (L. Koch, 1873) (Pseudoscorpiones, Chernetidae) phoretic on *Ephialtes manifestator* (Lin., 1758) (Hymenoptera, Ichneumonidae, Pimplinae). – *Newsletter of the British Arachnological Society* 132: 5–7
- Legg G & Jones RE 1988 Pseudoscorpions (Arthropoda: Arachnida). Keys and notes for the identification of the species. Synopses of the British Fauna (New Series), No. 40. Brill/Backhuys, Leiden. 159 pp.
- Mašán P & Křišťofík J 1992 Phoresy of some Arachnids (Acarina and Pseudoscorpionidea) on synanthropic flies (Diptera) in the south Slovakia. – *Biológia* 47: 87–96
- Mederos J & Zaragoza JA 2017 Nueva cita de *Pselaphochernes scorpioides* (Hermann, 1804) (Pseudoscorpiones: Chernetidae) en asociación forética con *Achyrolimonia decemmaculata* (Loew, 1873) (Diptera: Limoniidae). – *Revista Ibérica de Aracnología* 31: 133–135
- Opatova V & Štáhlavský F 2018 Phoretic or not? Phylogeography of the pseudoscorpion *Chernes habnii* (Pseudoscorpiones: Chernetidae). – *Journal of Arachnology* 46: 104–113 – doi: [10.1636/17-042.1](https://doi.org/10.1636/17-042.1)
- Poinar GO, Čurčić BPM & Cokendolpher JC 1998 Arthropod phoresy involving pseudoscorpions in the past and present. – *Acta Arachnologica* 47: 79–96 – doi: [10.2476/asjaa.47.79](https://doi.org/10.2476/asjaa.47.79)
- Ressl F 1965 Über Verbreitung, Variabilität und Lebensweise einiger österreichischer Afterskorpione. – *Deutsche Entomologische Zeitschrift* 12: 289–295 – doi: [10.1002/mmnd.19650120402](https://doi.org/10.1002/mmnd.19650120402)
- Ressl F 1970 Weitere Pseudoskorpion-Funde aus dem Bezirk Scheibbs (Niederösterreich). – *Berichte des Naturwissenschaftlich-medizinischen Vereins in Innsbruck* 58: 249–254
- Ressl F 1983 Die Pseudoscorpione Niederösterreichs mit besonderer Berücksichtigung des Bezirkes Scheibbs. In: Ressler F (ed.) *Naturkunde des Bezirkes Scheibbs. Die Tierwelt des Bezirkes Scheibbs, Band 2. Naturkundliche Arbeitsgemeinschaft des Bezirkes Scheibbs*. pp. 174–202
- Ricarte A, Zaragoza JA & Marcos-Garcia M 2016 First record of a phoretic association between a hoverfly (Diptera, Syrphidae) and a pseudoscorpion (Arachnida, Pseudoscorpiones) in the Iberian Peninsula. – *Boletín de la Asociación Española de Entomología* 40: 527–530
- Ruiz de la Cuesta Santiago JL & Zaragoza JA 2017 Primera cita de foresia para Europa sobre un evánido (Hymenoptera, Evaniidae) y nuevos casos sobre icneumonidos (Hymenoptera, Ichneumonidae) por pseudoscorpiones (Pseudoscorpiones, Chernetidae). – *Boletín de la Asociación Española de Entomología* 41: 293–309
- Ssymank A & Muster C 2010 *Anthrenochernes stellae* Lohmander, 1939 – ein Pseudoskorpion des Anhangs II der FFH-Richtlinie neu für das Saarland. – *Delattinia* 35/36: 387–391
- Szymkowiak P, Górski G & Bajerlein D 2007 Passive dispersal in arachnids. – *Biological Letters* 44: 75–101
- Weygoldt P 1969 The biology of pseudoscorpions. Harvard University Press, Cambridge. 145 pp.
- White PS, Morran L & Roode J 2017 Phoresy. – *Current Biology* 27: R578–R580 – doi: [10.1016/j.cub.2017.03.073](https://doi.org/10.1016/j.cub.2017.03.073)
- Zaragoza JA & Ruiz de la Cuesta Santiago JL 2017 Primera cita mundial de foresia por Pseudoscorpiones sobre Diptera, Rhinophoridae. – *Revista Ibérica de Aracnología* 31: 147–149
- Zeh DW & Zeh JA 1992 Failed predation or transportation? Causes and consequences of phoretic behavior in the pseudoscorpion *Dinnocheirus arizonensis* (Pseudoscorpionida: Chernetidae). – *Journal of Insect Behavior* 5: 37–49 – doi: [10.1007/BF01049156](https://doi.org/10.1007/BF01049156)