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The retrolateral tibial apophysis in spiders—shaped by sexual selection?

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The functional significance of the retrolateral tibial apophysis (rta) on the male pedipalps in four spider species with different mating positions is investigated with the help of histological serial sections prepared after freeze-fixing copulating pairs with liquid nitrogen. The results of this study, as well as most data in previous works, suggest that the rta is mostly used to fix the male pedipalp to the female epigyne in order to ensure the intromission of the sperm transferring embolus. This is in accordance with the female choice hypothesis on genitalia which predicts that species-specific genial structures should directly or indirectly contact the female during copulation and thus be shaped by sexual selection.

ADDITIONAL KEY WORDS:—genital mechanics - freeze-fixation - species-specificity.

CONTENTS

INTRODUCTION

A retrolateral tibial apophysis (rta) can be found on the pedipalps of adult male spiders in a great number of families. Coddington & Levi (1991) considered it to be the essential synapomorphy of about 38 entelegyne families (rta-clade) comprising about 18 000 named species. These authors quote only two papers as to the function of the rta: Bennett (1988) and Sierwald & Coddington (1988). In both papers, the rta is thought to stabilize the expanded genital bulb internally during copulation.

Theoretical considerations, however, led to the prediction that the rta contacts

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the female during copulation: according to Eberhard (1985), sexual selection is the principal cause for species-specificity in genitalia. The rta is highly species-specific and therefore figured in many taxonomic studies and identification guides (e.g. Heimer & Nentwig, 1991). Thus it may be predicted that physical contact (direct or indirect via other species-specific structures) with the female during copulation should be given as a prerequisite for mate choice.

The present paper presents the results on four species that exhibit the four dominant mating positions within the rta-clade and provides for the first time a summary and discussion of previous data on the function of the rta.

MATERIAL AND METHODS

Dictyna uncinata Thorell, 1856 (Dictynidae), *Misumenops tricuspidatus* (Fabricius, 1775) (Thomisidae) and *Philodromus aureolus* (Clerck, 1757) (Philodromidae) were collected as penultimates and adults on the Donauinsel in Vienna, Austria, during May. *Euophrys lanigera* (Simon, 1871) (Salticidae) was found on the terrace of the Zoological Institute, Vienna, in April and May. Males were introduced to the females in the laboratory and shock-fixed with liquid nitrogen during copulation at the moment of maximum hematodochal expansion. Histological serial sections of the coupled genital organs were prepared on an ultramicrotome after embedding in ERL-4206 epoxy resin (Huber, 1993). The individual genital organs were additionally investigated in the scanning electron microscope (Jeol JSM-35CF).

RESULTS

This paper is concerned primarily with the rta. However, as there are few works that treat genital mechanics in spiders, data on functions other than the rta are also briefly discussed.

Dictyna uncinata

Figure 1A shows the mating position of *D. uncinata*. The male approaches the female anteriorly and inserts his genital bulbs one at a time. First, the tip of the rta, which has two distinctive cone-shaped structures (‘ctenidia’; Figs 1B, 2A) is pressed into a lateral cuticular fold (‘fovea’; f in Fig. 2B) on the female opisthosoma (Figs 1E, 10). Then the tip of the conductor, which bears small cuticular denticles (Fig. 1D), is inserted into the membranous genital atrium of the female. Through the groove of the conductor (basal part shown in Fig. 1C) the embolus is pushed forward by the expanding and rotating hematodocha into the female insemination duct. Glands in the conductor open into the conductorial groove that bears and guides the embolus (Fig. 1F). The tip of the conductor is inserted into the genital atrium up to a highly sclerotized part with a diameter of only about 3.5 µm (asterisk in Fig. 2B) that only allows the embolus to pass.

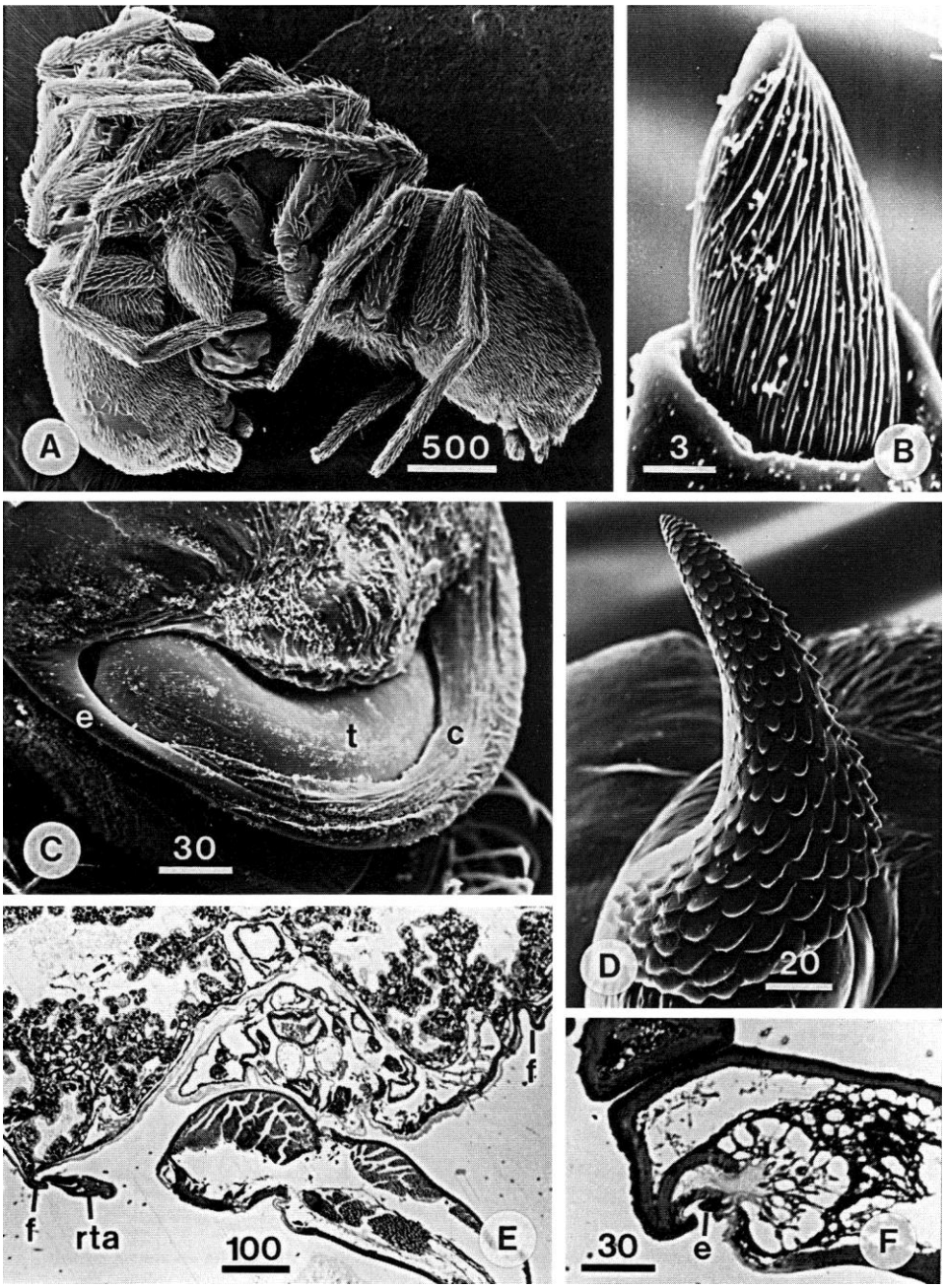
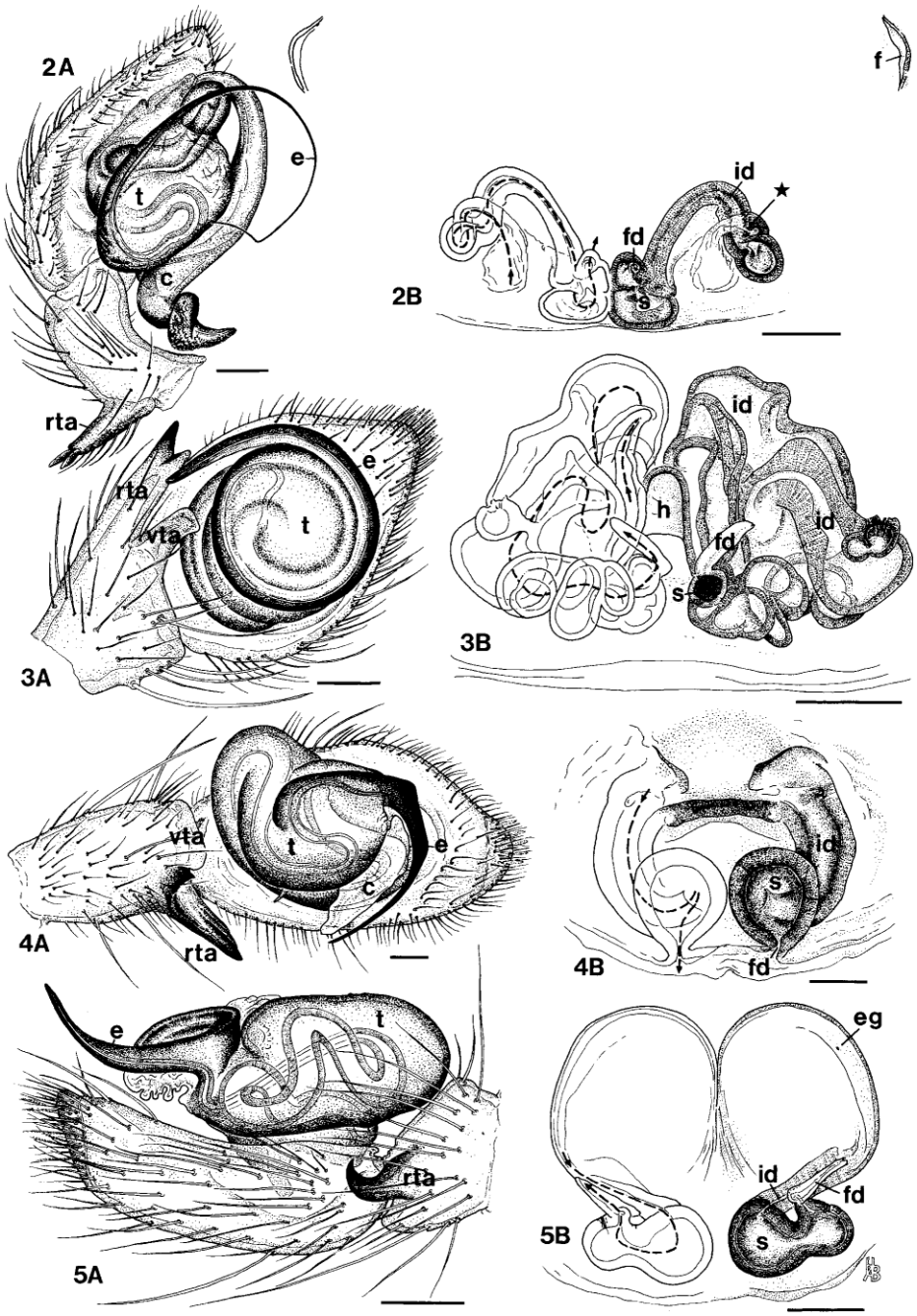


Figure 1. *D. uncinata*. A, Mating position, pair fixed in copula with liquid nitrogen, female on left side, SEM. B, One of the two 'ctenidia' at the tip of the male rta, SEM. C, Embolus (e) and conductor (c) in natural position, t = tegulum, SEM. D, Tip of the conductor with denticles, SEM. E, Semithin section, showing the position of the rta in the 'fovea' (f) during copulation. F, Semithin section, showing the embolus (e) in the conductorial groove and the glands opening into this groove. Scale bars in μm.



Figures 2-5. KOH preparations of the genital bulbs and vulvae of the species examined in this study. Scale bars = 0.1 mm. Broken lines show the course of sperm in the female vulvae. Fig. 2. *D. uncinata*. A, Left bulb, prolateral aspect; the embolus is pulled out of the conductorial groove; B, Vulva, dorsal aspect, with opisthosomal folds (f); asterisk marks sclerotized part up to which the conductor is inserted. Fig. 3. *M. tricuspidatus*. A, Right bulb, ventral aspect; B, Vulva, dorsal aspect. Fig. 4. *P. aureolus*. A, Left bulb, ventral aspect; B, Vulva, dorsal aspect. Fig. 5. *E. lanigera*. A, Right bulb, retrolateral aspect; B, Vulva, dorsal aspect. Further abbreviations: c = conductor; e = embolus; eg = epigyneal groove; fd = fertilization duct; h = hood of female epigyne; id = insemination duct; s = spermatheca; t = tegulum; vta = ventral tibial apophysis.

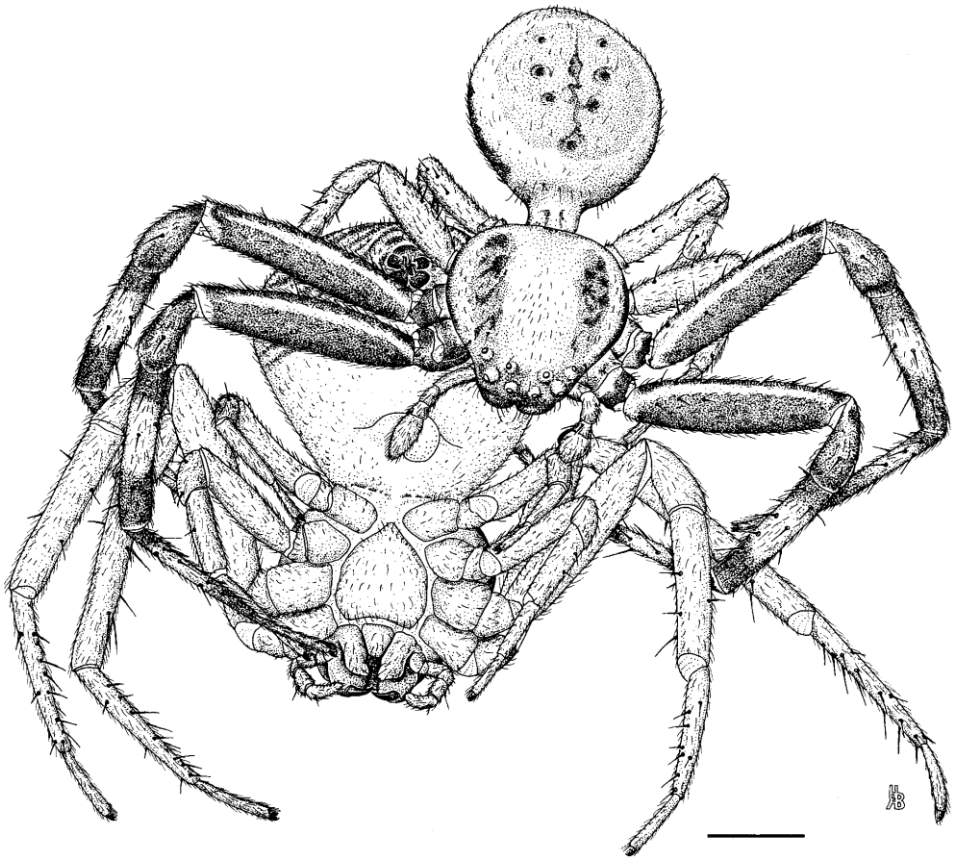


Figure 6. *M. tricuspidatus*. Mating position, drawn from a pair fixed in copula with liquid nitrogen. Scale bar = 1 mm.

Misumenops tricuspidatus

This species shows a mating position typical for many crab spiders (Fig. 6). As in *D. uncinata*, the rta is the first male structure that establishes a well defined contact with the female. The more pointed and sclerotized tip of the rta (Figs 3A, 7A) is inserted into a median hood of the epigyne (h in Figs 3B, 11). Many single slit sensilla are situated at the basis of the rta (also true of the two following species). The ventral tibial apophysis (vta) is hooked into a spiral groove of the tegulum (Fig. 7B) and thus guides the rotation of the tegulum produced by hematodochal expansion. This rotation drives the flexible embolus into the female insemination duct without the help of a conductor.

Philodromus aureolus

Philodromids show an intermediate mating position between that of *Misumenops* and that shown by most secondary hunting spiders (von Helversen, 1976). Exact positioning of the male pedipalp in relation to the copulatory orifice of the female is accomplished by the rta whose long spur (Fig. 4A) is inserted into

the epigastric furrow (indicated by the posterior line in Fig. 4B). The expanding hematodocha rotates the tegulum, thus driving the embolus into and through the insemination duct to the spherical spermatheca (Fig. 4B).

Rotation is apparently stopped by the membranous ‘conductor’ that finally becomes arrested by contact with the ventral tibial apophysis. It is unclear whether this ‘conductor’ also assists the introduction of the embolus into the insemination duct. The small spur at the tegulum (Fig. 8A) has no apparent function during copulation.

Figure 8B shows a secretory plug in the genital atrium of a mated female. In histological sections as well as in SEM-micrographs of broken plugs (Fig. 8C) these turned out to consist of sperm and secretions.

Eyophrys lanigera

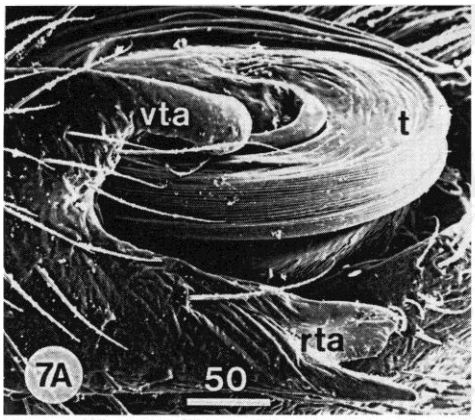
In a mating position typical for most secondary hunting spiders (von Helversen, 1976), the male expands the genital bulb after locking the pedipalp to the female epigyne. Again, locking involves the rta (Fig. 5A), which hooks into a membranous fold in the epigastric furrow (Figs 9C, 13). The inner surface of the curved rta is sculptured (Fig. 9A), presumably increasing the frictional resistance when hooked into the female. Expansion of the hematodocha rotates the bulbal sclerites and inserts the embolus into the insemination duct without the help of a conductor. The large epigyneal grooves (e.g. Figs 5B, 9B) probably function as funnels that receive and guide the rotating embolic division during hematodochal expansion.

DISCUSSION

Function of the rta in the genus Dictyna

Although genital morphology as well as mating behaviour are quite uniform among *Dictyna*-species (Chamberlin & Gertsch, 1958; Starr, 1988), data on the exact functioning of the rta are contradictory. Karpinski (1882) notes that in *D. arundinacea* (sub *D. benigna*) the rta of the right male pedipalp is locked into the right female genital orifice whilst the bulb is inserted into the left orifice, and vice versa. Billaudelle (1957) speculates that in *D. volucripes*, the rta of a given side is hooked into any of the two genital orifices and loses contact with it when the bulb is inserted. Both bulbs are assumed to be capable of being inserted into the same female genital opening. However, as expected from previous work (e.g. von Helversen, 1976) the present study confirms that, on the contrary, also in *Dictyna* right bulbs are inserted into right female copulatory openings. This is apparently a general rule for Entelegynae, and Karpinski’s as well as Billaudelle’s results are doubted in this respect.

Figures 7-9. Fig. 7. *M. tricuspidatus*. A, Male tibial apophyses, SEM; B, Semithin section of the male copulatory organ in copula. The vta is hooked into a groove of the tegulum. Fig. 8. *P. aureolus*. A, Spine on the male genital bulb, SEM; B, Female epigyne with epigyneal plug, SEM; C, Detail of epigyneal plug, SEM. Fig. 9. *E. lanigera*. A, rta with single slit sensilla at the basis, SEM; B, Epigyne, SEM; C, Semithin section, showing the tip of the male rta in a fold of the female epigastric furrow. Abbreviations: eg = epigyneal groove; id = insemination duct; s = spermatheca; t = tegulum; vta = ventral tibial apophysis. Scale bars in μm.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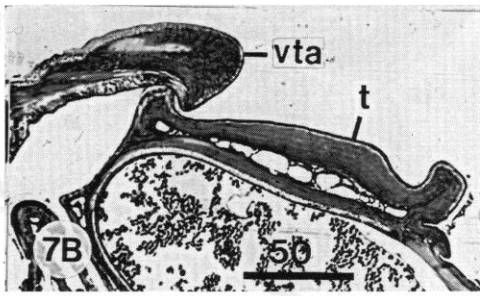
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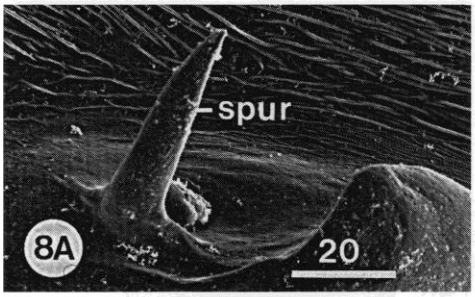
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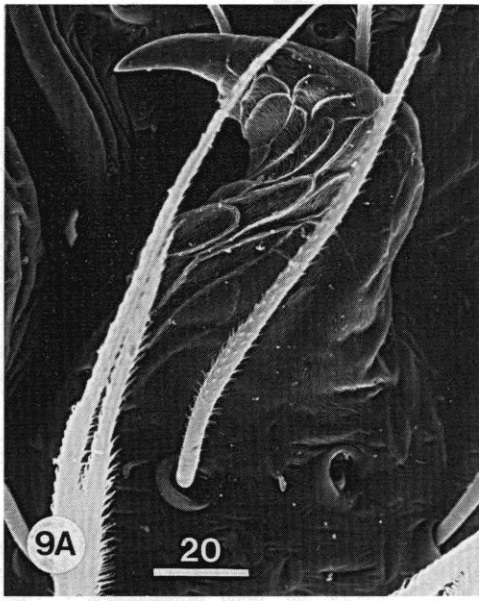
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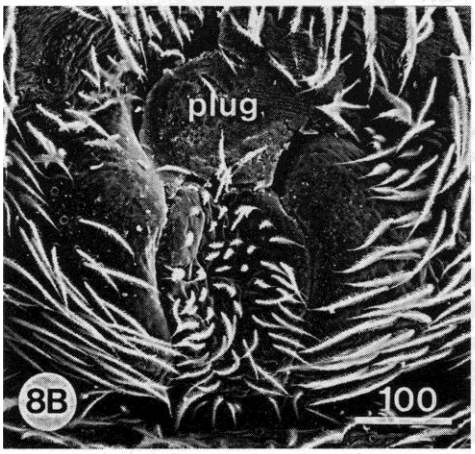
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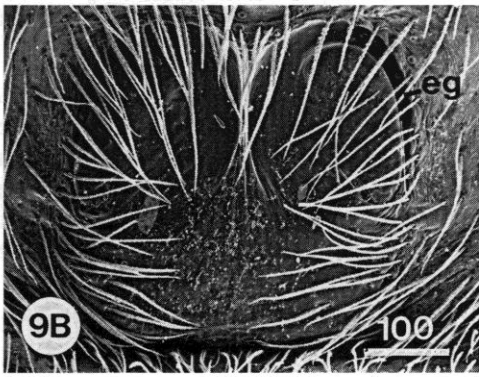
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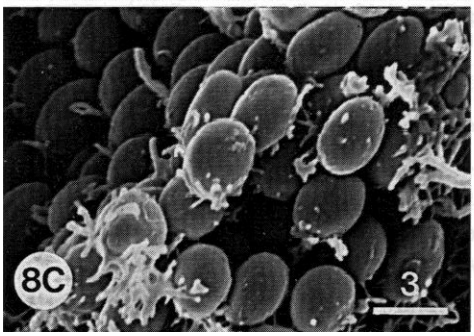
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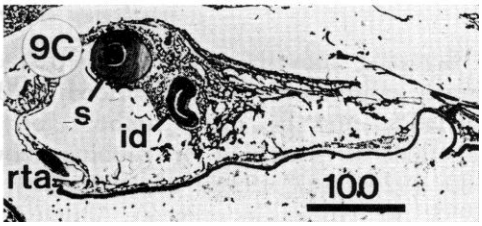
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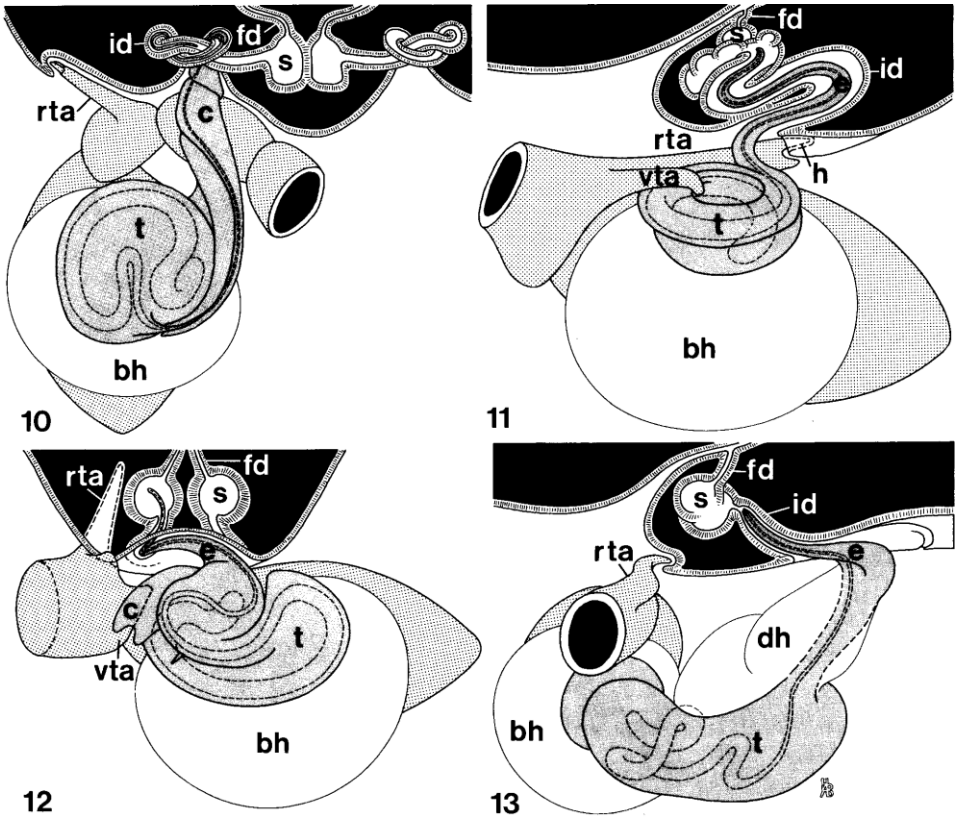

Figures 10-13. Schematic representation of the copulatory organs (right bulb, right vulva) in functional contact. Fig. 10. *D. uncinata*, frontal view. Fig. 11. *M. tricuspidatus*, lateral view. Fig. 12. *P. aureolus*, frontal view. Fig. 13. *E. lanigera*, lateral view. Abbreviations: bh = basal hematodocha; c = conductor; dh = distal hematodocha; e = embolus; fd = fertilization duct; h = hood of female epigyne; id = insemination duct; s = spermatheca; t = tegulum; vta = ventral tibial apophysis.

The function of the rta as shown for *D. uncinata* may probably be generalized for most species of the genus. Chamberlin & Gertsch (1958: 49) note that the presence of 'ctenidia' at the male tibial apophysis and of 'foveae' on the female opisthosoma distinguish the *Dictyna*-species 'from all related types'. Only the *spatula* group lacks 'ctenidia', and just in this group there are no 'foveae'. In the *longispina* group, where the male rta is extremely long, the 'foveae' are situated farthest away from the genital atria. A functional correlation of these structures is therefore predicted for the whole genus.

Significance of scraping movements

Scraping movements of the retrolateral side of the pedipalp against the female opisthosoma were described by Billaudelle (1957) and Jackson (1979) for dictynids, and by many authors for other families of the rta-clade (often described as 'searching' or 'rubbing' movements: e.g. Gerhardt, 1921: 132, 175, 180; 1924a: 107; 1924b: 25; 1928: 614; 1933: 29; Bristowe, 1926: 127; Gering, 1953: 56; Huber, in press c). Although stimulation cannot be excluded and is

not an exclusive alternative, I will argue that the main function of this behaviour is simply to find the female 'lock'. As soon as this is achieved, the genital bulb has an exactly defined position in relation to the female copulatory orifice so that a simple mechanical sequence of hydropneumatic movements introduces the embolus into the insemination duct.

In *P. aureolus*, *M. tricuspidatus* and *E. lanigera*, the large number of slit sensilla at the basis of the rta probably explains how male spiders realize that the pedipalp has assumed a correct position. The same sensory function could be fulfilled by the 'ctenidia' (sensilla?) on the tip of the rta in *Dictyna* species (there are no slit sensilla at the basis of the *D. uncinata* rta!).

Bulbal glands and mating plugs

Bulbal glands that do not open into the sperm duct have so far only been described in *Amaurobius fenestralis* (Suhm, 1992). In this species they are supposed to produce a secretory plug that closes the female genital opening and probably serves in paternity assurance. In *D. uncinata*, the glands that open into the conductorial groove might rather serve in the lubrication of this duct that narrows down to 3.5 µm, which is also the diameter of the distal part of the embolus. No mating plug could be found in mated *D. uncinata* females.

No functional interpretation can be given in respect to the secretory 'plug' found in mated females of *P. aureolus*. Such plugs have been found in a great variety of spiders (Austad, 1984) and have often been interpreted as devices of paternity assurance. However, detailed investigations would be needed to show whether such plugs really can influence further insemination attempts (Jackson, 1980; Masumoto, 1993) or whether alternative hypotheses should be considered (e.g. simply superfluous sperm; protection against desiccation of sperm in the spermatheca; protection against flowout of sperm).

Rta-function, an overview

Table 1 presents an overview of papers dealing with or mentioning the function of the rta. Zodariidae are included although their position within the rta-clade may not be correct (Coddington & Levi, 1991, placed them among 'lower entelegynes' with uncertain affinities; but see Lehtinen, 1967).

In most species/genera where the rta is supposed to arrest the male bulb internally during copulation, data are rather doubtful for methodical reasons: Harm (1935), Weiss (1979, 1982, 1989) and Bennett (1988) inferred the function from the investigation of artificially expanded genital bulbs. It has been documented in *Nesticus cellulanus* (Huber, in press a) that artificial expansion can result in completely different spatial relations of the bulbal sclerites than natural expansion during copulation. A similar movement of the distal bulbal sclerites towards the rta during artificial expansion occurred in most representatives of the rta-clade investigated by the present author in this respect (*E. lanigera*, *M. tricuspidatus*, *P. aureolus*, *Histopona torpida*, *Clubiona pallidula*; see also Shear, 1967). This suggested a functional correlation of these structures. During actual copulation, however, the rta is already fixed to the epigyne when the bulb is expanded, and the bulbal sclerites are primarily guided and stabilized by female structures. The same criticism might be applied to Sierwald & Coddington

TABLE 1. Overview of works mentioning the function of the retrolateral tibial apophysis in spiders

Taxon	Author	rta fixes the male pedipalp to the female	rta arrests the genital bulb internally
Dictynidae			
Dictyna arundinacea (Linnaeus, 1758)	Karpinski, 1882 (sub *D. benigna*)	X	
Dictyna civica (H. Lucas, 1850)	Billaudelle, 1957	X	
Dictyna uncinata Thorell, 1856	This paper	X	
Salticidae			
Evarcha arcuata (Clerck, 1757)	Harm, 1935 (sub *E. marcgravi*)		X
Phlegra spp.	Weiss, 1979		X
Sitticus pubescens (Fabricius, 1775)	Gerhardt, 1921 (sub *Attus p.*)	X	
Euophrys lanigera (Simon, 1871)	This paper	X	
Thomisidae			
Heriaeus spp.	Loerbroks, 1983	X	
Misumena vatia (Clerck, 1757)	Loerbroks, 1984	X	
Misumenops tricuspidatus (Fabricius, 1775)	This paper	X	
Xysticus lanio C. L. Koch, 1824	Bristowe, 1931	X	
Heteropodidae			
'*Sparassus* sp.'	Gerhardt, 1928	X	
Eusparassus walckenaeri (Audouin, 1826)	Gerhardt, 1933	X	
Micrommata virescens (Clerck, 1757)	Bristowe, 1926	X	
	Gerhardt, 1925	X	
Philodromidae			
Philodromus aureoles (Clerck, 1757)	Gerhardt, 1923	X	
	Bristowe, 1929	X	
	This paper	X	

(1988) where the function of the rta is inferred from a genital bulb fixed *in copula*, but sprung away from the epigyne.

When these cases of doubtful internal arresting are removed, there remain almost only species in which the rta is brought into contact with the female. All but one of these works are based on observations of copulation (exception: Loerbroks, 1983) and are therefore reliable from a methodological point of view. Many different possibilities of functional correlation have evolved, which may be due in part to the great variety of mating positions, but the principal function always seems to be the correct positioning of the pedipalp prior to hematodochal expansion. Gerhardt (1921: 201, 1923: 126) and Bristowe (1929: 342) have expressed the idea that this is the general function of the rta. Exceptions were found in Agelenidae (Osterloh, 1922; Gering, 1953; Huber, in press b), and in two of these cases (*Agelena gracilens* and *Histopona torpida*) it is the patellar apophysis that serves the function of positioning the pedipalp.

These results are in accordance with the prediction that highly species-specific

TABLE 1.—*continued*

Taxon	Author	rta fixes the male pedipalp to the female	rta arrests the genital bulb internally
Agelenidae			
Agelena gracilens C. L. Koch, 1841	Osterloh, 1922 (sub *A. similis*)		X
Agelenopsis spp.	Gering, 1953		X
Textrix denticulata (Olivier, 1789)	Huber, in press b	X	
Histopona torpida (C. L. Koch, 1834)	Gerhardt, 1927	X	
	Huber, in press b		X(?)
Cybaeidae			
Cybaeota nana Chamberlin & Ivie, 1937	Bennett, 1988		X
Clubionidae			
Clubiona germanica Thorell, 1870	Gerhardt, 1923	X	
Clubiona pallidula (Clerck, 1757)	Huber, in press c	X	
Clubiona brevipes Blackwall, 1841	Wiehle, 1961	X(?)	
Cheiracanthium inclusum (Hentz, 1847)	Gering, 1953	X	
Anyphaenidae			
Anyphaena accentuata (Walckenaer, 1802)	Huber, in press c	X	
Pisauridae			
Dolomedes tenebrosus Hentz, 1843	Sierwald & Coddington, 1988		X
Oxyopidae			
Oxyopes heterophthalmus Latreille, 1804	Gerhardt, 1933	X	
Oxyopes spp.	Weiss, 1989		X
Zodariidae			
Zodarion aurorae Weiss, 1982	Weiss, 1982		X

genital structures like the rta have been shaped by sexual selection and thus contact the female during copulation (at least in our case, where visual perception of the rta can be ruled out). The evolutionary mechanisms by which sexual selection might affect genital morphology (female choice by stimulations and/or mate choice by mechanical fit) have recently been outlined by Eberhard (1985) and Huber (in press d).

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