

The reproductive organs of the Plecopteron *Isoperla grammatica* (Poda, 1761)

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In a paper by the senior author (Brinck, 1955) the reproductive organs and mating habits of a series of stonefly species were dealt with. The specific sexual musculature, however, was described only partly, in a few cases when necessary for understanding the function of complex organs. Therefore, it seemed that a complete description of the musculature, associated with the copulatory organs, should be presented when sufficient material of a representative species was available. In June 1957 a fairly rich material of mating specimens of *Isoperla grammatica* (Poda, 1761) was collected and these specimens were used for the following description. The study of the material also added to the knowledge of the histological structure of the reproductive organs.

The material originated from South Sweden, Scania: Stockamöllan, and was fixed in Bouin's mixture.

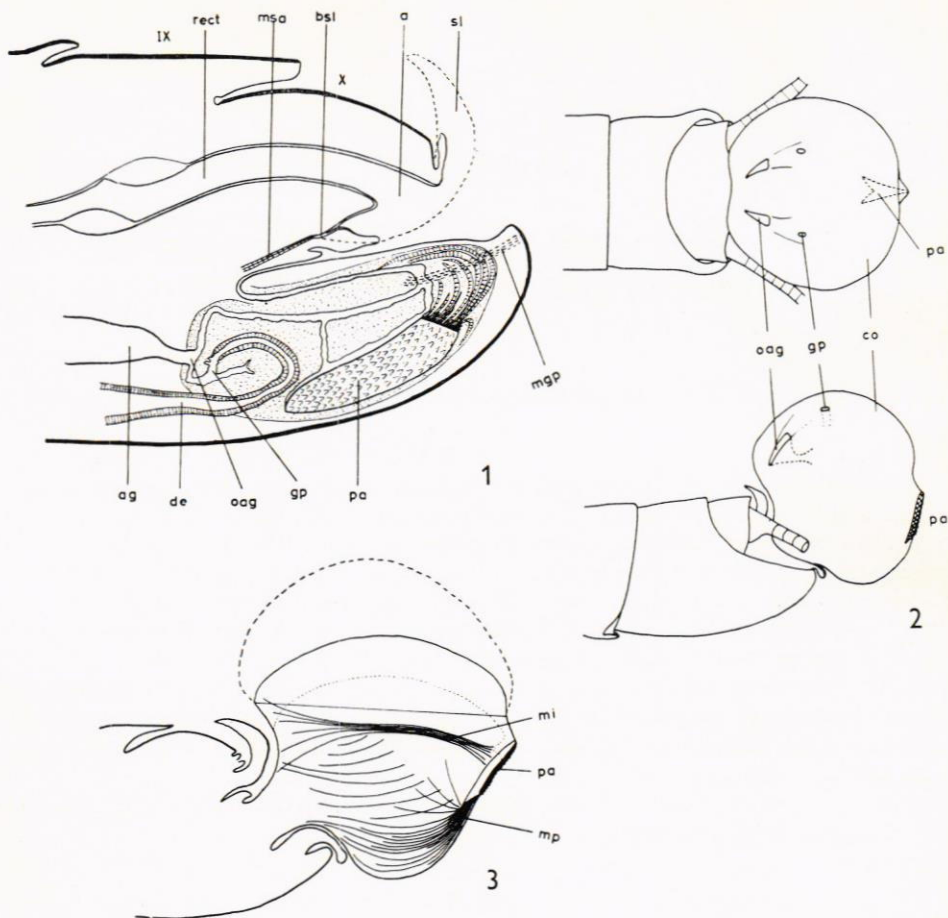
Male

(Figs. 1—5, 9—11)

General description of the copulatory organ

The male copulatory organ is a vesicle which is in rest completely concealed in the enlarged, ventral part of sternum IX where its various parts are folded in a complicated, more or less asymmetrical arrangement (cf. fig. 1). The gonopores (gp) are met with in the anterior part of the complex, in front of the penial armature (pa) which rests medially, near the sternal wall so that it might usually be seen through the sternum in ventral view, as a longitudinal, dark brown strip. The posterior parts of the ejaculatory ducts form part of the complex, while the "accessory glands" just open into it. When protruded the copulatory organ expands and contracts irregularly in live specimens, because of the movements of the contents. The latter vary to some extent. In male specimens, fixed in copula, the organ contains the whole of the accessory glands, the seminal vesicle, the ectal parts of the deferent ducts, the ejaculatory ducts and sometimes some Malpighian tubules.

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Figs. 1—3. — 1. Right half of the male abdominal apex, with the copulatory organ at rest, showing the positions of the penial armature, the openings, and the posterior genital muscle. (a=anus, ag="accessory gland", bsl=base of the subanal lobes, de=ejaculatory duct, gp=gonopore, mgp=posterior genital muscle, msa=subanal muscle, oag=opening of "accessory gland", pa=penial armature, rect=rectum, sl=subanal lobes.). — 2. Abdominal apex of preserved male specimen with protruded copulatory organ, showing the position of the orifices. A. Dorsal view. B. Lateral view. (co=copulatory organ, gp=gonopore, oag=opening of the accessory gland, pa=penial armature). — 3. Right ventral quarter of the protruded copulatory organ, showing the principal intrinsic muscles. (mi=internal bundle of muscles, mp=peripheral muscles, pa=penial armature.)

In specimens whose abdominal parts were pressed to extrude the copulatory organs or to retain these organs extruded, part of the intestine as well as large numbers of Malpighian tubules may also enter the organ. The shape of the fixed organ in such specimens is variable and frequently asymmetrical.

In all specimens the openings of the "accessory glands" are situated mesially and anteriorly (or ventrally) to the openings of the ejaculatory

ducts=the gonopores. In the fixed material the positions appear somewhat variable, as are also the relative distances between them. This is evidently due to the various degrees of distention of the organs at fixation. The gonopore is small. The external openings of the "accessory glands" are wider, mostly slit-like, and are formed by an invagination of the surface of the copulatory organ. Cf. fig. 2.

In the preserved material the armature is situated at the posterior part of the copulatory organ while the above mentioned openings are met with dorso-anteriorly. In actual copulation the organ is more protruded so that the armature becomes dorsal and the orifices anterior (cf. Brinck, 1955, p. 74, fig. 11 D).

Except for most of the "dorsal" surface, the copulatory organ is beset with small microtrichia of various shapes. The ventral ones are larger and conical.

The ventral knob of sternum VIII, besides a particular strong sclerotization, presents nothing remarkable. It serves in connection with the drumming: the habit of striking the substratum rapidly with the apical part of the abdomen.

Musculature

A. *Intrinsic muscles*

The copulatory organ is rich in intrinsic muscles. The main ones are inserted around the armature. The strongest muscles are fixed at the ventral part of the armature and run ventrad and laterad along the inner surface (cf. fig. 5, mp). Some of these fibres are short, others are long, extending to the peduncle of the copulatory organ.

The second important set — the internal muscles (fig. 3, mi) — takes its origin to the sides of the armature and runs forward, usually as a pair of well defined bundles, to the anterior part of the copulatory organ. There each bundle fans out above the peduncle, some of the fibres crossing to the other side. There are also, in this region, some superficial transverse fibres.

Thin, isolated fibres run in various directions. They are mostly peripheral.

B. *Extrinsic muscles*

The chief retractors of the copulatory organ arise from the ventro-lateral part of the anterior limit of segment IX (fig. 3, rm). Each retractor runs to the dorso-lateral part of the peduncle and fans out dorsally inside the copulatory organ. Evidently, they are modified internal sternal muscles.

From the sides of segment IX there extends a muscle composed of a series of bundles. Some of these run to the fold which is formed around the peduncle of the copulatory organ. Other bundles run to the ventral surface of the peduncle and fan out there, several fibres crossing to the other side, others proceeding into the peduncle. These muscles might be modified lateral muscles.

From the posterior, caudally extended portion of the 9th sternite, a pair of muscles (fig. 3, mgp) run to the dorsal part of the fold or, chiefly, to the dorsal surface of the peduncle. They run mesiad to the lateral muscles and laterad and dorsad to the retractors. Most of their fibres cross to the other side. These posterior genital muscles are probably modified external sternal muscles.

In the illustrations (figs. 4 and 5) a few other abdominal muscles are shown, as follows.

Near the origin of the retractor two other muscles originate, viz. the subanal and the ventral rectal muscles. Their origin is lateral to the retractor, the subanal more ventrally, the rectal more dorsally. The subanal muscles converge towards the base of the subanal lobes, situated under the anus. The ventral rectal muscles run to the rectum, to the region of the rectal "glands".

In fig. 5, right side, the three more ventral of the tergal muscles are illustrated. They are inserted at the ventral and lateral parts of tergum X.

C. *Function of the muscles*

The intrinsic muscles (mp and mi) are probably the most important for the ejaculation of the sperm. The muscle coat of the male efferent system is very weak (mgl) and would be inefficient for this purpose. The intrinsic muscles, when contracting, diminish the volume of the copulatory organ, thus forcing the sperms outside. The posterior extrinsic muscles (mgp) probably assist at this process, pressing down the dorsal wall of the peduncle, thus closing it and preventing the return of fluids to the body.

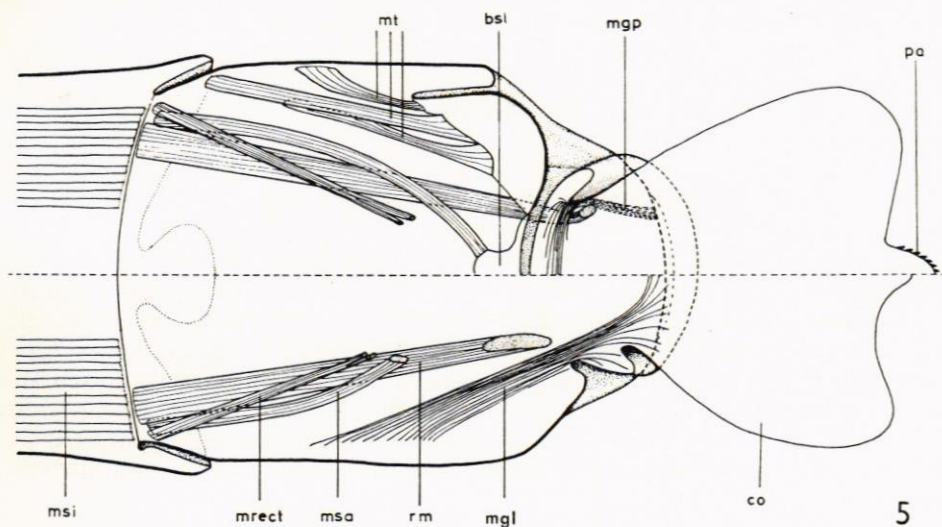
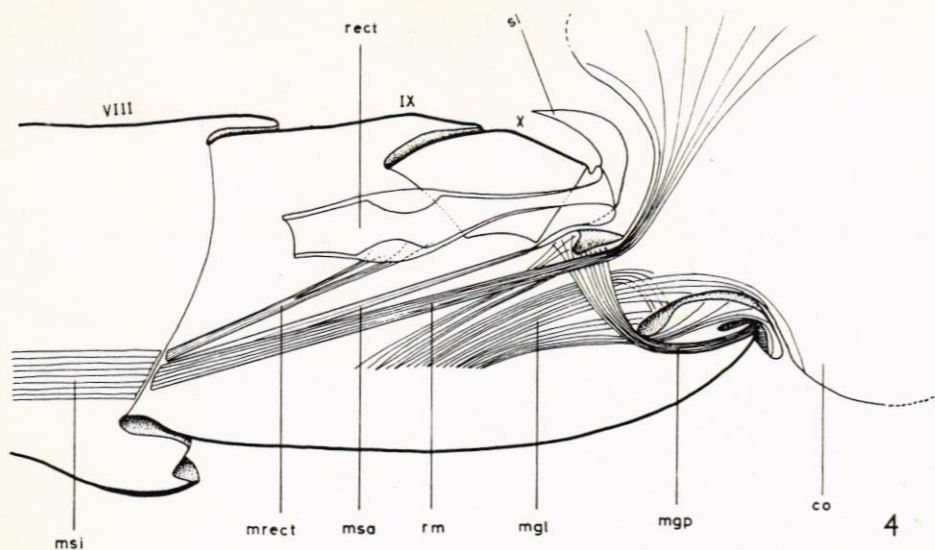
The retraction of the copulatory organ is brought about chiefly by the retractors (rm), but both the lateral (mgl) and, in the final stages, the posterior muscles (mgp) should be useful.

The lateral muscles (mgl) probably work also in the first stages of protrusion, enlarging, by their contraction, the opening through which the copulatory organ everts.

Some histological data

The epithelium of the deferent ducts, of the vesicle, and of the inner (ental) portion of the ejaculatory duct is thick, though somewhat thinner, of course, when these organs are dilated by sperms. It is glandular and is provided with a brush border. The investing muscular coat is very weak. The above mentioned parts of the efferent system are mostly filled up with spermatozoa mixed with a mucoid secretion. The outer (ectal) portion of the ejaculatory duct has a stronger muscular coat; its epithelium is much thinner and there is no brush border. It is usually empty. Cf. figs. 9—11.

The "accessory glands" have a very thin wall with very weak muscles (fig. 9, 11, ag). Except for some sparse basophilic material, their lumen is optically empty. The function of these sacs is enigmatic. They are hardly glandular.



Figs. 4—5. — 4. Right half of the male abdominal apex with the copulatory organ protruded, showing the genital musculature and some other muscles. Lateral view. (co=copulatory organ, mgl=lateral genital muscle, mgp=posterior genital muscle, mrect=rectal muscle, msa=subanal muscle, msi=internal sternal muscles, rect=rectum, rm=retractor muscle, sl=subanal lobe.). — 5. Ventral half of the male abdominal apex in dorsal view (left half sectioned at a lower level), showing the genital musculature and some other muscles. (bsl=base of the subanal lobes, co=copulatory organ, mgl=lateral genital muscle, mgp=posterior genital muscle, msa=subanal muscle, msi=internal sternal muscle, mt=tergal muscles, pa=penial armature, rm=retractor muscle.)

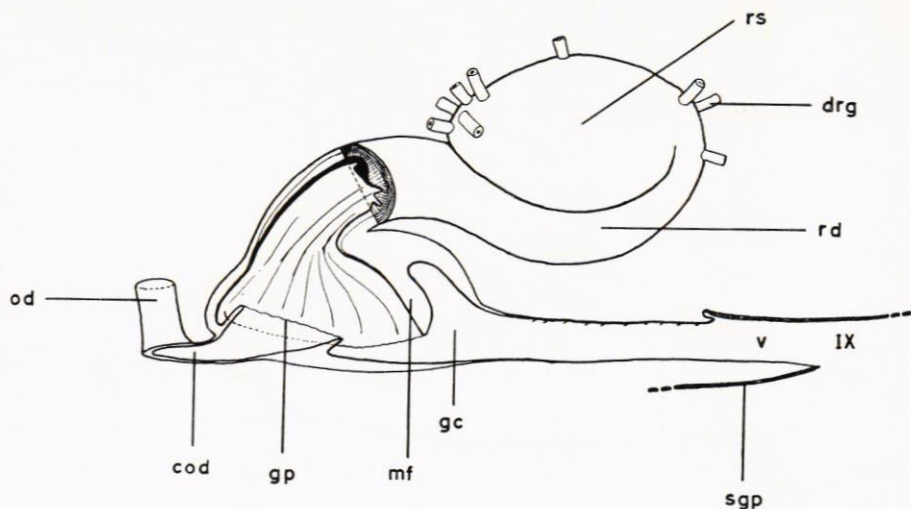


Fig. 6. Female genital cavity and associated structures. Slightly diagrammatic, lateral view, showing the elevated slit-like gonopore and the dorsal muscular fold which surrounds it. (cod=common oviduct, drg=ducts of the accessory receptacular glands, gc=genital cavity, gp=gonopore, mf=dorsal muscular fold, od=oviduct, rd=duct of the seminal receptacle, rs=seminal receptacle, sgp=subgenital plate, v=vulva.)

Female

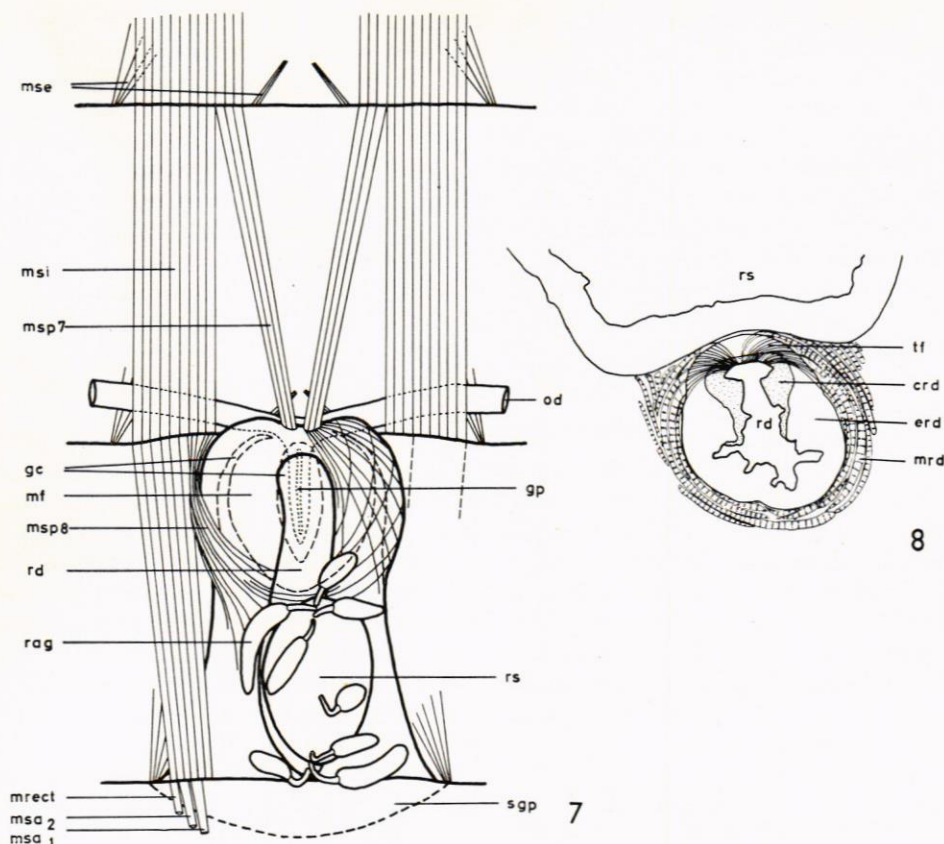
(Figs. 6—8)

General description of the sexual organ

The paired oviducts (od), of mesodermal origin, join to a very short common oviduct (cod) (fig. 7). The latter is directed backward and upward and projects into the anterior, muscular part of the genital cavity as an elongated ridge, which is higher anteriorly (cf. fig. 6). The gonopore (gp) is a slit along the edge of the ridge. The ridge is surrounded by a muscular, horseshoe-shaped dorsal flap (mf). The anterior ends of the flap are fused to the wall of the cavity. The ridge and the flap form a sluicing apparatus. In the central hollow of the horseshoe the opening of the receptacular duct is located.

The posterior part of the genital cavity is very wide and flat. Its walls are membranous. The dorsal wall is beset with microtrichia. The cavity opens via a broad genital aperture above the subgenital plate (sternum VIII).

Anteriorly, the genital cavity is connected with a moderately long receptacular duct (rd, fig. 6) which ends in the receptaculum (rs). The latter carries a variable number of receptacular glands: in 7 specimens examined the number varied from 6 to 13. These glands open along the mid-dorsal line of the receptaculum but are more concentrated at the ends. Usually a few of them open into the posterior part of the receptacular duct.



Figs. 7—8. — 7. Posterior part of the female reproductive organs in dorsal view (incl. the sternal muscles). (gc=genital cavity, gp=gonopore, mf=dorsal muscular fold of the genital cavity, mrect=ventral rectal muscle, msa₁ and msa₂=subanal muscles, mse=external sternal muscles, msi=internal sternal muscles, msp7=separate bundle of the internal sternal muscles of segment VII, inserted at the anterior part of the genital cavity, msp8=separate fibres of the internal sternal muscles of segment VIII attached to the genital cavity, od=oviduct, rag=receptacular accessory glands, rd=duct of the seminal receptacle, rs=seminal receptacle, sgp=subgenital plate.). — 8. Cross-section of the duct of the seminal receptacle, showing the thickened cuticle, the circular muscles, and their insertion through tonofibrils fixed in the cuticle. (crd=cuticle of the receptacular duct, erd=epithelium of the receptacular duct, mrd=circular muscles of the receptacular duct, rd=receptacular duct, rs=seminal receptacle, tf=tonofibrils.)

Musculature and histological data

The paired oviducts present a longitudinally folded epithelium which is low columnar and has no cuticle. It is surrounded by a muscle coat comprising circular as well as longitudinal muscles.

The very short common oviduct has a flat epithelium provided with a thin cuticle. Its muscular coat is strong.

The anterior part of the genital cavity is strongly muscular while the posterior part has membranous walls with sparse muscle fibres only.

The mesial fibres of the internal sternal muscles of segment VII form a pair of bundles which converge and insert at the anterior wall of the genital cavity. From around the insertion points of these muscles, numerous fibres originate. Part of them radiate around the wall of the genital cavity, part run into the muscular flap. All these fibres are more or less longitudinal.

The mesial fibres of the internal sternal muscles of segment VIII also serve the genital cavity. They run around the lateral wall of the muscular part of the cavity and fan out posteriorly, some crossing behind the receptacular duct, some inserting on the surface of the posterior, non-muscular part of the cavity. Some of the ventral fibres of the genital cavity intersect behind the receptacular duct; some, however, rise to cross over it or to insert at its dorsal wall.

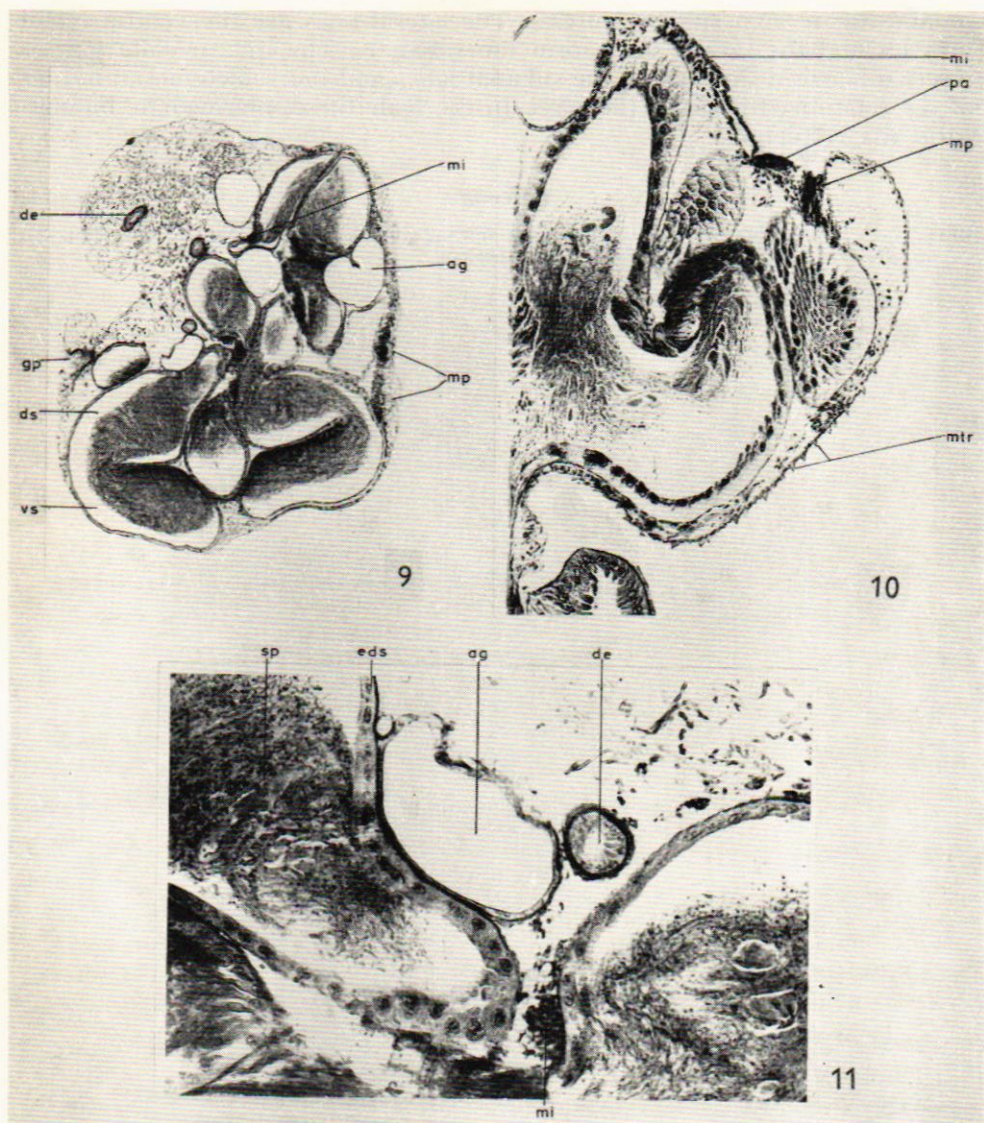
The whole of the genital cavity is covered by a flat epithelium and a rather thin cuticular lining.

The receptacular duct is rather rigid due to a thickening of the cuticular lining along two dorsal strips (cf. fig. 6 and fig. 8, crd). The epithelium of the duct is columnar and folded, except dorsally, where it is thinner and modified in connection with the insertion of circular muscles (fig. 8). The duct is surrounded by a strong layer of circular muscles (mrd), whose ends are inserted dorsally. The tonofibrils (tf) cross through the modified epithelium (erd) into the cuticle (crd). The receptaculum has a columnar glandular epithelium lined by a thin cuticle. Its muscle coat consists of a few scattered fibres. The receptacular glands produce a mucoïd secretion (stained blue with Azan). The ducts of these glands have a cuticular lining and are surrounded by a strong coat of longitudinal muscle fibres.

As mentioned above the anterior part of the genital cavity contains a sluicing apparatus, consisting of an elongated ridge, surrounded by a muscular horseshoe-shaped dorsal flap (cf. fig. 6). This apparatus seems to be a device for insuring fertilization of the eggs. An egg, issuing from the gonopore, is retained by the dorsal flap and rests below the receptacular duct. After fertilization, contraction of the various muscles pull the flap forward, thus liberating the egg. At the same time the contractions reduce the volume of the anterior part of the cavity and push the egg backwards via the membranous part of the cavity to the genital aperture.

In a female, fixed in copula, there is a mass of spermatozoa mixed with mucoïd secretion in the muscular genital cavity. The dorsal flap is retracted. Spermatozoa are also found in the receptacular duct and the receptaculum, in both mixed with red-staining secretion produced by their glandular epithelia.

Finally, some of the general muscles of the abdominal apex may be dealt with in a few words. In the 6th segment the external and internal sternal muscles are unmodified (cf. fig. 7). In the 7th segment the external sternal muscles are still unmodified, while the innermost bundles of the internal sternal muscles (msp 7) insert at the anterior part of the genital cavity. In the 8th segment the mesial bundles of the external sternal muscles have disappeared and the innermost parts of the internal sternal muscles (msp 8) are attached to the genital cavity. In the 9th segment there are three separate



Figs. 9—11. — 9. Transverse section of the copulatory organ at the level of one of the gonopores. Azan stain. (ag=accessory gland, de=ejaculatory duct, ds=seminal duct, gp=gonopore, mi=internal bundle of muscle fibres of the copulatory organ, mp=ventral peripheral muscle fibres of the copulatory organ, vs=seminal vesicle.) — 10. Sagittal section of the copulatory organ, ventral part. Azan stain. (mi=origin of the internal bundle of intrinsic muscles of the copulatory organ, mp=origin of some of the ventral peripheral muscle fibres of the copulatory organ, mtr=spiniform microtrichia on the ventral surface of the copulatory organ, pa=ventral end of the penial armature). — 11. The central parts of the copulatory organ, as shown in fig. 9. (ag=accessory gland, demonstrating its thin wall and empty appearance, de=ejaculatory duct with rather strong muscle coat, eds=epithelium of the seminal duct, mi=internal bundle of muscle fibres of the copulatory organ, sp=sperm mass inside the vesicular duct.)

bundles of internal sternal muscles. The lateral ones are the ventral rectal muscles and the mesial ones form the subanals. The intermediate pair is inserted between the base of the subanal lobes and the ventro-mesial border of the sclerotized bases of the cerci. In the male these intermediate bundles form the retractors.

Reference

- BRINCK, P. 1955. Reproductive system and mating in Plecoptera. *Opusc. Ent.* Vol. 21, pp. 57—127, 27 figs. Lund 1956 (printed 1955).