

of *T. parietina*. Roma Oxford assisted with our own collections.

## References

- AGNARSSON, I. 1996: Íslenskar köngulær. *Fjöðrit Náttúrufræðistofnunar* **31**: 1–175.
- BONNET, P. 1959: *Bibliographia Araneorum* **2**(5): 4231–5058. Douladoure, Toulouse.
- DAHL, M. 1931: Spinnentiere oder Arachnoidea, VI. 24. Familie. Agelenidae. *Tierwelt Dtl.* **23**: 1–46.
- LEHTINEN, P. T. 1967: Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. *Anns zool. fenn.* **4**: 199–468.
- MAURER, R. 1992: *Checkliste der europäischen Agelenidae nach der Roewerschen Systematik 1954 — unter Berücksichtigung angrenzender östlicher Gebiete*. I: 1–28; II: 1–99. Privately published, Holderbank, Switzerland.
- MILLER, F. 1971: Pavouci — Araneida. *Klíč zvířeny ČSSR* **4**: 51–306.
- OXFORD, G. S. 1999: *Tegenaria ferruginea* (Panzer, 1804): an agelenid spider new to the British list. *Newsl. Br. arachnol. Soc.* **84**: 10.
- PANZER, G. W. F. 1804: Systematische Nomenclatur über weiland Herrn Dr Jacob Christian Schäffers natürlich ausgewählte Abbildungen regensburgischer Insekten. In J. C. Schäffer, *Icones Insectorum Ratisbonensium* **4**: 1–260. Erlangen.
- PLATEN, R., BLICK, T., BLISS, P., DROGLA, R., MALTEN, A., MARTENS, J., SACHER, P. & WUNDERLICH, J. 1995: Verzeichnis der Spinnentiere (excl. Acarida) Deutschlands (Arachnida: Araneida, Opilionida, Pseudoscorpionida). *Arachnol. Mitt. Sonderband* **1**: 1–55.
- ROBERTS, M. J. 1995: *Collins field guide: Spiders of Britain & Northern Europe*. 1–383. HarperCollins, London.
- SAUER, F. & WUNDERLICH, J. 1985: *Die schönsten Spinnen Europas*. Fauna-Verlag, Karlsfeld.
- SIMON, E. 1875: *Les Arachnides de France* **2**: 1–361. Paris.
- SIMON, E. 1937: *Les Arachnides de France* **6**(5): 979–1298. Paris.

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## The web of *Trogloneta granulum* Simon (Araneae, Mysmenidae)

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### Summary

Spiders of the species *Trogloneta granulum* Simon, 1922 build tiny, three-dimensional webs in their humid environment. The basic building components which make up the design of a finished web are: hub, radial threads, and transverse threads which interconnect the radial threads. All parts of the web, with the exception of the hub, are covered with droplets of sticky secretion. The inner transverse threads, laid close to the hub, connect all the radial threads, whilst the transverse peripheral threads connect only two or three radii. The structure of the web shows elements typical of the “symphytognathoid” families. No wrapping behaviour occurs during prey capture.

### Introduction

Neither the web nor the spinning activity of *Trogloneta granulum* Simon, 1922 has been described so far. This paper describes the structure of the web, with notes on prey capture, and provides data useful in the study of mutual phylogenetic relations of orb-weaving spiders and their relatives. *Trogloneta granulum* is a rare spider whose body length rarely exceeds 1 mm. It was originally described from a cave in southern France (Simon, 1922), and was reported from a second French cave by Fage (1931). So far the most detailed morphological study has been published by Thaler (1975), who found this species in the Austrian northeastern Alps

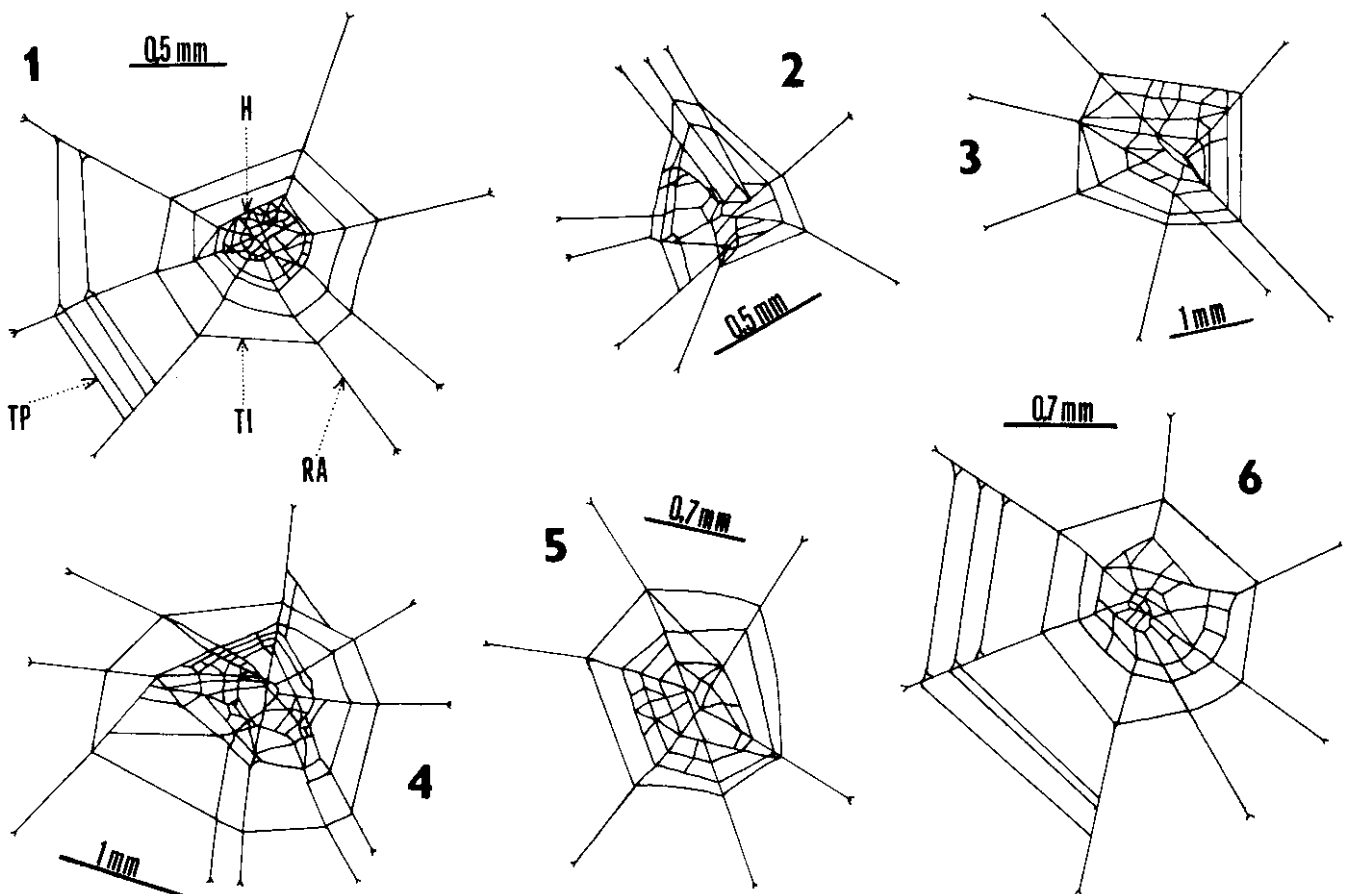
under stones deeply embedded in the forest floor, and as a preliminary classification he placed it in the family Symphytognathidae. Forster & Platnick (1977) transferred *Trogloneta* to the Mysmenidae. According to Růžička (1996) *T. granulum* is a very rare relict species found in stabilised stony debris without air circulation. Together with the Theridiosomatidae and Anapidae, both of the above-mentioned families form an important evolutionary line of so called “symphytognathoid” families (Coddington, 1990). In accordance with the cladistic classification formulated for the “Infraorder Araneomorphae”, the Anapidae and Symphytognathidae are closest to each other while all the “symphytognathoids” form part of the so-called “higher araneoids” (Coddington & Levi, 1991).

### Material and methods

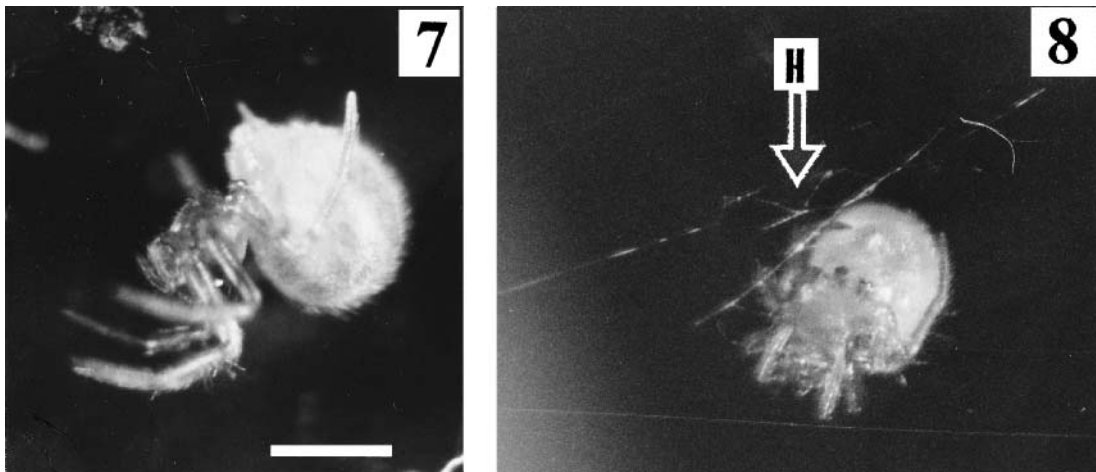
The observations were made exclusively in the laboratory between 4 April 1997 and 24 February 1998 and further in the period from 3 April to 22 May 1999, on a total of 41 specimens, consisting of 35 females and 6 males. Three of these males were collected as subadults and they reached maturity in the laboratory. All the studied material came from the locality of Vysoká Běta in the Blanský Les Protected Landscape Area (South Bohemia), where these spiders live among stony debris in a beech forest at an altitude of about 780 m. They build their tiny, to the naked eye practically invisible, webs directly on the surface of stones or on rotting leaves between stones at a depth of about 30–70 cm. The spiders were collected together with the wet leaves and placed in Petri dishes 100 mm in diameter and 15 mm high. They were later separated in the laboratory into groups of two or three in Petri dishes of the same dimensions or singly into small tube vials 50 mm long

and 9 mm in diameter, closed with moistened cotton-wool. Both types of containers were lined with black paper, which was shaped so as to simulate the surface of stones and leaves and which also enabled the spiders to orientate the central hub in any position. This substrate formed a contrasting background, suitable both for observation and for photographing the webs. The spiders were kept in a refrigerator at a temperature of 9–11°C. This temperature had been repeatedly measured in July and August at the above-mentioned locality during the collection of the spiders. A high relative humidity (97–100%), also corresponding to the natural environment, was maintained by wrapping wet filter papers around the outside of the Petri dishes and vials. Because of this high relative humidity and the condensation of water on the webs, it was not possible to distinguish explicitly droplets of water from droplets of sticky secretion. Therefore, some spiders were kept instead at 17–20°C and relative humidity 45–50% for a short period. After being kept for two or at most three days in these extreme conditions the spiders died. Normally, I removed the paper lining from the Petri dishes and vials at intervals of 3 to 5 days, exceptionally after longer intervals (maximum 16 days). Thus I acquired a comparative collection of webs built by the same as well as by different individuals on differently shaped surfaces,

and at the same time I prevented the excessive formation of mildew which always covered the moist paper after several days. The webs thus acquired were then kept in a deep-freeze. The web microstructure was studied with a stereoscopic microscope as well as by a scanning electron microscope. A videomicroscope equipped with a CCD (Charge Coupled Device) camera was also used to study the building of webs and the method of prey capture; this device enables the microscope image to be transmitted on a TV screen. *Trogloneta granulum* is a photophobic species which in the event of illumination moves away from the web and if disturbed repeatedly does not return to an incomplete web and does not finish the building. Therefore, when observing living spiders it was necessary to use so-called cold light (circular fibre illuminator KVO) and avoid overheating and consequential death of these very delicate animals. The food remains found in the remnants of webs in the natural environment consisted mainly of springtails (Collembola) and also tselontails (Protura). In the laboratory I fed the spiders with insects of a suitable size (*c.* 1–2 mm) caught in a sweepnet. During the winter, owing to lack of other, more suitable food, I inserted fruitflies (*Drosophila melanogaster* Meigen) into the thickly woven part of the peripheral mesh. A total of 78 completed webs were studied, 47 of them built in a



Figs. 1–6: Webs of *Trogloneta granulum*, from above. 1–5 Webs of adult females; 6 Web of subadult male. There are no two identical web patterns. The web design depends on the configuration of the substrate and on spatial conditions. Abbreviations: H=hub, RA=radial threads, TI=inner transverse threads, TP=transverse peripheral threads.



Figs. 7–8: *Trogloneta granulum*, adult female. **7** Side view; **8** Ventral view (H=hub). Scale line=0.5 mm.

humid environment (i.e. under conditions when water condensed on the threads) and 31 in an environment precluding water condensation.

## Results and discussion

### Web

The web of *T. granulum* as a whole is three-dimensional. Its shape, dimensions and the arrangement of the individual components depend on the available space, quality of the substrate, and distances apart of points at which the threads can be anchored by attachment discs (Figs. 1–6). Subadult males build webs of the same type as adult females (Fig. 6). Adult males, however, stayed on the webs they had built during their subadult stage and if they were removed from them they were not able to weave new webs. The design of a complete, finished web consists of three basic components: hub, radial threads, and transverse threads interconnecting the radial threads (Fig. 1). Threads of peripheral mesh (see below) appear later on the periphery and in the immediate vicinity of older webs, outside the frame (from the 4th or 5th day).

The hub is oriented mostly horizontally (Fig. 9). I have never observed any hub in a completely vertical position. The diameter of this part of the web varied in the range of 0.5–1.0 mm and it did not exceed the length of a sitting spider. There are no two identical hub patterns, not even those woven by the same individual. The spider sits on the hub, waiting for prey, always with the dorsum directed downwards (Figs. 7, 8). Whitish puffs of silk are clearly visible in the hubs of completed webs (Fig. 9). These puffs are created by the accumulation of a larger or smaller mass of free spirally wound unstretched threads (Fig. 10). I believe that they are homologous with the “white specks” described by Eberhard (1987) at the centre of the hub in the web of *Patu* sp. (Symphytognathidae) and *Mysmena* sp. (Mysmenidae).

Radial threads (or radii) form the supporting system of the web. They are used for prey capture, and their vibrations signal to the spider sitting at the hub when prey contacts the web. In newly built webs each radial

thread consists of two filaments which are often clearly separated by an interstice (Fig. 11). However, in older webs the radii may be formed by several parallel filaments of various thickness joined together. The length of the radii represented about 2–6 times that of the diameter of the hub and their number varied from 6–11 (mean=8.6). The complete web of *T. granulum* is three-dimensional, especially owing to some of the radial threads which extend from the hub at an angle both upwards and downwards to anchoring points on the surface of objects. The attachment discs, by which the web threads and drag lines are attached to the ground, are very simple.

If we study the structure of the web from the centre to its periphery we can see transversely oriented threads which interconnect the radial threads (Fig. 1). Around the hub these are inner transverse threads which connect all the radii and are laid in the form of concentric circles, because of which the webs of *T. granulum* acquire the appearance of very small orbs of orb-weaving spiders of the family Araneidae. Distally there are other, transverse peripheral threads in completed webs; these, however, usually interconnect only two (exceptionally three)

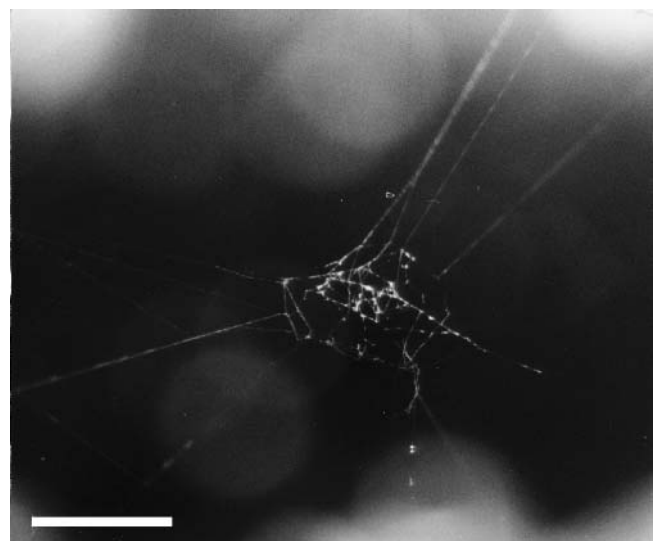
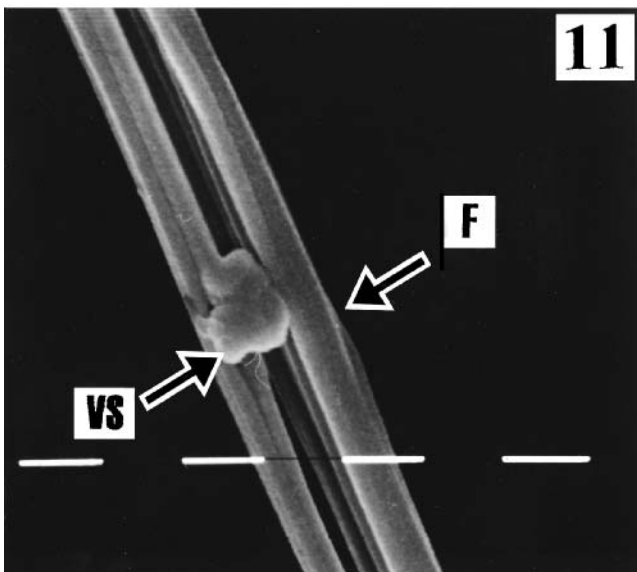
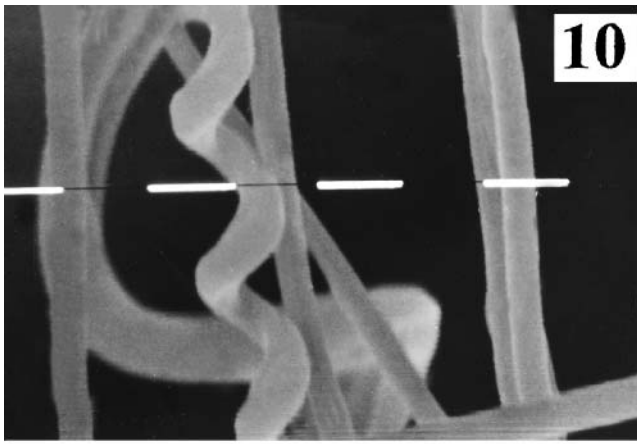


Fig. 9: Web of adult female *Trogloneta granulum*. Detail of hub with whitish puffs of silk (see Fig. 10). Scale line=0.5 mm.





Figs. 10–11: Details of threads. **10** Puffs of silk created by accumulation of a mass of unstretched spirally wound fibrils of silk fastened on hub threads; **11** Radial thread (F=filament, VS=dehydrated viscid secretion). Scale lines=1  $\mu$ m.

neighbouring radii. Their distance from the inner transverse threads is<sup>8</sup> conspicuous, especially in webs with relatively long radii. None of the webs shown in Figs. 1–6 was older than 75 hours. A tangle of threads of chaotic appearance appeared around the webs during later days (Fig. 12). The basis of this mesh consisted of the drag lines which the spiders trail behind themselves during their raids after prey, when moving around, and while searching the vicinity of the web. In laboratory conditions, when a larger number of individuals were kept in the enclosed space of the Petri dishes, a steadily thickening mesh interconnected the webs of individual spiders. In nature the distance between individuals of this species (tens of centimetres) is too great for such connections to occur. However, the mesh may connect several webs built by the same spider. In the confined space of the vials each of the eleven isolated females successively built 3–5 webs whose hubs were connected to each other by a tangle of threads, the density of which increased day by day. In such cases the spiders attacked insects caught anywhere in the space of the vials, and changed the hubs in which they waited for prey.

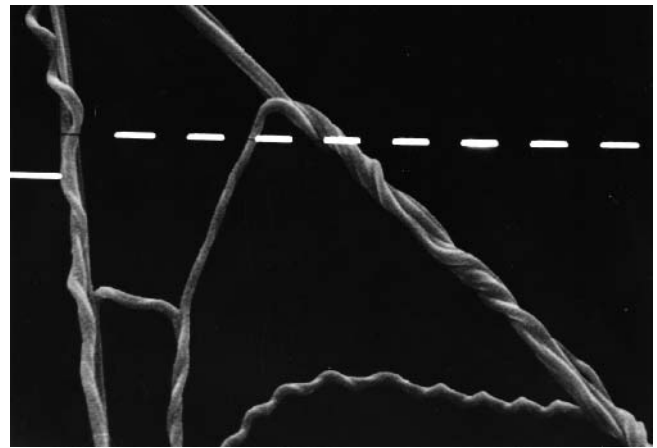


Fig. 12: Detail of threads forming peripheral mesh. Scale lines=1  $\mu$ m.

*Notes on prey capture*

A study of the webs woven under conditions with a lower relative humidity showed the presence of droplets of viscid secretion on all web components with the exception of the hub. These sticky droplets occur in a densely woven mesh. In the space of the Petri dishes or vials (i.e. in an unnatural habitat) prey capture was facilitated, in the case of newly built webs, by radial threads directed from the hub downwards, or by their distal, sticky parts, as well as by the transverse peripheral sticky threads which interconnect these distal ends of the radii (Fig. 13). Droplets of viscid secretion were present on the peripheral threads laid on later days, as well as in the early days. There is no doubt that condensed water, droplets of which can be found in any sector of the web (Fig. 13), also acts as an adhesive in the very humid microhabitat in which *Trogloneta* builds its webs.

The spider waits for prey on the central hub, suspended with the dorsum downwards. An insect adhering to the sticky threads of the web causes vibrations to

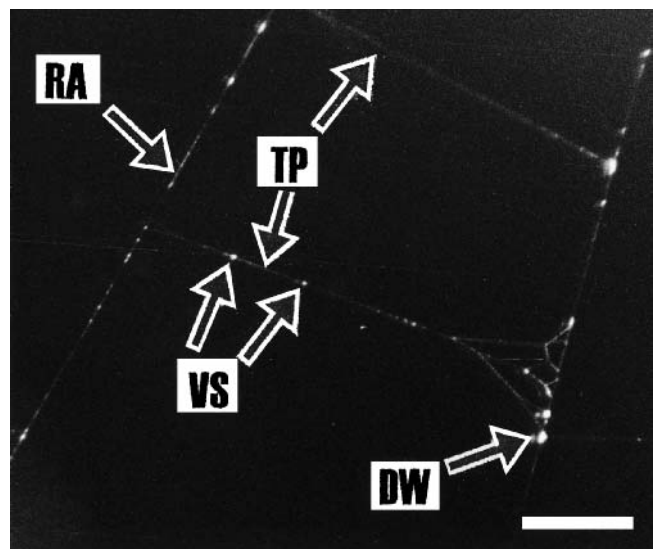


Fig. 13: Distribution of viscid secretion on threads of web of *Trogloneta granulum*. Abbreviations: RA=radial threads, TP=transverse peripheral threads, VS=droplets of viscid secretion, DW=larger, lustrous droplets of condensed water. Scale line=1 mm.

which the spider reacts with a fast movement (which resembles sliding along the threads) to the prey, which it bites with its chelicerae and disables by the released poison within 30 s to 3 min (depending on the volume or weight of the prey; 22 observations). I never observed wrapping behaviour comparable with the complete wrapping of the prey with silk, which occurs not only in orb-weavers of the family Araneidae but also in spiders of many other families. At the most it was possible to observe individual threads on the attacked insect or on its sucked-out remains; these threads did not form a complete silk cover. The immobilised insect is carried to the centre of the hub and sucked out there. The duration of sucking was 43–68 min in eleven cases when the size of the insect varied from 0.7–1.1 mm. The spider then removes the sucked-out insect from the web. The manner in which *T. granulum* manipulates prey closely resembles the behaviour of the spider *Comaroma simoni* Bertkau (Anapidae) described by Kropf (1990). If an insect gets caught in the tangle of threads of the peripheral mesh of an older web, it will also be attacked by *Trogloneta*. When I inserted with forceps into the mesh, specimens of *Drosophila melanogaster* with body size 3.0–3.5 mm, the spiders were able to kill them with their poison and later suck them out without carrying them to the centre of the web.

### Conclusions

The systematic position of any taxon cannot be determined without thorough analysis of all biological data. There are several works (Coddington, 1986, 1990; Eberhard, 1981, 1982, 1987) which demonstrate on the basis of a large amount of data that the spiders of all four symphytognathoid families (Theridiosomatidae, Anapidae, Mysmenidae and Symphytognathidae) modify the hubs of their webs in a unique way at the end of web construction and have a tendency to leave the primary radii in the web so that the resulting orbs are three-dimensional (Coddington, 1990). Wrap-attack during the capture of prey has not been proven in any of the studied species which belong to the symphytognathoid families (Coddington, 1990).

The results of this study of the construction of webs by *T. granulum* show the existence of the above-mentioned characters as well as the validity of these characters for the reconstruction of the evolution of

spider webs and spinning activity, and for investigating the phylogenetic relationships between orb-weaving spiders and their probable relatives. The hub, radii and transverse threads in the webs of *T. granulum* represent construction elements of considerable taxonomic importance.

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### References

- CODDINGTON, J. 1986: The monophyletic origin of the orb web. In W. A. Shear (ed.), *Spiders: webs, behavior and evolution*: 319–363. Stanford University Press.
- CODDINGTON, J. A. 1990: Ontogeny and homology in the male palpus of orb-weaving spiders and their relatives, with comments on phylogeny (Araneoclad: Araneoidea, Deinopoidea). *Smithson. Contr. Zool.* **496**: 1–52.
- CODDINGTON, J. A. & LEVI, H. W. 1991: Systematics and evolution of spiders (Araneae). *A. Rev. Ecol. Syst.* **22**: 565–592.
- EBERHARD, W. G. 1981: Construction behaviour and the distribution of tensions in orb webs. *Bull. Br. arachnol. Soc.* **5**: 189–204.
- EBERHARD, W. G. 1982: Behavioral characteristics for the higher classification of orb-weaving spiders. *Evolution* **36**: 1067–1095.
- EBERHARD, W. G. 1987: Web-building behavior of anapid, symphytognathid and mysmenid spiders (Araneae). *J. Arachnol.* **14**: 339–356.
- FAGE, L. 1931: Araneae. Cinquième série, précédé d'un essai sur l'évolution souterraine et son déterminisme. *Archs Zool. exp. gén.* **71**(2): 99–291.
- FORSTER, R. R. & PLATNICK N. I. 1977: A review of the spider family Symphytognathidae (Arachnida, Araneae). *Am. Mus. Novit.* **2619**: 1–29.
- KROPF, C. 1990: Web construction and prey capture of *Comaroma simoni* Bertkau (Araneae). *Acta zool. fenn.* **190**: 229–233.
- RŮŽIČKA, V. 1996: Spiders of stony debris in South Bohemian mountains. Pavouci kamenitých sutí jihočeských pohoří. *Silva Gabreta* **1**: 186–194.
- SIMON, E. 1922: Description de deux Arachnides cavernicoles du midi de la France. *Bull. Soc. ent. Fr.* **1922**(15): 199–200.
- THALER, K. 1975: *Trogloneta granulum* Simon, einere weitere Reliktart der Nordostalpen (Arachnida, Aranei, "Symphytognathidae"). *Revue suisse Zool.* **82**(2): 283–291.