

Sinarachna nigricornis and genus-specific host utilization of *Araneus* spiders by the genus *Sinarachna* (Hymenoptera: Ichneumonidae)

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Abstract. The ichneumonid parasitoid *Sinarachna nigricornis* (Holmgren, 1860) was associated only with *Araneus sturmi* (Hahn, 1831) in the studied locality. The normal capturing orb web of *A. sturmi* was always vertical and had a median of 18 radii and 9 spirals in laboratory conditions. When spiders did not build capture webs, they built resting and molting webs which consisted of a few threads between the ends of the provided tree twigs. There were no significant differences in the number of radials and spirals between unparasitized spiders and spiders parasitized by early instar parasitoid larvae. *Araneus sturmi* under manipulation by *S. nigricornis* built a modified cocoon web, serving parasitoid larva pupation. *S. nigricornis* exhibited high plasticity in the architecture of the cocoon web induced by its penultimate instar larva. The most common cocoon web was of 3D architecture with a small central silk platform, from which the wasp cocoon was suspended by its apical end (72% of webs). In 22% of cases, the cocoon web consisted only of a few threads, presumably resembling a molting web. In one case, the manipulated spider built a 3D tangle, though radials and the central hub (typical for the normal capturing web) were also present. The genus specificity of the cocoon web architecture described here, in which the typical cocoon web exhibits a sparse but strong 3D architecture and in which the wasp cocoon is suspended by its apical end at the center, is expected for the genus *Sinarachna*.

Keywords: Koinobiontism, spider host, host-parasitoid interaction, host range, life strategy

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Parasitoids, organisms that live in close association with their hosts during larval development and which ultimately kill them before reaching maturity, exploit various developmental stages of various holometabolous and hemimetabolous insects (e.g., Gal & Libersat 2008; Libersat et al. 2009). A few specific parasitoid groups of hymenopterans and dipterans have evolved in specific association with spiders (Fitton et al. 1987; Schlinger 1987; Kurczewski et al. 2017). One of the most host-specialised groups of koinobiont parasitoids is the *Polysphincta* group of genera from the family Ichneumonidae (Ephialtini). They are exclusively external koinobiont parasitoids of spiders, whose larvae are attached to the dorsal side of the spider's opisthosoma (rarely, the prosoma in more basal species) (Takasuka et al. 2018), where they develop while the spider continues foraging (Fitton et al. 1987; Eberhard & Gonzaga 2019). When the polysphinctine larva reaches the final instar, it injects behavioural modulators into the spider body (Kloss et al. 2017) and induces alterations in the web-building behaviour of the spider host in order to provide a safe place for pupation against enemies and the environment (e.g., Eberhard 2000; Korenko et al. 2014, 2018b; Eberhard & Gonzaga 2019). Several studies have been devoted to host-parasitoid interactions between polysphinctine wasps and orb web weaving spiders from the family Araneidae (e.g., Fitton et al. 1988; Messas et al. 2017; Takasuka 2019).

Here, we studied the genus *Sinarachna* Townes, 1960, a small genus comprising four described species and one subspecies from the Northern Hemisphere. *S. nigricornis* is widely distributed in the Palaearctic and *Sinarachna pallipes* (Holmgren, 1860) is widely distributed in the Holarctic, with a subspecies, *S. p. strigis* (Howard, 1892), widely distributed in

the Nearctic (Yu et al. 2012). There are two additional described species with unknown ecology: *Sinarachna maculata* He & Ye, 2006 from China (Yunnan and Guizhou provinces) (He et al. 2006 and *S. ceylonica* (Ashmead, 1896) from Sri Lanka (Yu et al. 2012). The host range of the genus *Sinarachna* seems to be very narrow and restricted to the group of orb web building spiders from the family Araneidae. *Sinarachna nigricornis* was documented to be reared from spiders of the genus *Araneus* Clerck, 1757 (Fitton et al. 1988), and *S. pallipes* seems to be specialised on the genus *Araniella* Chamberlin & Ivie, 1942 (Fitton et al. 1988; Korenko et al. 2014). The biology of the other two *Sinarachna* species from China and Sri Lanka, is still unknown.

The aim of the present study was to investigate the interaction between the hymenopteran parasitoid *S. nigricornis* and its spider host *A. sturmi*, with an emphasis on the alteration of spider web building behaviour induced by the penultimate instar larva before the killing of the spider and pupation on its web. We expected that *S. nigricornis* exhibits the same or at least similar traits of interaction with orb web building spider hosts as closely related wasps of the genus *Sinarachna* such as *S. pallipes*, whose cocoon web built by the manipulated spider is a sparse 3D tangle in which the pupa always takes up position at the center (Korenko et al. 2014). Details about the interaction of *S. pallipes* with spider hosts is documented in Korenko et al. (2014). We also expected that the cocoon web architecture of *Sinarachna* wasps (i.e., the architecture of the silk structure built by the spider after manipulation by the penultimate instar larva of the parasitoid) is genus-specific, because the cocoon web of *S. nigricornis* and the cocoon web of *S. pallipes* do not differ considerably.

Parasitoids for laboratory observations were collected as larvae attached to the abdomens of the spider *A. sturmi* in the ecotone of coniferous forest with dominant *Picea abies* L., 1881 and groups of shrubs of *Corylus avellana* L., 1753 and *Crataegus laevigata* (Poir.) DC., 1825 in the Králiky locality (N 48°43.81883', E 19°1.89877'), district of Banská Bystrica, Slovakia from autumn 2017 to autumn 2018. Spiders were collected by beating tree canopies (between 30 and 200 cm above the ground), with a square-shaped beating net (1-m² area) placed beneath. Parasitized spiders were identified visually, placed separately into tubes, and kept for wasp rearing and laboratory observations.

The web architecture of parasitized and non-parasitized spiders was studied by placing spiders individually into experimental arenas (100×100 mm base, 130 mm height), each with an installed twig providing support for a spider web. Spiders were kept at room temperature (20–23 °C) under a natural LD regime and fed with a surplus of fruit flies (*Drosophila melanogaster* Meigen, 1830). The web building activity of parasitized spiders was recorded until the larva killed and consumed the spider and built the cocoon. In the case of non-parasitized spiders, spider activity was observed when a spider captured prey (in a capture web), rested (in a resting web), and molted (in a molting web). Hatched wasps were identified using Fitton et al. (1988). The nomenclature for polysphinctines follows Fitton et al. (1988) and Yu et al. (2012). Voucher specimens were deposited in the collection of the Czech University of Life Sciences, Prague (Czech Republic).

We recorded the web building behaviour of both unparasitized and parasitized spider hosts – specifically, the presence/absence of particular elements of an orb web, such as the central hub, and radial, spiral, and frame threads – in various periods of the spider life history. This included periods of resting, capturing, and molting, and the production of the cocoon web (under manipulation by the penultimate instar parasitoid larva). Once the orb web was built, the number of radials and spirals were counted on horizontal and vertical lines, counting from the center to the edge of the web (from center to up/-down/-right/-left). The greatest number of spirals was used for analyses.

The architecture of silk structures was photographed using a Canon EOS 500 digital camera with an EFS 18–55mm DC III objective and an EF 100mm f/2.8L IS USM macro objective.

The Mann-Whitney U test was used to reveal differences in the numbers of radials and spirals between the orb webs of unparasitized spiders and those of parasitized spiders with early instar parasitoid larva. GraphPad InStat software v. 3.06 was used.

We inspected 211 individuals of *A. sturmi* in the Králiky locality during the 2017/18 season, and found 9.5% of spiders to be parasitized ($n = 20$). All reared wasps ($n = 15$) were identified as *S. nigricornis*. This is the first record of this species in Slovakia. Other parasitoid wasps were reported to be in association with spiders of the family Araneidae; *Polysphincta boops* Tschek, 1868, and *Polysphincta tuberosa* Gravenhorst, 1829 were reared only from spiders of the genus *Araniella*, while *Reclinervellus nielsenii* (Roman, 1923) was reared only from the spider *Cyclosa conica* (Pallas, 1772) (Table 1).

Table 1.—Community of orb web building spiders from the family Araneidae in the Králiky locality. f – female; m – male; juv – juvenile spider; p – average parasitism incidence per year; N – number of sampled spiders

Species	f	m	juv	p (%)	N
<i>Aculepeira ceropegia</i> Walckenaer, 1802			2		2
<i>Araneus diadematus</i> Clerck, 1757		1	9		10
<i>Araneus sturmi</i> (Hahn, 1831)	12	6	193	9.5	211
<i>Araneus triguttatus</i> (Fabricius, 1775)	2				2
<i>Araniella alpica</i> (L. Koch, 1869)	3				3
<i>Araniella cucurbitina</i> (Clerck, 1757)	3	3			6
<i>Araniella</i> spp.			104	9.6	104
<i>Cyclosa conica</i> (Pallas, 1772)	1		15	13.3	16
<i>Hyssosinga sanguinea</i> (C. L. Koch, 1844)			1		1
<i>Mangora acalypha</i> (Walckenaer, 1802)			1		1
unidentified			1		1
Total	21	10	324	10.2	357

Typical web building behaviour of the host *A. sturmi*.—In the control group, juvenile unparasitized spiders of *A. sturmi* ($n = 5$) and juvenile parasitized spiders with early instar larvae (the first and second instar) ($n = 10$) constructed only normal 2D orb capturing webs (60 days of observation of each individual). The normal capturing orb web of unparasitized spiders was always vertical and had a median of 18 radii (min no./max no. = 17/20) and nine spirals (min no./max no. = 8/14) in vertical orientation (Fig. 1a). The normal capturing orb web of spiders parasitized by early instar larvae was also vertical and had a median of 18 radii (min no./max no. = 15/22) and nine spirals (min no./max no. = 8/14) in vertical orientation. There were no significant differences in the number of radials and spirals between the webs of unparasitized spiders and spiders parasitized by early instar parasitoid larvae ($U = 23$, $P = 0.85$ and $U = 22$, $P = 0.76$, both $n = 15$). In the period of satiation (the period in which spiders do not catch prey), spiders built “resting webs”, which consisted of a few threads between the ends of the provided tree twigs. When the spider molted, it built a “molting web” consisting of a few threads, then molted as it hung on one of the threads.

Variability of web building behaviour of *A. sturmi* under manipulation.—The penultimate instar larvae of *S. nigricornis* induced unique changes in the web-building behaviour of its spider host, when the spider under manipulation built a modified web, also called a cocoon web, sustaining parasitoid larva pupation ($n = 18$). The wasp *S. nigricornis* exhibited high plasticity in the architecture of the cocoon web induced by its penultimate instar larva. In one case, the manipulated spider built a 3D tangle, though radials and the central hub (typical for the architecture of the normal capturing web) were also present (Fig. 1b). The most common cocoon web was of 3D architecture with a small central silk platform, from which the wasp cocoon was suspended by its apical end ($n = 13$, Fig. 1c). In four cases, the cocoon web consisted of only a few threads (resembling a molting web) (Fig. 1d). The wasp cocoon was placed vertically in the center of a silk tangle (if present). The wasp’s cocoon enclosing the pupa was narrowly fusiform, light brown–yellowish in colour, and densely woven with a tight outer cover of coarse fibers.

We found that *S. nigricornis* was associated only with the arboreal orb-web weaving spider *A. sturmi* in the studied

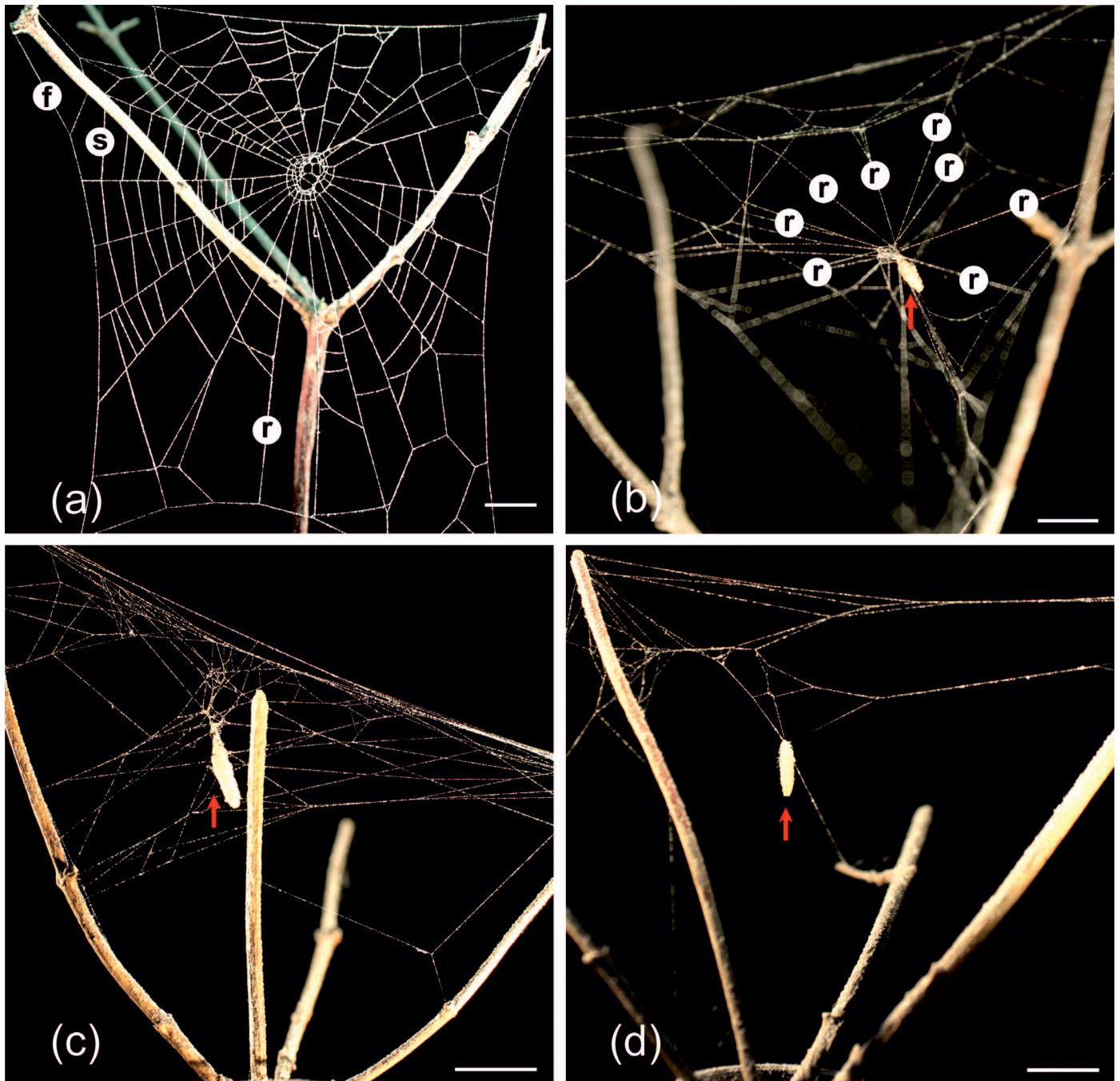


Figure 1.—(a) Web architecture of unmanipulated spider; (b) web architecture of manipulated spider: radials of normal web still presented; (c) 3D tangle web only; (d) extremely simplified cocoon web resembling spider molting web. f – frame thread, r – radial thread, s – spiral thread, arrow – shows position of cocoon with wasp pupa. Scale = 10 mm.

locality. Other spiders of the genus *Araneus* with similar ecology could be potential hosts, e.g., *A. diadematus*, as noted by Fitton et al. (1988) and Shaw (1994), but we did not confirm this in this study area. *Sinarachna nigricornis* seems to possess high association with *A. sturmi*, at least in the studied locality. The penultimate instar larvae of both species induced almost identical alterations in spider web building behaviour to provide a safe shelter for parasitoid pupation (see Korenko et al. 2014; this study). In addition, the architecture of the

cocoon produced by larvae before pupation was morphologically identical.

Variability of cocoon web architecture.—Eberhard (2010) observed that a tangle web building spider, *Anelosimus* sp. (Theridiidae), manipulated by the penultimate instar of *Zatypota solanoi*, Gauld 1991, appeared to adjust cocoon web architecture to local conditions: the large flat leaves from environs were integrated as parts of the upper and lower sheets of the cocoon web (Eberhard 2010). A further example of

cocoon web architecture variability within one parasitoid species is documented in the wasp *Zatypota kauros* Gauld, 1984 in association with *Trichonephila plumipes* (Latreille, 1804) in Australia (Korenko et al. 2018b). In 71% of observations, *T. plumipes*, under manipulation of the penultimate larva, built a 3D cocoon web in the center of which the wasp placed its pupa (typical architecture of cocoon web). The architecture of some cocoon webs differs considerably from the typical cocoon web. In one case, the spiral and some radials of the normal web were removed by the manipulated spider and the cocoon web consisted of the reduced number of radial threads and the central silk platform, which served as support for the parasitoid pupa. In another case, the spider did not modify the normal web at all and the larva pupated in a small tangle at the edge of the orb web, attached to the central hub (Korenko et al. 2018b). In *A. sturmi*, studied here, three types of cocoon web architecture induced by parasitoid penultimate instar larvae were distinguished. Spiders under manipulation by *S. nigricornis* mostly built sparse 3D structures, although, in one case, the cocoon web resembled the normal orb web in having radial lines converging on a hub-like structure, but differed by the absence of sticky spiral lines, and in another, the cocoon web resembled the simple web architecture of the molting web. Here, we documented another example of the intraspecific variability of cocoon web architecture, but the source of this variability is not yet explained.

Genus specific alteration of web architecture.—Some features of the cocoon web architecture are species/genus specific, others are common (Eberhard 2013; Korenko et al. 2014). Some orb web weavers under manipulation modified their 2-D orb web into a 3-D tangle structure (e.g., Gonzaga & Sobczak 2007; Eberhard 2013; Korenko et al. 2014; this study). Other species only somewhat modify their 2-D webs; for example, some parts are left out and others are reinforced (e.g., Eberhard 2001; Matsumoto & Konishi 2007; Korenko et al. 2015). The genus specificity of cocoon web architecture was documented in *Polysphincta* Gravenhorst, 1868 in Europe—in *Polysphincta boops* Tschek, 1869, *Polysphincta tuberosa* (Gravenhorst, 1829) (Korenko et al. 2014), and *Polysphincta longa* Kasparyan, 1976 (Korenko et al. 2017), when the penultimate instar larvae forced the spider host to build a dense 3D cocoon web with a high thread density, within which the pupa was positioned horizontally. This study on *S. nigricornis*, supported by the study on *S. pallipes* by Korenko et al. (2014), proposes the genus specificity of cocoon web architecture in the genus *Sinarachna*. This genus specificity must be confirmed by more data on a cocoon web architecture of other wasps of genus *Sinarachna*. In both the wasp species that have been studied, the typical cocoon web was of a sparse but strong 3D architecture and the wasp's cocoon was suspended vertically by its apical end at the center of the web. This type of cocoon web architecture, i.e., a sparse but strong 3D architecture, is also documented in the Indo-Australian genus *Eriostethus*—specifically, in a group of species associated with orb web building spiders from the family Araneidae (Korenko et al. 2018a); however, the architecture of the cocoon (another structure protecting the parasitoid pupa) is considerably different (see Korenko et al. 2018a).

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LITERATURE CITED

- Eberhard WG. 2000. Spider manipulation by a wasp larva. *Nature* 406:255–256.
- Eberhard WG. 2001. Under the influence: webs and building behaviour of *Plesiometa argyra* (Araneae, Tetragnathidae) when parasitized by *Hymenoepimecis argyraphaga* (Hymenoptera, Ichneumonidae). *Journal of Arachnology* 29:354–366.
- Eberhard WG. 2010. New types of behavioral manipulation of host spiders by a parasitoid wasp. *Psyche*: 950614.
- Eberhard WG. 2013. The Polysphinctine wasps *Acrotaphus tibialis*, *Eruga ca. gutfreundi*, and *Hymenoepimecis tedfordi* (Hymenoptera, Ichneumonidae, Pimplinae) induce their host spiders to build modified webs. *Annals of the Entomological Society of America* 106: 652–660.
- Eberhard WG, Gonzaga MO. 2019. Evidence that *Polysphincta*-group wasps (Hymenoptera: Ichneumonidae) use ecdysteroids to manipulate the web-construction behaviour of their spider hosts. *Biological Journal of the Linnean Society* 127:429–471.
- Fitton MG, Shaw MR, Austin AD. 1987. The Hymenoptera associated with spiders in Europe. *Zoological Journal of the Linnean Society* 90:65–93.
- Fitton MG, Shaw MR, Gauld ID. 1988. Pimplinae Ichneumon-flies. Hymenoptera Ichneumonidae (Pimplinae). Handbooks for the Identification of British Insects 7(1):1–110.
- Gal R, Libersat F. 2008. A parasitoid wasp manipulates the drive for walking of its cockroach prey. *Current Biology* 18:877–882.
- Gonzaga MO, Sobczak JF. 2007. Parasitoid-induced mortality of *Araneus omnicolor* (Araneae, Araneidae) by *Hymenoepimecis* sp. (Hymenoptera, Ichneumonidae) in southeastern Brazil. *Naturwissenschaften* 94:223–227.
- He J, Chen X, Ma Y, Ye S. 2006. Ichneumonidae (in Chinese with English summary). Pp. 571–575. In *Insects from Fanjingshan landscape (Insect Fauna from National Nature Reserve in Guizhou Province VI)*. (Z Li, Jin D, eds.). Guizhou Science and Technology Publishing House, Guiyang, Guizhou, China.
- Kloss TG, Gonzaga MO, de Oliveira LL, Sperber CF. 2017. Proximate mechanism of behavioral manipulation of an orb-weaver spider host by a parasitoid wasp. *PLoS ONE* 12, e0171336.
- Korenko S, Hamouzová K, Kysilková K, Kolářová M, Kloss TG, Takasuka K. et al. 2018a. Divergence in host utilisation by two spider ectoparasitoids within the genus *Eriostethus* (Ichneumonidae, Pimplinae). *Zoologischer Anzeiger* 272:1–5.
- Korenko S, Isaia M, Satrapová J, Pekár S. 2014. Parasitoid genus-specific manipulation of orb-web host spiders (Araneae, Araneidae). *Ecological Entomology* 39:30–38.
- Korenko S, Kysilková K, Černecká Ľ. 2017. Further records of two spider parasitoids of the genus *Polysphincta* (Ichneumonidae, Ephialtini) from Central Europe, with notes on their host interactions. *Arachnologische Mitteilungen* 54:28–32.
- Korenko S, Pekár S, Walter GH, Korenková V, Hamouzová K, Kolářová M. et al. 2018b. One generalist or several specialist species? Wide host range and diverse manipulations of the hosts'

- web building behaviour in the true spider parasitoid *Zatypota kauros* (Hymenoptera: Ichneumonidae). *Insect Conservation and Diversity* 11:287–299.
- Korenko S, Satrapova J, Zwakhals K. 2015. Manipulation of araneid spider web architecture by the polysphinctine parasitoid *Zatypota picticollis* (Hymenoptera: Ichneumonidae: Pimplinae). *Entomological Science* 18:383–388.
- Kurczewski FE, Edwards GB, Pitts JP. 2017. Hosts, nesting behavior, and ecology of some North American spider wasps (Hymenoptera: Pompilidae), II. *Southeastern Naturalist* 16:1–82.
- Libersat F, Delago A, Gal R. 2009. Manipulation of host behavior by parasitic insects and insect parasites. *Annual Review of Entomology* 54:189–207.
- Matsumoto R, Konishi K. 2007. Life histories of two ichneumonid parasitoids of *Cyclosa octotuberculata* (Araneae), *Reclinervellus tuberculatus* (Uchida) and its new sympatric congener (Hymenoptera: Ichneumonidae: Pimplinae). *Entomological Science* 10:267–278.
- Messas YF, Sobczak JF, Vasconcellos-Neto J. 2017. An alternative host of *Hymenoepimecis japi* (Hymenoptera, Ichneumonidae) on a novel family (Araneae, Araneidae), with notes on behavioral manipulations. *Journal of Hymenoptera Research* 60:111–118.
- Schlinger EI. 1987. The biology of Acroceridae (Diptera): True endoparasitoids of spiders. Pp. 319–327. *In Spider Ecophysiology*. (Nentwig W, ed.). Springer, Heidelberg.
- Shaw M. 1994. Parasitoid host ranges. Pp. 111–144. *In Parasitoid Community Ecology* (Hawkins B, Sheehan W. eds). Oxford University Press, Oxford.
- Takasuka K. 2019. Evaluation of manipulative effects by an ichneumonid spider-ectoparasitoid larva upon an orb-weaving spider host (Araneidae: *Cyclosa argenteoalba*) by means of surgical removal and transplantation. *Journal of Arachnology* 47:181–189.
- Takasuka K, Fritzen NR, Tanaka Y, Matsumoto R, Maeto K, Shaw MR. 2018. The changing use of the ovipositor in host shifts by ichneumonid ectoparasitoids of spiders (Hymenoptera, Ichneumonidae, Pimplinae). *Parasite* 25:17. doi: 10.1051/parasite/2018011.
- Yu DS, van Achterberg C, Horstmann K. 2012. Taxapad 2012. Ichneumonoidea 2011. Taxonomy, biology, morphology and distribution. Ottawa, Ontario. Online at <http://www.taxapad.com> (accessed – 1st August 2017). Now available online at <https://www.catalogueoflife.org/data/dataset/1068>.
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