

## Genital morphology and copulatory mechanics in *Anyphaena accentuata* (Anyphaenidae) and *Clubiona pallidula* (Clubionidae: Araneae)

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(With 3 plates and 5 figures in the text)

The spiders *Anyphaena accentuata* (Walckenaer, 1802) and *Clubiona pallidula* (Clerck, 1757) are investigated with respect to the functional morphology of their genital organs. Copulatory mechanics is directly analysed by freeze-fixation of copulating pairs and subsequent preparation of serial sections of the clasped genitalia. Data on courtship behaviour are included. Beyond the discussion of specific findings, the general usefulness of copulatory mechanics for phylogenetic research and the supposed function of male genitalia as stimulators are addressed.

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### Introduction

When arachnologists became aware of the high complexity of spider genitalia at the end of the last century, it was generally thought that genitalia would offer a large number of useful characters not only for taxonomic but also for phylogenetic research. Eventually, however, it became clear that genital structures are often difficult to homologies (see e.g. Lehtinen, 1978;

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Coddington, 1990; Sierwald, 1990) and convergences occur abundantly. Therefore, a number of authors proposed the use of the function in addition to descriptive morphology (e.g. van Helsdingen, 1969; Grasshoff, 1975; Lehtinen, 1978; Weiss, 1981, 1982; Weiss & Heimer, 1982). However, due to technical difficulties, a very few spider species have been investigated in detail with respect to the functional morphology of their copulatory organs. The frequently applied method of artificial expansion has turned out to provide rather doubtful conclusions on actual function (Huber, In press). Therefore, a new method that combines freeze-fixation of the copulating spiders with subsequent preparation of histological serial sections of the clasped copulatory organs, was applied to provide new data for the evaluation of functional mechanics for phylogenetic research.

These data also allow new insights into the general function of copulatory organs. In addition to the primary function of sperm transfer, genitalia have also been considered to act as stimulators that might influence female choice (Thornhill, 1983; Eberhard, 1985). This was proposed as one possible cause for the species-specificity in genitalia (Eberhard, 1985). Although functional morphology cannot directly show phenomena of sexual selection, it may help to investigate the possibility of certain mechanisms that are considered to be involved. Thus, for example, the investigation of the female structures that actually come into contact with the male genital structures during copulation should help to evaluate the possible significance of stimulation for internal courtship and cryptic female choice. A prerequisite of such studies, however, is the detailed knowledge of copulatory mechanics.

In the present paper, representatives of the presumably closely related (Coddington & Levi, 1991) families Anyphaenidae and Clubionidae are investigated with respect to the function of their genitalia. On the basis of these results, the usefulness of copulatory mechanics in phylogenetic research as well as the significance of genital stimulation during copulation can be addressed.

## Materials and methods

*Anyphaena accentuata* (Walckenaer, 1802) was collected in a mixed forest in the Mühlviertel near Linz, Upper-Austria. Until mid-December, the spiders were found at night in great numbers on the bark of beech and pine trees. During winter they occurred under the bark of dead trees. *Clubiona pallidula* (Clerck, 1757) was found under tree barks in March in the Prater-woods and on the Donauinsel in Vienna.

The penultimate-stage spiders of both species were reared individually (for housing conditions and feeding see Huber, 1993) until reaching maturity.

Some days (2-16) after the final moult of the female, a male was introduced into her container. Courtship and copulation of some pairs were observed under the dissection microscope and recorded.

Seven pairs of *Anyphaena accentuata* and three pairs of *Clubiona pallidula* were shock-fixed during copulation. This was done either by immersing the copulating spiders (in their container) into liquid nitrogen (-196°C) or by pouring it over them. Subsequently, the pair was transferred into cold ethanol (80%, -25°C) and kept at that temperature for about 3 weeks. The copulatory organs were then dissected from the animals, dehydrated and embedded in ERL-4206 epoxy resin after vacuum impregnation. Historical serial sections (1 µm) of the clasped copulatory organs were prepared on an ultramicrotome (Reichert OmU3) with diamond knives. The sections were stained with a mixture of azure 2 (1%) and methylene blue (1%) in an aqueous borax solution (1%) at 80°C for about 10 sec.

Since nitrogen fixation caused some damage to the soft tissues, the copulatory organs were also fixed in Duboscq-Brasil solution (Romeis, 1989). Embedding, sectioning and staining was as above.

The copulatory organs were further investigated with the scanning electron microscope (Jeol JSM-35CF), both individually and in functional contact (one pair of each species). Classical techniques like clearing the genital organs in KOH (10%, 80°C, 60 min) or concentrated lactic acid (80°C, 15 min) and expanding them

artificially (Shear, 1967) were also applied. Reconstruction of the serial sections and volume estimations were aided by a computer program (PC-3D).

## Results

### *Anyphaena accentuata*

#### *Male copulatory organ (Fig. 1)*

The conformation of the male copulatory organ, the genital bulb, is in accordance with the general condition in entelegyne spiders. It is situated at the cymbium which is the distal pedipalpal segment. A spirally folded, membranous sac, the basal hematodocha, connects the cymbium to the basal sclerite of the bulb, the subtegulum. This is distally connected to the tegulum by a 'joint' on one side, and a membrane (median hematodocha) on the other side. The tegulum is provided with several processes: a hook-shaped conductor (for discussion of terms see below), a median apophysis that is provided distally with a great number of small teeth (Plate Ib) and an embolus (Plate Ic). The actual sperm containing organ, the sperm duct, is a blind tube that originates in the subtegulum, passes through the tegulum into the embolus and opens at its tip. Before entering into the embolus, the sperm duct passes through a highly complicated system of cuticular folds inside the tegulum (Plate Iib). Glands open into the sperm duct along its full length, except in the embolus. Sperm duct volume is about  $6 \times 10^6 \mu\text{m}^3$ .

In the male pedipalp, femur and tibia are provided with conspicuous spines that do not occur in the female (and subadult male) pedipalp. The male tibia carries a prominent outgrowth that is

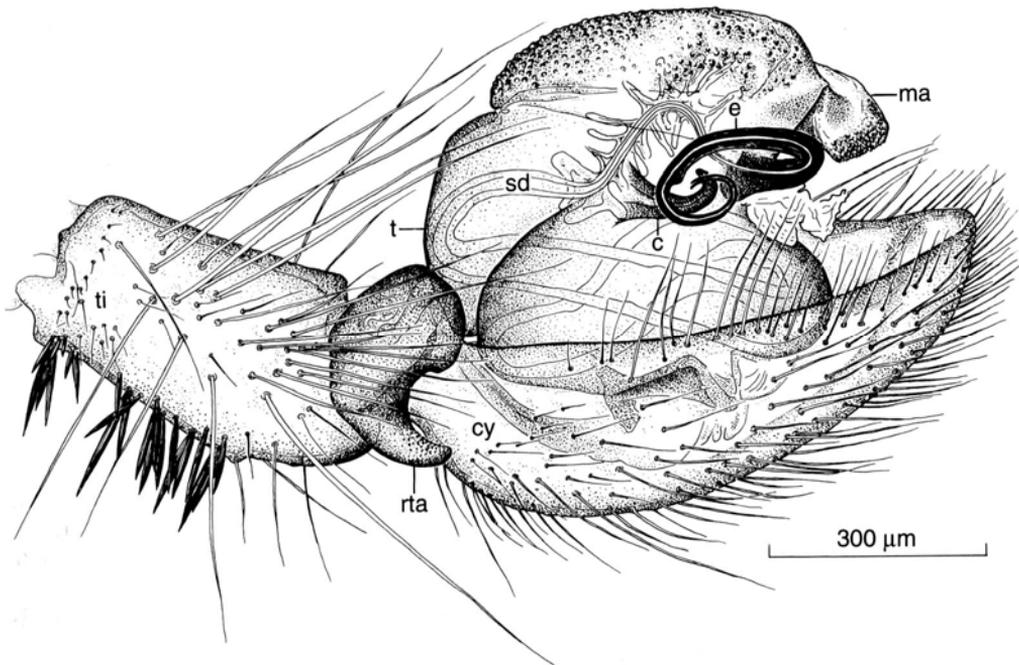


FIG. 1. *Anyphaena accentuata*, left male genital bulb cleared in KOH, retrolateral view. For explanation of abbreviations see p. 702.

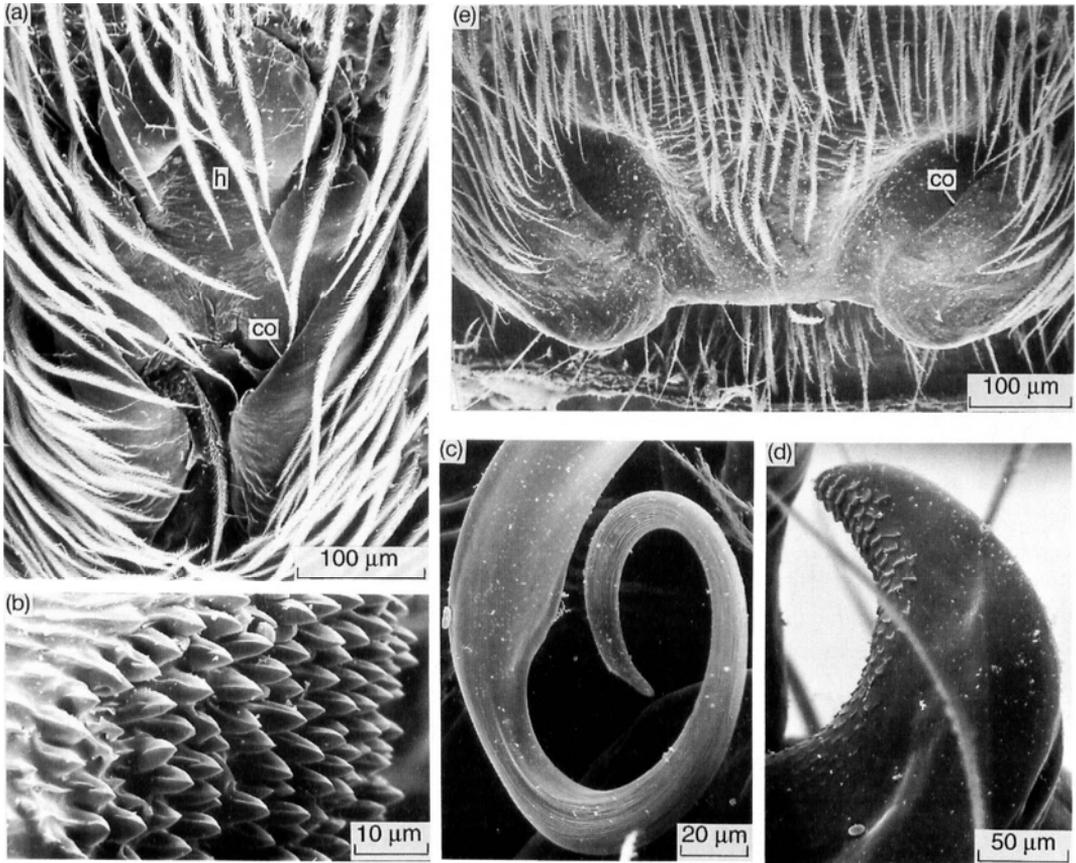


PLATE I. (a-d) *Anyphaena accentuata*: (a) female epigyne; (b) teeth on male median apophysis; (c) embolus; (d) 'finger' of the retrolateral tibial apophysis; (e) *Clubiona pallidula*, epigyne. For explanation of abbreviations see p. 702.

situated retrolaterally and is therefore termed the retrolateral tibial apophysis (rta). The 'finger' of this apophysis is provided with teeth at the concave side (Plate Id).

#### *Female copulatory organ (Fig. 2)*

The female copulatory organ is situated ventrally on the opisthosoma, anterior to the epigastric furrow. From a median field that is bordered by lateral folds (Plate Ia), the insemination ducts lead into the spermathecae (volume: each about  $1.5 \times 10^6 \mu\text{m}^3$ ). These are connected to the uterus externus by the fertilization ducts. Heavily sclerotized ducts lead from the insemination ducts to a pair of small hollow spheres (each  $1.5 \times 10^4 \mu\text{m}^3$ ). These 'diverticula' are distally provided with glands, as are the spermathecae.

Anterior to the median field, a heavily sclerotized hood lies medially, opening caudally.

#### *Courtship and copulation*

Since this study was primarily designed to elucidate copulatory mechanics, only slight attention

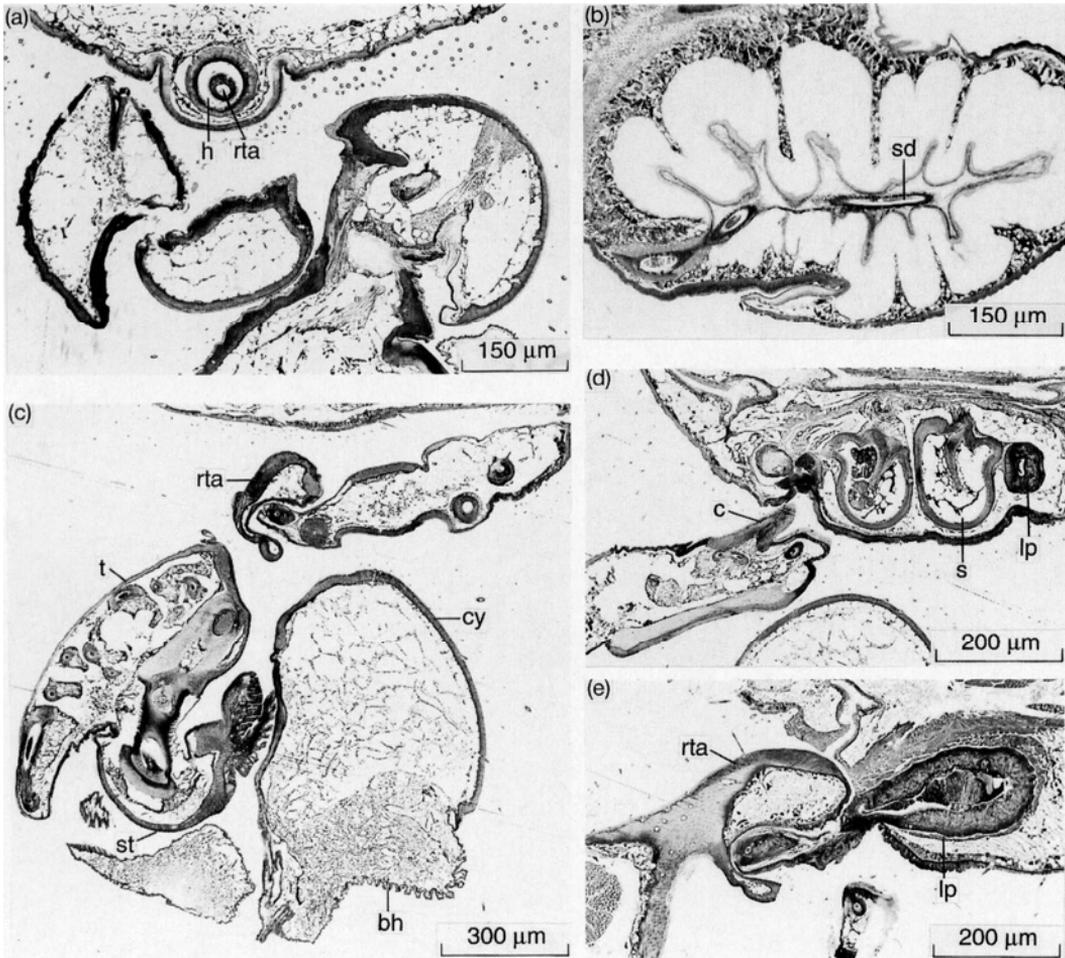


PLATE II. Semi-thin sections. (a-b). *Anyphaena accentuata*: (a) the 'finger' of the male tibial apophysis is locked into the 'hood' of the female epigyne (transverse section through female); (b) the male sperm duct passes through a complex system of cuticular folds, associated with glands. (c-e) *Clubiona pallidula*: (c) clasped copulatory organs, transverse section through female; (d) the conductor lies in a lateral depression of the epigyne; (e) sagittal section through female, the rt clasps the epigyne. For explanation of abbreviations see p. 702.

was paid to courtship behaviour. However, as little data exist about *Anyphaena accentuata*, the observations are briefly reviewed here.

Successful courtship was observed 17 times. Duration ranged from 4 to 148 min (mean 62 min), the pattern of events was quite constant and will therefore be summarized in the present tense.

After introduction of the male into the female container the male immediately courts intensively, vibrating with pedipalps and opisthosoma. This results in the female rushing out of her tent a short way towards him. The male immediately stops any movement and only after some seconds to half an hour he again begins, now very gently, knocking with the opisthosoma and drumming with the pedipalps. Courting intensity then steadily increases, until the knocking

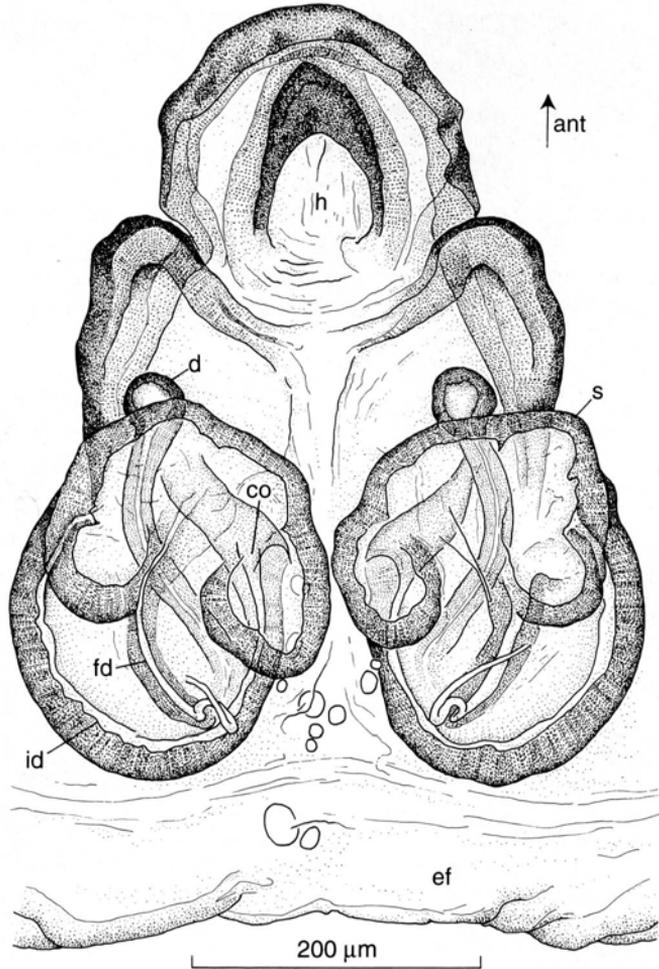


FIG. 2. *Anyphaena accentuata*, female vulva cleared in KOH, dorsal view. For explanation of abbreviations see p. 702.

of the opisthosoma against the plastic container is audible from a distance of up to one metre. The frequency increases up to about 30 knocks per minute and towards the end of precopulatory courtship the knocking is sometimes interrupted by short high-frequency vibrations of the opisthosoma and seemingly convulsive movements of the four anterior legs.

Finally, the male enters the female tent and mounts her, either from an anterior or posterior position. Still knocking with pedipalps and opisthosoma he brings himself into the appropriate position for copulation (position of the secondary hunting spiders, von Helversen, 1976). Then the male passes the pedipalp down to the epigyne between the third and fourth legs of the female, lifts her up and scrapes his pedipalp against the epigyne until the 'finger' of the tibial apophysis gets a hold in the female hood. As soon as this is accomplished, the basal hematodocha is expanded, driving the embolus into the insemination duct. First insertions were observed 11 times, average duration was 89.1 min (S.D. = 16.1). The basal hematodocha is rhythmically expanded (synchronously, leg spines are erected) and partially collapsed, the ratio of total:

subtotal expansion being about 5:5 sec in the beginning and about 10:150 sec towards the end of insertion.

After extraction of the first bulb, the male rests medially on the female for up to 10 min before passing the other pedipalp down on the other side and inserting the second bulb. Second insertions were only observed seven times (the other copulations were interrupted for experimental reasons). Average duration was 129.7 min (S.D. = 51), indicating that second insertions are significantly longer (*t*-test for paired measurements;  $P < 0.04$ ). In all seven cases observed, it seemed to be the male that terminated copulation. After extraction, the male usually spends some more minutes medially upon the female before leaping away. Both animals then engage in cleaning their copulatory organs until calming down within one hour.

There was no obvious copulatory or post-copulatory courtship behaviour (for working-definition see Eberhard, 1991).

Four mated and two half-mated females were repeatedly confronted with virgin males up to eight days after copulation. Despite fairly intensive and long courtship (up to three hours), the males were never accepted. The investigation of freshly mated (and half-mated) epigynes (dissecting microscope and serial sections) revealed no mating plugs.

#### *Copulatory mechanics* (Fig. 5a)

As already pointed out, the 'finger' of the tibial apophysis catches in the median hood of the female epigyne (Plate IIa). This brings the genital bulb into the correct position in relation to the

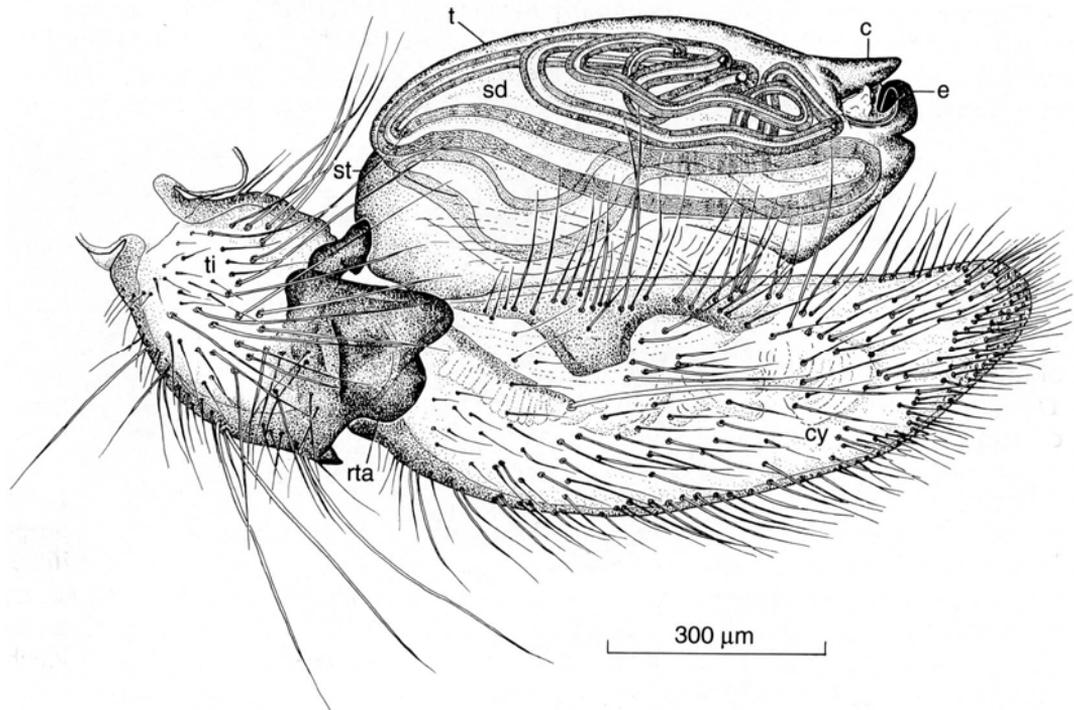


FIG. 3. *Clubiona pallidula*, left male genital bulb cleared in KOH, retrolateral view. For explanation of abbreviations see p. 702.

insemination duct. Then the expanding basal hematodocha drives the embolus into the insemination duct up to the spermatheca (left embolus into left insemination duct).

Since only fully expanded bulbs were freeze-fixed, no details can be given in respect to the process of insertion itself. The situation at full locking suggests, however, that the flat part of the rta might serve as a functional conductor, guiding the embolus into the insemination duct. It is surprising that neither the median apophysis nor the conductor seem to serve a special function during copulation. The femoral and tibial spines all point towards the female during copulation, touching the ventral side of her opisthosoma.

### *Clubiona pallidula*

#### *Male copulatory organ* (Fig. 3)

The *Clubiona*-bulb is principally of the same conformation as described in *Anyphaena*. The tegular processes are less elaborate, the embolus being a short hook, the conductor a simple cone and the median apophysis apparently lacking. The sperm duct is wound in a highly complicated way, not haphazardly, but according to a precisely given pattern. Its volume is about  $2.2 \times 10^6 \mu\text{m}^3$ . Glands are associated with it along its full length. Also in clubionids, the tibia is provided with a species-specific retrolateral apophysis (rta).

#### *Female copulatory organ* (Fig. 4)

Except for the funnel-like entrances into the insemination ducts (Plate Ie), no other sclerotized external structures are visible in the *Clubiona pallidula*-epigyne. The funnels narrow down to an inner diameter of  $2 \mu\text{m}$ . In this region the insemination ducts are highly sclerotized. They then increase in diameter and lead into lateral pouches that are characterized in sections by lamellar

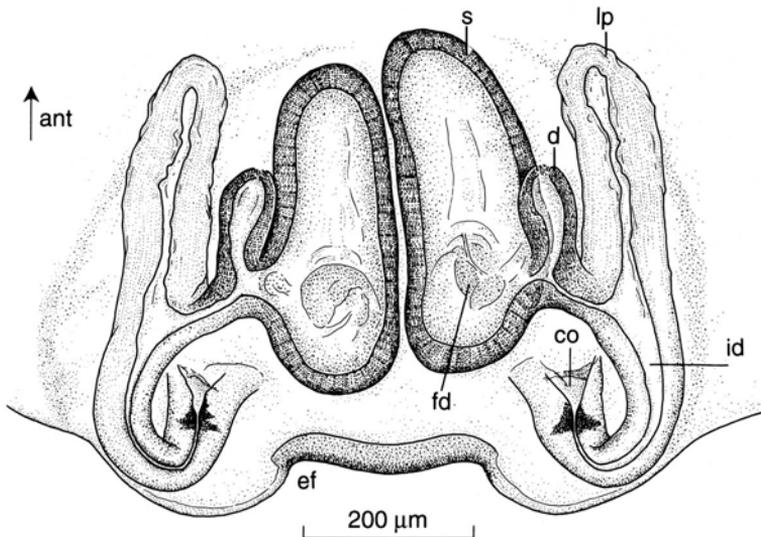


FIG. 4. *Clubiona pallidula*, female vulva cleared in KOH, dorsal view. For explanation of abbreviations see p. 702.

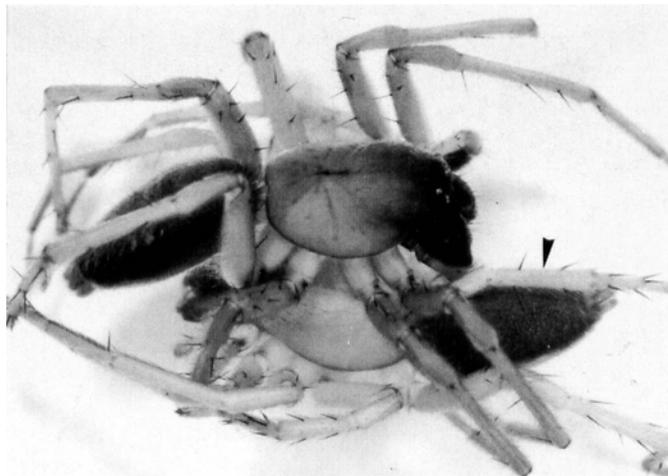


PLATE III. *Clubiona pallidula*, freeze-fixed pair in copulation. The right male pedipalp is applied. Note the position of the right female leg IV (arrow).

cuticula. Medially, narrow ducts connect these pouches to big median spermathecae from which the fertilization ducts arise. A pair of small diverticula originate at the insemination ducts at their entrance into the spermathecae. The approximate total volume of median spermatheca, lateral pouch, and diverticulum of one side is  $2.9 \times 10^6 \mu\text{m}^3$ . All these structures are provided with glands.

The posterior rim of the epigyne is medially impressed and well sclerotized.

#### *Courtship and copulation*

Only three copulations were achieved in *Clubiona pallidula* and these were all interrupted by nitrogen fixation. Courtship in these cases was rather short and less diverse than in *Anyphaena accentuata*. The males immediately performed quick bursts of vibration with their whole bodies as soon as they came into contact with female silk. The females responded with 'aggressive' rushes out of their tents (with spread chelicerae) but the males did not seem to be discouraged and mounted the females within a few minutes, still knocking with the opisthosoma.

The copulatory position is the same as in *Anyphaena accentuata*, and also in *Clubiona pallidula*, the male passes the pedipalp down to the epigyne between the third and fourth legs of the female (Plate III).

#### *Copulatory mechanics* (Fig. 5b)

As in *Anyphaena accentuata*, so in *Clubiona pallidula* the rta is the first male structure that establishes contact with the female epigyne. In contrast to *Anyphaena accentuata*, however, the female 'lock' is situated behind the copulatory orifices: the tong-like rta grips the well sclerotized posterior rim of the epigyne (Plate IIc, e). The expansion of the basal hematodocha results in a rotation of the tegulum that leads the short embolus into the funnel-like entrance of the insemination duct. Embolus and rta together provide secure mechanical locking as long as the

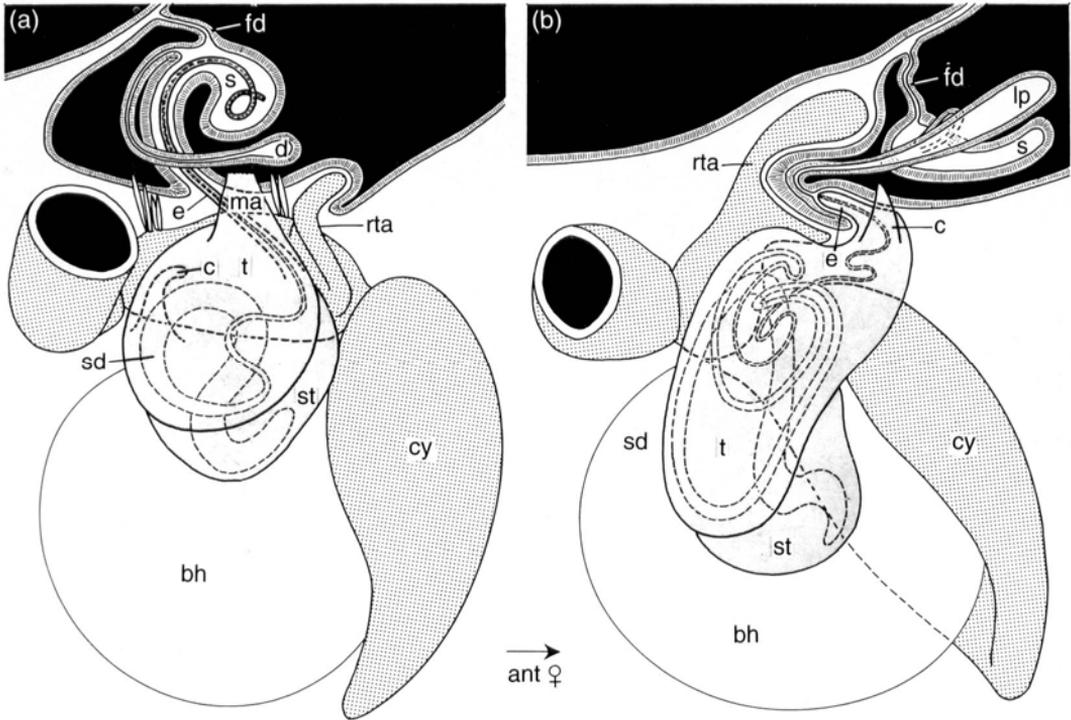


FIG. 5. Schematic illustration of the copulatory mechanics of *Anyphaena accentuata* (a) and *Clubiona pallidula* (b). The right male pedipalps are applied to the right half of the female vulva. For explanation of abbreviations see p. 702.

hematodocha is expanded. The conductor simply lies in a small lateral depression but has no locking function (Plate II d).

## Discussion

### *Morphological and behavioural aspects*

The nomenclature of the various genital structures in this paper has largely adopted that of previous authors, and it cannot therefore be concluded that homonymous structures are homologous. It is doubtful, for example, whether the 'conductor' in anyphaenids (Platnick, 1974) is homologous to the 'conductor' in clubionids (Wiehle, 1965). Brescovit (1992, in a partial revision of *Aysha*: Anyphaenidae) interpreted the 'conductor' of Platnick (1974) as median apophysis. For detailed discussions of homology in bulbar sclerites see Coddington (1990) and Sierwald (1990).

In the clubionid vulva, the functional significance of the various parts is still unclear, consequently, neutral terms have been used. Engelhardt (1910), who compared eight *Clubiona* species, called the lateral pouches "receptaculum I", the median spermathecae "rec. II" and the small diverticula "rec. III". In Wiehle (1965) the corresponding parts are called "Atrium", "Receptaculum" and "Drüse". In serial sections of the present study, sperm has been found in all parts, and glands are not only associated with Wiehle's "Drüse", indicating that the functioning of the vulva may be much more complex than often assumed and not restricted to mere storage of sperm. The same is true in

*Anyphaena accentuata*. Sperm were also found in the small diverticula in three females that were freeze-fixed after 9, 10 and 27 min, respectively, of copulation. There is no information about how the sperm passes through the long and narrow ducts so quickly. The position of this diverticulum, together with the fact that it is associated with glands, indicate that it may be a homologue to the “head of spermatheca” in Sierwald (1989) and the “accessory bulb” in Carico & Holt (1964).

Braun (1958), who observed two copulations of *Anyphaena accentuata*, speculated that the sperm duct is emptied during copulation. This is not the case, however, as is already indicated by the volume-ratio of sperm duct and spermatheca (4:1). Serial sections of the bulbs of two males that had copulated with one bulb only (and were then interrupted and rapidly fixed) showed that only a small percentage (about 15%) of the sperm was actually transferred to the female. The same is true of many other spider species (pers. unpubl. data), which may be able to copulate repeatedly without renewed sperm uptake. The termination of copulation can therefore not be induced by the “feeling of emptiness” but rather seems to be controlled by the central nervous system as indicated by Rovner (1966, 1967).

A surprising finding of Braun (1958) was the great plasticity of the copulatory pattern in *Anyphaena accentuata*. All the observations in the present study are in accordance with only one of the two patterns described by Braun (as mentioned above, he observed only two pairs). It is assumed that this is the “normal” pattern that is very constant as it is in most other spiders and that Braun’s second pair had some morphological abnormality (as had many of his males).

Courtship behaviour in clubionids may generally appear less elaborate than in anyphaenids, but it is definitely not lacking as claimed by some authors (e.g. Bristowe, 1929, Platnick, 1971). Courtship was described in *Clubiona germanica* (Gerhardt, 1923) and *Chiracanthium* sp. (Gerhardt, 1928) and is sometimes missing in the descriptions of this author simply because he found the pairs already in copulation (Gerhardt, 1923, 1924, 1930). Platnick (1971) classified clubionid courtship in his category “level I”, i.e. only involving direct contact, without the perception of pheromones. In their review article on pheromones in spiders, however, Pollard, Macnab & Jackson (1987) report of pheromones on the silk of *Clubiona cambridgei*-females and the present study indicates that in *Clubiona pallidula* female silk also carries pheromones.

The general copulatory position of both spiders investigated closely resembles the position of most other secondary hunting spiders (review: von Helversen, 1976). The specific situation of the male passing the pedipalp down to the epigyne between the third and fourth leg of the female has to my knowledge not been previously described. However, it seems to be quite common as some photos in literature suggest (e.g. in Salticidae: Preston-Mafham & Preston-Mafham 1984; in Philodromidae: Kullmann & Stern, 1981). It may be that some authors did not pay attention to it and this is probably the case in Gerhardt (1923) where an illustration of a copulating *Clubiona germanica*-pair shows the male passing the pedipalp down behind the fourth leg. It cannot be excluded, however, that both situations may occur within one family, even within one genus.

#### *Copulatory mechanics and phylogenetics*

Although the results in this paper do not allow definitive generalizations, two conclusions can be drawn regarding the usefulness of copulatory mechanics for phylogenetic research.

First, it seems to be limited to the hierarchy of genera and species-groups (Lehtinen, 1978). Both van Helsdingen (1969) and Grasshoff (1975) investigated very closely related species, and even within this small range it proved difficult to reconstruct evolutionary changes. This may be a result of the rapid and divergent evolution of genitalia (see Eberhard, 1985) that obviously does

not only include genital morphology, but also copulatory mechanics. Thus, convergences are likely to occur: a locking mechanism of the rta in an anterior median hood as described for *Anyphaena accentuata* was also found in crab spiders (Loerbroks, 1983, 1984; also in *Misumenops tricuspidatus*, pers. unpubl. data). On the other hand, presumably homologous structures may serve different functions within one family. The rta of four funnel-web spiders was found to serve four different functions (Huber, 1994). A similar situation obviously occurs in clubionids: Gering (1953) described the locking mechanism in *Chiracanthium inclusum* and it is quite unlike that of *Clubiona pallidula*. Still another completely different locking mechanism was described by Shinkai, Yoshida & Ito (1991) for *Chiracanthium japonicum*. The function of the rta in *Clubiona germanica* (Gerhardt, 1923) and *Clubiona brevipes* (Wiehle, 1967), however, seems to be similar to that in *Clubiona pallidula*, but the simple descriptions and illustrations, respectively, of these authors do not allow a detailed comparison.

Secondly, relatively simple genitalia like that of *Anyphaena* and *Clubiona* show rather simple copulatory mechanics in relation to genitalia of e.g. Araneidae (Grasshoff, 1975) or Linyphiidae (van Helsdingen, 1969). Therefore, from the perspective of phylogenetics, it will be more fruitful to investigate complex genitalia with many functional characters (as was done by the above-mentioned authors) rather than simple ones with a few characters only.

Summing up, the usefulness of functional mechanics for phylogenetic research seems to be restricted to closely related species with complex genitalia.

#### *Do male spider genitalia act as stimulators?*

The stimulatory function of male genitalia was proposed as one possible reason for the rapid and divergent evolution of genitalia (Eberhard, 1985). Females that discriminate between males on the basis of male genital morphology, subject male genitalia to strong selective pressure. A prerequisite for male genital stimulation, however, is an appropriate sensory basis in the female. According to the coevolution of male traits and female preferences that is assumed by theoretical models of sexual selection (Fisher, 1930; Lande, 1981), the female sensory system should be equally subjected to selection towards optimized reception as the male genitalia are towards increased stimulation. Therefore, one may put the introductory question in this manner: are female spiders able to perceive male genitalia and to discriminate between minimal morphological variants?

The investigation of the female contact zones during copulation does not point to such an ability in *Anyphaena accentuata* and *Clubiona pallidula* (thus corresponding to the results on *Nesticus cellulanus* in Huber, 1993). In contrast to nearly all the rest of the female body-surface, the contact zones appear free of mechanoreceptors. Tactile hairs and slit-sensilla were not found at the contact zones. Internal mechanoreceptors in spiders are restricted to membranous chitin, and have so far only been found in leg-joints (Foelix & Choms, 1979; Seyfarth, 1985).

These theoretical considerations do not disprove the existence of genital stimulation, but shed some doubt on its significance for rapid, divergent evolution and species-specificity in male spider genitalia. For example, the scraping movements of the pedipalp against the female epigyne before definitive locking as described in *Anyphaena accentuata* (and many other spiders), may have a stimulatory function, but the male structures that come into contact with the female during these movements are not those that are species-specific. An exception in *Anyphaena accentuata* is the rta, but the species-specific form of this apophysis can fully be explained by its locking and guiding function. In addition, some males performed only one single scrape. This indicates that this behaviour serves more of a searching than a stimulatory function.

*Species-specificity of spider genitalia*

An alternative mechanism to female choice based on stimulation is female choice by mechanical fit (Eberhard, 1985; Huber, 1993). According to this hypothesis, the female receives no sensory input and does not exert active choice, but passively chooses, e.g. by the morphology of her genital organs. In the standard theoretical model of sexual selection, female genital morphology would represent the female's preference that discriminates between variants of the male genitalia by the number of sperm that are transferred. The prediction that the fitting of genitalia is actually correlated to the number of sperm transferred appears logical but remains untested. Further research should concentrate on the number of sperm in female spermathecae and on the question, whether this can really be the limiting factor for offspring number.

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### Abbreviations used in plates and figures

ant	anterior	id	insemination duct
bh	basal hematochocha	lp	lateral pouch
c	conductor	ma	median apophysis
co	copulatory orifice	rta	retrolateral tibial apophysis
cy	cymbium	s	spermatheca
d	diverticulum	sd	sperm duct in the male bulb (spermophore)
e	embolus	st	subtegulum
ef	epigastric furrow—anterior border	t	tegulum
fd	fertilization duct	ti	tibia
h	hood		