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COPULATION WITH CONTRALATERAL INSERTION IN ENTELEGYNE SPIDERS (ARANEAE: ENTELEGYNAE: TETRAGNATHIDAE)

by

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ABSTRACT

Contralateral insertion, the application of the right male pedipalp to the left female genital opening is for the first time described in entelegyne spiders, *Leucauge mariana*, *Tetragnatha extensa*, *T. montana* and *Pachygnatha clercki* (Tetragnathidae). It is argued that the absence of a strict "lock-and-key" fit between male and female genitalia allowed the switch from the usual ipsilateral to contralateral insertion.

KEY WORDS: copulation, contralateral insertion, spider, Entelegynae, Tetragnathidae.

Since Gerhardt's (1921-1933) extensive observations of courtship and copulation it has been taken as certain that all entelegyne spiders show ipsilateral insertion during copulation: the right pedipalp is applied to the right side of the epigynum and inseminates the right spermatheca, and vice versa (GERTSCH, 1979: 93). Ipsilateral insertion has been observed in spiders with all kinds of copulatory positions. This led VON HELVERSEN (1976) to argue that this is a highly conservative character which cannot easily be changed once it is established due to the "lock-and-key" like fit of male and female genitalic structures. Two apparent contradictions to this pattern were reinvestigated by EXLINE & WHITCOMB (1965) and HUBER (1995), and in both cases (*Peucetia*: Oxyopidae; *Dictyna*: Dictynidae) it came out that right bulbs are inserted into right female genital openings.

This note reports for the first time unequivocally contralateral insertion in four entelegyne spiders, the Central American *Leucauge mariana*, and the European *Tetragnatha extensa*, *T. montana* and *Pachygnatha clercki* (Tetragnathidae). In *L. mariana*, more than 30 pairs have been observed with a dissecting microscope during copulation (EBERHARD & HUBER, in prep.).

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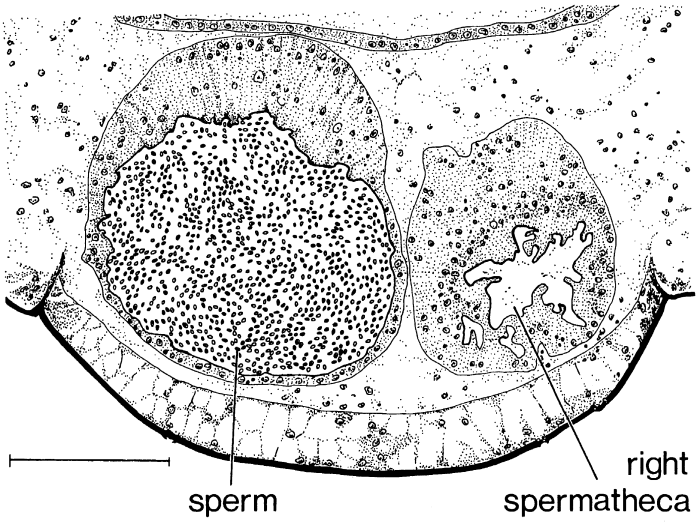

Fig. 1. Drawing of a semithin (1 μm) cross section through the vulva of a *Leucauge mariana* female, in which the left spermatheca contains sperm after the application of only the right male genital bulb. Scale bar: 0.1 mm.

In one pair the male was separated from the female after the first insertion (with the right pedipalp), and serial sections of the female vulva clearly revealed sperm only in the left spermatheca (fig. 1). Pairs of *T. extensa*, *T. montana* and *P. clercki* were freeze fixed during copulation with an industrial medium used for testing electronics ("Givrant 50" from Siceront KF, France) and then freeze dried. Whole mounts clearly revealed that right emboli were in contact with left spermathecae, and vice versa (fig. 2).

Although many entelegynes have been investigated, we know of only four tetragnathid species (including nephilines, metines and tetragnathines) in which ipsilateral insertion was said to occur: *Tetragnatha extensa* Linné (BERTKAU, 1875; GERHARDT, 1923); *Pachygnatha clercki* Sundevall (GERHARDT, 1923) (the same author observed some other *Tetragnatha* and *Pachygnatha* species, but only states that the mechanism of copulation is the same, without explicitely dwelling on the mode of insertion); *Meta merianae* C. L. Koch (GERHARDT, 1927); and *Nephila clavipes* (Linné) (HIGGINS, 1989). Both Bertkau and Gerhardt were obviously wrong regarding this detail in *Tetragnatha* and *Pachygnatha*. GERHARDT's (1927) observation on *Meta* needs confirmation. HIGGINS (1989) reported that "three experimental matings with right-side castrated males resulted in females with the right spermathecal sac virgin and the left inseminated". More data on other

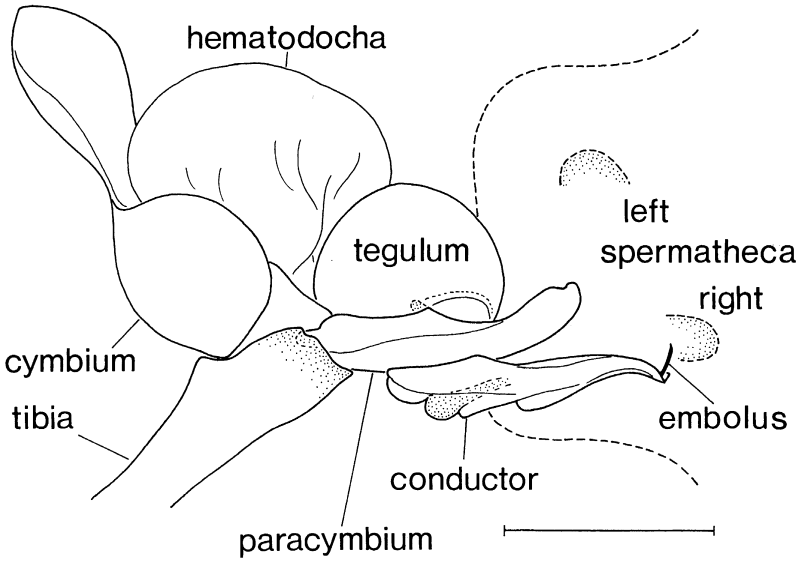

Fig. 2. Genitalia of *Tetragnatha montana* in functional contact (whole mount, vulva in dorsal view). The left male pedipalp is applied to the right female spermatheca. Scale bar: 0.5 mm.

genera are needed to evaluate the distribution of contralateral insertion in tetragnathids.

The force of VON HELVERSEN's (1976) argument that once ipsilateral insertion is established it cannot easily be changed, is greater for genitalia that have a more elaborate mechanical fit between male and female. In a sense our data confirm his ideas because there is almost no "lock-and-key" fit at all between males and females in the three species investigated. In *Leucauge mariana*, behavioural observations (EBERHARD & HUBER, in prep.) suggest that only the thread-like embolus is inserted into the soft entrance to the female genital system. There is no other structure (perhaps with the exception of some hairs) that serves to anchor the bulb appropriately to the female during hematodochal expansions. In *T. extensa*, *T. montana* and *P. clercki* both the conductor and the paracymbium are inserted into the vulva. The tip of the paracymbium is pressed against the soft dorsal membrane of the vulva in a median position. The conductor reaches to the entrance of the spermatheca, but is not locked in a "lock-and-key" fashion. Thus, there is no major obstacle to a switch from ipsi- to contralateral insertion and phylogenetic inferences should be made with caution.

Two additional findings should be briefly mentioned in this context. First, *Leucauge mariana* males climb on top of the threads to spin the sperm webs and to deposit the sperm, whereas *Tetragnatha* and *Pachygnatha* spin and ejaculate upside down (GERHARDT, 1923, 1924, 1928). The same difference appears to separate linyphiids from micryphantids (VAN HELSDINGEN, 1983). Second, sperm uptake in *Leucauge* follows the widespread pattern of alternately dipping the two bulbs into the drop of sperm. In *Tetragnatha* and *Pachygnatha*, both bulbs are simultaneously dipped into the drop (GERHARDT, 1923, 1924, 1928).

In conclusion, comparisons of courtship and mating behaviour which have been largely neglected since the promising efforts of Gerhardt, may give valuable data for understanding the evolution and phylogeny of spiders.

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