

Notes on brooding in the arachnid order Schizomida

Authors: Giribet, Gonzalo, and Moreno-González, Jairo A.

Source: The Journal of Arachnology, 49(3): 410-414

Published By: American Arachnological Society

URL: https://doi.org/10.1636/JoA-S-20-091

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.

SHORT COMMUNICATION

Notes on brooding in the arachnid order Schizomida

Gonzalo Giribet¹ and Jairo A. Moreno-González²: ¹Museum of Comparative Zoology & Department of Organismic and Evolutionary Biology, 26 Oxford Street, Cambridge, MA 02138, U.S.A. E-mail: ggiribet@g.harvard.edu; ²Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Caixa Postal 11461, 05422-970, São Paulo, SP, Brazil. E-mail: hansenochrus@gmail.com

Abstract. The scattered literature on schizomid brooding is reviewed and discussed in reference to the number of eggs, number and position of young as well as the brood chamber. In addition, novel brooding observations are provided for the Neotropical species *Hansenochrus tobago* (Rowland & Reddell, 1979), *Dumitrescoella decui* (Dumitresco, 1977), *Piaroa* sp. and *Surazomus* sp.

Keywords: Development, parental care, Thelyphonida

https://doi.org/10.1636/JoA-S-20-091

Schizomida is one of the so-called "smaller" or "lesser known" arachnid orders (e.g., Harvey 2003), comprising two families, three subfamilies and about 360 described accepted species (Monjaraz-Ruedas et al. 2020) restricted to tropical and subtropical regions around the world. With an amber fossil record extending back to the Cretaceous (Selden & Ren 2017; Müller et al. 2020), in addition to the earlier known fossils from Miocene Dominican amber (Dunlop 2010; Krüger & Dunlop 2010), their phylogenetic relationships to other arachnid orders are well established. Schizomida is the sister group of Uropygi, from which they diverged around the Upper Carboniferous, and started diversifying during the Permian-Triassic (Clouse et al. 2017). Together with Amblypygi, they constitute the clade Pedipalpi (e.g., Latreille 1810; Shultz 1990, 1999; Giribet et al. 2002; Shultz 2007; Garwood et al. 2017; Huang et al. 2018), a clade supported (although sometimes without sampling Schizomida) in broad-scale phylogenomic analyses (Sharma et al. 2014; Fernández et al. 2018; Ballesteros et al. 2019; Ballesteros & Sharma 2019; Lozano-Fernandez et al. 2019, 2020). Pedipalpi is characterized, among other features, by having a brood sac attached to the ventral surface of the female's opisthosoma, the embryos feeding on the yolk of the eggs. This differs from brooding in Pseudoscorpiones, in which embryos depend on maternal secretions (Weygoldt 1969; Shultz 1990).

Despite being a synapomorphy of Pedipalpi, little is known about the brooding habits of schizomids when compared to those of Uropygi or Amblypygi (e.g., Weygoldt 1971, 2000). In Schizomida, the female glues her eggs to the abdomen using a secretion (Alberti & Palacios-Vargas 2015) and carries her first instar young (Gravely 1915; Rowland 1972), but details about where the secretion is produced and the timing of the entire process are not well understood. At least in some regions, schizomids reproduce throughout the year (Adis et al. 1999, 2001).

Gravely (1915: Pl. XXIV, fig. 27) illustrated the underground brood chamber of *Schizomus crassicaudatus* (O. Pickard-Cambridge, 1872) from Sri Lanka kept in captivity, the female carrying seven eggs arranged in a ring of five, one in the center, and another one on top of the central egg. His illustration shows a female with the opisthosoma bent 90° upwards carrying five eggs in the sternal side (see Fig. 1A here). The eggs did not hatch.

The only study following the whole reproductive process, from fecundation to postembryonic development, is the widely cited paper on *Hubbardia pentapeltis* Cook, 1899 (as *Trithyreus pentapeltis*) by Rowland (1972). This study placed a male and a female from Riverside Co., California, in a glass chamber with 5 cm of loosely

packed soil and 2 cm of oak leaf litter on top, with artificially made holes, where the individuals spent hours motionless. After 55 days, the female spent five days making a round chamber, the radius of her body, in one of the holes. On day 71, the female was noticed to have a distended opisthosoma, with the developing eggs inside. On day 72, the female was found on the bottom of the chamber with a hemispherical mass of 30 eggs attached to the venter of the opisthosoma (Rowland 1972: fig. 1). Until day 102, the female remained active within the chamber; by then the eggs had elongated, with the long axis parallel to the female's body. By day 108, the young had already hatched, the appendages were recognizable but not the telson, and they surrounded the mother's opisthosoma, aligned along the A-P axis of the female, parallel to her (Rowland 1972: fig. 2). The young kept developing slowly until the first two molted on day 146 (74 days after the eggs were first observed). On day 147, about half of the young dropped off the mother and were on the floor of the chamber, and by day 148, all had dropped off the mother, sluggishly moving about inside the chamber. By day 157, the mother finished the rearing by breaking a hole in the chamber wall, exiting to the surface, followed by all but four of the young. There are some indications that the male may have eaten some of the young; the female was found dead on day 167.

Rowland (1972) observed six instars, one embryonic and five postembryonic. He also examined two vials at the American Museum of Natural History, New York, with two collections containing young from caves in Mexico collected by R.W. Mitchell and J. Reddell, and it is unclear whether they used chambers. He also mentioned not having observed the animals to eat anything during the time he kept them in captivity, but Gravely (1915) did observe an adult schizomid eating a symphylan (*Scutigerella* sp.).

However, other than these two studies, observations on schizomid reproduction and brood care are rare and few have been reported. Under the Comments section of their redescription of *Schizomus crassicaudatus*, Reddell & Cokendolpher (1991: 7) mention a series of papers discussing the "habitat and behavior (including egg brooding and defensive secretion) of this species". From the cited papers (Gravely 1911, 1915; Silvestri 1947; Rémy 1961), only Gravely (1915) and Silvestri (1947) have information on brooding, the other two focusing on descriptions of the habitat where specimens were found, but Rémy (1961) did report on collecting several young in Sri Lanka, during the wet season in 1959. We therefore provide a compilation of the existing but scattered literature as well as additional personal

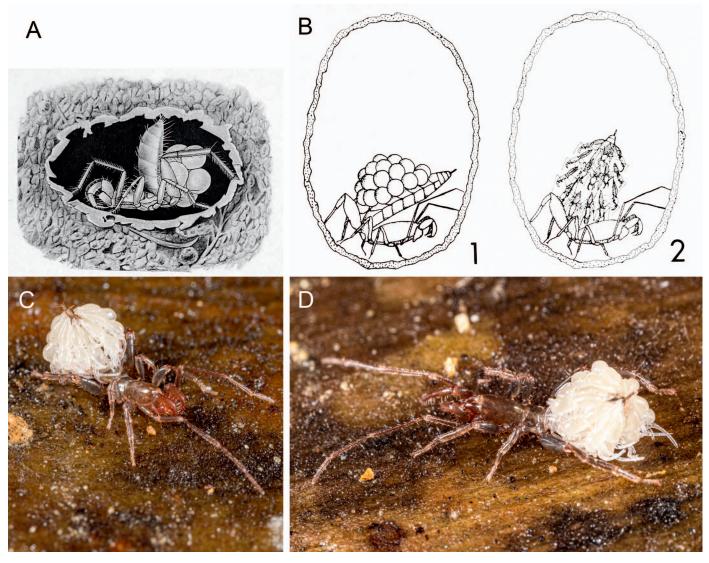


Figure 1.—A, Reproduction of the original illustration of the brooding chamber of the female *Schizomus crassicaudatus* by Gravely (1915); B, Reproduction of the original illustration by Rowland (1972) of the brooding chamber of a female *Hubbardia pentapeltis*, with eggs (left) and young (right); C, D, *Hansenochrus tobago* (MCZ IZ-144144), female with young instars, Gilpin Trail, Tobago, Trinidad & Tobago, May 23rd, 2017 (photographs by GG).

observations related to the reproductive behavior of Schizomida (see also Table 1).

- Silvestri (1947: 30) reported a female of *Bamazomus siamensis* (Hansen in Hansen & Sörensen, 1905) in a nest of *Macrotermes barneyi* (Hexapoda, Blattodea, Termitidae) in "Taipò Market (Kowloon, Cina meridionale)", probably the old Tai Po Market, Hong Kong; the female carrying on the dorsal side of the abdomen a "bag" ["borsetta"] with eggs or small larvae ["larvette"].
- Lawrence (1958) observed a cluster of ten eggs and some embryos of *Afrozomus machadoi* (Lawrence, 1958) in an individual vial separated from vials containing adult females collected in Dundo, Angola.
- Lawrence (1969) reported a female with 11–12 eggs in *Schizomus vinsoni* Lawrence, 1969 from Riviere des Anguilles, Mauritius.
- Sekiguchi & Yamasaki (1972) maintained under laboratory conditions some gravid females of *Orientzomus sawadai* (Kishida, 1930) collected in Chichi-Jima Island, Bonin Islands (the Ogasa-

- wara Islands), Japan. They were fed during four months with *Drosophila* flies but laid no eggs.
- Brach (1976) provided observations on the parthenogenetic species Stenochrus portoricensis Chamberlin, 1922 (as Schizomus floridanus Muma, 1967) from Key Biscayne, Florida, kept in captivity, which unlike in Rowland's (1972) study, were observed to feed on small insects. The study provided some behavioral observations about gregariousness and agonistic displays. A female captured in the field in August was observed with eight embryos attached to the underside of the opisthosoma, in a loosely-compacted mass, at the stage when embryos are still spherical. A second female was captured the same day carrying a mass of several larval exuviae on the dorsal side of the opisthosoma, shed shortly after capture. Large numbers of second-instar young were observed in the forest litter. In the lab, in April, a female was observed with three larvae attached to the opisthosoma (Brach 1976: fig. 1). The larvae were large, sticky on their ventral surface and the female did not carry the abdomen erect. No protective envelope was observed. As in H. pentapeltis, five post-embryonic molts were observed.

Table 1.—Summary of observations reported with information on taxonomy, locality and date.

Species	Reference	Locality/ Origin	Date	Observation
Schizomus crassicaudatus (O. Pickard-Cambridge, 1872)	Gravely (1915)	Sri Lanka	1915	Female carrying 7 eggs
Bamazomus siamensis (Hansen, 1905)	Silvestri (1947)	Hong Kong	26.iv.1925	Female carrying eggs or larvae
Schizomus vinsoni Lawrence, 1969	Lawrence (1969)	Riviere des Anguilles, Mauritius	x.1957	Female carrying 11–12 eggs
Hubbardia pentapeltis (Cook, 1899)	Rowland (1972)	Riverside, California, U.S.A.	14.i.1971	Female carrying 30 eggs/ hatchlings
Orientzomus sawadai Cokendolpher & Tsurusaki, 1994	Sekiguchi & Yamasaki (1972)	Chichi-Jima Island, Bonin Islands, Japan	iv.1972	Gravid females laid no eggs in laboratory
Stenochrus portoricensis Chamberlin, 1922	Brach (1976)	Key Biscayne, Floria, U.S.A.	10.i.1973	2 females with 8 and 3 young
Bamazomus siamensis (Hansen, 1905)	Howarth & Montgomery (1982)	Oahu, Hawaii, U.S.A.	7.iii.1979	Female carrying 6 young
Stenochrus portoricensis Chamberlin, 1922	de Armas (1989)	El Laguito, Playa, Havana, Cuba	18.x.1972	3 females: with 16 eggs, 12 eggs, and 15 young
Draculoides vinei (Harvey, 1988)	Humphreys et al. (1989)	Cape Range, Western Australia	1989	Female carrying 9 eggs
Stenochrus portoricensis Chamberlin, 1922	de Armas & Abud Antun (1990)	Ruinas de Engombe, Distrito Nacional, Cuba	13.viii.1990	Female with 4 young, 6 embryos and 1 egg
Stenochrus portoricensis Chamberlin, 1922	de Armas & Abud Antun (1990)	La Cienaguita, Bonao, Monseñor Nouel, Cuba	28.viii.1990	Female carrying 8 eggs
Rowlandius toldo Armas, 2002	de Armas (2002)	Moa, Holguín, Cuba	vi.1997 and ix.1998	2 females with 9 and 8 young
Undescribed genus	de Armas (2010)	Petit, Falcón, Venezuela	12.iv.2006	Female carrying ~10 young
Rowlandius pedrosi Giupponi, Miranda & Villarreal, 2016	Giupponi et al. (2016)	Santa Quitéria, Ceará, Brazil	iii–iv.2014	Female near a dropped egg mass of > 9 eggs
Stenochrus portoricensis Chamberlin, 1922	Bellman (2016)	Frankfurt, Germany	2004–2006	Female carrying ~7 young
Calima embera Moreno- González & Villarreal, 2017	Moreno-González & Villarreal (2017)	Santuario, Risaralda, Colombia	17.x.2012	Female carrying 6 young and a subadult male inside mud chamber
Hansenochrus tobago (Rowland & Reddell, 1979)	Present contribution	Main Ridge Forest Reserve, Tobago, Trinidad and Tobago	23.v.2017	Female carrying 10 young
Piaroa sp.	Present contribution	Yotoco, Valle del Cauca, Colombia	15.viii.2010	Female carrying 5 young
Dumitrescoella decui (Dumitresco 1977)	L. F. de Armas (pers com.)	Sierra de Anafe, Caimito, Artemisa, Cuba	ii.2016 and i–iii.2017	2 females with 12 eggs and 15 eggs
Belicenochrus pentalatus de Armas & Víquez, 2010	Gil Wizen (blog)	Belize	colony established in 2013	Parthenogenetic females with 5–6 eggs, hatching and post-hatching development
Surazomus sp.	C. Y. Quijano (iNaturalist)	Pital, Huila, Colombia	28.ix.2020	Female carrying ~8 young

- Howarth & Montgomery (1982) observed a female of *Bamazomus siamensis* (as *Trithyreus* sp.) carrying six young in an earthen cell attached to the underside of a flat rock, similar to the brooding chamber of *H. pentapeltis*, in a collapsed sinkhole in a quarry at the University of Hawai'i at Mānoa, in Oahu, Hawaii.
- de Armas (1989) observed in El Laguito, Playa, Havana City, two females of *Stenochrus portoricensis* inside individual brooding chambers, one female carrying 16 eggs and another 12 eggs. In the same field trip, a female was observed inside a brooding chamber with 15 hatchlings on her opisthosoma.
- Humphreys et al. (1989) reported different aspects of the biology of Draculoides vinei (Harvey, 1988), from caves in Cape Range,

- Western Australia. A female kept in captivity produced nine eggs, none of which hatched.
- de Armas & Abud Antun (1990) reported in Ruinas de Engombe, Distrito Nacional, Cuba, one female of *Stenochrus portoricensis* with four hatchlings, six embryos in different development phases, and a single egg. They also reported another female carrying eight eggs in La Cienaguita, Bonao, Monseñor Nouel, Cuba.
- de Armas (2002) observed in Moa, Holguín, Cuba, two females of *Rowlandius toldo* de Armas, 2002, one buried 15 cm deep into the soil and carrying nine young and another one buried 10 cm deep into the soil and carrying eight young. All young had their prosoma oriented anteriorly.

- de Armas (2010) observed a female of an undescribed genus in Petit, Falcón, Venezuela, carrying around ten young on her abdomen. This species was observed in sympatry with *Piaroa* sp. and *Rowlandius arduus* de Armas, Villarreal & Colmenares, 2009.
- Giupponi et al. (2016: fig. 8F) observed a female of Rowlandius pedrosi Giupponi, de Miranda & Villareal, 2016 walking near a dropped egg mass composed of at least nine eggs, inside a cave in Santa Quitéria, Ceará state, Brazil.
- A photograph of an unidentified species (probably *Stenochrus portoricensis*) by insect biologist Heiko Bellmann has appeared in a couple of publications, including his popular spider book (Bellmann 2016). The photo shows at least seven young aligned along the female's opisthosoma.
- Moreno-González & Villarreal M (2017) observed two females of Calima embera Moreno-González & Villareal M, 2017 in the Parque Natural San Rafael, Santuario, Risaralda, Colombia, each with six young, which were abandoned after becoming stressed. A subadult male of the same species was observed inside a small mud chamber, like the one illustrated by Gravely (1915) and Rowland (1972).

Unpublished observations:

- The photographs presented here (Fig. 1C–D) show a female of *Hansenochrus tobago* (Rowland & Reddell, 1979) (MCZ IZ-144144), found in Main Ridge Forest Reserve, Tobago, Trinidad & Tobago, bearing ten young on the opisthosoma, aligned with the A–P axis of the mother, their flagellum meeting with the flagellum of the mother, the legs facing the opisthosoma. All the young were completely depigmented and remained largely immobile.
- A female of an undescribed *Piaroa* species was observed by JAMG at Bosque de Yotoco, Valle del Cauca, Colombia, with five hatchlings on the opisthosoma. A few additional females were observed carrying hatchlings, but these were not collected.
- Two females of *Dumitrescoella decui* (Dumitresco, 1977) were observed in Sierra de Anafe, Caimito, Artemisa province, Cuba, carrying 12 and 15 eggs, respectively (L. F. de Armas pers. comm.).
- A series of photographs by Cristian Yamith Quijano published in iNaturalist shows a female of *Surazomus* sp. carrying at least six (probably eight if accounting for spacing) young observed in Pital, Huila, Colombia (https://www.inaturalist.org/observations/61423222).
- An internet blog by entomologist and nature photographer Gil Wizen, dated June 17th, 2019, reports different aspects of the reproductive biology of *Belicenochrus pentalatus* de Armas & Víquez, 2010 kept in captivity (https://gilwizen.com/schizomids/), a species that can reproduce parthenogenetically. Wizen reports the egg sac containing five or six relatively large eggs. Once hatched, the young climb on the mother's opisthosoma and stay there for two weeks before dropping off and starting their independent lives. He also reports that brooding females drop the babies at any disturbance.

Here we have compiled published (mostly obscure) and novel observations on schizomid brooding including the citizens science portal iNaturalist, which is becoming a powerful tool for biodiversity research (e.g., Heberling & Isaac 2018). Both authors have spent many hours searching for edaphic fauna, indicating that these observations are rare. Most studies show the existence of three to multiple young aligned with the opisthosoma of the female, converging on the flagellum. One study, however, has showed an illustration with many small young surrounding the mother's opisthosoma in multiple layers (Rowland 1972: fig. 2 [see Fig. 1B here])—as if ornaments on a Christmas tree. This position seems at odds with all other observations (Gravely 1915; Brach 1976; Bellmann 2016), including the ones provided here (Fig. 1C–D). While this could be due to the large number of eggs/young reported for *Hubbardia pentapeltis*, the illustration is a drawing and should be confirmed with

new observations. Another aspect worth studying seems to be their brooding chamber, reported for some of the species (Gravely 1915; Rowland 1972), as well as in some of the observations reported here. Similar chambers have also been reported for *Rowlandius potiguar* Santos, Ferreira & Buzatto, 2013 kept in captivity, although in this case they were supposedly built for shelter (de Oliveira & Ferreira 2014: fig. 6). Rowland (1972) also provides the possibility that cave species may brood without the use of chambers in caves, but this remains to be studied, as an observation from Hawaii reports the building of an earthen cell attached to the underside of a flat rock in a collapsed sinkhole (Howarth & Montgomery 1982).

Schizomids continue to be a fascinating order of arachnids, with only a few aspects of their biology well characterized (Beccaloni 2009). Few studies have focused on the transfer of spermatophores and mating (e.g., Sturm 1958, 1973), and a few more provide anecdotal data on brooding. More detailed experimental studies are certainly needed, both in the laboratory and in the field. We hope this report stimulates behavioral and developmental work on this poorly understood group of soil animals.

ACKNOWLEDGMENTS

Ligia Benavides, Julia Cosgrove and Gustavo Hormiga accompanied GG in the field trip to Trinidad & Tobago that produced some of the observations here reported. Fieldwork was funded by the Putnam Expedition Program of the MCZ. This work was supported by the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) (under Grant 2015/18376-2) to JAMG. Associate Editor Mark Harvey and two anonymous reviewers provided detailed comments that improved this note.

LITERATURE CITED

- Adis J, Cokendolpher JC, Reddell JR, Rodrigues JMG. 2001. Abundance and phenology of Schizomida (Arachnida) from a secondary upland forest in Central Amazonia. Revue suisse de Zoologie 108:879–889.
- Adis J, Reddell J, Cokendolpher J, de Morais JW. 1999. Abundance and phenology of Schizomida (Arachnida) from a primary upland forest in Central Amazonia. *Journal of Arachnology* 27:205–210.
- Alberti G, Palacios-Vargas JG. 2015. Fine structure of the ovary of *Schizomus palaciosi* (Arachnida: Schizomida). *Soil Organisms* 87:153–168.
- Ballesteros JA, Santibáñez López CE, Kováč Ľ, Gavish-Regev E, Sharma PP. 2019. Ordered phylogenomic subsampling enables diagnosis of systematic errors in the placement of the enigmatic arachnid order Palpigradi. *Proceedings of the Royal Society B: Biological Sciences* 286:20192426.
- Ballesteros JA, Sharma PP. 2019. A critical appraisal of the placement of Xiphosura (Chelicerata) with account of known sources of phylogenetic error. *Systematic Biology* 68:896–917.
- Beccaloni J. 2009. Arachnids. The Natural History Museum, London. Bellmann H. 2016. Der Kosmos Spinnen-führer. Kosmos.
- Brach V. 1976. Development of the whipscorpion *Schizomus floridanus*, with notes on behavior and laboratory culture. *Bulletin of the Southern California Academy of Sciences* 74:97–100.
- Clouse RM, Branstetter MG, Buenavente PAC, Crowley LM, Czekanski-Moir J, General DEM, et al. 2017. First global molecular phylogeny and biogeographical analysis of two arachnid orders (Schizomida and Uropygi) supports a tropical Pangean origin and mid-Cretaceous diversification. *Journal of Biogeography* 44:2660–2672.
- de Armas LF. 1989. Adiciones al orden Schizomida (Arachnida) en Cuba. *Poeyana* 387:1–45.
- de Armas LF. 2002. Nuevas especies de Rowlandius Reddell &

- Cokendolpher, 1995 (Schizomida: Hubbardiidae) de Cuba. *Revista Ibérica de Aracnología* 6:149–167.
- de Armas LF. 2010. Schizomida de Sudamérica (Chelicerata: Arachnida). Boletín de la Sociedad Entomológica Aragonesa 46:203–234.
- de Armas LF, Abud Antun AJ. 1990. El orden Schizomida (Arachnida) en República Dominicana. Poeyana 393:1–23.
- de Oliveira MPA, Ferreira RL. 2014. Aspects of the behavior and activity rhythms of *Rowlandius potiguar* (Schizomida: Hubbardiidae). *PLoS One* 9:e91913.
- Dunlop JA. 2010. Geological history and phylogeny of Chelicerata. Arthropod Structure & Development 39:124–142.
- Fernández R, Kallal RJ, Dimitrov D, Ballesteros JA, Arnedo MA, Giribet G, et al. 2018. Phylogenomics, diversification dynamics, and comparative transcriptomics across the Spider Tree of Life. Current Biology 28:1489–1497.
- Garwood RJ, Dunlop JA, Knecht BJ, Hegna TA. 2017. The phylogeny of fossil whip spiders. BMC Evolutionary Biology 17:105.
- Giribet G, Edgecombe GD, Wheeler WC, Babbitt C. 2002. Phylogeny and systematic position of Opiliones: a combined analysis of chelicerate relationships using morphological and molecular data. *Cladistics* 18:5–70.
- Giupponi APdL, de Miranda GS, Villarreal OM. 2016. Rowlandius dumitrescoae species group: new diagnosis, key and description of new cave-dwelling species from Brazil (Schizomida, Hubbardiidae). ZooKeys 632:13–34.
- Gravely FH. 1911. The species of Ceylon Pedipalpi. *Spolia Zeylanica* 7:135–140.
- Gravely FH. 1915. Notes on the habits of Indian insects, myriapods and arachnids. *Records of the Indian Museum* 11:483–539.
- Harvey MS. 2003. Catalogue of the smaller arachnid orders of the World. CSIRO Publishing, Melbourne.
- Heberling JM, Isaac BL. 2018. iNaturalist as a tool to expand the research value of museum specimens. *Applications in Plant Sciences* 6:e01193.
- Howarth FG, Montgomery SL. 1982. Notes and exhibitions: Trithyreus? sp. (Schizomidae: Schizomida). Proceedings of the Hawaiian Entomological Society 4:8.
- Huang D, Hormiga G, Xia F, Cai C, Yin Z, Su Y, et al. 2018. Origin of spiders and their spinning organs illuminated by mid-Cretaceous amber fossils. *Nature Ecology & Evolution* 2:623–627.
- Humphreys WF, Adams M, Vine B. 1989. The biology of Schizomus vinei (Chelicerata: Schizomida) in the caves of Cape Range, Western Australia. Journal of Zoology, London 217:177–201.
- Krüger J, Dunlop J. 2010. Schizomids (Arachnida: Schizomida) from Dominican Republic amber. Alavesia 3:43–53.
- Latreille PA. 1810. Considérations générales sur l'ordre naturel des animaux composant les classes des Crustacés, des Arachnides, et des Insectes; avec un tableau méthodique de leurs genres, disposés en familles. F. Schoell, Paris.
- Lawrence RF. 1958. Whipscorpions (Uropygi) from Angola, the Belgian Congo and Mossambique. Publicações Culturais da Companhia de Diamantes de Angola 40:69–79.
- Lawrence RF. 1969. The Uropygi (Arachnida: Schizomidae) of the Ethiopian Region. *Journal of Natural History* 3:217–260.
- Lozano-Fernandez J, Tanner AR, Puttick MN, Vinther J, Edgecombe GD, Pisani D. 2020. A Cambrian-Ordovician terrestrialization of arachnids. Frontiers in Genetics 11:182.
- Lozano-Fernandez J, Tanner AR, Vinther J, Giacomelli M, Carton R, Edgecombe GD, et al. 2019. Increasing species sampling in chelicerate genomic-scale datasets provides support for monophyly of Acari and Arachnida. *Nature Communications* 10:2295.
- Monjaraz-Ruedas R, Francke OF, Prendini L. 2020. Integrative

- systematics untangles the evolutionary history of *Stenochrus* (Schizomida: Hubbardiidae), a neglected junkyard genus of North American short-tailed whipscorpions. *Biological Journal of the Linnean Society* 130:458–479.
- Moreno-González JA, Villarreal M O. 2017. Two new species of *Calima* Moreno-González and Villarreal, 2012 (Arachnida: Schizomida: Hubbardiidae) from the Colombian Andes, with a discussion on the male flagellar microsetae of Hubbardiinae. *Journal of Natural History* 51:2681–2700.
- Müller SP, Dunlop JA, Kotthoff U, Hammel JU, Harms D. 2020. The oldest short-tailed whipscorpion (Schizomida): A new genus and species from the Upper Cretaceous amber of northern Myanmar. Cretaceous Research 106:104227.
- Reddell JR, Cokendolpher JC. 1991. Redescription of *Schizomus* crassicaudatus (Pickard-Cambridge) and diagnoses of *Hubbardia* Cook, *Stenochrus* Chamberlin, and *Sotanostenochrus* new genus, with description of a new species of *Hubbardia* from California (Arachnida: Schizomida: Hubbardiidae). *Pearce-Sellards Series Texas Memorial Museum* 47:1–24.
- Rémy PA. 1961. Sur l'écologies des Schizomides (Arachn. Uropyges) de mes récoltes, avec description de trois *Schizomus* nouveaux, capturés par J. van der Drift au Surinam. *Bulletin du Muséum National d'Histoire Naturelle, 2e Série* 33:406–414.
- Rowland JM. 1972. The brooding habits and early development of Trithyreus pentapeltis (Cook) (Arachnida, Schizomida). Entomological News 86:69–74.
- Sekiguchi K, Yamasaki T. 1972. A redescription of "Trithyreus sawadai" (Uropygi: Schizomidae) from the Bonin Islands. Acta Arachnologica 24:73–81.
- Selden PA, Ren D. 2017. A review of Burmese amber arachnids. *Journal of Arachnology* 45:324–343.
- Sharma PP, Kaluziak S, Pérez-Porro AR, González VL, Hormiga G, Wheeler WC, et al. 2014. Phylogenomic interrogation of Arachnida reveals systemic conflicts in phylogenetic signal. *Molecular Biology and Evolution* 31:2963–2984.
- Shultz JW. 1990. Evolutionary morphology and phylogeny of Arachnida. *Cladistics* 6:1–38.
- Shultz JW. 1999. Muscular anatomy of a whipspider, *Phrynus longipes* (Pocock) (Arachnida: Amblypygi), and its evolutionary significance. *Zoological Journal of the Linnean Society* 126:81–116.
- Shultz JW. 2007. A phylogenetic analysis of the arachnid orders based on morphological characters. Zoological Journal of the Linnean Society 150:221–265.
- Silvestri F. 1947. Seconda nota su alcuni termitofili dell'Indocina con una appendice sul *Macrotermes Barneyi* Light. *Bollettino del Laboratorio di entomologia Agraria di Portici* 7:13–40.
- Sturm H. 1958. Indirekte Spermatophorenübertragung bei dem Geißelskorpion *Trithyreus sturmi* Kraus (Schizomidae, Pedipalpi). *Die Natur-wissenshaften* 45:142–143.
- Sturm H. 1973. Zur Ethologie von Trithyreus sturmi Kraus (Arachnida, Pedipalpi, Schizopeltidia). Zeitschrift für Tierpsychologie 33:113–140.
- Weygoldt P. 1969. The Biology of Pseudoscorpions. Harvard University Press, Cambridge.
- Weygoldt P. 1971. Notes on the life history and reproductive biology of the giant whip scorpion, *Mastigoproctus giganteus* (Uropygi, Thelyphonidae) from Florida. *Journal of Zoology*, *London* 164:137–147.
- Weygoldt P. 2000. Whip spiders (Chelicerata: Amblypygi). Their Biology, Morphology and Systematics. Apollo Books, Stenstrup.

Manuscript received 17 November 2020, revised 30 December 2020.