

Comparative Morphology of Female Genitalia and the Copulatory Mechanism in Trypetimorphini (Hemiptera, Fulgoromorpha, Tropiduchidae)

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ABSTRACT A comparative morphological study of the female genitalia in Trypetimorphini shows that *Caffrommatissus trimaculatus* has a monotrysian condition, while species of *Trypetimorpha* and *Ommatissus* are ditrysian. Dissection of *Trypetimorpha biermani* Dammerman in copula shows that spermatozoa are first deposited in the bursa copulatrix and probably are transferred secondarily into the spermatheca. Maintenance of copulatory position is achieved by the male's gonostyli gripping the female's VIII gonapophyses, by endosoma inflation, and by eversion of antero-ventrally directed endosomal processes. Existence of the ditrysian condition in Fulgoromorpha is disputed and the presence of a copulatory-duct has to be interpreted as a neoformation in Tropiduchidae, although within this group it could have evolved several times independently.

Although male genitalic structures have been one of the most important sources of character information in Fulgoromorpha systematics since the beginning of this century, little is known about female genitalia and even less about the functional roles of the various components of the genitalia in both sexes during copulation. However, information on these topics is essential in order to understand the homologies of genitalic structures and their significance for phylogenetic interpretation.

For the Trypetimorphini, only two recent papers have provided valuable information about the structure of male genitalia: one on the genus *Ommatissus* Fieber 1872 (Asche and Wilson, '89) and one on the genus *Trypetimorpha* Costa 1862 (Bourgoin and Huang, '90). Female genitalia were also described in the first of these publications, and in the second the authors mentioned that, as in many other Tropiduchidae, females of *Trypetimorpha* and *Ommatissus* show a ditrysian genitalic conformation (i.e., two separate genital openings in the female) while those of *Caffrommatissus* (Fennah '67), the third trypetimorphine genus, have a monotrysian condition (one opening only).

Little information is available on the functional morphology of Fulgoromorpha with the exception of studies by Weber ('30), Asche ('85), Hoch and Remane ('85), and Heady and Wilson ('90).

Combining our interests in fulgoromorph morphology (T.B.) and trypetimorphine systematics (J.H.), the present report deals with comparative female genitalia morphology in the three recognized genera of the Trypetimorphini (Asche and Wilson, '89): *Trypetimorpha* Costa, *Ommatissus* Fieber, and *Caffrommatissus* Fennah. It also presents a functional morphological study of the copulatory mechanism in *Trypetimorpha*.

MATERIALS AND METHODS

Female genitalia were examined in about 60 dried specimens of different species of *Trypetimorpha*, including *T. biermani* (Dammerman in Bierman, '10), *T. fenestrata* (Costa, 1862), *T. japonica* (Ishihara, '54), *T. canopus* (Linnavuori '73), and four other new species of *Trypetimorpha* still unnamed; of two species of *Ommatissus*, *O. binotatus* (Fieber, 1876) and *O. lybicus* (Bergevin, '30); and of two specimens of *Caffrommatissus trimaculatus* (Fennah '67), this last genus being monospecific. After a 10% KOH bath (raised to boiling for 5–10 min) and an endocuticular staining with chlorazol black E (Carayon, '69), the specimens were dissected in glycerin. For functional morphology, one pair of dried *T. biermani*, preserved in copula, was placed still joined in a lukewarm 10% KOH bath for 5 hr. After 2 hr, both male and female thoraces were dissected and in the last 20 min the

specimens, still in KOH, were stained with chlorazol black E. Specimens were transferred to distilled water for dissections and observations for drawings.

Terms used for the female genitalia are those of Scudder ('61, '71) and for the male genitalia those of Bourgoïn ('88) and Bourgoïn and Huang ('90).

RESULTS

Genitalia in females of Trypetimorphini (Figs. 1-3)

Segmental and appendicular structures

As in all Hemiptera, genitalia in females of Trypetimorphini are of the ovipositor type, or type II according to Scudder ('71). The two gonocoxa of the abdominal segment VIII (Gx VIII)—the first valvifers of Snodgrass ('33)—are inserted ventrally below the laterotergites VIII bearing the eight spiracles. Gonocoxae VIII are more or less rectangular and bear the gonapophyses VIII (Gy VIII), the first valvulae. These two valves are strongly sclerotised with small teeth on their dorsal and ventral margins. Disposition and number of these teeth were used by Fennah ('82) in his revision of the tribal classification of the family. In segment IX, each gonocoxa IX (Gx IX)—the second valvifer—carries two processes: an anterior gonapophyses IX (Gy IX) or second valvula, and a postero-dorsal gonoplac (Gp) or third valvula. Gonapophyses IX are fused together on their inner-lateral margin and are strongly reduced but well sclerotised. The gonoplares are two thick, more or less membranous lobes and are devoid of teeth.

Interiorly a chitinated lobe is situated between the gonoplares and gonapophyses IX. This is known as "the mediocephalic process of the second valvula" (Asche and Wilson, '89) or the "basal unpaired apodeme of the second valvula" (Emeljanov, '79). We propose instead the term "gonospiculum" (nom. nov.) (Gl) as this structure appears as a sclerotised invagination of the body wall: an internal extension of the anterior wall of the gonoplares posteriorly and of the posterior wall of the fused gonapophyses IX anteriorly. The gonospiculum is indeed independent of the gonapophyses IX, as it is still present in (all?) female eurybrachids even though gonapophyses IX are completely lost.

Complex of the ectodermal genital ducts

In females of *Caffrommatissus* (Fig. 1) only one opening, the gonoporus (g), occurs between gonapophyses VIII and IX as in most Fulgoromorpha. In contrast, the complex of the ectodermal ducts opens by two openings in all *Trypeti-*

morpha (Fig. 2) and *Ommatissus* (Fig. 3), which are thus ditrysian. The posterior opening, "oviporus" (o) (Boulard, '66, '90), opens, as above, between the gonapophyses VIII and fused gonapophyses IX. The anterior opening, "copulaporus" (c) (Boulard, '66, '90), is located in the intersegmental fold VII-VIII and is separated anteriorly from gonocoxae VIII by a sternal VIII membranous area.

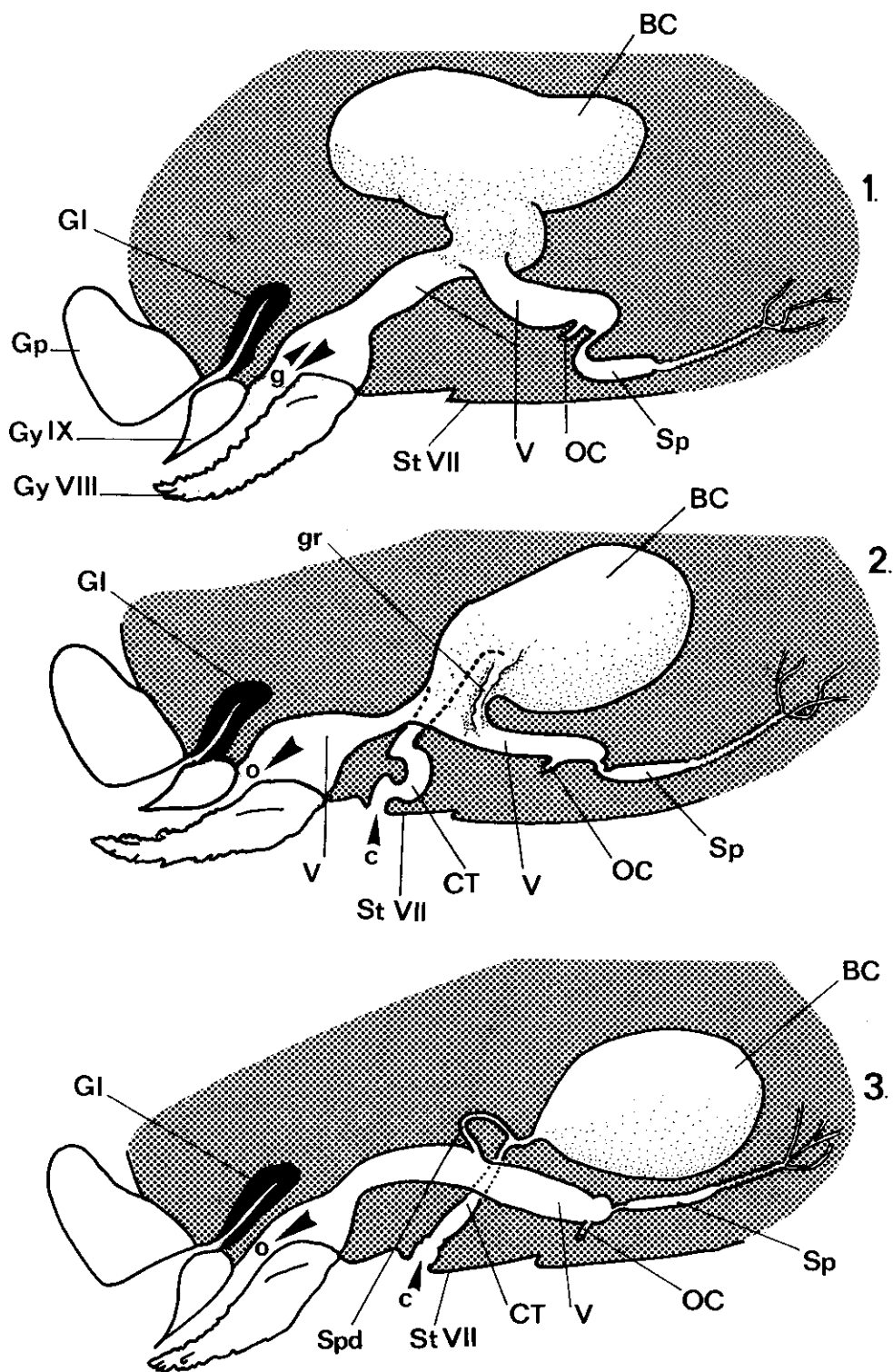
In *Caffrommatissus* females (Fig. 1), the ectodermal ducts show dorsally a large dorso-vaginal pouch or bursa copulatrix (BC) which opens directly into the vagina (V). In this species, the vagina has a laterally branched anterior part which gives off the common oviduct (OC) antero-ventrally and the spermatheca (Sp) apically. The posterior part of the vagina opens externally via the gonoporus.

In *Trypetimorpha* females (Fig. 2) ducts used in oviposition and copulation are different. The copulation-track leads from the copulaporus through a thin copulatory-duct which enters directly into the bursa copulatrix. The bursa then joins the oviposition track by opening broadly into the vagina, which divides into an anterior branch with common oviduct and spermatheca and a swollen posterior part that opens externally at the oviporus. In *T. canopus* the copulatory-duct is distinctly sclerotised and projects beyond the postero-dorsal wall of the bursa copulatrix. Posteriorly the vagina swells into it. It is interesting to note that in this genus, chlorazol black E, applied directly in KOH, did not stain the spermatheca. It remained practically uncoloured, an unusual condition for female fulgoromorphs. In two *Trypetimorpha* species, *T. fenestrata* and *T. biermani*, and more particularly in one of the new undescribed species (from New Guinea) and in *T. canopus*, a strengthened groove (gr) extends from the region where the copulatory-duct opens into the bursa copulatrix along the wall of the bursa to the anterior part of the vagina.

Ommatissus females (Fig. 3) show a similar conformation to that of *Trypetimorpha* but structures of the oviposition-track and of the copulation-track are only connected by a thin membranous duct, the spermoductus (Spd) (nom. nov.), running from the base of the bursa copulatrix to the middle of the vagina. The copulatory-duct opens into the spermoductus close to the base of the bursa copulatrix.

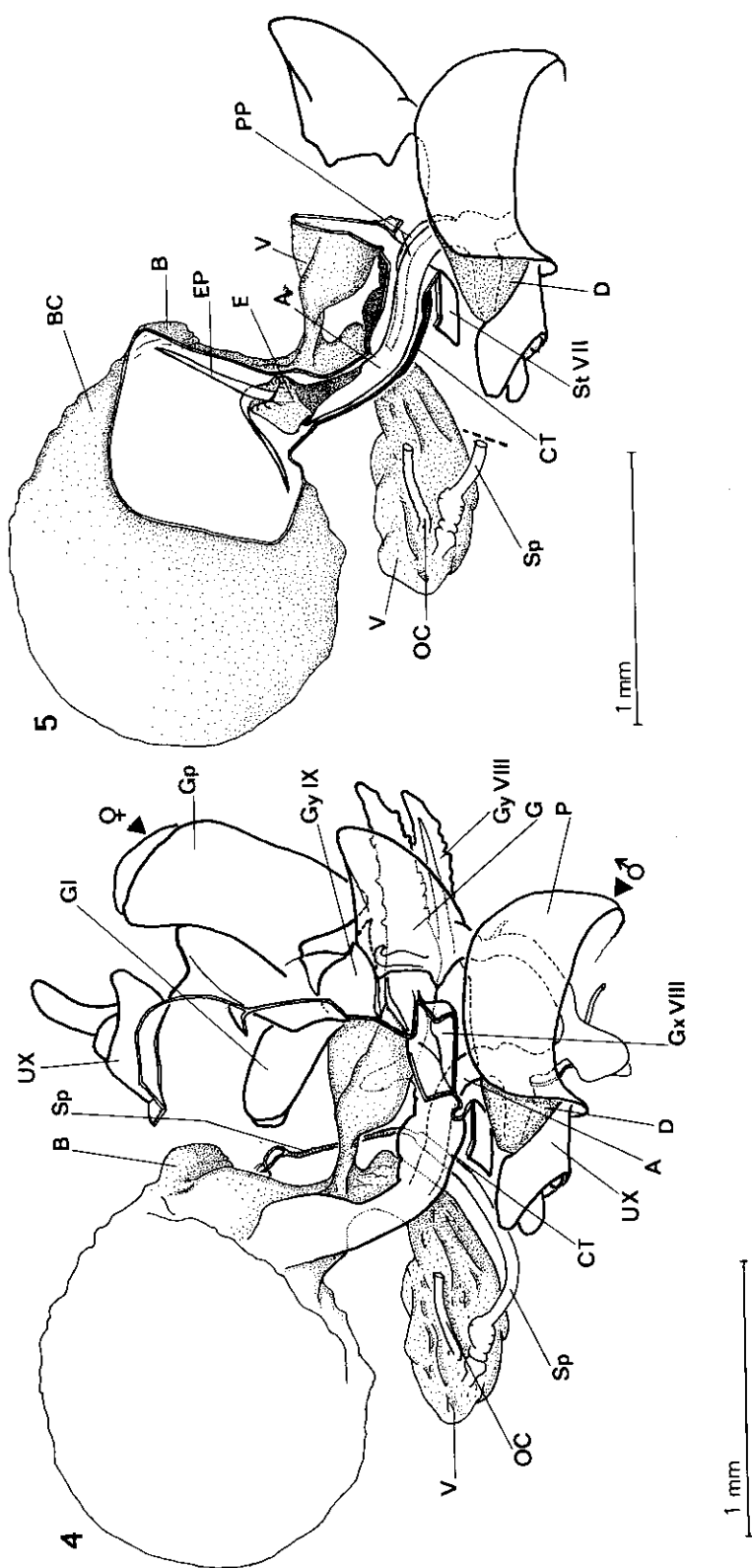
Copulatory mechanism in Trypetimorpha (Figs. 4, 5)

Protected dorsally by the anal tube—mainly urite X (UX)—and ventro-laterally by the gonostyli when not in use, the male genitalia in *Trype-*



Figs. 1-3. Diagrammatic parasagittal sections (not to scale) of female genitalia in the three Trypetimorphini genera: (1) *Caffrommatissus trimaculatus* Fennah 1967; (2) *Trypetimorpha* sp.; (3) *Ommatissus* sp. BC, bursa copulatrix; c, copulaporus; CT, copulatory-duct; g, gonoporus; gr, strength-

ened groove of bursa copulatrix; GI, gonospiculum; Gp, gonoplac; Gy VIII, Gy IX, gonapophyses VIII, IX; o, oviporus; OC, common oviduct; Sp, spermatheca; Spd, spermoduct; St VII, sternite VII; V, vagina.



Figs. 4, 5. Lateral aspect of male and female genitalia of *Trypetimorpha biermani* (Dammerman in Bierman) 1910 in copula. Abdominal segments I-VIII of male and segments I-VII and laterotergite VIII of female are omitted from the drawings. In Figure 5, the bursa copulatrix and copulatory duct are opened laterally to show the aedeagus in place; posterior parts of terminalia not drawn. A, aedeagus; b, bump

of bursa copulatrix; BC, bursa copulatrix; CT, copulatory duct; D, diaphragma; E, endosome; EP, endosomal process; G, male gonostylus; Gf, gonapophyses VIII, IX; Gp, gonopod; Gx VIII, gonapophyses VIII, IX; o, ovipositor; OC, common oviduct; P, pygofer; PP, perandrium lateral process; Sp, spermatheca; St VII, sternite VII; UX, uncus; V, vagina.

timorpha are everted during mating. This movement is effected by contraction of muscles that pull down and separate the gonostyli (G) and raise the anal tube (Fig. 4), movements certainly aided by hemolymph pressure. The diaphragm (D) becomes visible laterally. During copulation, the gonostyli enclose each of the female gonapophyses VIII on their median external side (Fig. 4).

The aedeagus (A) and the unpaired perianthrium lateral process (PP) are inserted together into the female copulatory-duct (Fig. 5). The copulatory-duct is lightly twisted at rest but becomes practically straight during mating. The lateral process of the perianthrium reaches the middle of the copulatory-duct. It is inserted into the region of the tube that has the thickest wall. The aedeagus reaches the base of the bursa copulatrix. While the endosoma (E) is being everted, the endosomal processes (EP) first project postero-dorsally into two strengthened bumps (B) of the bursa copulatrix wall. When the endosoma is fully everted, these processes point latero-ventrally onto the floor of the bursa copulatrix. At this time, the ductus seminis opens at the base of the bursa copulatrix near the entrance into the anterior part of the vagina (Fig. 5). It seems that the membranous endosoma cannot evert more.

DISCUSSION

Comparative morphology of female genitalia in Trypetimorphini

Females of *Caffrommatissus* show a general conformation seen in most fulgoromorph females, although the lateral branching of the anterior part of the vagina represents an apomorphic condition (Fig. 1). This conformation differs fundamentally from the more advanced ditrysian condition found in *Trypetimorpha* and *Ommatissus* females and in those of some other species of tropiduchids.

In females of *Trypetimorpha* (Fig. 2), the copulatory-duct opens into the bursa copulatrix, which has retained a large and direct opening into the vagina. Between these two openings an open strengthened and longitudinal groove may be found. In *Ommatissus* females (Fig. 3), the bursa copulatrix has lost its direct connection to the vagina: the pathway used in laying eggs is independent of that used in copulation. Spermatozoa must pass from the copulation-track to the oviposition-track—from bursa copulatrix to the vagina (not the ductus receptaculi as drawn by Asche and Wilson, '89, Fig. 31)—via the spermoductus. It is likely that the spermoductus is an evolutionary advance derived from the condition of an open strengthened groove like in fe-

males of *Trypetimorpha*. Spermoductus and groove may thus be considered homologous, and if so the spermoductus probably represents an apomorphic condition. It is interesting to note that this duct is similar to the fecundation canal known in females of most Heteroptera gerromorphs (Heming-Van Battum and Heming, '86), and furthermore that it derives from the bursa copulatrix wall as in gerromorph females.

We agree with Asche and Wilson ('89) that the new tribal classification system of Tropiduchidae proposed by Fennah ('82) may be considered as purely phenetic rather than phylogenetic, a distinction especially applicable to the Trypetimorphini which cannot be considered as a monophyletic group (Bourgoin and Huang, '90). At present it is difficult to decide if the spermoductus represents an autapomorphic character for the unique genus *Ommatissus* or for a suprageneric taxon not yet identified.

The ditrysian condition

The ditrysian condition is known in some females of other fulgoromorph species, including *Phenax variegata* Olivier (Boulard, '66) and *Fulgora* sp. (Bourgoin, '85), and in females of entire higher taxonomic groups such as stenocranine Delphacidae (Asche, '85) and, according to Asche ('88), most tropiduchids. From unpublished data of the senior author, we can state that probably all females of fulgorids and dictyopharids are also ditrysian, but that females of several species of tropiduchids (e.g., *Numicia*, *Tropiduchus*) remain monotrysian as in *Caffrommatissus trimaculatus*.

We recognize at present that there are at least three ditrysian arrangements in female fulgoromorphs: one in Dictyopharidae and Fulgoridae where the copulaporus opens directly into the base of the vagina without a differentiated copulatory-duct; a second type in stenocranine Delphacidae and in some other tropiduchid genera (e.g., *Rhynodictya*) in which a thin copulatory-duct joins the vagina at a higher level; and a third type in *Trypetimorpha* and *Ommatissus* females—and probably some other female tropiduchids—in which the copulatory-duct opens directly into the bursa copulatrix.

We do not think that these differing ditrysian conditions are step-wise variations of the same ontogenetic mechanism, but that they have evolved independently several times. In fulgorids and dictyopharids, the ditrysian condition may have arisen in the same way as in the females of cicadomorph Cicadidae where, in the last larval instar, the developing gonapophyses VIII secondarily divide the gonoporus (Boulard, '66, '90). It is not obvious, however, that the same

event occurs in females of ditrysian tropiduchids and in those of stenocranine Delphacidae. Indeed, in females of the tropiduchid genus *Haliartus* instead of the copulatory-duct, there is a parasagittal ectodermic blind tube completely independent of the genital ducts—which are of normal conformation—although in wide contact with the bursa copulatrix. This blind tube and the copulatory duct are probably homologous. Thus the blind tube could show either a regression to the monotrysian condition resulting from loss of a connection between the copulatory-duct and the bursa copulatrix or it could represent an early step in evolution of the ditrysian condition in tropiduchids, different in its ontogenesis from that in dictyopharids and fulgorids. The copulatory-duct may therefore be interpreted as a neoformation, appearing independently several times: once in stenocranine Delphacidae and at least once in ditrysian tropiduchids.

Deposit and storage of spermatozoa

During copulation in *Tettigometra* sp. (Fulgoromorpha Tettigometridae) the male's endosoma does not enter the bursa copulatrix but enters into the first part of the spermatheca and most of spermatozoa are directly deposited into the apical and swollen portion of the ductus receptaculi; thus the spermatheca appears to be a real receptaculum seminis (unpublished data).

In *Trypetimorpha*, spermatozoa are deposited into the bursa copulatrix. If, as we think, the spermatheca in females of all fulgoromorphs is also a real receptaculum seminis—the different parts of a typical and functional spermatheca exist—then spermatozoa must be transferred into it. This may be by the way of the chitinised groove in the floor of the bursa copulatrix. We do not know if spermatozoa migrate actively or if they are moved passively by action of vaginal muscles, or more probably by a combination of the two. McMillan ('63) has observed spermatozoa both in the spermatheca and bursa copulatrix just after mating in adults of *Sogata orizicola* (Delphacidae), and has noted both sperm movement and pulsations of muscles in both of these organs. Abdominal contractions in male and female during mating, observed in two other species of delphacid, *Prokelisia dolus* Wilson and *P. marginata* (Van Duzee) (Heady and Wilson, '90, personal communication), could also help the migration of spermatozoa.

Maintenance of copulatory position between male and female

Holding pairs together during copulation does not appear to be difficult to maintain. In *Trype-*

timorpha this is achieved principally by the male's gonostyli gripping the female's gonapophyses VIII by their outer sides. Inflation of the endosoma and the antero-ventrally directed endosomal processes could assist in maintaining the aedeagus inside the female's exit ducts. In Cixiidae, Weber ('30) has shown that contact is maintained in *Cixius* sp. by a double hooking of the male's gonostyli, which grip the outer side of gonapophyses VIII, and by the settling of the anal tube into the intersegmental sternal fold between abdominal segments VI and VII. As in *Trypetimorpha*, two hook-like sclerotised endosomal processes maintain the aedeagus inside the female's exit ducts. Asche ('85) has observed a similar holding mechanism in the ditrysian delphacid, *Stenocranus major* Kirshbaum. In a cixiid genus, Hoch and Remane ('85) have described a different method of maintenance of copulatory position by a triple hooking in *Hyalesthes obsoletus* Signoret and *H. mlokosiewicz* Signoret. The distal, hook-like parts of the gonostyli pass between the female's gonapophyses VIII, the anal tube seems to act as a suction disk, and the paired asymmetric spined processes of the pygofer come to settle in the membranous sternal fold between sternite VIII and gonocoxa VIII. In this genus, gripping of the inner sides of the female's gonapophyses VIII opens the gonoporus more widely to facilitate entrance of the aedeagus. This pattern may have phylogenetic value, possibly demonstrating an apomorphy, and may also indicate the evolutionary significance of physiological modifications.

Additional studies of functional aspects of the genitalia morphology in Fulgoromorpha are required to support this suggestion. Recently, Heady and Wilson ('90) have shown that male gonostyli of *Prokelisia dolus* and *P. marginata* are placed posterior to the produced anterior end of the gonocoxa VIII and anterior to the gonapophyses VIII of the female. Nothing else maintains the copulatory position. Male gonostyli are in constant motion before insemination. Thus they may have a stimulatory function in preparing the female to receive and to store the spermatozoa; also they may reproductively isolate these sympatric and synchronic species.

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