

A Comparative Study of
the Genital Segments and the Genital Chamber in

Female Trichoptera

By ANKER NIELSEN

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Synopsis

Detailed studies of the genital segments, the genital chamber and their musculature have been undertaken in the same 26 species as in my 1957 paper on the males. In addition two other species have been studied more cursorily. For comparison with the genital segments a brief description is given of the pregenital segments and their musculature. More often the genital chamber has an extremely complex shape, no doubt unrivalled among insects. Most Trichoptera have a bursa copulatrix, to all probability homologous with those in Mecoptera and Lepidoptera. Various special glands are briefly described. Some speculations have been made as to the plesiomorphic condition in Trichoptera. A theory is put forward, explaining the backward shift of the gonopore in insects other than Thysanura and Ephemeroptera.

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List of Abbreviations

- a. (as a prefix): anterior part of
 ac.: antecosta
 add.: additional
 an.: anus
 an.tb.: anal tube
 ap.: apodeme of
 bs.: bursa copulatrix, bursae
 c.: cercus
 c.e.: cut edge of
 co.dt.: colleterial duct
 co.gl.: colleterial gland
 d. (as a prefix): dorsum, dorsal part of
 dm: dorsal muscle
 d.pl.: dorsal plate
 dt.: ductus, duct of
 dt.bs: ductus bursae
 dt.sp.: ductus spermathecae
 dvm: dorso-ventral muscle
 e. (as a prefix) external part of
 g.ch.: genital chamber
 gchm: extrinsic muscle associated with the genital chamber
 gl.: glandula, gland of
 gon.: gonopod
 gonm: muscle associated with a gonopod
- i. (as a prefix): internal part of
 int.pr.: intermediate process
 m.(as a prefix): middle part of
 m (as a suffix): see IX–Xm
 op.: opening of
 ov.: oviductus communis
 p. (as a prefix): posterior part of
 pl.: pleural membrane of
 po.pr.: posterior process
 pr.sp.: processus spermathecae
 r.: rectum
 scl.: sclerite
 sp.: spermatheca, spermathecae, spermathecal
 spir.: spiracle
 sp.scl.: spermathecal sclerite
 st.: sternum
 t.: tergum
 v. (as a prefix): venter, ventral part of
 valv.: lateral valve of segment VIII
 vm: ventral muscle
 V–X: abdominal segments five to ten
 VIIa (in *Ecnomus*): sclerotized bottom of latero-ventral recess
 between segments VII and VIII
 IX–Xm: intersegmental muscle between segments IX and X

Preface

The present study is a *pendant* to my previous paper on the males (1957). The same 26 species, representing all subfamilies in North Europe (with the exception of "*sedae incertis*" *dubius* Steph., which possibly is the sole European representative of a distinct subfamily), have been investigated. In addition *Rhyacophila fasciata* Hagen has been included for comparison with *R. nubila* Zett., and *Limnephilus rhombicus* L. for comparison with *L. flavicornis* F.

In order to conform with modern nomenclature, and especially Fischer's invaluable Catalogus, some generic and specific names have been changed from those used in my 1957 paper. In these cases the name used in 1957 is given below the headline.

During my studies I ran into some difficulties. As in the males, and perhaps even more so, dissections are necessary. In preserved specimens, however, the bulky colleterial glands often have bursted, and their contents hardened to a rubber-like substance, gluing all internal organs together. Moreover, due to the increa-

sing pollution of our running waters it was difficult, if not impossible, to procure fresh material of many of the forms studied. Hence, not all my dissections have been satisfactory. In internal organs I may have overlooked some thin muscle layers, which I might have detected with polarized light.

As is customary in papers on insect morphology membranous areas are indicated with a dotting of fine points in the drawings. Parallel lines of fine points indicate muscles, though this special signature sometimes is omitted and substituted by simple dotting, e.g. in the spermatheca.

I take the opportunity to correct a misprint in my 1957 paper: On p. 7, line 25 it shall read "venter X" instead of "Venter IX".

I wish to express my thanks to my colleague, Dr. S. L. Tuxen, Zoological Museum, Copenhagen, who many years ago proposed the study of the genitalia to me, and to this Institute for excellent facilities during my work.

Introduction

Previous literature. The genitalia of female Trichoptera have been even less studied than those of the males, no doubt due to the fact that they in most genera do not provide good specific characters, or perhaps rather that these characters are not easily recognizable in pinned specimens. It is true that there exist a great number of more or less accurate descriptions and figures of the external genitalia. Especially may be mentioned Ulmer (1909, 1951), Marlier (1947: *Limnephilus*), Schmid (1953–54: Apataniinae, 1974: *Rhyacophila*), Kumanski (1963: *Rhyacophila*) and Novák (1963: *Rhyacophila*). The best descriptions, however, probably are those of *Tinodes* by Fisher (1977) and of the Hydropsychidae by Denning (1943), Tobias (1972) and McFarlane (1976).

Only a couple of papers deal with the genital chamber itself. Stitz (1904) gives diagrammatic figures of cross-sections through the genital chambers of *Molanna angustata* Curt. and *Limnephilus bipunctatus* Curt. They do not, however, convey any idea of the structure of this organ, nor do the brief remarks Unzicker (1968) makes on several species. Morton (1902) and I (1943) have described the genital chamber of *Apatania*; both descriptions need corrections and supplements.

A greater number of papers are concerned with the appendages to the genital chamber: bursa copulatrix, spermatheca and colleterial glands. Stitz (1904) confused the terms bursa copulatrix and spermatheca (receptaculum seminis), an error which has been repeated by several other authors, including myself (1943) and Gower (1967). This mistake probably was

due to the fact that in Trichoptera the sperm is transferred directly to the spermatheca, whereas in Lepidoptera (at least in Ditrysia) it first enters the bursa copulatrix. Unzicker (1968) uses the right terms.

Stitz (1904) has described the appendages mentioned above in *Molanna angustata* Curt., *Oligotricha striata* L. (*Phryganea striata* auct.), *Limnephilus rhombicus* L. and *L. bipunctatus* Curt. Various species have been treated by Cholodkovsky (1913), Dodson (1935), Khalifa (1949), Gower (1967) and Unzicker (1968: 47 species, representing all major groups of the order). In most cases the descriptions are rather summary and the figures more or less rough. I cannot confirm all the statements made by the authors mentioned above. Their papers will be further discussed on the following pages.

Pregenital segments. In the vast majority of female Trichoptera the abdomen is broadest and highest at or a little in front of the middle and tapers in an anterior and especially in a posterior direction. In *Beraea*, however, it is roughly cylindrical and has approximately the same thickness for most of its length.

In segment I the tergum is narrow in front and widening in a posterior direction. As is usually the case in winged insects it is firmly united with the metanotum. The sternum is very much reduced and indistinguishably united with the acrosternite II. The combined sclerite has a very concave, roughly parabolic anterior margin. The long, outward and especially forward directed corners form a simple articulation with the lateral margin of the tergum, the pivot for movements between thorax and abdomen.

The following description refers more particularly to the segments from III onwards.

Generally the tergum and the sternum are approximately equal in width. In *Wormaldia* and *Ecnomus*, however, the sterna are broader than the terga. In *Athripsodes*, quite on the contrary, the terga are broader and more vaulted than the sterna. The two sclerites invariably are separated by copious pleural membranes.

In some few cases the sclerites are pale and weakly defined. They always, however, easily can be distinguished from the pleural membranes by the fact that the sclerites are smooth (though provided with tiny, close-set microtrichia), whereas the membranes have fine, longitudinal wrinkles. More often the postero-mesal part of the sclerites is pale and possibly very weakly sclerotized and devoid of setae. In some few forms the sterna do not reach the posterior ends of the segments, but in *Sericostoma* the posterior margins of both the terga and the sterna are reflected, and the same is the case in *Oligoplectrum*, though only when the abdomen is contracted to form an "egg cup" (p. 146).

The antecostal suture on the tergum runs close to the anterior margin, so that the acrotergite is very short. Sublaterally, however, the suture is bent somewhat backward, and the acrotergite hence longer. This part of the sclerite is produced into a shorter or longer, laterally and more or less forward directed tongue, of which at least the distal end most often has an apodemal character. More often the antecostal suture, bent forward again, runs into the posterior margin of this extension. It rarely, however, reaches its distal end, and in a great many forms it does not enter the extension at all. In *Wormaldia*, however, the lateral end of the antecosta is much dilated and covers the whole extension, and in *Silo* there is a reinforcement in the front margin of the extension besides the antecostal suture in its hind margin.

Tergum I has, for its whole length, a very strong suture at the lateral margin. At some

distance from the posterior end it is forked. The following terga also have a pair of lateral sutures, but they run in a varying, though always small distance from the lateral margin. They are not as strong as the sutures on tergum I, and in some few cases they are even indistinct, especially on the posterior segments. In *Agraylea* and *Hydroptila* there is no connection between the antecostal suture and the longitudinal suture, but in other forms the latter issues from the top of the sublateral, backward bend of the antecostal suture. In a great many forms, however, the antecostal suture does not extend beyond the anterior end of the longitudinal suture. The latter then appears as a backward bent continuation of the antecostal suture.

As to the length of the longitudinal suture there is a very great variation. It never reaches the posterior margin of the tergum, though in many forms it extends for most of the length of the segment. On the other hand, in *Psychomyia*, *Polycentropidae* and *Silo* it only covers one half or even less of the length of the tergum. It often becomes shorter and perhaps also less distinct on the posterior segments, but in *Psychomyia* it quite on the contrary becomes longer.

That part of the tergum which lies laterally to the suture often is paler than that lying mesally to the suture, perhaps more weakly sclerotized and devoid of setae.

A paired mesal longitudinal suture, in front issued from the antecostal suture, is found in *Lype*, *Psychomyia*, *Hydroptilidae*, *Eclisopteryz*, *Apatania* and *Silo*. It never reaches half the length of the segment, and most often it is considerably shorter. It is situated approximately in the middle of each half of the tergum. In *Beraea* an unpaired longitudinal suture is slightly indicated on the anterior segments.

The front margin of the sternum, from III onward, is built as in the tergum, and like the terga the sterna have a pair of longitudinal sutures, though they are lacking in *Rhyacophila*, *Agapetus*, *Wormaldia* and the *Hydroptilidae*, and

indistinct in *Agrypnia*, especially on the posterior segments. Conditions, however, rarely is exactly as in the terga. In *Lasiocephala* the lateral end of the antecostal suture is much dilated and covers the whole extension of the anterior corner, as is the case on the tergum in *Wormaldia*. In *Oligoplectrum* the antecostal suture apparently proceeds not into the hind but into the front margin of the extension of the anterior corner; this part of the suture, however, probably is a secondary structure. In *Silo* there is, as on the tergum, a reinforcement in the front margin of the extension besides the antecostal suture in the hind margin. As to conditions in *Sericostoma* see p. 158.

More often the sternal longitudinal suture appears as a backward continuation of the antecostal suture, or there is no connection between the two sutures. In *Sericostoma* the anterior end of the longitudinal suture is forked, and the same is the case on sternum V in *Lype*. The tendency for the suture to become shorter and perhaps more or less indistinct on the posterior segments is even stronger than on the terga.

In *Psychomyia* a mesal longitudinal suture is found on sternum II. It is unpaired and extends for the anterior half of the sternum. In front it is connected with the antecostal suture.

A strong transverse suture is found on the sternum in *Rhyacophila*, *Agrypnia* and the Limnephilidae as well as in *Agapetus*, though in the latter genus only on sternum V (see p. 34). On the anterior sterna it is situated at or somewhat behind the middle, on the posterior segments it is shifted backward. On sternum VII the transverse suture is lacking in *Rhyacophila* and *Apatania*, and only its lateral ends are found in *Limnephilus*, *Potamophylax* and *Ecclisopteryx*; the same is the case on sternum VI in *Apatania*. In *Agrypnia* the suture is paired in all segments; in this form its length is subject to great individual variation, but it is always shorter on the posterior segments, and on segment VII it is very short.

In *Rhyacophila*, in which lateral longitudinal

sutures are lacking, the transverse suture extends for most of the width of the sternum. Otherwise it may form a bridge between the longitudinal sutures near their posterior ends, or it may appear as a mesally bent continuation of these sutures, or there may be no connection at all between the longitudinal sutures and the transverse suture.

In most cases the costae corresponding to the sutures described above are developed only as reinforcements of the cuticle and hence appear as lines of darker colour. Some sutures, however, are developed as typical sulci. This is the case with the antecostal sutures of sterna III and IV in *Agraylea* and *Orthotrichia*, and in the former also with those on tergum and sternum II. In *Rhyacophila* and especially in *Agapetus* the transverse sternal sutures are developed as sulci. In *Sericostoma*, *Athripsodes* and *Odontocerum* the longitudinal sutures are in part developed as sulci, in *Odontocerum*, however, on the terga only. In *Agraylea* and *Orthotrichia* the antecostal suture of sternum V is developed as a shallow, rounded sulcus, and this is the case with all sutures in *Beraea* and *Lasiocephala*. Thus all types of sutures are found in the abdomen of Trichoptera, except that shown in fig. 1 B (p. 9).

A small unpaired tooth is found on sternum VI in *Rhyacophila*, *Agapetus*, Hydroptilidae and Limnephilidae; in *Potamophylax* there are even three small teeth. In the Limnephilidae this tooth is situated immediately in front of the transverse suture. In *Beraea* there is, strangely enough, a tooth on sternum VII, but not on sternum VI.

In *Rhyacophila*, *Tinodes*, *Wormaldia*, *Polycentropus*, *Orthotrichia* and *Athripsodes* spiracles are lacking in segment VII, and in *Holocentropus* in segments V and VI as well. In some small forms (*Agapetus*, *Lype*, *Psychomyia*, *Ecnomus*, *Agraylea* and *Hydroptila*) abdominal spiracles seem to be very feebly developed or entirely lacking.

The setae generally are more close-set and thicker, sometimes also longer on the sterna

than on the terga, though some particularly long setae may be found on the terga. On the anterior terga setae are more sparse than on the posterior ones, and on tergum I in *Agraylea* they are entirely lacking. The difference between terga and sterna in this respect no doubt is due to the fact that the terga in repose are covered by the wings.

In addition to setae there are tiny sensilla campaniformia. They are often concentrated on the acrotergites and acrosternites or parts of these. In *Agraylea* a pair of very large sensilla campaniformia is found on each tergum.

Suture and sulcus. In entomology the term suture has been misused, i.a. by myself, to designate an ecdysial line or a narrow membranous stripe between two sclerites. It should be reserved, however, for the external expression of an internal reinforcing ridge, a costa. Sutures, thus defined, take various shapes (fig. 1).

A: It is merely a rather broad and relatively shallow depression, something like corrugated iron. B: It is an open, narrow and often very deep cleft, as in the pterothoracic phragmata of many insects. C: The costa is largely solid, and the cleft is reduced to a less deep and more often sharp furrow, a sulcus. This is the typical insect suture. D: The costa is a thickening of the cuticle without any external furrow. In this case the suture generally appear only as a darker coloured line in the cuticle. All intermediates of course are found.

In recent entomological literature it has been proposed to substitute the term suture with the term sulcus. The term suture, lent from human anatomy, and meaning a line along which two things are sewn together, of course is a misnomer in entomology. In insects a suture very rarely-though sometimes-has arisen by fusion of originally separated sclerites, e.g. the suture separating e.gon. VIII and IXc in *Tinodes* (fig. 11 B, p. 39). Still, I do not recommend the procedure mentioned above. In the same insect serially homologous sutures, and in different

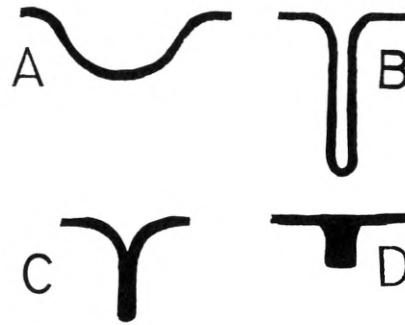


Fig. 1. Diagrammatic cross-sections through the cuticle of various types of sutures. It will be noted that the suture in all cases is represented by a furrow in the epidermis.

insects homologous sutures, may belong to either of the types. To me it seems meaningless to call a suture of type D a sulcus, which means a furrow or a cleft.

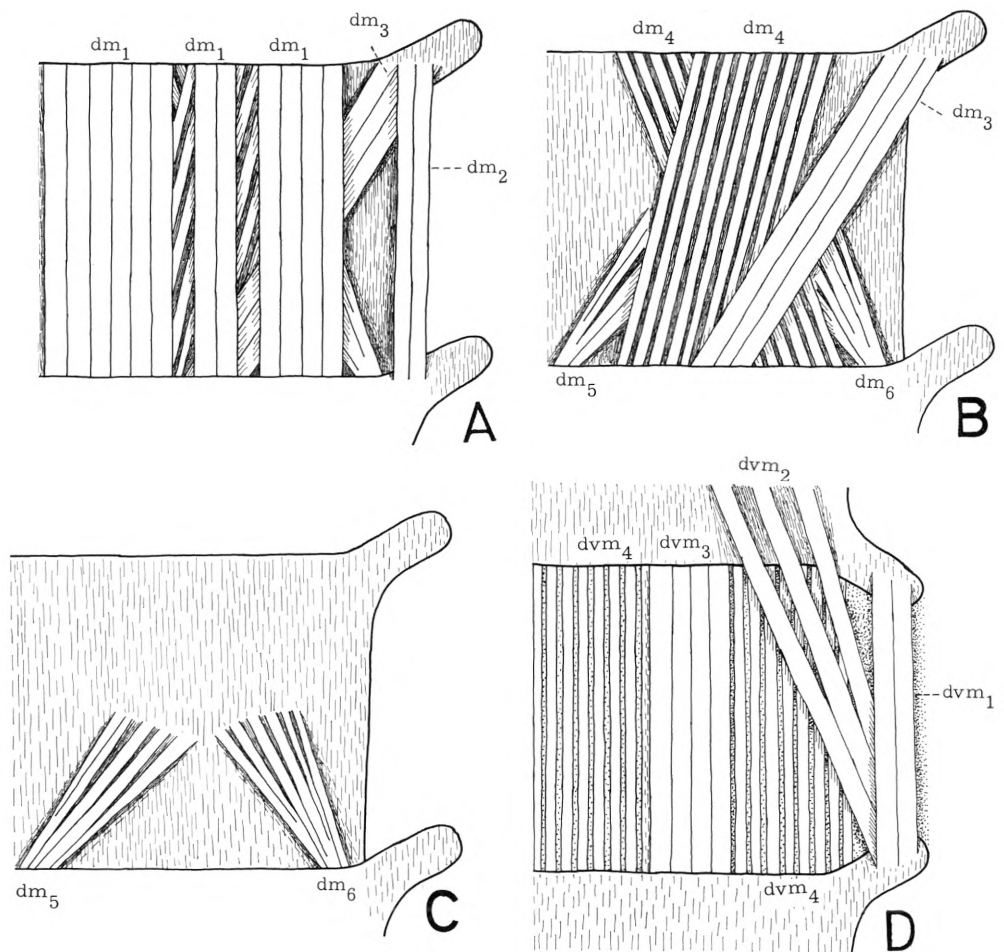
As mentioned above, the type D is by far the prevailing one in the abdomen of Trichoptera, and generally the costa is rather low at that. When a suture exceptionally belongs to type C, I have used the phrase "a suture developed as a sulcus", though this can be said to be a contradiction in terms.

Finally, it can be added that an enforcing ridge may, though not very often, be developed not internally but externally. In this case it is called a carina, e.g. VIIIa and IXc in *Tinodes* (fig. 11 B, p. 39).

The glands in segment V. In about half the forms investigated a pair of small glands is found in this segment. From a systematic point of view their occurrence is very irregular, and rather closely related forms may differ in this respect. No doubt they belong to the typical outfit of the Trichoptera.

Each gland (fig. 74, p. 145) has a pear-like to globular reservoir covered with tricellular elements. The opening is near the anterior corner of the sternum behind the antecostal suture, and mesally to the longitudinal suture if the latter is

Fig. 2. Diagrammatic representation of the musculature in a pregenital segment. A: Left dorsal muscles as seen from the inside. B: Same, internal muscle layer removed. C: Same, external layer only. D: Dorso-ventral muscles, left side as seen from the inside.



present. In *Oligoplectrum* (fig. 74, p. 145) and especially in *Sericostoma* (fig. 50 E, p. 106) and *Beraea* (fig. 56 A, p. 116) the opening apparently is in front of the backward curved antecostal suture. A closer examination, however, reveals that it actually is not so. In *Polycentropus*, *Holocentropus*, *Agraylea* and *Hydroptila* the opening is on a finger-like process. In the two hydroptilids mentioned and in the limnephilids (except of course in *Silo*, in which it is lacking) the gland is provided with an obturator muscle which, however, is not homologous in the two systematic groups.

Since the gland generally occurs in both sexes, it probably is repugnatorial, though both its size and the situation of its opening seem inadequate for this purpose. In those forms in which the gland is lacking in the female, but present in the male, it perhaps is developed as a sexual scent organ in the latter sex. At least this seems to be the case in *Agapetus* and *Hydropsyche*.

Muscles in the pregenital segments (fig 2). This musculature is subject to some variation. The muscles listed below are those present when the musculature is most complete. All muscles are flat, though the most narrow ones may approach

the cylindrical shape. Longitudinal muscles can be identified by their anterior and posterior attachments. Thus a V–VI muscle connects the segments V and VI. The dorsoventral muscles, however, are intrasegmental. If a muscle during its course approaches the mesal plane, it is said to converge; if it deviates from this plane, it diverges.

Dorsal muscles: A broad muscle (dm_1) connects successive antecostae and covers most of the width of the tergum. It most often is composed of three portions, the mesal one being the broadest, the middle one the most narrow. In the Hydroptilidae, *Odontocerum* and *Agrypnia* there are only two portions, the mesal one the broadest. In *Limnephilus* a thinner muscle (dm_{1a}) lies superficially to the mesal portion; it is narrower than the latter.

A narrow muscle (dm_2), generally consisting of two units, connects the extensions of the anterior corners of successive terga. In *Odontocerum* the broader lateral unit is a little fan-like widening in a posterior direction and partly attached to the pleural membrane.

An oblique muscle (dm_3) has its anterior attachment superficially to dm_2 . It converges more or less in a posterior direction, passing superficially to the lateral and the middle portion of dm_1 , and generally has its posterior attachment superficially to the middle portion of this muscle.

Another oblique muscle (dm_4) is superficial to dm_3 . It is approximately half as broad as each half of the tergum, very thin and composed of one layer of very fine and distinctly separated units. It may be convergent in a posterior direction, but more often is divergent. It sometimes is divided into two portions which diverge or converge, resp., to a different degree in a posterior direction. Or one portion may be convergent, the other divergent, in which case the two portions cross each other.

It is fairly certain that both dm_3 and dm_4 are lacking in the hydroptilids.

Most superficial are two short muscles, a mesal and a lateral one. The posterior attachment is to the antecosta. In an anterior direction the mesal muscle (dm_5) diverges, whereas the lateral one (dm_6) converges. Both widen fan-like toward the anterior attachment, which generally is approximately in the middle of the segment. In *Molanna* dm_5 has an almost transverse course. In *Odontocerum* this muscle is divided into two portions. Often either the mesal or the lateral muscle is lacking, and in *Oligoplectrum* both seem to be lacking.

The ventral musculature to some degree is a replica of the dorsal one, but there are some differences. The muscle vm_1 most often consists of only one portion, which covers the mesal half or even less of each half of the sternum. (The right and the left muscle, however, are separated by an interval, in which the central nervous system is situated). In return the muscle is rather thick. In *Agrypnia* and the limnephilids a thin muscle (vm_{1a}), consisting of two units, lies superficially to vm_1 . In *Molanna* and *Odontocerum* the mesal unit of this muscle is present, it lies partly mesally to vm_1 . The same is the case in *Athripsodes*, but only in segments II–III and III–IV. In II it has its anterior attachment in the middle of the segment, in III–IV it extends from antecosta to antecosta. It is fairly certain that the muscles vm_3 and vm_4 are lacking in the hydroptilids. Of the short muscles often either the mesal (vm_5) or the lateral one (vm_6) is lacking. In *Agraylea* and *Hydroptila* only vm_5 is found, and only in segments V–VI, it acts as an obturator muscle of the efferent duct of the gland in segment V (p. 10). In *Orthotrichia* a short muscle has its posterior attachment approximately on the middle of each half of the antecosta. Since it converges in an anterior direction, it probably represents the lateral muscle, vm_6 . In *Odontocerum* the mesal muscle is so short that it must be able to act as an extensor of the following segment. In *Agapetus* vm_6 is divided into two portions.

Dorsoventral muscles: A slender muscle

(dvm₁) connects the extensions of the anterior corners of the tergum and the sternum, passing laterally to the main tracheal trunk. Another slender muscle (dvm₂) has its ventral attachment to the anterior corner of the sternum. It passes mesally to the main tracheal trunk as well as to the muscles dm₂ and dm₃, spreads out fan-like, and is attached to the tergum along a longitudinal line. The attachment sometimes is to the anterior part of the tergum; in *Hydropsyche* some of the units even are attached to the preceding tergum. In others the dorsal attachment may be to the posterior part of the tergum; in *Odontocerum* some of the most posterior units are attached to the antecosta of the following tergum. The more posterior, the more mesal the attachment is. In *Psychomyia* the ventral attachment of this muscle is shifted to the pleural membrane, at the segment boundary, and the dorsal attachment is to the most posterior part of the tergum. A broad, perpendicular muscle (dvm₃) connects the lateral margins of the tergum and the sternum, passing laterally to the main tracheal trunk. Sometimes it is situated in the middle of the segment, sometimes farther backward. A layer of very fine and distinctly separated muscle units (dvm₄) is situated in the pleural membrane, i.e. each unit has numerous attachments to the bottoms of the furrows separating the fine longitudinal wrinkles of the pleural membrane. Barth (1963) has described this muscle in segments V and VI of the Brazilian odontocerid *Barypenthus* in connection with a male scent organ. It is, however, common to all pregenital segments (and often to segment VIII as well) in both sexes of all Trichoptera, and probably also to other insects with ample pleural membranes. In *Psychomyia* one unit, at the segment boundary, is considerably stronger than the others; it is lacking between segments VII and VIII.

Segment VII is almost invariably longer and more tapering than the preceding segments. It is deviating also in other respects, at least as to the ventral VII–VIII musculature. In *Agapetus*, *Ec-*

nomus, the hydroptilids, *Lasiocephala*, *Agrypnia* and especially in *Oligoplectrum* the deviations are greater than in other forms, and in *Wormaldia* this segment is very much modified.

Segment VIII. In most Integripalpia and in *Psychomyia* this segment, though shorter, apparently does not deviate much from segment VII (as to the subgenital plate see below, p. 17), being provided with a tergum and a sternum. A closer examination, however, reveals that these sclerites are not true serial homologues of the preceding terga and sterna, i.e. not occupying exactly the same areas of the segment. In *Beraea* the posterior part of the sternum is modified, and in *Oligoplectrum* the whole ventral side of the segment is strongly modified. The apparently plesiomorphic character of the segment thus probably is secondary. Nor is segment VIII in the Lepidoptera built as the preceding segments.

The really plesiomorphic shape of segment VIII probably is found in *Rhyacophila* (figs. 3, 4 and 8, pp. 28, 29 and 34). Here the anterior part of the segment is strongly sclerotized and synscleritous, forming a collar (a. VIII) from which a pair of valves (valv.) are produced backward. In *Rh. nubila* Zett. they are long and cover to the greater extent the posterior part of the segment, which is largely membranous and retractile. In *Rh. fasciata* Hag. (fig. 8) they are considerably shorter. In *Agapetus* (fig. 9, p. 35) part of the segment is synscleritous, and the valves can easily be recognized, though they are not so pronounced as in *Rhyacophila*. In *Lype* (fig. 14, p. 45), too, the segment is synscleritous, but laterally the sclerite is weakly defined, and here the antecosta is interrupted. In *Agapetus* the posterior part of the segment is membranous and retractile, in *Lype* the posterior end is membranous. In *Orthotrichia* (fig. 46 and 47, pp. 100 and 102) the segment is synscleritous, and the same in the case with the anterior part in *Hydroptila occulta* Eat. (fig. 45 A, B, p. 98). In the latter the posterior part (fig. 44, p. 90) is extremely

elongated and inverted as a very complicated tube, extending far forward.

In the remaining Annulipalpia (*Wormaldia*, *Tinodes*, *Psychomyia*, the polycentropids, *Hydropsyche* and *Agraylea*) there is a dorsal sclerite, which to some extent resembles the preceding terga. However, as in the Integripalpia various features prove that it is not serially homologous with the latter. In *Wormaldia* (fig. 19, p. 55) there is a larger ventral sclerite, which together with the smaller dorsal one cover most of the circumference of the segment. In *Agraylea* (figs. 39 and 40, pp. 89 and 90) there is a ventral sclerite, which is longer and broader than the dorsal one; its posterior corners are continuous behind the latter. *Hydropsyche* (fig. 34, p. 80) has an unpaired ventral sclerite, which extends much farther dorsally than the lateral margins of tergum VII and, judged by the musculature, comprises also a part of the dorsum. *Ecnomus* (fig. 30, p. 73) has a pair of ventral sclerites, and in *Polycentropus* (fig. 22, p. 59) and *Holocentropus* (fig. 26, p. 67) the ventral side has a rather elaborate equipment of sclerites.

Traces of structures which possibly are homologues of the valves in *Rhyacophila* are found in *Orthotrichia*. In the polycentropids and in *Hydropsyche* the posterior corners of the ventral sclerites are produced into "ventral plates", no doubt homologues of the ventral parts of the valves in *Rhyacophila*. (Recently—1977—Fisher has described similar "ventral lobes" in *Tinodes assimilis* McL. and *T. machlachlani* Kimmins). In *Hydropsyche* they are joined by processes from the posterior corners of the dorsal sclerite. Even in *Agrypnia* among the Integripalpia the posterior corners are produced into a pair of small plates, which may be remnants of valves.

In *Rhyacophila*, *Agapetus*, *Hydroptila* and *Orthotrichia* the anterior margin of the sclerite on segment VIII are produced into a pair of rod-like apodemes (ap. VIII) of varying length. In *Wormaldia* and *Agraylea* the same apodemes are present, here issued from the ventral sclerite.

In the polycentropids, *Hydropsyche*, *Lasiocephala*, *Oligoplectrum*, *Agrypnia* and the limnephilids the plate formed of the gonopods (see p. 17) is not sharply delimited from the ventral side of segment VIII. As to *Hydroptila occulta* Eat. see p. 96.

In *Agapetus* (fig. 9 A, p. 35) and the hydroptilids (figs. 40, 44, A, 45, A, B, pp. 90, 96 and 98) segment VIII is provided with a structure (gl. VIII) which possibly is a gland. In the hydroptilids it has a very complicated build.

The dorsal VII–VIII musculature in the Integripalpia does not deviate from that in the preceding segments, but this may perhaps be a secondary condition, a male character acquired by the female, like the antlers in the reindeer doe. That structures characteristic of one sex are acquired by the other is not an unknown phenomenon among insects. Thus, in the bark-beetles (Scolytidae), "structures which in one species or genus characterize the male may, in another genus or species, be peculiar to the female" (Hopkins 1894, quoted from Richards 1927). In the Annulipalpia the muscles are fewer in number and not easily homologued with those of the preceding segments.

In *Rhyacophila*, *Agapetus* and *Wormaldia* there are only two muscles; one is at one end attached to the apodeme of segment VIII and no doubt is dm_6 , the other probably is dm_1 . In the hydroptilids there are, in addition to these two muscles, a third one which probably is dm_2 . In *Agraylea* and *Hydroptila* dm_6 is bipartite, in *Orthotrichia* even tripartite. In the polycentropids and in *Hydropsyche* three muscles are found, in the former possibly dm_1 , dm_3 and dm_6 , in the latter dm_2 , dm_3 and dm_6 (or dm_5 ?). As to the psychomyids my dissections were not successful, but conditions probably are as in the polycentropids.

The dorsoventral musculature in segment VII is developed as in the preceding segments, with the exception of *Wormaldia*, in which it is reduced and highly specialized.

Ventral VII–VIII musculature. This musculatu-

re does not seem to be serially homologous with that of the preceding segments. A muscle which to all probability is vm_6 is found in *Rhyacophila*, *Agapetus* and *Wormaldia*, and possibly also in *Sericostoma*, *Odontocerum* and the limnephilines. In *Agraylea* and *Orthotrichia* it is the only muscle present, and in *Hydroptila* it, too, is lacking. A possible vm_2 is seen in *Limnephilus* and perhaps in *Potamophylax* and *Apatania*.

In *Rhyacophila*, *Agapetus* and *Wormaldia* the ventral musculature is an exact replica of the dorsal one (as to muscles associated with the oviduct see, however, below), but whereas the lateral muscle probably is vm_6 , it is, considering conditions in other Trichoptera, doubtful that the mesal one is vm_1 .

In the Psychomyidae, the Polycentropinae and the Integripalpia there are, besides those mentioned above, an internal and an external muscle, the former passing above (dorsally to), the latter below (ventrally to) the lateral oviduct. The external muscle generally is convergent, the internal one divergent in a posterior direction.

The external muscle rather often is composed of two portions, generally with a different course. One or (*Potamophylax*) both may have the anterior attachment rather far behind the front end of sternum VII, and the same is the case with the single muscle in *Apatania*. It thus may have some resemblance to vm_5 , but to all probability does not represent this muscle. In *Potamophylax* one, in *Limnephilus* and *Apatania* the single muscle has its posterior attachment behind the front margin of segment VIII.

In *Polycentropus* and *Holocentropus* there is, in addition to the internal muscle, a transverse musculature above the common oviduct for almost the whole length of segment VII. Whether it in the middle is attached to the oviduct I have been unable to decide with certainty, but at least it adheres to the oviduct by dissection. It probably is a derivate of the internal muscle. In *Ecnomus* it is the only internal muscle present, and it is found in *Wormaldia*, too. A similar

structure is seen in *Lype*: the anterior end of the common oviduct receives fine muscle units both from the antecosta of sternum VII and from the ventral sclerite of segment VIII.

In *Molanna* and *Limnephilus* also the internal muscle has two portions, but none is attached to the oviduct. In *Sericostoma* and *Apatania* I have been unable to find the internal muscle.

In *Rhyacophila* a muscle has its posterior attachment to the front margin of segment VIII and its anterior attachment to the dorsal side of the common oviduct. It probably is a homologue of the internal muscle described above, its anterior attachment being shifted to the oviduct. Whether this muscle is present in *Agapetus* I have been unable to ascertain, but probably it is not. A similar muscle is found in *Hydropsyche*. The only other ventral muscle in this genus is a layer of fine bands for the whole width of sternum VII, below the oviducts.

The discrepancy between the ventral musculature in segment VII and that in the preceding segments, and especially the muscles crossing above the oviducts, may be explained by assuming that the shift of the gonopore from behind segment VII to behind segment VIII has been accomplished by the limbs of segment VII having united with each other and with segment VIII, which also explains that the apparent sternum VIII in many Trichoptera is not serially homologous with those of the preceding segments. In Thysanura the functional gonopore is behind segment VIII, but the ventral side of this segment is longitudinally cleft (Barth 1962). I am inclined to consider the apposed margins of the cleft as the gonapophyses VII, united with segment VIII. Conditions in Ephemeroptera, with paired though close-set gonopores behind segment VII, may very well be secondary, due to the lack of an ovipositor, which will seem to belong to the typical outfit of insects.

Segments IX–XI and the genital opening. Structures which probably are cerci are present in the Annulipalpia, though it is difficult to be certain,

since no musculature is associated with them. In *Agapetus* they are even two-segmented. Otherwise segment XI cannot be recognized as a separate entity. Nor is there any distinct boundary between segments IX and X, though in many Annulipalpia structures which may be termed segment IX and segment X, resp., are found, separated by membrane and even having a mutual articulation. However, certain features, i.a. the musculature, suggest that the division is secondary. The combined structure is extremely variable in shape.

As to those parts which with certainty can be attributed to segment IX, the most primitive condition apparently is found in some Integripalpia (*Sericostoma*, *Berae*, *Athripsodes*, *Molanna* and *Odontocerum*), in as far as sclerites which might be interpreted as tergum and sternum, resp., are present. However, as is the case in segment VIII, a closer examination reveals that they are not serially homologous with the pregenital terga and sterna. Nor is a primitive sternum to be expected in this segment. Since the spermatheca and the colleterial glands open on venter IX (cp. below and p. 17), at least the mesal part of the latter must enter into the composition of the genital chamber.

On the other hand, in *Rhyacophila*, *Wormaldia* and the hydroptilids the very slender segment IX, sclerotized to a varying degree and provided with apodemes like those of segment VIII, forms part of an extensile "Legeröhre". This, too, could be considered as primitive, since it is reminiscent of conditions in Mecoptera, though not in the Boreidae, which in my opinion are the most primitive representatives of the order in this respect. *Agapetus* also has a "Legeröhre", but segment IX is not much thinner than segment VIII.

As to the genital opening, however, I think that the most plesiomorphic condition is found in *Ecnomus* (fig. 30 C, p. 73). Here the rather large and conical segment IX is sclerotized for the greater part of its circumference, but has on

the ventral side a big, longitudinal, largely membranous furrow. For most of their length its margins are closely apposed, so that the furrow forms a functional tube. Quite in front, however, the margins diverge, but here the cleft is closed by a sclerotized structure (e.gon.VIII) which obviously belongs to segment VIII. The opening of the spermathecal duct is above this structure, which is entirely free of segment IX, that of the colleterial duct behind its posterior end, i.e. from a purely morphological point of view both are outside the genital chamber, a very primitive character indeed, which cannot be found in insects with the genital opening between segments IX and X. In my opinion it is likely that gon. VIII represents the united gonopods of segment VIII.

In a ventral view segments VIII and IX of *Tinodes* (fig. 11, p. 39) have in their main features, a great resemblance to those of *Ecnomus*, but the structure e.gon.VIII is coalesced with the margins of the cleft in segment IX. In this form, too, the openings of both the spermathecal and the colleterial duct from a morphological point of view are situated outside the genital chamber, and the same is the case with that of the colleterial duct in *Polycentropus* (p. 65) and *Holocentropus* (p. 70).

In *Rhyacophila* (fig. 3 B, p. 28, 4 A, p. 29) *Agapetus* (fig. 9 A, C, p. 35), *Wormaldia* (figs. 19, p. 55, 20, p. 56) and the hydroptilids (figs. 41, p. 92, 45 C, D, p. 98, 48, p. 103) a structure is found which clearly is homologous with e.gon. VIII in *Ecnomus* and *Tinodes*, but it extends much farther backward and has for its greater length coalesced with the margins of the cleft in segment IX, so that it forms a lower lip, not only of the functional but also of the morphological genital opening. (In the special descriptions it will sometimes be referred to as the ventral side of segment IX). Moreover, except in *Wormaldia*, it is largely membranous. In *Rhyacophila*, *Agraylea* and *Orthotrichia* the lip is slightly bilobed, suggesting a paired origin of e.gon.VIII. In

Wormaldia the dorsal (internal) side of the latter is bisected by a longitudinal furrow.

On the inside of the folds flanking the furrow in segment IX in *Ecnomus* (fig. 31, p. 75) and the psychomyids (figs. 12, p. 41, 14, p. 45, 15, p. 47; 18, p. 52) structures are found which suggest that they have arisen by fusion of originally paired organs with the ventral side of segment IX itself. These organs possibly must have been the gonopods of segment IX. In *Agapetus* and the hydroptilids the genital opening is surrounded by four lips, the ventral one mentioned above, a dorsal one (segment X, see below) and a pair of laterals. The latter possibly represent the distal ends of the gonopods of segment IX. (See also p. 17).

In *Polycentropus*, *Holocentropus* and *Hydropsyche* conditions are highly specialized and very complicated. An atrium with an upper and a lower lip is formed. *Holocentropus* (figs. 26, 28 and 29, pp. 67, 69 and 71) seems to be the least specialized. Both the out- and the inside of the upper lip is formed by segment IX, including its gonopods except for the most posterior part of the inside, which belongs to segment X. The posterior part of the outside and the whole inside of the lower lip is formed by the gonopods of segment VIII, which are not sharply delimited from the ventral side of segment VIII itself. An unpaired, sclerotized fold (p.i.gon.VIII) on the inside of the lower lip is reminiscent of the tongue e.gon. VIII in *Ecnomus* and *Tinodes*. A pair of sclerotized folds (gon.IX) on the inside of the upper lip possibly to their greater extent represents the gonopods of segment IX. The colleterial duct opens on the inside of the upper lip, outside the genital chamber.

In *Polycentropus* (figs. 22–25, pp. 61–67) the outside of the upper lip is formed by segment IX, which forms also the latero-anterior parts of the inside of the lower lip. At least most of the inside of the upper lip is formed by segment X, which also forms the meso-anterior part of the lower lip. The outside of this lip is made up of

the gonopods VIII, which form also the posterior part of the inside, and perhaps segment VIII itself. Paired structures on the inside of the lower lip, surrounding the opening of the genital chamber, probably represent part of gonopods VIII and IX and part of segment X.

In *Hydropsyche* (figs. 34, p. 80, 35 A, p. 82; 37 A, p. 84; 38 B, p. 86) the outside of the upper lip as well as the antero-lateral parts of the outside of the lower lip is formed by segment IX. The greater part of the lower lip is made up of the gonopods VIII. The antero-mesal part of the inside of this lip is formed by segment X, which forms also at least most of the inside of the upper lip. The lateral parts of the inside, however, seem to be formed by the gonopods IX.

In *Polycentropus*, *Holocentropus* and *Hydropsyche* segment IX carries a pair of glands.

In *Rhyacophila*, *Agapetus*, *Wormaldia*, *Holocentropus* (cp., however, p. 68) and the Hydroptilidae setae are lacking on segment IX, but in these forms, except *Agapetus*, *Holocentropus* and *Orthotrichia*, some sensilla campaniformia are found.

What probably is the most plesiomorphic condition among Integripalpia is found in *Sericostoma* (fig. 50, p. 106). As in the hydroptilids the genital opening is surrounded by four lips. The ventral one, carrying "sternum IX" and at the anterior end overlapped by a fold of venter VIII, possibly represents gonopods VIII, the lateral ones (e.gon.IX) the distal ends of gonopods IX.

Structures which possibly represents the distal ends of gonopods IX are found also in *Molanna* (fig. 61, p. 125) and *Odontocerum* (fig. 64, p. 130), but in *Molanna* (p. 130) the musculature suggests that they also contain parts of segment IX itself.

In *Lasiocephala*, *Oligoplectrum*, *Agrypnia* and the Limnephilidae the external parts of the gonopods are much reduced in size, or at least in length, and form MacLachlan's "vulvar scale". (As to *Oligoplectrum* and *Agrypnia* see pp. 146 and 151). In the three first mentioned genera

the "vulvar scale" has united with sternum VIII, leaving no distinct boundary. In the following the combined structure sometimes will be called the "ventral plate", which is not homologous with the ventral plates in the Polycentropidae and *Hydropsyche*. In the Limnephilidae the "vulvar scale" is rather clearly separated from sternum VIII, though less so in *Apatania*. This division, however, may be secondary.

In *Lasiocephala* and more distinctly in the Limnephilinae and in *Ecclisopteryx* the "vulvar scale" is divided into an unpaired middle lobe (e.gon.VIII) and a pair of side lobes (e.gon.IX). In *Apatania* the external parts of gonopods IX are still more reduced, but the musculature shows that the structure labelled IXd in fig. 96 A (p. 181) must contain parts of this gonopod. In *Silo* (figs. 98, p. 185, 99, p. 186) the side lobe has united with part of segment IX itself, forming a very elaborate structure. The two components, however, can easily be distinguished.

In *Silo* the middle lobe is slightly bilobed, suggesting a paired origin, and the same is the case with the posterior margin of the vulvar scale in *Oligoplectrum* and *Agrypnia*.

Therefore, I feel forced to conclude that the female gonopore in Trichoptera is not, as generally believed, situated between segments IX and X, but at the posterior end of the ventral side of segment VIII, as is usually the case in insects other than Thysanura and Ephemeroptera. The apparent posterior situation is due to the fact that the gonopods VIII and IX have coalesced with each other and those of segment IX with the segment itself. This theory probably is corroborated by the musculature described on pp. 25-26.

It implies that at least the posterior part of the lateral and ventral walls of the genital chamber with their generally very elaborate structures are formed by the gonopods.

Segment X. As mentioned above the exact boundary between this segment and segment IX cannot be stated. What may be called the exter-

nally visible part of segment X in the Annulipalpia is much shorter and generally also less wide and lower than segment IX. In *Rhyacophila*, *Agapetus* and the hydroptilids it forms a rather simple upper lip of the genital opening. In *Rhyacophila* and *Orthotrichia* the ventral side is transversely concave, and in the former genus the segment is slightly bilobed. In other Annulipalpia it is almost or entirely (*Psychomyia*, *Polycentropus*, *Hydropsyche*) divided into a pair of valves.

The segment has a single, unpaired sclerite or a pair of sclerites forming simple, often elastocuticular articulations with the sclerite of segment IX, generally with paired reinforcements of the latter. In *Tinodes* there is besides a pair of lateral sclerites an unpaired dorsal sclerite. In *Wormaldia* the lateral sclerotizations are continuous with the sclerite of segment IX, and there are no articulations. In *Ecnomus* the sclerites of segments IX and X do not articulate with each other, but that of segment IX sends an extension onto the postero-mesal part of segment X. In *Hydropsyche*, on the other hand, there is a very complicated articulation between segments IX and X.

In the Integripalpia segment X is comparatively larger than in the Annulipalpia, and generally has a very elaborate shape. Its sclerite is continuous with that of segment IX. In *Athripsodes* and especially in *Beraea*, however, the segment is largely membranous, probably due to a reduction.

Various things go to prove that segment X, at least in many forms, has encroached upon the dorsal wall of the genital chamber. Thus the anus is situated on the dorsal wall of the latter in *Rhyacophila*, *Agapetus*, the Psychomyiidae, *Wormaldia* and *Athripsodes*, in *Agapetus* and *Wormaldia* even rather far forward. In the Psychomyiidae, however, it is in that part of the chamber which from a morphological point of view is open ventrally. In the Hydroptilidae and in *Sericostoma* and *Odontocerum* the anus is just at the opening of the genital chamber. Further, a

study of the musculature gives evidence that in *Beraea*, *Lasiocephala*, *Agrypnia*, *Limnephilus*, *Potamophylax* and *Ecclisopteryx* a greater or smaller part of the dorsal wall of the genital chamber belongs to segment X.

In *Polycentropus* and *Hydropsyche* segment X forms the greater part of the inside of the upper lip of the atrium as well as the antero-mesal part of the lower lip. In *Holocentropus* the position of the opening of the colleterial duct shows that mesally only a small, posterior part of the inside of the upper lip belongs to segment X.

In *Wormaldia* a rather large, probably glandular sac opens through a narrow duct on the dorsal side of the genital chamber, between the anus and the opening of the colleterial duct. In *Hydropsyche* a great part of the inside of the upper lip of the atrium is inverted as an anal sac, the wall of which is partly glandular.

As to the equipment with sensilla it may especially be noted that a gradual transition from normal setae on the anterior end of segment X to sensilla campaniformia on the posterior end of this segment is seen in the Annulipalpia. On the same region there can be found, in one form typical setae, in another intermediates between setae and sensilla campaniformia, and in a third typical sensilla campaniformia. To me this seems to represent a genetical puzzle.

Cerci probably are represented in the Annulipalpia by a pair of small and slender, very thin-walled, fingerlike processes, carrying a small number of sensilla, on the posterior end of segment X. Generally they are unsegmented and at most a little more than half as long as segment X, or even shorter. In *Agapetus* (fig. 9, p. 35), however, the cercus is almost twice as long as segment X and by a constriction divided into two segments. In the polycentropids (figs. 22, 26, 30 and 31, pp. 59, 67, 73, and 75) and in *Hydropsyche* (figs. 34, 35 A, 37 A, pp. 80, 82, 84) the cercus is flanked, dorsally and ventrally, by a pair of similar, though a little different,

processes. No muscles are associated with the cerci, and in Integripalpia no trace of cerci is found.

The sensilla on the cercus generally are developed as sensilla campaniformia. It will seem that at least those distally on the cercus can have only a tactile function, and in fact Spinola & Chapman (1975) have shown by electrophysiological studies that sensilla campaniformia in cockroaches are sensitive to tactile stimuli. Distally on the cercus of *Hydropsyche* (p. 84) sensilla are found which, according to their general appearance, may be chemoreceptors.

Dorsoventral muscles in segment VIII is lacking in *Rhyacophila*, *Agapetus*, *Psychomyia* and the Hydroptilidae. In *Wormaldia* there is, as in segment VII, a specialized musculature, which cannot be homologized with that in the preceding segments. The Polycentropidae have one muscle, which possibly is dvm_3 , and *Polycentropus* in addition one, which possibly is dvm_1 . In *Hydropsyche* dvm_2 and dvm_4 are found, and in most Integripalpia dvm_1 , dvm_2 and dvm_4 are present, though in *Lasiocephala* dorso-ventral muscles are lacking, and in *Oligoplectrum* only dvm_4 seems to be present. The occurrence of dorso-ventral muscles in segment VIII, however, very likely is secondary (cp. p. 13: dorsal VII–VIII musculature).

The VIII–IX musculature. The muscles are fewer in number than in the pregenital segments, especially in those forms which possibly are plesiomorphic in this respect. In *Agrypnia* and *Limnephilus* conditions approach those in the pregenital segments, but this may very likely be a secondary phenomenon.

The dorsal muscles are very difficult to homologize with those of the preceding segments, and as to the ventral muscles this is still more the case, no doubt because the ventral side of "segment IX" is largely made up of the gonopods. The interpretation given in the table on p. 26 must be considered as quite tentative.

The muscle dm_1 generally consists of only one

portion, though sometimes there are two, in *Sericostoma* and *Silo* even three. In *Rhyacophila*, *Agapetus* and *Orthotrichia* the muscle interpreted as dm_2 might also be considered as a ventral muscle (vm_2) or perhaps a combination of these two muscles, in *Wormaldia*, *Agraylea* and *Hydroptila* maybe rather as vm_2 . Otherwise the only ventral muscle present (and not always) is vm_6 . Nor could ventro-mesal muscles be expected, since the mesal part of venter IX has entered into the composition of the genital chamber.

However, the muscle inserted to the spermathecal sclerite (see below) must be considered as a ventral VIII-IX muscle, perhaps vm_5 , but more likely a derivate of vm_6 .

In *Athripsodes*, *Molanna*, *Odontocerum* and *Ecclisopteryx* this musculature was not thoroughly investigated. The muscle vm_6 is present in *Molanna*, whereas it is rather certain that it is lacking in *Athripsodes* and *Odontocerum*.

In *Agrypnia* and in *Apatania* the muscle interpreted as dm_6 is divided into two portions.

VIII-IX muscles

1	dm_1	dm_2	dm_3	dm_{4a}	dm_{4b}	dm_5	dm_6	vm_6
<i>Rhyacophila nubila</i>	+	+	+			+	+	
<i>Agapetus fuscipes</i>		+				+	+	+
<i>Tinodes waeneri</i>	+							
<i>Lype phaeopa</i>	+		+					+
<i>Psychomyia pusilla</i>	+							+
<i>Wormaldia occipitalis</i>	+	+				+	?	+
<i>Polycentropus flavomaculatus</i>	+					?	?	
<i>Holocentropus dubius</i>	+					?	?	
<i>Ecnomus tenellus</i>	+		+				+	
<i>Hydropsyche</i>	+					+	+	+
<i>Agraylea multipunctata</i>		+				+	+	+
<i>Hydroptila occulta</i>		+					+	+
<i>Orthotrichia costalis</i>		+				+	+	+
<i>Sericostoma personatum</i>	+			+	+			
<i>Beraea maurus</i>	?			+	+	+		
<i>Athripsodes cinereus?</i>								
<i>Molanna angustata</i>	+	+			+	+		+
<i>Odontocerum albicorne?</i>	+	+		+	+			
<i>Lasiocephala basalis</i>	+					+		
<i>Oligopteryx maculatum</i>	+	+		+	+		+	+
<i>Agrypnia pagetana</i>	+	+			+		+	+
<i>Limnephilus flavicornis</i>	+	+	+	+	+		+	+
<i>Potamophylax latipennis</i>	+							+
<i>Ecclisopteryx dalecarlica?</i>								
<i>Apatania zonella (at least)</i>	+						+	+
<i>Silo nigricornis (at least)</i>	+				+		+	

The genital chamber varies much in length. In most Annulipalpia it reaches the anterior end of segment VIII or the posterior end of segment VII, but by retracted "Legeröhre" it extends in *Hydroptila occulta* beyond the middle of segment VII, in *Wormaldia* even far into segment VI. In *Ecnomus*, on the other hand, it reaches only the posterior end of segment VIII. In the Integripalpia the anterior end generally lies in the middle of segment VIII, but in *Molanna*, *Odontocerum* and *Potamophylax* it extends to the boundary between segments VII and VIII, in *Beraea* to the middle of segment VII, and in *Sericostoma* and *Apatania* even to the boundary between segments VI and VII; (in the latter genus the dorsal branch-see below-only). In *Athripsodes*, on the other hand, it reaches only the posterior end of segment VIII.

The genital chamber receives the common oviduct, the spermathecal duct and the colleterial duct. Further there is, in most forms, a ductus bursae opening between the common oviduct and the spermathecal duct.

In some forms the anterior part of the genital chamber is divided into a dorsal and a ventral branch. In *Athripsodes* (fig. 59, p. 122) the two branches are of equal length, in *Apatania* (fig. 96, p. 181) the dorsal, in the Hydroptilidae (fig. 42 C, p. 94) and in *Agrypnia* (fig. 78, p. 153) the ventral branch is the longer. In *Potamophylax* (fig. 90, p. 171), *Ecclisopteryx* and *Silo* (fig. 101, p. 191) there is a suggestion of a very short dorsal branch. The oviduct, the ductus bursae and the ductus spermathecae open into the ventral branch, the colleterial duct into the dorsal branch.

Apart from those described below no definite structures are seen in the genital chamber of *Rhyacophila*, *Agapetus* and *Wormaldia*, but this very likely is a secondary condition. In the Hydroptilidae also the genital chamber has a rather simple structure but this, too, may be considered as secondary. This opinion is substantiated by the fact that the genital chamber in

the very advanced genus *Oligoplectrum* has a much simpler structure than in its relatives.

The opening of the ductus spermathecae is on the dorsal wall of the anterior part of the genital chamber though, as mentioned above, in *Ecnomus* and *Tinodes* outside the morphologically closed part of the latter. That part of the dorsal wall which carries the opening may be horizontal or more or less steeply ascendent, even vertical (*Wormaldia*, *Holocentropus*).

In *Tinodes* (fig. 12, p. 41) the opening is on a membranous papilla, in all other forms it is on a spermathecal sclerite (and in *Tinodes* the papilla is flanked by sclerotized structures). Part or whole of the sclerite bulges into the lumen of the genital chamber as a processus spermathecae, the shape of which is extremely variable, often very complicated, and which may comprise also membranous parts; especially the opening of the duct often is on a membranous area. In *Agraylea*, *Hydroptila* and the Integripalpia the opening of the duct is on a longitudinal keel, superimposed on the processus; its posterior end often projects as a "toe", its anterior end sometimes as a "heel".

The processus spermathecae often, especially in the Hydroptilidae and the Integripalpia, projects tongue-like backward. In *Athripsodes*, *Potamophylax* and *Apatania* this tongue forms the lip between the dorsal and the ventral branch of the genital chamber. In *Agrypnia* and *Silo* this lip is behind the processus spermathecae. In the last mentioned genus it is sclerotized and of a very elaborate shape; (cp. also p. 21). In *Beraea*, *Oligoplectrum* and *Limnephilus* the tongue of the processus spermathecae forms the lower lip of the opening of the colleterial duct. (The elaborate tongue in *Silo*, mentioned above, may perhaps also be considered as a part of the processus spermathecae).

The ductus bursae opens between the processus spermathecae and the common oviduct. Its proximal part, which may be sclerotized, more often is horizontal, but in some forms it is more or less downward bent, even (*Limnephilinae*,

Ecclisopteryx and *Silo*) vertical. In most Annulipalpia and some Integripalpia the processus spermathecae forms the upper lip of the crescentic opening (which in *Hydropsyche*, however, is not much flattened), but in *Polycentropus* and *Holocentropus* another structure is intercalated between the process and the opening.

In most Integripalpia the opening is in a "window" in the spermathecal sclerite in front of the processus spermathecae. The "window", the anterior side of which often is incomplete, rarely (*Beraea*; in this form the "window" actually is in front of the spermathecal sclerite) is circular; generally it takes the shape of a transverse or angular cleft, or it is reniform or crescentic. In *Apatania* and *Silo* the opening is as broad as the genital chamber. In the latter genus (fig. 104 A, p. 194) the opening is a narrow, broken cleft: the middle part is transverse, the lateral parts diverge 45° in an anterior direction; the concavity thus is opposite to that of other forms.

In *Holocentropus*, *Ecnomus* and *Apatania* the lip between the ductus bursae and the common oviduct is very thick. In *Apatania* it is sclerotized, and in *Ecnomus* it has a rather elaborate shape. In *Wormaldia* this lip has united with the processus spermathecae.

The unpaired colleterial duct opens on the dorsal wall of the genital chamber. The position varies from just behind the processus spermathecae to near the posterior end. In *Tinodes*, *Holocentropus* and *Ecnomus* the opening is behind the morphologically closed part of the genital chamber, in *Holocentropus* on the inside of the upper lip of the atrium. When the genital chamber is divided into a dorsal and a ventral branch, the opening is in the anterior end (*Hydroptilidae*, *Athripsodes*) of the former, or dorsally (*Agrypnia*) or ventrally (*Apatania*) in the foremost part of this branch. In *Potamophylax*, *Ecclisopteryx* and *Silo* the opening also is in the short dorsal branch, which means far behind. In the other forms that part of the dorsal wall which carries the opening may be horizontal or more or less steeply ascendent. In

Odontocerum and *Limnephilus* it is horizontal, but the height of the genital chamber increases abruptly behind the opening.

In *Beraea*, *Molanna* (fig. 62, p. 127, 63, p. 128) and *Odontocerum* (fig. 68, p. 135) there is a short thick, membranous tongue just in front of (below) the opening of the colleterial duct. In *Odontocerum*, in which it perhaps can be considered as a part of the processus spermathecae, it is tripartite. In *Tinodes* (fig. 12, g.ch.f, p. 41) a sclerotized tongue is seen in front of (below) the opening; its sclerite is continuous with a sclerotized bulge behind the (in this form membranous) processus spermathecae, and with structures flanking the latter. In *Psychomyia* (fig. 18, p. 52) the opening of the colleterial duct is well behind the processus spermathecae, but the posterior part of this process is developed as a thin, colourless, but apparently stiff lamella, forming a valve for the opening. In the limnephilids (fig. 84, p. 163; 102, p. 191), except *Apatania*, the opening is flanked by a pair of blunt processes (g.ch.b), obstructing the lumen of the genital chamber. A pair of processes is found also in *Sericostoma* (fig. 52 C, g.ch.b, p. 110), but here they are situated in front of the opening. In *Lasiocephala* the colleterial duct opens on a papilla, which fills almost the whole lumen of the genital chamber.

Behind the opening of the colleterial duct the dorsal wall of the genital chamber may bulge somewhat into the lumen as an unpaired longitudinal fold. The posterior end of the latter sometimes forms a tongue in front of the anus (*Tinodes*, *Psychomyia*, *Agraylea*, *Hydroptila*) or separating the genital opening and the anus (*Orthotrichia*, *Molanna*). In *Ecnomus* (fig. 31, p. 75) there is a sort of valve behind the colleterial duct; it seems to be able to close both the latter and the genital chamber anterior to it. In *Rhyacophila* (fig. 7, p. 32) the opening of the colleterial duct is situated immediately behind the processus spermathecae, and behind the opening a slender and rather elaborate, sclerotized tongue

is found; the sclerite of this tongue is continuous with that of the processus spermathecae. In *Lasiocephala* the descendent dorsal wall behind the opening of the colleterial duct is sclerotized.

In forms other than those mentioned on p. 20 the lateral and ventral walls have an elaborate shape. On the posterior part of the ventral side a structure (i.gon.VIII), suggestive of i.gon.VIII in *Tinodes* (figs. 12, p. 41, 13, p. 43), is seen in *Sericostoma* (fig. 52, p. 110), *Beraea* (fig. 56, p. 118), *Lasiocephala* (fig. 72 A, p. 141), *Agrypnia* (figs. 77, p. 152, 79, p. 155) and *Apatania* (Nielsen 1943, fig. 5 B, 8) as well as, though less obvious, in *Athripsodes* and *Molanna*. A backward directed tongue on the ventral side of the genital chamber in the Hydroptilidae (fig. 42, p. 94) possibly is a homologue. In *Lasiocephala* and sometimes in *Molanna* the structure in question shows traces of a paired origin. It is considered here as a part of the gonopods VIII.

On the lateral side of the genital chamber there is, in most forms, a longitudinal fold or system of folds, which more often are sclerotized. In the Psychomyidae and most Integriplapia a dorsal and a ventral fold, sometimes subdivided, can be recognized. In *Polycentropus* there are two sets of folds, but the ventral one is rather inconspicuous. In *Ecnomus* (figs. 31, p. 75, 32, p. 77) and in *Holocentropus* (figs. 28 A, p. 69, 29, p. 71) there is only a single lateral fold. In the former genus it is a direct continuation of the margin of the ventral cleft in segment IX. In *Holocentropus* it is a sclerotized fold on the ventral side of the upper lip of the atrium (p. 16); only its extreme anterior end projects into the genital chamber. In the Limnephilinae and in *Ecclisopteryx* the folds by shortening of the genital chamber have become anterior and posterior in position; in *Limnephilus* the right and the left folds are continuous across the ventral wall of the genital chamber.

The folds on the lateral sides of the genital chamber here are considered as part of the gonopods IX. A study of the musculature supports this view.

The shape of the anterior part of the ventral wall in the genital chamber varies, but generally there is a pair of folds flanking the processus spermathecae. In *Lasiocephala* the two sides of the spermathecal sclerite are connected by a sclerotic bow across the ventral side of the genital chamber.

The common oviduct is flattened and provided with a rather strong circular musculature, and in *Silo* there is a thin external layer of longitudinal fibres. In *Rhyacophila*, *Agapetus* and *Wormaldia* the duct is S-like bent by retracted "Legeröhre". If it extends beyond the anterior end of segment VII, which is more often the case, the proximal ends of the lateral oviducts are bent forward, downward and backward.

The bursa copulatrix is a simple, roughly globular, elongate or pear-like sac. By Cholodkovsky (1913) it is called "birnförmige Drüse", and this term (in translation) is used also by Khalifa (1949) and Gower (1967). It is provided with a thin cuticle and generally a very thin epithelium. The ductus bursae has, at least for most of its length, a rather strong circular musculature. In the proximal portion of the duct part of or the entire wall often is sclerotized and non-muscular, and the sclerite is continuous with the spermathecal sclerite. The duct in most cases is flattened and more or less funnel-like dilated toward the opening.

Wormaldia is unique in having a paired bursa copulatrix. The two small sacs, which open through a common duct, have like the ductus bursae a strong circular musculature. The same condition is described by Unzicker (1968) in two other philopotamids, *Chimarrha* and *Sortosa*, but the sacs are stated to be of unequal size. In several other forms this author has described the bursa copulatrix as consisting of a larger "primary" and a smaller "accessory" sac, but these observations I have been unable to confirm. In *Brachycentrus subnubilis* Curt. the distal end of the bursa is bilobed (Dodson 1935); this author stresses that it is a peculiarity for the genus *Brachycentrus*.

The function of the burssa copulatrix is obscure. It can be considered certain that sperm never enters it. The term thus is misleading, but is used here since the organ to all probability is homologous with the bursa copulatrix in Lepidoptera (see below). It may perhaps have a secretory function in the late pupa or early pharate adult. In pharate adults of *Polycentropus* I found an 8μ thick epithelium, and the lumen filled with an unidentifiable substance. In a specimen of *Rhyacophila nubila* Zett. I found it filled with an amorphous substance, and in a specimen of *Hydropsyche* there was a loose, brownish substance in the bursa. Finally, in a specimen of *Agrypnia pagetana* Curt. it contained a brownish-yellow, hard substance. The three last mentioned cases, however, perhaps have been anomalies.

In one specimen of *Odontocerum albicorne* Scop. a seta was seen in the bursa.

In most cases the openings of the ductus bursae and the common oviduct are close together, but sometimes they are separated by a thicker lip, which may have a rather elaborate shape; (see *Wormaldia*, *Polycentropus*, *Holocentropus*, *Ecnomus*, *Apatania* and *Silo*).

A bursa copulatrix is lacking in the Psychomyiidae and the Hydroptilidae. In *Tinodes* (figs. 12 and 13 A, pp. 41 and 43) the ventral wall of the genital chamber just in front of (below) the opening of the common oviduct bulges downward and forward as a large, partly sclerotized sac, but this structure of course is not homologous with the bursa copulatrix in other forms. A similar, though much smaller, sac is seen in *Lype* (fig. 15, p. 47).

In entomology the term bursa copulatrix has been used rather indiscriminately, but to all probability the bursa in Trichoptera is homologous with those of Mecoptera and Lepidoptera. In *Panorpa* its wall is richly provided with large tricellular glands (Grell 1942). According to Unzicker (1968) it is bipartite as in *Wormaldia* but Grell, however, describes it as a simple sac.

In monotrysian Lepidoptera the relation be-

tween the common oviduct and the ductus bursae is the same as in Trichoptera (Williams 1941, 1947) but in the majority of Lepidoptera (Ditrysia) the bursa has a more or less ventral position. The first rudiment of the bursa, however, is dorsal (Verson & Bisson 1896, Amman 1954, Brumold 1957) and the final position is due to asymmetric growth of the wall of the genital chamber. In Lepidoptera Ditrysia the bursa opens not only into the genital chamber, but also to the exterior. This probably secondary condition is due to the fact that the two gonopods VIII fail to unite at their anterior (proximal) end.

The spermatheca is a large, thin-walled sac of somewhat varying shape which, like the bursa copulatrix, lies below the intestine. It often is divided into a proximal and a distal part by a more or less pronounced constriction, which in *Tinodes* even takes the shape of a narrow duct. Something similar is seen in *Rhyacophila* (cp. below and p. 49). According to Unzicker (1968) the spermatheca may be bilobed, but I think this statement must be due to some misinterpretation.

The spermatheca has a delicate cuticle and a thin epithelium, though the nuclei are large and close-set. A secretory function is not unlikely (cp. also below). In several forms I have, as also observed by Stitz (1904) and Khalifa (1949), seen a very small microtrichium to each cell in the distal part of the spermatheca. In *Potamophylax latipennis* Curt. there is, to each cell, a ca. 22μ broad comb with up to ten ca. 5μ long, distally directed teeth. In most cases the microtrichia are so tiny that they are difficult to see, especially since the wall often is thrown into fine wrinkles, so the structure may be more wide-spread than will appear from my observations. In many Integripalpia there is a funnel-like sclerotized ring at the junction of the spermatheca and its duct, as also observed by Khalifa (1949).

The ductus spermathecae, which issues from the posterior end of the sac or from the ventral wall close to the posterior end, varies much in

length. It may be short and almost straight, longer and S-like bent, or very long and convoluted. It always has, at least for the greater part of its length, a glandular epithelium and, at least for part of its length, a circular musculature. The extreme proximal end of the duct always is devoid of muscles, and in *Psychomyia* a musculature seems to be entirely lacking. The duct may be divided, more or less abruptly, into portions differing in thickness, width of the lumen etc. A part of the duct, either proximal or distal, may be developed as a bulb.

In *Apatania* and *Silo* the circular musculature of the duct proceeds for some distance on the spermatheca itself. In *Tinodes*, *Odontocerum*, *Lasiocephala*, *Limnephilus*, *Potamophylax* and *Ecclisopteryx* the spermatheca is provided with a circular musculature in its whole extent. Generally it is rather feeble, but in the thick part of the spermatheca in *Limnephilus* and *Potamophylax* it is very strong. In *Lasiocephala* there is a longitudinal muscle layer inside the circular one, i.e. nearest the wall of the spermatheca. Stitz (1904) has described muscles in the wall of the spermatheca in *Molanna*, too, but this I have been unable to see. However, considering the difficulty mentioned in the preface, it cannot be excluded that muscles in the wall are of more common occurrence than appears from the present study. In most figures the musculature is not indicated.

In most forms a gland opens into the ventral (anterior) side of the ductus spermathecae, though in *Lasiocephala* the opening has shifted to the left, in *Apatania* to the right side. Like the duct itself it varies much in length; it may be very long and very much coiled. In *Rhyacophila*, *Odontocerum* and the *Limnephilinae* the opening faces distally, i.e. toward the spermatheca, so that the gland appears as a continuation of the distal, thinner part of the ductus spermathecae. The epithelium in the gland very often is thinner than that of the duct itself. The proximal part may have a weak circular musculature. In

Sericostoma a distally directed valve is found in the spermathecal duct just proximally to the opening of the gland. In *Apatania* and *Silo* also a valve-like structure is seen in the duct.

In *Limnephilus lunatus* Curt. Gower (1967) calls this gland receptaculum seminis. Unzicker (1968), which calls it diverticulum spermathecae, considers it as a structure particular to the Trichoptera, on which topic I shall not venture any opinion, though it is not improbable that the "additional" gland described below is homologous with the spermathecal gland in (most) other insect orders. Unzicker states that it is lacking in all Annulipalpia (in which suborder he does not include Rhyacophilidae, Glossosomatidae and Hydroptilidae). I have, however, found it very well developed in *Hydropsyche* and present, though in a much reduced state, in *Polycentropus* and *Holocentropus*. In *Polycentropus* it shows traces of a paired origin. In *Tinodes* Khalifa describes two glandulae spermathecae, a proximal and a distal one, but I have found the gland to be lacking in the Psychomyidae as well as in the Hydroptilidae.

In *Rhyacophila*, the limnephelines and the drusines (p. 262) the gland is short. In the two last mentioned subfamilies there is, in return, a long "additional" gland opening into the spermatheca itself. The distal sac in *Rhyacophila* (p. 32) may be a similar structure.

This gland has been observed by Gower (1967) in *Limnephilus lunatus* Curt. He states that its size is 25 X 0.1 mm, i.e. about twice the length of the animal itself. Stitz (1904) describes it also in *Molanna*, but this I have not seen. According to Cholodkovsky (1913) and Khalifa (1949) it is general to all Trichoptera, and Unzicker (1968), too, describes it in a great number of forms. I am unable to confirm these observations. What has been called an "additional gland" is, at least in very many cases, an "appendix vermiformis", which often is seen at the distal end of the spermatheca.

In not a few cases I have seen a "spermatopho-

re" in the spermatheca. (It cannot be called a true spermatophore since it, as observed by Khalifa 1949, is not used for sperm transfer, but is formed within the body of the female). It is pale with a slight iridescence, spherical or pear-like, with the "neck" lying in the entrance to the spermatheca itself. It occupies only a small fraction of the latter, though occasionally two "spermatophores" may be found in the same animal. In some cases an amorphous substance filled the remainder of the spermatheca.

These "spermatophorenartige Gebilde" have been observed already by Cholodkovsky (1913). Khalifa (1949) states that they are lacking in some families, e.g. the Leptoceridae. I have found, however, "spermatophores" in the leptocerid *Athripsodes*, and I think that they are general to all Trichoptera.

The colleterial glands are the most bulky part of the genital system. Together with the ovaries they fill so much of the abdominal cavity that active respiration will seem to be impossible, and in fact the abdominal spiracles are so small that they often are difficult to find. In the Annulipalpia the shape of the colleterial glands is simple, sausage-like, tapering toward the distal end. In the Integripalpia each gland is divided into at least two branches (*Molanna*, *Oligoplectrum*, *Apatania*), an anterior and a posterior one, and more often one or both of these branches is again subdivided, so that in all three, four or even six (*Athripsodes*) branches are seen. In *Sericostoma* one of the four branches differs from the others by having a longitudinal wrinkled wall; it may perhaps serve as a reservoir.

The right and the left gland have a common part from which the wide colleterial duct goes downward. In those forms which have a "Lege-röhre" the duct is S-like bent when it is retracted. In *Polycentropus* the duct first goes forward and then is bent backward. The duct has a strong circular musculature, and in *Silo* a thin external layer of longitudinal fibres. In *Ecnomus*, however, its most proximal part is a non-muscular

"stalk". The duct in *Sericostoma* is unique in having a very elaborate structure.

Muscles of the gonopods. It is possible to recognize three muscles or three sets of muscles. One (gonm₁) originate on the anterior margin or the anterior part of the sclerotization on venter VIII and is inserted to gonopod VIII. The second muscle(s), gonm₂, originate(s) on the sclerite of segment IX and is also inserted to gonopod VIII. (Also in the thorax of insects a limb muscle may originate in an adjacent segment). Finally gonm₃ originates on the sclerite of segment IX and is inserted to gonopod IX. In *Beraea* and *Lasiocephala* there are two muscles. In the former one, in the latter both are inserted to structures in the genital chamber, and the same is the case with the single muscle in *Tinodes*, *Sericostoma*, *Molanna* and *Agrypnia*. In this respect, external versus internal insertion, *Orthotrichia* occupies an intermediate position.

In less than half the forms studied all three (sets of) muscles are present. When one is lacking, it rarely is gonm₁. Only in *Limnephilus*, *Potamophylax*, *Silo* and perhaps *Apatania* two (sets of) muscles are lacking.

A transverse musculature extended between parts which here are considered as formed by the gonopods is found in *Agapetus* (p. 39), *Wormaldia* (p. 58), *Ecnomus* (p. 79), *Hydropsyche* (p. 88), *Agraylea* (p. 96), *Hydroptila* (p. 99), *Sericostoma* (p. 114), possibly in *Lasiocephala* (p. 142), *Apatania* (p. 184) and *Silo* (p. 195), and perhaps in *Molanna*. (p. 139). This musculature generally passes below the genital chamber, which here is considered as a secondary structure, but in *Ecnomus* and *Hydropsyche* it passes above the genital chamber. In *Hydropsyche* there possibly is, in addition, a muscle passing below the genital chamber.

It is obvious that muscles passing above the genital chamber cannot be strictly homologous with muscles passing below the latter. However, both may be homologous with muscles found in other insect orders. In some insects having an

undisputable ovipositor, e.g. Psocoptera (Badonnel 1934) and Rhabdidoidea (Mickoleit 1973) the two sides of this organ are connected by a transverse musculature. In the beetle *Atomaria ruficornis* Marsh. (Evans 1961) a pair of sclerites which may be interpreted as parts of gonopods IX (cp. p. 15) are connected by a transverse musculature. This homologization being correct, it lends support to the theory (p. 17) that the "ventral side of segment IX" is formed of the gonopods VIII and IX.

IX-X muscles. In half the forms studied only one pair of muscles connects these two segments, but there may be as many as four (*Hydropsyche*). In *Wormaldia* the anterior, in *Lype* all bands of the only muscle have their posterior attachment to a sclerite which here is designated as part of segment IX, proving that the apparent boundary between segments IX and X is a secondary one.

In some forms one of the muscles or (*Athripso-des*) the only muscle is inserted to the anal tube. One of the muscles may be inserted to the postero-dorsal part of the genital chamber, and this is the case with the only muscle in *Ecclisopteryx*. The attachment to the genital chamber proves that segment X enters into the composition of the latter.

Extrinsic muscle of the genital chamber (gchm). This muscle in most cases is inserted to the spermathecal sclerite or (*Rhyacophila*, *Agapetus*, *Ecnomus*) a sclerotized part of the ductus bursae. In *Polycentropus* and *Holocentropus*, in which the spermathecal sclerite is much reduced, it is inserted to a membranous part of the genital chamber. It generally has its origin somewhere on the ventral sclerotization of segment VIII, varying from the anterior to the posterior part. In *Lasiocephala* it is on a sclerotized furrow between sternum VIII and tergum VIII, in *Beraea* even on tergum VIII. This is one of many things going to prove that tergum and sternum VIII, when distinguishable, are not strictly homologous with those of the preceding segments.

In *Rhyacophila* and *Hydropsyche* the origin of

this muscle has shifted to segment IX, in the former genus to the apodeme of this segment, in the latter to the dorsal part of its antecosta. In the Psychomyidae, *Wormaldia*, *Oligoplectrum* and probably *Orthotrichia* the muscle gchm is lacking.

Intrinsic musculature in the genital chamber. The genital chamber has a circular musculature, which is a direct continuation of that in the common oviduct, and which also covers possible bulges of the chamber. In *Wormaldia*, *Ecnomus*, the Hydroptilidae and *Agrypnia* this musculature does not quite reach the posterior end of the chamber, nor does it reach the front end of the dorsal branch in the last mentioned genus.

In *Ecnomus* and in the Psychomyidae the muscle-rings of course are interrupted by the ventral cleft in segment IX, here the incomplete rings are at each end attached to the sclerite of segment IX. In *Lype* and *Psychomyia* the posterior ones of the complete rings pass through the structure considered as gonapods VIII. The muscle rings may be interrupted also dorsally at the spermathecal sclerite, by various apodemes of the latter, or in other places, and of course at the insertions of extrinsic muscles.

The circular musculature of the genital chamber generally, though not always, is confluent with those of the ductus bursae and the colleterial duct, sometimes with that of the anal tube, but rarely with that of the ductus spermathecae.

In *Rhyacophila*, *Agapetus*, the Polycentropidae and *Sericostoma* there is an internal layer of longitudinal muscle fibres. In the Polycentropidae it is restricted to the ventral side and is paired; in *Ecnomus* it extends farther backward than the circular musculature. In *Sericostoma* it is found only in the dorsal wall behind the opening of the colleterial duct. Finally, in *Silo* there is, laterally and ventrally on the front end of the genital chamber, an external layer of longitudinal fibres, continuing such a layer on the common oviduct. With a polarization microscope it might perhaps be found that longitudinal fibres are of more common occurrence.

When the anterior part of the genital chamber

is divided into a dorsal and a ventral branch, each generally has its own circular musculature. In *Apatania*, however, the most posterior parts of the two branches have a circular musculature in common, and in the Hydroptilidae the division externally is entirely obscured by a common musculature.

In *Apatania* and especially in *Limnephilus*, *Potamophylax* and *Silo* the intrinsic musculature is more complicated than is usually the case.

In *Apatania* and probably in *Ecclisopteryx* there is a feeble transverse musculature in the processus spermathecae.

Special Part

Rhyacophila nubila Zett.

Pregenital segments (cp. *R. fasciata* Hag. fig 8, p. 34). Immediately in front of the transverse suture on sternum VI a low, unpaired, but sometimes bifid tooth is seen. The gland in segment V is large. It opens rather far behind the antecostal suture, at about one third of the distance between the latter and the transverse suture.

Segment VIII (figs. 3 and 4) is very much modified. Its extreme anterior end, which normally is overlapped by segment VII, forms a strong, synscleritous "collar" (a.VIII), which is a little thicker than the rest of the segment. This "collar" has three indentations, an unpaired dorsal one and a pair of laterals. In the middle of the dorsal side (fig. 4 C) and latero-ventrally the posterior margin of the "collar" is a sharp, backward directed edge. In the middle of the ventral side (fig. 4 D) there is no sharp boundary between the "collar" and the anteromesal corners of the valves mentioned below; (the "collar" can be said to be discontinuous on the ventral side). The two structures together form a backward directed lamella.

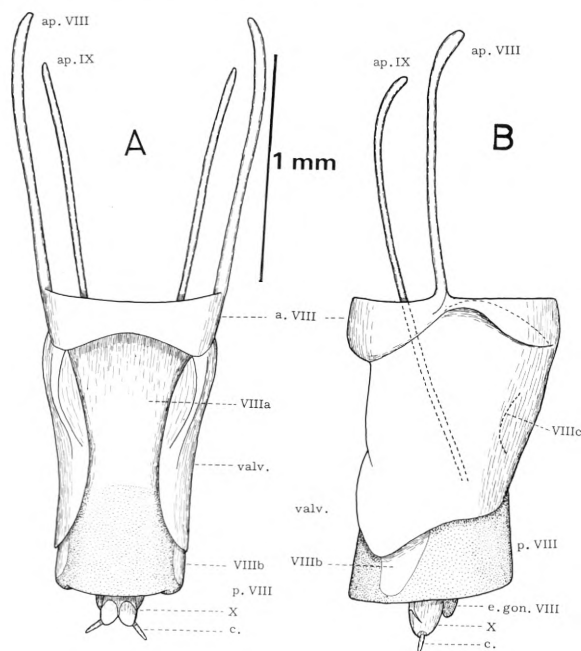
From the "collar" a pair of large valves (valv) is issued. They cover most of the rest of the segment and reach almost the posterior end of the latter. Dorsally the two valves are widely separated and have convex mesal (or dorsal) margins, along the anterior half of which a submarginal carina runs on each valve. Ventrally they are separated by a V-like indentation, at the extreme anterior end of which the two valves are continuous.

The rest – and by far the greater – part of the

segment is tube-like. The dorsal side is slightly sclerotized. The sclerite (VIIIa), which is continuous with the inside of the valves, has, however, a broad and deep posterior indentation, the posterior corners thus projecting as a pair of tongues (VIIIb). At the anterior corners, and concealed by the valves, there is a patch, about 125 μ wide, of close-set and rather strong (40–50 by 6 μ) spines.

The ventral side is membranous except for a minor, slightly concave sclerite (VIIIc) of some-

Fig. 3. *Rhyacophila nubila*. Segments VIII-X in a dorsal view (A) and as seen from the right side (B).



what varying shape (as shown in fig. 4 B), which is finely wrinkled and rough with minute ($6\ \mu$ long and $4\ \mu$ thick) spinules.

In the middle of the lateral side the anterior margin of segment VIII is produced into a long, rod-like apodeme (ap.VIII), which reaches the posterior end of segment VI. Its downward bent anterior end is a little thickened.

Segment IX (fig. 5) is normally, except for the extreme posterior end of the ventral side (fig. 4), withdrawn into segment VIII. It is about one third as long and only a fraction as thick as the latter. In a posterior direction it tapers slightly. Except for the ventral side s.str. the posterior three fourths of the segment are feebly sclerotized. On the lateral side there is a strong, rod-like and slightly ascendent reinforcement, the anterior end of which issues both a short dorsal and a

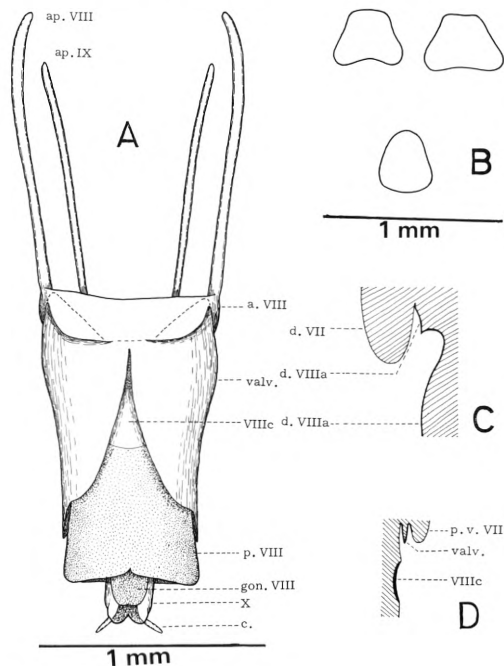
short ventral branch along the anterior margin of the sclerotization, so that the whole reinforcement takes the shape of a T with a long stem. By a small area of thick and flexible elastocuticle the latter is united with another rod lying on the lateral side of the anterior, otherwise membranous part of the segment. This rod is produced into an apodeme (ap.IX), which resembles that of segment VIII, though it is a bit more slender. The apodeme of segment IX lies dorsally and mesally to that of segment VIII and extends scarcely as much forward as the latter.

The posterior end of the membranous ventral side (which probably represents the united gonopods VIII; pp. 15–16) forms a thick and almost imperceptibly bilobed lip of the genital opening. The sides of this lip extend forward as a pair of deep furrows, in which a pair of very narrow sclerotic rods lies for almost the entire length of the segment.

The whole segment, with the exception of the ventral side s.str. is provided with sensilla campaniformia (not shown in fig. 5) similar to the large ones on segment X, but is devoid of setae. The sclerite has a sculpture of exceedingly fine, in a posterior direction divergent furrows. On the ventral side there are tiny spinules, resembling miniature rose-thorns, with downward and forward directed points.

Segment X (figs. 4 and 5) is about two fifths as long, but just as broad and almost just as high as segment IX. It forms a slightly bilobed upper lip for the genital opening, which projects farther backward than the lower lip. The membranous ventral side is concave in a transverse direction, forming half a cylinder. The dorsal side is weakly sclerotized, but has a more strongly sclerotized area in the shape of a transverse plate, the posterior margin of which is produced into three rays, a longer and broader median one and a pair of shorter and narrower laterals. The anterior corner of the transverse sclerotization is connected with the lateral rod on segment IX by a small area of flexible elastocuticle.

Fig. 4. *Rhyacophila nubila*. A: Segments VIII–X in a ventral view. B: Various shapes of the sclerite VIIIc. C: Diagrammatic longitudinal section through the posterior end of segment VII and the anterior end of segment VIII, dorsal side. D: Same, ventral side. C and D are not drawn to scale.



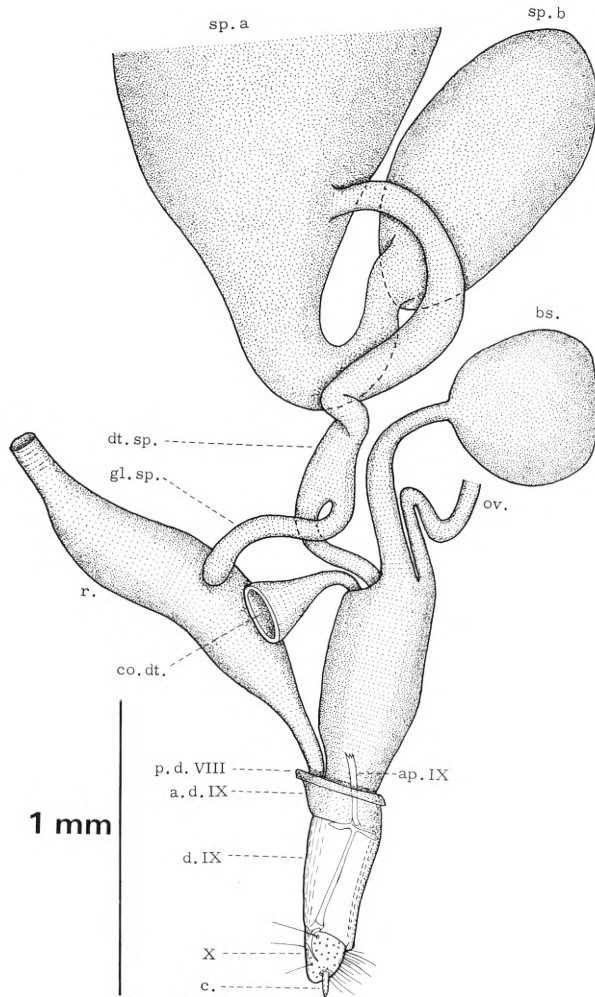


Fig. 5. *Rhyacophila nubila*. The genital chamber etc. as seen from the right side.

On the dorsal side there are three pairs of strong setae. A fringe of similar setae is seen on the ventral side, on the margin of the half-cylinder. The sclerotized dorsal side is densely clothed with 3-6 μ wide sensilla campaniformia, among which a still denser (mutual distance about 8 μ) clothing of smaller (about 1.5 μ wide) sensilla campaniformis is seen; the latter is not shown in the fig.)

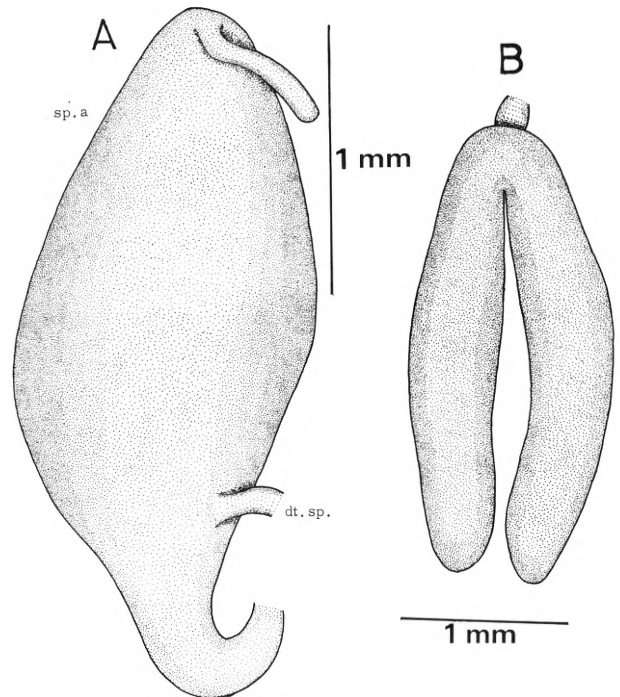
A pair of short, finger-like cerci arises from small membranous areas a little ventrally on the

posterior end of the segment. The cercus is rather thin-walled, and the still more thin-walled distal end carries three sensilla campaniformia. Two, with a diameter of ca. 2 μ , are subdistal and lateral, the third one, with a diameter of 4 μ , is almost terminal (though a little mesal) and might be mistaken for a rudimentary second segment.

“Legeröhre”. Segments VIII–X form an extensible “Legeröhre”. Normally it is retracted so much that segment IX is (almost) entirely concealed, and sometimes even segment X is concealed. In the latter case the posterior projections on the dorsal sclerite of segment VIII (fig. 3, VIIIb) are bent inwards. Likewise segment VIII can be more or less completely retracted into segment VII.

The genital chamber (fig. 5) is long and slender. By retracted “Legeröhre” it extends into the

Fig. 6. A: *Rhyacophila nubila*; proximal part of the spermatheca (sp.a) as seen from the right side. B: *Rhyacophila fasciata*; colleterial glands in a dorsal view.



posterior part of segment VII. Its posterior portion almost fills up the interior of segment IX; in an anterior direction it becomes a little wider. It is of a rather simple shape; apart from the processes described below its wall is membranous and without definite structures.

The processus spermatheca (fig. 7), which is situated on the anterior, here about 45° ascendent, dorsal wall of the genital chamber, has the shape of two low cone segments placed one upon the other. Posteriorly and laterally they are separated by a fine furrow on the distal end of the proximal segment, in front their surfaces are flush. Details will appear from fig 7. The distal end of the second segment carries excentrically, shifted in a ventral direction, on its backward and downward directed surface, the opening of the ductus spermathecae.

The anterior side of the processus spermathecae is continuous with the sclerotized and in a transverse section crescentic (dorsally concave) wall of the ductus bursae. A view of the intact genital chamber might give the impression that the opening of the ductus bursae has a more anterior position, but this is due to the fact that the proximal part of the ductus has a circular musculature in common with the genital chamber itself.

Just behind the processus spermathecae the dorsal wall of the genital chamber is vertical for a very short reach, and here the opening of the colleterial duct is seen as a narrow, transverse cleft. Behind this opening a small, sclerotized "intermediate process" (int. pr.) projects into the lumen. It is about half as broad as the latter, has a somewhat descendent ventral side and an almost vertical posterior side. In a transverse direction its mesal part is concave, whereas the anterior half of the lateral parts form rounded ridges, continuous with the sclerite of the processus spermathecae on each side of the opening of the colleterial duct.

Behind the "intermediate process" again a short portion of the dorsal wall is vertical and

bulges into the lumen as a long, sclerotized "posterior process" (po.pr.) of a rather elaborate shape, extending into the anterior part of segment IX, i.e. almost to the posterior end of the genital chamber. The "intermediate" and the "posterior" processes are sclerotically continuous, though separated by a narrow furrow, curved with a posterior concavity. Immediately at its base the ventral side of the "posterior process" bulges downward, and the bulge has a concavity conforming to a convexity on the posterior side of the "intermediate process", a sort of monocondylic articulation thus being formed.

In the middle of the dorsal side of the "posterior process" there is a pair of deep, longitudinal furrows. It seems a reasonable assumption that they receive the parameres of the male during copulation.

Though the processus spermathecae is continuous with the "intermediate process" and through this with the "posterior process", the two latter processes cannot be considered as parts of the processus spermathecae, since they arise behind the opening of the colleterial duct.

At the level of the "intermediate process" the wall of the genital chamber has a pair of latero-ventral processes, which partly fills up the interval between the processus spermathecae and the "posterior process". In a lateral view the fill scarcely, in a dorsal or ventral view far from half the lumen of the genital chamber.

Behind the broadest part of the "posterior process" the genital chamber tapers in a posterior direction.

The common oviduct by retracted "Legeröhre", lies in a very much dorso-ventrally compressed, S-like figure, in the direction from the genital chamber: forward-downward-backward-downward-forward.

The bursa copulatrix (fig. 5) is a rather small, roughly globular sac, which in one specimen was filled with an amorphous substance. The ductus bursae is sclerotized in its posterior part (fig. 7).

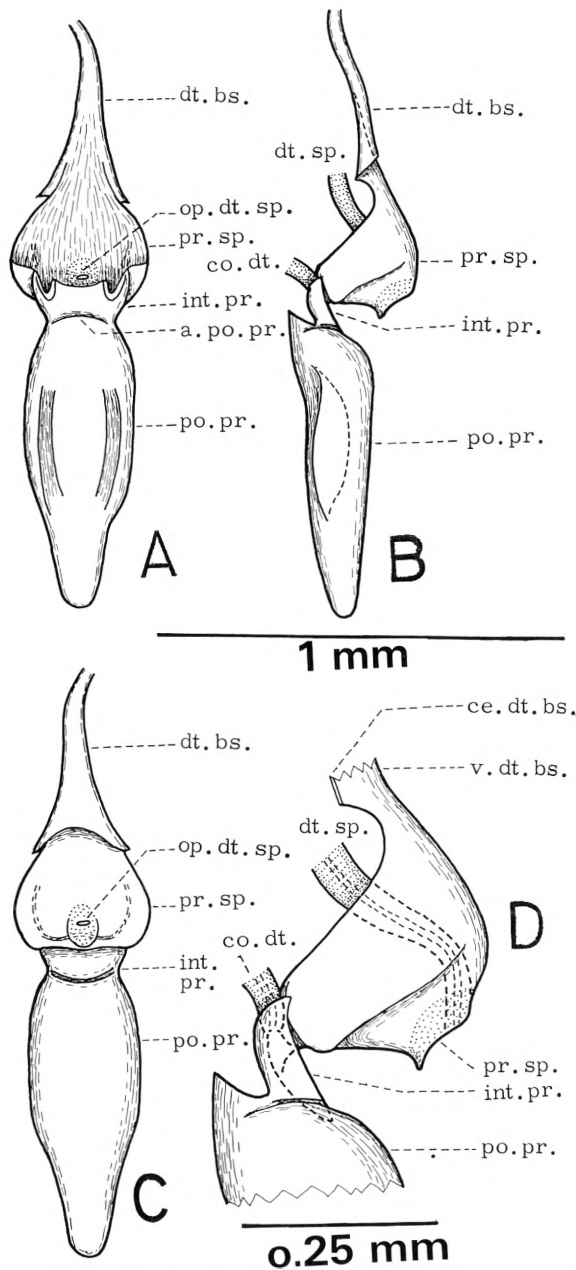


Fig. 7. *Rhyacophila nubila*. Processus spermathecae in a dorsal view (A), as seen from the right side (B) and in a ventral view (C). D: Details of B.

The sclerotization first is cylindrical, but toward the opening in the genital chamber it widens and becomes crescentic in a transverse section.

The spermatheca (figs. 5 and 6 A) is divided into two parts. One is sac-like and of much varying size in the specimens dissected by me. In some it extended into segment III, in others only to the anterior end of segment V. From its anterior end a long and very slender appendix is issued, from its posterior end two ducts at a great mutual distance. The ventral one is the ductus spermathecae. The dorsal one, which proximally is considerably thicker than the ductus spermathecae, but decreasing in width in a distal direction, leads into a much smaller sac lying behind and below the large sac. It has a thicker epithelium than the large sac, but none is muscular. The small sac may be an additional gland. It must be stressed, however, that the additional gland in the limnephilines and drusines opens ventrally into the spermatheca.

The ductus spermathecae is long and slender and somewhat convoluted. In a distal direction its width increases, and that of the lumen even more so. Whereas the lumen proximally occupies only a small fraction of the diameter, it distally counts for most of that, including the circular musculature.

The glandula spermathecae, which opens subproximally into the duct, is short, its length being about the same as the width of segment VIII. Its opening faces distally, so that it has the appearance that the thicker, distal part of the duct bifurcates, one branch being the gland, the other the proximal part of the duct.

The colleterial glands (fig. 6 B) are of a simple shape and extend, tapering, to the middle or anterior end of segment V. The thicker hind end is situated in the posterior part of segment VII. The muscular duct is funnel-like, though flattened toward its opening, which has been described above. By retracted "Legeröhre" the duct is bent like a reflection of the oviduct.

The anus is situated on the dorsal wall of the genital chamber in the posterior part of segment IX, a cloaca thus been developed.

Musculature. A rather strong muscle, probably

VII–VIII dm_1 , originates on the lateral half of the antecosta of tergum VII and is inserted latero-dorsally on the anterior margin of segment VIII. Another, not particular strong muscle, probably dm_6 originates at the posterior corner of tergum VII and is inserted to the distal end of the apodeme of segment VIII. The ventral VII–VIII muscles have exactly the same arrangement as the dorsals. However, whereas the lateral muscle probably is vm_6 , it is doubtful that the mesal one is vm_1 . The mesal muscles are retractors, the laterals extensors of segment VIII.

In addition there is ventrally a muscle, which is somewhat weaker than the mesal ventral muscle described above, and originates on the anterior margin of segment VIII. The left and the right muscle converge in an anterior direction, passing above (dorsally to) the common oviduct and are inserted to the front end of the latter, which lies in the anterior part of segment VII. It may be interpreted as an internal VII–VIII muscle (p. 14), the anterior attachment of which has shifted to the oviduct. (Cp. *Hydropsyche*, p. 88).

The muscle VIII–IX dm_1 is rather weak and rather mesally situated. It extends between the anterior margin of segment VIII and the bottom of the furrow between this segment and segment IX. The strong dm_2 connects the distal ends of the apodemes of segments VIII and IX. This muscle – which might also be considered as vm_2 , or a combination of dm_2 and vm_2 – probably is a retractor of segment IX. A muscle, which probably is dm_3 , and is stronger than dm_2 , extends from the distal end of the apodeme of segment VIII to the bottom of the furrow between segments VIII and IX, where it is inserted dorsally to the root of the apodeme of the latter segment. A strong muscle, probably dm_6 , originates on the posterior end of the sclerotic extension VIIIa (fig. 3) and is inserted to the distal end of the apodeme of segment IX. It is the only extensor of this segment. A muscle,

which may be dm_5 , and which is much stronger than VII–VIII dm_6 and vm_6 , originates mesally on the distal part of the apodeme of segment VIII and is inserted latero-ventrally to the bottom of the furrow between segments VIII and IX. Probably this muscle partly is a retractor of segment IX, partly it can, together with dm_3 , give this segment a nodding movement, in which other muscles may also be implied.

A muscle, which I have interpreted as $gonm_1$, conforms exactly to dm_1 . The muscle $gonm_2$ originates dorsally on segment IX. The line of origin is ascendent: the anterior ones of the numerous units originate on the anterior end of the rod-like reinforcement (fig. 5), the posteriors rather mesally to the latter. It is inserted to the ventral sclerotic rod. This muscle can raise the ventral side of segment IX, and hence the rods generally are seen lying in deep furrows.

The rather strong IX–X muscle, consisting of several units, originates on the dorsal arm of the T-formed reinforcement on segment IX. The left and the right muscle converge in a posterior direction, passing mesally to $gonm_2$, and have a common insertion on the anterior margin of segment X. They must be levators of this segment.

The muscle $gchm$, which is of about the same strength as VII–VIII dm_6 , originates on the distal end of the apodeme of segment IX and is inserted to the posterior part of the ductus bursae.

The genital chamber has an external circular and an internal longitudinal musculature. The former extends to the middle of segment IX, the latter is closer to the wall of the chamber.

Rhyacophila fasciata Hag.

In the structure of segment VIII definite differences between this species (fig. 8) and *R. nubila* are seen. The valves are much shorter. On the dorsal side their posterior corners extend into a pair of mesally directed tongues, which almost

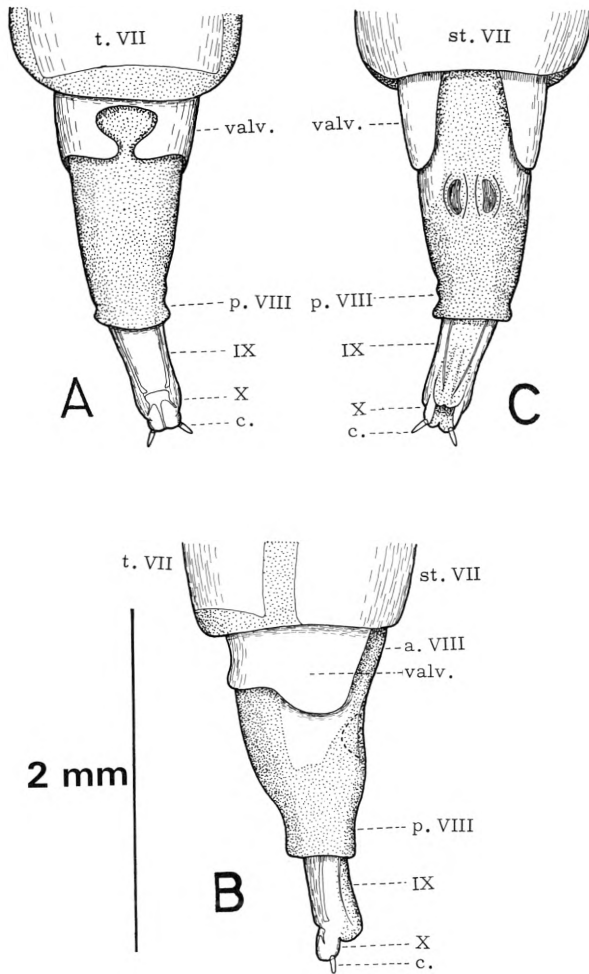


Fig. 8. *Rhyacophila fasciata*. Posterior end of abdomen in a dorsal view (A), as seen from the right side (B) and in a ventral view (C).

touch each other, and moreover the dorsal indentation is not nearly as deep as in *R. nubila*. The ventral indentation is much wider and has a broadly rounded bottom. Instead of an unpaired ventral sclerite on the posterior part of segment VIII there is a pair of small, but deep, sclerotized depressions.

Novák (1963) has studied segment VIII as a means for identifying species in the females of twelve *R.* spp. *R. obliterated* Mcl. resembles *R.*

fasciata in the length of the valves and the shape of the dorsal indentation, but the two species are easily distinguished by the shape of the ventral indentation and especially by the shape of the valves in a lateral view. In *R. glareosa* McL. the dorsal indentation only is found, and it is less deep, in *R. tristis* Pict. this indentation, too, is lacking. Unlike all the other species *R. hirticornis* McL. has a dorsal and a ventral valve. These characters are best seen in fluid-preserved specimens; in pinned specimens they will generally be obscured by the retraction of segment VIII into segment VII.

Agapetus fuscipes Curt.

Pregenital segments. On sternum V there is, in addition to the antecostal suture, a strong transverse suture in the shape of a sulcus. Laterally it is issued, jointly with the antecostal suture, from the anterior corners of the sternum. The greater, mesal part of this suture is strongly backward bent, so that the suture in the middle almost touches the posterior margin of the sternum. The anterior edge of the sulcus projects as a backward and downward directed, 16.5 μ broad lamella. In a lateral view it therefore has the appearance that sternum V at its posterior margin carries a very short, pointed tooth. No glands are found on this segment.

Sternum VI (fig. 9 A) has a short, but strong, sagittally compressed, backward directed tooth near its posterior margin.

Segment VII (fig. 9 A) differs somewhat from the preceding segments. It is relatively longer than segment VI, much more tapering in a posterior direction, and somewhat sagittally compressed. Both the tergum and the sternum are broader than those on segment VI. At the anterior end the pleural membrane is almost as wide as on segment VI; the margin of the tergum is descendent, so that eventually the pleural membrane is very much reduced in width. The lateral longitudinal suture on the

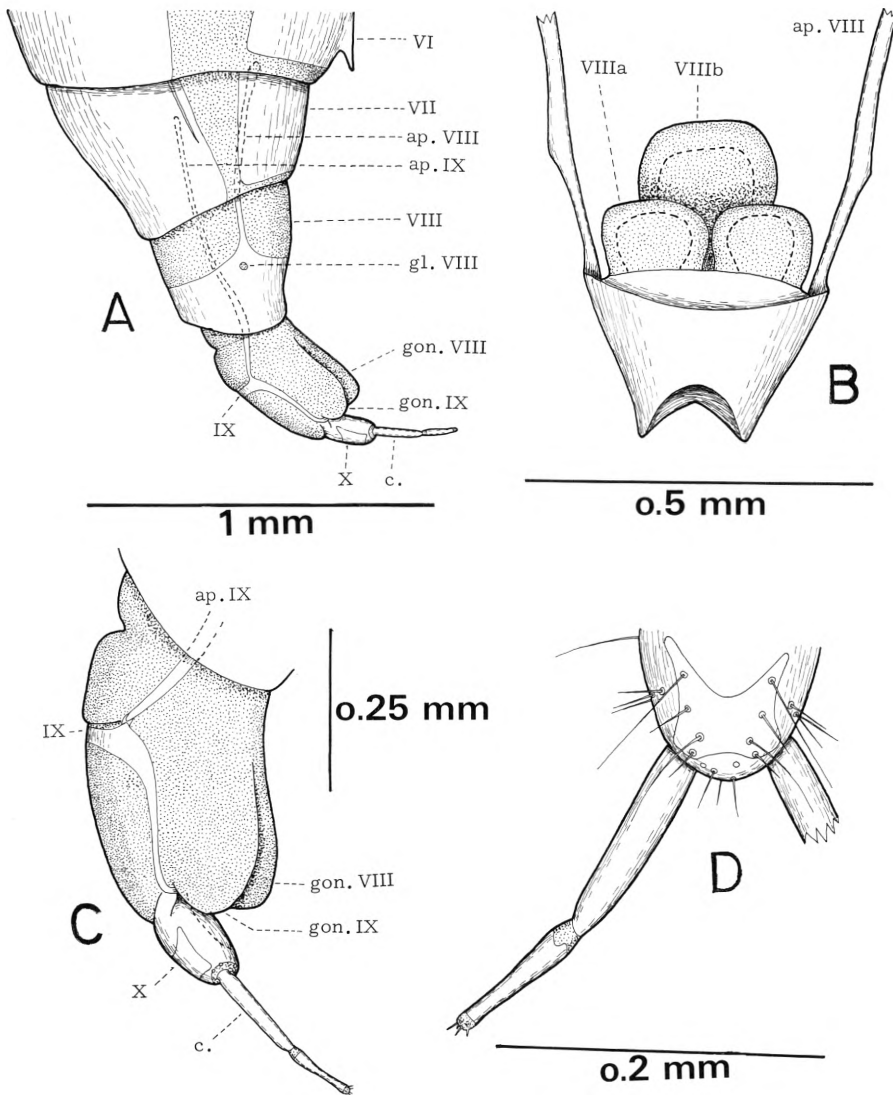


Fig. 9. *Agapetus fuscipes*. A: Posterior end of abdomen as seen from the right side. B: Segment VIII in a dorsal view. C: Segments IX and X as seen from the right side. D: Posterior end of segment X in a dorsal view.

tergum extends only for about half the length of the segment.

Segment VIII (fig. 9 A, B) is very much modified. It is much narrower than segment VII and rather much sagittally compressed. In a dorsal or ventral view it tapers much, in a lateral view only a little toward the posterior end.

Segment VIII is synscleritous, but the sclerite is restricted to approximately the posterior half

of the external part (see below) of the segment. Ventrally to the middle of the lateral side the anterior margin extends into a small triangle, from the apex of which a longitudinal sclerotic rod issues. At the anterior end of the segment this rod continues as an apodeme (ap.VIII), which reaches the posterior end of segment VI when the "Legeröhre" is extended, the anterior end when it is retracted. At the base of the

triangle a small, 9 μ wide, pale, circular spot (gl.VIII) is seen; it is probably the opening of some gland. The posterior margin of the sclerite has a rounded indentation on both the dorsal and the ventral side. There is no antecosta.

By dissection it is revealed that the segment has the character of a tube. The posterior part of the inside is sclerotized. In contrast to the external sclerite the anterior margin of this internal sclerite bulges forward on the dorsal and the ventral side, whereas it has lateral indentations. Dorsally and ventrally the internal sclerite extends farther, laterally not so much forward as the external one. The posterior margin of the tube is sharp, but I am inclined to believe that there is no sclerotic connection between the external and the internal sclerite.

The longer, anterior part of the inner wall of the tube is membranous and extends well into segment VII. When the "Legeröhre" is protruded to its full extent part of this membrane is visible externally.

The anterior margin of the inner sclerite carries three peculiar, large, tongue-like, forward directed apodemes, a pair of dorsals (VIIIa) and a much larger, unpaired ventral one (VIIIb). Though stiff they are colourless or rather slightly opalescent, and they have distinct, cleft-like lumina. The cuticle (probably elastocuticle) of these apodemes is enormously thickened. At the posterior end of the ventral apodeme the wall is 24.5, at its anterior end even 33 μ thick, and here the lumen is 8 μ wide. In the dorsal apodemes the wall is "only" 16.5 μ thick, but the lumen is just as wide as in the ventral one. I am unable to imagine the function of these apodemes.

The tube-like, sclerotized structure of segment VIII to all probability is homologous with the valves in *Rhyacophila*.

The external sclerite of segment VIII is clothed with rather scattered setae similar to those on segment X (see below). The group of small setae, however, is not represented.

Segment IX (fig. 9 C) is about as long as (the external part of) segment VIII, almost as broad and high as the posterior end of this segment, and somewhat sagittally compressed. It is largely membranous and, when fully extended, separated from the membranous part of the internal tube of segment VIII by a slight constriction. Latero-dorsally, on about the posterior two thirds of the segment, a pair of strong, sclerotic rod lies. The posterior end of the rod is bent downward and inward, into the "mouth angle" between segments IX and X, where it is widened and forms a simple articulation with the ventral sclerite of segment X (see below).

The anterior ends of the rods are bent a little upward and connected by a broader, dorsal bridge. At the anterior corner thus formed the sclerite is produced into a very small triangle, which is bent about 45° inward, and by a minute area of flexible elastocuticle connected with an ascendent rod lying on the anterior third of the segment. The latter rod is produced into an apodeme (ap.IX) which extends scarcely as much forward as that of segment VIII, to which it is dorsal in position.

In the middle of the dorsal side the posterior margin of segment IX curves a little backward. The ventral side, which projects a little farther backward as the dorsal side, forms a thick lower lip of the genital opening. There is also a pair of broad lateral lips. These lips probably represent the distal ends of the gonopods VIII and IX, resp. The cleft between the ventral lip and the laterals extends forward as a pair of more or less pronounced longitudinal furrows, which are associated with muscle attachments.

Segment IX is entirely devoid of setae.

Segment X (fig 9, C, D) is very short, about two thirds as broad and a little more than one third as high as segment IX; the dorsal sides of the two segments are flush. Segment X, which forms the upper lip of the genital opening, is to its whole extent feebly sclerotized. Two unpaired, more strongly sclerotized areas are seen, a dorsal

and a ventral one. The latter forms the articulation with the latero-dorsal rod on segment IX. The posterior end of this rod is bent downward, into the "mouth angle", and then inward at almost a right angle.

The posterior half of the dorsal side, the posterior two thirds of the ventral side, and almost the whole of the lateral sides are covered with rather strong setae. Posteriorly, especially on the dorsal and lateral sides, most of the setae are relatively short and thick and have thick, rounded apices. As to numbers there is a rather great though not complete symmetry, as well as a great though not complete similarity between various specimens. Moreover, three ca. $3\ \mu$ wide sensilla campaniformia are found on each side of the segment, one dorsally on the posterior end and two laterally on the margin of the membranous area surrounding the base of the cercus.

As far as Trichoptera go the cerci, which are implanted a little ventrally into circular membranous areas, are very long and slender, almost twice as long as segment X. By a constriction the cercus is distinctly divided into two segments. There is no true articulation between the two segments, but proximally on the smaller second segment the cuticle is pale and possibly somewhat flexible. The distal end is membranous and carries four tiny ($4\ \mu$ long), but relatively thick ($0.65\ \mu$) sensilla, which taper rather little toward the rounded apices and are provided with alveoli.

"*Legeröhre*". Segments VIII–X form a "Legeröhre", which normally is so much retracted that of segment VIII only most of the posterior, sclerotized part is seen, segment IX entirely concealed by segment VIII, and of segment X only the posterior end with the cerci is seen. By the greatest possible extension the rather ample intersegmental membrane between segments VII and VIII as well as segment IX and the (in repose) anterior, membranous part of the lateral tube of segment VIII are exposed. Judged by

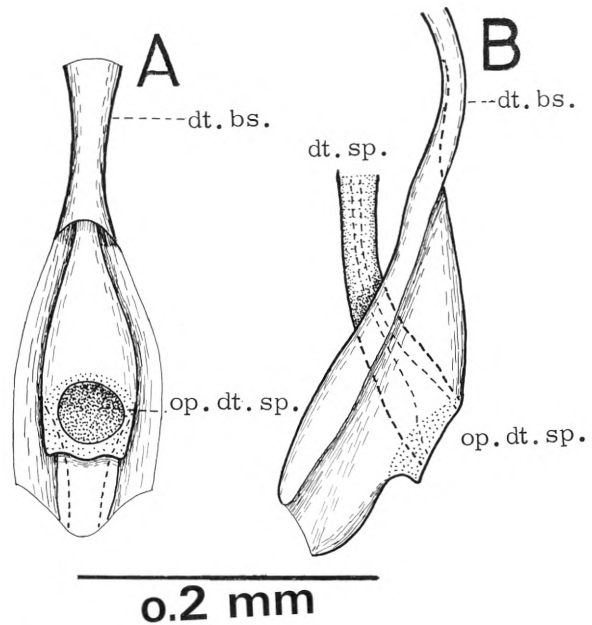


Fig. 10. *Agapetus fuscipes*. Processus spermathecae in a ventral view (A) and as seen from the right side (B).

preserved specimens the extension is accompanied by a rather strong downward flexion of segment IX.

The sclerites on segments VIII and IX are darker than those on the pregenital segments, whereas segment X has the same colour as the latter.

The genital chamber has a similar shape as in *Rhyacophila*, long, slender and tapering in a posterior direction. By extended "Legeröhre" it reaches about the middle of the ventral, tongue-like apodeme (VIIIa) of segment VIII. As in *Rhyacophila* the anterior end tapers gradually into the ductus bursae.

The spermathecal sclerite (fig. 10) covers a little less than the anterior third of the dorsal wall and is continuous with a dorsal sclerotization in the ductus bursae. Its lateral margins are bent downward, its mesal part bulges into the lumen as a rounded ridge, the processus spermathecae. In front this ridge is quite narrow and

proceeds as a rounded dorsal fold into the ductus bursae.

On the posterior three fourths of the sclerite the ridge increases gradually and strongly in width and height. Somewhat in front of its posterior end it has a membranous area, and here the large, funnel-like opening of the ductus spermathecae is seen. Behind this membranous area the ridge suddenly decreases in width and height and here, as well as at the membranous part, its base is a little constricted.

The ridge continues for a short distance behind the sclerite as a membranous fold, immediately behind which the colleterial duct opens. A little farther backward, approximately in the middle of the genital chamber, the anus is found on the dorsal side, a cloaca thus being formed.

Apart from those described above no differentiations are seen in the wall of the genital chamber.

Bursa copulatrix and spermatheca. I did not succeed in dissecting these organs, nor the ductus spermathecae.

The colleterial glands are of a simple shape. In some of the specimens studied they extended into the anterior part of segment III, in others only into the anterior part of segment IV.

Musculature. A rather thin muscle layer, probably dm_1 , originates on the whole antecosta of tergum VII and is inserted to the bottom of the furrow between the segments VII and VIII. Another muscle, no doubt dm_6 , originates laterally on the posterior margin of tergum VII and is inserted laterally to the anterior end of the apodeme of segment VIII. The ventral VII–VIII musculature is an exact replica of the dorsal one, but whereas the lateral muscle to all probability is vm_6 , it is doubtful that the mesal one is vm_1 (cp. p. 13). Whether there is an extrinsic muscle associated with the oviduct I have been unable to decide with certainty.

The muscle VIII–IX dm_1 seems to be lacking. An ascendent muscle connecting the anterior ends of the apodemes of segments VIII and IX

probably is dm_2 . A very strong muscle, probably dm_5 (cp. *Agraylea multipunctata*, p. 95), originates dorsally on approximately the posterior third of the apodeme of segment VIII and is inserted to approximately the mesal half of the transverse dorsal sclerotization on segment IX. The insertions of the left and the right muscle are almost continuous. A muscle, probably dm_6 , which seems to be stronger than the corresponding ventral muscle, originates dorsally on the posterior margin of the external sclerite of segment VIII and is inserted to the distal end of the apodeme of segment IX. Its ventral counterpart, vm_6 , has similar attachments.

The muscle $gonm_1$ is very strong. It originates mesally on the distal end of the apodeme of segment VIII and is inserted ventrally to the anterior end of segment IX. The muscle $gonm_2$ is composed of fine bands originating on the posterior part of the longitudinal sclerotization on segment IX and inserted to the ventral furrow on the same segment (cp. *Rhyacophila*, p. 33). The muscle $gonm_3$ may be lacking, though one of the muscles interpreted as a IX–X muscle may actually be the $gonm_3$.

With the above mentioned reservation there are three IX–X muscles. One is rather strong, originates on about the mesal part of the dorsal transverse sclerotization on segment IX and is inserted to the anterior margin of the dorsal reinforcement on segment X. The left and the right muscle are closely apposed, though distinctly separated; their insertions occupy almost half the width of segment X. Another muscle, consisting of fine bands, originates more laterally, partly on the internal surface of the transverse sclerotization on segment IX, partly on the anterior portion of the membranous areas behind this sclerotization. The bands converge, the anteriors being 45° , the posteriors much more steeply descendent, and are inserted to the posterior part of the lateral side of the genital chamber. The third muscle, also consisting of fine bands, originates on the ventral furrow on

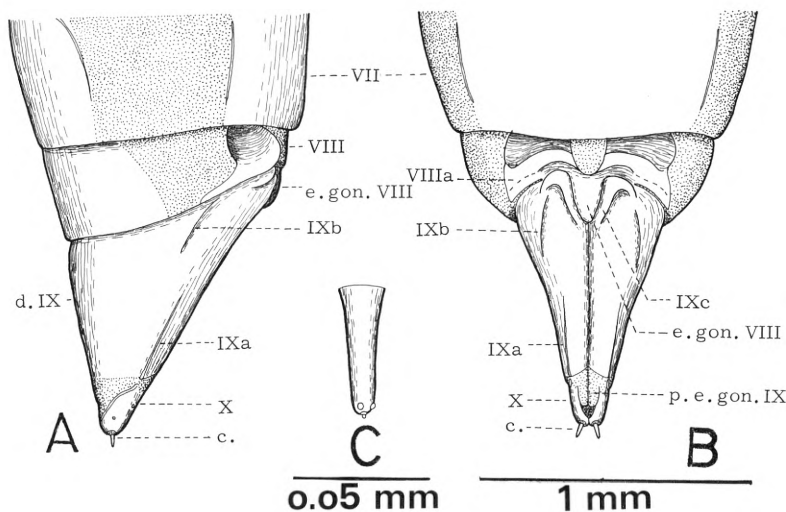


Fig. 11. *Tinodes waeneri*. Posterior end of abdomen as seen from the right side (A) and in a ventral view (B). C: Right cercus in a lateral view.

segment IX, behind the insertion of gonm₂. The very much fan-like convergent bands are inserted to the lateral side of the genital chamber, behind the second muscle. That the two last mentioned muscles are considered as IX-X muscles is because they are inserted behind the anus. As to the third muscle it is with no little doubt, since it seems to have relations to the gonopods.

The two sides of segment IX are connected by numerous, rather fine muscle bands, passing below the genital chamber.

The muscle gchm is much forward directed toward its insertion to the ductus bursae.

As in *Rhyacophila* the genital chamber has an external circular and an internal longitudinal musculature. Both layers extend to the "mouth angle".

Tinodes waeneri L.

Pregenital segments. The gland on segment V opens a little behind the sternal antecosta.

The genital segments (fig. 11). Whereas segment VIII dorsally and laterally overlaps segment IX to some degree, it is, in the middle of the ventral

side, impossible to state the boundary between the two segments with certainty.

Segment VIII is much longer dorsally than ventrally. It has a weakly defined dorsal sclerite, which for the sake of convenience may be called a tergum, though it hardly is serially homologous with the pregenital terga. It is relatively broader than those and increasing in width in a posterior direction. It has no lateral longitudinal sutures.

On the ventral side there is a pair of stronger sclerites, separated by a membranous area, though at the posterior end connected by a narrow, sclerotic bridge. The posterior corner of the sclerite is produced into a long tongue along the posterior margin of the segment; it does not, however, reach the tergum. The larger, anterior part of the sclerite is occupied by a deep depression. In fig. 11 B about the anterior half of the depression is overlapped by segment VII. Behind the depression, on each side of the posterior end of the membranous area, there is a transverse, rounded and slightly curved (posterior concave) carina (VIIIa).

From the bridge connecting the two sclerites, as well as from the mesal parts of the sclerites

themselves, an unpaired, rather short, tongue-like, in a transverse section very convex process (e.gon.VIII) issues. A comparison with *Ecnomus* (p. 74) suggests that this structure represents part of the gonopods of segment VIII.

The ventral sclerites on segment VIII and the tongue e.gon.VIII are devoid of setae.

Segment IX is much longer than segment VIII. It is conical, strongly tapering in a posterior direction, and somewhat sagittally compressed, especially in its anterior part. The dorsal side is flush with that of segment VIII, the ventral side is ascendent. Except for its very posterior end it is entirely covered by a sclerite, though the dorso-posterior part of this sclerite is rather feebly developed.

Latero-ventrally, on the posterior third to half of the sclerite, there is a pair of ascendent, rod-like reinforcements (IXa). Also latero-ventrally, though a bit more dorsal, on the sclerite a pair of narrow and not very well pronounced sulci (IXb) is seen.

For its whole length the ventral side of segment IX is split by a longitudinal cleft. In by far the greater, posterior part of the segment the broadly rounded margins of the cleft are in close contact, at least in repose, the cleft thus having the appearance of a deep furrow. At their anterior end the margins diverge, flanking the tongue e.gon.VIII. Here the sclerite of segment IX coalesces with that of the tongue, forming a pair of costae (fig. 12, e.gon.VIIIa) which, toward their edges, are bent laterally. Externally the costae appears as sutures in the shape of sulci. The latter again are flanked by a pair of rounded carinae (fig. 11 B, IXc), the anterior ends of which are bent laterally and a little backward.

For its whole circumference segment IX is provided with an antecosta which, however, is divided into a larger dorsal and a much smaller ventral part. The latter is coincident with the anterior and lateral margin of the carina IXc; it is of course paired, though the left and the right

half are connected by a rather indistinct cuticular thickening at the base of the tongue e.gon.VIII. The ventral antecosta is separated from the costa between this tongue and the carina IXc by a small interval. The lateral (or ventral) ends of the dorsal antecosta are situated in front of the lateral ends of the ventral antecosta.

The sclerite, except for those parts adjacent to the tongue e.gon.VIII, is clothed with setae, which are larger and more close-set than on the preceding segments.

The posterior end of the ventral side forms a membranous lower lip (figs. 11 B, 12, p.e.gon.IX) of the genital opening, lying between the ventral margins of the valves formed by segment X (see below). The lip is of course divided by the longitudinal cleft, but the two halves are closely apposed; its posterior end only is slightly bilobed. These lobes probably represent the distal ends of the gonopods IX.

Segment X is small and forms, so to speak, the rounded top of the cone of segment IX. On the dorsal side it is almost entirely, on the ventral side (fig. 11 B) entirely divided into a pair of valves, which are concave on the mesal side. On the dorsal side and posteriorly on the ventral side the valves are separated by a narrow cleft, on the greater, anterior part of the ventral side they are widely separated. Segment X projects farther backward than the lower lip of the genital opening, formed by segment IX.

Quite dorsally the anterior ends of the mesal sides of the valves are sclerotized (fig. 12, a.d.X). The two sclerites, left and right, are continuous at the bottom of the dorsal cleft and have, in a dorsal view, the shape of a hair-pin. Moreover, the posterior end and most of the lateral side of the valve is covered by a sclerite which, however, is rather weakly developed except for a narrow band along the ascendent dorsal margin. The rather acute anterior corner of the sclerite, which is situated latero-ventrally, forms a simple articulation with the sclerite of segment IX at the

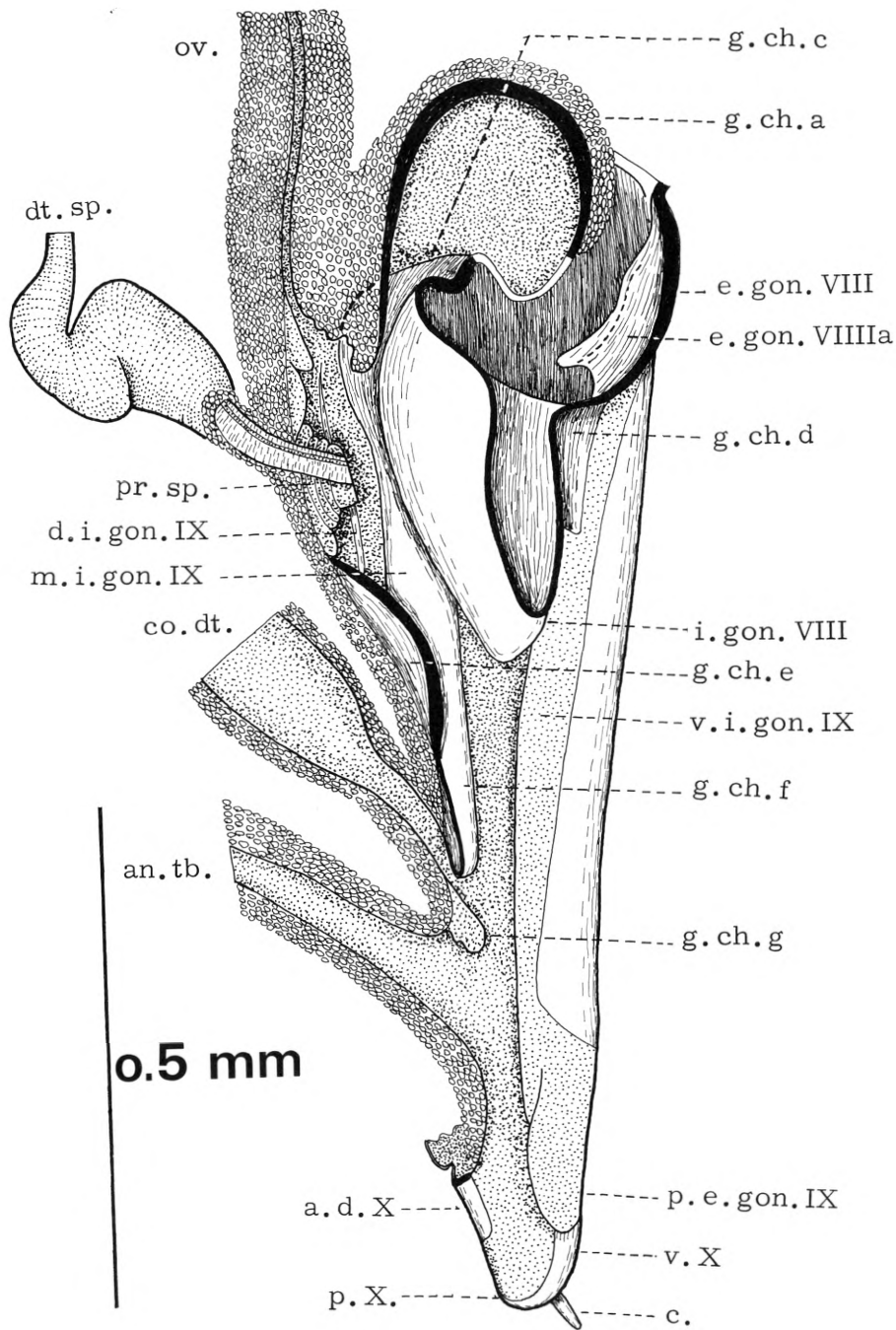


Fig. 12. *Tinodes waeneri*. Sagittal section through the genital chamber; left side as seen from the inside.

posterior end of the reinforcement IXa on the latter.

On the posterior end of the segment and along the posterior half of its ventral margin the sclerite is clothed with 3 μ wide sensilla campaniformia, so close-set that they almost touch each other, among which a very few, tiny (ca. 8 μ long), normal setae are found. Postero-ventrally on the lateral side there are extremely short, peg-like setae, which gradually merge with the sensilla campaniformia mentioned, all intermediates being found. Finally there are on each sclerite two larger, ca. 5 μ wide sensilla campaniformia, one laterally and one latero-ventrally; the former has a more posterior position than the latter.

The small and slender, finger-like cercus (fig. 11 C) is implanted into a small membranous area on the posterior end of the valve. It carries three sensilla, two sensilla campaniformia laterally and subdistally, and on the apex a tiny, peg-like seta like those on segment X.

The genital chamber (figs. 12, 13 A) fills up a great part of the lumen of segment IX. Here it is morphologically, though – at least in repose – not functionally, open on the ventral side. Conforming to the shape of segment IX its posterior part is very narrow. Forward it extends, widening, to the anterior end of segment VII.

The posterior end of the tongue e.gon.VIII is continuous, though only by a narrow, triangular strip through the cleft in segment IX, with the lower side of a rather elaborate structure (fig. 13 B, i.gon.VIII), which projects backward in the anterior part of the genital chamber and, in a dorso-ventral direction, fills most of the lumen. It has the shape of a sclerotized tongue which, as seen from the dorsal side, has a rather narrow base, broadens for most of its length, and eventually tapers somewhat toward the distal end, which is divided into two rounded lobes. The dorsal side is trough-like; during copulation the phallus of the male probably lies in this trough, the margins of which are rather much

thickened. In a longitudinal direction the bottom of the trough is slightly curved with a dorsal convexity. The tongue extends approximately to the middle of segment IX.

The ventral base of i.gon. VIII as well as the, in a dorsal direction broader, triangular strip which connects it with e.gon.VIII are continuous with a pair of strong, brown sclerites (figs. 12, 13 B, g.ch.d), lying ventrally and laterally in the wall of the genital chamber and not extending as far backward as i.gon.VIII. The dorsal margins of the sclerites g.ch.d again are continuous with the ventral sides of a pair of sclerotic folds (m.i.gon.IX) dorsally on the lateral sides of the genital chamber; in a transverse section they are roughly triangular; the dorsal side, which lies at a level a bit more dorsal than the upper side of i.gon.VIII, is horizontal. These folds, which extend farther backward than i.gon.VIII, are higher near the base of the latter, but also here the right and left fold are separated by an interval. In an anterior direction the folds become a little lower, posteriorly they soon become much lower and at the same time shifted toward the dorsal side of the genital chamber.

In front of the base of the tongue i.gon.VIII the dorsal side of the latter, the sclerites g.ch.d and the dorsal sides of the folds m.i.gon.IX are continuous and form the sclerotized mesal part of a thick lip (g.ch.c) which projects forward and has a rounded margin. Above this lip a rather narrow, transverse cleft leads into an anterior, sac-like extension (g.ch.a) of the genital chamber. In a dorsal view this sac is roughly triangular with rounded anterior and lateral corners. Its posterior side bulges a little into the base of the tongue e.gon.VIII. To their greater extent the walls of the sac are colourless, though stiff. The dorsal side, which is a little concave in a transverse direction, is sclerotized and brownish, and the sclerite continues, though only one third as broad and indistinctly delimited, over the anterior and ventral sides.

The common oviduct lies dorsally to g.ch.a

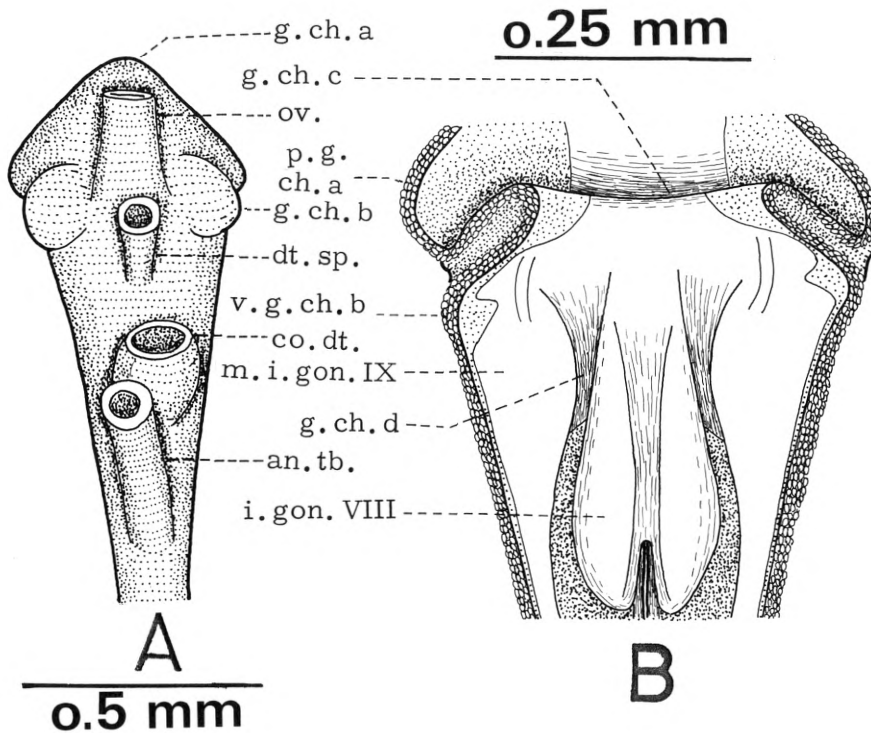


Fig. 13. *Tinodes waeneri*. A: The genital chamber in a dorsal view. B: Anterior part (except anteriormost part) of the floor of the genital chamber in a dorsal view.

and opens behind the entrance to this sac, above the base of the tongue i.gon.VIII. Since the sac g.ch.a is ventral to the oviduct, it cannot be a bursa copulatrix – which is lacking – though from a functional point of view it perhaps deserves this name better than the structure so-called in other Trichoptera. During copulation it very likely receives the distal, membranous and perhaps distensible end of the lower branch of the male phallus.

The opening of the oviduct is flanked by a pair of much smaller sacs (g.ch.b) issued from the dorsal side of the genital chamber. The anterior parts of these sacs lie laterally on the dorsal side of the sac g.ch.a. The sclerites on the dorsal sides of the folds m.i.gon.IX send small extensions into the ventral walls of the sacs.

The processus spermathecae (pr.sp.) is situated in a shallow concavity on the dorsal side of

the genital chamber, immediately behind the opening of the oviduct, above the middle of the tongue i.gon.VIII. Unlike conditions in other Trichoptera it is membranous, a rather small and low, circular wrinkled papilla with the opening of the ductus spermathecae in the middle.

Just behind the concavity with the processus spermathecae the dorsal wall of the genital chamber forms a low, unpaired, sclerotized bulge (g.ch.e) into the lumen. It is flanked by a pair of small, sclerotized folds (d.i.gon.IX) which are sclerotically continuous with the posterior part of its sclerite. The muscle gonm₃ suggests that they belong to the gonopods IX. They extend forward, narrow and rather sharp, on each side of the concavity with the processus spermathecae. They extend also, broader and rounded, behind g.ch.e and eventually unite

with the posterior ends of the folds m.i.gon.IX to form an unpaired, sclerotized tongue (g.ch.f) below the opening of the colleterial duct. In a transverse section this tongue is much curved, ventrally concave.

Behind the tongue e.gon.VIII the margins of the ventral cleft in the genital chamber project upward as a pair of narrow and low folds (v.i.gon.IX). The mesal sides of these folds are partly sclerotized, the sclerites being a direct continuation of the sclerite of segment IX.

The *spermatheca* consists of two rather large and equal, rounded sacs, connected by a narrow duct. It is doubtful, however, whether this condition is homologous with that in *Rhyacophila* (p. 32), since the sacs are posterior and anterior (or proximal and distal. Unzicker in his paper, 1968, apparently has interchanged his drawings of *Rhyacophila* and *Tinodes*). As far as I have been able to see, the sacs are provided with a feeble musculature, but I am not quite certain on this point.

The long ductus spermathecae is swollen and S-like curved subproximally (fig. 12). In this part of the duct the lumen is wide and the epithelium thick; a glandular function must be assumed. In the short proximal part of the duct the epithelium is just as thick, but the lumen very narrow and the cuticle thicker. In the long, thin and straight distal part of the duct the lumen is wide, the cuticle and the epithelium thin.

The proximal part of the spermathecal duct, the swelling included, has a strong circular musculature. In the distal part the latter is weak.

There is no glandula spermathecae.

The *common oviduct* is ascendent and broadens a little toward its cleft-like opening.

The *colleterial glands*, which have a simple shape, extend into segment V.

The *anus* is situated on the dorsal wall of the genital chamber a short distance behind the opening of the colleterial duct and separated from the latter by a membranous, finger-like process (g.ch.g). The position is immediately in

front of the dorsal side of segment X. Since this part of the genital chamber morphologically is open on the ventral side it perhaps is not correct to speak of a cloaca.

Musculature. The external ventral VII–VIII muscle has its anterior attachment laterally on the antecosta of segment VII and its posterior attachment mesally on the antecosta of segment VIII. In the internal muscle the anterior attachment is mesally, the posterior one laterally. In segment VIII one dorso-ventral muscle is found, namely dvm₄. There is only one VIII–IX muscle, probably dm₁. It is, though not very distinctly, divided into a larger mesal and a much smaller lateral portion.

The muscle gonm₁ originates on the ventral sclerite of segment VIII, in front of the middle of the depression on this sclerite. It “rolls” over the mesal side of the depression and is inserted in front of the costa flanking the tongue e.gon.VIII. The function of this muscle is puzzling, unless it plays some role during the final moult. The strong gonm₂ originates latero-ventrally on the sclerite of segment IX, below the anterior end of the sulcus IXb. Its bands converge fan-like toward the insertion on the posterior part of the costa e.gon.VIIIa (fig. 12). Since the latter attachment no doubt is the fixed one, the function of the muscle probably is to cause a deformation of the sclerite of segment IX and thus open the ventral cleft in this segment. The morphological value of this muscle perhaps is a little doubtful. The strong muscle gonm₃ is very steeply ascendent, though not entirely vertical. It originates latero-dorsally in segment IX. Its bands are slightly convergent toward the insertion to the anterior part of the fold d.i.gon.IX (fig. 12) near its junction with g.ch.e.

The IX–X muscle, which is rather strong, originates on the sclerite of segment IX above and behind the origin of gonm₂, but still below the sulcus IXb. It is inserted by means of a long tendon to the lateral sclerite of segment X

dorsally to the articulation between this segment and segment IX. It is perhaps both a levator and an adductor of the valves of segment X.

The muscle gchm is lacking.

The genital chamber, including g.ch.a and g.ch.b, has a circular musculature. The bands of course are interrupted by the ventral cleft in segment IX. Here they are attached to the sclerite of this segment.

Lype phaeopa Steph.

Pregenital segments. On the middle of each half of the tergum there is a longitudinal suture, which in front is connected with the antecostal suture. On the anterior segments it extends for two fifths of the length of the tergum, on the posterior segments it is shorter, and on segment VII it is very short. The sternum has a lateral longitudinal suture, which appears as a backward bent continuation of the antecostal suture. On segment V, however, it does not reach the latter, but its anterior end is forked. This fork might be supposed to enclose the opening of the gland of segment V, but this gland is lacking in *Lype*.

Segment VIII (fig. 14) is much shorter and less than half as broad as segment VII. In front it is almost as high as this segment, but its dorsal side is approximately 45° descendent. Its anterior end is rather much overlapped by segment VII, especially on the ventral side.

Segment VIII is synscleritous, but the dorsal and pleural regions are rather weakly defined. Laterally, though shifted a little in a ventral direction, there is a broad and deep, membranous anterior indentation (seen only in fig. 14 C; VIIIa), comprising one third both of the length and the height of the segment. The antecosta is divided into a dorsal and a ventral portion. The former extends also in front of the dorsal half of the anterior indentation, and thus comprises more than half of the circumference of the segment, whereas the ventral portion is devel-

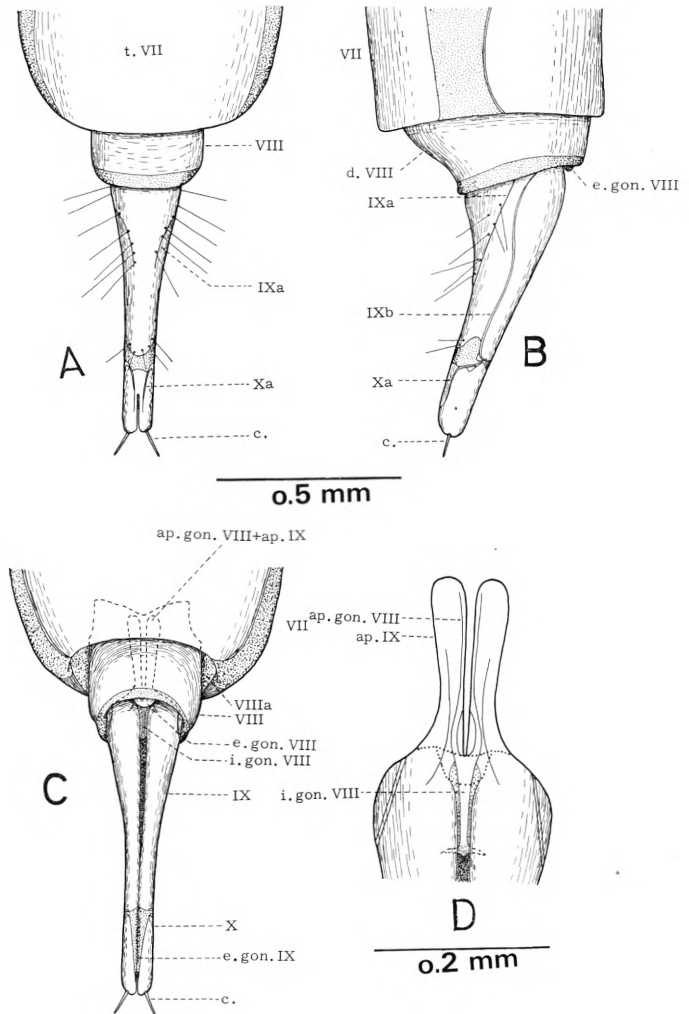


Fig. 14. *Lype phaeopa*. Posterior end of abdomen in a dorsal view (A), as seen from the right side (B) and in a ventral view (C). D: The apodemes of segments VIII and IX etc. in a ventral view.

ped only between the two indentations. Here the anterior margin again is indented in the shape of a very flat V.

Externally there is no connection between the sclerites of VIII and IX. However, a comparison with *Tinodes* (pp. 39 and 42) and *Ecnomus* (pp. 74 and 76) suggests that the structures e.gon.VIII and i.gon.VIII, described below, be-

long to segment VIII and represent the gonopods of this segment.

Segment IX is very long and slender, much more so than in *Tinodes*, strongly tapering in a posterior direction, and somewhat sagittally compressed. For its whole length the ventral side is divided by a longitudinal cleft. In the specimen shown in fig. 14 C the cleft gapes a little, and I have seen specimens in which it gapes even more. Normally, however, the margins of the cleft are closely apposed, except quite anteriorly, where they first diverge strongly, and finally again converge somewhat (fig 14 D). This part of the cleft, however, is concealed by the tongue e.gon.VIII.

Apart from the extreme posterior end the external parts of segment IX are entirely covered by a sclerite. Latero-dorsally on the anterior part of the segment there is a pair of fine, in a posterior direction convergent furrows (IXa). For the whole length of the lateral side a very strong, slightly S-like curved suture in the shape of a sulcus with a corresponding strong costa is seen (IXb). The posterior end of this suture is bent hook-like downward and forward.

Above each of the furrows IXa row of 3–7 (more often 7) long setae is seen. A transverse, curved row of 2–7 rather large setae is found dorsally on the posterior end of the sclerite. The other setae are small and scattered, but there is a rather dense clothing of sensilla campaniformia.

As mentioned above the anterior part of the ventral cleft in segment IX is covered from below by a tongue (e.gon.VIII). The latter is short and broadly rounded. The anterior half of its ventral side (concealed by overlapping of segment VIII) is membranous, the posterior half of the ventral side and the whole dorsal side is sclerotized. (See also below; the genital chamber).

Segment X is long and slender and forms, as it were, the posterior end of segment IX. It is divided by a longitudinal cleft, dorsally for about its posterior half, ventrally for its whole length.

To its greatest extent segment X is covered by an unpaired sclerite, but the closely apposed margins of the ventral cleft are bordered by membranous stripes, which are narrow behind, broad in front. Together they form a slightly bilobed lip for the genital opening, which does not project as far backward as the dorsal side of the segment. These membranous areas, however, probably are part of segment IX, representing the distal ends of the gonopods, though their cuticle is continuous with the sclerite of segment X. (Cp. p. 48).

Latero-ventrally the sclerite of segment X forms a simple articulation with the suture IXb, but otherwise the sclerites of the two segments are separated by copious membrane. Above the articulation the anterior margin of the sclerite of segment X has a reinforcement. On the dorsal side the latter bends backward, the two reinforcements (left and right) converging, but not reaching the posterior end of the segment.

On the posterior end of the sclerite of segment X, and in a broad belt along its ventral margin, there are close-set sensilla campaniformia, densest on the posterior end, among which some few, tiny normal setae are seen. On the lateral side, somewhat behind the middle, a little larger (ca. 4 μ wide) sensillum campaniformium is found. Quite posteriorly on the lateral side there are tiny, but comparatively thick, peg-like setae, intermediates between setae and sensilla campaniformia. On the rest of the sclerite normal, small setae are found.

The short, slender, distally tapering cerci arise from a pair of small, circular, membranous areas on the posterior end of segment X. In a short, proximal part of the cercus its wall is 1 μ thick. Quite proximally, however, there is a slight constriction in which the wall is still thinner. In the larger, distal part of the cercus the wall is so thin that its thickness cannot be measured with the light microscope, but here it is strengthened by ring-like thickenings. Occasionally these "taenidia" divide into two. Hense, in an optical

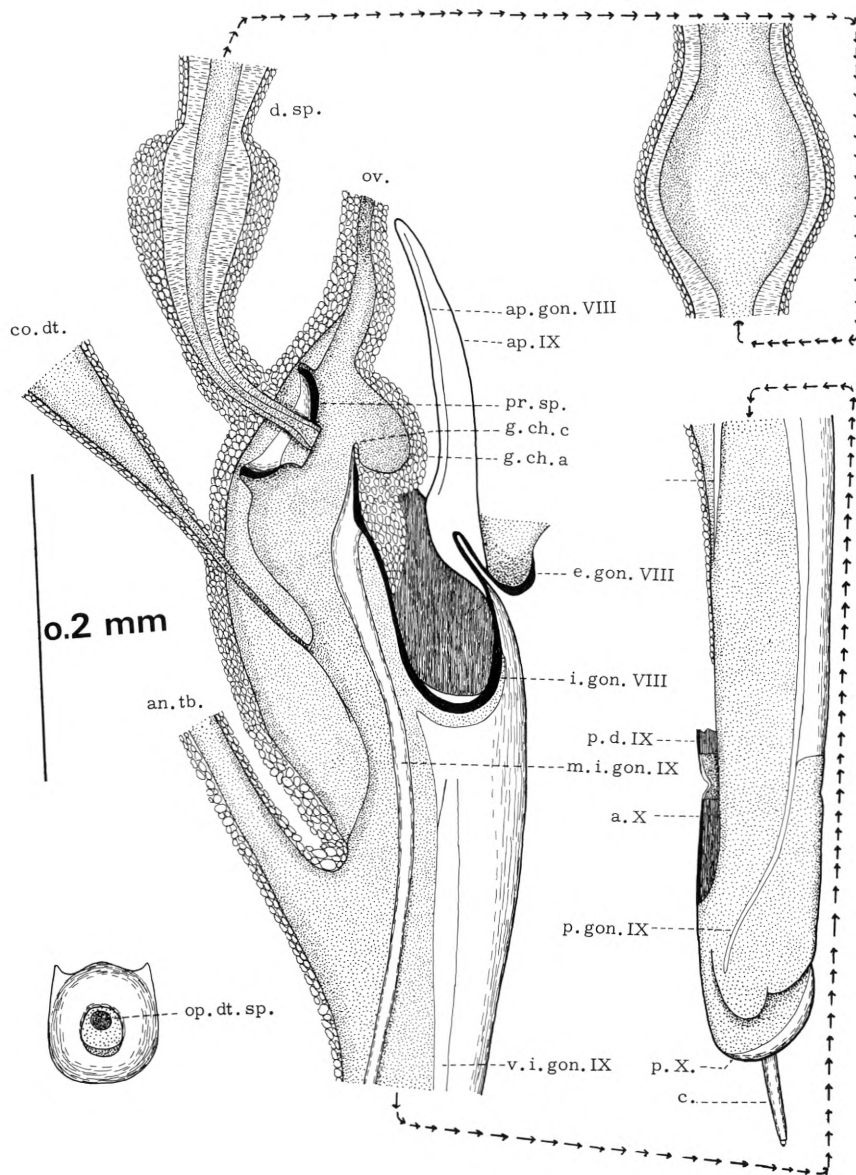


Fig. 15. *Lype phaeopa*. Sagittal section through the genital chamber; left side as seen from the inside. Left lower corner: The spermathecal sclerite in a ventral view.

longitudinal section (fig. 16 B) their number is not necessarily the same on the two sides. Distally the rings become lower, and quite distally they are entirely lacking. Here again the wall seems to be a little thicker.

The apex of the cercus carries a structure, which perhaps may be described as an interme-

diate between a sensillum basiconicum and a sensillum styloconicum; the wall, which in itself is extremely thin, has a ring-like portion which seems to be still thinner.

The genital chamber. For about the anterior fifth the membranous insides of the valves, formed by segment IX, are connected by a thick

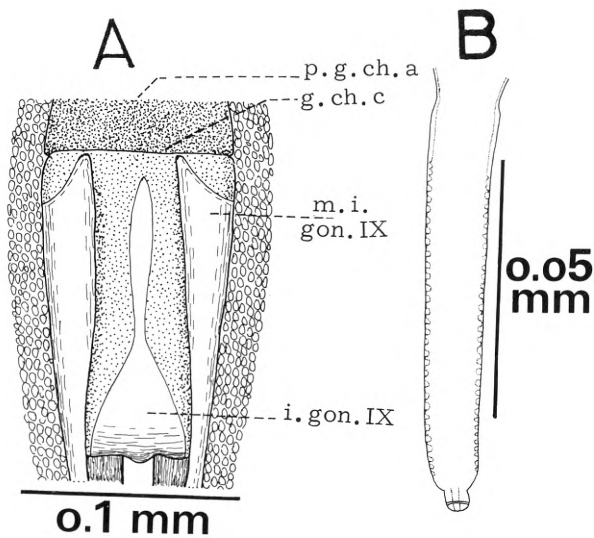


Fig. 16. *Lype phaeopa*. A: The anterior part (except the anteriormost part) of the floor of the genital chamber in a dorsal view. B: Optical longitudinal section through the right cercus.

tongue (figs. 14 C, D, 15, i.gon.VIII) which is several times as long as e.gon.VIII. (The tongue i.gon.VIII thus has no lateral sides). The very broadly rounded posterior margin of this tongue is sclerotized in almost its entire width. In the middle it has a low, rounded carina, which in a ventral or dorsal view appears as a low, rounded tooth. In front of the carina the sclerotization continues on the ventral side as a very narrow, rod-like sclerite, which gradually increases in width, and at its extreme anterior end suddenly becomes very broad. Here it is continuous, laterally with the inward turned lateral (or ventral) parts of the sclerite of segment IX, mesally with the dorsal side of e.gon. VIII. From the furrow between these structures a pair of forward directed, spoon-like apodemes (ap.IX) is issued. Together the two apodemes resemble a pair of hare's ears; their thickened mesal margins (fig. 14 D, ap.gon. VIII) lie rather close to each other.

The sclerite on the posterior margin of i.gon.

VIII continues on its dorsal side, but soon narrows to a lanceolate rod, (fig. 16 A) which does not quite reach the anterior end of the tongue. The latter appears as a rather thin lamella, forming a sort of lip (g.ch.c) of a ventral bulge (fig. 15, g.ch.a) of the anterior end of the genital chamber. This structure no doubt is homologous with the sac g.ch.a. in *Tinodes* (figs. 12 and 13, pp. 41 and 43), but of considerably smaller dimension. Immediately in front of it the common oviduct opens.

The genital chamber (fig. 15) extends into segment VIII. As in *Tinodes* it is morphologically open for the greater, posterior part of its length. Below and behind the tongue i.gon.VIII the sclerite of segment IX extends for some distance onto the wall of the here sagittally compressed genital chamber. For almost its entire length the margin of this sclerotization has a reinforcement (v.i.gon.IX), which proceeds beyond the sclerite of segment IX as a narrow rod on the "internal valve" of segment X described below. Slightly S-like curved it approaches the dorsal side.

The membranous areas seen in fig. 14 C (cp. p. 46) between the sclerite of segment X and the ventral cleft are the ventral sides of a pair of chiefly membranous internal valves (fig. 15 p.gon.IX), which do not project as far backward as the external valves. The two valves (left and right) are closely apposed.

On the lateral side of the genital chamber there is a narrow, sclerotized fold (m.i.gon.IX). Its anterior end lies close to and is partly issued from the dorsal side of the tongue i.gon.VIII. In a posterior direction the fold approaches the dorsal side, decreases much in size, and finally disappears entirely in the posterior part of segment IX. A structure homologous with d.i.gon.IX in *Tinodes* and *Psychomyia* does not seem to be found in *Lype*.

The processus spermathecae (fig. 15) is situated quite anteriorly on the dorsal wall of the genital chamber. It is a low, sclerotized dome. Its posterior side is transverse, though with a broad,

but low ridge in the middle, flanked by a pair of shallow, rounded furrows, sharp posterior corners thus being formed. In the middle of the dome there is a smaller, membranous papilla, on the distal surface of which the opening of the spermathecal duct is found excentrically, near the anterior side.

There is no *bursa copulatrix*.

The *spermatheca* is a large, somewhat elongate sac. Its anterior end lies at the boundary between segments V and VI, its posterior end in the middle of segment VII. The most proximal part of the ductus spermathecae (fig. 15) appears as a club-like swelling, by a slight constriction separated from another, fusiform swelling. Distally to the latter the duct tapers gradually and strongly. In the swellings, and especially in the club-like bulbus, the epithelium is thick and appears to be glandular, whereas there is no separate glandula spermathecae. The circular musculature of the duct is especially strong in the bulbus.

The *colleterial glands*, which have a simple shape, extend into the posterior end of segment V. They have a thick common part, lying transversely in segment VII, from which the rather thin colleterial duct issues. The latter is S-like curved: backward into segment VIII, downward and forward, and then downward and backward again. It opens above the tongue *i.gon.VIII*, on the anterior end of a membranous fold on the dorsal wall of the genital chamber, immediately behind the *processus spermathecae*.

The *anus* is found just behind this fold, a little in front of the middle of segment IX.

Musculature. The external ventral VII–VIII muscle converges, the internal one diverges in a posterior direction. In addition the dorsal side of the front end of the common oviduct receives fine muscle bands from the anterior margins of both segments VII and VIII. This musculature no doubt is a derivate of the internal muscle.

There are two dorsal VIII–IX muscles, which I have interpreted as dm_1 and dm_3 . The former

originates mesally on the antecosta of segment VIII and is inserted latero-dorsally to segment IX. The latter originates laterally on the antecosta of segment VIII, extending onto that part which lies in the anterior indentation of the sclerite, crosses externally to dm_1 , and is inserted dorso-mesally to segment IX. The muscle vm_6 originates on a large, lateral part of the sclerite of segment VIII and is inserted to the lateral margin of the spoon-like apodeme *ap.IX* (fig. 14 D).

In segment VIII the muscle dvm_4 is present in the anterior indentation of the sclerite.

The strong $gonm_1$ originates on the ventral antecosta of segment VIII for almost the entire width of the latter and is inserted to the tongue *e.gon.VIII*. The muscle $gonm_2$ originates on that part of the ventral side of segment IX which flanks *e.gon.VIII* and is inserted to the posterior end and somewhat less than the posterior half of the dorsal side of *i.gon.VIII*. The anterior bands are approximately 45° ascendent, the posterior ones almost horizontal. I did not find a $gonm_3$.

A strong muscle, which in a dorsal or ventral view is fan-like converging in an anterior direction, originates on the middle of the costa of the suture IXb (fig. 14 B). The ascendent muscle is inserted to the sclerite of segment IX in a transverse line at a level a little in front of the posterior end of *e.gon.VIII*. Most of the insertion is below the suture IXb, but some bands are attached above this suture, extending toward the furrow IXa. If the interpretation of this muscle as a IX–X muscle is correct, it indicates that the apparent boundary between segments IX and X is secondary.

The muscle *gchm* is lacking.

The circular musculature of the genital chamber of course has the character of a true circular musculature only in the anterior part of the chamber. The most posterior rings lie on the middle of the dorsal side of *i.gon.VIII*. Behind that point the rings are interrupted ventrally. As far as the posterior end of *i.gon.VIII* they seem

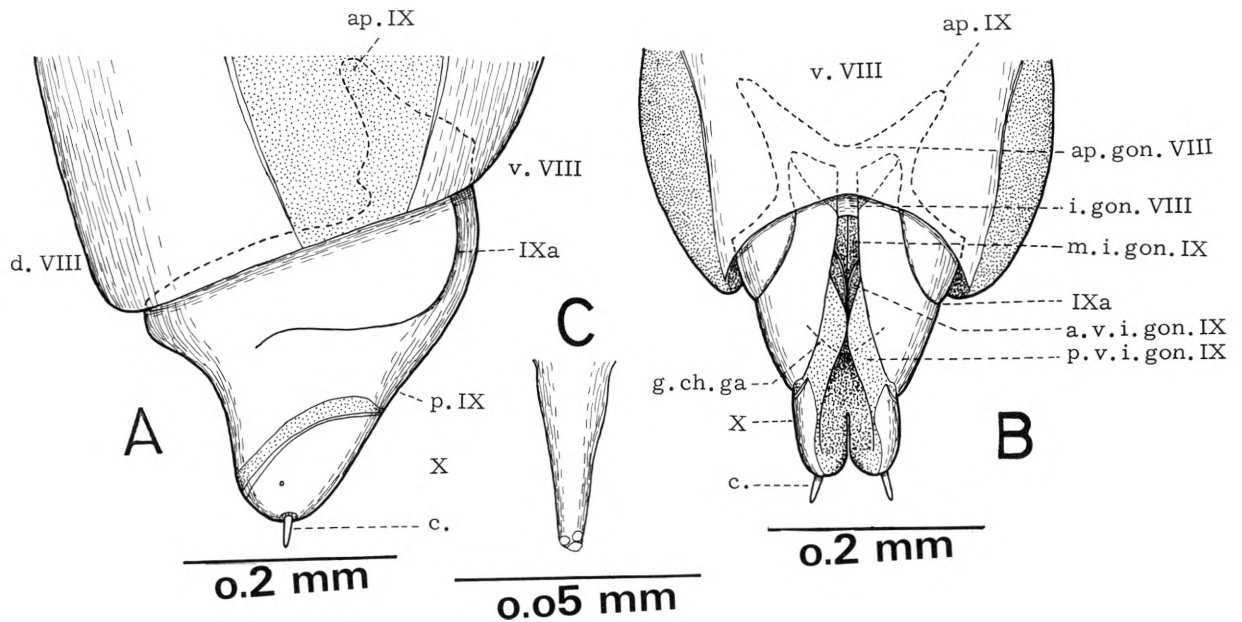


Fig. 17. *Psychomyia pusilla*. Posterior end of abdomen as seen from the right side (A) and in a ventral view (B). C: Right cercus in a lateral view.

to be attached to m.i.gon.IX, and then to the sclerite of segment IX near the ventral cleft.

Psychomyia pusilla F.

Pregenital segments. There is, on the tergum, a mesal, paired longitudinal suture, which extends for about one fourth of the length of the segment. There is no gland on segment V.

Segment VIII (fig. 17) does not differ much from the pregenital segments. A comparison with *Tinodes* and *Lype*, however, makes it unlikely that the tergum and sternum are serially homologous with those of the preceding segments. In a posterior direction the tergum and sternum, which are provided with the same sutures as the pregenital terga and sterna, approach but are far from reaching each other. Ventrally the posterior margin of the segment (fig. 17 B) is indented for its whole width.

Segments IX and X together are, quite unlike conditions in *Tinodes* and *Lype*, very short, subconical, and much sagittally compressed. In a lateral view the dorsal side is slightly S-like curved, the ventral side ascendent. The boundary between the larger segment IX and the smaller segment X is only indicated by a rather narrow membranous stripe.

For its whole length the ventral side of segment IX is divided by a longitudinal cleft, which always gapes, in front only a little, at the posterior end for almost the whole width of the segment.

Apart from two small, triangular membranous areas bordering the anterior end of the ventral cleft (and to their greatest extent concealed by the overlapping posterior margin of segment VIII) segment IX is covered by a strong sclerite, which also extends a little onto the internal side of the cleft. Here its margin projects as a 12–15 μ broad lamella, which vanishes a little in front of the posterior end of the segment.

Approximately in the middle of the lateral

side the sclerite of segment IX has a vertical, slightly S-like bent carina (fig. 17 A, IXa), which ventrally bends evenly forward. The vertical part of this carina is less sharply defined, ca. 135° in cross section, than the ventral longitudinal part, which is ca. 90° in cross section. The most anterior part of the carina, however, is indistinct. On the ventral side the anterior part of the sclerite, laterally bounded by the carina, has a sculpture of very fine, labyrinthine wrinkles. Colour differences might suggest a division of the sclerite of segment IX, but this division has no relation to skeletal morphology.

Segment IX has no antecosta, at least not a distinct one.

The ventral side of segment X is almost twice as long as the dorsal side. The segment is entirely divided into a pair of valves, which are concave on their membranous internal sides. Dorsally the cleft between the valves is narrow, ventrally their margins are widely separated. The external side of each valve is covered by a sclerite, the ventro-anterior corner of which forms a simple articulation with the sclerite of segment IX. Except for a reinforcement along the ascendent anterior margin the sclerites of segment X are rather weakly defined. The dorsal part of the reinforcement is not only wider, but also stronger, brownish, than the lateral part.

The cerci (fig. 17 C), which are implanted into small membranous areas on the posterior end of the segment, are short, tapering distally, and very thin-walled. The thickness of the wall is proximally 1.5, distally 0.5 μ . The still more thin-walled apex carries three flat, dome-like sensilla, a larger one distally and two smaller ones subdistally and laterally. They may be either sensilla campaniformia or chemoreceptors.

Segments IX and X are clothed with small setae. In a broad fringe along the posterior half of the ventral cleft on segment IX they are very strong. On segment X, below the cercus and on the posterior part of the ventral side of the

sclerite, there are close-set sensilla campaniformia. Two somewhat larger ones are found on the anterior part of the lateral side and on the posterior end, a little above the cercus, resp. Intermediates between setae and sensilla campaniformia are found above the cercus and on the posterior part of the lateral side.

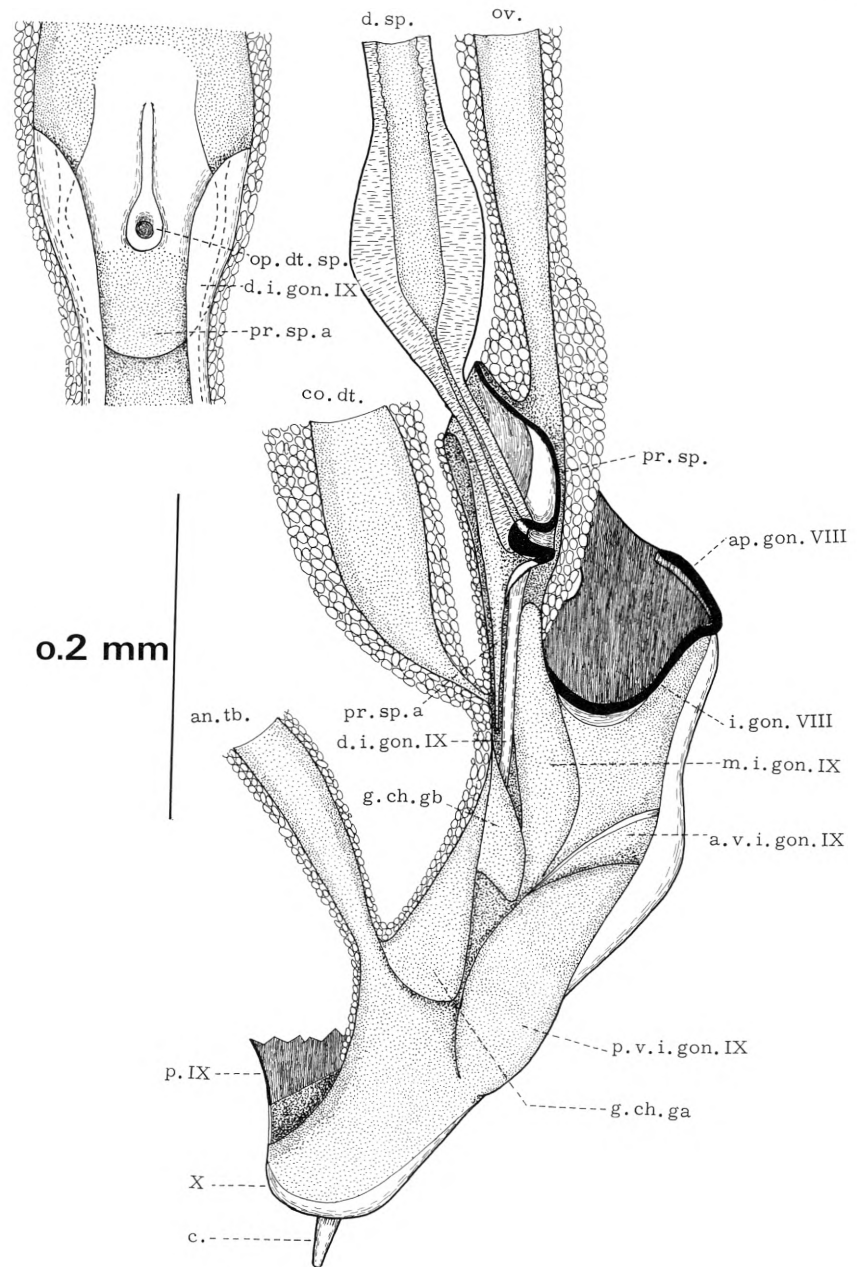
The genital chamber (fig. 18) extends approximately to the anterior end of segment VIII. Ventrally its posterior part is, not only from a morphological but also from a functional point of view, open, though a sort of closure is effectuated by the folds mentioned below. There is not the slightest trace of an anterior dilation as in *Tinodes* and *Lype*, nor is there any bursa copulatrix, and hence the boundary between the common oviduct and the genital chamber is not sharply defined. The former extends to the anterior end of segment VII.

At the anterior end the two valves formed of segment IX, as in *Lype*, are connected by a thick tongue (figs. 17 B, 18, i.gon.VIII). Its dorsal side is membranous, its very broadly rounded posterior margin, which in a ventral view is a little concave, as well as its whole, ascendent ventral side are sclerotized. The anterior end of the ventral side is continuous with an apodeme (ap.gon.VIII), which here is ca. 45° descendent. The lateral, and not descendent parts of the apodeme are formed by the sclerite of segment IX. In this way a sclerotic connection between this sclerite and the tongue i.gon.VIII is formed. The anterior corners of the apodeme are produced into forward and outward directed extensions (ap.IX). The ventral side of these extensions faces also laterally, and hence they both in a ventral (fig. 17 B) and in a lateral view (fig. 17 A) appear narrower than they really are.

On the dorsal side of the apodeme ap.gon.VIII there is an unpaired longitudinal costa, which in an anterior direction becomes higher and broader.

On the membranous interior side of the valve of segment IX two longitudinal folds are seen,

Fig. 18. *Psychomyia pusilla*. Sagittal section through the genital chamber; left side as seen from the inside. Upper left corner: Anterior part of the upper wall in a ventral view.



one posterior and more ventral (v.i.gon.IX), another anterior and more dorsal (m.i.gon.IX). The narrow anterior end of the latter lies above the tongue i.gon.VIII. The former is divided by an oblique, in an anterior direction divergent, furrow into a posterior (p.v.i.gon.IX) and a

much smaller anterior fold (a.v.i.gon.IX). The posterior end of m.i.gon.IX lies above a.v.i.gon.IX. The folds are membranous, except for the sharp edge of a.v.i.gon.IX, which is sclerotized. At its anterior and ventral end this rod-like sclerite is hook-like bent upward and outward

and eventually is continuous with the sclerite of segment IX.

The right and the left folds m.i.gon.IX and a.v.i.gon.IX are closely apposed, and the same is the case with the anterior ends of the folds p.v.i.gon.IX. In a posterior direction the two last mentioned folds diverge and eventually merge with the ventral margins of segment X. At the boundary between segments IX and X this fold has an area with slender, 13 μ long and 1.5 μ thick, pale microtrichia.

Dorsally on the lateral side of the genital chamber there is a low and narrow, though in an anterior direction somewhat higher and broader, sclerotic fold (d.i.gon.IX). Its anterior end extends beyond the fold m.i.gon.IX, its posterior end not quite so far backward as this fold.

I think it is justified to consider these folds as homologous with the structures given the same designations in *Tinodes* (p. 42).

The processus spermathecae can be described as a rather narrow, but very high, backward directed transverse fold on the anterior part of the dorsal wall of the genital chamber, between the front ends of the folds d.i.gon.IX. Its ventral side almost touches the membranous dorsal side of the tongue i.gon.VIII. On the anterior two thirds of the fold a sclerite, which becomes broader in a posterior direction, lies on the ventral side. On the greater, posterior part of this sclerite there is again a high longitudinal ridge in the middle. For most of its length it is very narrow, but its hind end is roundish expanded. On this part there is a deep and very thick-walled, pot-like depression, no doubt destined to receive the "beak" of the male phallus (Nielsen 1957, pp. 41–42) during copulation, in the bottom of which the opening of the ductus spermathecae is found.

The posterior part of the fold is developed as a thin, colourless, but apparently stiff lamella (pr.sp.a), forming a valve for the opening of the funnel-like colleterial duct.

The anus is situated on the dorsal wall of the

genital chamber, approximately in the middle of segment IX. Just in front of it there is a thick, backward directed, membranous tongue (g.ch.ga). Proximally on the ventral side this tongue has a pair of longitudinal folds, the posterior ends of which project as a pair of pointed, membranous processes (g.ch.gb). The ventral side of the tongue, including the folds, is clothed with slender, 13 μ long and 1 μ thick, pale microtrichia. Though the genital chamber, as in *Tinodes* and *Lype*, is a cloaca, the anus and the egg passage to some extent are separated by this tongue.

The ovaries are well developed and fill most of the abdomen, even in newly emerged females.

The spermatheca is a pear-like sac extending from the boundary between segments VI and VII to the boundary between segments IV and V. In the most proximal part of the ductus spermathecae (fig. 18) the lumen is narrow, the epithelium thick and probably glandular. Then follows a fusiform swelling with a wide lumen and a still thicker epithelium, and finally a rather long reach of the same width throughout, in which the lumen is wide and the epithelium thinner (though probably still glandular). Toward the spermatheca, however, the thickness of the epithelium increases, the width of the lumen decreases. In the spermathecae itself the epithelium is thin. I was unable to see any muscles in the wall of the duct.

There is no glandula spermathecae.

Colleterial glands. The position of their anterior ends varies from segment III to segment II.

Musculature. The muscle dvm₄ is present until and including segment VII. One band, at the segment boundary, is considerably stronger than the others. This band is found also at the boundary between segments VI and VII, but not at the boundary between segments VII and VIII. In the latter segment no dorsoventral muscles are found.

The external ventral VII–VIII muscle is composed of a number of fine bands. The internal

muscle consists of two strong bands, which both diverge in a posterior direction.

In my opinion the only VIII–IX muscles present are dm_1 and vm_6 . The latter originates on the posterior margin of segment VIII and diverges somewhat toward its insertion to the ventral side of ap. IX.

The muscle $gonm_1$, consisting of several bands, extends from the ventral antecosta of segment VIII to the base of the tongue i.gon.VIII. The mesal bands are approximately longitudinal, the lateral bands converge. The not particularly strong $gonm_2$ is composed of one layer of bands, which originate on the longitudinal part of the carina IXa. They go in a mesal and a little anterior direction and are inserted, partly to the ventral side of the tongue i.gon.VIII, partly (the most anterior bands) to the longitudinal costa on ap.gon.VIII. I found no $gonm_3$.

The IX–X muscle is not very strong. It originates on the sclerite of segment IX behind the dorsal end of the carina IXa. The rather few bands are a little descendent and a little convergent toward their insertion to the anterior margin of the sclerite on segment X. Since the insertion is laterally to the articulation between the sclerites of segments IX and X, this muscle probably must act as an abductor of the valves of segment X.

The muscle $gchm$ is lacking. The circular musculature of the genital chamber is developed approximately as in *Lype* (pp. 49–50). The complete rings extend for the whole membranous dorsal side of the tongue i.gon.VIII, the “broken rings” to the posterior end of segment IX, i.e. behind the anus.

Wormaldia occipitalis Pict.

Pregenital segments. The sterna are considerably broader than the terga. There is no gland on segment V.

Segment VII, already, is much modified. It is

considerably thinner than segment VI and tapering in a posterior direction. In the specimen shown in fig. 19, in which the “Legeröhre” was at least partially extended, neither the tergum nor the sternum did reach the posterior margin of the segment. There is no lateral longitudinal suture on the tergum.

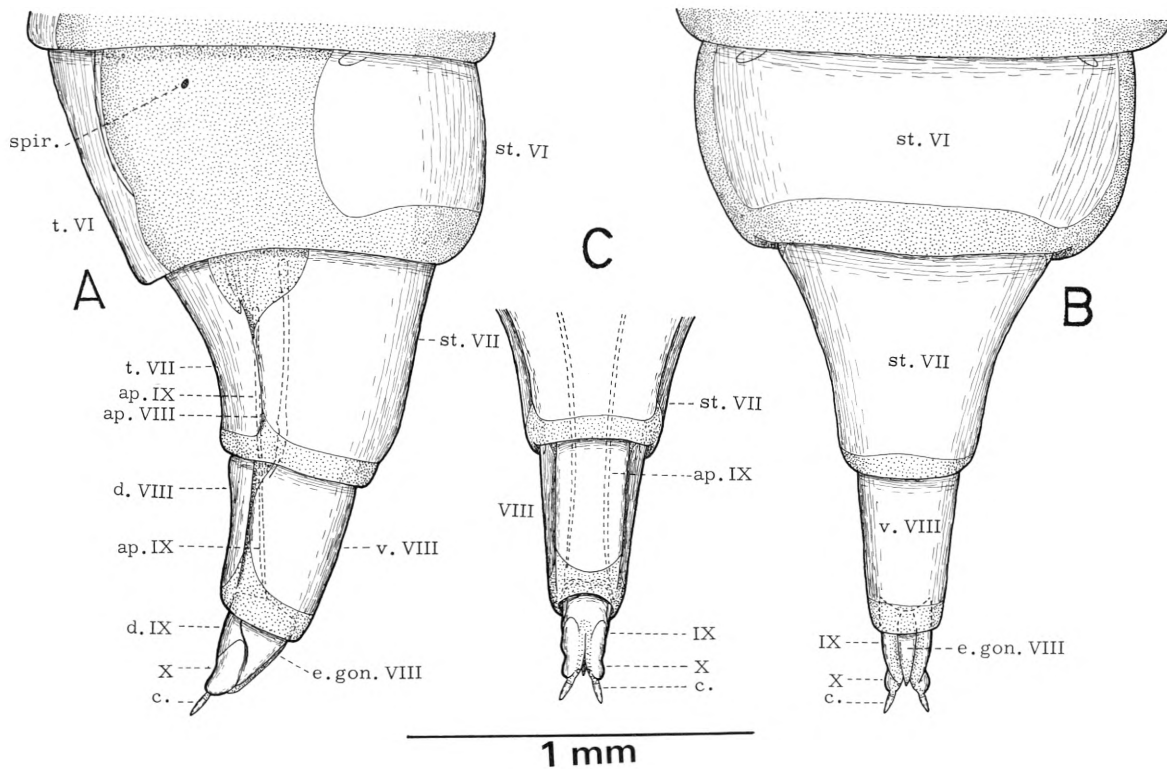
For their posterior half the lateral margins of the tergum and the sternum touch each other. The margins of the sclerites, and especially that of the tergum, are bent inward, a latero-dorsal longitudinal furrow thus being formed. The sternum, which is considerably broader than the tergum, is visible in a dorsal view.

In the anterior part of the segment the margins of the sclerites recede from each other, leaving a broad pleural membrane, which shows a fan-like figure of fine longitudinal wrinkles.

Segment VIII is much more slender than segment VII, but only tapering a little toward the posterior end, and slightly sagittally compressed. Otherwise this segment to some degree is a duplicate of segment VII. However, the tergum and the sternum are separated for their whole length, though the middle of the lateral margin of the sternum almost touches that of the tergum. Moreover, none of these sclerites reaches the anterior end of the segment, except for the anterior corner of the sternum, which is produced into a narrow rod. This rod continues forward as a thin, though at the anterior end a little dilated, apodeme (ap.VIII), which by fully retracted “Legeröhre” must reach the posterior end of segment VI.

Normally the anterior end of segment VIII is much overlapped by the posterior end of segment VII.

Segments IX and X (figs. 19, 20 A) are so firmly united that the boundary cannot be stated with any degree of certainty. Together they form a small terminal segment of the abdomen. It is narrower and lower than the posterior end of segment VIII and rather much sagittally compressed. In a dorsal and ventral view it tapers only



a little, in a lateral view much toward the posterior end.

For its whole length the ventral side of the combined segment is divided by a gaping longitudinal cleft. This cleft, however, is closed by an unpaired tongue (e.gon. VIII), the anterior two thirds of which have coalesced with the margins of the cleft in segment IX and ventrally are covered by a transversely convex sclerite. The membranous distal end of the tongue is sagittally compressed, and more so in a posterior direction, so that in a ventral view it is acutely pointed. The membranous and, especially at the posterior end, thin-walled dorsal side is bisected by a deep longitudinal furrow, suggesting a paired origin. The tongue probably represents the gonopods of segment VIII.

Also dorsally the combined segment is divided, but only for a little more than one third of its length. To their greater extent the margins of

Fig. 19. *Wormaldia occipitalis*. Posterior end of abdomen as seen from the right side (A) and in a ventral view (B). C: Posterior end of segment VII and segments VIII-X in a dorsal view.

the dorsal cleft are closely apposed, but at the hind end the cleft gapes widely, a pair of small, divergent processes thus being formed (fig. 20 B). In a dorsal or ventral view these processes are separated from the rest of the combined segment by a slight constriction.

The combined segment is largely covered by an unpaired sclerite which, however, does not reach the anterior end of the segment, nor the dorsal and ventral clefts. The sclerite, which is pale and rather weakly defined, has some reinforcements. The strongest one is along more than the dorsal half of the anterior margin, which in the middle has a slight, V-like indentation. Another, narrow, descendent and a little S-

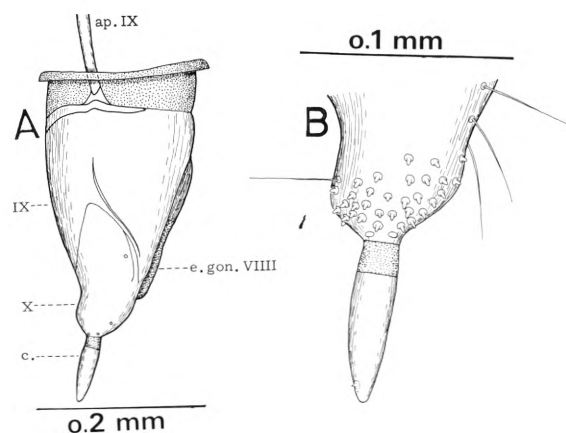


Fig. 20. *Wormaldia occipitalis*. A: Segments IX and X as seen from the right side. B: Posterior end of segment X with right cercus in a lateral view.

like curved one is in the middle part of the lateral side. On the posterior part of the lateral side of the segment there is a line in the shape of a V, the rounded bottom of which points forward, and behind which the sclerite has a little darker colour. This line might perhaps be considered as the boundary between segments IX and X, but the musculature (p. 58) proves that this is not the case. The posterior half of the ventral leg of the V has the character of a reinforcement.

On the otherwise membranous mesal sides of the posterior processes there is a pair of strong, rod-like, vertical sclerites, which have no connection with the large sclerite.

A little dorsally to the middle of the lateral side a triangular area of thick, but elastic cuticle connects the anterior margin of the large sclerite with a short, longitudinal rod, which proceeds forward as a slender, black apodeme (figs. 19 A, C, 20 A, ap.IX), which lies above the apodeme of segment VIII, and by retracted "Legeröhre" must extend far into segment VI. Dorsally the elasticuticular, triangular area has a group of very close-set sensilla campaniformia.

The sclerite of segment IX (as defined above

by the V-shaped line) has a dense clothing of sensilla campaniformia, but no setae. The anterior part of the sclerite of segment X is clothed with slender, up to $32\ \mu$ long, pale setae, densest and longest along the ventral margin. On the posterior processes (fig. 20B) the sclerite is richly provided with intermediates between setae and sensilla campaniformia: $1.5\ \mu$ long and $1\ \mu$ thick setae with rounded apices set in $4\ \mu$ wide alveoles. Moreover there are (always?) four typical sensilla campaniformia, two above each other at the base of the cercus, one more ventrally and anteriorly, and one above the middle of the reinforced part of the ventral leg of the V. Finally there is a small, $8\ \mu$ long setae mesally to the cercus. The ventral tongue is devoid of setae.

The cercus is situated on the posterior end of segment X, mesally to the posterior margin of the external sclerite. It is short and slightly fusiform. The wall is $1.2\ \mu$ thick (as compared with $2.5\ \mu$ on segment X itself). In the distal fourth, however, the wall is still thinner, but here it has irregular, ring-like thickenings. The cercus carries only one sensillum, a tiny, $1.5\ \mu$ long and $1\ \mu$ thick, conical setae with a comparatively large alveole, situated subdistally and medio-dorsally. It is probably tactile in function.

The "Legeröhre". Segment VIII can be retracted so much into segment VII that the posterior, membranous parts of the latter are concealed. Segments IX and X can be retracted entirely into segment VIII.

The genital chamber (fig. 21) is long and slender and extends even more forward than the apodemes of segment IX. In an anterior direction it becomes gradually a little wider. Its thin, membranous wall is thrown into irregular folds, but apart from the processus spermathecae (and its immediate surroundings) there are no definite structures.

Immediately above (or behind) the opening of the common oviduct the dorsal wall of the genital chamber is vertical for a short reach and bulges into the lumen of the chamber. The

bulge is bisected by the crescentic (dorsally concave) opening of the ductus bursae. The larger, dorsal section is the processus spermathecae, which thus form the dorsal wall of the opening of the ductus bursae.

The processus spermathecae (fig. 21) is a rather low, approximately circular knob. Apart from the ventral side, which is membranous or at most weakly sclerotized, the knob is strongly sclerotized. On its posterior (morphologically: ventral) surface there is an only half as thick and

half as high process, which is sclerotized only quite proximally. In the center of the posterior surface of this process, again, the opening of the ductus spermathecae is situated.

The ovaries are rather small, but seem to be fully developed in newly emerged females.

The common oviduct is S-like bent by retracted "Legeröhre".

The bursa copulatrix is unusual by being paired, but the two bursae open through a common duct. Each is slender, club-like, and the wall is thrown into numerous, irregular wrinkles. Both the bursae themselves and the duct are surrounded by a rather strong circular musculature.

The spermatheca is comparatively small, pear-like, the ductus spermathecae rather long. For most of its length the duct is very slender. Approximately in the middle there is a slight swelling, and proximally a considerably stronger swelling. The latter does not represent any widening of the lumen, which in the extreme proximal end decreases to a small fraction of its former width. In that part of the duct which lies proximally to the middle swelling the internal wall is clothed with microtrichia, ca. $13\ \mu$ long (a little more than half the width of the lumen) and $0.5\ \mu$ thick.

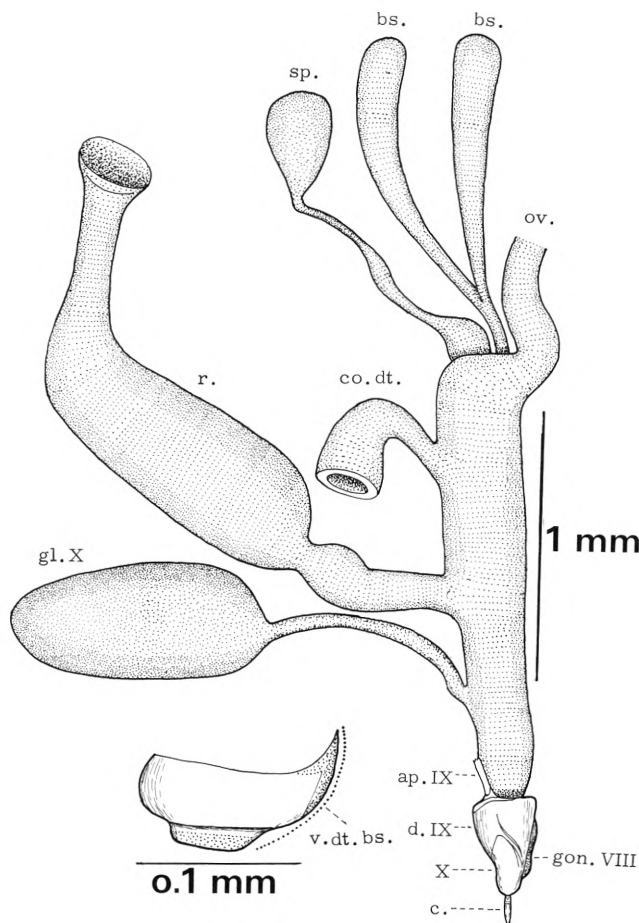
In the two swellings of the ductus spermathecae the epithelium is thick and probably glandular, but there is no glandula spermathecae. The circular musculature is rather weak, except in the proximal swelling, where it is strong.

The colleterial duct opens not far behind the processus spermathecae. Its proximal part is upward and forward directed, then it bends backward and becomes funnel-like.

The anus is situated approximately in the middle of the dorsal wall of the genital chamber.

An unusual organ (gl?X) lies dorsally in segment VI and extends for some distance into segment VII. It is elongate and considerably larger than both the spermathecae and the bursae copulatrices. In preserved specimens it appears white and solid. From its posterior end a

Fig. 21. *Wormaldia occipitalis*. The genital chamber as seen from the right side. Lower left corner: Processus spermathecae as seen from the right side.



slender duct leads to the genital chamber, on the dorsal wall of which it opens, midway between the anus and the anterior margin of segment IX. The organ may have a glandular function.

Musculature. There are two dorsal VII–VIII muscles, interpreted as dm_1 and dm_6 , resp. The former is in front attached to the antecosta of tergum VII, behind to the anterior border of tergum VIII. The anterior attachment occupies only a fraction of the antecosta VII, the posterior one not the entire margin of tergum VIII. The muscle dm_6 is stronger than dm_1 . It originates on the posterior corner of tergum VII and is inserted to the anterior end of the apodeme of segment VIII.

A thin, but rather broad layer of muscle bands originates on the antecosta of sternum VII and is inserted to the anterior margin of sternum VIII. At the anterior attachment the right and the left muscle are separated by an interval, which is approximately as broad as the anterior end of segment VIII. A transverse muscle is perhaps inserted to the oviduct. It may be interpreted as an internal VII–VIII muscle, (p. 16), the posterior attachment being shifted to the oviduct. A rather strong muscle (vm_6) originates on the posterior corner of sternum VII and is inserted to the anterior end of the apodeme on segment VIII.

The weak muscle VIII–IX dm_1 originates on the anterior margin of tergum VIII and is inserted dorsally to the anterior margin of the sclerite on segment IX. A muscle (dm_2) extends between the anterior ends of the apodemes on segments VIII and IX. (This muscle perhaps rather should be called ventral, but here it is called dorsal as its homologue in *Rhyacophila*). A muscle originates dorsally on the anterior end of the apodeme on segment IX and is inserted to the middle of the dorsal side of the same segment, between the two muscles dm_1 . For its posterior half this muscle, which probably is dm_5 , its origin being shifted from the posterior end of segment VIII to the anterior end of

segment IX, appears unpaired. The rather strong muscle vm_6 originates on the posterior corner of sternum VIII and is inserted to the anterior end of the apodeme on segment IX.

^ In both segments VII and VIII a dorso-ventral musculature, much deviating from conditions in other Trichoptera, is found. Fine bands originate along a longitudinal line, approximately in the middle of each half of the tergum and are inserted to the furrow between the latter and the sternum. In segment VIII the bands are stronger, but shorter than in segment VII.

A muscle, interpreted as $gonm_1$, originates on the ventral side of the apodeme of segment VIII for almost its whole length and is inserted ventrally to the anterior margin of the sclerite on segment IX. This muscle, together with dm_5 , probably can give segment IX a nodding movement. The muscle $gonm_2$ is composed of some few bands, which originate on the anterior reinforcement of the sclerite on segment IX, below the connection with ap.IX. They go downward, backward and inward, and are inserted to the middle of the furrow between segment IX and the tongue $gon.VIII$. I found no muscle which could be interpreted as $gonm_3$.

Between the last mentioned muscle on one side and the anterior and the ventral margin of the sclerite of segment IX on the two others there is a small triangular area. On this area originates a small bundle of transverse muscle bands, those of the left and those of the right side being continuous below the genital chamber.

One layer of about 45° descendent muscle bands is inserted dorsally to the lateral side of the sclerite of segments IX and X. The most posterior bands are inserted to a part of the sclerite which possibly belongs to segment X, and the muscle thus may be considered as a IX–X muscle. If so, it proves that the fine, V-shaped line is not the true boundary between segments IX and X. The origin is partly on the

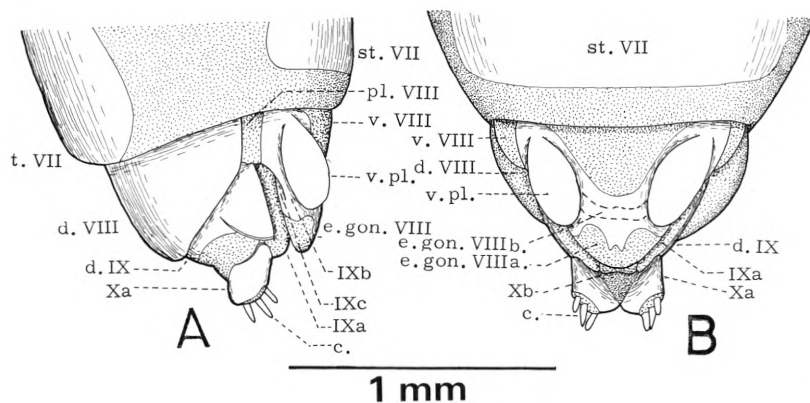


Fig. 22. *Polycentropus flavomaculatus*. Posterior end of abdomen as seen from the right side (A) and in a ventral view (B).

anterior reinforcement above the connection with ap.IX, partly along the mesal line to a point approximately midway between the anterior margin and the dorsal longitudinal cleft. The anterior bands are shorter than the others.

The muscle gchm is lacking. The circular musculature of the genital chamber does not seem to extend beyond the anterior margin of segment IX.

Polycentropus flavomaculatus Pict.

It cannot be excluded that some of the specimens studied belong to the species *irroratus* Curt., which may account for some minor – and from a morphological point of view insignificant – differences observed.

Pregenital segments. The gland on segment V opens on the apex of a process, which is situated in the angle between the antecosta and the lateral longitudinal suture. This process has a conical basal part, ca. 185 μ long and ca. 185 μ broad, and a slender, finger-like distal part, ca. 312 μ long and ca. 33 μ thick. The length of the whole structure is about five seventh of that of the segment.

Sternum VII (fig. 22) differs from the preceding ones by not reaching the posterior end of the segment.

On the terga there are, besides numerous

smaller ones, some few larger setae, though not as large as the big ones on the ventral plate. In addition to setae both terga and sterna are provided with tiny sensilla campaniformia like those on the ventral plates.

The genital segments (fig. 22) which together are very much smaller than segment VII, have a very complicated structure. Segments VIII, IX and X are so intimately united that the boundaries cannot be stated with certainty. An atrium has been formed, with a transverse, horizontal “mouth”, the “mouth angle” of which in fig. 22 A lies just in front of the pleural membrane of segment VIII (pl. VIII). The upper lip of the atrium is formed of segment IX, which on its posterior end carries the small segment X, the lower lip of the posterior part of segment VIII, though parts of segment IX also must enter in the composition of this lip.

The cavity of the atrium extends farther forward than its “mouth angle”. Both the dorsal and the ventral wall are concave, though on the latter the concavity is largely masked by the cushion (i.gon.VIII, e.gon.IX, Xd) described below.

Dorsum VIII, at least to some extent, has preserved its individuality. Its posterior margin bulges very strongly backward, so that the dorsum in a mesal line is more than twice as long as its lateral parts and the pleural membranes. It is

entirely covered by a tergum, which is relatively broader than the pregenital terga, but like those rather weakly defined. Its lateral margins project as narrow folds over the dorsal parts of the pleural membranes. There is a well developed antecostal suture, but no lateral longitudinal sutures. The tergum has the same covering of setae as the pregenital terga, though there are none of the large setae.

Venter VIII is partly covered by a sclerite; the musculature, however, shows that the mesal part of this sclerite belongs to the gonopods VIII (e.gon.VIIIa). Its anterior margin has in the middle a broad and deep, parabolic indentation. The posterior margin has a rather elaborate shape, which will appear from fig. 22 B. The anterior corners of the sclerite are produced into narrow, upward directed, more strongly sclerotized tongues (fig. 23B; in fig. 22 A concealed by the overlapping posterior margin of segment VII), which perhaps may be considered as lateral parts of an incomplete antecosta.

From small, longitudinal, subelliptic areas of this sclerite, near the anterior corners, a pair of oval, flattened ventral plates (figs. 22, 23 B, v.pl.) arise; they probably are the homologues of the ventral parts of the lateral valves in *Rhyacophila* (p. 28). Their external sides face ventrally and laterally. This side is densely clothed with setae which, as to size, form two distinct groups. The larger ones, few in number, are situated distally. Among the setae tiny sensilla campaniformia are seen. On the distal part of the internal side, as well as on the ventral sclerite itself, some few setae exceptionally may be found. Otherwise venter VIII and the lower lip are devoid of sensilla.

The upper lip of the atrium. Conforming to the posterior bulge of dorsum VIII this lip is short in the mesal line, much longer laterally. In a lateral view the dorsal side is steeply descendent and slightly convex. In a dorsal view the lip generally is concealed by dorsum VIII.

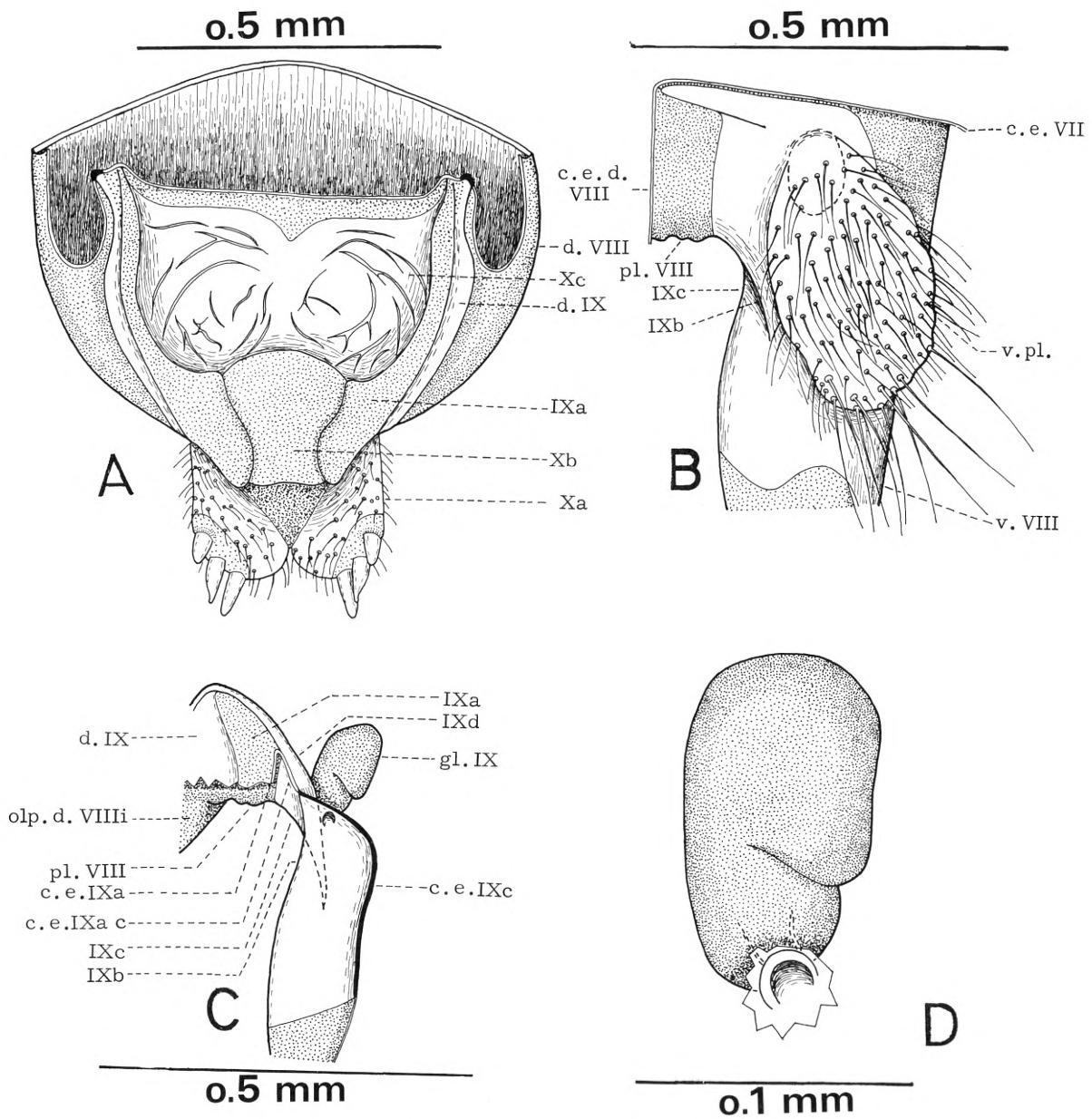
The greater part of the external side of the lip

is covered by a sclerite (d.IX), which may be called tergum IX, and which has a well developed antecosta. Its posterior margin has a broad and deep indentation, so that the tergum is very short in the mesal line. The posterior and mesal margin of the tongue flanking the indentation is reinforced, and the reinforcement proceeds forward for some distance in front of the bottom of the indentation. Ventrally (or laterally) to this part of the reinforcement 1–4 setae of the same size as the small ones on the ventral plate are seen. There are no other sensilla on the upper lip.

The lateral margin of the upper lip (fig. 23 A) is rather thick. It is divided into a mesal and a lateral fold by a fine furrow, which receives the ridge IXc on the lower lip, described below. The mesal fold (IXa), which projects much more ventrally than the lateral one (d.IX), is membranous. (In fig. 22 A the atrium gapes a little, and hence the fold IXa is seen). The tergum extends onto the lateral fold, which thus is sclerotized.

The internal side of the lip, also, is partly covered by a sclerite (Xc), which extends onto the "cheeks" of the lip, and which has a peculiar sculpture of „brain-like" convolutions. Its anterior margin has a narrow, V-like, the posterior margin a broad, rounded indentation. On the middle of the sclerite there is a weakly defined longitudinal keel, conforming to a furrow on a cushion (i.gon.VIII, e.gon.IX, Xd) on the lower lip described below. The relations to the anus and to the gonopore (cp. p. 63) prove that the mesal part of this sclerite belongs to segment X. The muscle gonm₃ (p. 66), however, if rightly interpreted, shows that its lateral parts belong to the gonopods IX. The posterior part of the internal side of the upper lip is membranous and divided into three folds, a broader and unpaired mesal one (Xb) and a pair of laterals (IXa). The latter represent dilations of the mesal fold of the lateral margin.

The lower lip of the atrium (figs. 22, 24, 25 A–B), formed by the gonopods of segment VIII, and



perhaps in part by this segment itself, is a direct posterior continuation of venter VIII. It is shorter and narrower than the upper lip, but like the latter tapering in a posterior direction, of a parabolic outline. (The lateral and posterior parts of the upper lip are visible in a ventral view, fig. 22 B).

Fig. 23. *Polycentropus flavomaculatus*. A: Upper lip of the atrium in a ventral view. B: Anterior part of the left side of the lower lip of the atrium as seen from the right side. C: Anterior part of the lower lip of the atrium as seen from the inside. D: Detail of C: The gland of segment IX.

The sclerite of venter VIII extends round the lateral margin of the lower lip onto the rather

high internal part of the "cheek" (fig. 23 C) and eventually is continuous with the sclerite e.gon. VIIIb, described below. On the anterior part of the margin the sclerite has a longitudinal furrow, flanked by two ridges. The sharper mesal one of these (IXc) fits into the longitudinal furrow on the margin of the upper lip. The more rounded lateral ridge (IXb) is descendent in a dorsally slightly concave curve. In a lateral view (fig. 22 A) it crosses the mesal fold and gradually disappears on the lateral side of the lip.

In repose the anterior part of the lateral, sclerotized fold on the margin of the upper lip (fig. 23 A, d.IX) lies in the furrow between the two ridges. In an anterior direction the bottom of the furrow proceeds as an upward bent, rod-like sclerite (fig. 23 C, IXd) which, concealed by the pleural membrane VIII, eventually joins the antecosta of tergum IX. This as well as the feature mentioned below, show that the anterior part of the margin of the lip and the internal "cheek" must belong to segment IX.

On the anterior part of the sclerotized inside of the "cheek", i.e. in the atrium, a gland (fig. 23 C, gl.IX, fig. 23 D) opens. It is short and tubular, but relatively thick. The outer part of its duct is sclerotized. This gland probably is homologous with a structure which in *Hydropsyche* is found on tergum IX (p. 81).

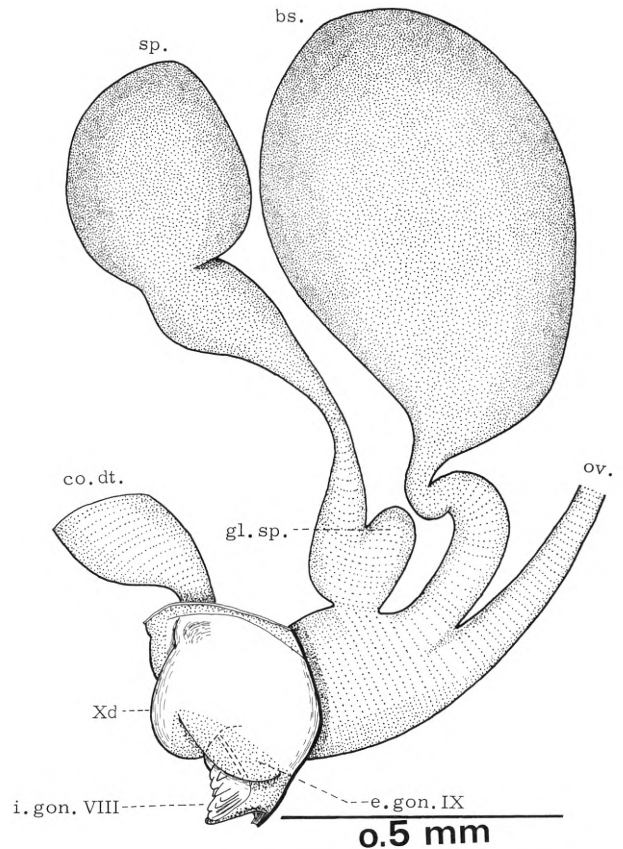
As mentioned above the internal side of the lower lip is strongly concave, but this is largely masked by the fact that the greater, middle part is raised into a cushion (figs. 24, 25 A, B, i.gon.VIII, e.gon.IX, Xd), which practically fills up the concavity of the upper lip. At its posterior end this cushion is divided into three pairs of lobes. The two mesal ones (Xd, i.gon.VIII) form the upper and the lower lip, resp., of the genital opening, which in repose has the shape of a horizontal cleft; the lower of these two lips, which has a rather sharp posterior edge, projects farther backward than the upper lip. The third pair of lobes (e.gon. IX) embraces laterally

the bases of i.gon.VIII and Xd. It is membranous and thin-walled and seems normally to be thrown into a couple of irregular folds. In figs. 24 and 25 B it is shown distended, which condition probably can be achieved by blood pressure. The dorsal part of its mesal wall is a direct continuation of a posterior fold in the genital chamber.

In repose the fold Xb on the upper lip (fig. 23 A) lies upon the dorsal side of i.gon.VIII and thus closes the genital opening from behind.

At the extreme anterior end the cushion occupies the whole width of the atrium, but otherwise it is separated from the rest of the

Fig. 24. *Polycentropus flavomaculatus*. The genital chamber etc. as seen from the right side.



floor of the latter by a sharp furrow. Ventrally in this furrow, encircling the cushion laterally and posteriorly, a roughly crescentic sclerite (e.gon. VIIIb) lies. Its mesal and narrower part is shown in fig. 22 B by broken lines. Its anterior part is, as mentioned above, continuous with the sclerotized parts of the "cheeks".

Laterally the anterior, undivided part of the cushion is sclerotized, and the sclerite extends onto the dorsal wall of the furrow separating the cushion from the rest of the floor. (On the ventral side of this furrow the crescentic sclerite mentioned above lies). It likewise extends onto the dorsal side of the cushion, but here the two sclerites, left and right, are separated by a membranous area, broader in front, narrower in the rear. The lateral part of the sclerite has a large depression, which dorsally at the anterior end is delimited by a sharp lamella. The sclerites also cover the dorsal side of the lobes Xd, between which there is a small, unpaired and low membranous lobe. From the posterior end of Xd a very strong suture with a very high costa extends forward on the dorsal side for the whole length of the sclerite.

The lobe i.gon.VIII is membranous except for a sclerite dorsally on the somewhat downward facing lateral side (fig. 24). This sclerite has some sharp, irregular folds.

From a topographical point of view the lobes Xd and the basal part of the cushion lie in front of the genital opening, but this is a result of the formation of an atrium. From a morphological point of view they are posterior (or dorsal) to the genital opening. Since in other Trichoptera segment X forms the upper lip of the genital opening, the antero-mesal part of the dorsal side of the lower lip of the atrium, including the lobes Xd, must belong to this segment. The same is true for the sclerite on the inside of the upper lip (fig. 23 A, Xc), which is substantiated also by the musculature.

The lobes i.gon.VIII no doubt are part of the gonopods VIII (cp. p. 66: the muscle gonm₂),

and the folds e.gon.IX may represent the gonopods IX.

Segment X, as mentioned above, enters into the composition of the atrium. The rest of the segment (figs. 22, 23 A) appears as a pair of incompletely separated folds, which together form a ventrally open, thick-walled half-cylinder, the ventral margins of which is considerably longer than the dorsal side. The folds are sclerotized, but both dorsally and ventrally (i.e. both on the out- and the inside of the folds) the two sclerites, left and right, are separated by membranous, triangular areas; the bases of the triangles are anterior. On the outside of the sclerite there is along the ascendent anterior margin, a narrow reinforcement. The rounded anterior corner forms a very simple articulation with the latero-posterior corner of tergum IX. The sclerites are clothed with setae, which are somewhat smaller than those on the ventral plate, but relatively thick.

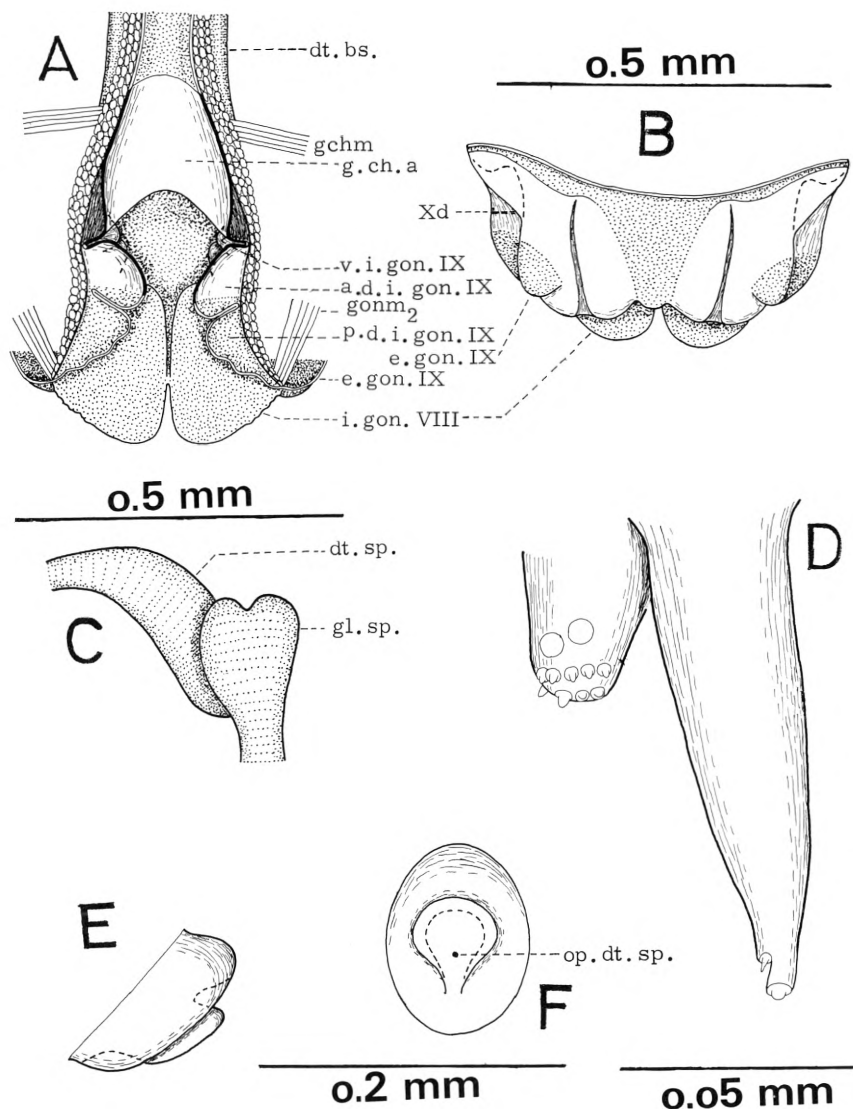
The anterior end of the half-cylinder is "closed" by the thickened posterior end of the fold Xb on the internal side of the upper lip of the atrium. Above this lobe, i.e. just inside the wall of the half-cylinder, the anus is situated.

The ascendent posterior margin of each fold of segment X is membranous and carries three processes above each other. The middle one of these processes probably is the cercus, whereas the two others are structures peculiar to the Polycentropidae and the Hydropsychidae.

The slender cercus (fig. 25 D) tapers toward the distal end. Subdistally and laterally it carries a tiny, conical seta (cp. *Wormaldia occipitalis*, p. 56), distally to which the thickness of the cercus decreases abruptly. The distal end of the cercus is entirely occupied by a semiglobular sensillum and its alveolus. It is difficult to tell whether these sensilla are tactile or chemoreceptive in function. Proximally the wall of the cercus is 2 μ thick. In a distal direction the thickness decreases, and in the slender distal end it is only 0.5 μ .

The two others, a little shorter processes do

Fig. 25. *Polycentropus flavomaculatus*. A: Floor of the genital chamber in a dorsal view. After removal of the structures shown in B. C: Part of the spermathecal duct. D: Left cercus and apex of adjacent dorsal process in a ventral view. E: Processus spermathecae as seen from the right side. F: Same in a postero-ventral view.



not taper as much toward their rounded distal ends. Proximally the wall is just as thick as on the cercus, in a distal direction the thickness decreases, and quite distally it is so small that it cannot be measured with the light microscope. Apically each process carries a small and a little varying number of very short and thick sensilla set in alveoli, possibly intermediates between setae and sensilla campaniformia. On the dorsal process

they are shifted a little in a dorsal direction, on the ventral one a little in a ventral direction. The latter process carries, moreover, a little more proximally two larger typical sensilla campaniformia. Such ones are not found on the dorsal process.

The genital chamber (figs. 24, 25 A) is short, extending to the boundary between segments VII and VIII. For its whole length is about 45°

ascendent. The processus spermathecae (fig. 25 E, F) is situated in the dorsal wall as a low, somewhat elongate, sclerotized knob, the width of which is about half that of the lumen of the genital chamber. The ventro-posterior surface of the knob is concave, and from the middle of the concavity arises a smaller, sclerotized process, which is widened toward its distal (ventro-posterior) surface. The latter has a pear-like shape, narrowing in a ventro-anterior direction, and in front of its middle the small opening of the ductus spermathecae is found.

For its whole circumference the processus spermathecae is surrounded by a ring-like, membranous fold, which is just as high as the processus itself. The ventral (or anterior) part of this fold forms the upper lip of the crescentic opening of the ductus bursae. The lower lip of this opening (fig. 25 A, g.ch.a) is sclerotized and has a concave posterior margin. The posterior corners of the sclerite are produced into a pair of sclerotic folds, flanking the ring-fold round the processus spermathecae.

On the posterior part of the genital chamber (fig. 25 A) there are two successive folds. The anterior one (a.d.i. gon.IX) is sclerotized, except for its posterior side, and below its anterior end two small, imperfectly separated, sclerotic processes (v.i.gon.IX) are seen. The posterior fold (p.d.i.gon.IX) is entirely membranous, irregularly folded, and continuous with the mesal side of the lobe e.gon.IX (p. 94).

On the ventral wall of the posterior part of the genital chamber there is a pair of broad, but low folds, separated by a faint longitudinal furrow. They are continuous with the dorsal sides of the lobes i.gon.VIII.

The oviduct. The two lateral oviducts unite at the boundary between segments VI and VII.

The bursa copulatrix is unusually large, considerably larger than the spermatheca, and pear-shaped. The cuticle is thin, but in pharate adults the epithelium is thick (ca. 8 μ), but otherwise without indications of secretory activity, though

the lumen was filled with an unidentified substance. The greater, proximal part of the duct is thick (though thinner than the common oviduct), and somewhat flattened. The much narrower distal part makes a single spiral turn.

The spermatheca has approximately the same length as the bursa copulatrix, but is considerably more slender. By a constriction it is divided into a proximal, elongate, pear-like part, and a distal, very roughly spherical part. Already the proximal part of the ductus spermathecae is rather thick, and in a distal direction the diameter increases further for some distance. Subproximally there is an anterior (or ventral) slightly bilobed bulge (fig. 25 C), the lumen of which is flattened and for its greater part divided into a left and a right portion. This bulge no doubt represents the reduced glandula spermathecae. Distally to it the duct tapers gradually. The epithelium, especially in the proximal part of the duct and in the bulge, is thick. Both the duct and the bulge are surrounded by a strong circular musculature.

The colleterial glands, which have a simple shape, extend to the boundary between segments IV and V. They are very bulky, especially in their posterior part, which fills up most of the segments VII and VIII. The colleterial duct has the shape of a funnel with a long stalk. The funnel is forward directed to circumvent the anterior wall of the atrium; the stalk then bends backward. The opening is situated approximately in the middle of the undivided part of the cushion i.gon.VIII, e.gon.IX, Xd on the dorsal side of the lower lip of the atrium.

Musculature. As to the dorsal VII–VIII muscles see p. 13. The external ventral VII–VIII muscle is divided into two portions. One is broad, but thin, and composed of numerous bands, which originates mesally, a little behind the antecosta of sternum VII and are inserted to the boundary between segments VII and VIII (i.e. not to the ventral sclerite of segment VIII). The other is a strong, flat muscle band origina-

ting laterally to the former muscle, approximately in the middle of each half of the antecosta of sternum VII. This muscle diverges somewhat in a posterior direction and is inserted to the upward directed projection of the anterior corner of the ventral sclerite on segment VIII (fig. 23 B). The internal muscle (which, however, is ventral to the second of the two muscles mentioned above) is transverse and extends for the whole length of segment VII. It is composed of several bands, which all are very tender, though the posterior one is stronger than the others. The bands are perhaps attached to the dorsal side of the oviduct; at least they adhere to the latter by dissection.

There are two dorso-ventral muscles in segment VIII, probably dvm_1 and dvm_3 . The former, which is very weak, has its ventral attachment on the base of the upward directed projection of the anterior corner of the ventral sclerite on segment VIII. The latter is strong and composed of several fine bands. It originates on an oblique, ascendent line, laterally on tergum VIII. (This line, at least often, has a little darker colour than the rest of the tergum). The bands converge fan-like, pass just anterior to the "mouth angle" of the atrium, and are inserted to the ventral sclerite of segment VIII just in front of the ventral plate.

There are three VIII-IX muscles. One probably is dm_1 , the two others I have, though with some hesitation, interpreted as dm_5 and dm_6 .

The muscle $gonm_1$ is rather strong. It originates on the anterior margin of the ventral sclerite on segment VIII, just in front of the ventral plate. It goes inward and backward, approaching a transverse course, approximately parallel to the anterior margin of the sclerite. Its insertion is to the same sclerite; the two muscles, left and right, are widely separated. The very strong, but flat muscle $gonm_2$ originates on the sclerotic bridge which connects the furrow between the ridges IXb and IXc on the margin of the lower lip of the atrium (fig. 23 C) with the

antecosta of tergum IX, and is inserted to the reinforced anterior corner of the sclerite on the fold i.gon.VIII (fig. 24). The muscle $gonm_3$ is rather strong, but short, approximately cylindrical and very steeply ascendent, almost vertical. It originates on the rounded, sclerotized margin of the upper lip of the atrium, and is inserted laterally to the anterior part of the sclerite Xc on the dorsal wall of the atrium (fig. 23 A). This muscle might also be considered as a IX-X muscle. A comparison with *Holocentropus* (p. 72), however, suggests that it is $gonm_3$. This being the case, the lateral parts of the sclerite Xc must belong to the gonopods IX.

There are two IX-X muscles. One originates on the dorsal part of the antecosta of tergum IX. It is strongly fan-like convergent and inserted to the anterior margin of the external sclerite on segment X (p. 63). The other, much weaker muscle originates mesally to the former and is inserted to the internal sclerite on segment X, just above the anus; the two muscles, left and right, are separated by a large interval.

The strong muscle $gchm$ originates on the base of the upward directed extension of the anterior corner of the ventral sclerite on segment VIII (fig. 23 B) and is inserted to the anterior end of the genital chamber. The latter has the usual circular musculature.

Holocentropus dubius Steph.

Pregenital segments. The gland on segment V is developed as in *Polycentropus* (p. 59). The process is as long or a little longer than sternum V. Sternum VII does not extend to the posterior end of the segment.

There are some few, rather big setae on the posterior parts of the terga. Both terga and sterna are provided with sensilla campaniformia like those on the ventral plates.

The genital segments. There is a great resemblance to, but also considerable differences from, conditions in *Polycentropus*. As in this

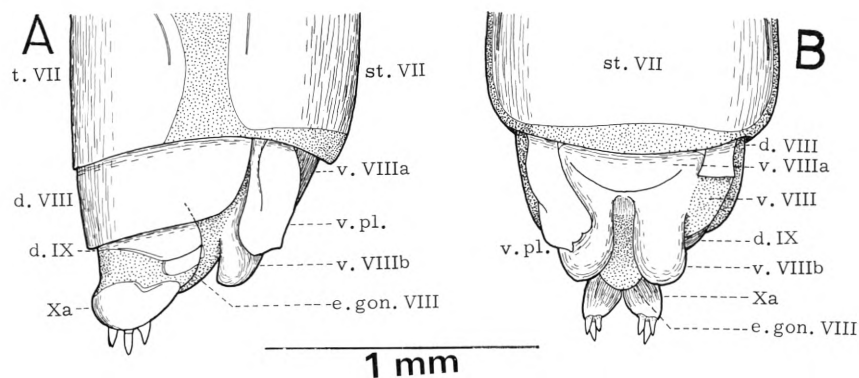


Fig. 26. *Holocentropus dubius*. Posterior end of abdomen as seen from the right side (A) and in a ventral view (B).

genus an atrium is formed. However, the boundary between the latter and the genital chamber is not sharply defined, and no part of segment IX seems to enter into the formation of the lower lip.

Dorsum VIII (fig. 26) is entirely covered by a sclerite, which resembles the pregenital terga and may be called tergum VIII. Its lateral part lies behind the pleural membrane VII and in front of the lateral parts of the lower lip of the atrium. Its lateral margin overlaps the dorsal edge of the ventral plate a little, its posterior margin overlaps tergum IX to a considerable degree and covers the "mouth angle" of the atrium.

Tergum VIII has a well developed antecosta. In one specimen I found a rudiment of a lateral longitudinal suture. It was much removed from the lateral margin of the sclerite, i.e. it had the same position as in the pregenital segments. The muscle dvm_3 originated laterally to this suture for the whole length of the segment.

Venter VIII is largely membranous. On its anterior part it carries a large, roughly semicircular sclerite (v.VIIIa). The straight or slightly concave front margin of the sclerite does not quite reach the anterior end of the segment, its lateral corners are rather far removed from the margins of the venter. (In fig. 26 B the membranous area in front of the sclerite is concealed by the overlapping posterior end of segment VII).

The sclerite has no antecosta. It carries a pair of large, plump, finger-like, backward directed processes (v.VIIIb). The musculature (p. 72) indicates that the posterior part of the sclerite v.VIIIa belongs to the gonopods VIII (e.gon. VIII), the processes v.VIIIb perhaps also belong to this structure, suggestive of its paired origin.

The ventral plates (fig. 26, v.pl., 27 C), lying in planes which form angles of about 45° with the sagittal plane, are narrower than in *Polycentropus flavomaculatus*, and have a more elaborate shape. A basal, longitudinal carina near the dorsal edge will especially be noted. The plates arise directly from the membranous venter. In front of the plate, only, there is a narrow, triangular sclerite, continuous with the plate and extending in a dorsal and anterior direction. It is neither continuous with the sclerite v.VIIIa, nor with the tergum.

Except for the ventral plates venter VIII is devoid of both microtrichia and setae. These plates, on the other hand, carry numerous setae. Among these some few, at the dorso-posterior corner, are considerably larger than the others. Scattered between the setae, particularly basally, tiny sensilla campaniformia are seen. When the microscope is focused deeply their diameter is 1.5μ , but when it is focused highly only 0.5μ . We are thus concerned with partly lowered sensilla.

The upper lip of the atrium, the dorsal side of

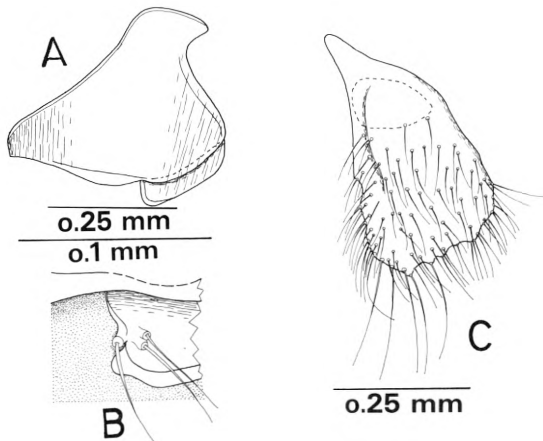


Fig. 27. *Holocentropus dubius*. A: Tergum IX as seen from the right side. B: Dorso-posterior corner of hind part of tergum IX. C: Right ventral plate.

which is approximately horizontal, is clearly visible in a dorsal view, since the posterior margin of dorsum VIII, as opposed to conditions in *Polycentropus*, is only slightly convex. A sclerite, which may be called tergum IX, has a very broad and deep posterior indentation and therefore covers only partly the external side of the lip; in the middle the tergum merely forms a sclerotic transverse bridge.

On the lateral side, flanking the indentation, the tergum has a broad, but relatively short, tongue-like extension (fig. 27 A), resembling the postero-lateral part of the tergum in *Polycentropus*, but of a somewhat more elaborate shape. It is separated from the anterior part of the tergum by a narrow, rounded, overlapping fold of the latter, which continues as a broad reinforcement along both the lateral and the posterior margin of the main portion of the sclerite without, however, reaching neither the anterior end nor the middle line of the segment. The anterior, projecting and somewhat downward bent corner of the tergum seems to be of an apodemal character. The anterior end of the lateral reinforcement possibly indicates the root of the apodeme.

The tongue itself has a narrower reinforcement along the dorsal margin and the dorso-posterior corner. In one specimen the tongue carried on the left side three (fig. 27 B), on the right side two large setae, at the dorsal margin and at the dorso-posterior corner, resp. Otherwise the external side of the upper lip is devoid of both setae and sensilla campaniformia.

Tergum IX forms a little more than half of a cylinder, and therefore is visible also in a ventral view (fig. 26 B). For its whole width it has an antecosta in the shape of a marginal reinforcement.

The inside (or ventral side) of the upper lip (fig. 28 A) of the atrium is rather much convex in a transverse direction, continuing the curvature of tergum IX. It is to a great extent covered by a pair of yellow sclerites (gon.IX), the shape of which will appear from the figure. They probably represent the gonopods IX, though the position of the opening of the gland mentioned below proves that the antero-lateral part of the sclerite belongs to segment IX itself. The mesal edges of the sclerites project as a pair of rounded, mesally directed folds. In a lateral or mesal view (fig. 29) the folds are very elongately egg-like with the thick end forward. In a ventral view they have convex mesal sides, which diverge somewhat in an anterior direction. Both the anterior and the posterior end of the folds project as a pair of rounded processes. Each fold carries a seta approximately in the middle of its ventral side.

In repose the folds gon.IX, which are separated by a membranous area, lie in the lateral concavities of the sclerotic ridge p.i.gon.VIII on the lower lip (fig. 28 B; see below), but they can be abducted as shown in fig. 28 A.

A gland (fig. 28 A, gl.IX, fig. 29) similar to that found in the lower lip of *Polycentropus* (p. 62) and to all probability homologous with that on segment IX in *Hydropsyche* (p. 82), opens in *Holocentropus* on the upper lip, proving that structures which in *Polycentropus* form part of the

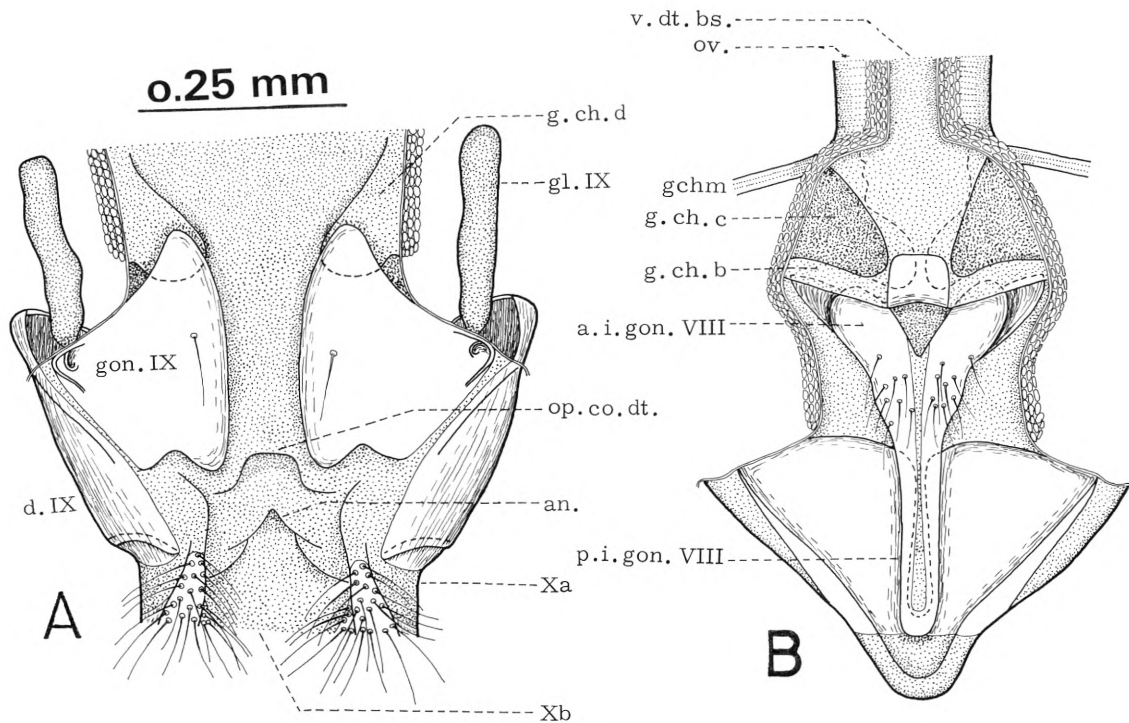


Fig. 28. *Holocentropus dubius*. A: Posterior part of the dorsal wall of the genital chamber and anterior part of the dorsal wall of the atrium in a ventral view. B: Floor of the genital chamber and lower lip of the atrium in a dorsal view.

lower lip in *Holocentropus* enter into the composition of the upper lip. The opening is in a depression, in front and laterally bordered by steep walls, at the latero-anterior corner of the sclerite gon. IX, i.e. near the "mouth angle" of the atrium. In some preparations the gland appears straight and extending almost to the anterior end of segment VIII, in others it is curved. In one specimen its distal end was slightly bifurcate.

The lower lip of the atrium (figs. 26, e.gon. VIII, 28 B), which tapers toward its rounded posterior end, forms a direct continuation of venter VIII. In repose the lateral margins of the lip overlap tergum IX a little; its posterior end is developed as a membranous scale, which is bent upward into the half-cylinder formed of segment X (see below) and covers the anus. (In fig. 29 the upper and the lower lip of the atrium are removed a little from each other, an artifact).

Conforming to the convexity of the upper lip, the inside (or dorsal side) of the lower lip (fig. 28 B) is concave. Apart from the posterior "scale" it is covered by a sclerite which, however, only at its posterior end reaches the lateral margin. In its middle there is an unpaired, high, but rather narrow longitudinal ridge (p.i.gon. VIII), which forms a posterior continuation of the folds a.i.gon. VIII in the genital chamber, described below. The ridge has a very narrow base and hence strongly concave lateral sides. The base does not extend to the posterior margin of the sclerite on the lip, but the hind end of the ridge projects as a very short, rounded process. On the dorsal side of the ridge

there is a narrow membranous area, which in an anterior direction becomes still narrower, and which does not reach the posterior end.

This ridge is reminiscent of the tongue e.gon. VIII in *Ecnomus* (p. 74) and i.gon. VIII in *Tinodes* (pp. 39–40).

In repose the ridge p.i.gon.VIII lies between the folds gon.IX on the inside of the upper lip, which then are very much less separated than shown in fig. 28 A. Their mesal edges fit into the lateral concavities of the ridge.

Segment X (fig. 26) in principle is built as in *Polycentropus*, but the cleft between the two halves is deeper, so that the segment actually is divided into a pair of valves, which as in *Polycentropus* are clothed with setae on both the external and the internal sides. On the former side the sclerite has an approximately right-angled indentation, along which a narrow marginal reinforcement is seen. Ventrally to this indentation the anterior margin of the sclerite approaches the posterior margin of the lateral tongue on tergum IX, though still separated from it by rather copious membrane.

As in *Polycentropus flavomaculatus* the sclerite of segment X carries some large sensilla campaniformia, one on the ventral edge near the base of the ventral process flanking the cercus, and three to four scattered over the lateral side. The subdistal sensillum on the cercus is shorter than in *Polycentropus*, and apically there seem to be more (three?) sensilla.

The genital chamber (figs. 28, 29) is short and wide, extending to the posterior end of segment VII. As mentioned above, there is no sharp boundary between the atrium and the genital chamber s.str. At the level of the "mouth angle" of the atrium the width, in an anterior direction, suddenly decreases to about half that of the atrium. This point lies much in front of the opening of the colleterial duct, and thus cannot be homologous with the opening of the genital chamber in *Polycentropus* (pp. 62 and 65).

In the anterior end of the genital chamber the

dorsal wall is vertically ascendent, and here the processus spermathecae is situated. The latter is a short-oval, knob-like structure, approximately half as broad as the width of the lumen of the genital chamber. Its (from a topographical point of view) dorsal side is entirely sclerotized, whereas the lateral sides and especially the ventral side are membranous basally. Ventrally the process is surrounded by a membranous ring-wall, forming the upper lip of the crescentic opening of the ductus bursae. On the rear side the processus carries a quite low, cylindrical projection, on the posterior surface of which, again, the small opening of the ductus spermathecae is found in a very excentric position, shifted in a ventral (from a morphological point of view: anterior) direction.

Below the processus spermathecae the ventral wall of the genital chamber bulges outward as a large sac (g.ch.a) which, however, is almost entirely filled up by the very thick and plump, membranous lower lip (g.ch.b) of the opening of the ductus bursae. This lip, which in the middle of the posterior margin has a small sclerite, occupies the whole width of the genital chamber, which thus at the level of the lip has no lateral sides; this fact of course is concealed by the musculature. Basally the dorsal surface of the lip is very concave, conforming to the crescentic shape of the opening of the ductus bursae. In a posterior direction the concavity rapidly decreases, but is still seen on the posterior end of the lip, which thus is slightly bilobed.

On the dorsal surface of the lip there is a pair of large and deep lateral depressions (g.ch.c), which project as processes into the lumen of the lip (i.e. into the haemocoel), almost touching each other in the mesal line; they are sclerotized on the posterior side.

Behind the lip, latero-ventrally on the wall of the genital chamber, a pair of high, but relatively narrow, strongly sclerotized folds (a.i.gon.VIII) is seen. The anterior ends of the folds are twisted around their axes, so that their rounded

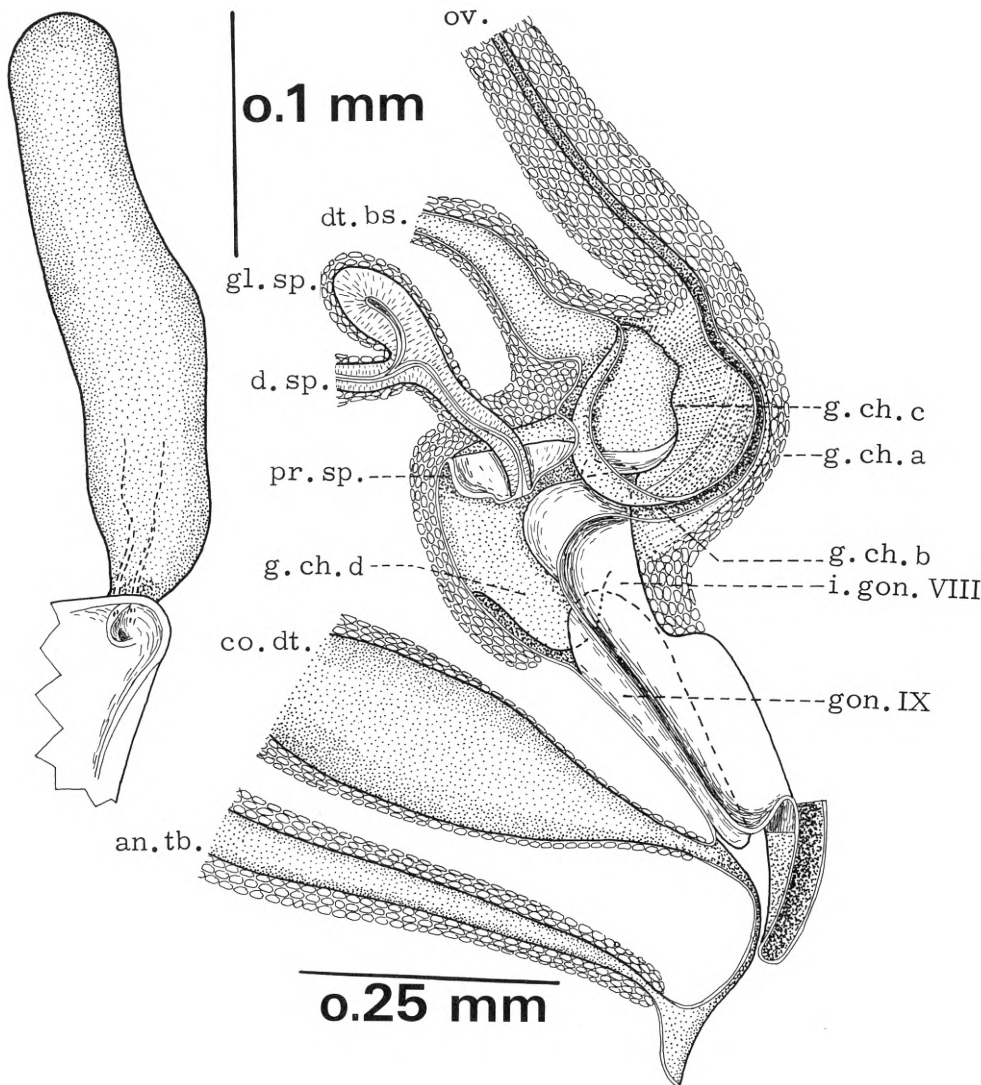


Fig. 29. *Holocentropus dubius*. Right gland of segment IX in a ventral view. Sagittal section of the genital chamber etc.; left side as seen from the inside.

edges face straight upward. The folds soon descend onto the ventral wall of the genital chamber and unite into an unpaired fold. Their sclerites, however, do not become continuous, but are separated by a membranous stripe, which is continuous with the membranous stripe on the dorsal side of the ridge p.i.gon.VIII on the lower lip of the atrium, just as this ridge is a continuation of the folds in the genital chamber.

At the level of union of the two folds each carries 7-9 small setae.

At the "mouth angle" there is, on the dorsal side of the genital chamber, a pair of small, finger-like, membranous processes (g.ch.d), the apices of which lie above the the anterior processes of the folds gon.IX on the ventral side of the upper lip of the atrium (fig. 28 A).

The bursa copulatrix is built as in *Polycentropus*

(p. 65). The thin part of the duct is extremely short, almost only a constriction between the bursa and its duct. The latter is about half as broad as the common oviduct.

The *spermatheca* is a large, simple sac. The short ductus spermathecae has the same thickness for its whole length, except for an anterior bulge, as in *Polycentropus*. The bulge, which no doubt is a much reduced glandula spermathecae, is not bilobed, and its lumen, which like the lumen of the duct itself is flattened, is undivided. The whole duct, including the bulge, has a glandular character. In *Cyrnus* Khalifa (1949) describes the gland as a short, thick, muscular part of the duct.

The *colleterial glands* are built as in *Polycentropus* (p. 65). The opening of the colleterial duct has an unusual posterior position, on the upper lip of the atrium behind the folds gon.IX, only a little in front of the anus (fig. 28 A).

Musculature. As to the dorsal VII–VIII muscles see p. 13. Very numerous fine muscle bands have their anterior attachment on sternum VII, the most mesal bands a little in front, the most lateral ones a little behind the middle of the sclerite, the posterior attachment is at the boundary between segments VII and VIII. In the rear most bands thus are not attached to any sclerite; some few of the most lateral bands, only, are attached to the mesal half of the ventral plate. The most mesal bands are longitudinal, the most lateral ones rather much converging in a posterior direction. A somewhat, but not very much, oblique and very strong muscle has its anterior attachment on the antecosta of sternum VII, just mesally to the point where the latter bends backward. The posterior attachment is to the upward directed sclerite issued from the base of the ventral process (p. 67; cp. *Polycentropus*, p. 60). The transverse muscle is developed exactly as in *Polycentropus* (p. 66).

A vertical, flat muscle, possibly *dvm*₃, composed of numerous fine bands, originates laterally on (but not on the lateral margin of) tergum VIII

and is inserted to the ventral sclerite on segment VIII (v. VIIIa) laterally to the base of the process v.VIIIb (fig. 26 B).

The VIII–IX musculature is developed as in *Polycentropus* (p. 66).

The strong muscle *gonm*₁ originates on the lateral half of the base of the ventral plate and is inserted to the sclerite v.VIIIa immediately postero-mesally to the process v.VIIIb; (cp. *Polycentropus*: p. 66). This muscle is about 45° descend and of course convergent toward the sagittal plane. I did not find the muscle *gonm*₂. The muscle *gonm*₃ originates on the most lateral (or ventral) part of the antecosta on tergum IX and is inserted to the lateral part of the posterior margin of the sclerite on the ventral side of the upper lip of the atrium (fig. 28 A, gon.IX).

As in *Polycentropus* (p. 66) there are two IX–X muscles. In addition strongly ascendent muscle bands originate on the ventral margin and the ventral half of the postero-lateral tongue on tergum IX (fig. 27 A, B) and are inserted in the vicinity of the anus, perhaps to the lateral side of the posterior part of the anal tube.

The muscle *gchm* originates on the upward directed sclerite issued from the base of the ventral plate (p. 67, cp. *Polycentropus*, p. 66). The circular musculature of the genital chamber extends to the “mouth angle” of the atrium. There are also paired, internal ventral longitudinal muscles which go from the anterior side of the bulge *g.ch.a* of the genital chamber into the anterior part of the ridge *a.i.gon.VIII* on the lower lip of the atrium (fig. 29).

Exnomus tenellus Ramb.

Pregenital segments. Whereas the abdomen gradually tapers in a posterior direction, the absolute width of the terga remains practically the same. The sterna are broader, but show the same tendency.

There is no gland on segment V.

Segment VII (fig. 30), already, is modified.

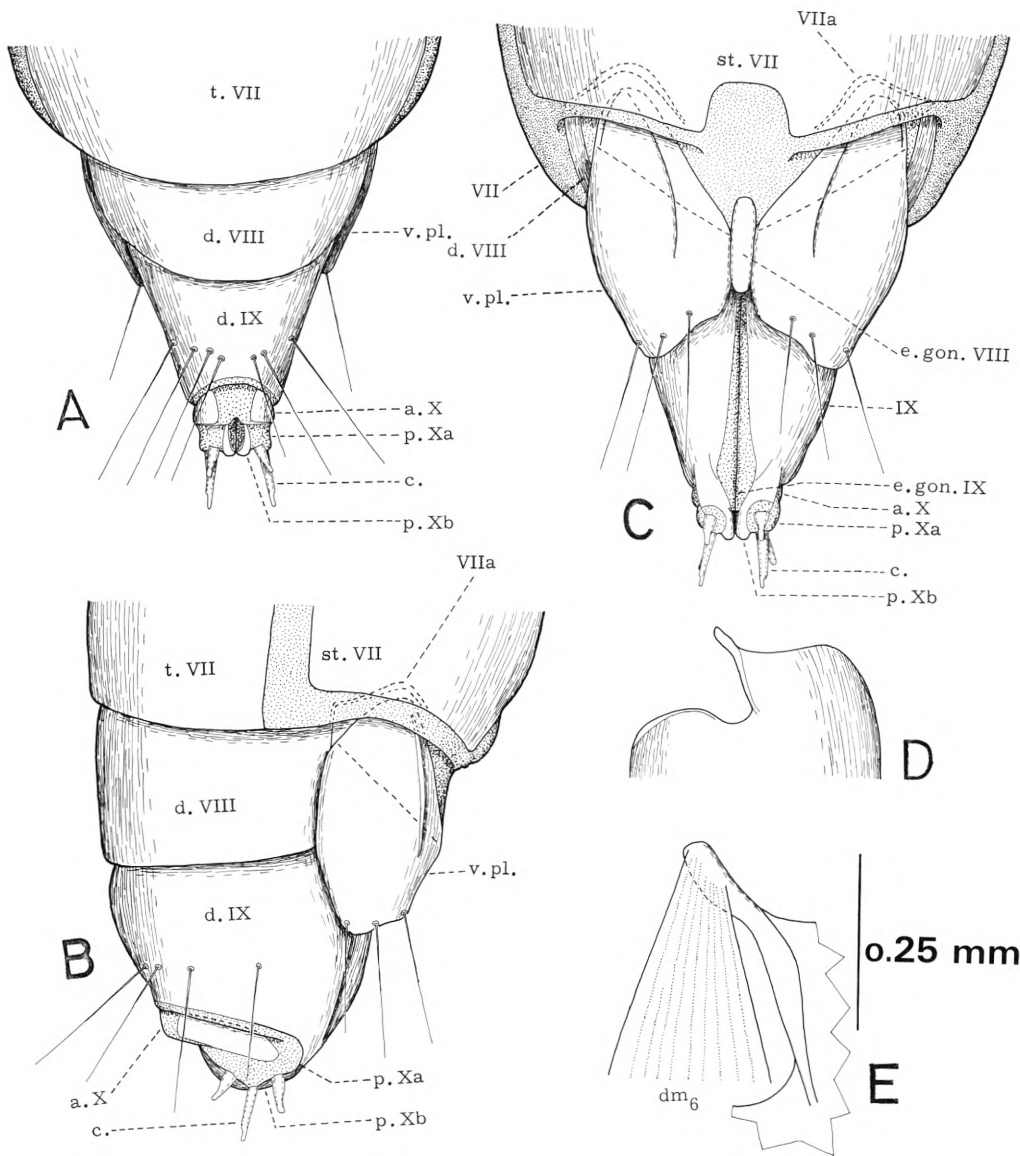


Fig. 30. *Ecnomus tenellus*. Posterior end of abdomen in a dorsal view (A), as seen from the right side (B) and in a ventral view (C). D: Right anterior corner of tergum IX in a lateral view. E: Left anterior corner of tergum IX as seen from the inside.

The tergum is developed as on the preceding segments, though the lateral longitudinal suture is still shorter, extending only for one third of the length of the segment. The sternum is broader than on the preceding segments. Its posterior margin has an unpaired, narrow, but relatively deep indentation, the membrane of which is continuous without boundary with the mesal, membranous part of venter VIII. Laterally to this indentation the posterior margin of

segment VII overlaps the anterior end of segment VIII. Here there is, moreover, a pocket-like recess of the furrow between the two segments. The bottom of the pocket is sclerotized, and this sclerite (VIIa) is by a sclerotic bridge connected with the anterior corner of tergum VIII. The latero-anterior part of the sclerite on venter VIII lies on the dorsal wall of the pocket.

Segment VIII is both much shorter and much narrower than segment VII. The tergum is

developed as on the preceding segments, though considerably broader, extending behind the pleural membrane VII. Its posterior corners are sharply rounded. It has a well developed antecosta, but no lateral sutures.

On the anterior part of the venter a pair of roughly triangular (the exact shape will appear from fig. 30 C) sclerites lies, separated by a large membranous area. As mentioned above the broadly rounded latero-anterior corner of the sclerite is situated in the pocket under the posterior margin of venter VII. Its latero-posterior margin is produced into a large and rather thick ventral plate (v.pl.), the convex dorsal (or lateral) edge of which overlaps tergum VIII and segment IX a little, except quite in front. This plate probably is homologous with the ventral part of the lateral valve in *Rhyacophila* (p. 28). The internal side of the plate, as well as that part of venter VIII covered by it, are membranous.

At the latero-anterior corner of the ventral sclerite, but not extending onto the ventral plate, there is a marginal reinforcement. On the sclerite and the basal part of the ventral plate a strong longitudinal suture with a high costa is seen. The lateral side of the suture projects as a low carina.

The sclerites mentioned, including the ventral plates, are covered with numerous small setae. Along the distal margin of the plate there are always three very large setae. Otherwise venter VIII is devoid of microtrichia and setae.

The mesal edge of the ventral plate is less than half as long as the lateral (or dorsal) edge. The two plates, left and right, are separated from each other only by a narrow interval, the greater, anterior part of which, however, is occupied by an, in a ventral view, finger-like, sclerotized process (e.gon.VIII; the actual shape of the process, after removal of the ventral plates, is described below, p. 76). The ventral wall of the process proceeds for a short distance forward as a sclerotic ridge on the mesal, otherwise membranous part of venter VIII. This ridge, as well

as the process itself, is devoid of microtrichia and setae.

The process e.gon.VIII is reminiscent of the structure so labelled in *Tinodes* (p. 39). It will be noted that it decidedly belongs to segment VIII and is entirely free of segment IX.

Segment IX is longer than segment VIII (the ventral plates excluded), but narrower, rather much sagittally compressed, and tapering in a posterior direction. In a transverse section the segment narrows in a dorsal direction into a very broadly rounded ridge.

For its whole length the ventral side of the segment, as in the psychomyids, is divided by a longitudinal cleft, the margins of which are closely apposed, except at the anterior end. Here they are much divergent, forming a pair of folds, which partly overlap the dorsal side of the process e.gon.VIII and have some relation to a pair of folds (figs. 31, 32 A, i.gon.IX) in the genital chamber.

Segment IX is almost entirely covered by a sclerite which, however, neither reach the posterior end of the segment (cp., however, below: segment X), nor the margins of the ventral cleft. The anterior margin has, concealed by the overlapping segment VIII, an unpaired indentation of a somewhat irregular shape, which will appear from fig. 30 D, and comprising about the dorsal half of the sclerite. An antecosta runs along the greater, mesal part of the indentation, and along the somewhat descendent lateral limit of the indentation there is a marginal reinforcement. The latter proceeds forward as a short, a little upward directed apodeme, extending beyond the middle of tergum VIII.

Somewhat in front of the posterior margin of the sclerite there is a transverse row of 7-9 (on each side 3-5) large black setae and moreover, in front of this row, some few small pale setae.

Segment X forms, as it were, the posterior end of segment IX and is, like this segment, much sagittally compressed. On the dorsal and especially on the lateral side the membranous poste-

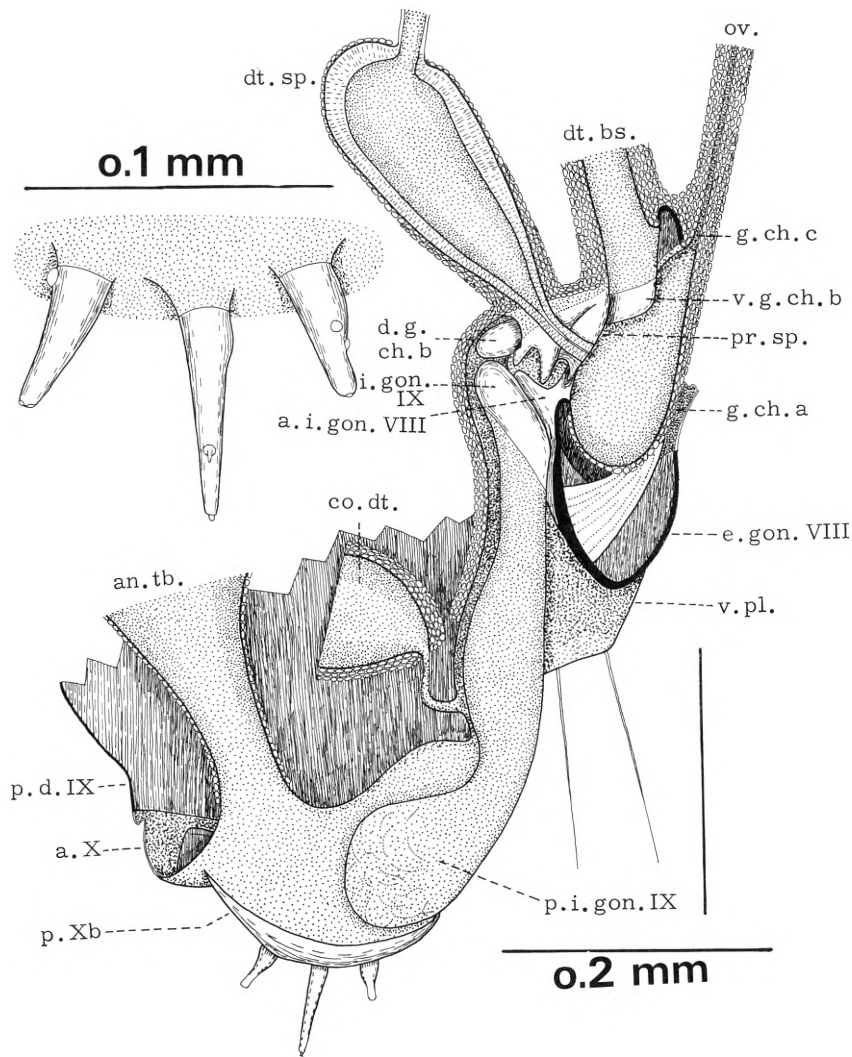


Fig. 31. *Ecnomus tenellus*. A: Sagittal section through the genital chamber etc.; left side as seen from the inside. Upper left corner: Right cercus and adjacent processes in a lateral view.

rior end of segment IX overlaps segment X a little, whereas there is no boundary between the two segments on the ventral side. For about the dorsal third of its circumference segment X is divided into an anterior higher, and a posterior, lower part. The former overlaps the latter a little. Dorsally the posterior part is divided by a longitudinal cleft, ventrally the whole segment is divided by a continuation of the cleft in segment IX. The dorso-posterior part of the segment thus is divided into a pair of rather thick valves,

each of which again is very incompletely divided by a vertical furrow into a thicker lateral and a thinner mesal valve (fig. 30 C); the latter projects farther backward.

Laterally on the anterior part of segment X (fig. 30 A, B) there is a transverse, rather narrow, steeply descendent, almost vertically placed sclerite, the anterior margin of which is reinforced. Dorsally the two sclerites, left and right, are separated by a broad membranous area. They have a dense covering of very small

setae, which extends also somewhat onto the dorsal membrane. The posterior corner of the sclerite on segment IX sends an extension (figs. 30 and 31, p.Xb) onto the ventral and posterior sides of the mesal valve on segment X. This sclerotization, too, is covered with small setae.

Ventrally segment IX does not extend as far backward as segment X, but the thickened posterior ends of the margins of the ventral cleft in segment IX bend upward for a short distance as a pair of thickened, innermost valves of segment X (fig. 31, p.i. gon.IX), which are very thin-walled and finely wrinkled. These valves, as well as the margins of the cleft in segment IX, possibly represent the gonopods IX. The sclerotized valves p.Xb may also in part belong to these gonopods, though the position of the anus as a vertical cleft between them proves that the bases of their mesal sides must belong to segment X.

The lateral, membranous valve of segment X carries as in other polycentropids three small processes above each other on its posterior side (fig. 31), the middle and largest of which probably is the cercus. Each of the two other processes is divided, though with no definite boundary into a longer and thicker proximal part and a shorter and more slender distal part. Proximally the wall of all three processes is less than one μ thick. In a distal direction the thickness decreases so much that it cannot be measured with the light microscope.

Dorsally or mesally on the base of the dorsal process a large sensillum campaniformium is found. The ventral process has, at the constriction two large sensilla campaniformia, ventrally and latero-ventrally, resp. Apically the dorsal process carries two small sensilla campaniformia, the ventral process only one. At the distal fourth of the cercus a very short, peg-like sensillum is seen; its position appears to vary, even on the two sides of the same animal, from dorsal to lateral. Another sensillum is found on the apex; it is short, but relatively thick and may be either an intermediate between a seta and a

sensillum campaniformium, or a sensillum basi-conicum.

The genital chamber (figs. 31, 32 A) extends only into the posterior part of segment VIII. From a morphological point of view its greater, posterior part is open ventrally. This part is also very low; since its dorsal wall is very much closer to the ventral than to the dorsal side of segment IX; it is compressed to a rather narrow, horizontal cleft. The short anterior part of the genital chamber, on the other hand, is rather high, and from its ventral wall a bulge (g.ch.a) extends into the base of the process e.gon.VIII between the ventral plates (cp. *Tinodes*, p. 42).

In a ventral view this process (fig. 32 B, C), as mentioned above, appears finger-like. Actually it is very much sagittally compressed. Its lateral side has a deep anterior indentation, along which the thick, membranous posterior margin of venter VIII is attached. The sclerite proceeds a little internally to the line of the attachment as a crescentic apodeme (ap. gon. VIII). About midway between the indentation and the posterior end the lateral side has a small depression, which dorsally is bounded by a sharp edge.

On the dorsal side of the process (fig. 32 A) the sclerite extends almost twice as far forward as on the ventral side and becomes gradually many times as broad as on this side. (In fig. 30 C this is concealed by the ventral plates). Roughly it has the shape of a broad isosceles triangle with slightly S-like curved sides. Its greater anterior part is somewhat descendent in a gentle curve (fig. 31) and transversely concave. By a deep parabolic indentation it is divided into two branches, and each of these again is divided into two branches by a smaller indentation.

The mesal one of the two last mentioned branches extends farther forward than the lateral one, and is raised into a low and narrow, somewhat ascendent, sclerotic fold (i.gon.VIII) on the lateral side of the anterior part of the genital chamber. The broadly rounded anterior end of this fold (in fig. 31 concealed by the

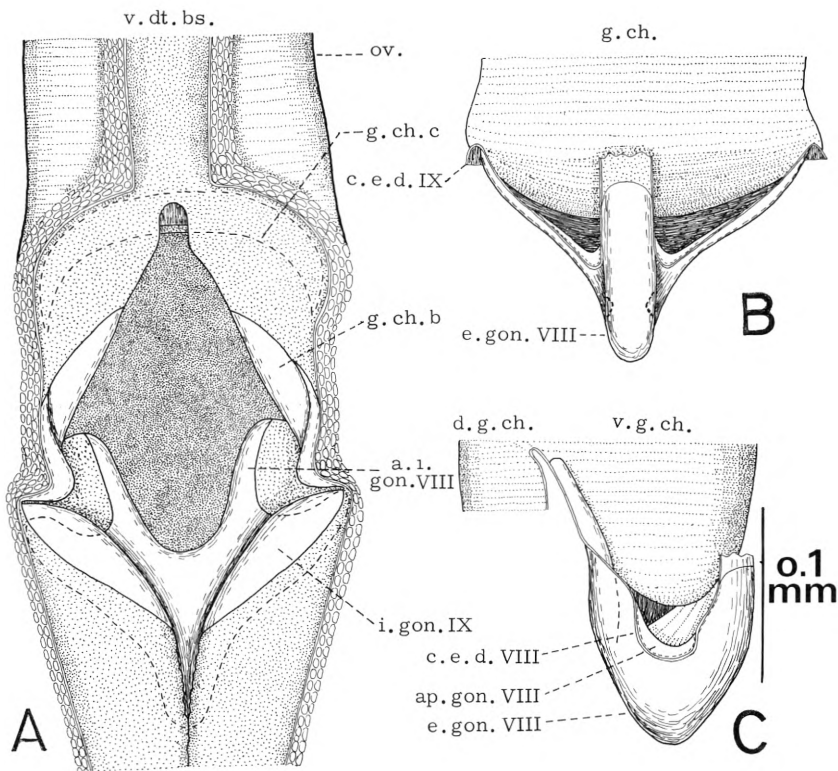


Fig. 32. *Ecnomus tenellus*. A: Floor of the genital chamber in a dorsal view. B: The process e.gon.VIII etc. in a ventral view. C: Same, as seen from the right side.

processus spermathecae) comprises also part of the membranous indentation between the two branches.

The anterior end of the shorter lateral branch lies in the "mouth angle", a narrow cleft between venter VIII and segment IX.

A broad horizontal furrow divides the lip between the openings of the ductus bursae and the oviduct into two (fig. 31), of which the dorsal one (g.ch.b) is by far the larger. The ventral lip (g.ch.c) has the shape of a narrow crescent (fig. 32 A; broken lines). The dorsal lip (fig. 32 A) is almost entirely divided into two by a large, V-like indentation, in the bottom of which there is an additional, small, U-like notch (through which the mesal part of the lower lip can be seen in a dorsal view). The halves of the dorsal lip have the character of a pair of almost vertical folds (g.ch.b) on the lateral sides of the genital chamber, framing the processus spermathecae,

and perhaps belonging to the gonopods IX (cp. *Tinodes*, p. 43).

The furrow between the dorsal (g.ch.b) and the ventral lip (g.ch.c) is sclerotized. The sclerite covers almost the whole dorsal side of the lower lip and almost the whole ventral side of the upper lip. On the latter it gradually encroaches upon the mesal and dorsal sides, so that the dorsal (or posterior) part of this lip is entirely sclerotized. Its, a little elaborate, hind end forms a sort of articulation with the fold i.gon.IX formed of the lateral margin of segment IX. The two folds join each other at an approximately right angle.

As mentioned above, the strongly divergent anterior parts of the margins of segment IX partially overlap the dorsal side of e.gon.VIII. For its anterior two thirds this part of the margin forms a sclerotized fold (i.gon.IX).

At the anterior end of the genital chamber the

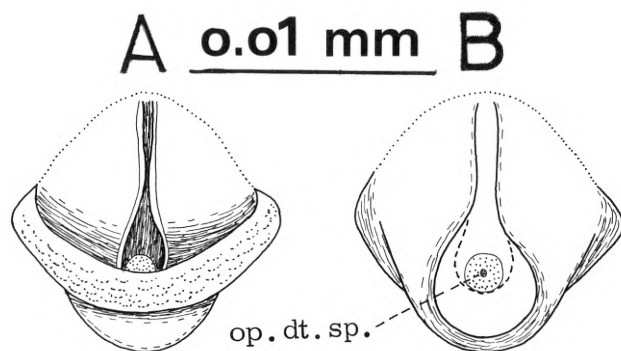


Fig. 33. *Ecnomus tenellus*. Processus spermathecae in a dorsal (A) and in a ventral view (B).

dorsal wall is very steeply ascendent, and on this part of the wall the complicated processus spermathecae (figs. 31 and 33) is situated. It may be described as a largely sclerotized elevation of the wall of the genital chamber, the backward directed side of which is divided into three lips above each other. The dorsal lip is the broadest, the middle lip projects farthest backward. In the middle the dorsal lip is covered with some very low, $6.5\ \mu$ broad, rounded nodules.

The ventral lip, which is much narrower than the two others, has the most elaborate shape. In a ventral view it is club-like, the "head" and the "shaft" approximately equal in length. The posterior, some what egg-like head is attached to the ventral surface of the middle lip on an area which is much shorter and much narrower than the ventral surface of the head. On this surface the small opening of the ductus spermathecae is found on a membranous area. The "shaft" is a narrow, longitudinal keel on the anterior part of the ventral surface of the middle lip.

Bursa copulatrix. An intact bursa was not preserved in any of my preparations. The ductus bursae has a rather wide lumen and a thin cuticle.

The spermatheca. My dissections were not successful. The ductus spermathecae is sharply divided into two parts. The proximal one is club-like or elongately pear-like. Quite proximally the

lumen is very narrow, but then it widens so much that it constitutes by far the greater part of the diameter. The epithelium is thick and no doubt glandular. This part of the duct has a circular musculature, the thickness of which however, decreases much in distal direction. The width of the distal part of the duct is only a small fraction of that of the proximal part, but the lumen is relatively wide. The epithelium is thin and there is no musculature.

A glandula spermathecae is not found.

The colleterial glands are of a simple shape, sausage-like, and united only for a short distance. The funnel-like colleterial duct (fig. 31) opens through a short, flattened, non-muscular "stalk" in the posterior part of segment IX. A little behind the opening the height of the genital chamber increases abruptly. In this way a downward directed fold is formed. It seems to be a sort of valve, not only for the opening of the colleterial duct, but also for the more anterior parts of the genital chamber.

Musculature. The list given below perhaps is not complete, but those muscles which have the greatest morphological significance possibly have been observed.

As to the dorsal VII–VIII muscles see p. 13. There is only one external ventral VII–VIII muscle. It is strong, fan-like, consists of numerous fine bands and originates rather laterally on the antecosta of sternum VII. It is inserted to the boundary between segments VII and VIII just mesally to the sclerite (fig. 30, B, C, VIIa) in the bottom of the ventral pocket described above. The internal muscle is developed as in *Polycentropus* (p. 66) and *Holocentropus* (p. 72).

In segment VIII there is one dorso-ventral muscle, interpreted as dvm_3 , composed of several parallel muscle bands. Its dorsal attachment is laterally on (but not on the lateral margin of) tergum VIII, the ventral attachment to the longitudinal costa on the ventral sclerite and the ventral plate of segment VIII (fig. 30 B, C, v.pl.).

There are three VIII-IX muscles, which I have interpreted as dm_1 , dm_3 and dm_6 . The last mentioned muscle originates on the posterior part of tergum VIII at the level of the lateral part of the anterior indentation in the sclerite of segment IX, and is inserted to the apodeme of segment IX (fig. 30 E). The whole origin thus lies dorsally to the insertion. Since, however, the overlapping of segment IX by segment VIII is more copious ventrally to the insertion than dorsally to it, the most likely function of this muscle is an elevation of segment IX.

A rather strong muscle, interpreted as $gonm_1$, originates on the reinforcement at the latero-anterior corner of the ventral sclerite on segment VIII. The right and the left muscle converge, and their bands also converge toward their insertion at the "mouth angle" between venter VIII and segment IX. I found no muscle $gonm_2$. The muscle $gonm_3$ originates latero-ventrally on the sclerite of segment IX, behind the middle, (a little in front of and a little more ventrally than the most lateral seta shown in fig. 30 B). This muscle is almost vertical, though the bands diverge not a little toward their insertion to the lateral margin of the sclerite on segment IX, behind the process e.gon.VIII.

In front of and a little ventrally to $gonm_3$ a strong muscle bundle originates. The muscle bands of the left and the right side are continuous with each other. Behind the origin of $gonm_3$ there is a similar, but much weaker muscle. Both these muscles, which no doubt represent the transverse musculature mentioned on pp. 25-26, pass above the flat "stalk" of the colleterial duct.

The muscle $gchm$ originates, like $gonm_1$, on the reinforcement at the latero-anterior corner of the ventral sclerite on segment VIII. It is inserted to the upper lip (figs. 31, 32 A, g.ch.b) between the ductus bursae and the common oviduct.

There are two IX-X muscles. One originates on the greater part of the antecosta of segment

IX; on the dorsal side there is only a small interval between the left and the right muscle. The very strong, fan-like muscle is inserted by means of a slender tendon rather ventrally to the margin of the sclerite on segment X, which here has an obtuse-angle bend. The other IX-X muscle is composed of some very feeble bands, which originates on the posterior part of the ventral margin of the sclerite on segment IX. They pass deeply below the former muscle and seem to be inserted to the posterior part of the anal tube.

The circular musculature of the genital chamber, which of course is truly circular only in the anterior part of the chamber, does not by far reach the opening of the colleterial duct. There is, moreover, a paired ventral longitudinal musculature which, at least in part, is attached to the dorsal side of the process e.gon.VIII (fig. 31). At its anterior end this musculature is internal, but it goes farther backward than the circular musculature.

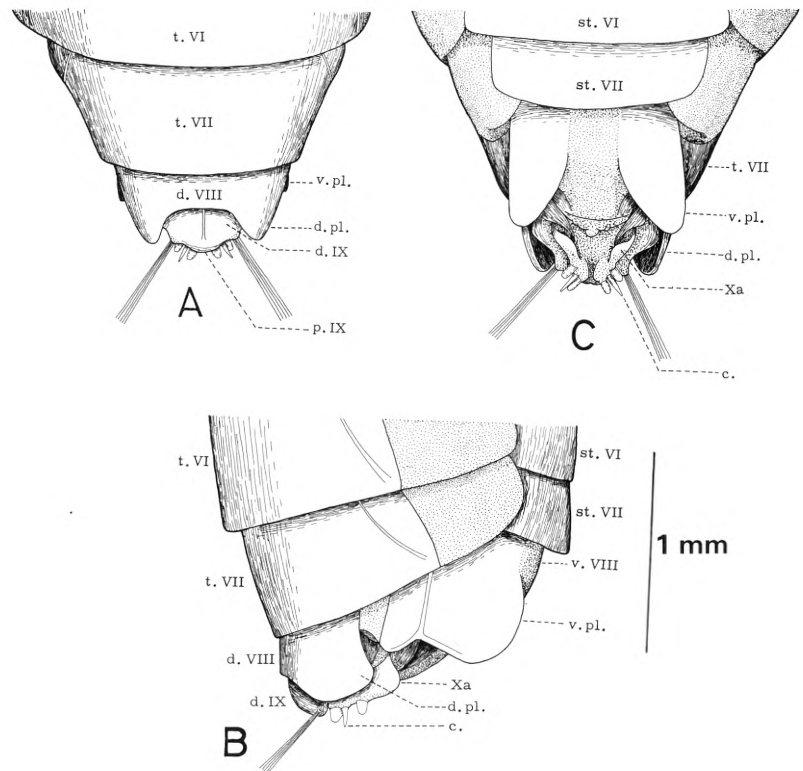
Hydropsyche Pict.

When my dissections and drawings were made, Tobias' key (1972) to the females of the genus was not published, and hence I paid no attention to the species used. At least two species are represented, *siltalai* Döhler (fig. 35 A) and *pellucidula* Curt. (figs. 35 C and D, 36 A-D). As to species represented in the other figures I cannot say anything, but very likely *angustipennis* Curt. is.

Pregenital segments. In a posterior direction the abdomen tapers considerably more in a dorsal (or ventral) than in a lateral view. There are no glands on segment V.

The genital segments (fig. 34). Segments VIII-X are very much modified. Together they are about as long as segment VII, but in contrast to this segment considerably longer on the ventral than on the dorsal side. The anterior end of the genital complex is as broad as the posterior end

Fig. 34. *Hydropsyche*. Posterior end of abdomen in a dorsal view (A), as seen from the right side (B) and in a ventral view (C).



of segment VII; in a posterior direction it continues the general tapering of the abdomen. Like the pregenital segments it is sagittally compressed.

Segment VIII has both dorsal and ventral sclerites, separated by a pleural membrane, which is considerably narrower than those on the pregenital segments. Its width varies according to the state of contraction of certain muscles, described below.

The dorsal sclerite, which may be called tergum VIII, is considerably narrower than tergum VII. (The pleural membrane VIII lies behind the sublateral parts of tergum VII). It is provided with a well developed antecosta, and its corners are produced into downward directed extensions. When the pleural membrane is relaxed, the extension lies in front of the dorsal half of it, when the membrane is contracted, as in fig. 34 B, it almost touches the ventral sclerite.

For almost its whole length tergum VIII is developed as a free, backward projecting lamella, which is sclerotized also on the inside, and which covers most of segment IX. The posterior margin of the lamella has, however, a broad, unpaired indentation, through which part of segment IX is visible in a dorsal view (fig. 34 A). The lateral margin of tergum VIII is somewhat concave. Thus a pair of broad posterior corners, dorsal plates (fig. 34 A, B, d.pl.), is formed. No doubt they are homologous with the dorsal part of the valves of segment VIII in *Rhyacophila* (p. 28). That part of the pleural membrane which is visible in fig. 34 B, and which of course does not extend as far backward as the dorsal plate, also overlaps segment IX.

On tergum VIII the setaceous covering is restricted to a narrow fringe along the posterior and lateral sides. The setae of the two sides are separated by a narrow interval. Along the lateral

half of the posterior margin they are particularly close-set and long (up to 210 μ).

The ventral side of segment VIII (fig. 34 C) is provided with a pair of sclerites, which for their greater part are separated by a rather broad, membranous area, but in front connected by a not quite narrow sclerotic bridge (in fig. 34 B and C concealed by the overlapping posterior border of VII). The lateral (or dorsal) parts of these sclerites lie behind the lateral parts of tergum VII.

The posterior margin of the ventral sclerite on segment VIII is produced into a ventral plate (v.pl.; lateral plate Denning 1943), which approximately is as long as the sclerite itself. As compared with conditions in the polycentropids this plate is very broad, and its greater, lateral part has an almost vertical position. By an obtuse-angled indentation the posterior margin is divided into a larger mesal and a smaller, but more strongly sclerotized lateral part. The inside of the mesal part has a crescentic sclerotization along the distal margin; otherwise the inside of the plate is membranous. The ventral plates no doubt are homologous with parts of the valves in *Rhyacophila* (p. 28).

The ventral sclerite of segment VIII has only quite laterally a feebly developed antecostal suture. Approximately from its middle a strong longitudinal suture runs to the indentation in the margin of the ventral plate. Here it divides into two branches, one to each side of the indentation. The part laterally to the longitudinal suture is by Denning called "pleurosternum, which is fused to the dorsal margin of the eighth sternum".

Mesally to the longitudinal sutures the ventral plates have a clothing of small setae. Otherwise venter VIII is devoid of setae.

The atrium. As in *Polycentropus* (p. 59) and *Holocentropus* (p. 66) an atrium is found, and as in *Polycentropus* the upper lip is formed of segment IX (and X), whereas both parts of segment VIII and parts of segment IX enter

into the composition of the lower lip. The position of the "mouth angle" is indicated with an arrow in fig. 35 A.

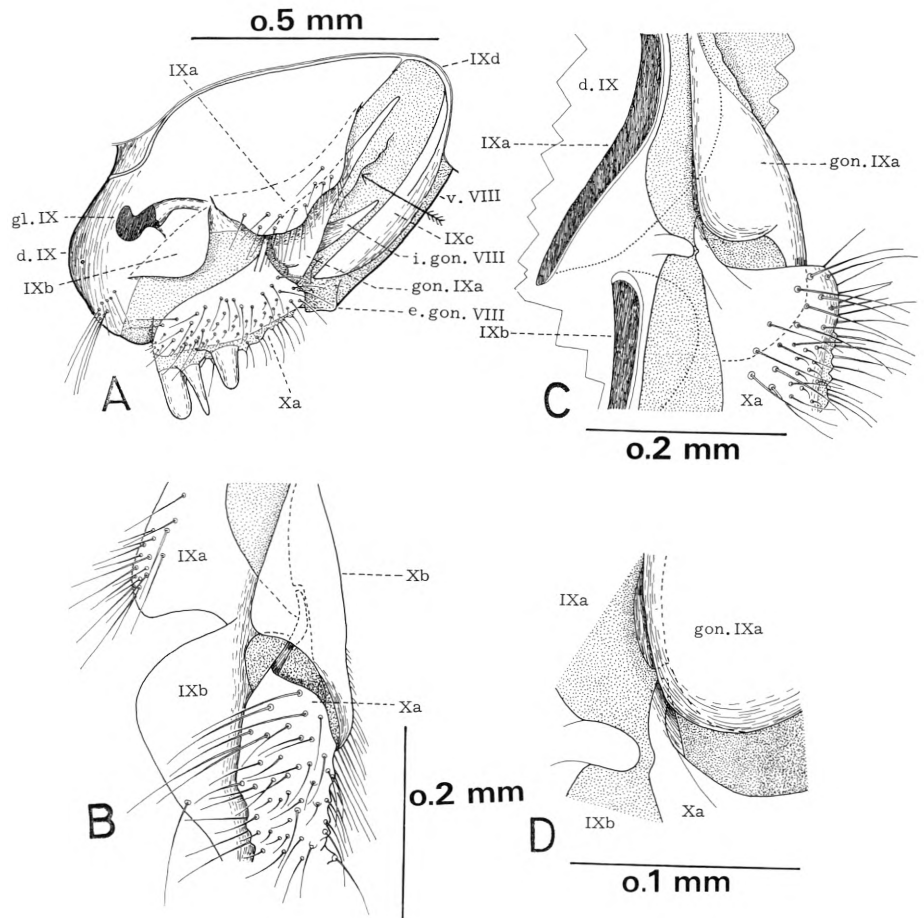
The upper lip of the atrium (fig. 35 A). The dorsal and lateral sides are entirely covered by a sclerite, which may be called tergum IX. The anterior margin of this sclerite is, like the whole dorsum, indented for its entire width, so that the length in the mesal line is a little more than half the length of the lateral side. (In fig. 34 A the anterior half of the mesal part is concealed by tergum VIII).

Tergum IX has a well developed antecosta. In the middle it is rather much removed from the anterior margin of the sclerite, being bent backward in the shape of a V. From it an unpaired longitudinal suture extends to the posterior margin of the tergum which, on each side of the suture, is slightly bulging.

On the lateral side, near, but not on, the lateral margin, the tergum has two outward and downward directed, tongue-like lamellae (figs. 35 A-C, 37 A). The anterior one (IXa; lateral lobe Denning 1943, Ventrallobus Tobias 1972) lies at a more lateral level than the posterior one (IXb; "second prominent lobe" Denning, Dorsallobus Tobias) and is considerably larger than the latter. (In fig. 34 B the greater part of IXa as well as the base of IXb are concealed by the pleural membrane VIII). Both these structures are lacking in the genus *Diplectrona* Westwood (Tobias).

Above the anterior end of the lamella IXa there is, on the lateral side of tergum IX, an ascendent, rounded furrow (clasper groove Denning, Zangenrinne Tobias), which dorsally widens into the irregular and in shape, specifically and apparently also individually, somewhat varying entrance to a rather shallow, but very spacious, sclerotic cavity (gl.IX; clasper receptacle Denning, Zangengrube Tobias). The ventral (or lateral) margin of the opening (fig. 36 A) is rather rounded, but the other margins project as sharp lamellae, on the lower part of

Fig. 35. *Hydropsyche*. A: Segments IX and X as seen from the right side. B: The articulation between segments IX and X (see p. 125) in a ventral view. C: Same as seen from the right side. D: Detail of C.



the posterior side as a tongue, which proceeds ventrally to the opening. The epithelium covering the cavity is very thick and probably contains tricellular glands. In situ the organ is concealed by the dorsal plate of segment VIII.

This structure possibly is homologous with the gland which in *Polycentropus* (p. 62) and *Holocentropus* (p. 68) opens into the atrium. If so, parts of segment IX which in *Hydropsyche* are external in these two genera enter into the composition of the inside of the atrium. The structure gl.IX is lacking in the genera *Diplectrona* Westwood (Tobias) and *Arctopsyche* McL. (Denning) and it is also poorly developed or entirely lacking in some few American species of *Hydropsyche* (Denning).

Denning describes "A distinctly marked heavily pigmented suture" between the two gl.IX. Tobias speaks of a "dorso-laterales Begrenzungslinie der Dorsalkappe des IX. Tergits". I found only a not always too distinct boundary between the anterior (or dorsal) darker part and the posterior lighter part of tergum IX.

It has been shown (Denning, Tobias, Statzner 1975) that gl.IX receives the distal end of the male harpago during copulation.

On the hind end of tergum IX there is, on each side, a group of 4-5 large setae and some few smaller ones (dorso-laterales Borstenbündel Tobias). In some specimens the large setae were concentrated as a pencil on a membranous papilla. Tobias does not describe such an arran-

gement in any European *H.* species, but in *Diplectrona felix* McL. It is certain, however, that the genus *Diplectrona* is not represented in my material. Moreover there is, behind the middle of the dorsal side, a pair of large sensilla campaniformia. Finally the lamella IX has a rather sparse covering of small setae on the lateral side and on the edge. Other sensilla are not seen on tergum IX.

The ventral side of the upper lip (fig. 37 A) is chiefly membranous, but laterally there is a pair of sclerotized folds (gon.IXa; lateral plates Denning 1943. This author's "only remaining sclerotized portion of the ninth sternum" probably is their anterior ends), which converge somewhat in a posterior direction. The hind and especially the front end of the fold is very narrow, the middle part is considerably broader. In details the fold has a rather elaborate shape. The broad middle part has a vertical mesal side, which in a posterior direction becomes rather high, and a flat ventral side, which is much broader than the base of the fold. On the narrow posterior part, mesally to the anterior end of the fold of segment X, the vertical mesal side is clothed with 40–60 μ long microtrichia.

The homology of this fold is difficult to decide. I have considered it as part of the gonopod IX, since it is reminiscent of the fold gon.IX in *Holocentropus* (p. 68), and since gonopods IX seem to enter into the composition of the lateral part of the upper lip in *Polycentropus* (pp. 60 and 66). The membranous area (Xb) belongs to segment X, as proved by the positions of the anus and the genital opening.

Approximately the anterior half of the ventral side of the upper lip, between the folds gon.IXa, is inverted as a large, slightly bilobed sac (Xc). The steep posterior side of the sac, which in the middle bulges a little forward, and the posterior parts of the lateral sides are feebly sclerotized. (This is Denning's "medial plate", which he has pictured in a wrong position; Pl. XVIII, fig. 1 B). Here the epithelium is very thick (ca. 40 μ) and probably glandular. A pair of cushions of similar epithelium is found in front on the lateral sides. The rest, i.e. the greater part, of the sac has an alveolar structure, being clothed with rounded ca. 6 μ broad nodules. The anus is found on the anterior part of the dorsal side of the sac.

The sac possibly is homologous with the structure gl?X in *Wormaldia* (p. 57). In one preserved

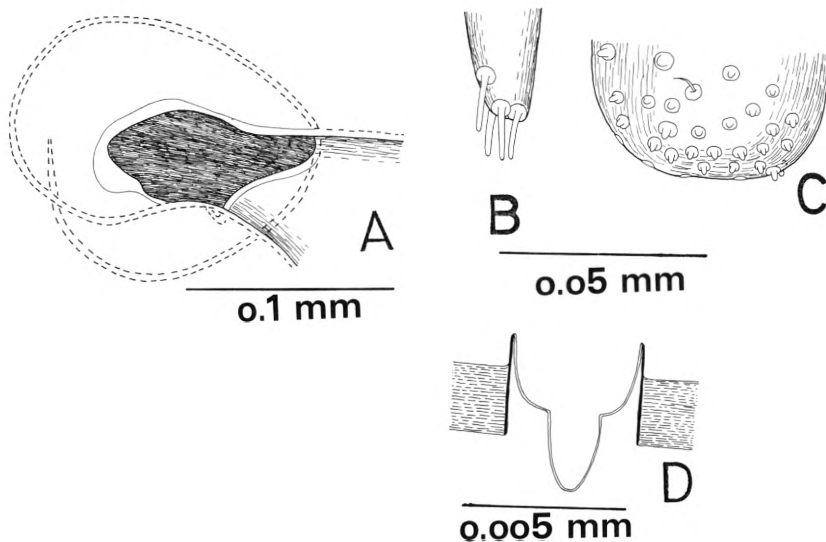
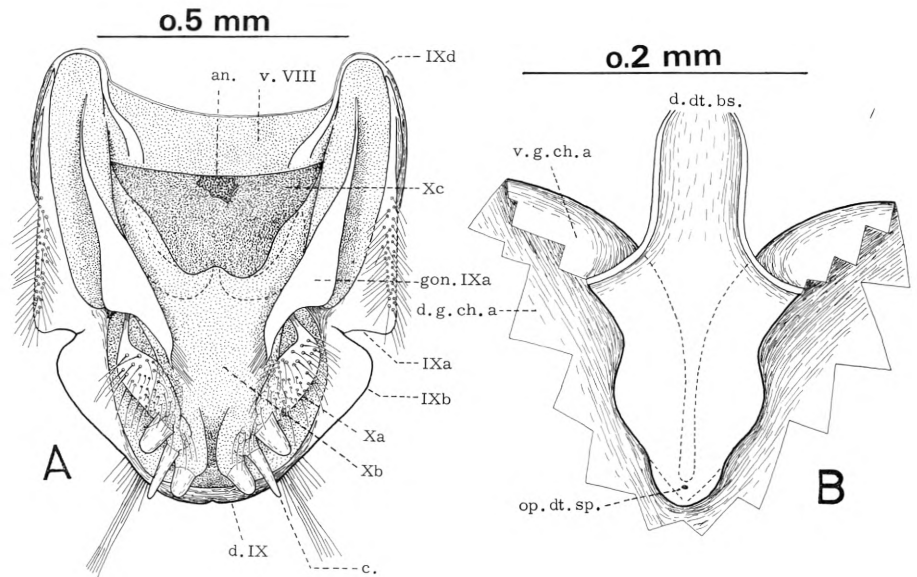


Fig. 36. *Hydropsyche*. A: Detail of fig. 35 A. B: Distal end of right cercus in a lateral view. C: Distal end of the process dorsally to the right cercus in a lateral view. D: Diagrammatic section through sensillum on the latter.

Fig. 37. *Hydropsyche*. A: Upper lip of the atrium in a ventral view. B: Processus spermathecae in a ventral view.



specimen the atrium gaped very much, and the sac (though not its sclerotized posterior side) was partly everted. It is uncertain whether this can be considered as a normal phenomenon.

Segment X. A comparison with the male (Nielsen 1957, pp. 63–64) may suggest that the large setae on the posterior part of segment IX actually belong to segment X, and as mentioned above this segment also contributes much to the formation of the atrium. Otherwise segment X (figs. 35 A, 37 A) is developed only as a pair of longitudinal folds on the posterior, steeply ascendent part of the ventral side of the upper lip. The posterior (or dorsal) ends of the folds almost touch each other, in an anterior (or ventral) direction the folds diverge. The lateral side of the fold carries a sclerite (Xa). At the anterior end this sclerite covers the whole fold (also the mesal side), which here has the shape of a rather sharp, somewhat mesally bent lamella. The folds probably can be actively moved.

The fold, except for the sclerotized part of the mesal side, is clothed with small setae of two orders of magnitude. On the membranous parts

most setae are placed on small processes. The smaller setae have a peculiar shape, being somewhat hook-like bent.

On the posterior (or ventral) side of the fold there are, as in the polycentropids, three processes above each other, the middle one probably being the cercus. The latter, which is much nearer to the dorsal than to the ventral one of the two other processes, is conical, though with a rounded apex. The two other processes are much thicker, the larger dorsal one almost cylindrical, the smaller ventral one somewhat tapering toward the rounded distal end. In the dorsal and ventral process the wall is 2 μ thick. In the cercus it is 1.5 μ thick; at the apex, however, too thin to be measured with the light microscope.

The dorsal and ventral process have on the distal end (fig. 36 C), especially laterally, a dense covering of tiny, peg-like setae set on dome-like alveolar membranes in deep alveoli (fig. 36 D), no doubt intermediates between setae and sensilla campaniformia, and in fact rather close to the latter. Among these sensilla some minute,

typical setae may be found. Quite apically there are true sensilla campaniformia, and more proximally on the process a much sparser covering of small, but relatively thick setae. The cercus carries four slender, cylindrical sensilla placed in alveoli, three on the apex, one subdistally and laterally (fig. 36 B). They probably are sensilla basiconica, i.e. chemoreceptors.

The articulation between segments IX and X (figs. 35 B–D). There is a rather complicated articulation between the fold gon.IXa, the sclerite Xa, and tergum IX. In front the lateral, dorsal edge of the sclerite Xa is produced into a somewhat reinforced, forward and downward directed, rod-like extension, which forms an articulation with a reinforcement laterally on the base of the broad part of the fold gon.IXa. Between the tongues IXa and IXb the lateral margin of tergum IX is produced into an obtuse-angled triangle, the base of which extends from the middle of IXa to the middle of gon.IXa. The top of the triangle again is produced into a short, reinforced rod, which forms a simple articulation with the dorsal side of the extension from the sclerite Xa.

The lower lip of the atrium (figs. 34 C, 35 A, 38), issued from the posterior end of venter VIII is shorter and narrower than the upper lip. It extends as a thick, chiefly membranous tongue backward between the two folds gon.IXa on the ventral side of the upper lip, and does not by far reach the posterior end of this lip. Laterally on the ventral side there is a pair of sclerites (fig. 35 A, IXc; cp. below, p. 87; the muscle dm_6), which narrow toward both ends. At the anterior end the mesal margin is reinforced and through a narrow bridge (figs. 35 A, 37 A, IXd), which curves round the “mouth angle” of the atrium, this reinforcement is continuous with the antecosta of tergum IX, suggesting that the sclerite IXc really belongs to segment IX, including part of the gonopod, as does the musculature (pp. 87–88). The posterior end of the lip is very thin-walled and irregularly wrinkled. Moreover

there is a rather slender, likewise thin-walled and wrinkled process, which is partly inverted, but possibly erectile.

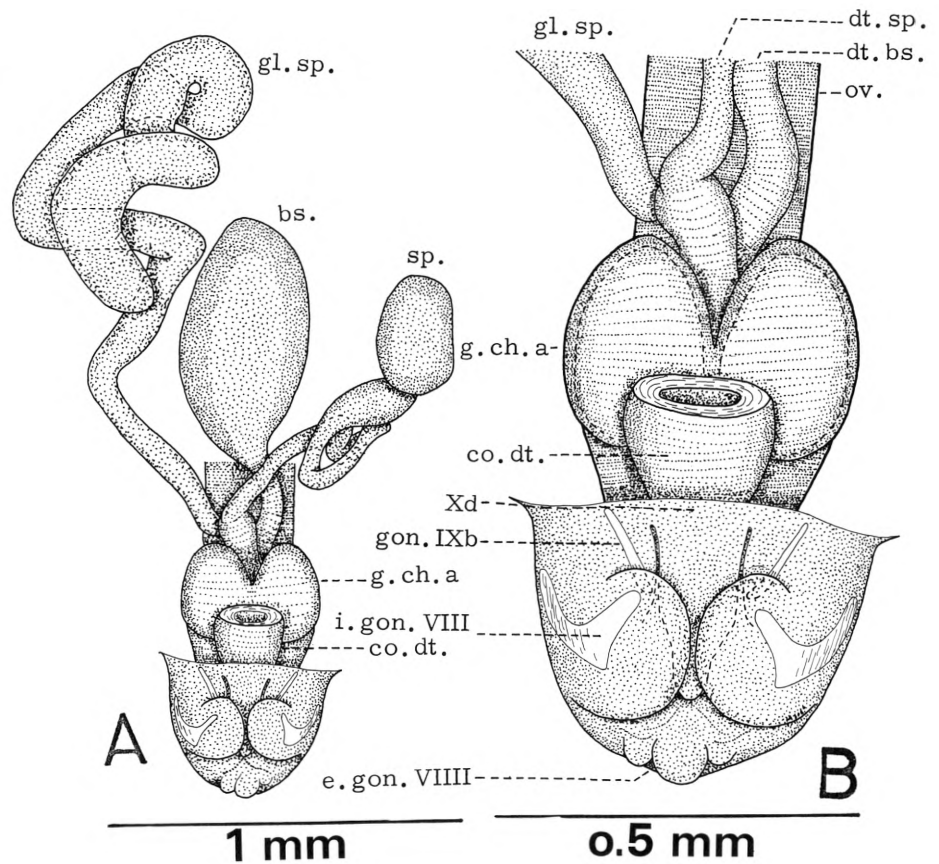
The genital opening is found on the anterior part of the dorsal side of the lower lip. (Thus the intestine and the genital tract have not a common opening as claimed by Denning, unless the “mouth” of the atrium is considered as the common opening). It is surrounded by five lobes, a long and slender, tapering anterior one (Xd) and two successive pairs of laterals (gon.IXb and i.gon.VIII). All five must be said to be dorsal in position; the ventral boundary of the genital opening is formed of the lower lip itself (e.gon.VIII). Of the paired lobes the posterior ones (i.gon.VIII) are by far the larger. They overlap the hind ends of the anterior lobes (gon.IXb), and the two posterior lobes almost touch each other above the distal part of the unpaired lobe (Xd). On each of the paired lobes there is a sclerite. On the anterior lobe it is small and rod-like (probably Denning’s “remains of the tenth sternum”), on the posterior lobe larger and biramous, but on this lobe, too, it covers only a small part of the surface.

The anterior, unpaired lobe (Xd) no doubt belongs to segment X, since it from a morphological point of view is situated behind the genital opening; (one imagines the the inside of the lower lip rolled backward and downward). The paired lips may represent parts of the gonopods VIII and IX, resp.

In one specimen each of the lobes i.gon.VIII carried two rather strong setae behind the sclerite, 50 (dorsal) and 70 μ (ventral) long, resp.

The genital chamber (fig. 38) is short, extending only to the front end of segment VIII. The anterior part of its dorsal wall bulges outward as a large sac, which is imperfectly divided into two egg-like vesicles (g.ch.a; roughly indicated by Denning–Pl. XVIII, fig. 1 C—as “internal plates”), which project both backward and, especially with the narrower ends, forward. The vesicles are stiff and thick-walled throughout, but pos-

Fig. 38. *Hydropsyche*. A: Lower lip of the atrium with the genital chamber etc. in a dorsal view. B: Detail of A.



sibly sclerotized only in their mesal, brownish halves. The broad ridge between the two vesicles widens somewhat toward its free, flat surface. It is the much ascendent processus spermathecae, the shape of which will appear from fig. 37 B. The small opening of the ductus spermathecae is found near the dorso-posterior end.

On the lateral sides of the genital chamber there are two successive pairs of folds, separated by sharp furrows, which are stiff and thick-walled, but possibly not sclerotized. The anterior folds, by far the shorter, are situated at the entrances to the dorsal vesicles (g.ch.a), flanking the processus spermathecae. In a posterior direction the rear folds gradually become lower, and disappear near the base of the unpaired

lobe (Xd) at the genital opening. These folds possibly are part of the gonopods IX.

The common oviduct arises at the boundary between segments VI and VII by union of the flat lateral oviducts, which carry the ovarioles on their ventral sides. Two sections may be distinguished. The anterior one is very delicate and narrows until the rear end of segment VII, where the short posterior section begins. The latter has parallel sides and is muscular.

The bursa copulatrix is a large, elongate sac. In one of the dissected specimens it was filled with a loose, brownish substance. At the posterior end the ductus bursae is sclerotized, continuous with the processus spermathecae. More distally it has a circular musculature.

The *spermatheca* is divided into two parts, connected by a short duct. The more slender proximal part is fusiform, the distal part approaches the spherical shape.

The ductus spermathecae is divided into a short and thick proximal part and a long and slender distal part; the latter is somewhat coiled. The difference in thickness is due only to the fact that the proximal part is provided with a circular musculature, the distal part not. At the opening the lumen of the duct is very narrow. It soon increases to 6 μ , and immediately before the transition into the slender part there is a spherical dilation with a diameter of 37 μ . In these parts the epithelium is 10 μ thick. In the slender distal part of the duct the lumen is 27 μ thick, the epithelium thin.

The long glandula spermathecae is exceptionally thick. It opens into the spherical dilation of the lumen of the ductus spermathecae. Proximally the gland is a little thicker than the slender distal part of the ductus spermathecae, in a distal direction the thickness increases gradually and strongly. The thick apical part is loosely coiled up. For a short, proximal part of the gland the epithelium is 24.5 μ thick, but the thickness soon decreases to 10 μ , quite distally even less. The gland has no musculature.

Colleterial glands. None of the specimens studied had mature ovaries, and the colleterial glands were small, extending only to the middle or the anterior end of segment VI. The unpaired section, lying in the posterior end of segment VII and in segment VIII, was the most voluminous section. The very strongly muscled, a little fusiform duct opens into the most posterior part of the genital chamber.

Musculature. Ventrally the front margins of segments VII and VIII are connected by a layer of fine longitudinal muscle bands for the whole width of sternum VII, below the oviducts. The anterior portion of a muscle, associated with the common oviduct and described below, may represent an internal muscle, the anterior attach-

ment of which has been shifted to the oviduct (cp. *Rhyacophila*, p. 33).

In segment VIII the dorso-ventral muscles dvm_2 and dvm_4 are present. As to the latter, the most posterior bands, lying in the fold overlapping segment IX, are considerably stronger than the others.

There are four VIII–IX muscles, which I have interpreted as dm_1 , dm_5 , dm_6 and vm_6 . The first mentioned is rather slender; it originates approximately in the middle of each half of the antecosta of tergum VIII and is inserted latero-dorsally to the antecosta of segment IX. The muscle dm_5 is still more slender. It originates on tergum VIII, behind the antecosta and somewhat ventrally to the middle of each half of this tergum. In a posterior direction the muscle converges toward the insertion to the membranous furrow between terga VIII and IX, the left and the right muscle quite close to each other. The rather strong, subcylindrical muscle dm_6 originates on the ventral sclerite of segment VIII (fig. 34 B, v.pl.) and is inserted to the lateral part of the antecosta on segment IX. The interpretation of this muscle involves that the dorsal and ventral sclerites on segment VIII are not serially homologous with the terga and sterna on the preceding segments. The very flat muscle vm_6 has one attachment to the ventral sclerite of segment VIII, laterally to the longitudinal suture (fig. 34 B, v.pl.) and from the antecosta in front of this suture. Its bands converge somewhat toward their other attachment on the mesal reinforcement of the sclerite IXc (fig. 35 A). The posterior attachments of this muscle and that of dm_6 are not quite symmetrical in relation to the "mouth angle" of the atrium. Considering that the attachments are so close to the curvature of the antexosta on segment IX (fig. 37 A, IXd) their most likely function seems to be extension and retraction, resp., of the upper lip. By simultaneous contraction they possibly can cause also an opening of the atrium.

In addition I found a muscle, which is inserted to the anterior end of the rear, muscular part of the common oviduct (p. 86), its converging bands at least in part continuous across the latter. It consists of two portions. One originates on the anterior corner of the ventral sclerite on segment VIII, the other mesally on the anterior end of the sclerite IXc (fig. 35 A). As mentioned above, the first may be considered as an internal VII–VIII muscle. The second may be considered as a transverse muscle associated with the gonopods (p. 25). If so, the sclerite IXc must contain part of the gonopod IX.

The rather slender muscle $gonm_1$ originates on the ventral sclerite of segment VIII mesally to the longitudinal suture (fig. 34 B, v.pl.) and is inserted to the lower lip of the atrium mesally to the sclerite IXc (fig. 35 A). The flat muscle $gonm_2$ originates on the posterior half of the mesal reinforcement on IXc and is inserted to the mesal edge of the sclerite on the lobe i.gon.VIII (fig. 38). The muscle $gonm_3$ also is flat, but rather strong. It extends in front of the "mouth angle" of the atrium between the dorsal and the ventral part of the antecosta on segment IX. The dorsal attachment is approximately on the middle of each half of the dorsal antecosta, the ventral attachment on the anterior half of the mesal reinforcement on the sclerite IXc. It is probably a closer of the atrium.

Several fine muscle bands originates on the lateral margin of the sclerite on i.gon.VIII (fig. 38). They pass forward, upward and inward, laterally to and in front of $gonm_2$. The bands of the left and the right side are continuous above the posterior part of the genital chamber. Another transverse muscle, possibly associated with the gonopods, has been described above.

The IX–X musculature is very complicated. One muscle originates on the antecosta of segment IX opposite the attachment of VIII–IX dm_1 (p. 87), another on the surface of tergum IX. They pass in front and behind, resp., gl.IX (fig. 35 A) on segment IX. Both are ribbon-like

and both are inserted to the sclerite Xa. Considering the rather complicated articulation between the segments IX and X (p. 85) it seems likely that they cause an outward rotation of the sclerite Xa and thus an abduction of the folds of segment X. The anal sac (fig. 37 A, Xc) is rather well provided with muscles. One originates on the sclerite of segment IX above the base of the tongue IXa (fig. 35 A); its bands converge fan-like toward their insertion. Another is unpaired and originates on the triangular area of tergum IX in front of the antecosta (p. 81). Both are inserted to the posterior margin of the entrance to the anal sac, and their function probably is to widen this opening. Below the glandular epithelium on the posterior side of the anal sac fine muscle bands are seen.

The slender muscle $gchm$ originates on the dorsal antecosta of segment IX, somewhat above dm_6 (p. 87). It is inserted to the sclerotized part of the ductus bursae.

The genital chamber has the usual circular musculature. The anterior ends of the two dorsal vesicles (fig. 38, g.ch.a) have each a circular musculature of its own.

Agraylea multipunctata Curt.

Pregenital segments. On terga III–VII there is, in addition to the lateral suture, a short paired, mesal longitudinal suture. It appears as a backward bending of the antecostal suture, since the latter is only feebly developed between the two longitudinal sutures. On the sterna II, III and IV the antecosta, quite on the contrary, is more strongly developed in the middle. This is less so on sternum V, still less on sternum VI, and not at all on sternum VII.

The gland on segment V is slightly pear-like, 205–222 μ long and 62–82 μ thick. It opens on a short, finger-like process, situated near the anterior corner of the sternum and directed obliquely backward. Hence its anterior side is longer (62 μ) than the posterior side (33 μ); the thickness is

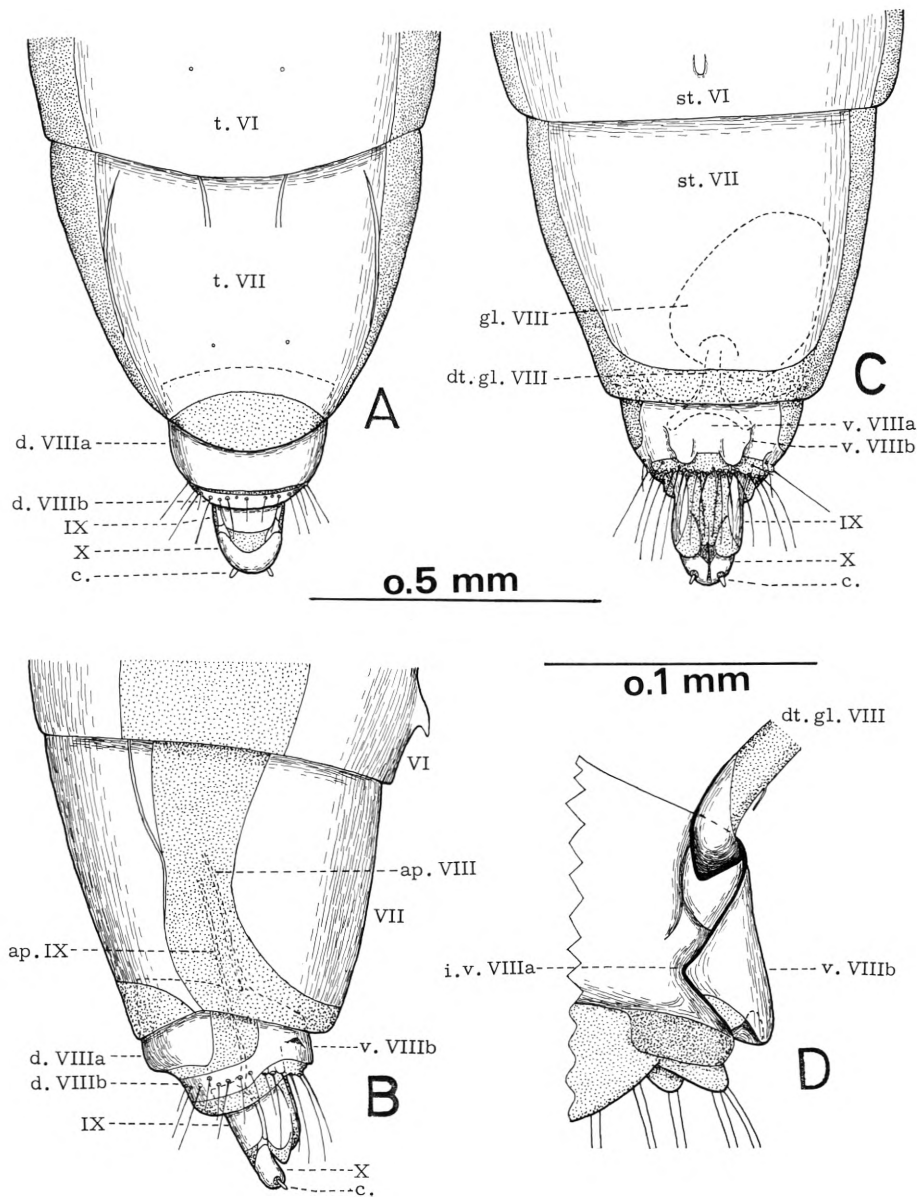


Fig. 39. *Agrylea multipunctata*. Posterior end of abdomen in a dorsal view (A), as seen from the right side (B) and in a ventral view (C). D: Sagittal section through ventral side of segment VIII; left side as seen from the inside.

25 μ . Apically the process carries a pencil of a large, up to 145 μ long, setae. The gland opens subdistally (i.e. proximally to the pencil) and laterally on the process. The opening is difficult to see, since the outer part of the efferent duct is ribbon-like compressed, and the opening therefore has the shape of an, in relation to the

process longitudinal, cleft. As mentioned below (p. 95) it can be opened by means of a muscle.

Near the posterior margin of sternum VI there is an unpaired, backward directed and somewhat sagittally compressed tooth (fig. 39 B, C).

On each tergum, also on tergum I, there is a

pair of very large sensilla campaniformia. On segment I they are situated approximately in the middle of the tergum, on the following segments they gradually move backward.

Segment VII (fig. 39 A–C) is slightly modified. It is longer than segment VI. In front it is just as broad as this segment, in a posterior direction it tapers more. The posterior margin of the dorsum is rather much convex, but in return the posterior margin of the tergum has a broad indentation. The sternum does not reach the posterior end of the segment, and the pleural membrane is scarcely as broad as on the preceding segments.

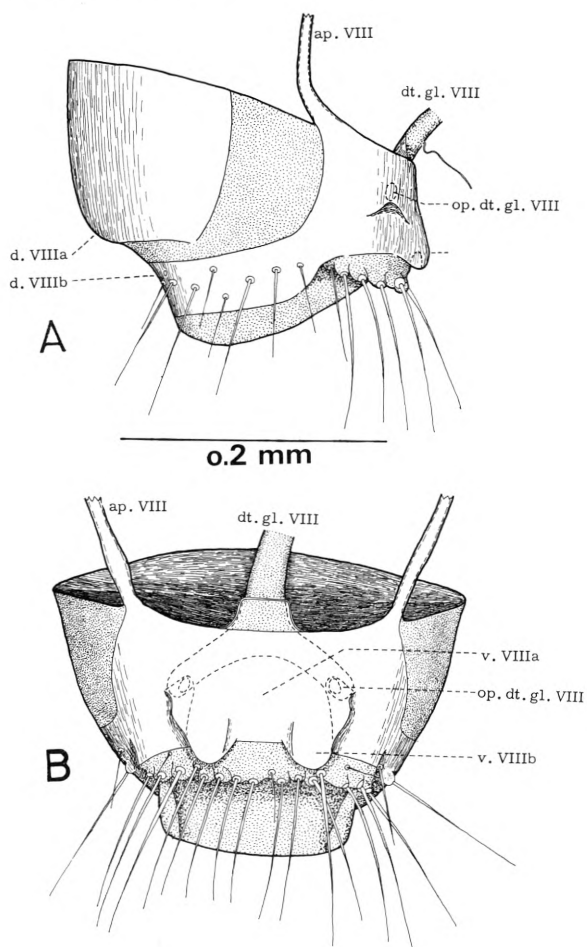
Segment VIII (figs. 39 A–C, 40) is highly modified. It is somewhat narrower than the posterior end of segment VII but only a little tapering, except at the extreme posterior end. Its dorsal side is scarcely half as long as segment VII, but a little more than twice as long as the ventral side. This difference, however, is obscured by the fact that segment VII overlaps more dorsally than ventrally.

The anterior two thirds of the dorsal side is covered by a sclerite (d.VIIIa). On the ventral side there is a stronger sclerite (v.VIII), which does not quite reach the posterior end of the segment, and is separated from the dorsal sclerite by a rather ample pleural membrane. The anterior corners of the ventral sclerite are produced into a pair of very slender, slightly S-like curved apodemes (ap.VIII), which in the specimens shown in fig. 39 A–C extend beyond the middle of segment VII. From the posterior corners of the sclerite a pair of extensions is issued. They meet on the dorsal side of the segment and coalesce, forming a posterior, transverse sclerotic bridge (d. VIIIb) which, like the surrounding membrane, lies on a “shelf” at a lower level than the anterior sclerite. The bridge has a lighter colour than the ventral sclerite; this colour boundary might be mistaken for the margin of the ventral sclerite.

A not quite regular circle of strong setae is

seen along the posterior margin of segment VIII. They are shortest dorso-mesally, longest ventro-laterally. The ventral setae are placed on high processes on the posterior, membranous part, the dorsal setae on the transverse sclerotic bridge (d.VIIIb). In addition to these setae there often, but not always, are some few, smaller setae on the posterior corners of the ventral sclerite itself. Some setae on the more posterior of the pregenital segments may be even longer than the large setae on segment VIII, but the setae of course are more conspicuous on this

Fig. 40 *Agraylea multipunctata*. Segment VIII as seen from the right side (A) and in a ventral view (B).



otherwise (almost) naked segment. A little in front of the dorsal row of setae a pair of large sensilla campaniformia is found, as in the pregenital segments.

On the ventral side of segment VIII a peculiar structure is seen. In the middle the sclerite has, for its whole length, a funnel-like depression (v.VIIIa; see especially fig. 39 D), flanked by a pair of rounded longitudinal ridges (v.VIIIb). The hind ends of the latter project as a pair of short, tongue-like lamellae with sharp edges. Since the lamellae are curved in a transverse direction they appear, however, rounded both in a lateral (fig. 40 A) and in a ventral view (fig. 40 B). In the middle of the lateral side the ridge has a deep, inward and forward directed impression, ventrally bordered by a sharp edge, in front of which the ridge is less pronounced. Dorsally, near the bottom of the depression, the paired opening of a, strangely enough, unpaired structure is found. The latter is a large, elongate, sac-like organ (fig. 39 C, gl.VIII) which lies in the posterior part of segment VII, ventrally to the oviduct. The posterior end of the sac is lowered into a hilus, from which a short and slender duct (dt.gl.VIII) issues. At the boundary between segments VII and VIII the duct divides into two branches, which together form a flat curve with a posterior concavity. Near the opening the paired duct narrows gradually and strongly, and hence the opening is rather small.

The relations between the unpaired duct, the posterior part of venter VII and the anterior part of venter VIII, which in this region has a narrow, anterior membranous extension, will appear from figs. 39 D and 40 B. The posterior part of the dorsal side of the duct is sclerotized, and the same is the ventral side after having entered the region of the ventral sclerite (v.VIIIa) of segment VIII. The branches, too, are sclerotized. These sclerotized parts of the duct coalesce with the sclerite of segment VIII, and hence the branches of the duct may appear as a curved suture on this sclerite.

The wall of the sac is quite thin, but to all probability we are concerned with a scent organ. In some specimens examined, the sac – the size of which varies rather much – contained a whitish substance. Perhaps a secretion takes place in the pharate adult, and the glandular epithelium then degenerates. There are, however, no muscles in the wall of the sac, nor does there seem to be other means of emptying, unless this can take place by means of general movements of the abdomen. Neither is there any closing mechanism. However, it is possible that in the living animal segment VIII is more deeply retracted into segment VII than in the specimens shown in fig. 39 A–C and some closure thus achieved.

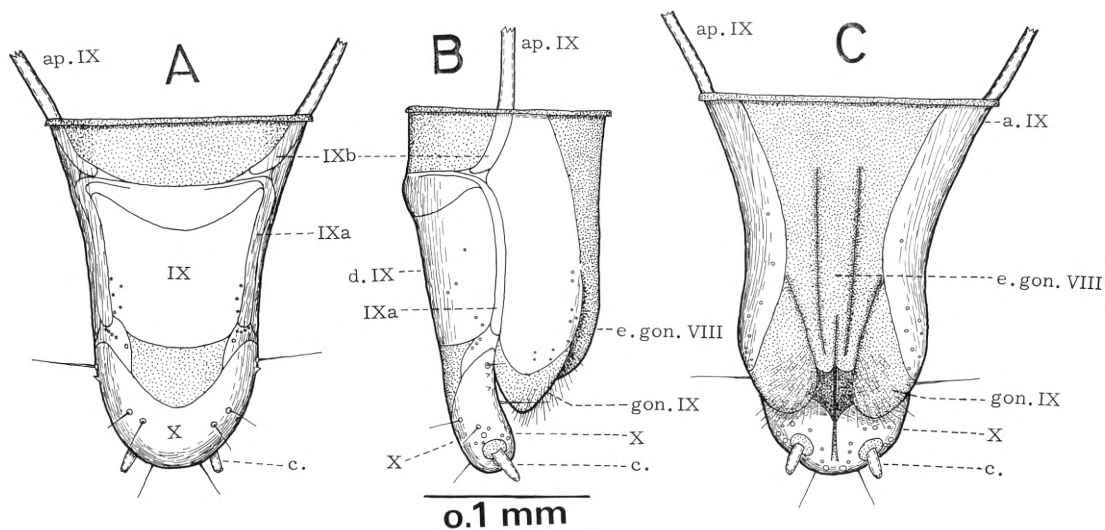
This organ perhaps is homologous with that described in *Agapetus* (p. 36).

Segment IX (fig. 41) is a little more than half as long as segment VIII and much more slender, subcylindrical. In the specimens shown in fig. 39 A–C it is rather much retracted into segment VIII, but in some specimens examined the whole segment was withdrawn.

Though pale, the dorsal and lateral sides are weakly sclerotized. The dorsal side, however, has for its whole width a relatively shallow membranous indentation at the anterior end. Behind this indentation there is, a little dorsally to the middle of the lateral side, a longitudinal, rod-like, brown reinforcement of the sclerite (IXa). Ventrally to the rod IXa the sclerite proceeds beyond the posterior end of the latter as a tongue-like extension. The anterior end of the rod IXa bends upward and continues, narrower, along the lateral part of the anterior indentation. It is, so to speak, superimposed by a much broader reinforcement which runs between the anterior ends of the two rods IXa and has a backward curved posterior margin. Laterally this transverse reinforcement is only feeble, mesally it is very strong.

On the short anterior part of the segment there also is a pair of, even broader, reinforce-

Fig. 41. *Agraylea multipunctata*. A: Segments IX and X in a dorsal view (A), as seen from the right side (B) and in ventral view (C).



ments (IXb), here running along the dorsal margins of the sclerite. The two rods, the anterior (IXb) and the posterior one (IXa), are connected by a small, thickened, elasticuticular area – almost the usual form of articulation in the genital segments of female Trichoptera. The rods IXb proceed forward as a pair of slender, but strong apodemes (ap.IX), reaching (in the specimens shown in fig. 39 A–C) the middle of segment VII, i.e. almost as much forward as those of segment VIII, in relation to which they are dorsal. The posterior ends of the apodemes of segment VIII lie at a more lateral level than those of segment IX, but since the latter diverge more, the anterior ends of the two sets of apodemes lie in the same sagittal plane.

The greater mesal part of the ventral side, broader both at the anterior and at the posterior end, is membranous. Its hind end forms an, apparently very thin-walled and often irregularly wrinkled, bilobed lower lip of the genital opening. Continuing the indentation between the two lobes an unpaired longitudinal furrow proceeds forward for a short distance. The anterior part of this furrow is flanked by a pair of much deeper furrows which, slightly divergent in an anterior direction, extend for more

than half the length of the ventral side. The ventral side of segment IX (e.gon.VIII) probably represents the gonopods of segment VIII, and the bilobed posterior end reveals the paired origin of this structure.

Laterally the genital opening is bordered by a pair of rounded lobes (gon. IX), each of which is much broader and proceeds much farther backward than the lower lip. The latero-posterior extension of the sclerite of segment IX lies laterally on the base of the lobe gon.IX. The membranous posterior end of the latter is clothed with pale, $16\ \mu$ long and $1\ \mu$ thick, stiff microtrichia. The lateral lobes probably represent (part of) the gonopods of segment IX.

The indentations between the lobes gon. IX and the lower lip (e.gon.VIII) continue forward toward the lateral margin of the sclerite on segment IX as a pair of divergent furrows. In a cross section the lower lip becomes broader, the lateral lobes (gon.IX) narrower in a dorsal direction.

Segment IX carries no setae, but on the sclerotized as well as on the elasticuticular parts a number of sensilla campaniformia is seen. Their distribution will appear from fig. 41.

Segment X is only a little more than half as

long, but at its anterior end just as broad as segment IX. It forms a parabolic upper lip of the genital opening, and is less than half as high as segment IX. It is almost entirely covered by an unpaired sclerite. On the dorsal side the latter has a deep anterior indentation. Here the sclerites of the two segments thus are separated by copious membrane, and the exact boundary cannot be stated. The anterior corners of the sclerite on segment X are connected with the posterior ends of the rods IXa on segment IX by a pair of rather large, roughly triangular, elastocuticular areas. On the lateral side, near the anterior end of the sclerite, a small tooth will be noted; more rarely there are, as in fig. 41 B, two small teeth behind each other. On the ventral side an unpaired, longitudinal, membranous furrow is seen.

The sclerite of segment X carries on each side (4–) 5 small setae in a regular order, which will appear from figs. 41 A and B. Moreover, there is a greater number of sensilla campaniformia laterally and ventrally on the posterior part of the segment. A pair of very large sensilla ventrally on the posterior end will especially be noted.

The small, peg-like cerci issue from a pair of small, circular, membranous areas latero-ventrally near the posterior end of the segment. The rounded apex of the cercus is almost entirely covered by three sensilla campaniformia.

The genital chamber (fig. 42) is somewhat flattened, extends to the posterior third of segment VII and has a rather simple shape. It is broadest a little in front of the middle, where the width further is increased by a pair of low lateral bulges. It tapers slightly toward the anterior end, more strongly in a posterior direction.

The most anterior part of the dorsal wall is a little ascendent. Then, still near the anterior end, a short vertical part follows. On this part the funnel-like colleterial duct opens through an approximately cylindrical "stalk". Behind this

opening the lumen of the genital chamber is bisected by a horizontal lamella (g.ch.b), the hind edge of which lies at the level of the lateral bulges mentioned above, and the posterior part of which is sclerotized. From a morphological point of view the anterior base of the lamella of course lies in front of the opening of the colleterial duct. Externally this division of the genital chamber is concealed by the circular musculature.

The rather flat processus spermathecae (fig. 43) arises from the anterior, ascendent part of the dorsal wall. Since it is directed straight backward, below the lamella (g.ch.b) mentioned above, it follows that the ventral side is much longer than the dorsal side. In a ventral view (fig. 43 B) the anterior half has almost parallel sides, whereas the posterior half is roughly triangular. The extreme posterior end, however, is much sagittally compressed; it is partly membranous, but apparently stiff. On the dorsal side the membrane proceeds until the base as a longitudinal ridge, which in an anterior direction becomes lower.

On the ventral side, too, there is a longitudinal ridge. In front it is rather broad, in a posterior direction it tapers gradually and strongly, and also becomes lower. At the posterior fourth the height suddenly decreases (fig. 43 A), a small backward and downward facing area thus being formed. The latter is membranous, and on it the small opening of the ductus spermathecae is found.

The hind corners of the anterior broad half of the processus spermathecae are produced into a pair of narrow rods (figs. 42 B, 43, sp.scl.b), which in curves proceed backward latero-ventrally on the wall of the genital chamber, and eventually are continuous with the anterior corners of a sclerite, lying on the dorsal side of a tongue (i.gon.VIII) issued from the ventral wall of the genital chamber (fig. 42 B). The tongue is directed backward, but does not reach the posterior end of the genital chamber, nor does the

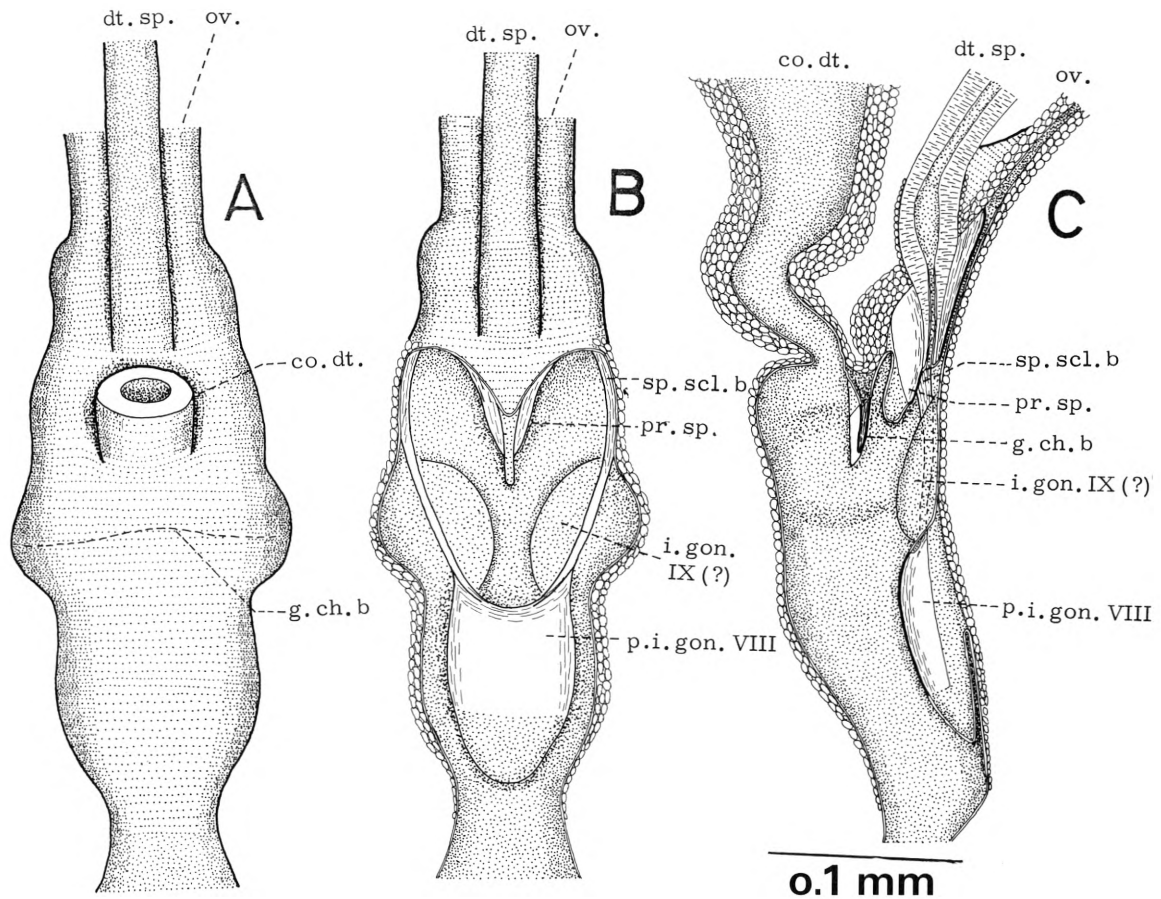


Fig. 42. *Agrylea multipunctata*. A: The genital chamber in a dorsal view. B: Same after removal of the dorsal wall behind the spermathecal sclerite. C: Sagittal section through the genital chamber; left side as seen from the inside.

sclerite reach the posterior end of the tongue. Behind the latter the ventral wall of the genital chamber is strongly ascendent, so that the genital opening takes the shape of a transverse cleft.

Finally there are, ventrally to the bulges of the lateral wall, and mesally to the the rods issued from the processus spermathecae, a pair of low membranous cushions (i.gon.IX), possibly representing part of the gonopods IX. They are densely covered with $2.5\ \mu$ broad and $1.5\ \mu$ high nodules.

The ovaries are of the "finger type", with very long ovarioles.

Bursa copulatrix. This structure is not found.

The spermatheca lies in the anterior part of segment VII and may extend into VI. The ductus spermathecae has a thick ($8\ \mu$) epithelium and thus probably is glandular. The lumen is $6.5\ \mu$ wide, but narrows in the processus spermathecae to $1.5\ \mu$. Only the proximal part of the duct has a feeble musculature. A glandula spermathecae is not found.

The colleterial glands are large, sausage-like, and extend into segment IV.

The anus is situated on the dorsal wall of the most posterior part of the genital chamber, separated from the genital opening s.str. by a

short, backward directed, membranous lobe. By the way, the intestine gives the impression of being rudimentary.

Musculature. The muscle vm_5 is found only in segments V–VI. Like the corresponding dorsal muscle it consists of only one band, but in an anterior direction it diverges much more. It enters the process at the anterior corner of sternum V and is inserted to the posterior side of the duct of the gland in this segment. No doubt it serves as an obturator muscle.

The muscles VII–VIII dm_1 and dm_2 are developed as in the preceding segments. On the lateral margin of tergum VII, at the point where the lateral longitudinal suture reach the latter, a slender muscle originates. It passes laterally to the apodeme of segment IX and is inserted to the base of the apodeme of segment VIII. Another slender muscle, inserted distally to the apodeme of segment VIII, originates either on the extreme anterior corner of tergum VII or on the pleural membrane at the boundary of segment VI and VII. I have interpreted the two last mentioned muscles as a bipartite dm_6 , which involves that the dorsal and ventral sclerites of segment VIII are not serially homologous with the terga and sterna on the preceding segments.

Of ventral VII–VIII muscles only vm_6 is

present. It originates laterally, not quite at the hind end, on sternum VII and is inserted to the distal part of the apodeme of segment VIII.

Dorso-ventral muscles are not found in segment VIII.

There are four VIII–IX muscles, which I have interpreted as dm_2 , dm_5 , dm_6 and vm_6 . The first mentioned muscle is composed of several bands, which connect the apices of the apodemes of segments VIII and IX; in one of my preparations this muscle appeared strongly fusiform. The strong muscle dm_5 originates on the dorsal sclerite of segment VIII, near the anterior corner. In a posterior direction it converges strongly, and the left and the right muscle are inserted quite close to each other in the bottom of the furrow between segments VIII and IX. The rather strong muscle dm_6 originates on the transverse reinforcement on the sclerite of segment IX (fig. 41) and is inserted distally to the apodeme of the same segment. That both attachments are in the same segment is remarkable, but may be explained by the shifting of one attachment from the sclerite of segment VIII to the apodeme of segment IX, just as the origin of the muscle $gchm$ in *Rhyacophila* (p. 33) and *Hydropsyche* (p. 88) appears to have shifted from segment VIII to segment IX. The muscle vm_6 originates on the ventral sclerite of segment VIII, at the root of the bridge $d.VIIIb$ (fig. 40 A), and is inserted to the distal part of the apodeme on segment IX.

The muscle $gonm_1$ originates mesally on the distal part of the apodeme on segment VIII and is inserted ventrally to the anterior margin of segment IX; the left and the right insertion are rather widely separated. I did not find any muscle representing $gonm_2$. The flat muscle $gonm_3$ originates laterally on the transverse reinforcement of the sclerite on segment IX (fig. 41). It is descendent and is inserted along a longitudinal line on somewhat less than the posterior half of the sclerite on segment IX, approximately midway between the reinforce-

Fig. 43. *Agraylea multipunctata*. Processus spermathecae as seen from the right side (A) and in a ventral view (B).

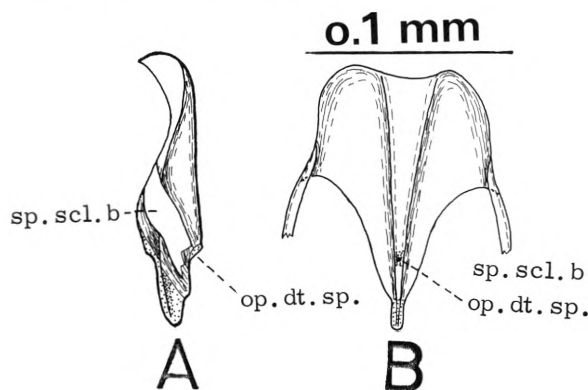
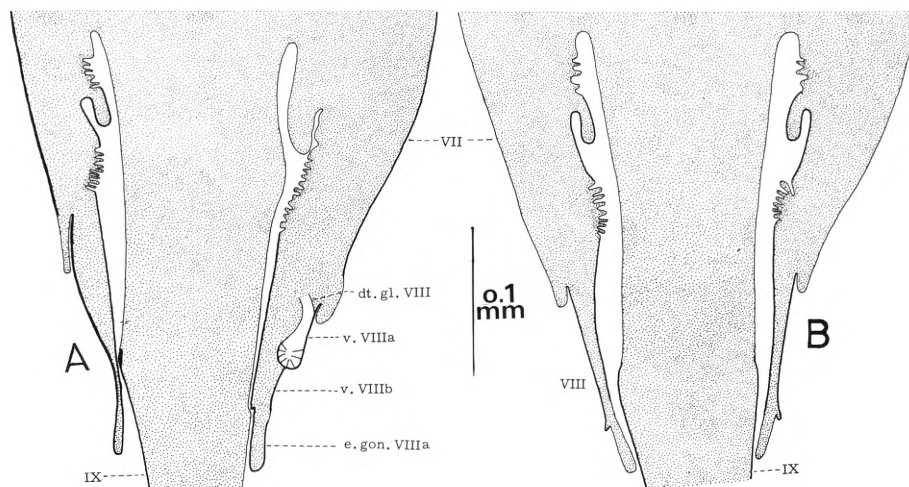


Fig. 44. *Hydroptila occulta*.
Diagrammatic sections
through posterior part of
segment VII, segment VIII,
and anterior part of seg-
ment IX. A: Vertical plane.
B: Horizontal plane.



ment IXa and the ventral side of the segment, i.e. to a part which probably is derived from the gonopod IX.

A transverse musculature is found in segment IX. It extends over the anterior half of that part of the segment which in fig. 39 A-C is seen projecting beyond segment VIII. It passes below the genital chamber.

The flat IX-X muscle originates on the transverse reinforcement of the sclerite on segment IX, mesally to and in part behind the origin of gonm₃. It is inserted dorsally to the anterior margin of the sclerite on segment X and probably is a levator of this segment.

The strong muscle gchm originates approximately on the middle of the lateral margin of the ventral sclerite on segment VIII. It passes ventrally to the apodeme of segment IX, but dorsally to the muscle gonm₁, and is inserted to the anterior end of the processus spermathecae.

The circular musculature does not quite reach the posterior end of the genital chamber.

Hydroptila occulta Eat.

I have previously (1951) given a short description of the genital segments in this species, a description which badly needs both supplements

and corrections. In the following differences from *Agraylea* especially have been stressed. There is a great resemblance between the two forms, but *Hydroptila* has many peculiarities of its own.

Pregenital segments. As in *Agraylea* the sternal antecosta is very strong in the middle on segments II-IV, less so on segments V and VI. The opening of the gland in segment V is situated on a setae-carrying process. I have been unable to find the large sensilla campaniformia seen in *Agraylea*.

Segment VII is long and both in a dorsal (or ventral) and in a lateral view much tapering in a posterior direction.

Segment VIII is very highly modified. The external parts (fig. 45 A, B; see below) of this segment taper in a posterior direction. The dorsal side is about twice as long as the ventral side; in a lateral view it is slightly S-like curved. The segment is synscleritous, though to its greatest extent pale and weakly sclerotized. On the dorsal side the sclerite reaches the posterior end, on the lateral and ventral sides it is separated from the latter by a short membranous area. A pair of slender, rod-like apodemes (ap.VIII) issues from the anterior margin a little ventrally to the middle of the lateral side. They are

extremely long, in the specimens studied extending to the anterior end of segment VI. Continuing the apodeme in a posterior direction a short, downward bent reinforcement is seen on the sclerite of segment VIII.

The posterior part (v.VIIIb) of the ventral side of this sclerite lies at a deeper (i.e. more dorsal) level than the anterior part (v.VIIIa). The boundary of the depressed area is transverse, though at the lateral ends somewhat backward bent. Latero-ventrally, at the extreme end of this boundary, there is a deep, pocket-like depression beneath the posterior margin of the sclerite. In a transverse section the pocket is triangular; its ventral and lateral sides are sclerotized, the mesal side is membranous. In the pocket the small opening of a glandular organ is found.

This organ is built in principle as in *Agraylea* (pp. 133–34). That part of the unpaired duct (dt. gl.VIII) which lies in segment VIII (as defined by the external part; see below), as well as the branches, are sclerotized and firmly coalesced with the ventral side of the sclerite on segment VIII which here, just in front of the depressed area (v.VIIIb), is reinforced. In my previous paper (1951) I called this reinforced part the “ventral plate”, erroneously considering the boundary of the depressed area as the genital opening.

At the point of division the duct is very wide and has a peculiar honey-combed appearance (fig. 44 B. v.VIIIa). The “cells” are ca. 4 μ wide, their walls ca. 5 μ high. Toward the outer, narrower part of the branches the lumen is almost entirely obstructed in this way. This structure has no small similarity to that on the distal part of the dorsal branch of the gonopods in the male (Nielsen 1951: “paramere”; cp. 1957, pp. 83–84).

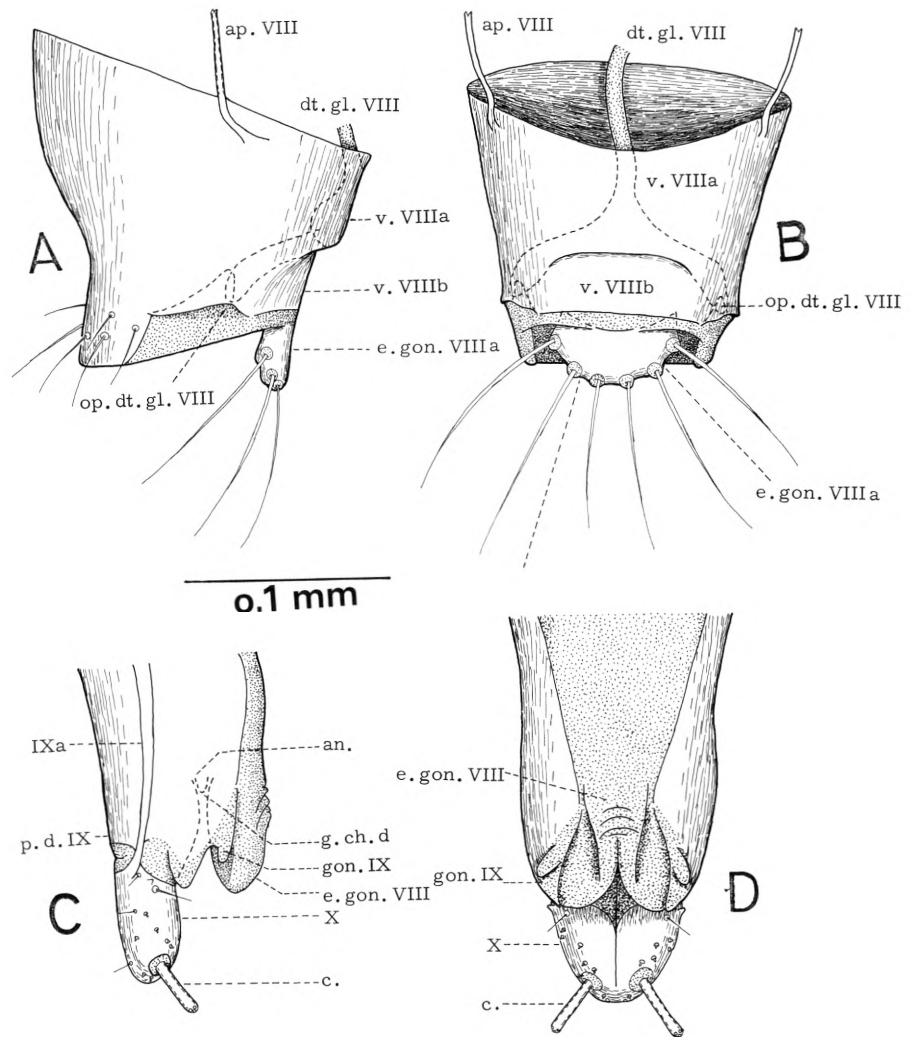
Ventrally a tongue-like lobe (fig. 45 A, B, e.gon.VIIIa) issues from the posterior margin of segment VIII. It is strongly sclerotized on both sides and closely appressed to the ventral side of

segment IX. Previously (1951) I, very inappropriately, called this tongue the “dorsal plate”. The lateral parts of the tongue are slightly overlapped by the membranous posterior end of segment VIII. The tongue probably represents part of the gonopods VIII. On its margin there are three pairs of very large setae. 5–6 much smaller setae are seen postero-dorsally on each side of the sclerite on segment VIII; they are 16–40 μ long, i.e. of about the same length as on the preceding segments. The large sensilla campaniformia seen in *Agraylea* are not found.

The posterior end of segment VIII is deeply invaginated, forming a tube (fig. 44) which in the specimens studied extends a little beyond the middle of segment VII. In the wall of the tube four sections can be distinguished. The hindmost and longest, which reaches the posterior end of segment VII, is sclerotized and continuous with the dorsal side of the external sclerite as well as with e.gon.VIIIa, though separated from the latter by a fine, backward directed ridge. The next section is thin-walled, membranous and thrown into numerous, regular circular folds. By a straightening of the folds this section must be able to increase its length considerably. The following section forms a larger double fold, which is sclerotized on the dorsal and the lateral sides, membranous on the ventral side. The foremost section again is membranous and thrown into fine folds; the latter, however, extend only over the dorsal and the lateral sides, i.e. they are horseshoe-shaped. Eventually the wall of the tube bends round into the wall of segment IX.

Segment IX (fig. 45, C, D). Conforming to the posterior invagination of segment VIII this segment is very long. Otherwise it in principle is built as in *Agraylea* (pp. 91–92) though the sclerite does not seem to extend in front of the dorsal transverse reinforcement, which in the specimens studied was situated a little in front of the posterior end of segment VIII, i.e. concealed in the internal tube of this segment. At least the

Fig. 45. *Hydroptila occulta*. External part of segment VIII as seen from the right side (A) and in a ventral view (B). Posterior end of segment IX and segment X as seen from the right side (C) and in a ventral view (D).



wall in front of the transverse reinforcement is very thin, at the anterior end so thin that its thickness cannot be measured with the light microscope. Moreover, the posterior (IXa) and the anterior (cp. fig. 41 IXb) rod-like reinforcements are connected by exocuticle. At the point of union there is, however, an upward directed "elbow" and perhaps some flexibility. The anterior rods proceed as a pair of apodemes, which is dorsally and mesally to those of segment VIII and extend scarcely as far forward. The anterior

part of the apodeme of segment IX is thickened, but in return has a distinct lumen, thus forming a thin-walled tube.

As in *Agraylea* the posterior part of the ventral side of segment IX forms a bilobed lower lip (e.gon.VIII) of the genital opening, but it is much broader than in *Agraylea* and stiff, perhaps even slightly sclerotized. On each half of the lower lip a deep longitudinal furrow is seen, and between these two furrows some few transverse folds. The lobes bordering the genital

opening laterally (gon.IX) are much narrower than each half of the lower lip, and pointed. Ventrally they carry a small, finger like, membranous process, which is so thin-walled that it is difficult to observe in a ventral view.

In my former paper on *Hydroptila occulta* (1951) I included that part of segment IX which lies behind the dorsal transverse reinforcement in segment X, and mistook the genital opening for the anus.

Segment X (fig. 45 C, D) is in principle built as in *Agraylea*. On the anterior part of the lateral side a small, rounded tooth is seen. Both on the dorsal and on the ventral side the sclerite has a V-like indentation. On the ventral side there is, as in *Agraylea*, a longitudinal furrow which continues on the membranous area in front of the sclerite. The anterior corners of the latter are continuous with the reinforcements IXa on segment IX, which here are bent a little upward.

The sclerite of segment X carries four pairs of small setae, the distribution of which will appear from fig 45 C and D. In addition there is on the lateral and ventral sides, as well as on the posterior end, a rather great number of small, peg-like sensilla, intermediates between setae and sensilla campaniformia. Among these two pairs placed symmetrically on the posterior end, dorsally and ventrally resp., will be noted. Finally a pair of large sensilla campaniformia is situated close to each other on the posterior end.

The cercus is more slender than in *Agraylea*. Its distal end carries three tiny sensilla campaniformia. (However, owing to the smallness of the object it is difficult to ascertain the number with certainty, even by the use of an immersion lens).

The genital chamber extends, in the specimens studied, beyond the middle of segment VII, a little farther forward than the internal tube of segment VIII. The lamella below the opening of the colleterial duct is sclerotized. It is extremely thin, but this is obscured by the fact that it is vaulted in a transverse direction, with a ventral concavity. In front the dorsal side of the sclerite

of the lamella has a reinforcement, which proceeds beyond the margins of the lamella as a pair of rods on the lateral wall of the genital chamber, flanking the opening of the colleterial duct. In an anterior or posterior view the whole structure is roughly semicircular. In my previous paper (1951) I have described it as a bridge connecting "the arms of the trident-like structure", a term taken over from Mosely. The "central piece" of the latter is the processus spermathecae and thus not situated on the ventral wall of the genital chamber.

The anus is found on the most posterior part of the dorsal wall of the genital chamber. It is separated from the genital opening s.str. by a short, backward directed, membranous tongue (fig. 45 C, g.ch.d).

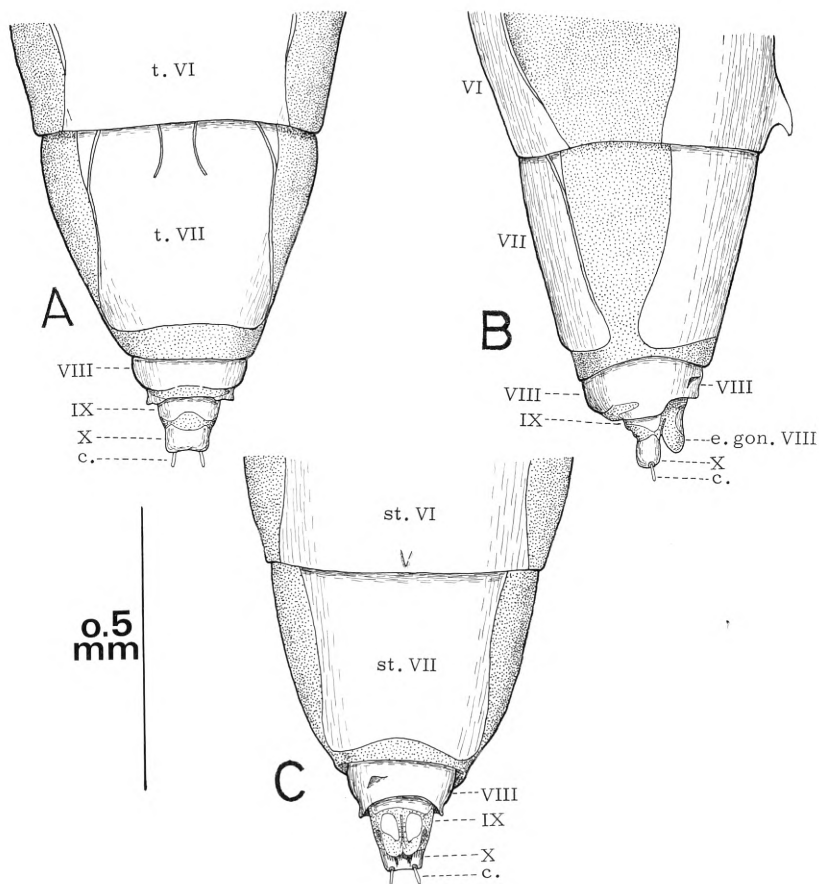
Musculature. As in *Agraylea* (p. 95) VII–VIII dm_6 is represented by two muscles. One passes laterally to the apodeme of segment VIII and is inserted to the anterior margin of this segment a little ventrally to the base of the apodeme. The other has a more posterior origin than the first mentioned muscle, to which it passes laterally toward its insertion subdistally to the dorsal side of the apodeme of segment VIII. In connection with the elongation of the apodeme of segment VIII the last mentioned muscle, as compared with *Agraylea*, has shifted its origin, in part also its insertion, and perhaps its function too. The muscle VII–VIII vm_6 seems to be lacking.

Among the VIII–IX muscles there is one less than in *Agraylea*: dm_5 is lacking, which probably has some connection with the deep invagination of segment VIII.

Also the muscle $gonm_1$ seems to be lacking.

The transversal muscles in segment IX have their attachment latero-ventrally in the segment and are continuous across the segment, curving round the ventral side of the genital chamber. This musculature extends, in an anterior direction, to near the front margin of the external sclerite on segment VIII. It might easily be confused with the circular musculature in the

Fig. 46. *Orthotrichia costalis*. Posterior end of abdomen in a dorsal view (A), as seen from the right side (B) and in a ventral view.



genital chamber. In many preparations, however, I have seen a distinct interval between the two sets of muscles.

Orthotrichia costalis Curt.
(*O. tetensii* Kolbe)

Pregenital segments. Terga III–VII have the same mesal longitudinal sutures (fig. 46 A) as in *Agraylea*. The sternal antecosta is very strong. On segments III and IV it is strongest in the middle, on segments VI and VII quite on the contrary more feeble in the middle. Near the posterior margin of sternum VI there is an unpaired, sagittally compressed, backward directed tooth (fig. 46 B, C). There is no gland in segment V.

Segment VII (fig. 46) is longer than segment VI and the longest segment in the abdomen. In a posterior direction it tapers rather much. Neither the tergum nor the sternum reach the hind end of the segment. On the dorsal side a thin fold overlaps segment VIII rather much, on the lateral and ventral sides this segment is only a little overlapped by a thicker fold. These conditions, however, no doubt vary according to the degree of extension and retraction, resp., of the “Legeröhre”.

Segment VIII (fig. 47). The length is only a fraction of that of segment VII. It is a little thinner than the posterior end of the latter segment, and only very slightly tapering in a posterior direction. The dorsal side is almost twice as long as the ventral side.

The segment is synscleritous. On the ventral side and on the lateral sides the sclerite reaches the posterior end. On the dorsal side there are broad membranous indentations both at the posterior and at the anterior end. The anterior indentation proceeds on the lateral side until the base of the apodeme mentioned below. The dorso-posterior membranous area has latero-dorsal extensions in front of the tongue valv. described below.

Approximately in the middle of the lateral side the anterior margin of the sclerite has a triangular extension, and the top of the triangle is produced into a slender apodeme (ap.VIII). The latter is long, though not as compared with conditions in *Agraylea* and *Hydroptila*. In the specimens shown in fig. 46 it scarcely reaches the middle of segment VII.

In the middle of the lateral side the posterior margin of the segment is produced into a short, backward directed and somewhat outward bent tongue (valv.), which is sclerotized on both sides. The dorsal end of the tongue is bent somewhat in a mesal direction, following the curvature of the segment, and here its sclerite, as mentioned above, is separated from the main sclerite of the segment by a membranous indentation. The tongue, though small in size, probably is homologous with the lateral valve in *Rhyacophila* (p. 28).

On the external side, near the posterior margin, the tongue valv. carries a row of 4–7 setae. Their length is 11–40 μ , the longer ones being best represented. They are shorter, but stiffer and possibly more thick-walled too, than the setae on the pregenital segments. Other setae are not found on segment VIII.

The same glandular organ as in *Agraylea* and *Hydroptila* is found. It differs, however, by having an unpaired opening (fig. 47, B, C), which is placed asymmetrically, shifted toward the right. Moreover, by the fact that the duct (dt.gl.VIII) does not narrow toward its opening, but quite on the contrary is funnel-like dilated,

especially in the horizontal plane. The opening has the shape of a rather large depression, which mesally is indistinctly delimited, laterally and in front bordered by a sharp edge. The depression has no anterior side; here is the opening of the gland. The duct is membranous, at least for the greater part of its length. It is closely applied to the ventral side of segment VIII, but as far as I could see not coalesced with the latter.

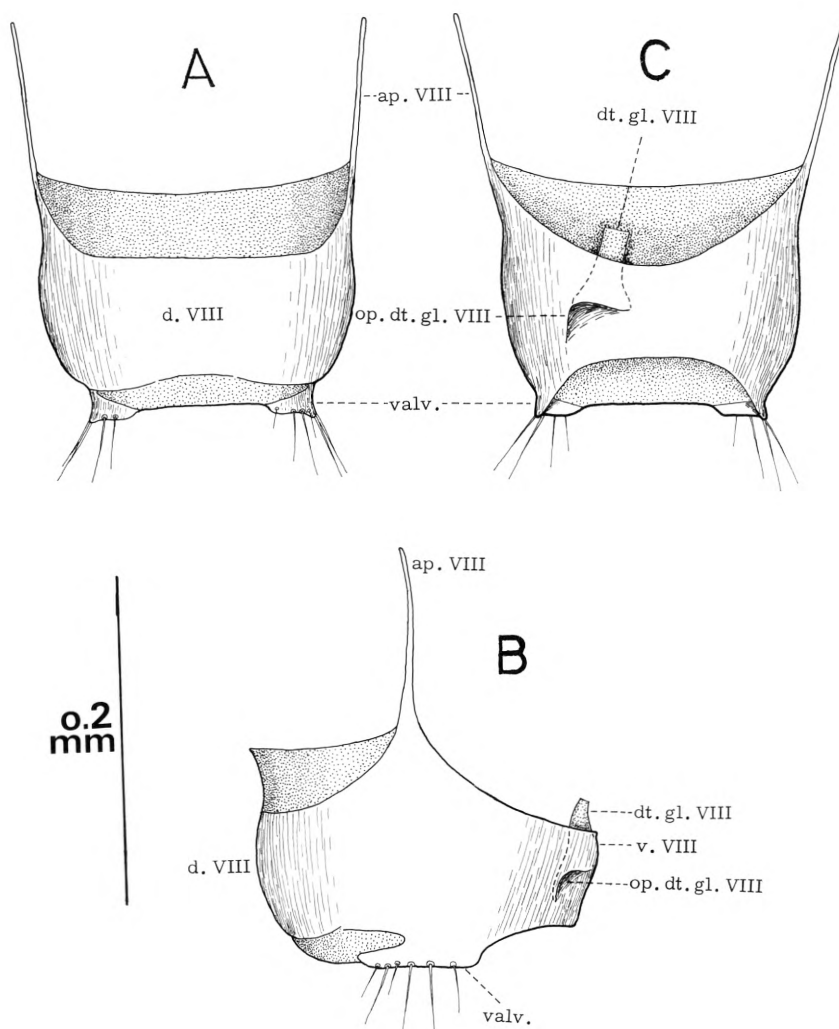
To all probability the condition in *Orthotrichia* is secondary, the left branch of the paired duct having been suppressed.

Segment VIII overlaps to a great degree segment IX, especially on the dorsal and the lateral sides. On the lateral side its posterior end is divided into two folds, an external sclerotic one (the tongue valv. mentioned above) and an internal membranous end. However, an internal tube as in *Hydroptila* is not formed.

Segment IX (fig. 48) is only a little shorter, but considerably narrower and lower than segment VIII, and tapers strongly in a posterior direction. The dorsal half of the segment is covered by a sclerite, which has a broad posterior indentation, broadly rounded posterior corners thus being formed. The ventral side is to a great extent membranous. There are, however, an unpaired sclerite (v.IX) and a pair of sclerites (e.gon.VIII) which, in contrast to the weak dorsal sclerite are strong.

The anterior ventral sclerite (v.IX) forms a transverse bridge at the front of the segment. For its whole width the posterior margin has a relatively shallow indentation. Laterally to the rounded posterior corner of this indentation the sclerite proceeds forward on the lateral side as a descendent and gradually narrowing rod, which again proceeds forward as a long (though as compared with conditions in *Agraylea* and *Hydroptila* short) and slender apodeme (ap.IX). In the specimens shown in fig. 46 it scarcely extends to the anterior end of segment VIII. Whereas the antero-ventral margins of the external rod and the apodeme form an even curve,

Fig. 47. *Orthotrichia costalis*. Segment VIII in a dorsal view (A), as seen from the right side (B) and in a ventral view (C).



the boundary on the dorsal side is marked by a sharp bend. At the latter the rod is connected with the anterior corner of the dorsal sclerite by a short and narrow, longitudinal and probably elastocuticular bridge.

The posterior ventral sclerites are roughly elliptical. Their front ends almost touch the posterior corners of the anterior sclerite, their hind ends are far removed from the posterior end of the segment.

The membranous posterior end of segment

IX forms a bilobed lower lip (e.gon.VIII) of the genital opening; the approximately semiglobular lobes are densely clothed with ca. 4μ long microtrichia. The incision between the two lobes proceeds forward as an unpaired furrow between the two postero-ventral sclerites. Laterally the genital opening is bordered by a pair of lobes (gon.IX), which are much shorter than the lower lip, approximately half as broad as each lobe of the latter, and also much more thin-walled. In a ventral view they are completely concealed by

the lower lip, in a lateral view almost entirely covered by the lateral parts of dorsum IX and by the upper lip of the genital opening, segment X.

The paired ventral sclerites on segment IX probably belong to the gonopods VIII, the anterior sclerite (v.IX) possibly includes both parts of these gonopods and of gonopods IX.

As in *Agraylea* and *Hydroptila* segment IX is devoid of setae, nor did I see any sensilla campaniformia.

Segment X (fig. 48) forms, in a dorsal view, so to speak a continuation of segment IX. It is much shorter than this segment, much broader than long, and approximately half as high as segment IX. Its posterior end is almost transverse, only very slightly concave. The segment forms an upper lip of the genital opening (and of the anus; see below), separated from the lower lip by a deep "mouth angle", extending beyond the middle of the postero-ventral sclerites of segment IX. In a transverse direction the ventral side of the upper lip is very concave, so that the thickness of the lip in the middle is only

about half of its total height. In an anterior direction the margins of the concavity become rather sharp.

Segment X is almost entirely covered by an unpaired sclerite, the dorsal side of which has a broad anterior indentation. The rounded anterior corners approach, but do not reach, the posterior corners of the dorsal sclerite on segment IX. Otherwise the two sclerites are separated by ample membrane. A ventral longitudinal furrow as in *Agraylea* and *Hydroptila* is not seen. The furrow in the two latter forms perhaps is a rudiment of the concavity in *Orthotrichia*.

The cercus, the base of which is surrounded by a small, ring-like, membranous area, is situated laterally on the posterior end of the segment, ventrally to the middle, but not in so ventral a position as in *Agraylea* and *Hydroptila*. It is slender and carries distally three sensilla campaniformia. The latter lend a somewhat angular shape to the apex, which in some specimens might give the impression that there are a couple of rudimentary distal segments.

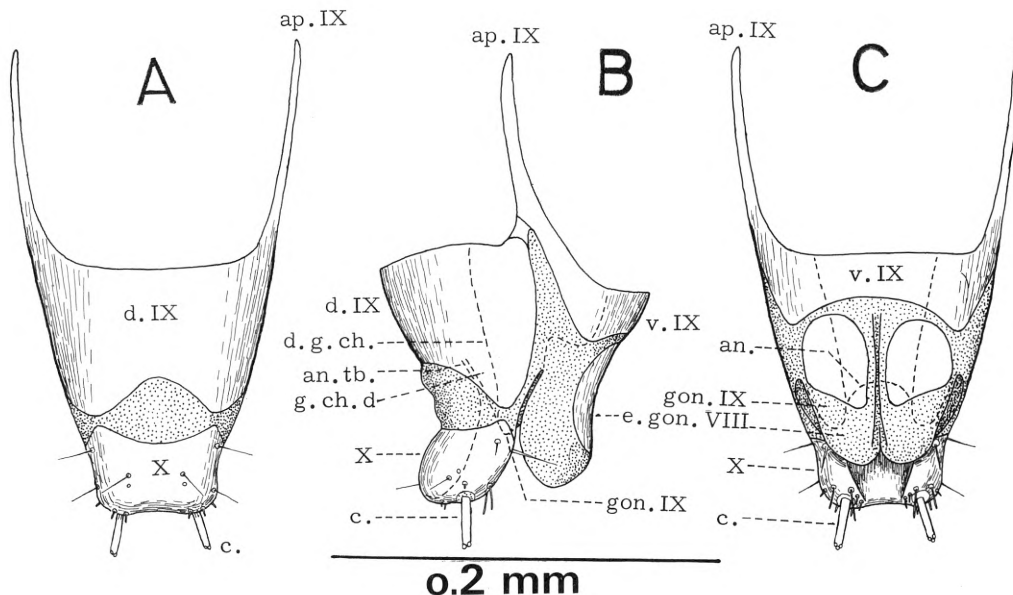
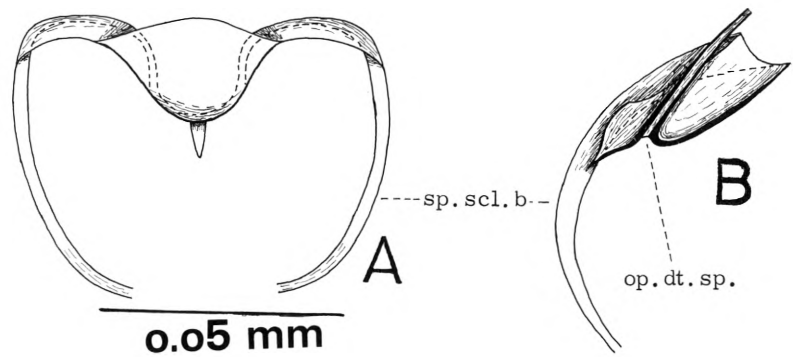


Fig. 48. *Orthotrichia costalis*. Segments IX and X in a dorsal view (A), as seen from the right side (B) and in a ventral view (C).

Fig. 49. *Orthotrichia costalis*. A: Processus spermathecae in a ventral view. B: Sagittal section through the processus spermathecae; left side as seen from the inside.



Segment X is provided with some setae, the distribution of which will appear from fig. 48. A circle of seven short, but relatively thick setae round the base of the cercus will especially be noted: two dorsals, two mesals, two ventrals, and a lateral one. The two ventrals are the longest; the five others tend toward intermediates between setae and sensilla campaniformia.

The genital chamber extends, in the specimens shown in fig. 46, scarcely to the middle of segment VII.

The processus spermathecae (fig. 49) has many features in common with those of *Agraylea* and *Hydroptila*, but there are distinct differences too. Two sections can be distinguished in the entirely sclerotized, approximately 45° ascendent process. The anterior section is a flat, parabolic tongue, which is not nearly as broad as the lumen of the genital chamber. The posterior section is very much narrower than the anterior one, much sagittally compressed and, especially in a lateral view, much pointed. Its ventral side lies at a deeper (i.e. more dorsal and more anterior) level than that of the anterior section. The opening of the ductus spermathecae is situated on the declivity between the two sections and hence not seen in an exact ventral view.

The anterior corners of the processus are produced into a pair of slender rods (sp.scl.b.). That part of the rod which is nearest to the processus lies transversely on the dorsal wall of the genital chamber, the rest of the rod on the

lateral wall of the latter. In a lateral view (fig. 49 B) the rod is curved with a ventral concavity. The two rods, left and right, eventually take the shape of a pair of reinforcements in the anterior margin of a feeble sclerite, lying on a low cushion on the ventral wall of the genital chamber. The posterior end of this cushion is not produced into a tongue as in *Agraylea* and *Hydroptila*, but behind it there is another cushion which almost obstructs the lumen of the genital chamber.

The mesal sides of the lateral lobes (fig. 48 B, C, gon. IX) at the genital opening proceed forward as a pair of membranous folds on the lateral walls of the genital chamber.

There is a lamella below the opening of the colleterial duct, but it does not seem to be sclerotized.

Bursa copulatrix is not found.

Spermatheca. My dissections were not successful, but I am rather sure that there is no glandula spermathecae. The proximal part of the ductus spermathecae is sclerotized.

The colleterial glands are bulky, but have a simple shape and extend to the middle of segment III.

The anus (fig. 48 B) cannot be said to lie in the genital chamber itself, but rather above its opening (but of course below its upper lip, segment X). The two openings are separated by a tongue (g.ch.d), the rather sharp posterior edge of which is concave. Its ventral side is sclerotized,

and the sclerite extends to the anterior end of segment X.

Musculature. The muscle VII–VIII dm_6 (cp. p. 13) is tripartite. One portion originates as a number of bands laterally on the posterior margin of tergum VII and is inserted distally to the apodeme of segment VIII. The second muscle originates at the anterior third of tergum VII, distinctly mesally to the lateral longitudinal suture; it is inserted to about the distal half of the apodeme of segment VIII. The third portion originates dorsally on the pleural membrane at the boundary between segments VI and VII and is inserted to the distal end of the apodeme of segment VIII. Of VII–VIII ventrals only vm_6 is found. It consists of a couple of feeble bands which originate quite laterally on the posterior margin of sternum VII and is inserted ventrally to the apodeme of segment VIII, approximately in the middle.

Dorso-ventral muscles are not found in segment VIII.

As in *Agraylea* (p. 95) four VIII–IX muscles are found. The muscle dm_2 is closely applied to the mesal side of the apodeme of segment VIII. The muscle dm_5 differs rather much from the corresponding muscle in *Agraylea*. It is composed of numerous bands, which converge fan-like toward their insertion dorsally on the base of the apodeme of segment IX. The ventral (or lateral) bands originate on the anterior margin of the sclerite on segment VIII, somewhat dorsally to the apodeme. The dorsal bands are almost vertical and originate latero-dorsally, approximately in the middle between the front and hind end of the sclerite on segment VIII. The strong muscle dm_6 originates latero-dorsally on the anterior margin of the dorsal sclerite on segment IX, passes laterally to dm_5 and is inserted to the distal end of the apodeme of the same segment; if the interpretation is correct, a shift of one of the attachments from one segment to another is involved. The muscle vm_6 also is strong. It originates latero-ventrally

near the posterior end of the sclerite on segment VIII, is ca. 45° descendent and is inserted distally to the apodeme of segment IX.

The very strong muscle $gonm_1$ has its anterior attachment on the front margin of the sclerite on segment VIII, ventrally to the apodeme. Half of the posterior attachment is ventrally on the basal fourth of the apodeme of segment IX, the other half to the anterior margin of the ventral unpaired sclerite on this segment. The muscle passes mesally to vm_6 . I did not find a muscle $gonm_2$. The muscle $gonm_3$ is composed of fine bands which originate latero-dorsally on the anterior part of the sclerite of segment IX. I am rather certain that the descendent and slightly divergent bands are inserted to the structure $gon.IX$ (fig. 48 B, C).

Transversal muscles are not found in segment IX.

The IX–X muscle originates on the anterior part of the sclerite on segment IX, mesally to the muscle $gonm_3$, and is inserted dorsally to the sclerite of segment X. The right and the left muscle have a common origin.

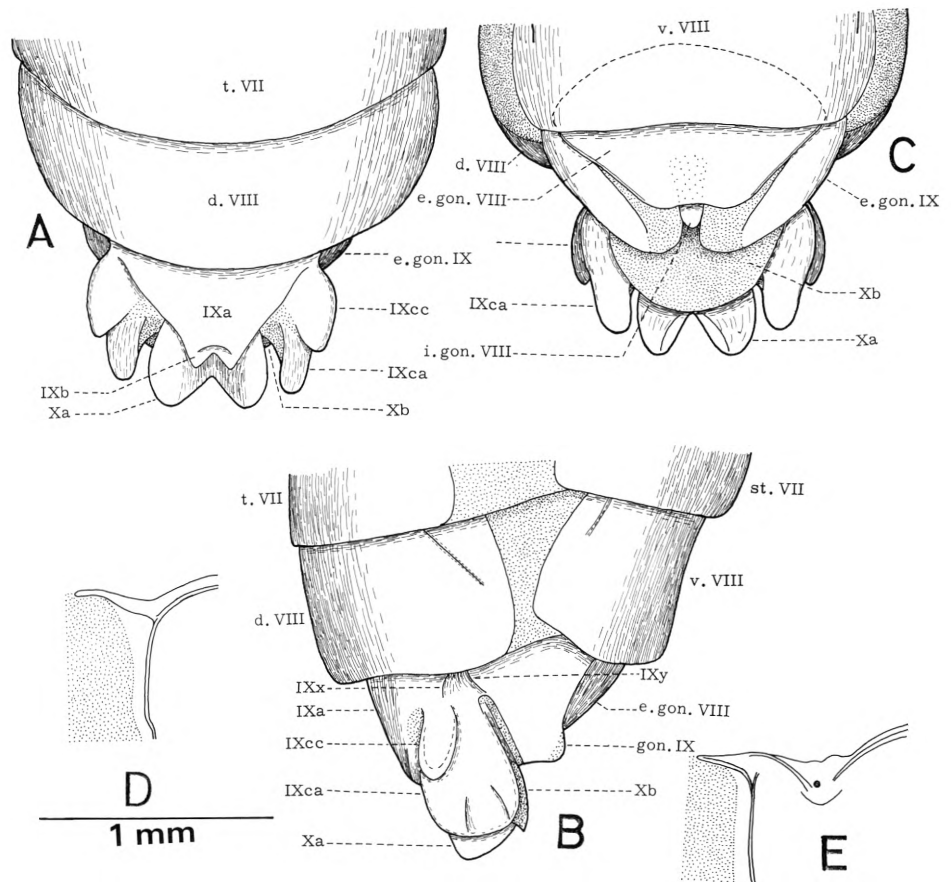
I have been unable to find the muscle $gchm$ and feel rather certain that it does not exist.

Sericostoma personatum Kirby & Spence (*S. pedemontanum* McL.)

There is some difference of opinion as to whether *S. pedemontanum* McL. is a valid species. The alleged specific characters probably is dependent on the functional state of the maxillary palp, which is a male scent organ (W. Müller 1887, Cummings 1914, Crichton 1957).

Pregenital segments. On the terga the middle of the antecostal suture is bent forward in an unpaired curve. Here the acrotergite therefore is very narrow, as the acrotergite generally is in Trichoptera, whereas its more lateral parts are unusually broad (fig. 50 D). The lateral, broader part of the acrotergite, including the extension of the anterior corner, is darker than the rest of

Fig. 50. *Sericostoma personatum*. Posterior end of abdomen in a dorsal view (A), as seen from the right side (B) and in a ventral view (C). D: Left anterior corner of tergum V. E: Right anterior corner of sternum V.



the tergum and densely covered with small sensilla campaniformia. At the base of the extension one or two larger sensilla campaniformia. Small, close-set sensilla campaniformia are also seen on the anterior part of the tergum laterally to the longitudinal suture.

On sternum V the antecosta is interrupted in front of the opening of the gland of this segment (fig. 50 E), and the two ends of the interruption are bent backward, flanking this opening, behind which a short and much narrower suture is seen. The latter is bent in a curve with anterior concavity.

The anterior end of the sternal longitudinal suture (fig. 50 E) is divided into two much weaker, strongly diverging branches, a quite

short mesal one and a longer lateral one, which together with the antecostal suture delimit an area roughly in the shape of an obtuse-angled triangle. This area has the same structure (sensilla campaniformia) and colour as the broad part of the acrotergite and, like the latter, proceeds onto the extension of the anterior corner. The antecostal suture is far from reaching the apex of this extension, the lateral branch of the longitudinal suture proceeds along its posterior margin. Mesally on the triangular area there is a larger sensillum campaniformium. That part of the sternum which lies laterally to the longitudinal suture is narrower than the corresponding part of the tergum, especially on the posterior segments.

On sternum VII the two branches of the longitudinal suture diverge so much that they together form a curve with anterior concavity. The dark area with sensilla campaniformia is lenticular.

Segment VIII (fig. 50 A–C) differs only a little from the pregenital segments. The tergum is broader than tergum VII, and since the lateral margin of the sternum is ascendent, its posterior corner approaches, but does not reach, the lateral margin of the tergum. The lateral longitudinal suture is still more divergent than on tergum VII, forming an angle of 45° with the longitudinal axis, and extends only to the middle of the segment. On the sternum the lateral longitudinal suture is much weaker than on the preceding segments and does not reach the middle of the segment. Its branches, however, delimiting the area with sensilla campaniformia, which as on segment VII is lenticular, are more strongly developed than on the preceding segments; In fig. 50 B, C they are concealed by the overlapping posterior margin of segment VII.

There is no spiracle on segment VIII.

Segments IX and X and the gonopods, (figs. 50 A–C, 51, 52 A, C). These two segments are so firmly united that the boundary cannot be stated with certainty. The combined segment, which is sclerotized to its greatest extent, is considerably narrower than segment VIII and has a rather elaborate shape. On the dorsal side a roughly triangular, antero-mesal area (IXa) is bounded by a distinct declivity which, however, does not quite reach the anterior end of the segment. The narrower hind end of this area is divided into a pair of small processes (IXb). From the indentation between the latter an unpaired apodeme arises.

Laterally to the declivity which forms the posterior boundary of the area IXa there is a large process (IXc), divided into a broader, but shorter and lower antero-dorsal branch (IXcc) and a narrower, but longer and higher postero-ventral branch (IXca). Part of the mesal side of

IXc is membranous. The lateral side of IXcc is flat and shining, forming a "mirror", the posterior and ventral sides of which project as a thin lamella.

Behind the area IXa a large bilobed process (Xa) is seen. Its dorsal side is trough-like, angular in a cross section. Basally its ventral side is connected with the tongue Xb. The latter, which forms the upper lip to the genital opening, is semicircular to short-parabolic. It does not project so far backward as the process Xa, but is considerably broader. Its wall is thin and hyaloid, but nevertheless the tongue apparently is stiff. The posterior and lateral margins are sharp. The tongue practically has no dorsal side. Posteriorly it, as mentioned, is continuous with the ventral side of the process Xa, anterolaterally with the ventral side of the process IXc. It is separated from the latter by a fine furrow, which is sclerotized.

The lateral side of the combined segment is largely occupied by a roughly trapezoidal sclerite (e.gon.IX). The narrower posterior end of this sclerite, however, covers only partly the lateral side of a large and otherwise membranous process, which forms the lateral boundary of the genital opening. In a ventral view this process is strongly convergent in a posterior direction, but the two processes, right and left, does not quite reach each other. They are separated from the tongue Xb by narrow clefts, which in an anterior direction extend to the bases of the processes IXc. In front of this process the sclerite is continuous with the area IXa, though separated from the latter by a deep depression, bounded by sharp edges (IXx and IXy). In front (in fig 50 B concealed by the overlapping hind margin of tergum VIII) this depression narrows to a longitudinal suture, which at the anterior end of the segment bends mesally and continues as an antecostal suture along the front margin of the area IXa. Ventrally to the suture the dorsal part of the sclerite e.gon.IX proceeds as a narrow strip to the

anterior end of the segment; otherwise it is rather widely separated from the latter.

Ventrally to the combined segment (IX + X), narrower than the latter and not projecting nearly as far backward, there is an unpaired sclerite (e.gon.VIII), which for half its length is covered by the overlapping posterior margin of sternum VIII. Its front margin is strongly convex, its lateral sides, along which there are faint sutures, converge about 45° in a posterior direction; the narrow and slightly concave hind margin forms a lower lip of the genital opening. In the middle of the anterior margin there is a reinforcement. On the postero-mesal part of the sclerite a small, unpaired, paler and possibly more feebly sclerotized area is seen.

The process Xa, together with the posterior part of the area IXa, can be bent downward to a vertical position. In this movement the tongue Xb of course takes part, an efficient closure of the genital opening thus being obtained.

As mentioned in the Introduction (p. 16) the structures e.gon.VIII and e.gon.IX (the latter including the membranous parts bordering the genital opening laterally) probably represent parts of the gonopods of segments VIII and IX, resp., though the VIII-IX musculature proves that the anterior end of e.gon.IX must belong to segment IX itself. The posterior attachment of one of the IX-X muscles suggests that the mesal part of the declivity bordering the area IXa is the boundary between segments IX and X. The tongue Xb, which is situated above (from a topographical point of view: behind) the anus (see below: the genital chamber), of course also belongs to segment X. A comparison with *Limnephilus* (p. 158), however, suggests that the process IXc belongs to segment IX.

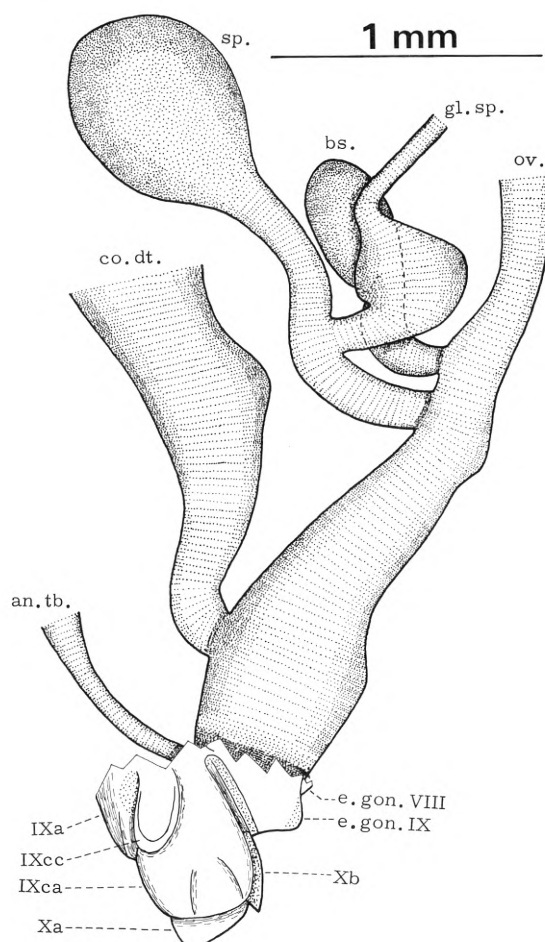
There are one or two large sensilla campaniformia at the anterior corner of e.gon.VIII and some few small ones on the posterior end of IXa, but otherwise the structures IXa, IXb, IXcc, e.gon.VIII and Xb are devoid of sensilla. The lateral side of IXca and the dorsal side of Xb

have a dense clothing of small setae, and in one specimen a large seta was seen on the left side at the base of IXca.

The genital chamber (fig. 51) is very long and has a very complex structure. A long and slender anterior section and a thicker, but only half as long, posterior section may be distinguished. In the foremost part of the posterior section the ventral wall is somewhat descendent.

The anterior half of the spermathecal sclerite (fig. 53), which covers the whole width of the dorsal side, is roughly semi-elliptical with a

Fig. 51. *Sericostoma personatum*. The genital chamber etc. as seen from the right side.



rounded anterior end. The posterior half tapers with concave lateral sides.

The extreme anterior end of the sclerite is concave in a transverse direction. Here the opening of the ductus bursae is found as a kidney-shaped "window". The anterior side of the "frame" of the latter actually is a sclerotization in the most proximal part of the ductus bursae seen from the edge. Behind the opening of this duct the sclerite for almost its whole width bulges into the lumen of the genital chamber as a low processus spermathecae. This transverse convexity of the dorsal wall proceeds beyond the broad anterior part of the spermathecal sclerite, but here it is only partly covered by the posterior, narrow part of this sclerite.

Behind the opening of the ductus bursae and extending a little onto the posterior, narrow part of the sclerite, there is an unpaired longitudinal ridge, which is composed of three successive and, so to speak, superimposed parts. The foremost and longest one (pr.sp.a) is broader in front and narrows somewhat in a posterior direction. In a lateral view the ventral surface of its anterior end bends upward in an even curve to the opening of the ductus bursae. The next part (pr.sp.b) is flat and constricted at the base. In a ventral view it is pear-shaped; its narrower anterior end arises from the posterior part of the first section. The last and smallest section (pr. sp.c) is a triangular, flattened tooth, which arises from the the ventral surface of the middle section, near its posterior end. This tooth is thin-walled and hyaloid, but apparently stiff and possibly sclerotized, at least to some degree. Centrally in the middle of pr.sp.b (i.e.at the boundary between the latter and pr.sp.c) an egg-shaped membranous area is seen, in the anterior end of which the small opening of the ductus spermathecae is situated.

The anterior, broader part of the spermathecal sclerite is continuous with a sclerite on the lateral wall of the genital chamber (fig. 52). In front, flanking the opening of the ductus bur-

sae, the transition between the spermathecal sclerite and the lateral sclerite is gradual, behind this opening the lateral sclerite is separated from the spermathecal sclerite by a sharp furrow. In front the lateral sclerite is only narrow; its ventral margin is descendent, so that the posterior end of the sclerite covers the whole lateral side of the genital chamber. For a little more than half its length the lateral sclerite is produced into a flat, backward directed tongue (sp.scl.b).

Another fold (a.v.i.gon.IX) extends between sp.scl.b and the hind end of the slender anterior part of the genital chamber, i.e. for almost half the length of the genital chamber. This fold covers the greater, dorsal part of the lateral side of the genital chamber. It is approximately semicircular in a transverse section. The right and the left fold occupy about half the width of the genital chamber, more in front, less behind. Quite in front, however, a.v.i.gon.IX gradually becomes lower and narrower.

The ventro-anterior end of a.v.i.gon.IX is overlapped by sp.scl.b. The latter fold has a shallow, backward facing ginglymus, which forms a simple articulation with a condylus on a.v.i.gon.IX (fig. 52 B). At the rear the fold a.v.i.gon.IX ends abruptly. Its about 45° ascendent posterior end forms a shallow ginglymus for the fold m.v.i.gon.IX, described below.

On the lateral sides of the posterior, wide part of the genital chamber two successive pairs of broad, but flat folds lie. The anterior one is more than 45° descendent, a little broader dorsally than ventrally and entirely covered by a sclerite (m.v.i.gon.IX), the dorso-anterior corner of which is a condylus, conforming to the ginglymus on the posterior end of the fold a.v.i.gon.IX. The slightly concave dorsal margin of the posterior fold (p.v.i.gon.IX) is considerably less than 45° descendent, this fold being roughly triangular. Antero-ventrally it has a membranous area, but is otherwise covered by a sclerite with parallel sides, the ventro-anterior

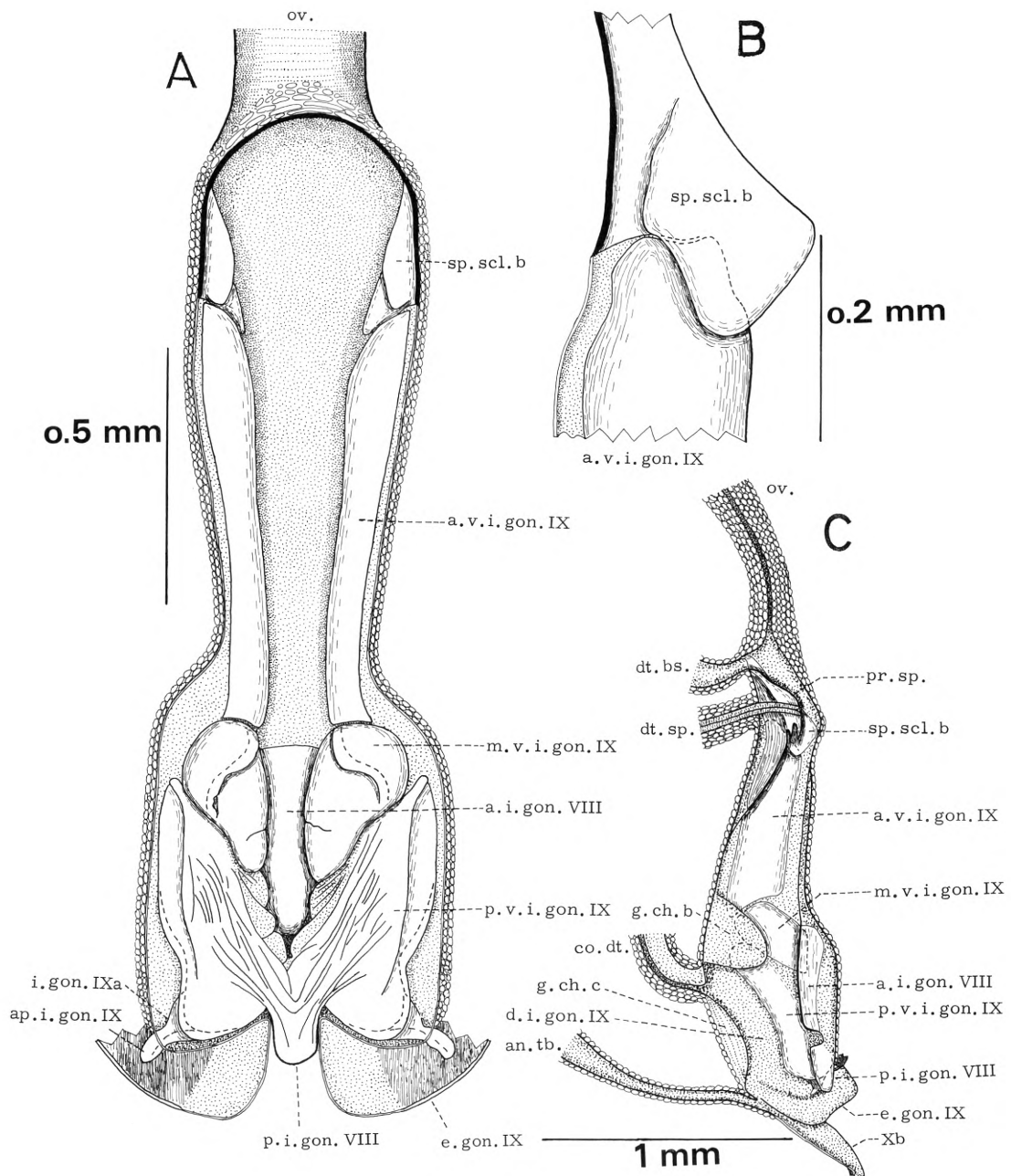


Fig. 52. *Sericostoma personatum*. A: Floor of the genital chamber in a dorsal view. B: Articulation between the spermathecal sclerite and gonopod IX; left side as seen from the mesal side. C: Sagittal section through the genital chamber; left side as seen from the inside.

margin of which, near its upper end, forms a simple articulation with the sclerite on m.v.i.gon. IX. Ventrally to this articulation the boundary between sclerite and membrane is indistinct. Both the membranous and the sclerotized part

of the fold p.v.i.gon.IX, except for the dorso-posterior part of the sclerite, are provided with fine, irregular, descendent ridges.

Ventrally both the anterior (m.v.i.gon.IX) and the posterior fold (p.v.i.gon.IX) overlap the floor of the genital chamber a little. Also, a little more than the posterior half of the dorsal margin, as well as the posterior end, of the sclerite on p.v.i.gon.IX overlaps the lateral wall a little. At the dorso-posterior corner the reflected margin of the sclerite is continuous with a small, outward and backward directed sclerite (fig. 52 A, i.gon.IXa), the distal end of which (ap.i.gon.IX) is apodemal.

Behind the tongue sp.scl.b the middle of the floor of the genital chamber gradually rises into an unpaired longitudinal fold. For less than its posterior half, where it is rather high (since the ventral wall of the genital chamber for a short distance is descendent), the fold is sclerotized (a.i.gon.VIII); its anterior part is membranous. The sclerite m.v.i.gon.IX and the membranous part of the fold p.v.i.gon.IX overlap the lateral parts of a.i.gon.VIII, with which m.v.i.gon.IX forms a simple articulation. A system of levers, sp.scl.b – a.v.i.gon.IX – m.v.i.gon.IX – a.i.gon.VIII, thus is formed; p.i.gon.IX, too, is involved in this system.

The posterior end of a.i.gon.VIII descends abruptly and is by an, in the bottom membranous, furrow separated from the structure p.i.gon.VIII. The latter is unpaired and spout-like, and its posterior end projects a little beyond the ventral lip of the genital chamber, between the two processes e.gon.IX (fig. 50 C). The nearly horizontal, though in a transverse section slightly concave, dorsal side is continuous with the sclerite on p.v.i.gon.IX, the wrinkles of which proceed onto the spout (fig. 52 A). The ventro-posterior corner of p.v.i.gon.IX, however, is overlapped by the posterior end of p.i.gon.VIII, and the right and the left sclerite on p.v.gon.IX are continuous behind the base of the posterior end of p.i.gon.VIII. The latter of

course also belongs to the system of levers mentioned above.

From the dorsal part of the cushion-like mesal side of the process e.gon.IX a low, membranous fold (d.i.gon.IX) proceeds forward for some distance on the lateral wall of the genital chamber, above the fold p.v.i.gon.IX.

The opening of the colleterial duct has a rather posterior position on the dorsal wall of the genital chamber. Just in front of the opening there is a pair of plump, membranous processes (fig. 52 C, g.ch.b). The length of the process is about half the height of the lumen of the genital chamber, and the right and the left process are far from touching each other.

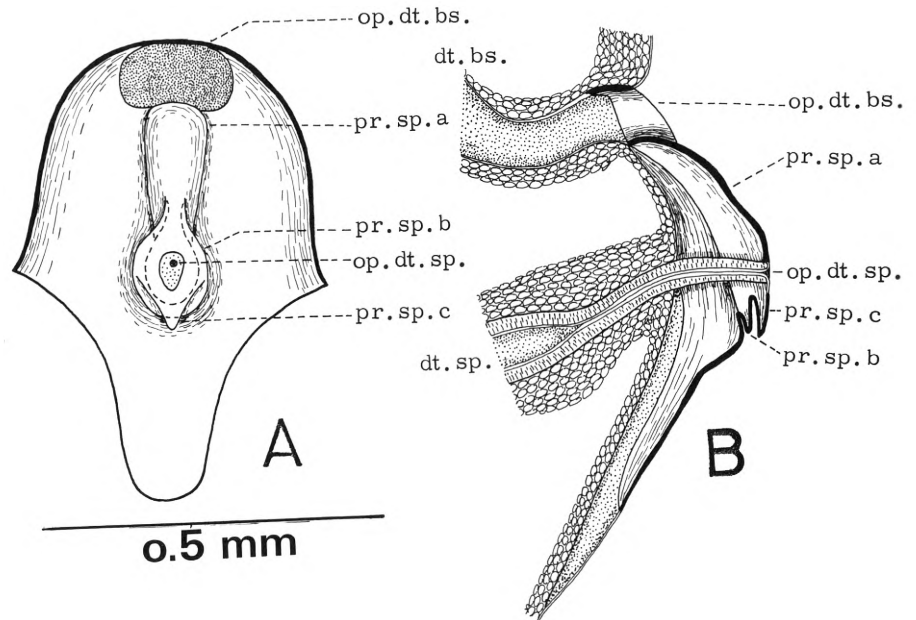
Behind the opening of the colleterial duct the dorsal wall bulges into the lumen as a short and low fold (g.ch.c), which is partly bisected by a narrow longitudinal cleft. Behind this fold, again, the anus is found between the two processes e.gon.IX. Since, however, the “mouth angle” of the genital chamber extends as far forward as does the margin of Xb, it is doubtful whether the genital chamber truly can be called a cloaca.

The bursa copulatrix (fig. 51) is a rather small, elongate sac. As compared with conditions in other Trichoptera its epithelium is thick. The duct, short and relatively thick, is bent downward, so that its proximal end is vertical. It has a wide lumen and a thin cuticle.

The spermatheca (fig. 51) is larger than the bursa copulatrix, but still, as compared with conditions in most other Trichoptera, small. The size of the pear-shaped sac, however, varied much in my preparations, and the same did the thickness of the epithelium, which in some specimens was much greater than in other Trichoptera.

The ductus spermathecae is rather short, but thick. The width of the lumen is only a fraction of the thickness of the duct. The glandula spermathecae opens a little proximally to the middle. Just proximally to this opening the anterior (or ventral) wall of the duct forms a

Fig. 53. *Sericostoma personatum*. A: Processus spermathecae in a ventral view. B: Sagittal section through the processus spermathecae; left side as seen from the inside.



thin, distally directed valve. The duct has a thin cuticle, a thick epithelium and a strong circular musculature. Distally the latter is thinner than the epithelium, proximally much thicker. A little beyond the opening of the gland, in a proximal direction, the width of the lumen decreases rather abruptly and very strongly, so that it in the most proximal part of the duct is extremely narrow; the thickness of the epithelium, however, remains the same.

The most proximal part of the glandula spermathecae is rather thick, and subproximally the gland widens rather much into a short, fusiform reservoir, as also noted by Unzicker (1968). Distally to the latter the gland is very long and thin and for the greater part of its length coiled up into a mass, the size of which is approximately the same as that of the spermatheca shown in fig. 51. In that part of the gland which lies proximally to the reservoir the histological structure is the same as in the spermathecal duct, though the epithelium is a little thinner. In the reservoir and in the distal part of the gland, the epithelium again is only half as thick so that, in

the distal part of the gland, the lumen occupies almost half the width of the gland. The latter is provided with a circular musculature which, however, is very thin in the distal part; it is thicker in the reservoir, and in the most proximal part of the gland it is thicker than the epithelium.

The colleterial glands. Each gland is divided into four tube-like lobes, three of which have a smooth wall, whereas the wall of the fourth and thickest one is finely longitudinally wrinkled. It seems a reasonable assumption that the three former are the true gland, and the latter is a reservoir. Two of the smooth tubes, a dorsal and a ventral one, are directed forward, the third backward. Laterally (and at the origin ventrally) to the latter the fourth tube, the possible reservoir, lies. Quite proximally it is directed outward and a little forward, in its further course it is S-like bent; at first upward, than in a sharp curve downward and backward, and eventually in a smoother curve forward. The posterior one of the smooth tubes is encompassed by the last mentioned curve.

The colleterial duct no doubt is one of the most elaborate ducts in the animal kingdom: its proximal half has an extremely complicated structure (fig. 54), the significance of which is a mystery to me. In the most proximal (or posterior) downward bent and thinner part of the duct there is a ventral longitudinal fold (a), which almost obstructs the lumen, so that the small opening of the duct is U-shaped. Farther forward (or distally), where the duct widens, there is a pair of mesally directed, thin folds (b) with rather sharp edges. In front they are quite low and arise almost in the middle of the ventral side, in a posterior direction they become higher and their bases shifted to a lateroventral posi-

tion. For their anterior two thirds the left and the right fold almost, but not quite, touch each other, in the posterior third they recede from each other, the folds again becoming lower. Their quite low posterior ends, flanking the anterior end of the fold a, are sclerotized, and mesally the sclerite extends for more than three fourths of the length, in front indistinctly delimited.

Above the folds b a pair of quite low, downward and outward directed folds (c) is seen latero-dorsally on the wall of the duct. The interval between these folds, on the dorsal side of the duct, is occupied by two rows of tongue-like, transverse lamellae (d), which to their

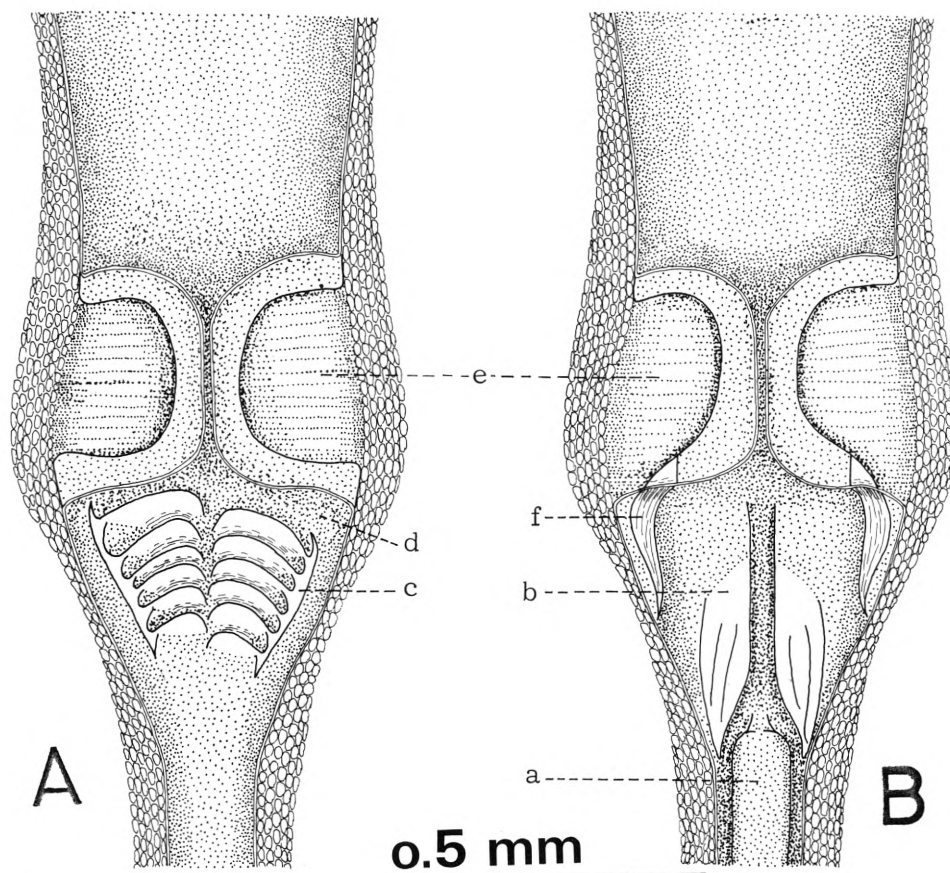


Fig. 54. *Sericostoma personatum*. Middle part of the colleterial duct. A: Dorsal wall as seen from the inside. B: Ventral wall as seen from the inside.

greater extent are sclerotized. Laterally their sclerites are connected with the mesal bases of the folds *c* by narrow bridges. In their natural position, inclined somewhat forward, these lamellae fill less than half the lumen of the duct.

Finally there is, in front of the structures *b*, *c*, and *d*, a pair of large, cushion-like, internal bulges (*e*) of the lateral walls of the duct, which almost entirely obstructs its lumen. Though colourless, they apparently are stiff. Just behind *e* a small, latero-ventral, rod-like sclerite (*f*) is seen. Its broader anterior end lies in the bottom of the furrow between *e* and the ventral side of the duct.

The circular musculature of the duct of course does not follow the structures described above.

Musculature. There is an almost unbroken layer of external ventral VII–VIII muscle bands which, however, is divided into a mesal and a much smaller lateral portion. The former converges slightly in a posterior direction, so that the distance between the right and the left muscle at the hind end is only half as great as at the front end. The anterior attachment of the lateral portion is rather far removed from the anterior margin of sternum VII. It diverges a little in a posterior direction, so that it at the hind end is distinctly separated from the mesal portion, whereas this is not the case at the front end. The last mentioned muscle, the lateral portion, may be *vm*₆. Other ventral muscles were not seen.

In segment VIII the dorso-ventral muscles *dvm*₁, *dvm*₂ and *dvm*₄ are found, but *dvm*₃ was not seen.

There are three VIII–IX muscles, which I have interpreted as *dm*₁ and *dm*₄, the latter divided into two portions, which is also sometimes the case in pregenital segments (p. 11). The first mentioned muscle is a couple of strong bands, which originate on about the mesal half of the antecosta of tergum VIII and are inserted to a little more than the lateral half of the dorsal

antecosta of segment IX. The muscle *dm*_{4a}, composed of numerous fine muscle bands, originates on about the lateral half of the antecosta on tergum VIII and are inserted to the sclerite *e.gon*.IX (fig. 50 B, C). The muscle *dm*_{4b} is superficial to *dm*_{4a}. The narrow muscle originates on the antecosta of tergum VIII, externally to the middle of *dm*₁, and is inserted quite laterally to the dorsal antecosta of segment IX.

The musculature of the gonopods is extremely complicated, and the following explanation must be considered quite tentative. There are three *gonm*₁ muscles. A mesal and a lateral muscle originate on the antecosta of sternum VIII and are inserted to the anterior margin of the sclerite *e.gon*.VIII (fig. 50 C). The mesal muscle has an unpaired anterior attachment and diverges in a posterior direction. The third muscle has an oblique course between the two first mentioned. It is much broader than the lateral of these, the anterior attachment of which it partly cover in a dorsal view.

There are two *gonm*₂ muscles. One is flat and originates near, but not on, the dorsal antecosta of segment IX along an ascendent line forming an angle of about 45° with the antecosta. It goes downward and backward and is inserted to the posterior part of the sclerite *e.gon*.VIII, flanking the more weakly sclerotized indentation. The other, narrower, but thicker muscle originates at the anterior corner of the area IXa (fig. 50 A). It, too, goes downward and backward and is inserted rather laterally to the sclerite *e.gon*.VIII (fig. 50 C).

The rather strong muscle *gonm*₃ originates mesally on the posterior part of the area IXa (fig. 50 A) and is inserted to the latero-posterior corner of the sclerite *p.v.i.gon*.IX (fig. 52 A, C).

A slender muscle which originates on the sclerite *e.gon*.VIII, behind the last mentioned of the two muscles *gonm*₂, and is inserted near the anterior end of *m.v.i.gon*.IX, I have been unable to try to homologize.

The sclerite *e.gon*.VIII is crossed by a very

complex transverse musculature, the bands of which in part are intertwined with those of the muscles gonm₁.

There are two IX-X muscles. One, rather strong, originates approximately in the middle of each half of the area IXa and is inserted to an unpaired apodeme issued between the two processes IXb. The other is composed of fine, transverse muscle bands, which originate approximately on the middle of each half of the latero-posterior margin of the area IXa. They are inserted latero-dorsally to the hindmost part of the anal tube.

The slender muscle gchm originates on the anterior corner of sternum VIII and is inserted to the front end of the spermathecal sclerite. The genital chamber has the usual circular musculature. Inside the latter, i.e. closer to the wall of the chamber, there is a longitudinal musculature in the fold g.ch.c.

Beraea maurus Curt.

The *pregenital segments* (fig. 55) deviate somewhat from the usual picture in Trichoptera. For almost its entire length, to and including segment VIII, the abdomen is approximately equal both in width and height. The sclerites are very well defined.

On the terga, except the foremost ones, the anterior margin is deeply indented for almost its whole width, deepest, and very deep, on the middle segments. The indentation, however, is entirely covered by the much overlapping posterior margin of the preceding segment. The extension of the anterior corner, at the point of bending of the antecosta, is separated from the rest of the front margin by a small, rounded indentation. The extension, like the most closely adjacent parts of the tergum, is darker and covered with small sensilla campaniformia. Similar sensilla, though more scattered, are found also on the rest of the acrotergite, except on its mesal part, which rather appear as an indistinct

extension of the antecostal suture. On the anterior terga an unpaired mesal longitudinal suture is slightly indicated.

The anterior margins of the sterna are straight.

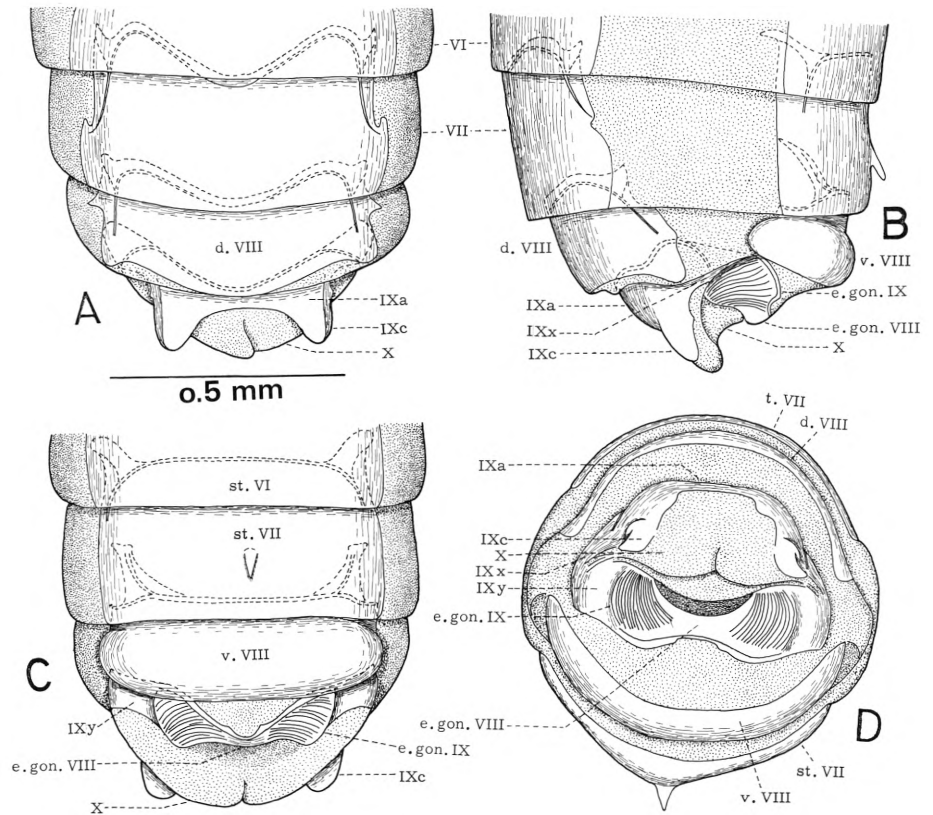
On sternum V the antecostal suture appears to make a bend behind the small opening of the gland (fig. 56 A), so that it might seem that the latter is situated on the acrosternite. However, in almost the mesal half of the area with the opening there is a suture as a direct continuation of the antecostal suture. From a morphological point of view it probably is most correct to say that the antecostal suture is interrupted in front of the gland opening, and that the curved suture behind the latter, continuing in the lateral longitudinal suture, is a secondary structure. Also, the roughly triangular area with the gland opening is devoid of sensilla campaniformia.

Sternum VII carries, a little behind the middle, an unpaired, strong, sagittally compressed tooth.

Segment VIII is much shorter, but scarcely narrower and only a little lower than segment VII. Like the pregenital segments it has a separate tergum and sternum. The former does not deviate much from the preceding terga. In front it is a little broader than tergum VII, and in a posterior direction the width increases. Hence the lateral longitudinal suture for its whole length is parallel to the lateral margin. The posterior margin has a pair of broad, but shallow indentations, the hind corners thus being produced into tongues. Along the posterior margin, and across the bases of these tongues, a fringe of strong setae is seen.

The sternum is more deviating. In front it is a little broader than sternum VII. The tongue at the anterior corner is directed almost straight forward and, as will appear from fig. 55 C, of another shape than on the preceding sterna. Moreover, it issues a little mesally to the anterior corner. Laterally the antecostal suture divides into two branches. One runs to the anterior

Fig. 55. *Beraea maurus*. Posterior end of abdomen in a dorsal view (A), as seen from the right side (B), in a ventral view (C) and in a posterior view (D).



corner of the sternum, the other approximately in the middle of the tongue. There is no lateral longitudinal suture on sternum VIII.

The posterior part of this sternum is very much vaulted in a longitudinal direction (fig. 55 B). It is broader, too, than the anterior part, with strongly convex sides (fig. 55 C) and densely covered with very strong setae. Half or more of the non-vaulted part is overlapped by the posterior margin of segment VII.

Segments IX and X and the gonopods. Together these two segments (fig. 55) are much narrower and somewhat lower than, but just as long as segment VIII. The combined segment forms an approximately semicircular, much descendent tongue, which is somewhat vaulted in a longitudinal direction. It is rather thick, but has a thin, though rounded posterior margin. It carries a

dorsal sclerite (IXa), which reaches the anterior end, but otherwise is separated from the margin of the tongue by membranous areas (see, however, below). The anterior margin of the sclerite is indented to the same degree as tergum VIII, but there is no tongue at the anterior corner, or rather, here the sclerite is continuous with the structure e.gon.IX as described below.

The posterior margin of the sclerite IXa has a broad and very deep indentation, especially conspicuous when seen from behind (fig. 55 D). The posterior corners of this indentation project beyond the margin of the tongue as a pair of free processes (IXc) which are sclerotized on the ventral sides too: the apices of these processes, however, do not project as far backward as the membranous middle of the tongue. In a cross section they are roughly triangular with a latero-

dorsal, a meso-dorsal and a ventral side; the first mentioned one is a little concave.

The sclerite IXa has an antecostal suture. In the middle it runs so close to the anterior margin of the sclerite that an acrotergite must be said to be lacking; laterally it bends backward as a short longitudinal suture.

The posterior, membranous part of the tongue (X) is bisected by a broad horizontal furrow (fig. 55 D). The ventral part, with an ascendent posterior side, forms the upper lip of the genital opening, the "mouth angle" of which is situated approximately at the same level as the base of the process IXc. The dorsal part is again bisected by a narrow, vertical cleft, in the bottom of which the anus is found. The position of the latter, the posterior attachment of the IX-X muscle, and a comparison with *Sericostoma* (pp. 107-08) suggest that the membranous part of the tongue represents segment X.

As to the structures IXx and IXy, see below.

The processes IXc are covered with rather strong setae, the only ones found on segments IX and X. In front of the processes there are numerous small sensilla campaniformia on IXa, in the greatest number mesally to the longitudinal sutures.

The gonopods form a very steeply ascendent lower lip of the genital opening. It is provided with a sclerite, which quite laterally reaches the anterior end, and here is more or less overlapped by the pleural membrane VIII, but otherwise is separated from sternum VIII by a large membranous area (fig. 55 C).

The sclerite has a rather elaborate structure. The middle and narrower (or shorter) part (e.gon.VIII) is smooth. Then a part (e.gon.IX) follows, which is more light-coloured, facing outward and backward, and provided with fine vertical wrinkles. Then again a smooth part (IXy) which is concave. In a lateral view (fig. 55 B) the latter is concealed by the most lateral, outward facing part (IXx), which is strongly convex, situated immediately laterally to the

longitudinal suture of segment IX and continuous with the sclerite IXa.

In front (or below) the middle part (e.gon.VIII) and the adjacent wrinkled parts (e.gon.IX) the sclerite has a reinforcement. It is strongest, stronger than any other suture on the abdomen, in front of e.gon.IX. The areas e.gon.VIII and e.gon.IX border the genital opening ventrally.

The muscles of the gonopods (p. 177) prove that the areas IXx and IXy belong to segment IX itself, the rest of the ventral sclerite to the gonopods, the wrinkled area (e.gon.IX) probably to gonopod IX.

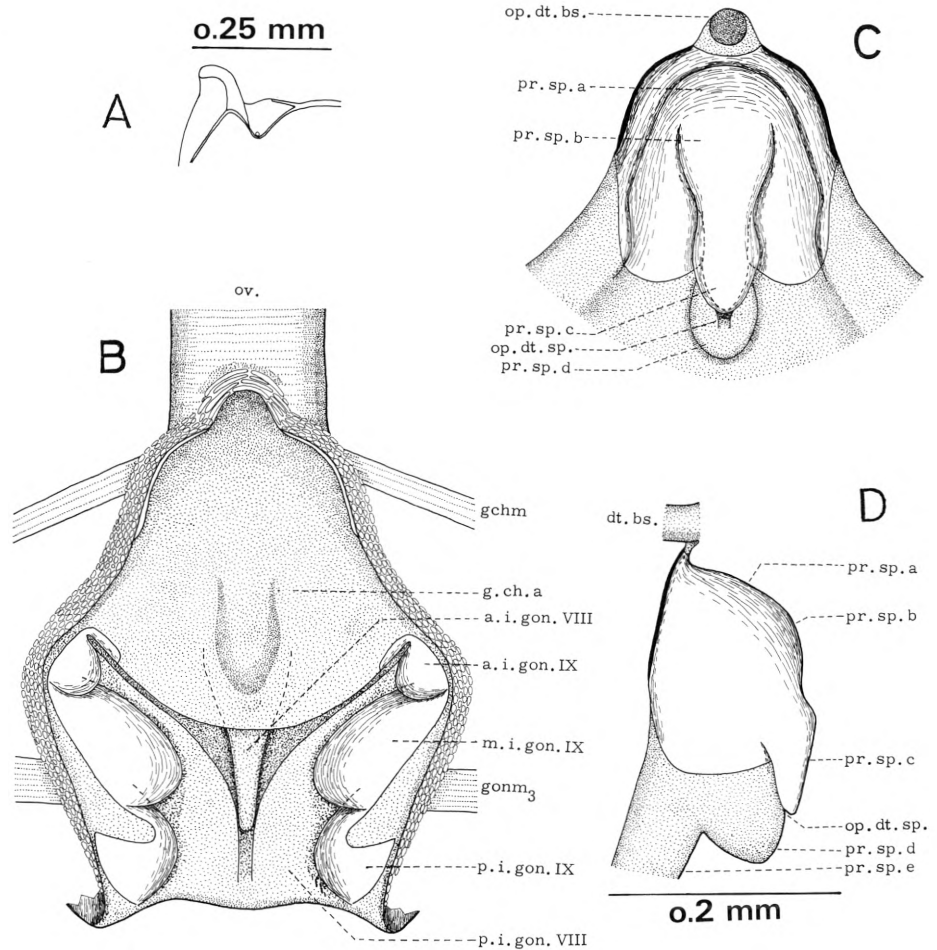
The gonopods are devoid of sensilla.

The genital chamber (fig. 56 B) is short and thick, thickest in the middle. It extends to a little behind the middle of segment VII. The ventral side is more than 45° ascendent, but in the following description it is thought to be horizontal.

The narrower anterior end of the spermathecal sclerite (fig. 56 C) has a shallow indentation, shortly in front of which the circular opening of the ductus bursae is found. The broader posterior margin of the sclerite is produced into a pair of tongue-like extensions. The greater middle and posterior part of the sclerite bulges into the lumen as an in a transverse section approximately semicircular processus spermathecae (fig. 56 C, D, pr.sp. a-d). The anterior end of the latter bends upward in an even curve. The bulge proceeds behind the sclerite as a membranous fold (pr.sp.e), which gradually becomes broader and less distinct. The postero-mesal part of this fold is developed as a lip below (or in front of) the opening of the colleterial duct, which is situated at the point where the genital chamber is broadest.

For the greater, posterior part of its length the processus spermathecae has again an unpaired longitudinal ridge (pr.sp.b-c), the shape of which will appear from fig. 56 C. At the rear the base of this ridge is somewhat constricted, and

Fig. 56. *Beraea maurus*. Right anterior corner of sternum V. B: Floor of the genital chamber in a dorsal view. C: Processus spermathecae in a ventral view. D: Same as seen from the right side.



its posterior end projects as a parabolic, dorsally somewhat concave process (pr.sp.c). Above the latter there is a blunt membranous process (pr.sp.d), which projects farther backward. The opening of the ductus spermathecae is situated basally on the ventral side of pr.sp.d.

In front of the posterior extensions mentioned above the spermathecal sclerite bends downward upon the lateral wall of the genital chamber.

At the broadest point of the genital chamber the ventral wall bulges, for its whole width, into

the lumen as a short, backward directed tongue (fig. 56 B, g.ch.a), a depression on the dorsal side of which receives pr.sp.c.

On the lateral wall of the genital chamber, behind the base of g.ch.a, there is a largely sclerotized longitudinal fold (i.gon.IX), which by approximately vertical, sharp furrows is divided into three rounded processes, the anterior one being the smallest, the middle one the largest. The anterior process (a.i.gon.IX) overlaps the base of the middle process (m.i.gon.IX) a little, and the latter again overlaps the posterior pro-

cess (p.i.gon.IX) a little. The two folds i.gon.IX are very far from reaching each other in the middle of the genital chamber.

On the ventral wall of the genital chamber, between the two folds i.gon.IX, there is a pair of low, membranous folds (p.i.gon.VIII). At the rear the right and the left fold are separated only by a short distance, in an anterior direction their mesal margins diverge, eventually running close to the margin of the tongue g.ch.a. The narrower posterior end of a shorter, unpaired, ventral, membranous fold (a.i.gon.VIII; its somewhat broader anterior end is covered by the tongue g.ch.a) is wedged in between the anterior ends of the two folds p.i.gon.VIII.

In front the base of the process a.i.gon.IX is continuous with the fold p.i.gon.VIII, which is sclerotized at its extreme anterior end. This sclerite is again continuous with a small sclerite lying quite laterally on the tongue g.ch.a.

Behind the opening of the colleterial duct the dorsal wall of the genital chamber bulges into the lumen as a broad, unpaired membranous fold.

The ductus bursae has a wide lumen.

The spermatheca is an approximately spherical sac. At the internal opening of the spermathecal duct there is a black, sclerotized ring, the diameter of which is much greater than the width of the lumen of the duct. It is clothed with distally (i.e. toward the spermatheca) directed microtrichia, forming a sort of "fish trap".

In the slide preparations made by me the proximal half of the spermatheca contained a "spermatophore", whereas the distal part was more or less collapsed.

The ductus spermathecae is short and built as in *Sericostoma* (p. 111). The glandula spermathecae, however, the distal part of which is coiled tightly up, is simple, thin and non-muscular (or at least without a strong musculature) to its proximal end, and there is no valve at its opening.

The colleterial glands are, as in *Sericostoma*,

richly branched, but the colleterial duct has a simple structure.

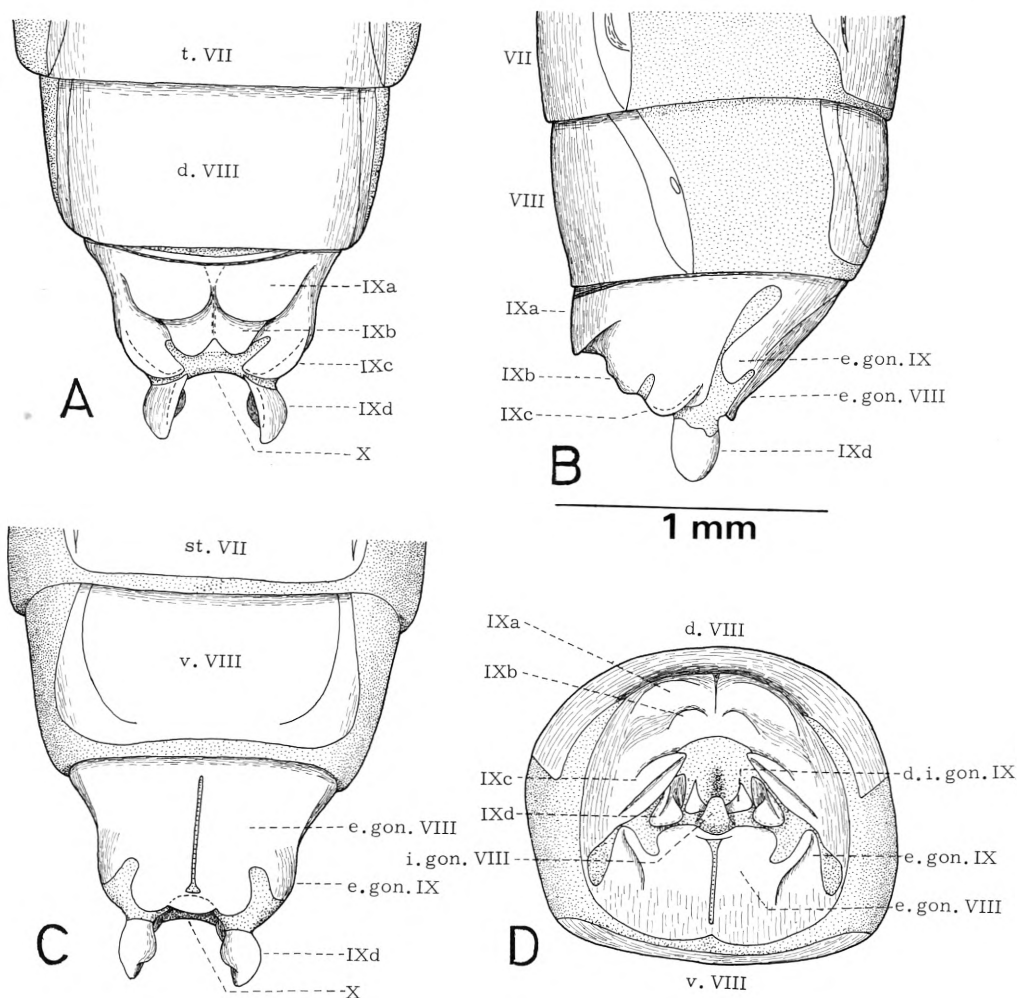
Musculature. The list given below cannot by any means claim to be complete. However, the most important muscles in the genital complex probably are included.

I was unable to decide whether the muscle VIII-IX dm_1 is present or not. The muscle dm_4 , however, is found and as in *Sericostoma* (p. 114) divided into two portions. The most lateral bands (dm_{4b}) are inserted to IXx (fig. 55 D). Moreover, dm_5 is present. It is a rather small muscle, which originates on the posterior end of the longitudinal costa on tergum VIII, and the parallel bands of which go in a mesal and dorsal direction the be inserted to the intersegmental membrane between segments VIII and IX.

There are four muscle gonm, gonm₃ being represented by two muscles. The first mentioned of these, and the muscles gonm₁ and gonm₂ are strong. The muscle gonm₁ is a ventral, longitudinal muscle, which is inserted to the reinforcement of the front margin of e.gon.VIII (fig. 55 C, D). The muscle gonm₂ originates on the anterior margin of IXx, dorsally to the attachment of dm_{4b} , and diverges fan-like toward its insertion laterally, though not quite laterally, on e.gon.VIII (fig. 55, C, D) for most of its length. This muscle is almost vertical. One of the muscles gonm₃ originates on the anterior margin of IXa (fig. 55 A, B), laterally to the longitudinal suture. It goes backward, downward and inward and is inserted to the reinforcement on the anterior margin of e.gon.IX (fig. 55 B-D). The other gonm₃ originates on IXx (fig. 55 D) and is inserted to the fold i.gon.IX (fig. 56 B) on the lateral side of the genital chamber.

There are two IX-X muscles. One is rather strong, originates on IXa (fig. 55 A, B), somewhat behind the antecosta and converges more than 45° in a posterior direction. The right and the left muscle has almost a common insertion on X. The other originates rather laterally on

Fig. 57. *Athripsodes cinereus*. Posterior end of abdomen in a dorsal view (A), as seen from the right side (B), in a ventral view (C) and in a posterior view (D).



IXa, has a vertical course and is inserted to the genital chamber near the "mouth angle".

The muscle gchm originates on tergum VIII (which is unusually; cp. pp. 12 and 26) and is inserted to the anterior end of this part of the spermathecal sclerite which is situated on the lateral wall of the genital chamber (p. 118).

The genital chamber has the usual circular musculature.

Athripsodes cinereus Curt.
(*Leptocerus cinereus* Curt.)

Pre genital segments. The terga are broader than the sterna and more vaulted in a transverse direction. There is no gland on segment V.

Segment VIII (fig. 57) does not deviate much from the preceding segments, though the longitudinal suture both on the tergum and on the sternum is more feeble. In a posterior direction

the sternum becomes a little broader, and the longitudinal suture hence farther removed from the lateral margin, and more so since the hind end of the suture bends in a mesal direction.

Segments IX and X and the gonopods. The segments IX and X are so firmly united that the boundary cannot be stated with any degree of certainty. Together with the gonopods they form a largely sclerotized, subconical structure, on the hind end of which a pair of vertical, spoon- or ear-like lamellae (IXd) is seen flanking the genital opening. These lamellae are sclerotized both on the mesal and lateral sides, but their sclerites have no connection with the sclerite on the rest of the combined segment. The muscle gonm₃ proves that they belong to segment IX itself, reminiscent of conditions in *Apatania* (pp. 180 and 184).

On the dorsal side an anterior, horizontal area (IXa) is delimited by a distinct declivity. In a dorsal view the latter forms two strong curves with posterior convexities, separated by an incision, which proceeds forward as an indistinct, in an anterior direction broader and still more indistinct furrow. The larger area behind the declivity is descendent with an, in a lateral view, sinuous outline. It has a posterior, membranous indentation, the shape of which will appear from fig. 57 A. It forms a thick, but indistinct upper lip of the genital opening; in a dorsal view it has a slightly concave hind margin.

The indentation (X) is surrounded, in front and laterally, by two pairs of low sclerotic bulges (IXb and IXc). The latero-posterior bulge (IXc) is produced into a sharp lamella.

The sclerite of segment IX proceeds, vertically placed, far down on the lateral side, behind more than the dorsal half of the pleural membrane VIII. For its whole width it is provided with an antecosta, which is much stronger than those on the pregenital segments. The acrotergite is rather broad.

The area IXc carries some rather strong setae, and the rest of the sclerite on segment IX is

richly provided with sensilla campaniformia. The lateral side of the process IXd is clothed with setae.

The gonopods form a rather flat plate (e.gon. VIII, e.gon.IX), which largely is sclerotized, though the posterior part of the sclerite by a pair of indentations is divided into an unpaired, broad mesal tongue and a pair of much narrower lateral tongues. The former reaches the posterior margin, the latter do not. The shape of the posterior margin of the mesal tongue varies. The trilobed condition shown in fig. 57 C is in fact a borderline case. In some specimens the posterior margin is evenly concave for its whole width. In the middle it apparently has a lenticular reinforcement, which however, is due to the shining through of a sclerite on the dorsal side of the plate, at the genital opening. The insertion of the muscle gonm₃ proves that the lateral tongues are parts of the gonopods IX.

The sclerite of the gonopods is almost entirely divided into two by a narrow longitudinal membranous stripe, which may reach the anterior margin. It stops shortly in front of the posterior margin with a small triangular extension.

The sclerite of the gonopods is separated from that of segment IX by a membranous area, which is narrow behind, broad in front. Quite in front, however, the two sclerites are continuous.

The gonopods are devoid of sensilla.

The genital chamber (fig. 58 and 59) is very short, its anterior end being situated at the boundary between sternum VIII and the gonopods, but very broad and high, and evenly increasing in thickness in an anterior direction. Its front end is divided into two branches, a thinner ventral one and a thicker dorsal one. The former appears as a continuation of the common oviduct, in the latter the colleterial duct opens, and in a lateral view it appears as a continuation of this duct, though separated from it by a constriction; in a dorsal view it is several times as broad as the colleterial duct and has prominent anterior corners.

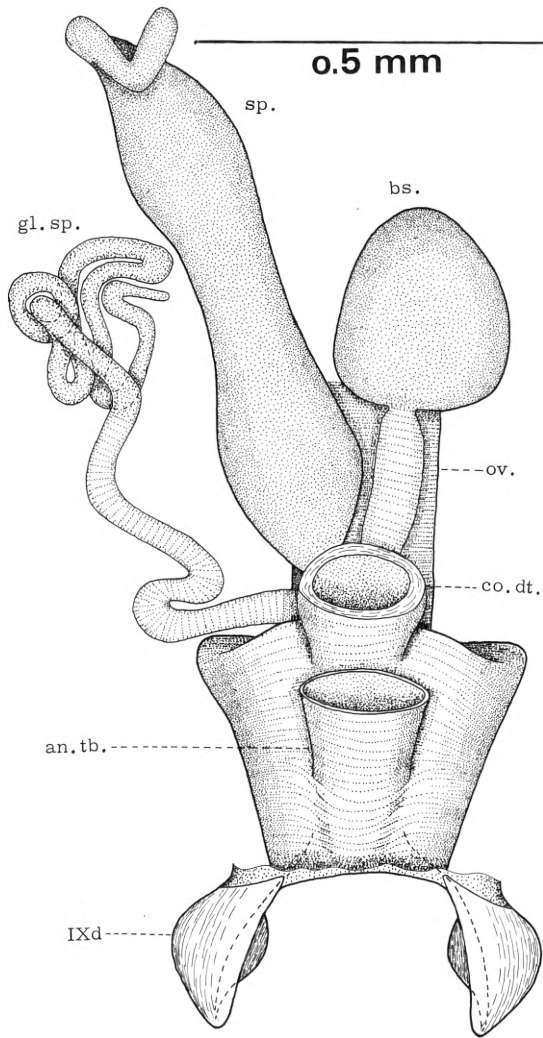


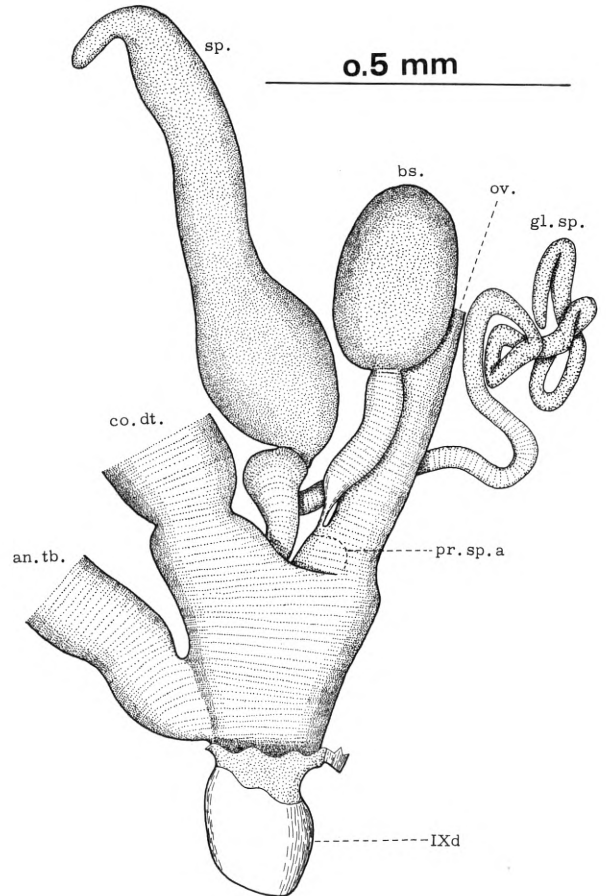
Fig. 58. *Athripsodes cinereus*. The genital chamber etc. in a dorsal view.

The sclerotic lip between the dorsal and the ventral branch of the genital chamber is produced backward, for the anterior two thirds of the genital chamber, as a processus spermathecae (fig. 60). In a dorsal or ventral view the latter has roughly the shape of an equilateral triangle, though with concave lateral sides and a slender, rounded posterior end. The processus is much flattened, but this is obscured by the ridge

mentioned below, as well as by the fact that it is much vaulted in a transverse direction, with a ventral concavity.

The ventral side of the processus spermathecae is continuous with the dorsal side of the sclerotic, funnel-like and likewise much flattened and much transversely vaulted posterior (proximal) part of the ductus bursae. Its anterior corners is produced into a pair of slender extensions, which unite with the dorsal sides of a pair of low sclerotic folds (v.i.gon.IX), situated latero-ventrally on the wall of the genital chamber. The furrows (sp.scl.b) between these folds

Fig. 59. *Athripsodes cinereus*. The genital chamber etc. as seen from the right side.



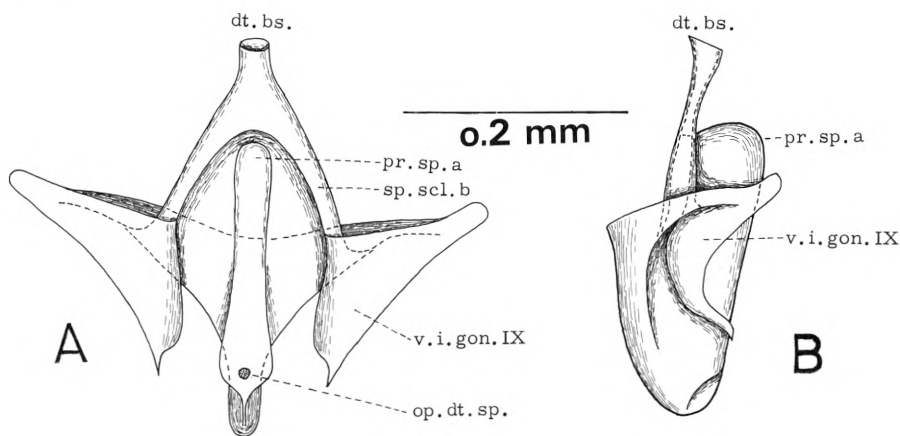


Fig. 60. *Athripsodes cinereus*. Spermathecal sclerite etc. in a ventral view (A) and as seen from the right side (B).

and the processus spermathecae proceed forward as the narrow lateral walls of the ductus bursae.

The ventral side of the processus is provided with a high, but rather narrow longitudinal ridge (pr.sp.a). The latter proceeds forward onto the dorsal wall of the ductus bursae, and projects ventrally through a parabolic "window" in the ventral wall of the duct (fig. 60 A). Its rounded anterior end must be able to partly close the opening of the oviduct. Near the posterior end the ridge pr.sp.a becomes somewhat broader, broader than the processus itself. On this part the ductus spermathecae opens. The hindmost part of the ridge is a thin sagittally compressed lamella.

The folds v.i.gon.IX, broad in front and much tapering in a posterior direction, extend for about the anterior half of the genital chamber. i.e. scarcely as far backward as the processus spermathecae.

A pair of sclerotic folds (d.i.gon.IX) extends for a little more than the posterior halves of the lateral sides of the genital chamber. Their narrow anterior ends lie above the likewise narrow posterior ends of the folds v.i.gon.IX. In a posterior direction the fold d.i.gon.IX becomes broader, eventually almost as broad as the height of the genital chamber. Its hind end is

almost, but not quite, continuous with the sclerite on the process IXd (fig. 57 D), which suggests that this process contains parts of the gonopods IX.

The posterior end of a low and narrow sclerotized fold, almost a sclerotic rod only, is intercalated between the folds v. and d.i.gon.IX. In an anterior direction it extends for the posterior two thirds of the dorsal branch of the genital chamber. The ventral wall of this branch is very concave in a transverse direction, and in the latero-ventral furrows thus formed the rods, probably derived from the gonopods IX, lie.

In front, between the two folds v.i.gon.IX, the ventral wall of the genital chamber is somewhat transversely convex. Farther behind it rises into a cushion, the posterior end of which projects as a membranous tongue (fig. 57 D, i.gon.VIII), just not beyond the genital opening.

The oviductus communis extends forward until the boundary between segments VII and VIII.

The bursa copulatrix is an elongate sac. It has a not quite thin epithelium and a very delicate cuticle. For most of its length the ductus bursae is membranous, but quite proximally it is, as mentioned above, sclerotized, funnel-like dilated, much flattened, and devoid of musculature.

The spermatheca is a long, sausage-like sac, which distally is produced into a short "proces-

sus vermiformis". It has a histological structure similar to that of the bursa copulatrix. In two of the dissected specimens it contained, in its proximal part, an iridescent "spermatophore".

The short ductus spermathecae has a strong circular musculature and is distally swollen into a bulbus. Subdistally it receives the long glandula spermathecae. Both the gland and the duct have a thick epithelium. The proximal part of the gland has a feeble circular musculature, its distal part is tightly curved up.

The colleterial glands extends into the anterior part of segment IV. Each gland is divided into two branches, an anterior and a posterior one which in their turn are divided into three branches, six in all. Among the anterior branches one, dorso-mesal, is slender, the middle one is shorter, but very thick, and the last, latero-ventral one is very small. The posterior branches are about equal in length and thickness. All branches have smooth walls.

The anus is situated on the hindmost part of the dorsal wall of the genital chamber.

Musculature. The external ventral VII–VIII muscle is divided into a mesal and a lateral portion. The internal muscle, which passes above the lateral oviduct, is narrow, but strong and diverges much in a posterior direction.

In segment VIII dvm_1 and dvm_4 are found, whereas dvm_2 and dvm_3 seem to be lacking.

I did not succeed in making a satisfactory dissection of the VIII–IX musculature.

The narrow and thick $gonm_1$ originates laterally on the ancosta of sternum VIII, converges in a posterior direction, and is inserted rather mesally on e.gon.VIII (fig. 57 C). The muscle $gonm_2$ also is rather strong, but flat. It originates along a slightly descendent line approximately on the middle of each half of IXa (fig. 57 A). Its insertion is divided into two portions, one in front of and another mesally to the posterior indentation between e.gon.VIII and e.gon.IX (fig. 57 C). The approximately cylindrical muscle $gonm_3$ has its ventral attachment just laterally

to this indentation; its dorsal attachment is to the lateral side of the process IXd, a little proximally to the middle. The slender IX–X muscle originates on the lateral side of the dorsal sclerite on segment IX, a little behind the antecosta. It passes mesally to $gonm_1$ and is inserted laterally, or perhaps rather lateroventrally to the posterior part of the anal tube.

The muscle $gchm$ is inserted to the sclerotic funnel of the ductus bursae.

The genital chamber has the usual circular musculature. The dorsal and the ventral branch of the anterior end have each a musculature of their own. The hindmost parts of the genital chamber and of the anal tube have a musculature in common.

Molanna angustata Curt.

Pregenital segments (fig. 61 A–C). In the middle of the pleural membrane there is a narrow and apparently slightly sclerotized longitudinal ridge. There is no gland on segment V.

Segment VIII deviates only a little from the preceding segments. The tergum and especially the sternum is a little broader than on segment VII, the posterior corners of the sternum are much more broadly rounded, and its hind margin forms a thick fold, since segment IX is considerably lower than segment VIII (fig. 61 B). The longitudinal sutures are much shorter than on the preceding segments. That on the tergum is just seen in fig. 61 A and B, that of the sternum is entirely concealed by the overlapping hind margin of segment VII. There is no longitudinal ridge on the pleural membrane.

Segments IX and X are so firmly united that the boundary cannot be stated with any degree of certainty. Together with the gonopods they form a short, broad and somewhat flattened, largely sclerotized structure, which in a transverse section is roughly rectangular.

The sclerite of segments IX and X, which has a very well developed antecosta, covers the

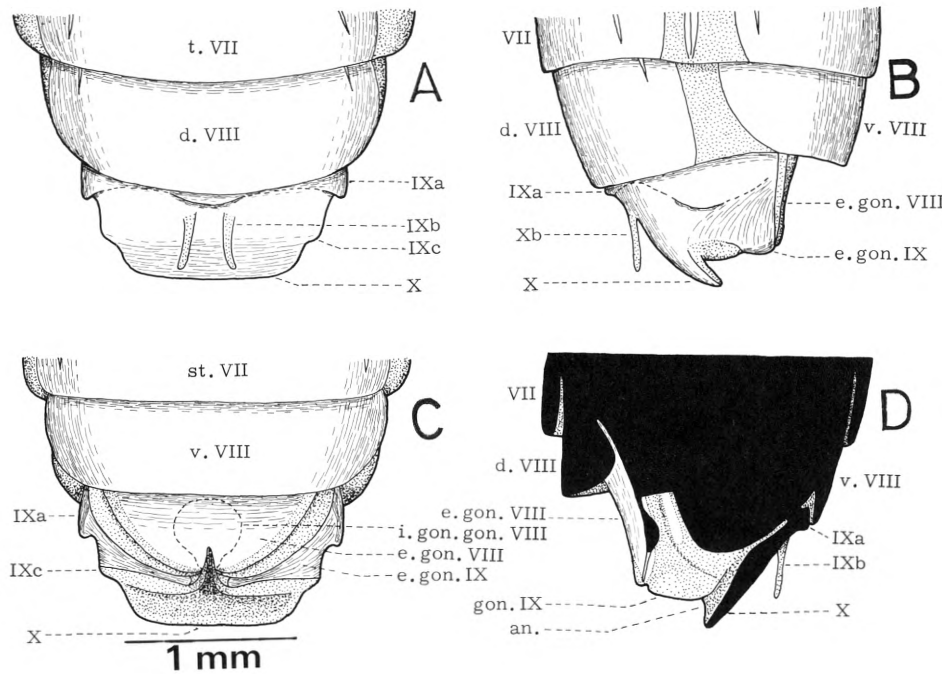


Fig. 61. *Molanna angustata*. Posterior end of abdomen in a dorsal view (A), as seen from the right side (B) and in a ventral view (C). D: Same, sagittal section; left side in a mesal view; black: haemocoel.

dorsal and lateral sides. It is divided into a short anterior part (IXa) and a longer posterior part by a declivity, which is well marked in the middle of the dorsal side and in the middles of the lateral sides, but otherwise rather indistinct. On the dorsal side the anterior part is very short, in the middle of the lateral sides it is longer.

In the middle of the dorsal side, at a short distance behind the declivity, a pair of finger-like, membranous processes (IXb) is found. Their position in relation to the muscle attachments makes it unlikely that they represent cerci. They are possibly homologous with the dorsal processes in the male (Nielsen 1957, fig. 56, p. 100). In the female they vary much in size, the two processes often differ in this respect, and sometimes both processes are quite inconspicuous.

Behind the declivity the dorsal side is descendent. Approximately in the middle it suddenly decreases in width, rounded posterior corners (IXc) thus being formed. The narrower poste-

rior part is a freely projecting lamella (X) with a straight hind margin and a membranous ventral side. The latter is separated from the posterior side of the combined segment by a deep, transverse furrow, in the middle of which the anus is found.

The posterior side of the combined segment is divided into a pair of high processes (fig. 61 A and B, e.gon.IX), flanking the genital opening, which has the shape of a vertical cleft. No doubt these processes are homologous with those so labelled in *Sericostoma* (pp. 107-08). They are largely membranous, though each process in the middle has a sclerite, which is continuous with the main sclerite of segments IX+X.

The external parts of the gonopods VIII form a plate (fig. 61 C, e.gon.VIII) which is both shorter and narrower than segments IX+X and roughly semicircular. It is separated from gonopod IX by a fine furrow, bordered by membrane on both sides. Otherwise the plate is covered by a slightly concave sclerite which, in a ventral view,

to a great extent is concealed by the overlapping posterior part of sternum VIII. The hind margin of the plate has in the middle a narrow, V-like incision, a sort of ventral extension of the genital opening. The shape of the incision varies somewhat. In one specimen a pair of tiny processes was seen in its bottom (cp. also below: the genital chamber). Apparently the incision is surrounded by a large, pear-like reinforcement (i.gon.VIII). This however, is due to the shining through of a sclerite on the ventral wall of the genital chamber. The plate has no antecosta.

Egg-laying. I have not seen this process, but from the difference between specimens containing eggs and specimens not doing so, as well as from morphological facts, the following may be deduced:

During egg-laying the plate e.gon.VIII is raised, i.e. drawn closer to the dorsal side of segment IX, and at the same time the posterior sides of the processes e.gon.IX come to lie in a horizontal plane, their sclerites being subjected to a torsion of 90° round their longitudinal axes. Moreover, the anterior part of the plate e.gon.VIII is drawn farther into segment VIII. In this way a ventral cavity arises on the posterior end of the abdomen. Behind it is bordered by the plate X, in front it extends into the posterior part of segment VII. In this cavity a spherical egg-mass is accumulated.

The female probably deposits the egg-mass while flying near the surface of the water. In September 1968 Solem (1973) found, in the lake Lille-Jonsvann in Norway, a great number of larvae "at a depth of 7 m, and since it was composed of very small larvae, the eggs must have been dropped and developed down to this depth." In shallow water I have myself found great numbers of egg-masses rolling freely on the bottom, and occasionally I have found them at a greater depth, even up to 14 m.

The genital chamber (figs. 62 A and 63) is long and slender, extending forward to the boundary between segments VII and VIII. In contrast to

conditions in (most) other Trichoptera the common oviduct tapers toward its opening in the genital chamber. In a dorsal view the latter has almost the same width for its whole length, apart from three slight dilations, one at the anterior end, one at the opening of the colleterial duct, approximately at the anterior third, and one in the posterior part, representing the latero-ventral bulges described below. At the anterior end, behind the opening of the ductus bursae, the dorsal wall is almost vertically ascendent. Then it is slightly descendent, but at the opening of the colleterial duct the height of the genital chamber increases suddenly and strongly. The foremost part of the ventral wall is ascendent.

The processus spermathecae (fig. 62 B, C) is situated on the anterior, steeply ascendent part of the dorsal wall. Hence its morphologically posterior end topographically is its dorsal side, its morphologically ventral side topographically its posterior side etc. In the following the terms dorsal, ventral etc. are used in their morphological sense.

The processus is a largely sclerotized fold, which has approximately the same height for its whole length. In front it covers most of the dorsal wall. From here it narrows strongly toward the rounded posterior end. The anterior side of the processus spermathecae bulges a little forward. About the basal half of this side is membranous.

On its greater middle part the processus has, on its ventral side, a not very well defined longitudinal ridge (pr.sp.a). The posterior two thirds of this ridge is membranous, and the ventral side of the membranous area is somewhat concave. On its middle the opening of the ductus spermathecae is found on a small elevation.

A sclerotic bridge (sp.scl.b) connects the processus spermathecae with a small sclerite (figs. 62 B and 63, sp.scl.c) lying on the anterior end of the lateral wall of the genital chamber. Its shape will appear from fig. 63. In front the

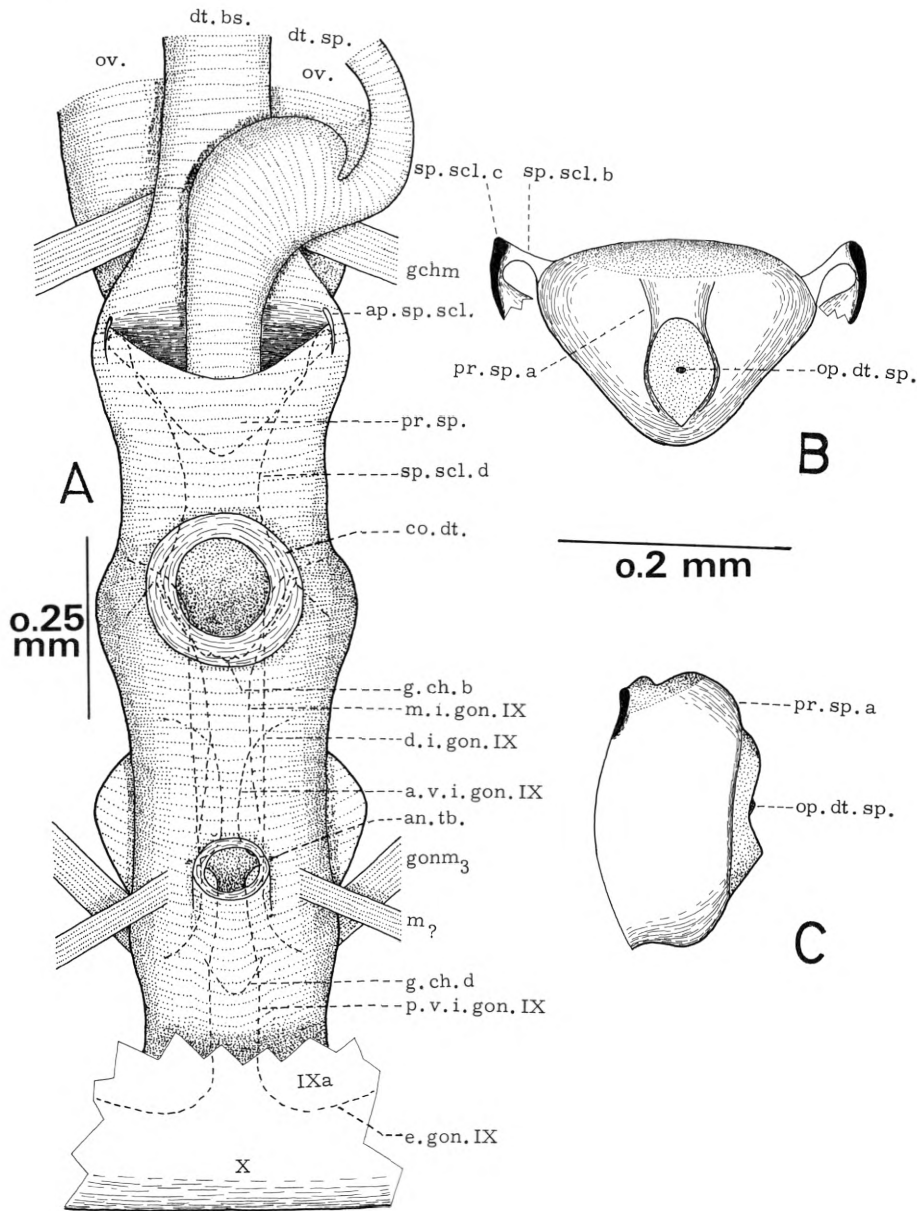


Fig. 62. *Molanna angustata*.
 A: The genital chamber etc.
 in a dorsal view; internal
 structures are shown by broken
 lines. Processus spermathecae
 in a ventral view (B) and as
 seen from the right side (C).

sclerite is produced into a tongue (sp.scl.a) on the latero-ventral side of the proximal, widened part of the ductus bursae. Behind the bridge sp.scl.b the sclerite sp.scl.c is continuous with the ventral side of a sclerotic fold (sp.scl.d), which lies dorsally on the lateral side of the genital

chamber and is rather narrow as compared with the latter. The tapering anterior end of the fold is bent downward, its free edge facing backward, and its ventral (or lateral) side is, as mentioned above, continuous with the sclerite sp.sc.c. At the line of union there is a deep and very

narrow, perhaps entirely closed, furrow, forming a small, forward directed apodeme (ap.sp.scl.) in the shape of a chordal section of a circle.

For most of its length the fold sp.scl.d is slightly descendent and its free edge facing mesally. In a posterior direction its height increases, and in the middle the two folds (right and left) occupy almost two thirds of the width of the genital chamber. Then the height again decreases, and the hindmost part of the fold, which is bent upward and forward, is extremely low and narrow, almost only a sclerotic rod just in front of the opening of the colleterial duct.

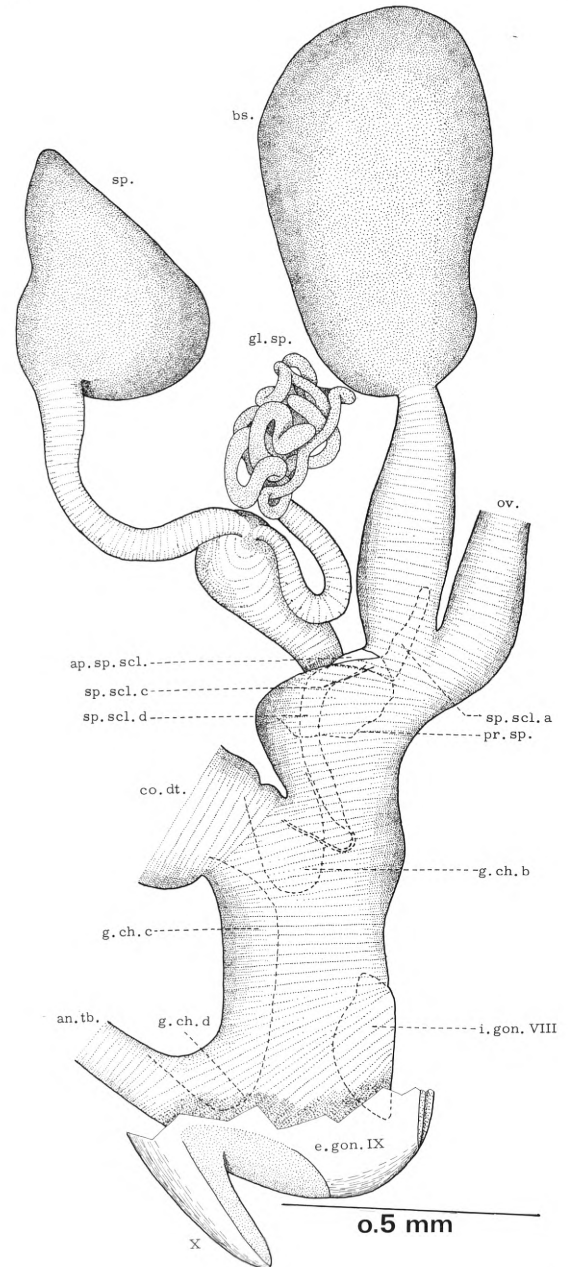
Below (or in front of) the opening of the colleterial duct there is a very thick, membranous, backward directed tongue (g.ch.b). Behind the opening the dorsal wall of the genital chamber bulges into the lumen as an unpaired longitudinal fold (g.ch.c). In unison these structures narrows the opening of the duct much and probably can close it entirely. The posterior end of the dorsal fold projects as a short tongue (g.ch.d), separating the anus and the genital opening.

On the lateral sides of the posterior, higher part of the genital chamber two pairs of longitudinal folds (fig. 62 A, i.gon.IX), a dorsal and a ventral one, are seen. The latter is entirely membranous, the former is at least slightly sclerotized. The anterior ends of the dorsal folds flank the opening of the colleterial duct and are situated above the hind ends of the anterior folds (sp.scl.d) described above. For more than two thirds of its length this fold is divided into a broader dorsal (d.i.gon.IX) and a narrower ventral part (m.i.gon.IX), both approximately semicircular in a cross section. The dorsal fold does not reach the posterior end of the genital chamber.

The ventral fold (v.i.gon.IX) does not proceed so far forward as the dorsal fold, but is higher than the latter; in front the right and the left fold almost touch each other. By a narrow

furrow, situated at the level where the division of the dorsal fold (into d.i.gon.IX and m.i.gon.IX) stops and this fold hence becomes narrow

Fig. 63. *Molanna angustata*. The genital chamber etc. as seen from the right side; internal structures are shown by broken lines.



wer, the ventral fold is almost completely divided into a shorter and narrower anterior part (a.v.i.gon.IX) and a broader posterior part (p.v.i.gon.IX). Behind the hind end of the dorsal fold (d.i.gon.IX, m.i.gon.IX) the fold p.v.i.gon.IX becomes still broader and eventually is continuous with the membranous mesal side of the process e.gon.IX (fig. 61, B, C).

At the posterior end the broad ventral wall of the genital chamber is strongly sclerotized (i.gon.VIII). The sclerite has in the middle a rounded longitudinal ridge, lying between the two folds p.v.i.gon.IX. The anterior part of this sclerite is broader than the genital chamber itself, and hence its broadly rounded anterior corners lie in latero-ventral bulges of the wall. In one of the dissected specimens the hind end of the ridge was divided into two tiny processes, visible externally.

The *bursa copulatrix*, which has the same histological structure as in *Athripsodes cinereus* (p. 123), is a large, elongate sac. The strongly muscleductus bursae is thickest in the middle.

The *spermatheca* is smaller than the bursa copulatrix. In one of the dissected specimens its distal end was produced into a bifurcate "appendix". Khalifa (1949) also has seen such a specimen. He considers the appendix as homologous with the "additional" gland in the Limnephilinae and Drusinae (pp. 165, 172 and 178), but this obviously is not the case. Stitz (1904) describes "fine bristles" in the distal part of the spermatheca, but I believe that this is an artifact.

The long ductus spermathecae is divided into a short and thick, somewhat clavate proximal part and a longer and slender distal part, the difference in thickness being due to the circular musculature. The long glandula spermathecae opens into the distal end of the thick part of the duct. It could also be said that the duct here bifurcates, one branch being the distal part of the duct, the other the gland. The proximal part of the latter has a weak circular musculature. Its

distal part is coiled tightly up and gradually becomes very thin, 18 μ or less thick.

The *colleterial glands* have only two branches, a dorsal and a ventral one. The former extends into segment IV or even segment II. Basally the ventral branch is directed forward, but it soon bends backward and mesally and extends, tapering, to the posterior end of X (fig. 61).

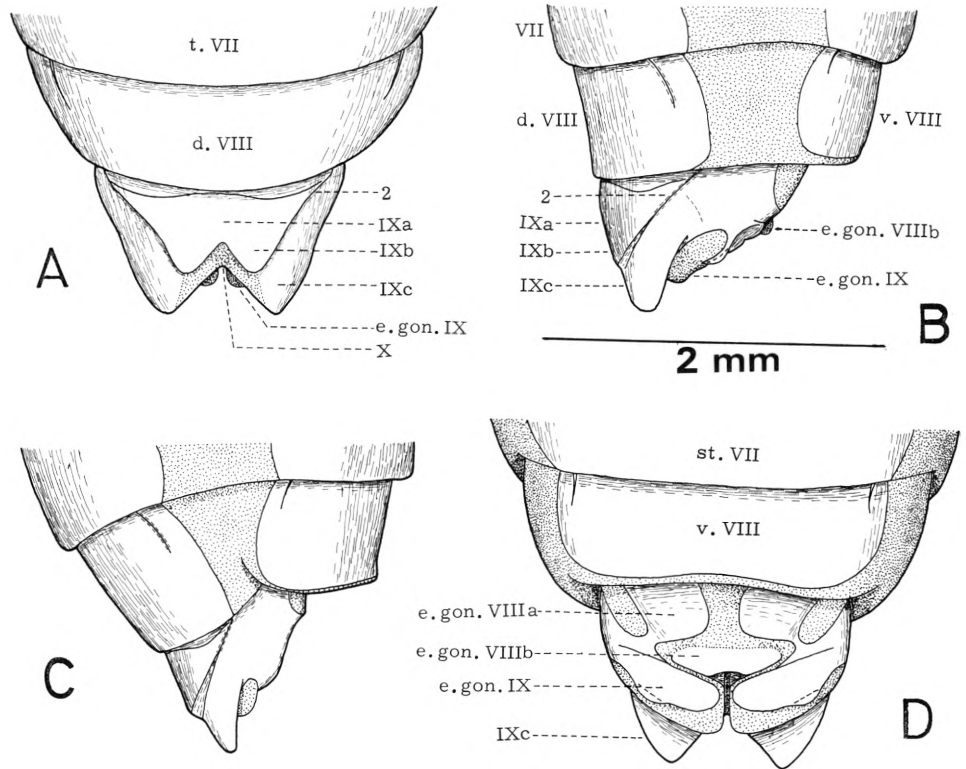
Musculature. In segment VIII dvm_1 , dvm_2 and dvm_4 is present, whereas dvm_3 is lacking.

There are five VIII-IX muscles which I have interpreted as dm_1 , dm_2 , dm_4 , dm_5 , and dm_6 . The muscle dm_2 diverges strongly in a posterior direction, so that a triangular area is seen between it and dm_1 . The muscle vm_6 has its posterior attachment to the anterior part of the lateral margin of the sclerite on segment IX.

The muscle $gonm_1$ is divided into two portions. One consists of fine muscle bands which originates over most of the surface of sternum VIII and converge toward an almost unpaired insertion on the anterior part of the plate e.gon.VIII (fig. 61 C). The other originates mesally on the antecosta of sternum VIII and is inserted to the middle of each half of the plate e.gon.VIII. The rather strong $gonm_2$ originates latero-dorsally on the sclerite of segment IX, at a short distance behind the antecosta. It has an almost vertical course and inserted to the lateral part of the plate e.gon.VIII, rather much behind the middle. The very slender $gonm_3$ originates on the sclerite of segment IX along a longitudinal line just behind the process IXb (fig. 63 A, B). It has a vertical course and is attached to the lateral side of the posterior part of the genital chamber.

There are two IX-X muscles. One is short and broad, but thin and rather diffuse. It originates laterally on the sclerite of segment IX, just behind the area IXa (fig. 61 A, B), and is inserted laterally on the plate X; it must probably act as a depressor of this plate. The other is very slender, but long. It originates laterally on the sclerite of segment IX, rather far behind the

Fig. 64. *Odontocerum albicorne*. Posterior end of abdomen in a dorsal view (A), as seen from the right side (B, C) and in a ventral view (D).



antecosta, but still on the area IXa. It is inserted latero-ventrally to the posterior part of the anal tube.

The homology of the two muscles mentioned below is a puzzle to me. One, consisting of only one slender band, was seen in one specimen only. It originated rather mesally on the sclerite of the process e.gon.IX (fig. 61 C) and was inserted to X behind the most mesal part of the first mentioned IX-X muscle. The other, likewise very slender, originates on the plate e.gon.-VIII, mesally to the insertion of the muscle gonm₂. It is inserted to the lateral wall of the genital chamber, in front of and dorsally to gonm₃. It may perhaps represent a transverse musculature.

The slender muscle gchm originates laterally on sternum VIII, a little behind the anterior corner, and is inserted to the sclerite sp.scl.a (fig. 63).

The genital chamber has the usual circular musculature.

Odontocerum albicorne Scop.

Pregenital segments. On the anterior sternum, and in part the terga too, the lateral longitudinal suture has a peculiar, sinuous course. There is no gland on segment V.

Segment VIII (fig. 64) does not deviate much from the preceding segments. The sternum is somewhat more strongly sclerotized than the preceding ones and also than tergum VIII, which in this respect resembles the pregenital terga. The lateral longitudinal sutures are shorter, on the tergum extending for a little more than half, on the sternum for a little more than one third of the length of the segment. The sternum does not quite reach the posterior end of the segment. Segment VIII overlaps segment

IX rather much, and more so the gonopods, here forming a very thick, membranous fold.

Segments IX and X and the gonopods are so firmly united that the boundaries cannot be stated with any degree of certainty. The dorsal and the lateral sides of the combined segment are largely covered by a sclerite, which has a well developed antecosta. In a lateral view the dorsal side is approximately horizontal, the ventral side rather steeply ascendent. In a dorsal view the combined segment tapers in a posterior direction, and the hind end has a large, triangular indentation.

An antero-mesal area (IXa) is delimited by a structure, which approximately is parallel to the side and hind margins of the combined segment, and thus also has a posterior, triangular indentation. This structure has on the dorsal side the shape of a broad and deep furrow. On the lateral side it narrows to an ordinary, strong suture, which extends toward, but does not reach, the anterior corner of the sclerite (fig. 65 A, 2). Near the lateral end the antecosta (ac) issues a short but broad side-branch (1). It approaches, but does not reach the suture 2. Laterally to the side-branch the antecosta is more weakly developed. Across the anterior part of the area IXa there is a fine, somewhat sinuous

transverse suture, which eventually joins the suture 2 (fig. 64 A, B).

That part of the dorsal side which lies behind the transverse furrow is developed as a pair of thick lobes (fig. 64, IXc + X). Behind the indentation in IXa their dorsal sides are membranous, laterally to the indentation they are, like the ventral sides, sclerotized. There is, however, no connection between the sclerites of the two lobes.

In the figure the membranous area is labelled X. The musculature (gonm₃, p. 201), however, suggests that it antero-mesally contains part of segment IX.

There are some few small sensilla campaniformia on the area IXa. Both the dorsal and the ventral sides of the lobes IXc + X are clothed with setae.

The posterior part of the lateral sides of the combined segment is developed as a pair of strongly convergent, almost transverse lobes (e.gon.IX), nearly touching each other in the sagittal plane, and separated from the lobes (IXc + X) mentioned above by a deep transverse furrow. To their greater extent these lobes are membranous, but each carries on its ventral side a tongue-like sclerite, which is continuous with the main sclerite of segments IX and X (fig. 66).

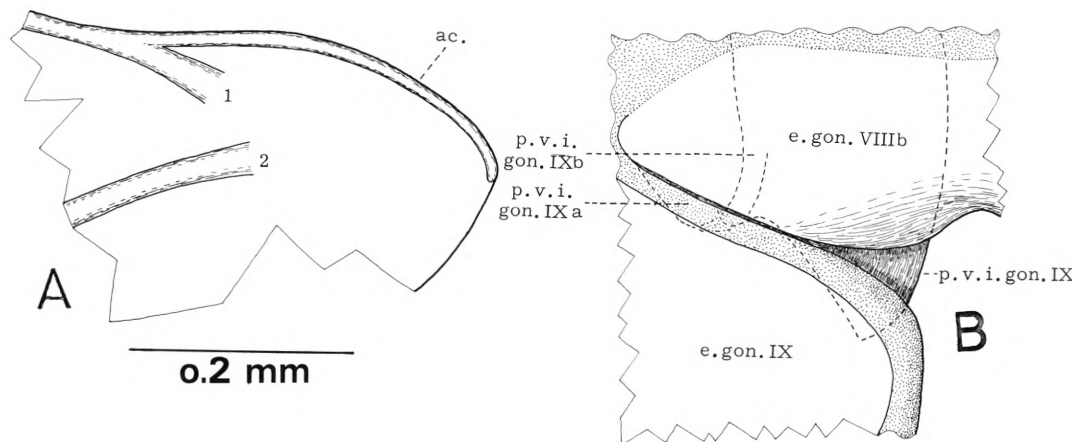


Fig. 65. *Odontoceram albicorne*. A: Right latero-anterior part of tergum IX. B: The relations between gonopod VIII and segment IX; right side in a ventral view.

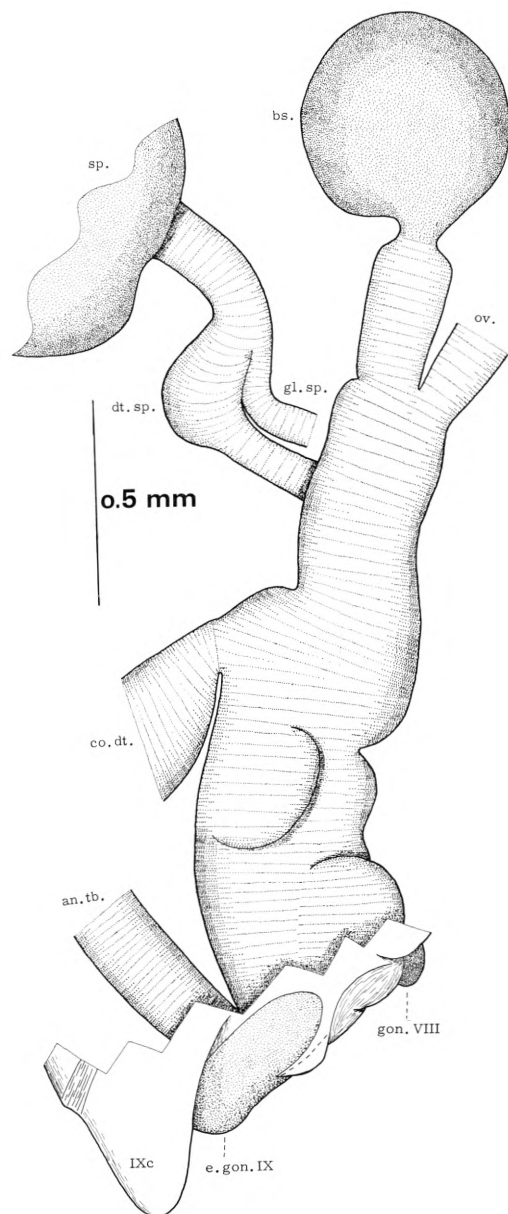


Fig. 66. *Odontocerum albicorne*. The genital chamber etc. as seen from the right side.

In a direction perpendicular to its long axis the sclerite is concave, and in the middle the posterior margin projects as a thin lamella (fig. 66).

The processes e.gon.IX form the lateral borders of the genital opening, and no doubt are

homologous with the processes so labelled in *Sericostoma* (p. 107). They are devoid of setae.

The external part of the gonopods VIII forms a steeply ascendent plate (e.gon.VIII), which is membranous to a great extent. It is provided with a pair of sclerites (e.gon.VIIIa) separated by a rather wide, unpaired, membranous area. They are separated also from the sclerite on segment IX by a pair of deep, but relatively narrow, anterior indentations, though their latero-posterior corners are connected with the roots of the sclerites e.gon.IX through narrow bridges. At the posterior end the membranous area between the two sclerites e.gon.VIIIa widens considerably, but here it is chiefly occupied by a transverse, weakly developed sclerite (e.gon.VIIIb). In the middle the hind margin of the latter, forming a lower lip of the genital opening, has a shallow indentation.

There are no sensilla on the plate e.gon.VIII.

Egg-laying. During this process the plate e.gon.VIII is raised very much, i.e. approached to the dorsal side of the sclerite on segments IX and X, and becomes strongly concave. The processes e.gon.IX also are raised and come to lie at a more dorsal level than the ventral sides of the lobes IXc, the antero-ventral margins of which then project as a sharp ridge. At the same time the whole complex is more deeply retracted into segment VIII. The final result is that the posterior end of the abdomen in a lateral view becomes a bilobed appearance. (The description given above is based on dissections of specimens empty of eggs; I have not seen the process itself). To all probability the egg-mass is carried between the two lips before deposition (cp. *Oligoplectrum maculatum*: p. 146).

The genital chamber (figs. 66 and 67) is long and narrow, extending into the posterior part of segment VII. In a dorsal view it shows three dilations, one, rather slight, at the anterior third, one a little behind the middle, and one, the largest, at the posterior end. The two last mentioned dilations represent dorso-lateral and

ventro-lateral, resp., bulges of the wall of the chamber. The opening of the colleterial duct is between the the anterior and the middle dilation. At this opening the height of the chamber increases abruptly.

For almost its whole extent the spermathecal sclerite (fig. 68) bulges into the lumen as a high and broad processus spermathecae. The posterior end of the latter gradually decreases in width and height. In a ventral view it is roughly triangular with a rounded apex. This relatively short, triangular area is, so to speak, framed by a more posterior, membranous fold, which gradually becomes broader and eventually projects as a short, tripartite tongue (pr.sp.d and e). The dorsal side of the middle lobe is clothed with stiff, 11 μ long and 1 μ thick microtrichia.

For about the posterior three fourths of the ventral side of the processus spermathecae there is an elaborate longitudinal ridge which, however, does not quite reach the posterior end. It can be said to be composed of two successive and in part superimposed sections. The anterior one (pr.sp.a) is egg-like with the broad end in front. The posterior one (pr.sp.b), the front end of which arises from the anterior section, has a very constricted base, broadest in the middle. At the hind end it is attenuated to a thin, vertical lamella (pr.sp.c). For the greater middle part the ventral side of pr.sp.b is dilated into a membranous "sole", slightly concave in a longitudinal direction and strongly convex in a transverse direction. On the posterior part of this "sole" there is a weak, oval sclerite which, behind its middle, carries the small opening of the ductus spermathecae.

The opening of the ductus bursae is a broad, but shallow indentation of the anterior margin of the spermathecal sclerite.

For the greater, anterior part of their length the lateral margins of the spermathecal sclerite are bent downward upon the lateral sides of the genital chamber. The lateral sclerite thus formed increases in height in a posterior direction,

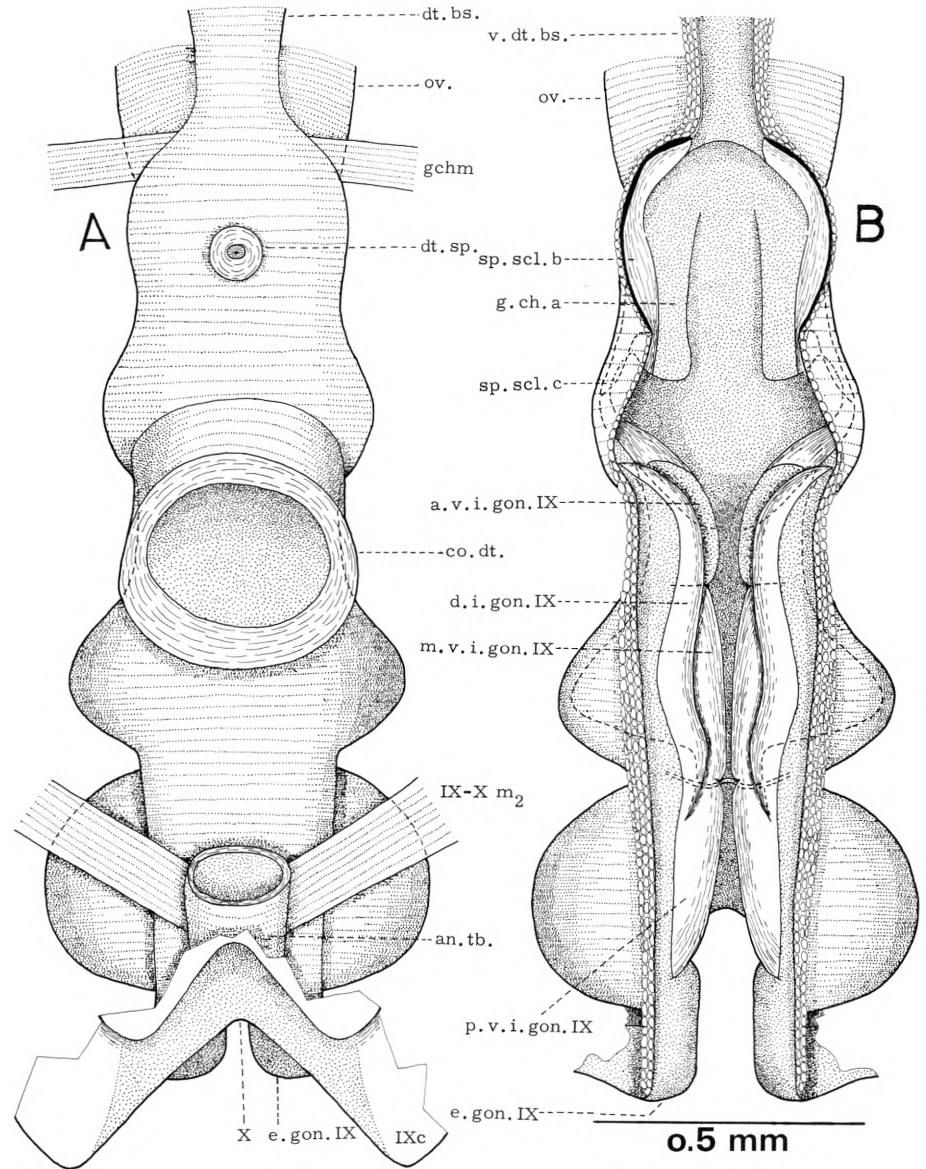
and for about half its length the ventral part of the sclerite again is bent inward and upward, forming a sclerotic groove (fig. 67 B, sp.scl.b) laterally on the floor of the anterior end of the genital chamber. The mesal sides of these grooves lie on a pair of otherwise membranous folds (g.ch.a) flanking the ridge (pr.sp.a-c) on the processus spermathecae. The groove proceeds beyond the fold on the lateral wall of the anterior of the three dilations of the genital chamber, here forming an approximately semi-circular arch (sp.scl.c) with a dorsal concavity. It gradually flattens out and eventually becomes continuous with the dorsal side of the fold a.v.i.gon.IX described below.

On the lateral wall of the posterior, higher part of the genital chamber there are two pairs of longitudinal folds (fig. 67 B), a ventral one (v.i.gon.IX) and a dorsal one (d.i.gon.IX). The former extends over the whole of this part of the chamber. Narrow, approximately vertical furrows divide it into three sections (a.v.i.gon.IX, m.v.i.gon.IX and p.v.i.gon.IX). The anterior section is the shortest, the two others about equal in length. The posterior ends of the two p.v.i.gon.IX almost touch each other in the middle of the genital chamber; otherwise the two folds v.i.gon.IX are separated by a somewhat greater distance.

The lower, anterior end of a.v.i.gon.IX is sclerotized. The sclerite, which extends farther backward on the ventral than on the dorsal side is, as mentioned above, continuous with the spermathecal sclerite through the arch (sp.scl.c) in the anterior dilation of the genital chamber. The greater, posterior part of a.v.i.gon.IX is membranous.

Both m.v.i.gon.IX and p.v.i.gon.IX are sclerotized, except at their bases. The furrow separating m.v.i.gon.IX from a.v.i.gon.IX is extremely narrow. The furrow between m.v.i.gon.IX and p.v.i.gon.IX is somewhat broader, but developed only on the ventral and in part the mesal side. The posterior end of m.v.i.gon.IX is slight-

Fig. 67. *Odontoceram albicorne*. A: The genital chamber etc. in a dorsal view. B: Floor of the genital chamber in a dorsal view.



ly convex, the anterior end of p.v.i.gon.IX slightly concave, a sort of simple articulation thus being formed. The posterior end of m.v.i.gon.IX projects farther ventrally than the anterior end of p.v.gon.IX. The projection is received by a depression in the membranous floor of the genital chamber.

On p.v.i.gon.IX the sclerite extends farther

laterally on the ventral side than on the dorsal side. On m.v.i.gon.IX the opposite is the case. On this fold the dorsal side even has a lateral, tongue-like extension, forming the sclerotic ventral wall of the narrow lumen of a dorso-lateral bulge of the genital chamber, the middle one of the three dilations seen in a dorsal view.

The fold d.i.gon.IX does not extend as far

forward as a.v.i.gon.IX, and its posterior end reaches only the anterior part of p.v.gon.IX. It is somewhat lower and considerably narrower than v.i.gon.IX and has a rather sharp free edge. Like v.i.gon.IX it is membranous at the base and sclerotized on the mesal part. On the posterior part of the fold, however, the sclerite, which as a whole is stronger than that on v.i.gon.IX, extends far in a lateral direction and forms the dorsal side of the lumen of the middle dilation of the genital chamber. In the bottom of this dilation it is united with the sclerite on m.v.i.gon.IX. The lower side of the sclerite on d.i.gon.IX unites with the dorsal side of p.v.i.gon.IX. The sclerotic folds form a sort of lever system between the processus spermathecae and the posterior end of the genital chamber.

The lower anterior ends of the folds d.i.gon.IX flank the process pr.sp.d and e, which lies above v.i.gon.IX.

The ventral side of the fold v.i.gon.IX is separated from the ventral wall of the genital chamber only by a narrow cleft. At the level of p.v.i.gon.IX this cleft is very much deepened, forming a latero-ventral bulge of the genital chamber, the posterior one of the three dilations seen in a dorsal view. The bulge is rather voluminous and apparently entirely membranous, though the articulatory sclerite between p.v.i.gon.IX and e.gon.IX, described below, may be said to lie on its posterior wall.

The membranous anterior side of the process e.gon.IX overlaps the posterior end of the fold p.v.i.gon.IX, especially on the ventral side (fig. 65 B; cp. fig. 64 D). The latero-posterior corner of the sclerite on this fold proceeds, reflected ventrally, in a lateral and a little posterior direction as an axelike extension (p.v.i.gon.IXa) into the furrow between e.gon.IX and p.v.i.gon.IX. This extension forms a very simple, hinge-like articulation with the sclerite e.gon.VIIIb. At the base of the extension there is a reinforcement (p.v.i.gon.IXb) along the lateral margin of the sclerite on p.v.i.gon.IX.

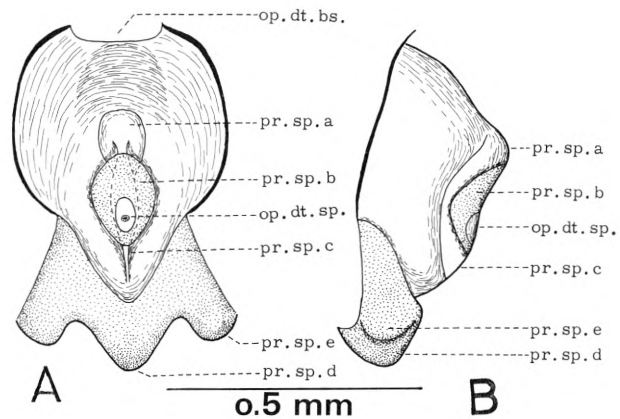


Fig. 68. *Odontoceram albicorne*. Processus spermathecae in a ventral view (A) and as seen from the right side (B).

In the posterior part of the genital chamber the dorsal wall bulges slightly into the lumen as an unpaired, membranous, longitudinal fold.

The bursa copulatrix (fig. 66) is a rather small, spherical sac. It is separated from the short ductus bursae by a constriction, due to the fact that the most distal part of the duct is devoid of muscles. The duct is somewhat funnel-like dilated toward its opening. Its thin cuticle is densely clothed with transverse rows of ca. 4 μ long microtrichia, directed distally, i.e. toward the bursa. In one specimen a tiny, ca. 12.5 μ long seta was seen. It was likewise directed distally.

The spermatheca (fig. 69 B) is a very large, elongate sac, extending to the anterior end of segment IV. It is provided with a rather feeble circular musculature (not indicated in the figs.), which toward the distal end takes a longitudinal course, the fibres remaining perpendicular to the tangent of the surface. In all the specimens dissected it contained a "spermatophore" in its proximal part, and the remainder, larger part of the lumen was filled by a solid, reddish mass.

The ductus spermathecae (fig. 66, 69 B) is short and S-like bent. In the middle it has a slight, fusiform swelling, proximally to which the duct is thinner than distally to it. The glandula spermathecae opens into the thicker,

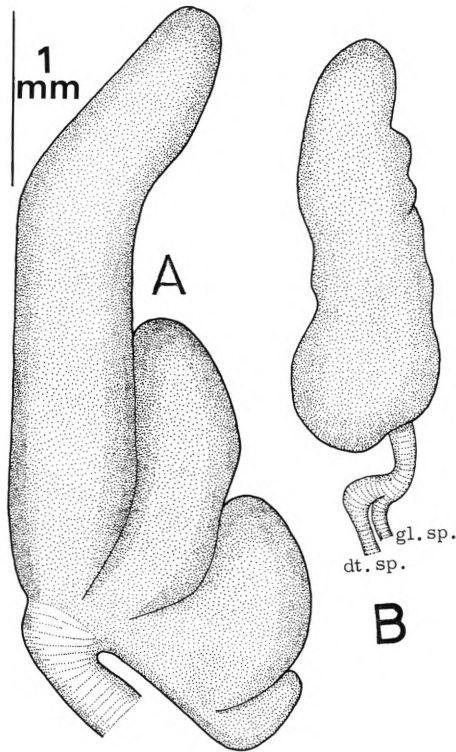


Fig. 69. *Odontoceram albicorne*. Left colleterial gland in a lateral view (A) and spermatheca as seen from the right side (B).

distal part in such a way that the opening is directed toward the spermatheca. The proximal part of the gland is like the duct provided with a circular musculature. Its distal part is thin and much coiled. The duct opens into the spermatheca on a papilla situated on the ventral wall near the posterior end. The top of the papilla is produced into a forward directed, sclerotic process.

The colleterial glands (fig. 69 A) are exceedingly voluminous and extend almost to the anterior end of the abdomen. Each gland is divided into two main branches, one forward and one backward directed. The two branches again bifurcate, four branches in all being formed. The length of these branches decrease very much in a ventral direction. The length of the second

branch is only one third to half of that of the uppermost branch, and the most ventral branch must be called tiny. The funnel-like colleterial duct is first directed backward, but then bent forward (fig. 66). It opens above (or behind) the process pr.sp.d-e (fig. 68).

The anus is found at the extreme posterior end of the dorsal wall of the genital chamber (fig. 66). Since it is situated between the processes e.gon.-IX, it perhaps cannot be said to be in the genital chamber s.str.

Musculature. The external ventral VII–VIII muscle is divided into two portions. The muscle vm_6 probably is present. It has its posterior attachment on the front corner of sternum VIII and converges slightly toward its anterior attachment, approximately in the middle of segment VII, mesally to the longitudinal suture.

In segment VIII dvm_1 , dvm_2 and dvm_4 are found. The muscle dvm_2 consists of only one band and is strictly intrasegmental, whereas it in the preceding segments is composed of several bands and is partly intersegmental, the posterior bands being attached to the antecosta of the following tergum.

There are four VIII–IX muscles, which, with some hesitation, I have interpreted as dm_1 (divided into two portions) dm_2 , dm_{4a} and dm_{4b} .

There are two muscles $gonm_1$. One is a group of fine bands, which originates closely behind the antecosta of sternum VIII. The origins of the right and the left muscle almost, but not quite, touch each other. The muscle diverges strongly toward its insertion, which is along a transverse line rather far behind on the sclerite e.gon.VIIIa (fig. 64 D). The other is broader, but likewise composed of fine bands. It originates laterally to the first mentioned muscle, approximately on the middle of each half of sternum VIII. It is inserted postero-laterally on the sclerite e.gon.VIIIa; the mesal half of the insertion is superficially to that of the first mentioned muscle. The rather strong muscle $gonm_2$ originates dorso-laterally on the anteco-

sta of segment IX. Its bands converge toward their insertion behind the mesal half of that of the first mentioned muscle gonm₁. A muscle, which I with some doubt have interpreted as gonm₃ (cp. p. 131) originates on the membranous area X (fig. 65 A) very close to the insertion of the IX-X muscle described below. Its bands diverge toward the insertion, which is in the angle between the dorsal wall of the genital chamber and the anal tube.

There are two IX-X muscles. One is rather strong and originates dorsally a little behind the antecosta of segment IX. Its bands converge strongly toward their insertion on the dorsal membranous area X (fig. 64 A) near the bottom of the indentation between the two IXb. The other, composed of several fine bands, originates on the suture on the lateral side of the sclerite on segment IX. Passing below the former muscle the bands converge toward their insertion laterally on the anal tube.

The narrow muscle gchm originates on the anterior corner of sternum VIII, has an almost transverse course and is inserted to the anterior corner of the spermathecal sclerite.

The circular musculature of the genital chamber is developed in the usual way.

Lasiocephala basalis Kol.

Pregenital segments (fig. 70). Near the hind margins of the terga paired groups of more light-coloured, slight elevations are noted. They are clothed with very large setae. On sterna III-VII the lateral end of the antecostal suture is spoon-like dilated, covering the extension of the anterior corners. The dilation is light-coloured, whereas the rest of the antecostal suture is dark-coloured. On segments V, VI and VII there are a slightly sclerotized longitudinal stripe on the broad pleural membrane. The spiracle is situated above this stripe. On segment IV it is at least very indistinct.

There is no gland on segment V.

Segment VII. This segment, already, is slightly modified, the sternum having a very broad, but relatively shallow posterior indentation. Quite laterally, only, does the sternum reach the posterior end of the segment.

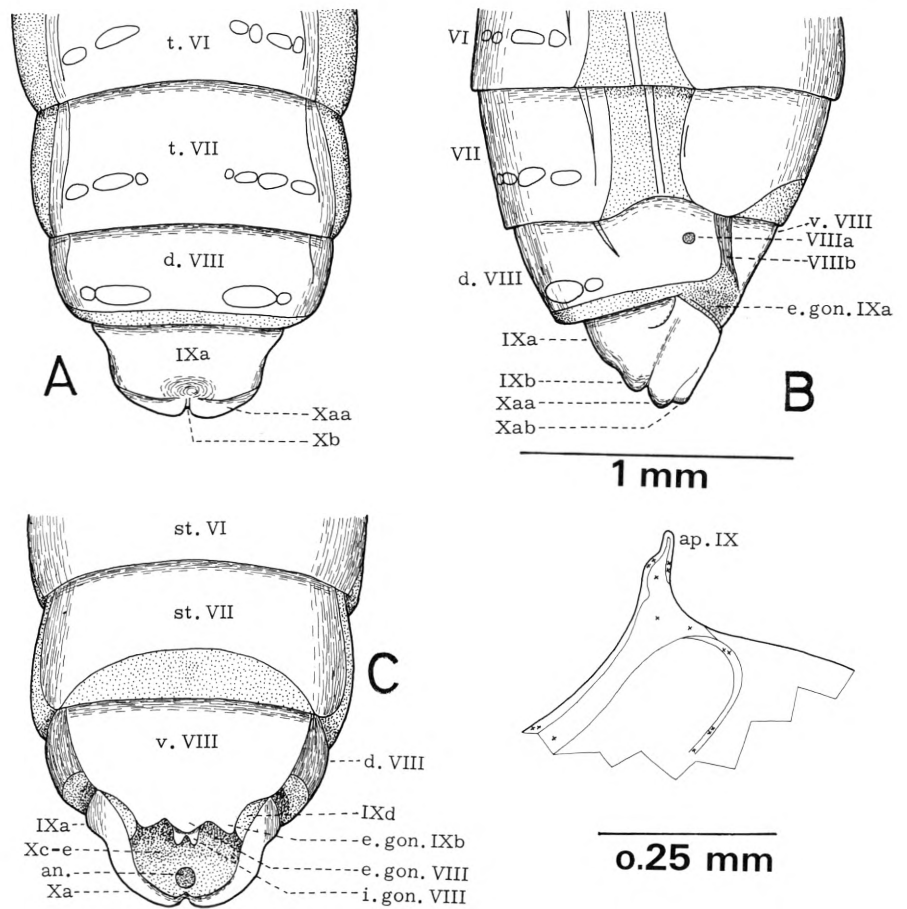
The genital segments. Segment IX is so firmly united with segment X that the boundary cannot be stated with any degree of certainty, and likewise the gonopods VIII and IX are firmly united with sternum VIII, forming a "ventral plate".

Tergum VIII is much broader than the preceding terga, extending far down on the lateral side of the segment, behind pleural membrane VII, and even behind the lateral part of sternum VII (fig. 70 B). The tergum thus covers considerably more than half the circumference of the segment and is visible also in a ventral view (fig. 70 C). The lateral longitudinal suture is shorter than on the preceding segments, but has the same position, and hence is far removed from the lateral margin of the tergum. The antecostal suture, however, proceeds beyond the longitudinal suture, about halfway to the anterior corner. The thick, membranous posterior margin of dorsum VIII overlaps segment IX to a great degree.

Tergum VIII has the same setae-bearing elevations as the preceding terga. On the lateral part of the tergum there is a small, circular, pale depression (VIIIa) without microtrichia. Maybe it is destined to receive some part of the male genitalia during copulation.

Segments IX and X form a short and broad structure, the shape of which will appear better from fig. 70 A and B than from descriptions. It is sclerotized on the dorsal, lateral and posterior sides. In a lateral view the ventral margin of the sclerite is somewhat ascendent. By two deep, approximately horizontal furrows its posterior end is divided into three parts (IXa-b, Xaa, Xb) of which the middle one (Xaa) projects farthest backward. The furrow separating IXa-b and Xaa proceeds, though much feebler and gradu-

Fig. 70. *Lasiocephala basalis*. Posterior end of abdomen in a dorsal view (A), as seen from the right side (B) and in a ventral view (C). D: Right anterior corner of tergum IX.



ally indistinct, on the lateral side of the sclerite. Both Xaa and Xab are partly bisected by a vertical furrow. On the dorsal side of Xaa an unpaired reinforcement (Xb) proceeds forward from this furrow. On IXb a similar division is slightly indicated by an unpaired, rather large, but shallow and not sharply delimited depression.

The three divisions of the sclerite differ in their surface structure. I.a. Xaa is densely clothed with setae, which are finer than on the preceding segments. This clothing continues as a broad fringe along the margin of the sclerite, in front of the furrow between Xaa and Xab. IXa-b is very sparsely clothed with setae, which are larger than on Xaa. Xab is also sparsely pro-

vided with setae, but here they are still smaller than on Xaa.

The anterior margin of the sclerite is divided into a dorsal, ascendent and a ventral, descendent part, separated by a corner forming an angle of about 90° . The apex of the corner is produced into a slender, short apodeme (fig. 70 D, ap. IX), the shape of which varies somewhat. The antecosta is developed only dorsally to this corner. It consists of a very broad, marginal reinforcement, which along the margin itself is, so to speak, superimposed by a narrow, still thicker reinforcement. Ventrally to the corner the antecosta bends, for some distance, backward and upward as a narrow, but strong reinforcement.

In situ the ascendent part of the anterior margin of the sclerite is concealed, being entirely overlapped by segment VIII, whereas the descendent part is visible to its greater extent. The sclerite is visible also in a ventral view (fig. 70 C), where its lateral and posterior parts form a frame round the membranous and strongly concave ventral side of the combined segment. On the posterior part of this side the anus is found. In the fig. it is shown open and circular; normally it is closed and difficult to see. Along the greater, postero-ventral part of the descendent anterior margin of the sclerite on segment IX there is a rather broad, membranous fold (IXd) flanking the "vulvar scale" (see below) and most clearly visible in a ventral view.

At the posterior end the processes Xab projects as a lamella ventrally to the membrane, which does not carry setae.

Sternum VIII and the gonopods. As mentioned above these structures are firmly united, forming a "ventral plate" (v.VIII, e.gon.VIII and e.gon.IX), which is rather much narrower than tergum VIII, ascendent to the same degree as the postero-ventral part of the sclerite on segments IX and X, and only slightly convex in a transverse direction.

For the greater, anterior part of the plate the lateral margins are a little convergent and slightly convex. Here there is, between the plate and the tergum, a rather broad longitudinal furrow (fig. 70 B, VIIIb), which, however is much narrower than the pleural membrane on the preceding segments. This furrow is sclerotized, and the sclerite is continuous with the "ventral plate", though separated from the latter by a sharp edge. The sclerite is in contact, but not continuous, with the lateral margin of the tergum. Behind the sclerite in the furrow there is a triangular, membranous area (e.gon.IXa), a widened continuation of the posterior, membranous part of dorsum VIII, but possibly belonging to the gonopods IX.

In the posterior part of the "ventral plate" the

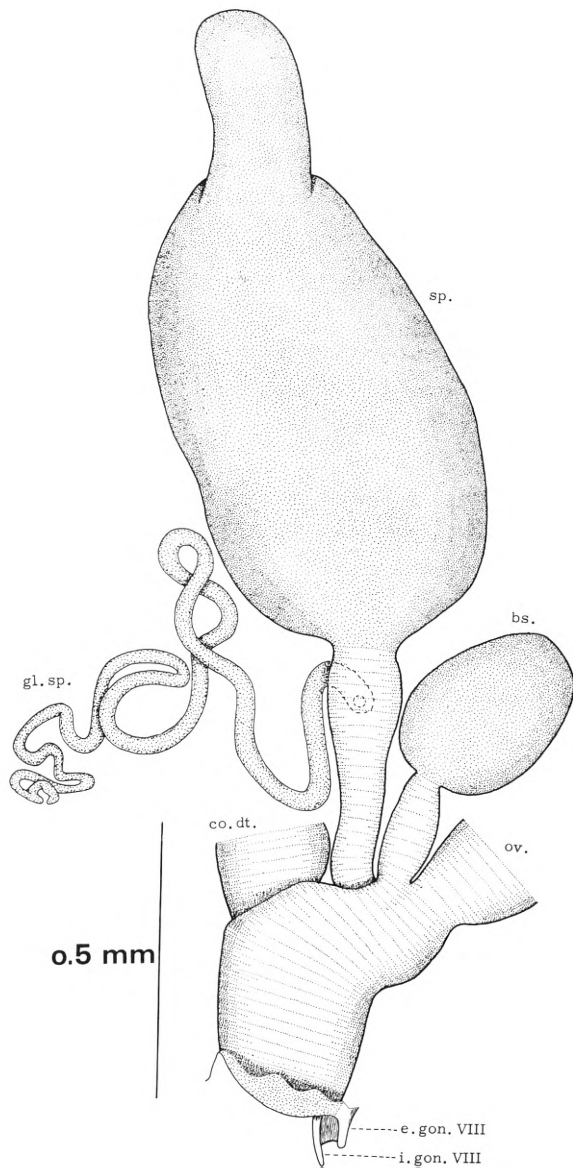


Fig. 71. *Lasiocephala basalis*. The genital chamber etc. as seen from the right side.

lateral margins are strongly convergent and rather much concave. The hind margin (the "vulvar scale" sensu MacLachlan), which is about half as broad as the anterior margin and placed far in front of the posterior end of segments IX and X, is divided into three lobes, an unpaired

“middle lobe” (e.gon.VIII) and a pair of “side lobes” (e.gon.IXb). The former and the mesal parts of the latter are rather thin and form the lower lip of the genital opening, whereas the lateral part of the “side lobe” is very thick. Its lateral side is membranous and rather much concave. This concavity (e.gon.IXa), which is visible only in a lateral view (fig. 70 B), is in front delimited by an approximately right-angled edge belonging to the membranous posterior part of dorsum VIII. Behind it is partly overlapped by the membranous fold IXd (fig. 70 C) described above, with the mesal base of which it is eventually continuous.

The musculature (gonm₂) proves that the gonopods VIII enter into the composition of the posterior part of the “ventral plate”. It then seems reasonable to suppose that the “middle lobe” is part of these gonopods, and that the “side lobes”, reminding of e.gon.IX in *Athripsodes* (p. 121) are parts of the gonopods IX.

The “ventral plate” is devoid of setae.

The genital chamber (figs. 71 and 72 A) is short, scarcely extending to the middle of segment VIII. It is divided into two parts, a very much shorter, narrower and lower anterior one and a longer, broader and higher posterior one. Especially in a dorsal view the two parts are sharply delimited toward each other. The anterior part is approximately circular in a cross section. The broad and rather flattened posterior part is roughly cordate, broadest near the anterior end, narrower toward the posterior end.

At the front end the dorsal wall is very steeply ascendent and bulges, for almost the whole width of the lumen, into the latter as a broad, but relatively low processus spermathecae (fig. 72 B, C). The forward and downward facing anterior side of the latter is, to the greatest extent basally, membranous, but otherwise the process is sclerotized. Its upward and backward facing posterior side is produced into a thick, but relatively flat and short tongue (pr.sp.b).

In the middle of the ventral side of the

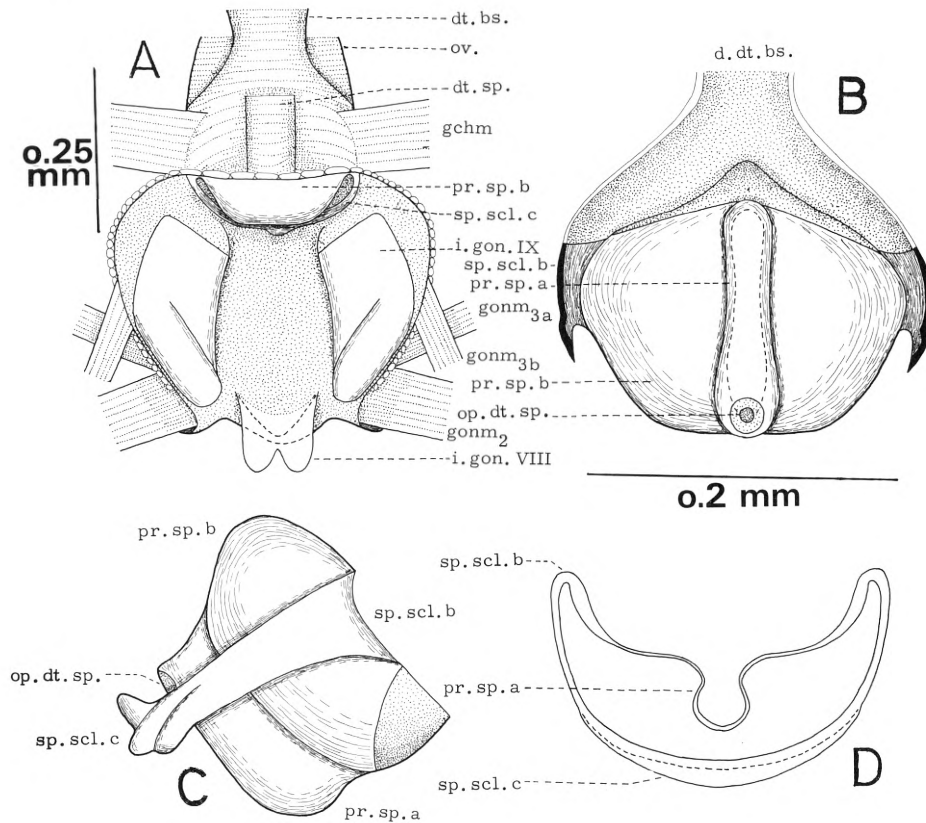
processus spermathecae there is a relatively narrow longitudinal ridge (pr.sp.a) arising from a somewhat constricted base; in a posterior direction it increases a little in width. The opening of the ductus spermathecae is situated near the hind end of this ridge, surrounded by a membranous area.

The processus spermathecae obstructs to a great degree the opening of the ductus bursae. It is flanked by grooves, forming a sort of continuation of the ductus bursae. The narrow posterior parts of these grooves (sp.scl.b) are sclerotized, the sclerite of the processus thus being continuous with a sclerotized bow (figs. 72 A, C and D, sp.scl.c) lying on the lateral and ventral sides of the genital chamber. Here the ventral wall of the chamber is ascendent, and the ventral part of the bow lies at the posterior end of the ascendent part. In a dorsal view the bow is almost conform with the margin of the posterior tongue (pr.sp.b) of the processus spermathecae. In a ventral direction the bow gradually becomes narrower; in the middle of the ventral side, however, it has a backward and upward directed extension (fig. 72 A, C), which is removed from the opening of the ductus spermathecae only by a short distance. The ventral part of the bow has a strong reinforcement.

Behind the processus spermathecae, i.e. at the anterior end of the broader, posterior part of the genital chamber, the dorsal wall for a short distance is ca. 45° ascendent. Here it bulges into the lumen as a large, membranous papilla, which almost fills the entire lumen and almost reaches the spout i.gon.VIII described below. The colleterial duct opens on the apex of this papilla.

The posterior, horizontal or slightly descendent part of the dorsal wall is covered by an unpaired sclerite.

A pair of longitudinal folds (fig. 72 A, i.gon.-IX) lies laterally on the ventral wall of the posterior, broader part of the genital chamber. They do not quite reach the posterior end of the

Fig. 72. *Lasiocephala basalis*.

A: Floor of the genital chamber in a dorsal view. Processus spermathecae in a postero-ventral view (B) and as seen from the right side (C). D: Transverse section through the processus spermathecae in a 45° descendent plane.

latter, but their hind ends can be said to lie on the dorsal side of the “side lobes” (fig. 70 C, e.gon.IXb) of the “vulvar scale”. Except for the antero-lateral part and the extreme anterior end the fold is sclerotized. The sclerite, especially at the hind end, is separated from the sclerite lying on the postero-dorsal wall of the genital chamber only by a short distance. Its mesal margin projects as a rather thin ridge. In the posterior half the lateral margin projects dorsally as a much thicker ridge.

Between the posterior ends of the folds i.gon.-IX, on the dorsal side of the “middle lobe” of the “vulvar scale”, a bilobed, pale, but apparently sclerotized spout (fig. 72 A, i.gon.VIII) projects backward, beyond the opening of the genital

chamber. The spout is supported by a triangular column, broader and quite low in front, narrower and higher in a posterior direction. This column is sclerotized and continuous with the “middle lobe” of the “vulvar scale”.

The bursa copulatrix (fig. 71) is a rather small, elongate sac. The short, muscular duct has a wide lumen. Toward the opening it is funnel-like dilated, but flattened.

The spermatheca is a very large, elongate sac, the distal end of which is produced into a short, plump, finger-like appendix. In the latter, and in the the distal third of the sac itself close-set microtrichia, 25 μ long and $1\frac{2}{3}$ μ thick, are seen. The spermatheca has a rather feeble circular musculature and for the greater, proximal part

of its length an also feeble longitudinal muscle layer inside the circular fibres (i.e. nearer the wall of the spermatheca). The musculature of the spermathecal sac is not indicated on fig. 71.

In some specimens an approximately spherical, white, shining "spermatophore" was seen in the proximal part of the sac.

The short ductus spermathecae is muscular. Its distal half is very slightly fusiform. On the left side of this part the glandula spermathecae opens. This gland has a wide lumen and a rather low epithelium. Distally to the opening of the gland the duct, which eventually widens slightly toward the spermatheca, is sclerotized.

The colleterial glands. Each gland is divided into two main branches. One is directed straight forward and extends into segment II. The other is basally divided into two branches. One of these is directed downward, but soon bent backward and extends, below the muscle gchm, into the "ventral plate". The other is directed straight backward and extends into segment IX. In all three branches fine longitudinal folds of the wall are seen. The colleterial duct is funnel-like.

Musculature. In segment VIII dorso-ventral muscles are not found.

There are three VIII-IX muscles, which I have interpreted as dm_1 , divided into two portions, and dm_5 . The two portions of dm_1 originate on the antecosta of tergum VIII, mesally and laterally, resp., to the longitudinal suture. They are both inserted to the dorsal side of the apodeme ap.IX (fig. 70 D), the first mentioned portion more basally. The muscle dm_5 originates on the posterior end of tergum VIII and is inserted to the lateral side of the apodeme ap.IX.

The muscle $gonm_1$ appears to be lacking. The rather broad, ribbon-like muscle $gonm_2$ originates on the sclerite of segment IX mesally (or dorsally) to the curved suture (p. 138; fig. 70 B). It goes downward, inward and a little backward, passes through the thick lateral part of the "side lobe" of the "vulvar scale" (fig. 70 B, e.gon.IXa)

and is inserted to this scale between the "middle" and the "side lobe". By its contraction it pulls the "vulvar scale" upward and forward, a furrow being formed between the scale and sternum VIII.

The $gonm_3$ is represented by two muscles. One originates very mesally on the furrow between IXb and Xaa (fig. 70 B), goes forward and is inserted to the membrane between the sclerite i.gon.IX (fig. 72 A) and the sclerite on the postero-dorsal wall of the genital chamber. The other originates on the apodeme ap.IX (fig. 70 D) and is inserted to the lateral margin of i.gon.IX near the posterior end.

There are three IX-X muscles. One originates at the slight furrow which in a lateral view (fig. 70 B) is seen on IXa and is inserted to the longitudinal reinforcement on Xaa; the insertion is practically unpaired. The rather strong muscle probably can cause a deformation of the sclerite on segments IX and X. Another originates on a rather broad area of IXa, laterally to the posterior depression on the latter. Its bands converge very strongly in an anterior direction, and so do the right and left muscle. They have a common insertion on the hind end of the postero-dorsal sclerite in the genital chamber, which here has an internal (i.e. haemocoelic), unpaired, short and low longitudinal ridge. The third muscle is slender and originates on IXa in front of the first mentioned muscle and above the posterior part of $gonm_2$. It passes above the former muscle and is inserted to the posterior part of the anal tube.

Finally there is a muscle, the homology of which I have been unable to decide. It is steeply ascendent, originates on what may be supposed to be the boundary between sternum VIII and the gonopods. (cp. p. 139) and is inserted to a rather large area of the sclerite i.gon.IX (fig. 72 A) at or a little in front of the middle. It may perhaps represent a transverse musculature in the gonopods IX (pp. 25-26).

The muscle gchm originates on VIIIb (fig.

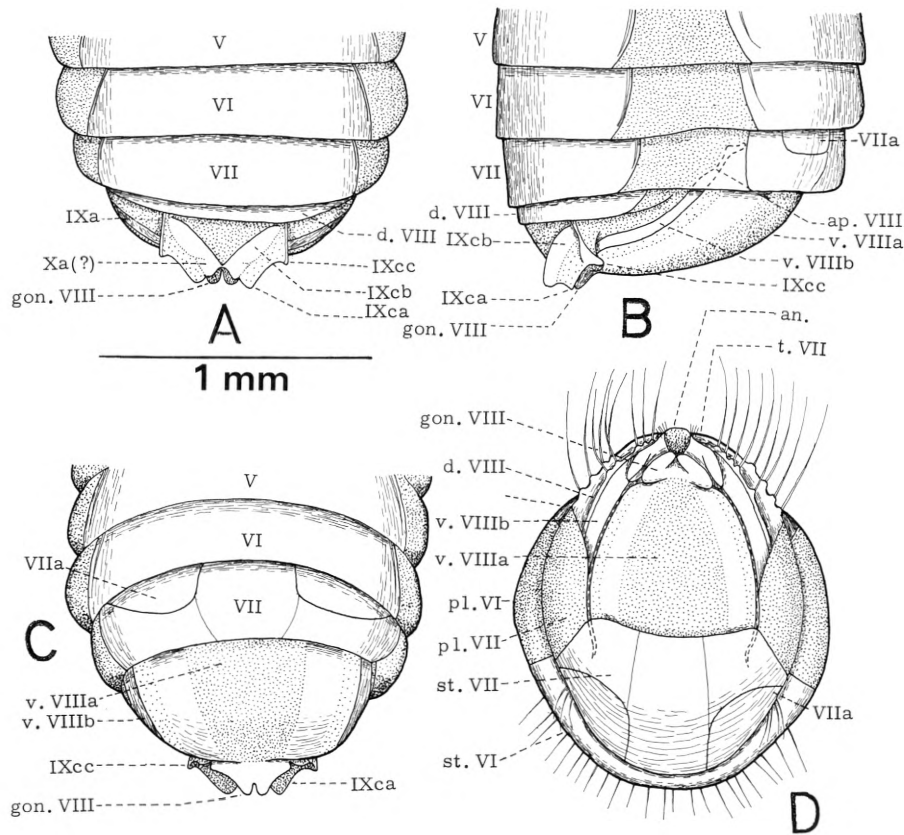


Fig. 73. *Oligoplectrum maculatum*. Posterior end of abdomen in a dorsal view (A), as seen from the right side (B), in a ventral view (C) and in a posterior view (D). The last after formation of an "egg cup," (p. 146).

70B) and is inserted to the bow sp.scl.c (fig. 72 a, C) as well as to the lateral wall of the genital chamber behind this bow.

Oligoplectrum maculatum Fourcr.

Pregenital segments. In the specimens shown in fig. 73 the posterior margins of the terga and sterna II–VII are reflected, and the abdomen hence short and plump. This probably is an initial stage to the formation of an "egg-cup" (see below). I have seen many specimens in which the abdomen was considerably more slender, and the hind margins of the said sclerites not reflected.

The anterior margin of the tergum has a shallow indentation, and in the middle of the latter the antecosta is interrupted, a feature

which perhaps is connected with the formation of an »egg-cup«.

The sternal lateral longitudinal suture is somewhat stronger than the tergal one and extends for about two thirds of the length of the sternum. By maximal contraction of the abdomen, during formation of an »egg-cup«, the whole of that part of the sternum which lies behind the lateral suture is reflected.

On the sternum the antecostal suture apparently proceeds into the front margin of the extension of the anterior corner (see p. 8). Between this part of the antecostal suture and the anterior end of the longitudinal suture there are a little less than twenty tiny, about 1.5μ broad sensilla campaniformia. Similar sensilla are found on the anterior corners of the terga, and in a small number (2–5) on the posterior

end of each sternal (but not tergal) longitudinal suture.

On terga II and III some few, very large setae are seen mesally to the posterior end of the longitudinal suture; on tergum IV a short transverse row of large setae proceeds in a mesal direction from this group. On terga V and VI the lateral groups of large setae are lacking, but in return there is a transverse row along the posterior margin of the tergum, interrupted only for a short distance in the middle. The base of each seta is surrounded by a circular, pale spot. A similar transverse row of somewhat smaller setae is seen on the sterna III–VII, though on sternum III it contains only a couple of setae. On these sterna there are also some large setae scattered over the mesal part of the sternum for most of its length. Small setae are almost entirely lacking.

Rather laterally on sternum V (fig. 74 B) the antecostal suture forms a backward bent curve. At the top of the curve, penetrating the antecosta the small, only 6 μ broad, a little backward directed opening of the gland of segment V is found. The gland is pear-shaped and has a wide lumen. The backward bent part of the suture probably is a secondary structure, the true antecosta being interrupted at the opening of the gland.

Segment VII. This segment, already, is somewhat modified. On the tergum the lateral suture is shorter than on the preceding segments. Quite in front the sternum is sclerotized for its whole width, and it has a well developed antecosta, but for most of its length the narrower, mesal part of the sternum is pale and weakly sclerotized. The lateral longitudinal suture extends only for the anterior third of the sternum. Behind it there is, on the lateral (entirely) sclerotized part of the sternum a large, darker and probably more strongly sclerotized area (VIIa).

In the specimens shown in fig. 73 B–C about the anterior third of the sternum and half of VIIa are concealed.

The tergum is provided with the same setae as the preceding terga. On the sternum there are only a few large setae just mesally to the posterior end of the longitudinal suture.

The genital segments. Segment IX is so firmly united with segment X, and sternum VIII with the gonopods VIII and IX, forming a “ventral plate”, that the boundaries cannot be stated with any degree of certainty. The segments VIII–X together form an approximately semiglobular structure. The shape, however, is somewhat dependent on the state of contraction. Before start of egg-laying the whole structure perhaps is more elongate.

Tergum VIII (d.VIII) is a little broader than, but only half as long as tergum VII. In the specimens shown in fig. 73 it is concealed to its greater extent by tergum VII, and overlaps itself segment IX to a great degree. The overlapping posterior margin of dorsum VIII proceeds for a short distance in a ventral (or lateral) direction as a membranous fold (fig. 73 B). The anterior margin of tergum VIII is built as in the preceding segments, i.e. the antecosta is interrupted in the middle, but the lateral longitudinal suture extends only for about half the length of the segment.

There is the same row of large setae as on the preceding terga.

Segments IX and X are only half as broad as segment VIII, and their height is only a small fraction of that of this segment (though it is difficult to state the anterior boundary of segment IX with certainty). In a dorsal view (fig. 73 A) the width of the combined segment increases a little in a posterior direction, in a lateral view (figs. 73 B, 74 A) the dorsal side is very much vaulted.

The posterior end for its whole width is produced into a short, but rather thick “scale”, which is bent, with a dorsal convexity, in a transverse direction and the mesal part of which forms the upper lip of the genital opening. A triangular incision divides the “scale” into a pair

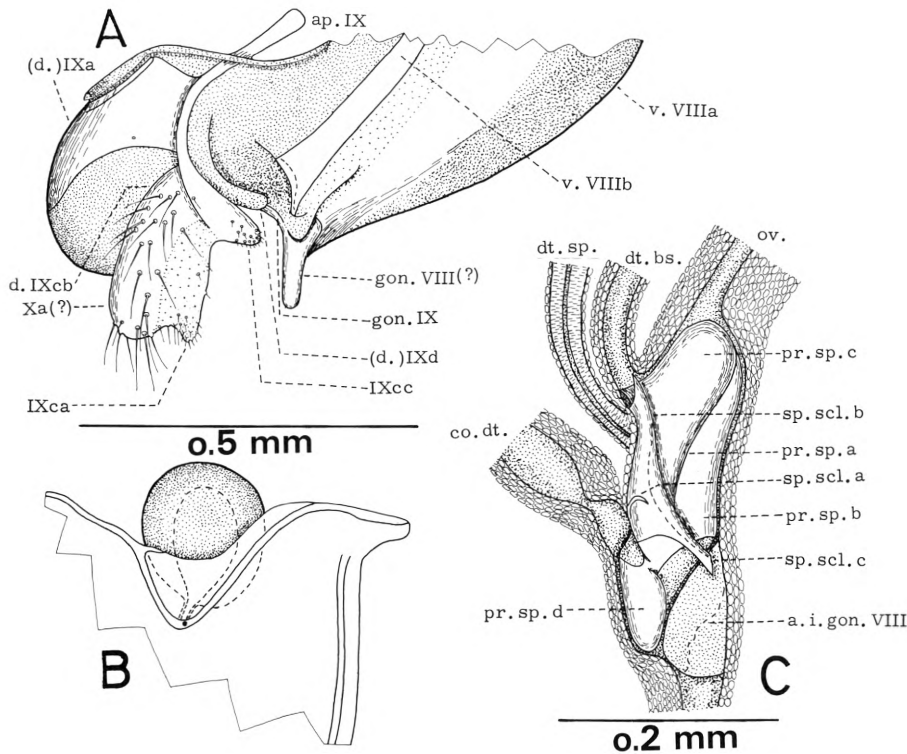


Fig. 74. *Oligoplectrum maculatum*. A: Postero-ventral part of segment VIII and segments IX and X as seen from the right side. B: Left anterior corner of sternum V with the gland of this segment. C: Sagittal section through the genital chamber (except the posterior-most part); left side as seen from the inside. The right side of sp.scl, however, is shown.

of lobes, each of which is again partly tripartite. The mesal one of these lobes (Xa?) lies at the most dorsal level, the lateral one (IXcc) at the most ventral level, whereas the middle one (IXca) projects farthest backward. Or rather, there are four pairs of lobes, for on the ventro-mesal side of the sagittally compressed lobe IXcc (fig. 74 A) there is a shorter, membranous tongue (IXd), the distal end of which normally is not seen. The anus is found between these lobes. Its lower lip has a very concave, almost semicircular posterior margin.

Segments IX and X are membranous to a great extent. A sclerite (IXa), which may be called tergum IX, is situated on the anterior part of the combined segment. (In fig. 73 A, B it is concealed by dorsum VIII, but it is seen in fig. 74 A). On the dorsal side its anterior margin is indented like that of the segment itself, and here

a well developed antecosta is seen. The dorsal part of the anterior margin is separated from the lateral part by obtuse-angled corner, and laterally to this corner the margin recedes, leaving a roughly triangular, membranous area.

The concave lateral margin of the sclerite IXa has a broad reinforcement, which proceeds forward, ventrally (or laterally) to the triangular membranous area mentioned above, eventually as a forward and downward directed apodeme (ap. IX), which increases somewhat in width toward the distal (or anterior) end. It proceeds also backward and downward, beyond the posterior margin of IXa, as a gradually broader, vertically placed sclerite, the dorsal margin of which projects as a low and narrow ridge, and the posterior end of which lies on the lateral side of the process IXcc. From the posterior end of this process to the distal end of the apodeme

ap.IX a strongly sclerotized arch with a ventral concavity thus is formed. Behind the posterior margin of the sclerite IXa there lies, on the dorsal side, a pair of rod-like, rather broad and strongly convergent sclerites (IXcb), separated by a triangular membranous area. Their posterior ends lie on the dorsal side of the processes Xa?

Near the backward curved posterior margin the sclerite IXa carries, on the dorsal side, a pair of very large sensilla campaniformia, on the lateral side a smaller sensillum campaniformium. The sclerites on the processes Xa? are clothed with small (37–74 μ long) but relatively thick (2.5 – 3 μ) setae. On the dorsal side of the process IXca and the lateral side of the process IXcc there are still smaller, only ca 8 μ , but relatively still thicker (up to more than 2 μ) setae. Other sensilla are not seen on segments IX and X.

The ventral plate (fig. 73 C). Venter VIII and the gonopods together form a parabolic, much vaulted and very much ascendent plate, which is about twice as broad as segments IX and X, below which it projects backward.

The greater mesal part of this plate, except for the “vulvar scale”, is very weakly sclerotized, and approximately the mesal half (v.VIIIa) is almost entirely membranous. Toward the lateral margin the sclerotization becomes somewhat stronger, especially in two longitudinal stripes. The mesal one of these is still rather weakly sclerotized. The lateral one, along the margin itself, is a strongly sclerotized, brown and sharply delimited rod (v.VIIIb). The anterior part of this rod is tapering, and its extreme anterior end forms a small, downward and inward directed apodeme (fig. 73 B, ap. VIII). The posterior part of the rod is separated from IXa by copious membrane. It is impossible to tell whether this membrane belongs to segment VIII or to segment IX.

The posterior end of the parabolic “ventral plate” is produced into a small “vulvar scale”

(gon.VIII). For a short, basal distance the latter becomes a little broader, then it narrows, with concave lateral margins, toward the bilobed apex (fig. 73 C). In relation to the main part of the “ventral plate” the “vulvar scale” is bent downward, so that it approaches a horizontal position. It forms the lower lip of the genital opening. Its ventral side and the greater, distal part of its dorsal side are weakly sclerotized. The ventral sides of the apical lobes are clothed with pale, 8–16 μ long and 2 μ thick, downward and a little forward directed microtrichia.

In a lateral view (fig. 74 A) the process IXd appears to be considerably longer than it really is. What looks like the greater, basal part of the process is in fact a cleft, which forms the entrance to a deep, inward and upward directed pocket. The reinforced posterior end of the rod v.VIIIb is bent inward and lies on the somewhat laterally facing ventral side of this pocket. (In fig. 74 A these features are distorted, since the cleft mentioned is unnaturally dilated).

In the “mouth angle” of the genital chamber there is a small, brownish rod (fig. 74 A, gon.-IX), which is bent in a quarter of a circle with posterior concavity. It lies behind the posterior end of the rod v.VIIIb and is continuous with the lateral side of the “vulvar scale”.

A study of the musculature of the gonopods corroborate the interpretation given above, though the gonopod VIII also must enter into the formation of the rod gon.IX.

Egg-laying. During this process the female sits in some sheltered place. An egg-mass gradually is formed, and at the same time the posterior end of the abdomen becomes concave. The egg-mass rests in this concavity (fig. 73 d), like an egg in an egg-cup, until it is deposited by the female descending below the surface of the water (Anker Nielsen 1937, 1943).

The initial stage of the process probably is a shortening of the abdomen. After that the dorsal region of the posterior segments is not subjected to any great change as compared with

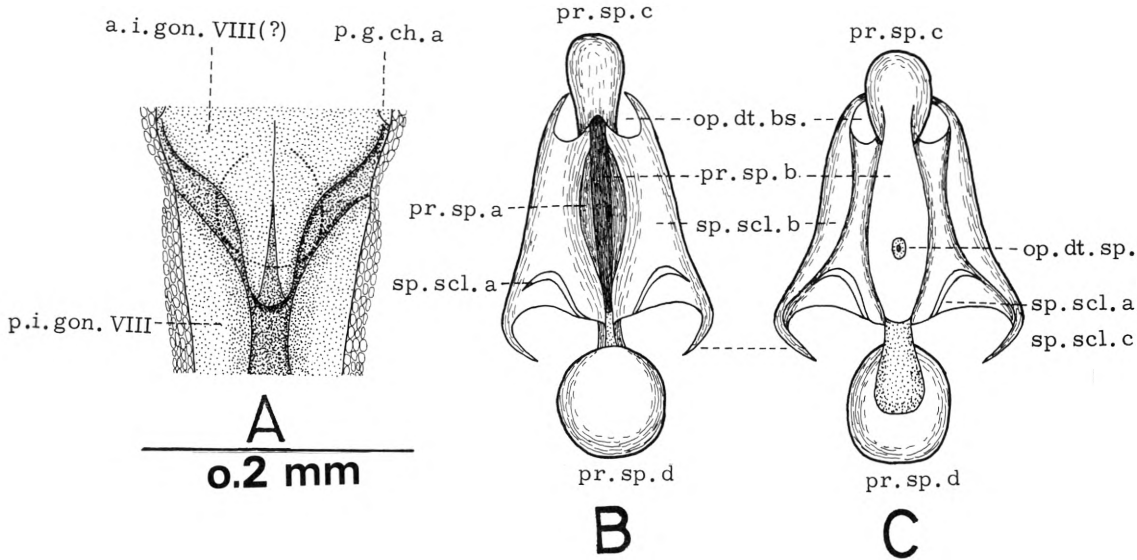


Fig. 75. *Oligoplectrum maculatum*. A: Middle part of floor of the genital chamber in a dorsal view. Processus spermathecae in dorsal view (B) and in a ventral view (C).

the descriptions given above and shown in figs. 73 and 74 A, but the ventral side undergoes a great deformation. Sternum VIII is strongly retracted, sternum VII being reflected along a line, which is lightly concave in the rear and just touches the anterior sides of the paired, more strongly sclerotized area. That part of the sternum which lies behind this line becomes vertical and strongly concave in a transverse direction. Sternum VII now is visible only in a posterior, neither in a lateral, nor in a ventral view. Part of the pleural membrane VII likewise is reflected. That part of the membrane which is visible in a lateral view is pointed ventrally. The posterior part of sternum VII overlaps sternum VIII as a much flattened fold. The greater, mesal part of the "ventral plate" becomes concave in both a longitudinal and particularly in a transverse direction.

The posterior "scale" on segments IX and X is somewhat deformed, the processes IXca and IXcc being bent inward and downward as well as a little forward. The "vulvar scale" (gon.VIII) is folded in a longitudinal direction, the lateral margins bent downward.

The posterior part of sternum VII and the

mesal part of the "ventral plate" form the evenly rounded bottom of the "egg-cup" (fig. 73 D). The walls are formed by the posterior, reflected part of sternum VI, a part of the pleural membranes VII, the rods v.VIIIb and the "vulvar scale".

The genital chamber (fig. 74 C) is very short, extending only to about the middle of the "ventral plate".

The spermathecal sclerite (figs. 74 C, 75 B, C) is approximately parabolic, narrower in front. It has an anterior indentation, forming a reniform "window" for the opening of the ductus bursae. However, the greater, antero-mesal part of the "window-frame" is lacking. The posterior margin of the sclerite has a pair of broad, but very shallow indentations. In front of each indentation a sickle-shaped, hollow carina (sp.scl.a) is seen.

As opposed to conditions in most other Trichoptera the spermathecal sclerite does not

bulge into the lumen of the genital chamber. Quite on the contrary, it is ventrally concave in a transverse direction, apart from a low longitudinal bulge (pr.sp.a) in the middle, which in a dorsal or ventral view is lentiform. On the ventral side of this bulge there is, again, a very high ridge (pr.sp.b), which from its narrow base is much dilated toward the rounded ventral side; the latter practically touches the floor of the genital chamber. In a ventral view the ridge pr.sp.b conceals pr.sp.a. It is broadest in the middle, somewhat behind which the small opening of the ductus spermathecae is found, surrounded by a small, membranous area.

Both the anterior and the posterior end of the ridge pr.sp.b projects beyond the ridge itself. The anterior projection (pr.sp.c) is pear-shaped, broader than the ridge itself in its broadest place, and somewhat sagittally compressed. It is forward and downward directed, bisects the opening of the ductus bursae, and projects into the posterior part of the common oviduct.

The posterior projection (pr.sp.d) is still broader, a circular or a little elongate and rather much flattened disc. It is connected with the ridge itself by a high, but rather much sagittally compressed shaft. Both the dorsal and the ventral side of the latter is membranous, and on the ventral side the membrane proceeds for a rather great distance onto the disc as a membranous ridge. The shaft bisects the opening of the colleterial duct, which is immediately behind the spermathecal sclerite.

Laterally the spermathecal sclerite (sp.scl.b) is bent downward and inward. The ventral, approximately horizontal parts of the sclerite lie on the bases of a pair of otherwise membranous folds (g.ch.a) on the lateral side of the genital chamber, flanking the ridge on the spermathecal sclerite. (In fig. 75 A only a very small part of these folds is seen). Thus there is formed a pair of sclerotic furrows, a sort of paired continuation of the ductus bursae. These furrows proceeds backward and downward upon a pair of

extensions (sp.scl.c) of the posterior corners of the spermathecal sclerite and, membranous, farther backward laterally to the cushion described below.

This membranous cushion (figs. 74 C, 75 A, a.i.gon.VIII?) lies on the floor of the genital chamber, below pr.sp.d, but proceeds farther backward than the latter. Its anterior end is almost as broad as the genital chamber, in a posterior direction it tapers considerably, with slightly S-like curved sides. In a lateral view it is quite low in front and highest near the posterior end, where it almost touches pr.sp.d. A longitudinal cleft divides the cushion into a pair of folds. In front the cushion is entirely bisected, but here the margins of the cleft are closely apposed. In a posterior direction they diverge (fig. 75 A), but in return the cushion here is only partly divided (fig. 74 C).

In the posterior part of the genital chamber there is a pair of not too well defined lateroventral folds (fig. 75 A, p.i.gon.VIII?). Their anterior ends flank the fold a.i.gon.VIII?. Behind the latter the two folds are separated only by a narrow interval.

A comparison with *Beraea* (p. 119) suggests the interpretation (i.gon.VIII) given above.

The common oviduct is long, extending to the anterior end of segment VII, very muscular, somewhat flattened and broader in an anterior direction.

The bursa copulatrix is rather large and approximately spherical. According to Dodson (1935) the distal end of the bursa is bilobed in the related *Brachycentrus subnubilis* Curt. The duct has a wide lumen.

The spermatheca is a slightly elongate sac. In the specimens dissected it was partly filled with an amorphous substance. A little less than the distal half of the ductus spermathecae, which is provided with a thin circular musculature, is somewhat dilated, fusiform. The glandula spermathecae opens just proximally to this swelling. Proximally the gland is just as thick as the duct.

It tapers in a distal direction and eventually is somewhat coiled.

The *colleterial glands* fill, immediately before egg-laying, most of the abdomen. Each gland has only two branches, one directed straight forward, the other straight backward. The very large colleterial duct is funnel-like.

Musculature. In the pregenital segments the muscles dm_5 , dm_6 and vm_5 seem to be lacking.

The internal one of the ventral VII–VIII muscles has its posterior attachment to the apodeme ap.VIII (fig. 73 B).

The muscle VIII dvm_4 is well developed. The (anterior) bands have their ventral attachment to the weakly sclerotized area which lies mesally to the rod v.VIIIb (fig. 73 B). See also below: VIII–IX muscles.

There are six VIII–IX muscles, which I have interpreted as dm_1 , dm_2 , dm_{4a} , dm_{4b} , dm_6 and vm_6 . The muscle dm_2 connects the apodemes ap.VIII (fig. 73 B) and ap.IX (fig. 74 A). The bands of dm_{4a} converge toward their posterior attachment on the rod-like sclerite which proceeds forward from the lateral reinforcement of the sclerite IXa (fig. 74 A). The muscle dm_6 connects the distal end of the apodeme ap.IX with the posterior part of tergum VIII, approximately at the level of the obtuse-angled anterior corner of IXa. Even in much distended specimens this muscle goes slightly backward. The slender vm_6 has its anterior attachment on the distal end of ap.IX and its posterior attachment to that part of v.VIIIb which is bent into the pocket below the process IXd (fig. 74 A).

A group of fine muscle bands, forming a sort of continuation of VIII dvm_4 , and perhaps to be considered as a posterior part of this muscle, has its dorsal attachment to the membranous area between the sclerite IXa (fig. 74 A) and the rod v.VIIIb. The ventral attachment is to the posterior part of this rod, though not to that part which is bent into the pocket below IXd.

The three following, rather strong muscles have each one attachment to the curved sclerite

(gon.IX) it the “mouth angle” of the genital chamber (p. 215). Their bands converge strongly toward this attachment. The muscle $gonm_1$ originates just in front of the base of the “vulvar scale”. Its middle axis is practically vertical. It is probably this muscle which causes the folding of the “vulvar scale” during the formation of an “egg-cup”. The ventral bands of $gonm_2$ originate laterally on the antecosta of IXa, the dorsal somewhat behind the latter. From its origin the muscle goes backward and somewhat downward. The muscle $gonm_3$ originates on the sclerite IXcb. It goes downward and forward.

A very slender IX–X muscle originates rather laterally on the antecosta of IXa and is inserted laterally to the posterior end of the anal tube.

The muscle *gchm* is lacking in *Oligoplectrum*.

Agrypnia pagetana Curt.

Pregenital segments. There are no glands on segment V.

Segment VII. On this segment the sternum is somewhat modified (fig. 76 B, C). The paired transverse suture is much shorter than on segment VI, and behind it, on each side, an indentation of the posterior margin is seen, so that the hind corners of the sternum do not reach the posterior end of the segment. Between the two indentations the hind margin of the sternum is convex, being produced rather much backward.

The genital segments (fig. 76). Segment IX is so firmly united with segment X, and venter VIII with the gonopods, forming a “ventral plate”, that the boundaries cannot be stated with any degree of certainty.

Segment VIII. Both the tergum and the sternum is considerably broader than on segment VII. In a lateral view (fig. 76 B) the pleural membrane appears only as a quite narrow stripe. Actually, however, it is a rather broad fold, which overlaps the lateral margin of the sternum, but this is seen distinctly only in a ventral

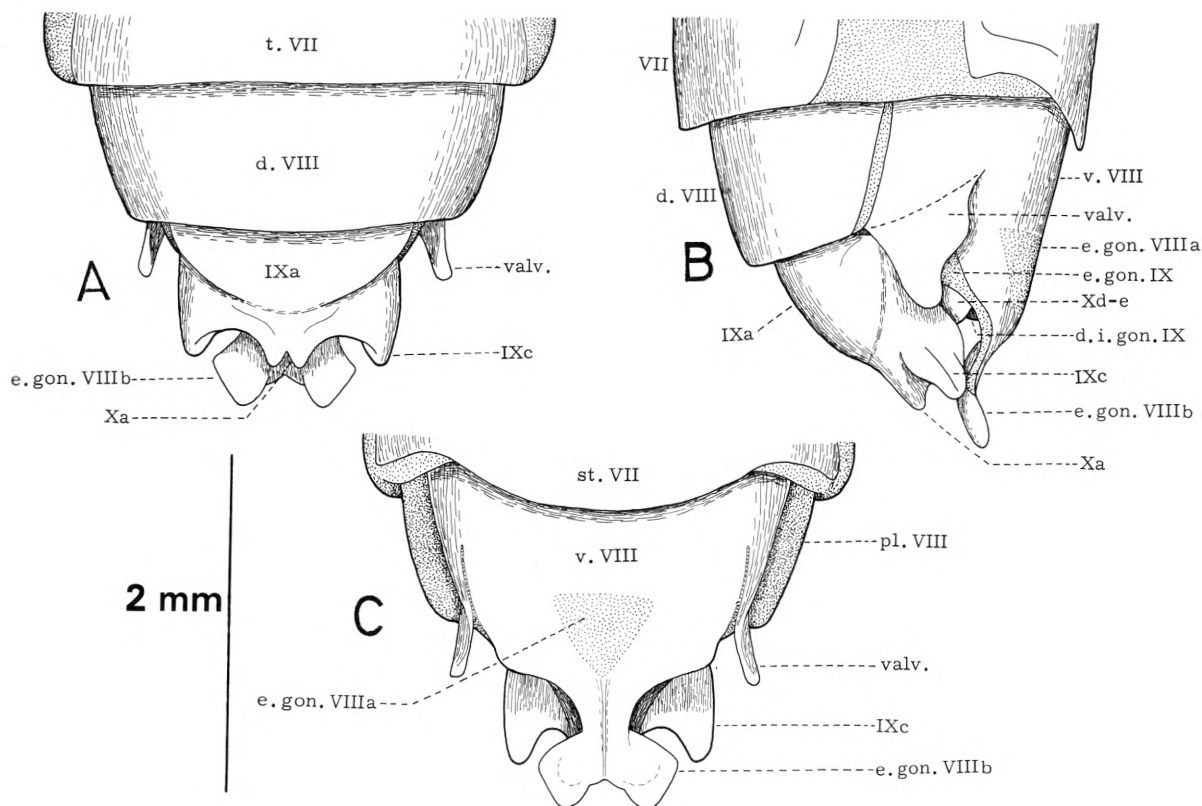


Fig. 76. *Agrypnia pagetana*. Posterior end of abdomen in a dorsal view (A), as seen from the right side (B) and in a ventral view (C).

view (fig. 76 C), since the tergum is much broader (though not higher) than the sternum. On the tergum the lateral end of the antecostal suture is bent backward, but a true longitudinal suture is not formed.

Segments IX and X are in front somewhat narrower than the posterior end of tergum VIII, but the width remains about the same for their whole length. They are approximately half as high as segment VIII, and in a lateral view the dorsal side is descendent. They are sclerotized to their greater extent.

An antero-dorsal area (IXa) is delimited by a horizontal, in a dorsal view strongly convex

furrow, which extends toward the anterior corners of the sclerite. The latter are produced into long and slender apodemes.

That part of the combined segment which lies behind the furrow is developed as a freely projecting "scale", sclerotized on both sides, the dorsal side of which is convex in a transverse direction. Its posterior end is divided into two processes (Xa and IXc). The ventral side (fig 77 A) is strongly concave. At the posterior end the concavity comprises only the smaller mesal processes Xa, which hence have the shape of thin lamellae. The process IXc is roughly triangular in a transverse section.

The concavity, which is sharply delimited, becomes broader in front, so that it eventually occupies the whole of the ventral side, i.e. it reaches the anterior corners of the combined

segment. From the concavity a tongue (Xc-e) arises along a posteriorly convex line. This tongue, which projects backward, though not as far as the processes Xa and IXc, actually is rather thick, but about its mesal half is strongly concave, the concavity being sharply delimited. Its posterior end therefore is in the shape of a thin lamella. The anus is found in the narrow furrow between this lamella and the processes Xa.

The ventral side of the tongue Xc-e, as well as the lateral, freely exposed parts of its dorsal side (fig 78, Xd-e) are sclerotized. On the ventral side, which is much longer than the dorsal side, the sclerite proceeds into the posterior end of the genital chamber (fig. 79), on the dorsal side of which it projects forward as a transverse fold, thicker in a lateral direction. The tongue Xc-e thus forms the upper lip of the genital opening. The IX-X muscles (see below) proves that it belongs to segment X, and the same no doubt is the case with the processes Xa.

Close to and in front of the furrow delimiting the area IXa (fig. 76 A) there are, on each side, a transverse row of some few yellow setae. They remind of the "brush" in the male (Anker Nielsen 1957, p. 116, fig. 65 C), though they are much smaller than the setae in question in this sex. Similar setae – and in a much greater number – are scattered on the dorsal side behind the furrow, as well as on the ventral sides of the processes IXc (fig. 77 A).

The "ventral plate". (fig. 76 B, C) is largely sclerotized. An almost flat and slightly ascendent ventral side and vertical lateral sides may be distinguished. However, the ventral side is by no means sharply delimited toward the lateral sides.

In front of the middle, at the possible boundary between sternum VIII and the gonopods (see below: the muscle gonm₁), the lateral side is produced into a backward directed tongue (valv.), arising from the "ventral plate" itself along a steeply ascendent line, the dorsal end of which lies at the level of the posterior corner of

tergum VIII. The area covered by this tongue is membranous, though the tongue overlaps the sclerite a little. The membrane overlaps as a short fold the structure Xd-e described below. This fold probably represents part of gonopods IX (see below: the muscle gonm₃).

The proximal part of valv. is closely applied to the "ventral plate" itself, and is membranous on the mesal side. The narrower, freely projecting distal part is sclerotized on the mesal side, as is the whole lateral side. The shape of the freely projecting part is subject to individual variation, also among specimens from the same locality. The tongue may be a remnant of a lateral valve as found in *Rhyacophila* (p. 28).

Quite laterally the sclerite of the "ventral plate" does not reach the anterior end of segment VIII, since triangular membranous areas are found at the anterior corners. Between these areas there is a well developed antecosta.

The "ventral plate" decreases in width in a posterior direction, and the hind margin, separated from the side margins by rounded corners, is a little more than half as broad as the anterior margin. In the middle it is produced into a large "vulvar scale" (e.gon.VIIIb), that part of the abdomen which projects farthest backward, at the base of which there is an unpaired, triangular, pale and weakly sclerotized area (e.gon.VIIIa), not sharply delimited.

The "vulvar scale" (figs. 77 B, 78 and 79) consists of an ascendent shaft and a broader, bilobed, horizontal or slightly downward bent distal part, which is pale, but apparently stiff. An indistinct, longitudinal keel is seen in the middle of the ventral side. Each half of the thin distal part is concave on the ventral side and convex on the dorsal side.

Both the dorsal and the ventral side of the "vulvar scale" is sclerotized, but the dorsal and the ventral sclerites are continuous only through the weak sclerotization on the distal lobes. The ventral sclerite is continuous with the main sclerite of the "ventral plate". In an anterior

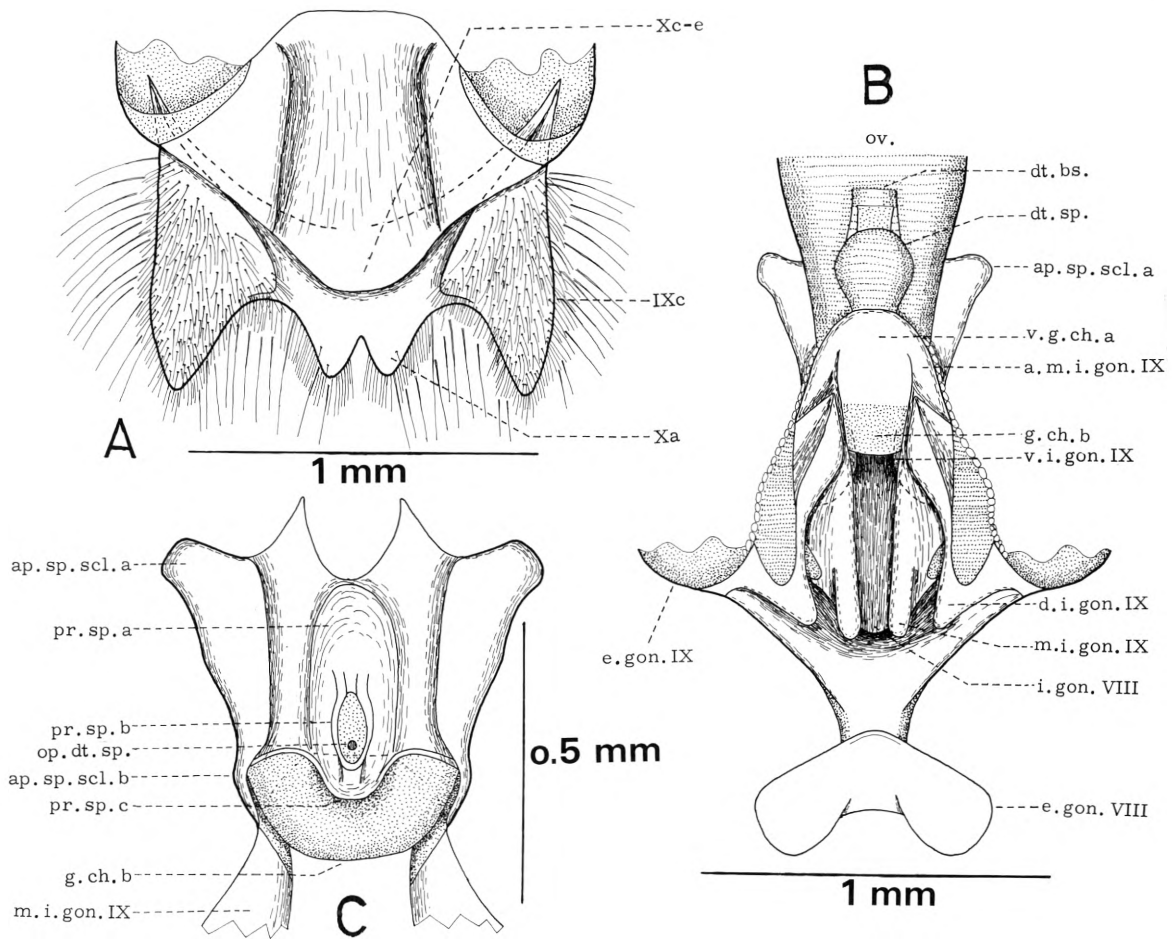


Fig. 77. *Agrypnia pagetana*. A: Segments IX and X in a ventral view. B: Floor of the genital chamber etc. in a dorsal view. C: Processus spermathecae etc. in a ventral view.

direction the dorsal sclerite is narrower than the ventral one. The two sclerites are separated by a membranous stripe on the lateral side of the shaft. This stripe proceeds, gradually broader, along the hind part of the main part of the "ventral plate" and eventually is continuous with the membrane (e.gon.IX) below the tongue valv.

The main part of the "ventral plate" has a sparse covering of very small setae. On the ventral side of the shaft of the "vulvar scale" the

setae are much larger and more close-set. The dorsal side of the shaft as well as both sides of the distal lobes are devoid of setae, but the dorsal sides of the lobes have, in contrast to the ventral sides, a dense covering of microtrichia.

The genital chamber (figs. 77 B, 78 and 79) is short, extending only to the anterior third of the "ventral plate". It is rather sharply divided into two parts, about equal in length. The posterior part is broader than the anterior one, and increases moreover considerably in width in a posterior direction. The ventral sides of the two parts are approximately flush, but the posterior part is about twice as high as the somewhat flattened anterior part. Dorsally its front end

bulges forward above the hind end of the anterior part, the genital chamber thus in front being divided into a longer ventral and a shorter dorsal (g.ch.a) branch. The colleterial duct opens on the upper side of the dorsal branch, the lower side of which is slightly sclerotized.

Including the apodemes described below the spermathecal sclerite (fig. 77 C) is roughly trapezoidal with the broad end in front. Laterally it is

bent sharply downward and inward, a pair of wing-like apodemes (ap.sp.scl.) thus being formed. The broader anterior end (ap.sp.scl.a) of this apodeme projects forward as a short tongue. In a posterior direction the apodeme becomes narrower, and its quite narrow posterior end (ap.sp.scl.b) is continuous with the sclerite on the fold m.i.gon.IX described below. Between the apodemes the anterior margin of the

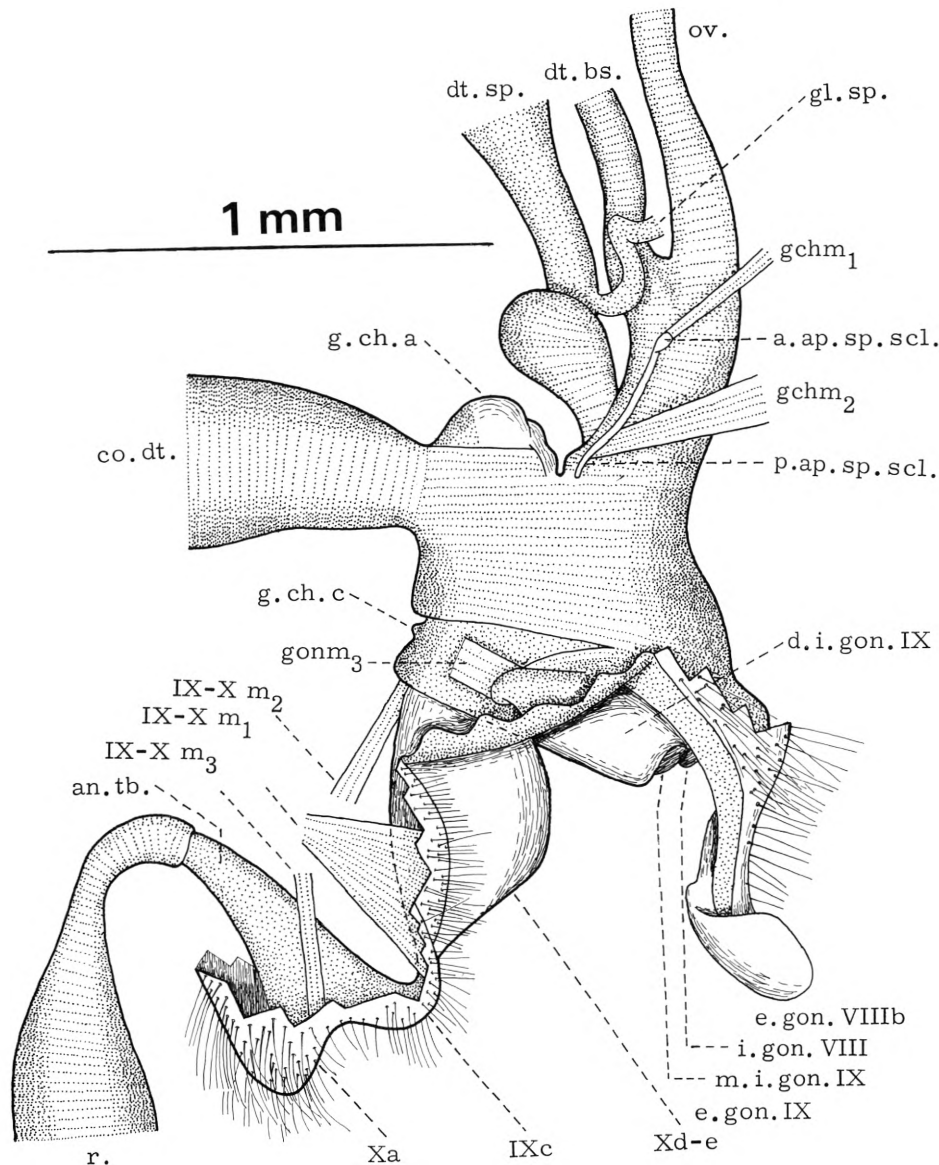


Fig. 78. *Agrypnia pagetana*. The genital chamber etc. as seen from the right side.

sclerite proceeds forward, but this extension is interrupted by an unpaired, parabolic indentation behind the opening of the ductus bursae.

The ventral side of the spermathecal sclerite is concave in a transverse direction except for its mesal half which bulges into the lumen as a rounded ridge, the processus spermathecae (pr.sp.a) which, in a ventral view, has rounded anterior and posterior ends. The latter projects backward, beyond the spermathecal sclerite, as a rounded process (pr.sp.c), laterally to which the sclerite forms a low and backward directed fold.

Superimposed, so to speak, on the posterior half of the processus there is a much narrower ridge (pr.sp.b), in the middle of which an elongate, membranous area is seen. The small opening of the ductus spermathecae is situated in the posterior part of this area.

The lip between the two branches of the anterior part of the genital chamber projects backward above and behind the processus spermathecae as a thick membranous tongue (figs. 77 B, 79, g.ch.b) which is almost as broad as the lumen of the genital chamber, but relatively short.

In the higher, posterior part of the genital chamber (figs. 77 B and 79) there are three pairs of longitudinal folds, a lateral one (d.i.gon.IX), a latero-ventral one (m.i.gon.IX) and one (v.i.gon.IX) below the anterior end of the latter. The rear end of the lateral fold (d.i.gon.IX) is rather low, but very broad and covers almost the whole lateral side of the genital chamber. It is sclerotized except for an area dorsally on its base. Its posterior end projects (fig. 78) as a large, in a lateral view roughly triangular, sagittally compressed process, the dorsal side of which lies at a more lateral level than the ventral one. This process is in situ just visible between the tongue Xd-e and the base of the "vulvar scale" (e.gon.-VIII, fig. 76 B). Dorsally its lateral side is overlapped by the fold Xd-e. In an anterior direction the fold gradually becomes much narrower and is shifted to a latero-dorsal posi-

tion. Eventually it enters the dorsal branch of the genital chamber (g.ch.a), where it is membranous and forms the fold co.dt.b described below.

At the posterior end of the genital chamber the fold m.i.gon.IX arises laterally on the ventral side. Here it is high, but rather narrow, and almost vertical, though inclined somewhat inward. It is sclerotized except for a small area dorsally on its base. Its posterior end projects as a tongue-like process, which is not nearly as broad (or high) as that formed by the fold d.i.gon.IX. In an anterior direction the fold m.i.gon.IX rather abruptly becomes much lower and narrower, and is shifted to a lateral position. Eventually it enters the lower side of g.ch.a as a narrow ridge (fig. 79, a.m.i.gon.IX). As mentioned above it is connected with the spermathecal sclerite by a narrow, sclerotic bridge (fig. 77 C, ap.sp.scl.b), which passes laterally to the tongue g.ch.b.

The posterior, sclerotized part of the third fold (v.i.gon.IX) lies ventrally on the lateral side of the genital chamber, below the anterior, narrow part of the fold m.i.gon.IX. It extends, membranous and gradually disappearing, into the ventral part of the genital chamber (fig. 77 B), flanking the processus spermathecae.

In the posterior part of the genital chamber the ventral wall is raised as an unpaired, sclerotized fold which in front, between the folds v.i.gon.IX is quite low, but gradually becomes higher. Its posterior end projects as a rather high, but quite short process (figs. 77 B, 79, i.gon.VIII).

At the posterior end of the genital chamber the sclerites on the structures d.i.gon.IX, m.i.gon.IX and i.gon.VIII are continuous with each other as well as with the sclerite on the dorsal side of the "vulvar scale".

On the dorsal side of the posterior, undivided part of the genital chamber there is a small sclerite (figs. 78 and 79, g.ch.c), which has a rounded suture along its hind margin.

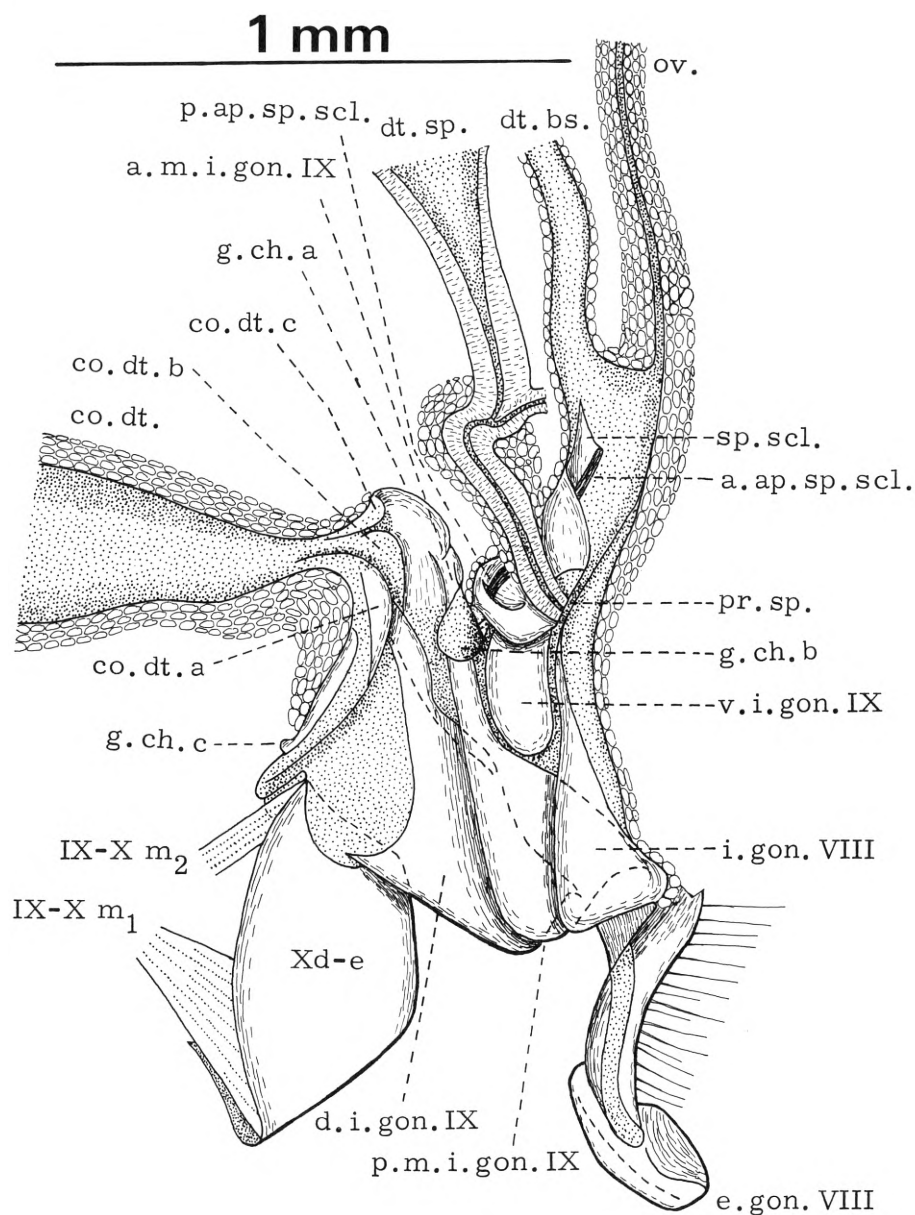


Fig. 79. *Agrypnia pagetana*.
Sagittal section of the genital
chamber etc.; left side as
seen from the inside.

The opening of the colleterial duct into the dorsal branch of the genital chamber (fig. 79, g.ch.a) is narrowed by three pairs of folds. One (co.dt.a) lies on the posterior side of the opening and continues on the dorsal side of the genital chamber until the sclerite on the tongue Xd-e, flanking the small sclerite g.ch.c. For a small part

of its extent, facing the lumen of g.ch.a, it is sclerotized, otherwise membranous. The other (co.dt.b), an anterior continuation of the fold d.i.gon.IX described above, lies on the lateral side, and the third (co.dt.c) on the anterior side of the opening. The two latter folds are entirely membranous.

The common oviduct extends to the middle of segment VII.

The bursa copulatrix is spherical and thin-walled. In one specimen it contained a brownish-yellow, hard substance. The short duct opens into the anterior indentation in the spermathecal sclerite.

The spermatheca is a large, thin-walled sac. In the distal part close-set, 21 μ long and $1\frac{2}{3}\mu$ thick microtrichia are seen. The short, proximal part of the ductus spermathecae (figs. 78 and 79) has a narrow lumen, a glandular epithelium, and a strong circular musculature, which increases in thickness toward the distal end. The very long and convoluted glandula spermathecae opens distally in this part of the duct. Beyond the opening of the gland the duct is devoid of musculature, widens gradually and passes into the spermathecae, its epithelium decreasing in thickness.

The colleterial glands are very voluminous. Each gland is divided into three branches. One extends into the foremost abdominal segments. The two others, a dorsal and a ventral one, are directed in a posterior direction and extend into segment IX. The vertical, funnel-like duct opens on the dorsal wall of the upper branch (g.ch.a) of the genital chamber.

Musculature. Among the ventral VII–VIII muscles there are, besides the usual external and internal muscles, two which no doubt is vm_5 and vm_6 . The former is rather broad, the latter consists of two narrow bands. Both have their anterior attachments close to each other, approximately in the middle of sternum VII.

The dorsal VIII–IX musculature is rather complete, only dm_3 lacking. The muscle dm_2 consists of only one band, which is narrower than each band in the preceding segments. The muscle dm_6 is divided into two portions, which originates on the lateral side and dorsally on the apex, resp., of the apodeme of segment IX (p. 150). Further vm_6 is present. It, too, originates on the apodeme of segment IX and is inserted to

the lateral margin of that part of the ventral plate which is overlapped by the lamella valv. (fig. 76 B).

The broad, but flat $gonm_1$ originates on the "cut off" anterior corner of sternum VIII (p. 151). It converges less than 45° in a posterior direction, and its bands also converges somewhat toward their insertion, approximately midway between the area e.gon.VIIIa and the lateral side of the "ventral plate" (fig. 76 C). The muscle $gonm_2$ originates behind the furrow separating the areas IXa and IXc (fig. 76 A) and is inserted to the lateral margin of the "ventral plate" behind VIII–IX vm_6 . The muscle $gonm_3$ (fig. 78) originates in front of the furrow mentioned above, passes vertically or steeply ascendent mesally to $gonm_2$, through the lateral part of the tongue Xd-e, and is inserted to the bottom of the deep furrow between this tongue and the membrane at the base of the "vulvar scale".

There are three IX–X muscles (figs. 78 and 79). One, IX–X₁, is rather strong. It originates mesally in front of the furrow behind IXa (fig. 76 A). Its bands diverge fan-like toward their insertion on the posterior half of the ventral side of the tongue Xd-e. The flat IX–X₂ originates in front of the process IXc. It passes forward, converging ca. 45° , and is inserted to the anterior part of the ventral side of the tongue Xd-e. The third muscle, IX–X₃, is very slender. It originates on IXa near, but not on, the antecosta, approximately at the middle of each half of the latter. It passes mesally to IX–X₁ and is inserted laterally to the posterior part of the anal tube.

Two muscles are associated with the spermathecal sclerite (fig. 78). One, $gchm_1$, slender and ca. 45° ascendent, originates at the anterior, "cut off" corner of sternum VIII (p. 151). Its bands converge a little fan-like toward their insertion on the apodeme ap.sp.scl.a (fig. 77 C). The other, stronger and more steeply ascendent muscle, $gchm_2$, originates on the ventral plate in front of the area e.gon.VIIIa (fig. 76 C) Its

bands converge fan-like toward their insertion on the posterior part of the apodeme of the spermathecal sclerite.

Except for its posterior end the genital chamber has a strong circular musculature. The circles, however, are complete only on two small parts of the chamber, namely at the anterior end and between the colleterial duct and the anterior end of the tongue Xd-e. In the region of the spermathecal sclerite they are interrupted by the apodemes of the latter. In the region of the colleterial duct the bands of course extend only to this duct. The ventral side and the whole anterior end of g.ch.a (fig. 78) are devoid of muscles.

Limnophilus flavicornis F.

(*Limnophilus flavicornis* F.)

Pregenital segments. On the segment to and including V the two longitudinal sternal sutures, right and left, near their posterior ends, at about the posterior third of the sternum, are connected by a distinct, transverse, a little backward bent suture. On sternum VI the anterior part only of the longitudinal suture is found, but the transverse suture still is present. Immediately in front of the latter a small, unpaired tooth is seen.

On segment VII the sternum is better defined than on the preceding segments; in the middle its posterior margin has a shallow, membranous indentation (fig. 80 B, C). The lateral ends only of the transverse suture are present. They are strongly bent, concave in a postero-lateral direction.

There is no gland on segment V.

The genital segments (fig. 80). Segment IX is so intimately united with segment X that the boundary cannot be stated with any degree of certainty. The much reduced external parts of the gonopods form a "vulvar scale" (e.gon.VIII and e.gon.IX) which is rather clearly separated from sternum VIII. This boundary, however, may very likely be secondary and not the true

one. The fact that sternum VIII projects farther backward than tergum VIII suggests this explanation.

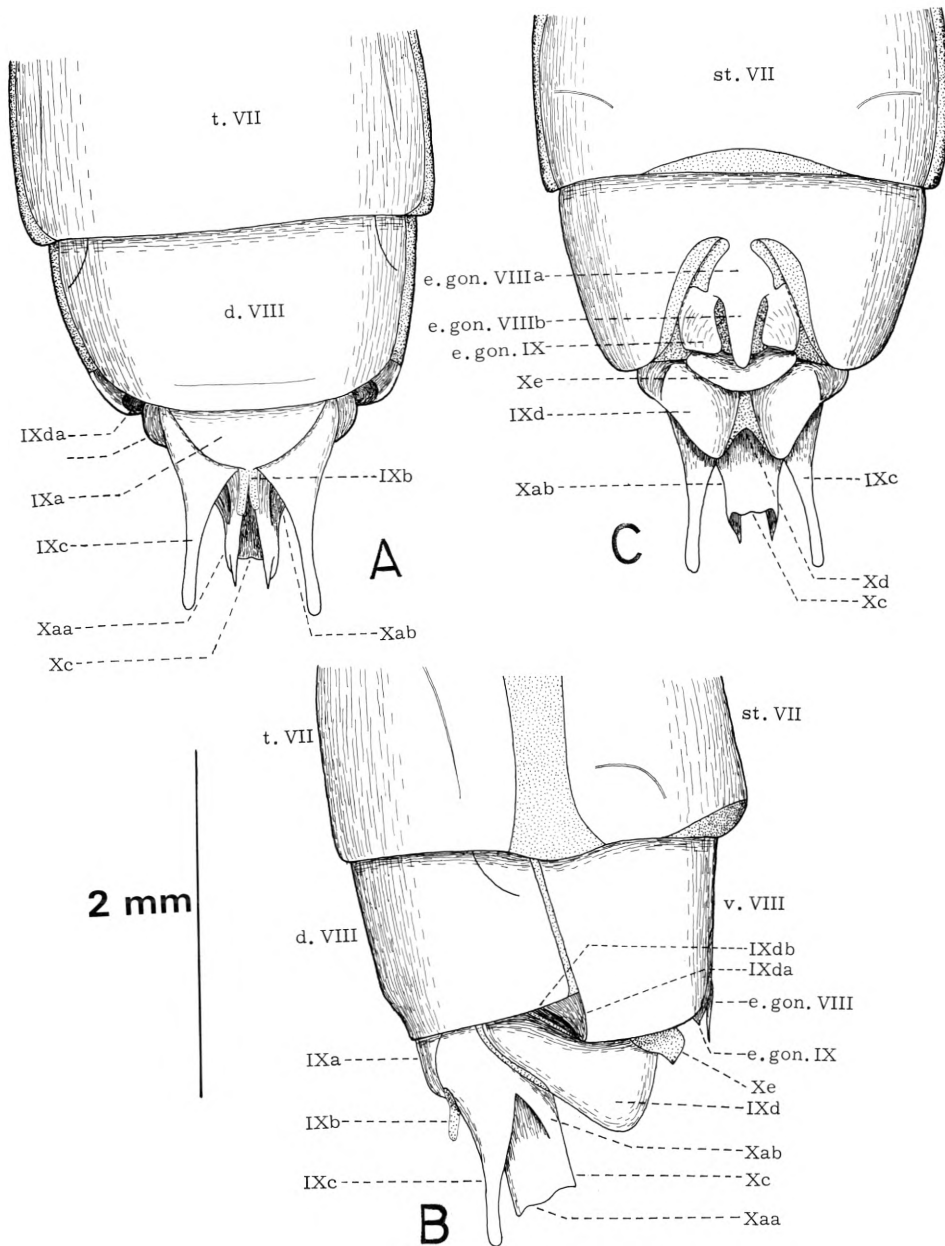
On segment VIII the tergum, and especially the sternum, are broader than on the preceding segments. The pleural membrane is partly inverted between the tergum and the sternum. In a lateral view (fig. 80 B) it appears only as a quite narrow stripe. In a dorsal view (fig. 80 A) it looks a little broader, since the sternum projects farther laterally than the tergum.

Tergum VIII, apart from its greater width, is developed as the preceding ones. The lateral longitudinal suture, however, is much shorter, extending for less than the anterior half of the tergum, and still more indistinct than on tergum VII; (in fig. 80 A, B it is largely concealed by the overlapping posterior margin of tergum VII). It is S-like curved, laterally convex in its anterior part, laterally concave in its posterior part.

Sternum VIII, as mentioned above, projects somewhat farther backward than tergum VIII. Behind the posterior corner of the latter there is a small sclerite, devoid of setae and of a rather complicated shape. By an approximately right-angled keel it is divided into two parts. One (IXda) lies behind the pleural membrane VIII, facing laterally, upward and a little backward. It is continuous with the lateral margin of sternum VIII, though separated from it by a narrow, upward directed ridge. This part of the sclerite is triangular and considerably broader than pleural membrane VIII, dorsally to which its anterior margin is overlapped by tergum VIII. The other part (IXdb), which is more strongly sclerotized, lies transversely, facing backward and a little upward. It is strongly concave, and ventrally the concavity is deepened to a pot-like depression, possibly destined to receive some part of the male genitalia during copulation. The musculature proves that at least this part of the sclerite belongs to segment IX.

Segments IX and X are considerably narrower than tergum VIII and of a very complicated

Fig. 80. *Limnephilus flavicornis*. Posterior end of abdomen in a dorsal view (A), as seen from the right side (B) and in a ventral view (C).



shape. The dorsal side is almost entirely sclerotized. A low, but distinct declivity delimits an antero-mesal area (IXa). That part which lies postero-laterally to the declivity is produced into a long process (IXc), which from a thick base tapers gradually for a little more than its proxi-

mal half, whereas the distal part is slender and finger-like. Except for the proximal part of the mesal side the process is entirely sclerotized. The lateral side reaches the anterior end of the combined segment, where it is not delimited against the area IXa.

Between the bases of the two processes IXc there is, on the dorsal side, a pair of small, finger-like, membranous processes (IXb). They probably are homologous with the processes IXb in *Molanna* (p. 125).

Below and between the two processes IXc a strongly sclerotized tube (Xa-c), carrying the anus, is seen. The posterior half of this tube (MacLachlan's "tubular piece") is slender. In its anterior half it becomes broader, owing to a pair

of latero-ventral, horizontal wings (Xab). In a dorsal view the tube has concave lateral margins. The ventral side, including the ventral side of the "wings", is flat. The dorsal side is cleft for its whole length by a narrow, V-like indentation.

By dissection it is revealed that the wall of the tube is double, i.e. it contains an extension of the haemocoel (fig. 81 B). The dorsal and lateral sides of the tube is continuous with the ventral side of the process IXc (fig. 80 B), the base of the

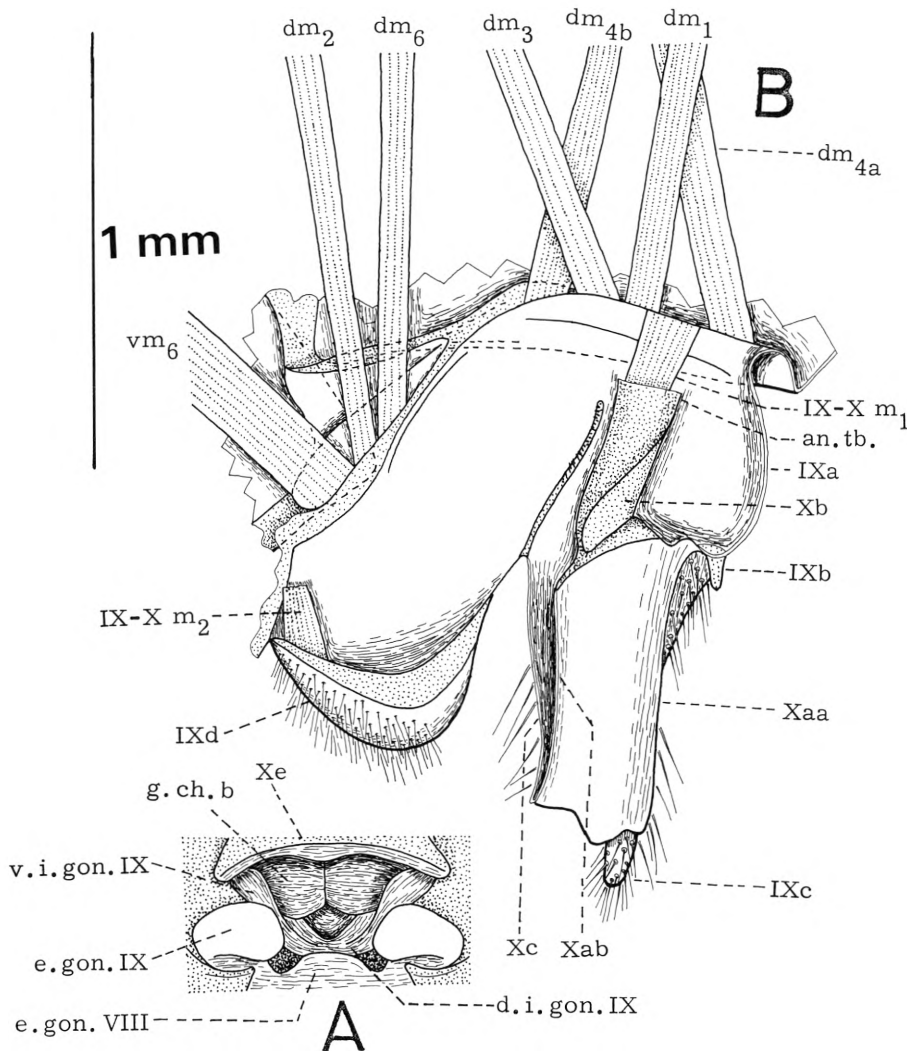


Fig. 81. A: *Limnephilus rhombicus*; the genital opening and its surroundings in a posterior view. B: *Limnephilus flavicornis*; sagittal section through segments IX and X; right side as seen from the inside.

“wing” Xab with the base of this process (fig. 80 B). Between Xab and the lateral side of IXc a broad, rounded furrow is seen.

The morphological anus probably is found in the bottom of the “tubular piece” (fig. 81 B). The anal tube, the ventral side of which is flush with that of the lumen of the “tubular piece”, is approximately half as high as the latter, but the anus is very much narrowed by a downward and backward directed, membranous tongue (Xb), issued from the dorsal side of the anal tube.

Below the processes IXc and the “tubular piece” there is a pair of very large, but rather short, subconical processes (figs. 80 and 81 B, IXd), which together are broader than IXa + IXc of both sides. The process IXd is somewhat sagittally compressed, and its lateral side is slightly concave. Except for the mesal side the process is sclerotized, though rather weakly. In the middle the ca. 45° descendent anterior margin of the sclerite has a narrow reinforcement (fig. 81 B). For its proximal half the process IXd is united with the process IXc, but the sclerites of the two structures are separated by a narrow, membranous stripe, except at the extreme anterior end.

To sum up: At the anterior end of the combined segment the sclerites IXa, IXc and IXd are continuous and separated by no boundaries. The base of the process IXd is to a rather great degree overlapped, ventrally by the membrane bordering the “vulvar scale” (fig. 80 C), dorsally by tergum VIII (fig. 80 A, B).

The membranous mesal sides of the processes IXd are united for more than their anterior half below the “tubular piece” (fig. 80 C). The ventral sides of the most proximal parts of the “tubular piece” and of the processes IXc are formed, so to speak, of the united processes IXd.

Below the processes IXd there is an unpaired, short tongue (figs. 80 B, C, 81 A, 83, Xe), approximately as broad as one of the processes IXd. The dorsal side of the tongue is membranous. On the longer ventral side there is a

strongly concave sclerite. It has a convex posterior margin, coinciding with the sharp posterior edge of the tongue, and a concave anterior margin. This sclerite, which is smooth and devoid of setae, forms the upper lip of the genital opening.

The processes IXb probably are homologous with those of *Molanna* (p. 125) and thus may mark the boundary between segments IX and X in the mesal line. The musculature, however, proves that the structures IXc and at least the lateral part of IXd belong to segment IX. Part of the mesal side of the latter, however, must belong to segment X and constitute, together with the “tubular piece” and the tongue Xe the externally visible parts of this segment.

The tongue Xe is reminiscent of the tongue Xb in *Sericostoma* (p. 107), but the positions of the two structures in relation to the anus proves that they cannot be homologous. But the membranous tongue Xb which narrows the anus in *Limnephilus* probably is homologous with the tongue Xb in *Sericostoma* and has been labelled accordingly. Still, the tongue Xe probably belongs to segment X, since this segment in Trichoptera in general forms the upper lip of the genital opening.

Except for a large anterior area, including the whole of IXa, and the ventral side of the tongue Xe, the sclerotized parts of segments IX and X are covered with setae, especially close-set on the distal parts of the processes IXc and IXd.

“*The vulvar scale.*” The posterior margin of sternum VIII (fig. 80 C) has a broad and deep indentation. In this otherwise membranous indentation there is a sclerite (e.gon.VIIIa), the basal part of the “vulvar scale”, which by an unpaired sclerotic bridge is connected with the sternum. The posterior, freely projecting part of the “vulvar scale”, forming the lower lip of the genital opening, is divided into an unpaired middle lobe (e.gon.VIIIb) and a pair of side lobes (e.gon.IX). The middle lobe projects farthest backward, though not as far as the tongue

Xe. It narrows gradually toward its rounded posterior end and is quite thin. The stouter, but a little shorter side lobes are thicker. Their proximal part is horizontal, their distal part is ascendent and concave. The side lobe thus has a sharp posterior edge, which is its only part seen in a lateral view (fig. 80 B).

All three lobes are sclerotized on the ventral as well as on the dorsal side, but on the latter (fig. 85 B), which on the side lobe is not half as long as the ventral side, the sclerites of the middle lobe and the side lobes are not directly continuous. (Cp. below: the folds d.i.gon.IX in the genital chamber).

The membranous area flanking the sclerite e.gon.VIIIa, as well as the latero-anterior parts of the side lobes are overlapped a little by sternum VIII, which forms a fine fold.

The "vulvar scale" is smooth and devoid of setae.

The genital chamber (figs. 82 and 85 B) is short, not extending much beyond the middle of the "ventral plate". In a dorsal view it is broadest at its posterior third. From here the chamber tapers rather strongly in anterior, more feebly in a posterior direction. The greater, anterior part of the genital chamber is flattened with a horizontal dorsal side. The latter rises abruptly into a short vertical part followed by a second horizontal part. The latter, however, is masked by the musculature of the colleterial duct.

For most of its length the dorsal wall of the genital chamber is covered by the brownish spermathecal sclerite (figs. 84 and 86). The narrow, crescentic, posteriorly concave opening of the ductus bursae is found in the anterior end of the sclerite. The anterior side of the "window", however, is not complete, but the anterior corners of the sclerite form a pair of forward and inward directed, spatulate extensions (sp.scl.a), flanking the opening.

That part of the spermathecal sclerite which lies on the anterior, horizontal part of the genital chamber is rather slightly convex in a transverse

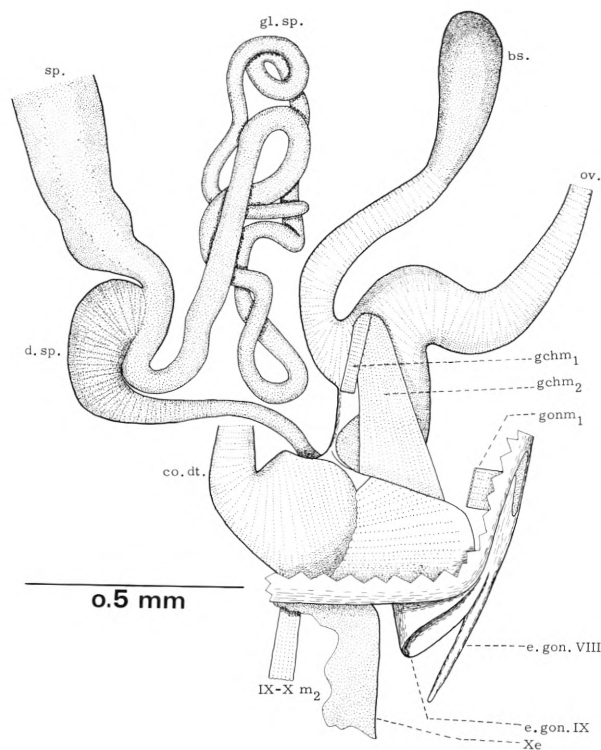


Fig. 82. *Limnephilus flavicornis*. The genital chamber etc. as seen from the right side.

direction. In the middle, however, it rises as a longitudinal keel (pr.sp.a), which is very broad in front, narrow behind. The shape of its anterior end varies. In some specimens it projects forward below the opening of the ductus bursae (fig. 86 B), in others it is gradually descendent (fig. 84). Superimposed on a little more than the posterior half of this keel there is another and narrower one (pr.sp.b), rising from a still narrower base. It is broadest approximately in the middle. Its posterior end (pr. sp.c), which projects farther backward than pr.sp.a itself, is very slender, especially in a lateral view, and carries near the extreme posterior end the opening of the ductus spermathecae. The flat ventral side of pr. sp.b almost touches the floor of the genital chamber.

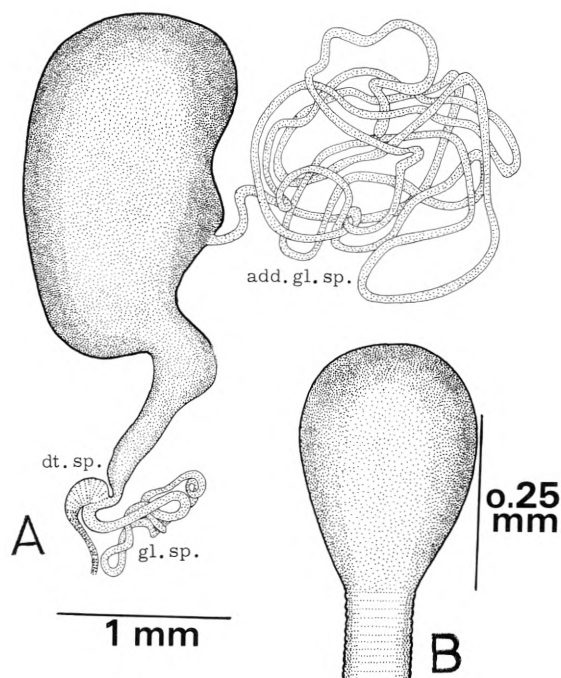


Fig. 83. *Limnephilus flavicornis*. A: The spermatheca as seen from the right side. B: Bursa copulatrix in a dorsal view.

That part of the spermathecal sclerite which lies on the vertical part and the posterior horizontal part of the wall of the genital chamber bulges into the lumen (fig. 84) as a large and plump, rounded process (pr.sp.d), the dorso-anterior corner of which is produced into an extension. The processes pr.sp.a and pr. sp.d together form the processus spermathecae. The ventral side of pr.sp.d has a membranous area above pr.sp.c.

Laterally the anterior, horizontal part of the spermathecal sclerite is bent downward as a wing-like apodeme (fig. 86 B, ap.sp.scl.), which is rather broad (or high) in front. Behind the middle its ventral margin is steeply ascendent, and at the hind end the apodeme is very narrow. Its rounded anterior end forms part of the spatulate extension (sp.scl.a) mentioned above. Its hind end is connected with the sclerite on the

fold v.i.gon.IX described below by a narrow sclerotic bridge (sp.scl.b).

On the lateral and ventral sides of the genital chamber (figs. 84 and 85 B) there is a sclerotic bow, which dorsally is considerably more than double as broad as ventrally, since its anterior margin is steeply descendent, its posterior margin steeply ascendent. Both the front end and the hind end of the bow bulges into the lumen as a pair of folds which, in each pair, is continuous across the ventral side of the genital chamber. Both pairs of folds are inclined much backward, and the anterior folds (v.i.gon.IX) extend almost as far backward as the, especially in the middle, narrower posterior folds (d.i.gon.IX). The folds v.i.gon.IX are entirely sclerotized only laterally; in the middle their dorsal (or anterior) side is membranous. The process pr.sp.c, carrying the opening of the ductus spermathecae, rests on this membranous area, in front of which there is a pair of longitudinal, membranous folds (fig. 85 B, g.ch.a), flanking the keel pr.sp.a.

The relations between these folds and the opening of the colleterial duct (fig. 84) suggest that they are homologous with the ventral (v.i.gon.IX) and the dorsal fold (d.i.gon.IX), resp., in other forms. Their positions in *Limnephilus* are due to a shortening of the genital chamber, in connection with which d.i.gon.IX (figs. 80 B, C, 84, 85 B) has shifted to a ventral and rather mesal position. As in *Apatania* (p. 182) it is the ventral fold which is connected with the spermathecal sclerite.

Between the folds v.i.gon.IX and d.i.gon.IX there is a broad, rounded, sclerotic furrow, which, however, is entirely filled by a pair of blunt, sclerotic processes (figs. 84, 85 B, g.ch.b), arising laterally on the dorsal wall of the genital chamber and flanking the opening of the colleterial duct. The posterior sides of their membranous bases are closely apposed to the upward bent front end of the ventral side of the tongue Xe. Mesally the two processes (right and left) touch each other and thus, together with the

ventral part of the folds d.i.gon.IX, obstruct the genital opening (as in fig. 81 A, drawn from *L. rhombicus*. In fig. 85 B they conceal the folds d.i.gon.IX).

The common oviduct is approximately two and a half times as long as the genital chamber. Near

its posterior end it is bent upward (figs. 82 and 84).

The bursa copulatrix (figs 82 and 83 B) is a small sac, which in a dorsal view is pear-like, but much flattened. The muscular ductus bursae is long. Near its posterior end (figs. 82 and 84) it is

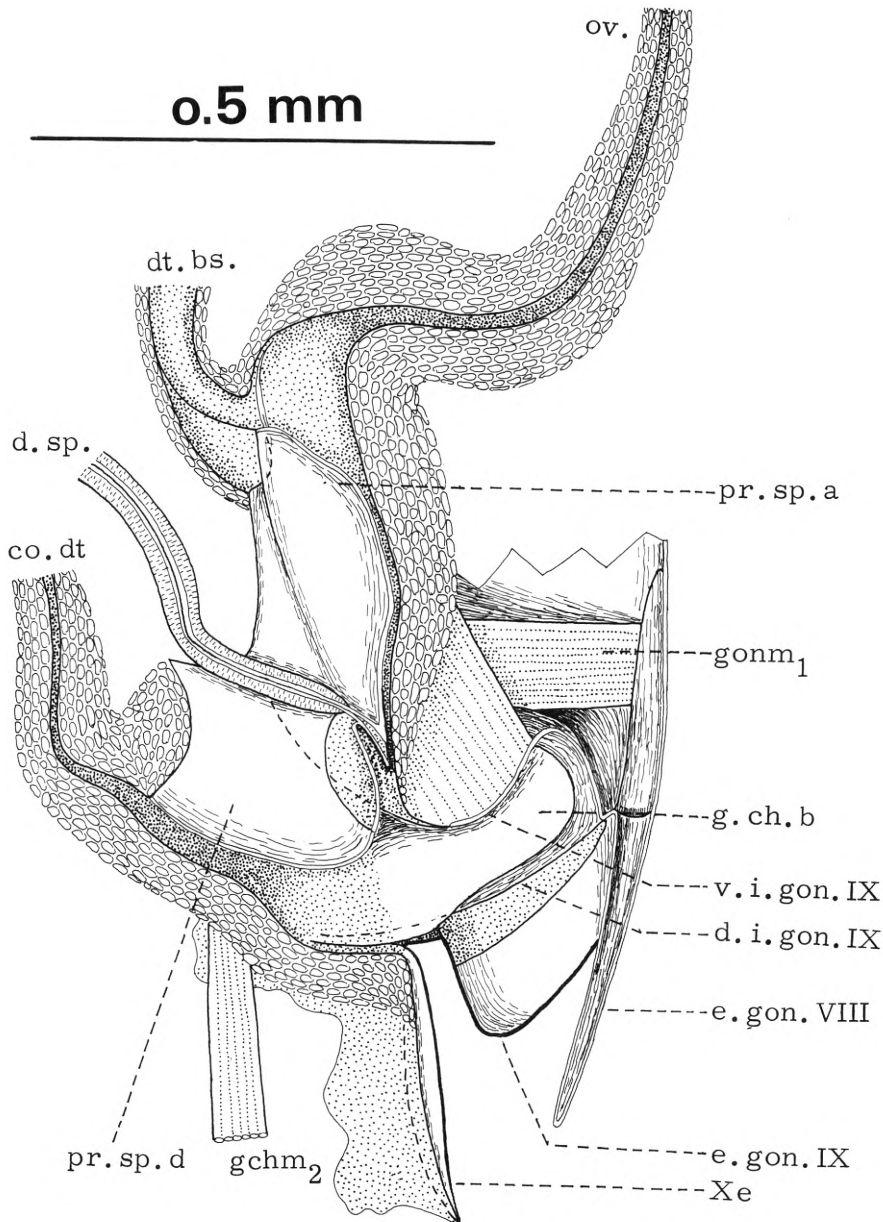
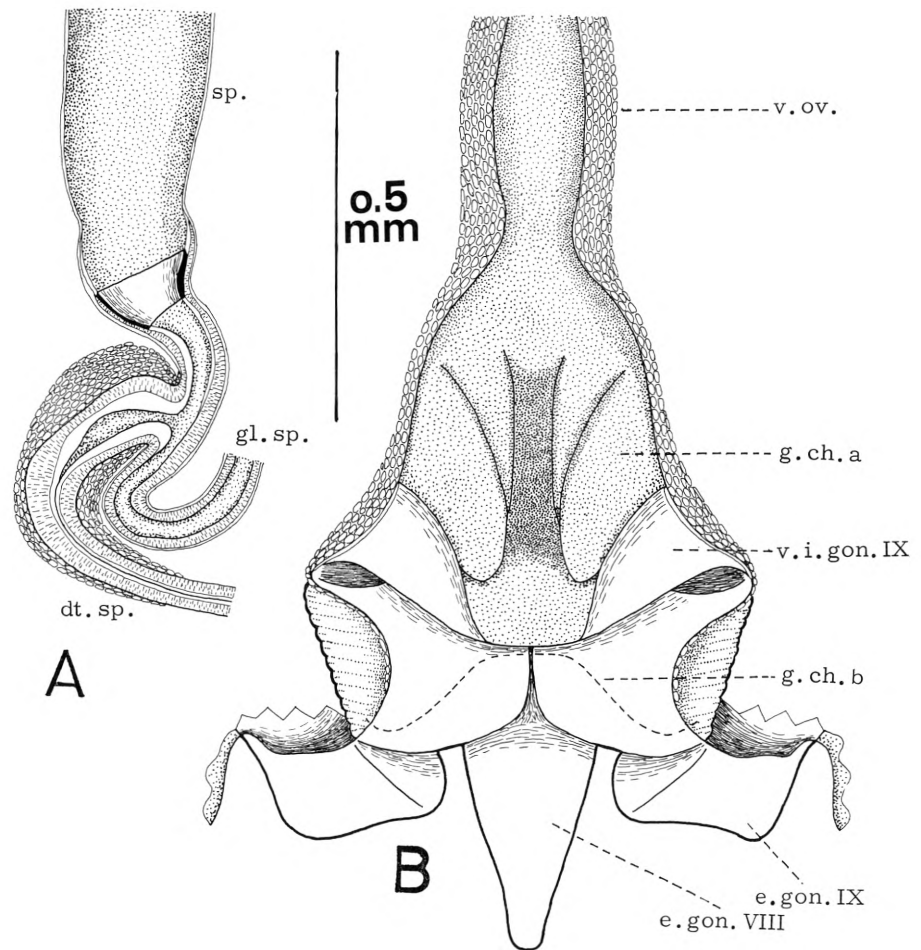


Fig. 84. *Limnephilus flavicornis*. Sagittal section through the genital chamber etc.; left side as seen from the inside.

Correction: for gchm₂ read IX-Xm₂.

Fig. 85. *Limnephilus flavicornis*. A: Sagittal section through the distal part of the ductus spermathecae and the proximal part of the spermatheca; left side as seen from the inside. B: Floor of the genital chamber in a dorsal view.



downward bent and funnel-like dilated, but flattened toward the crescentic opening.

The spermatheca (figs. 82 and 83 A) is very large, extending into the posterior part of segment IV. It consists of a slender proximal part in the shape of an elongate funnel, and a much longer and thicker distal part in the shape of an oblong sac; both are thin-walled. In the proximal part there is, at the transition into the ductus spermathecae, a short, somewhat funnel-like sclerotic ring (fig. 85 A).

The distal half of the slender part and the whole distal part are provided with a circular musculature, which toward the distal end takes a

longitudinal course, the fibres tangential to the surface. In the slender part the musculature is rather feeble, in the thick part it is very strong, consisting of several layers of fibres.

A little more than the proximal half of the ductus spermathecae (figs. 82, 83 A, 84, 85 A) is very slender and devoid of musculature. The lumen is very narrow and ribbon-like compressed dorso-ventrally. The distal part is thick and clavate. This is due partly to a strong circular musculature, partly to the fact that the lumen is wider, the cuticle, and to some degree the epithelium too, thicker. The relation between the ductus and the glandula spermathecae is

peculiar. The latter appears as a continuation of the lumen of the spermatheca itself, into which the duct opens dorsally.

The lumen of the glandula spermathecae, is wide, the epithelium is low but seems, as in the duct, to be glandular. This gland is coiled, but relatively short. In return an extremely long and very much coiled gland opens at about the posterior third of the ventral side of the distal part of the spermatheca. This is reminiscent of conditions in *Rhyacophila* (p. 32).

I have been unable to measure the length of this "additional" gland, but in *L. lunatus* Curt. Gower (1967) estimates it to be 25 mm, i.e. more than twice the length of the animal. According to Khalifa (1949) it is provided with muscles, but this I have been unable to confirm.

The colleterial glands. Each gland is divided into an anterior and a posterior main branch, each of which again is divided into a dorsal and a ventral branch. The dorso-anterior branch is the longest, more than twice as long as any of the others. The ventro-anterior branch is just as thick as the dorso-anterior one, the two posterior branches are much thinner. The dorso-posterior branch is directed straight backward, the ventro-posterior branch is directed downward at its base, but then bent backward. The colleterial duct opens in the extreme posterior end of the genital chamber, between the processes g.ch.b. and just behind the process pr.sp.d, which latter may be said to form the anterior wall of the opening (fig. 84).

Musculature (figs. 81 B, 82, 84, 85 B, 86 A). Among the ventral VII–VIII muscles the usual internal and external muscle are found. The former is divided into two portions, of which the smaller one is superficial to the larger one. The external muscle is convergent in a posterior direction, and the posterior attachments of the two muscles (right and left), which are just behind the antecosta of sternum VIII, are partly intermingled. In addition two muscles are found, which I have interpreted as vm_2 and vm_6 .

The former connects the anterior corners of sterna VII and VIII. The latter, which is composed of fine bands, has its posterior attachment laterally on the antecosta of sternum VIII and its anterior attachment approximately in the middle of each half of sternum VII.

As compared with the pregenital segments the equipment of dorsal VIII–IX muscles is rather complete, only dm_5 lacking. The muscle dm_4 is divided into two portions. Moreover the muscle vm_6 is present. It is strong, originates on the antecosta of sternum VIII, and is inserted to the middle part of the lateral margin of IXc.

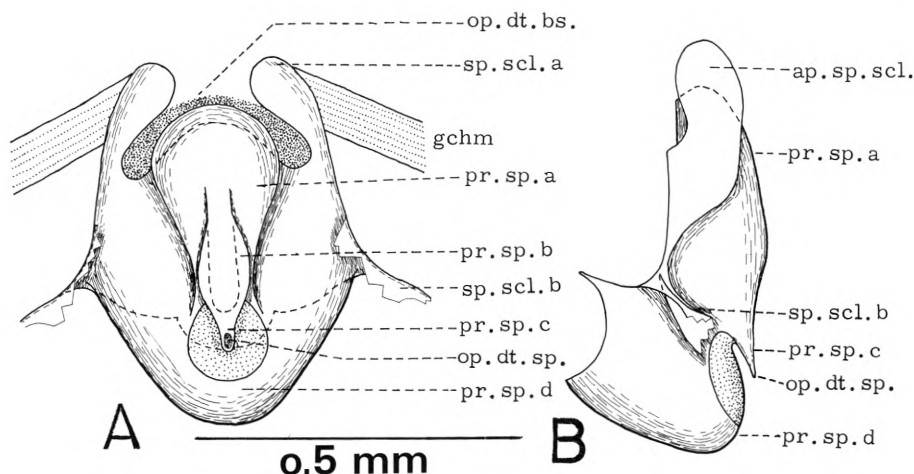
The muscle $gonm_1$ is flat, originates along the middle part of the lateral margin of sternum VIII, goes downward and inward and is inserted laterally to the side lobe of the "vulvar scale". Other muscles associated with the gonopods were not seen.

There are two IX–X muscles. One ($IX-Xm_1$) is thin, has its anterior attachment latero-dorsally on the front margin of segment IX, at the anterior end of IXc, and the posterior attachment to the bottom of the furrow between the structures Xaa and IXc. The other ($IX-Xm_2$) originates meso-ventrally and distally in the process IXd. The weak muscle goes forward and is inserted to the tongue Xe near the "mouth angle" of the genital chamber.

The rather narrow and flat $gchm_1$ originates on the posterior part of venter VIII and is inserted to the anterior end of the wing-like apodeme (ap.sp.scl.) of the spermathecal sclerite. Below its insertion a strong muscle originates (fig. 82, $gchm_2$). It goes slightly descendent backward, outside the circular musculature of the genital chamber, and its bands diverge a little fan-like toward their insertion to the ventral (or posterior) side of the fold v.i.gon.IX. The homology of this muscle is quite uncertain.

The circular musculature is more complicated than is usually the case. On the ventral side it extends in a posterior direction, and gradually thinner, to the base of the dorsal (or anterior)

Fig. 86. *Limnephilus flavicornis*. Processus spermathecae in a ventral view (A) and as seen from the right side (B).



side of the fold v.i.gon.IX. It is interrupted by the wing-like apodeme (sp.sp.scl.) of the spermathecal sclerite. Dorsally to this apodeme, i.e. on the outside of the spermathecal sclerite, there is no transverse musculature.

The circular musculature of the colleterial duct reaches the horizontal part of the base of the process pr.sp.d. Ventrally to this point (fig. 82) the bands are horseshoe-shaped, and attached at both ends to the vertical part of the base of pr.sp.d and, more ventrally, to the bridge sp.scl.b connecting the spermathecal sclerite with the fold v.i.gon.IX. Most of the last mentioned bands enter the base of the tongue Xe, but some are divided into two, the internal one being attached to the mesal side of the process g.ch.b.

On the outside of the furrow between the folds v.i.gon.IX and d.i.gon.IX a very strong muscle originates. It goes upward, the foremost and very short bands ca. 45° ascendent, the hindmost and long bands almost vertical (fig. 82). The bands eventually bend round and are inserted to the lateral side of the process g.ch.b. This muscle must be considered as a derivate of the circular musculature.

The process g.ch.b thus no doubt is movable, allowing for entrance to the genital chamber during copulation, and exit during egg-laying.

Limnephilus rhombicus L.

(*Limnephilus rhombicus* L.)

This species (fig. 87) is closely related to *L. flavicornis*, but there are distinct differences in the shape of segments IX and X. The area IXa is triangular rather than semicircular. It is sclerotically continuous with the process IXc only at the extreme anterior end; otherwise it overlaps the base of the latter a little. For most of its length this process is broad and flattened, only about the distal fourth is finger-like. The wing Xab is much thicker than in *L. flavicornis* and extends for the whole length of the "tubular piece", with slightly convex sides in a dorsal view. Hence the "tubular piece" appears much plumper than in *L. flavicornis*.

It must be observed that the processes IXb are present also in *L. rhombicus*. In the specimen figured they are shrivelled up, which may be the case also in (older?) specimens of *L. flavicornis*.

Potamophylax latipennis Curt.

(*Stenophylax stellatus* Curt.)

According to Nebois (1963) *stellatus* is a synonym of *latipennis*. Décamps (1966) has given some rough figures of the "vulvar scale" and the processus spermathecae ("pièce centrale") of *P. latipennis* Curt. and *P. cingulatus* Steph. Non

corresponds to conditions found by me in the species described here. The shape of the "vulvar scale" is subject to individual variation, and Decamp's preparations of the processus spermathecae may have been deformed by pressure.

Pregenital segments. The sternum has, rather far behind the middle, a very distinct transverse suture. On the segments to and including V it is connected with the antecostal suture by a pair of curved (laterally convex) longitudinal sutures. On sternum VI three small, sometimes multiple, teeth are found just in front of the transverse suture.

The gland on sternum V is rather large. The small opening is situated a little in front and a little laterally to the middle of that part of the sternum which is framed by the sutures, i.e. rather far behind the antecostal suture.

The genital segments (fig. 88). Segment IX is so intimately united with segment X that the boundaries cannot be stated with any degree of certainty, and sternum VIII is firmly united with the "vulvar scale".

Segment VIII tapers toward the posterior end. The tergum is broader than the preceding ones, and hence the longitudinal suture, which is shorter, is farther removed from the lateral margin. The pleural membrane is narrower than on segment VII, but much broader than in *Limnephilus flavicornis*.

The sternum is approximately as long as the tergum and not broader than sternum VII. Neither a longitudinal, nor a transverse suture is found. On the anterior corners there is a pair of not particularly deep, backward facing pockets; they probably are functionally related to the gonopods of the male.

Segments IX and X. A dorsal and a ventral lobe, separated by a rather large vertical, membranous area (IXe; cp.p. 173) can be distinguished. The former (IXa-c, Xa; fig. 89 B, IXf, Xc) is short and much narrower than segment VIII. In a transverse direction it is roughly semicircular. In a lateral view the ventral outline curves upward at the anterior end. (In fig. 88 B this is largely obscured by the overlapping posterior

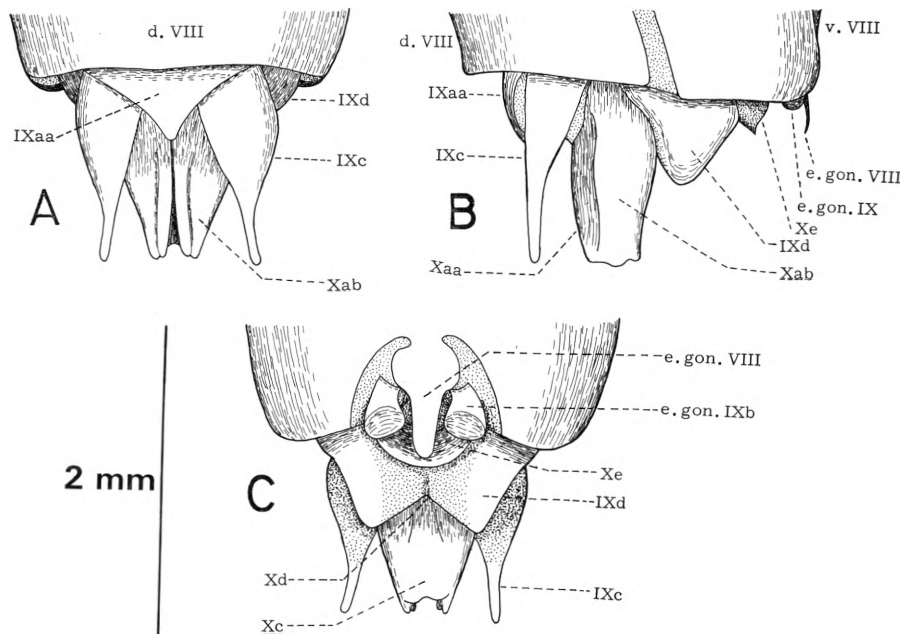
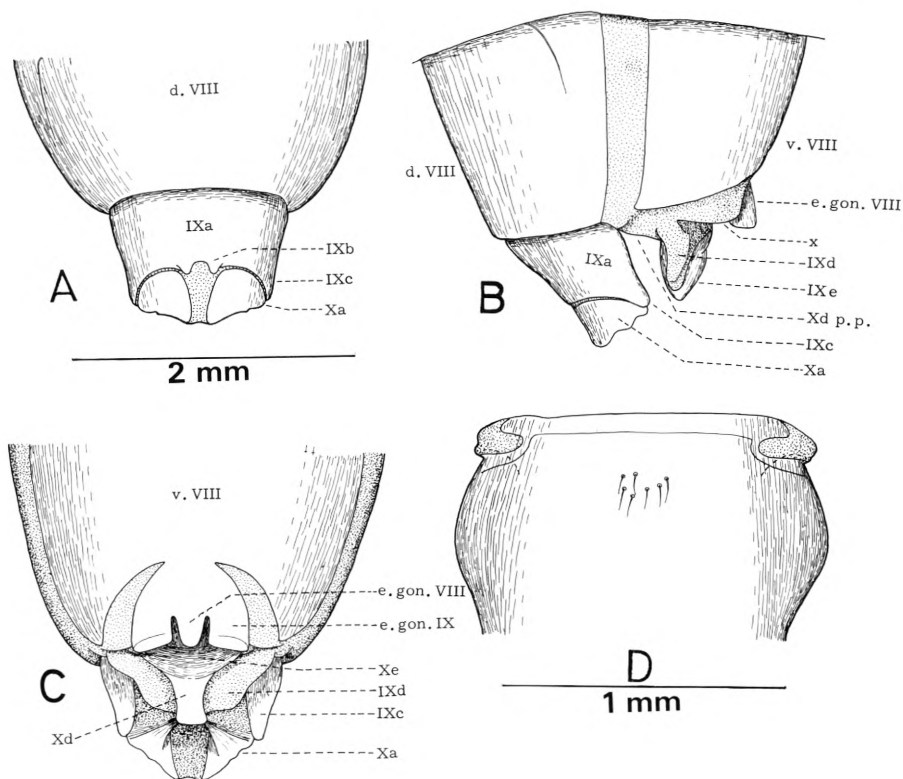


Fig. 87. *Limnephilus rhombicus*. Posterior end of abdomen in a dorsal view (A), as seen from the right side (B) and in a ventral view (C).

Fig. 88. *Potamophylax latipennis*. Posterior end of abdomen in a dorsal view (A), as seen from the right side (B) and in a ventral view (C). D: Anterior part of segments IX and X in a dorsal view.



margin of dorsum VIII. In the specimen figured the dorsal lobe was bent rather much downward). The dorsal and lateral sides of this lobe are sclerotized to their greater extent. The sclerite proceeds for some distance onto the ventral side, where it projects as a pair of rounded folds (IXc) "above" (i.e. ventrally to) the otherwise membranous ventral side. Their posterior ends form a pair of short processes. These folds and processes perhaps are homologous with the processes IXc in *Limnephilus flavicornis* (p. 158).

The sclerite IXa-c has an antecosta. At the anterior corner it has a small membranous indentation of a rather complicated shape, which will appear from fig. 88 D. The antecosta proceeds along the indentation. Here it is narrower, but stronger, whereas it between the inden-

tations is represented only by a rather slight thickening of the cuticle.

At the posterior end (fig. 89 A) the sclerite IXa has, for its whole width, a deep, rounded indentation; just in front of its middle a pair of more or less distinct, short and rounded, backward directed, sclerotic processes (IXb) is found. In some newly emerged specimens these processes were seen to carry each a thin filament, reminiscent of the process IXb in *Limnephilus flavicornis*, though longer and thinner.

The posterior indentation of the sclerite IXa is largely occupied by a pair of sclerites (Xa), which also proceed onto the posterior end of the dorsal lobe, flanking the anus, as well as onto the ventral side of the lobe (fig. 89 B) and onto the posterior part of the lateral side of the anal tube. The sclerite has a rather complicated shape,

being divided into several portions by various keels. Moreover, the shape varies according to the state of contraction of certain muscles. By full relaxation of these the hind margin of the dorsal side of the lobe is irregularly convex (fig. 88), by full contraction it is concave (fig. 89).

The posterior end of the ventral side (fig. 89 B) has, for its whole width a shallow, V-like indentation, flanked by the ventral parts of the sclerites Xa. Apart from these it is membranous, which is also the case with a very small, backward directed process (Xc) in the bottom of the V-like indentation. This process, together with the sclerites Xa, probably are homologous with the "tubular piece" in *Limnephilus flavicornis* (p. 235).

Near the anterior end the sclerite IXa carries a small, unpaired group of some few setae (fig. 88 D). The posterior ends of the folds IXc, as well as the sclerites Xa, are densely clothed with setae (fig. 89).

The ventral lobe (fig. 88 B and C, IXd, Xd-e) is almost as broad as, but much shorter than the dorsal lobe. It is a chiefly membranous tongue. On the anterior part of its ventral side there is a concave sclerite (Xe), forming the upper lip of the genital opening. From the middle of its posterior margin a raised, sclerotic area (Xd) issues. The latter, the width of which varies rather much, bends round the posterior end of the tongue onto the dorsal side. The ventral lobe probably is homologous with the tongue Xe in *Limnephilus flavicornis* (p. 159), though the muscle IX-X₂ (p. 173) proves that it also contains part of the process IXd (p. 160). The membranous parts of the ventral lobe are clothed with setae.

The "vulvar scale". The posterior end of sternum VIII has, for its whole width, an indentation in which the "vulvar scale" lies (fig. 88 C). The latter is very similar to that of *Limnephilus flavicornis*. The following differences may be noted: The bridge connecting it with the sternum is much broader. The middle lobe is much

smaller, smaller than the side lobes, but relatively thick. The membranous fold (fig. 88 B, x) bordering the "vulvar scale" is connected with the lateral side of the side lobe, the sclerite of which hence has a very deep proximal indentation. The "vulvar scale" is rather richly provided with microtrichia, but devoid of setae.

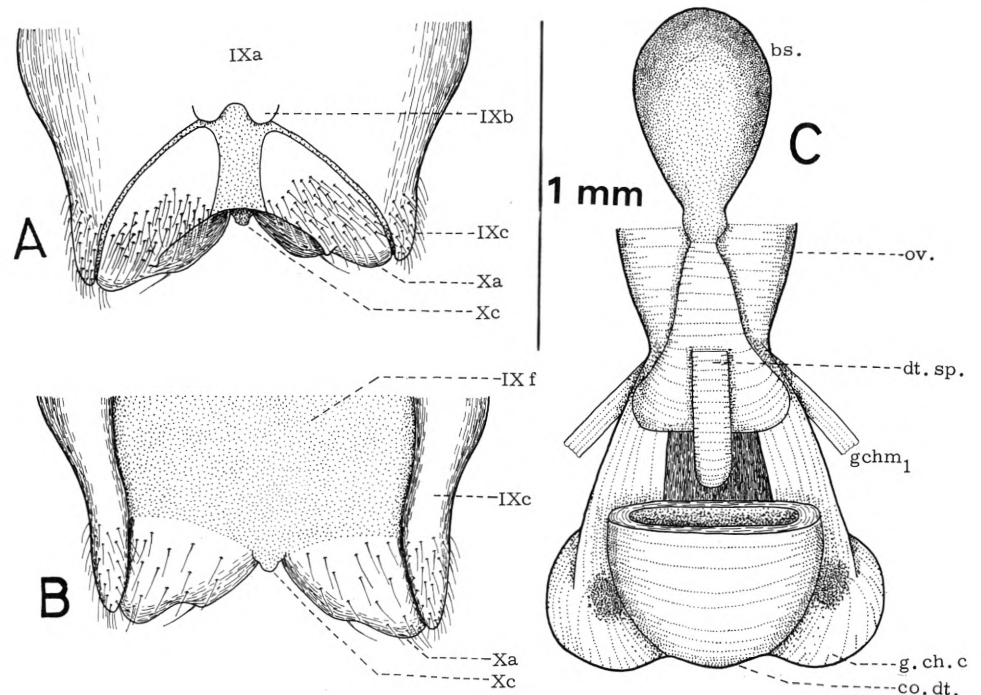
The genital chamber (figs. 89 C, 90) is short, extending to the posterior end of segment VII. A short and narrow anterior part and a longer and wider posterior part can be distinguished. The width of the latter part is due to a pair of latero-dorsal outward bulges (g.ch.c) of the wall, as well as to an unpaired ventral bulge in the most posterior part.

In the anterior part of the genital chamber the dorsal wall is ascendent in an even curve. It is covered by the spermathecal sclerite which, for nearly its entire length and width, bulges into the lumen as a processes spermathecae (fig. 91), almost touching the posterior, descendent part of the dorsal wall (see below). A large, anterior part of the lateral side of this process is pale and perhaps more weakly sclerotized.

At the anterior end the ventral side of the processus spermathecae bends upward into a low, approximately vertical area. The short part of the spermathecal sclerite lying in front of the latter is transversely concave toward the lumen. Here the opening of the ductus bursae is found in the shape of a transverse, in the middle backward bent, cleft which extends for almost the whole width of the sclerite.

Along a little more than the anterior third of the base of the processus spermathecae, as well as along the sclerite in front of the latter, the spermathecal sclerite is bent downward upon the lateral wall of the genital chamber for a short distance. This lateral sclerotization (sp.scl.a) is broadest (highest) at the anterior end. Here it sends a short and narrow extension (sp.scl.e) onto the lateral wall of the common oviduct. That part of the spermathecal sclerite which carries the opening of the ductus bursae sends

Fig. 89. *Potamophylax latipennis*. The posterior end of segments IX and X in a dorsal (A) and in a ventral view (B). C: The genital chamber etc. in a dorsal view.



short, tongue-like extensions onto both the dorsal and the ventral wall of the ductus bursae (sp.scl.c and sp.scl.d, resp.). The former extension is continuous with the anterior side of the processus spermathecae. The narrow posterior end of sp.scl.a proceeds backward as a downward bent sclerotic bridge (sp.scl.b), connecting the spermathecal sclerite with the sclerite i.gon. IX described below.

Somewhat in front of the middle of the ventral side of the processus spermathecae a much narrower, backward and slightly downward directed process (pr.sp.c) issues from a still narrower base. Especially in a lateral view its apex, which does not project nearly as far backward as the processus spermathecae itself, is pointed. The oblong opening of the ductus spermathecae is situated on its ventral side, at the extreme posterior end.

A sclerotic bow lies on the lateral and ventral walls of the posterior part of the genital chamber (fig. 90). On the ventral side it is continuous with

the sclerite on the dorsal side of the "vulvar scale". Both the anterior and the posterior margin of the sclerite is raised into a pair of rounded sclerotic folds (v.i.gon. IX and d.i.gon. IX, resp.), which are placed almost vertically. The posterior fold is broad, the anterior one is narrower, but higher; its anterior side is continuous with the spermathecal sclerite through the bridge (fig. 91 B, sp.scl.b) mentioned above. In each pair the abruptly rounded ends of the two folds almost touch each other on the ventral side of the genital chamber.

In the bottoms of the two posterior bulges described above (p. 249) a pair of cylindrical processes (g.ch.b) issues. The base of the process entirely fills the lumen of the bulge (fig. 89 C, g.ch.c). Its middle flanks the posterior end of the processus spermathecae, and its distal part lies in the rounded furrow between the folds v.i.gon. IX and d.i.gon. IX. The right and the left process touch each other and thus occlude the lumen of the genital chamber.

The colleterial duct opens near the posterior end of the genital chamber, between the dorso-lateral bulges (g.ch.c). Behind the opening the dorsal wall of the genital chamber is almost vertically descendent. (Hence the genital opening is much lower than the posterior part of the genital chamber). The sclerite Xe bends up onto this part of the dorsal wall, where it has a deep, V-like, anterior indentation.

The bursa copulatrix (fig. 90) is a small, pear-like sac with a thin cuticle. The duct has a rather thick cuticle and a strong circular musculature. For its whole length, though especially in the posterior part, it is funnel-like dilated, but at the same time increasingly flattened. Its proximal end is bent much downward.

The spermatheca, which is smaller than in *Limnephilus flavicornis*, consists of a slender,

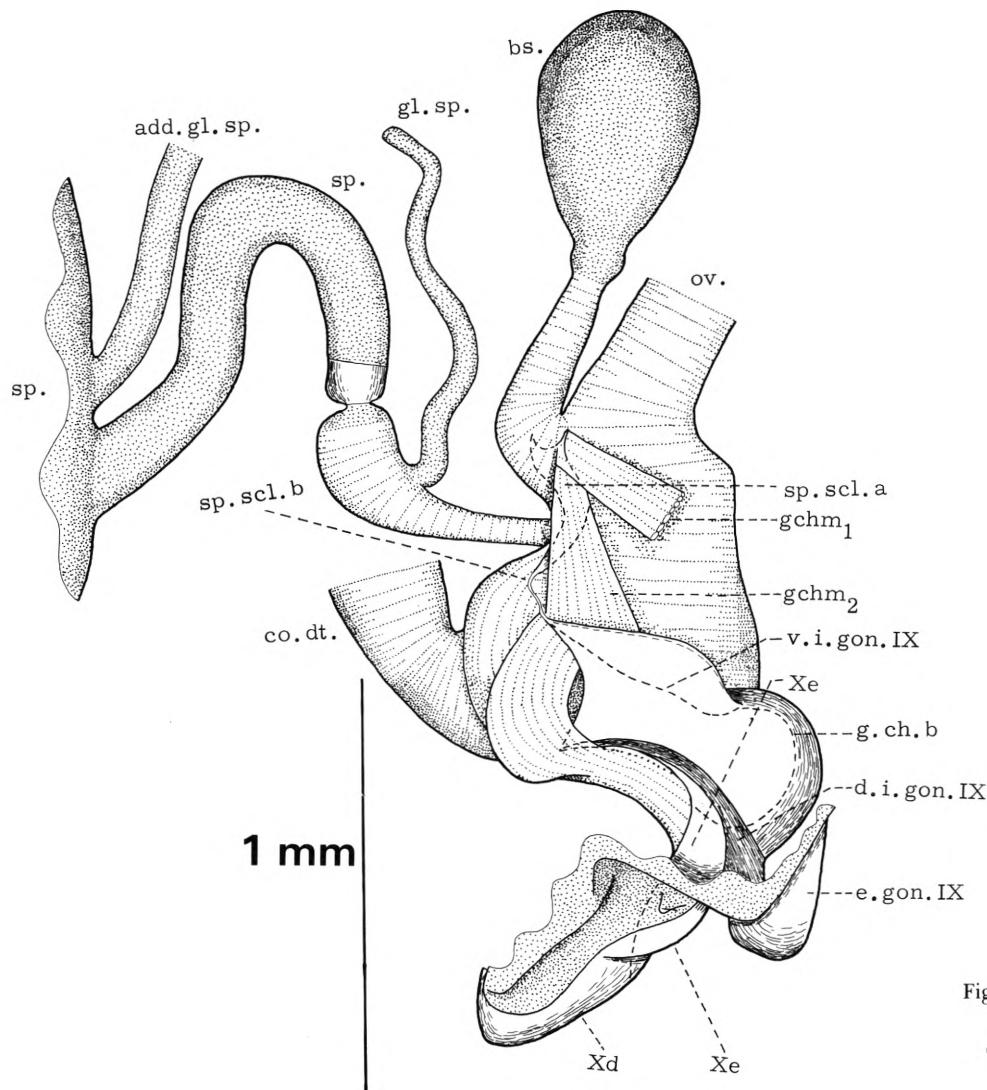
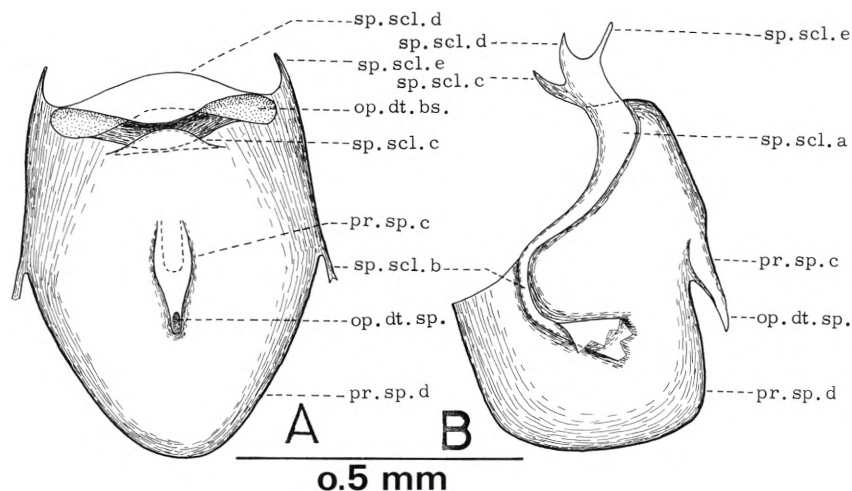


Fig. 90. *Potamophylax latipennis*. The genital chamber etc. as seen from the right side.

Fig. 91. *Potamophylax latipennis*. Processus spermathecae in a ventral view (A) and as seen from the right side (B).



tube-like proximal part, opening into the ductus spermathecae through a sclerotized funnel, and a twice as long, sac-like distal part. In the latter the wall is clothed with microtrichia in the shape of ca. 22 μ broad combs, each with up to ten tiny, ca. 5 μ long, distally directed teeth, one comb to each epithelial cell.

The spermatheca has a circular musculature, developed as in *Limnephilus* (p. 164).

The short ductus spermathecae is clavate. The opening of the glandula spermathecae, facing toward the spermatheca, is on its ventral side, a little distally to the middle. This gland is very much reduced, short, thin and almost straight. In return there is, as in *Limnephilus*, another gland which opens ventrally into the sac-like part of the spermatheca, just in front of the tube-like part. This gland is still longer than in *Limnephilus*. It has a subproximal swelling, provided with circular muscles. Its distal part is tightly coiled up and fills almost as much as the spermatheca itself.

Musculature. A special ventral muscle is found in segment V. It is small and has its anterior attachment on the sternal antecosta, a little mesally to each half of the latter. It diverges in a posterior direction, and its bands converge fan-like toward their insertion on the efferent duct

of the gland of this segment. The muscle, the homology of which is quite uncertain, no doubt is an obturator of the gland.

The external ventral VII–VIII muscle is divided into two. One has its anterior attachment a little behind the antecosta. It extends rather far into segment VIII, being attached approximately at the anterior third and rather mesally on sternum VIII. The other, composed of fine bands, has its posterior attachment behind the antecosta VIII. It has a very transverse course, and the anterior attachment is quite laterally on sternum VII, approximately in the middle of the segment. The bands converge a little toward their anterior attachment. The internal muscle is undivided. Moreover, the muscle vm_6 seems to be present. It is divided into two portions with posterior attachment on and just mesally to, resp., the pocket on the anterior corner of sternum VIII (p. 167). The former, which may also represent vm_2 , converges a little in an anterior direction, and does not quite reach the antecosta of sternum VII. The latter converges 45° in an anterior direction and is attached approximately to the middle of each half of sternum VII.

In segment VIII the muscles dvm_1 , dvm_2 and dvm_4 are found, whereas dvm_3 is lacking.

As compared with *Limnephilus* the VIII–IX muscles are few in number. On the dorsal side there are two muscles, which I have interpreted as portions of dm_1 . The mesal one is very broad and has its anterior attachment to the greater part of antecosta VIII. The narrow lateral portion consists of only two fine bands and thus is reminiscent of dm_2 . It cannot be this muscle, however, since it passes mesally to dvm_2 . It has its posterior attachment to the membranous area between the dorsal and the ventral lobe of segment IX. The muscle vm_6 has its posterior attachment to the same area; the anterior attachment is on sternum VIII, a little in front of the middle.

As in *Limnephilus* there is only one pair of muscles associated with the gonopods, $gonm_1$. The rather strong muscle originates laterally on sternum VIII, approximately in the middle. It has an almost transverse course, and its bands converge fan-like toward their insertion at the base of the side lobe of the “vulvar scale”.

There are three IX–X muscles. The rather strong IX– X_1 originates partly on the antecosta of segment IX, behind the indentation at the anterior corner (fig. 88 D), partly behind the antecosta. Its bands converge fan-like toward the insertion on the dorsal side of the sclerite Xa (fig. 88 A). IX– X_2 is a slender muscle originating on the dorsal sclerotization (Xd; cp. p. 169) on the ventral lobe of segment IX, approximately in the middle of the latter. It diverges in an anterior direction and is inserted to the posterior part of the lateral side of the genital chamber, as far as I have been able to see to the posterior margin of the sclerite d.i.gon.IX and v.i.gon.IX. This muscle might be interpreted as $gonm_3$, but a comparison with *Limnephilus* (p. 165) suggests that it actually is a IX–X muscle. The muscle IX– X_3 consists of some fine bands inserted to the posterior part of the anal tube. As far as I have been able to see, they originate on the sclerotic fold IXc.

The muscle $gchm_1$ originates laterally on ster-

num VIII. Its bands converge a little fan-like toward the insertion, which is on the anterior end of the downward bent extension of the spermathecal sclerite (fig. 90, sp.scl.a). As in *Limnephilus* (p. 244) another and strong muscle ($gchm_2$) originates beneath $gchm_1$. Its bands diverge a little fan-like and are inserted to the outside of the fold v.i.gon.IX.

The circular musculature of the genital chamber is only developed on the ventral and lateral sides. The posterior, dorso-lateral bulges have rather a longitudinal musculature. Some of the bands have an anterior attachment anterolaterally on the spermathecal sclerite, others a posterior one on the sclerite Xe, and some proceeds into the processes g.ch.b (p. 170).

Ecclisopteryx dalecarlica Kol.

(*E. guttulata* Pict.)

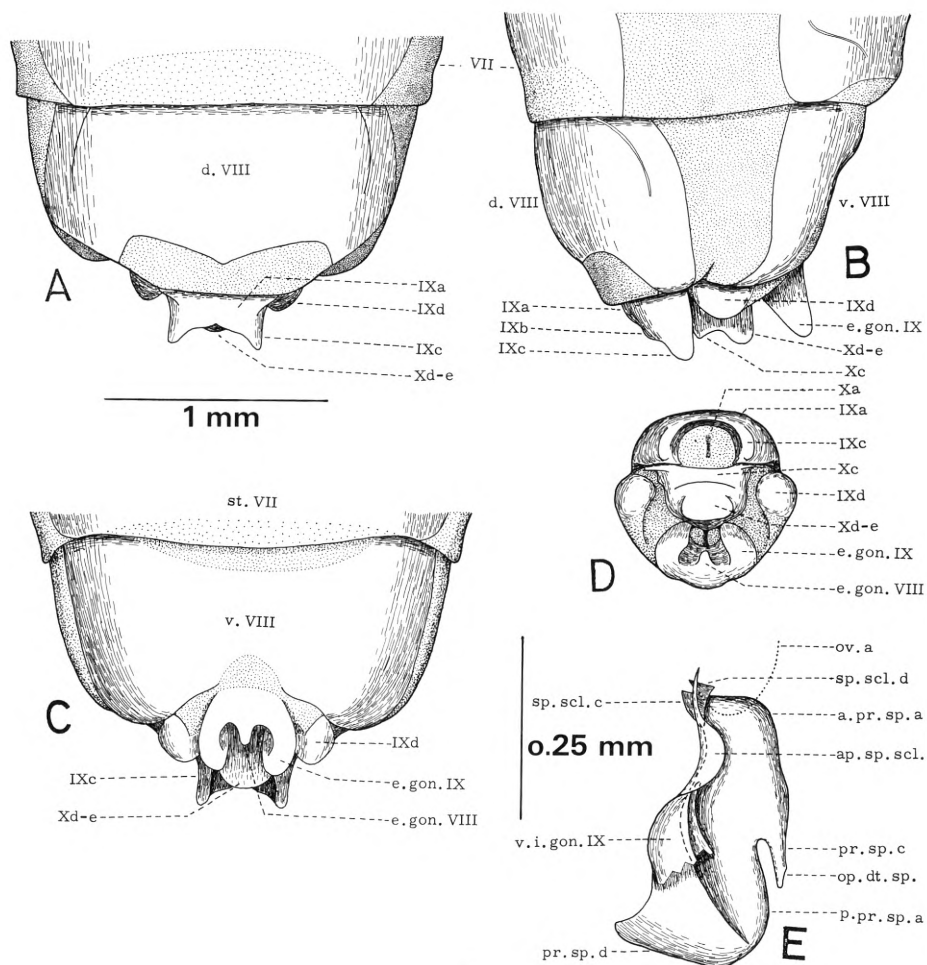
According to Svensson & Tjeder (1975) *E. guttulata* is not found in North Europe, and the males described by me in 1957 belong to the species *E. dalecarlica*.

Pregenital segments. On sternum VII (fig. 92) as on sternum II, the most lateral parts of the transverse suture only are present. They are slightly S-like curved.

The gland in segment V opens a short distance behind the antecostal suture, but rather much mesally to the longitudinal suture. It is oblong and very large, 535 μ long and 410 μ thick, extending into the posterior part of segment IV. The outer part of the efferent duct, for a length of ca. 95 μ , is strongly sclerotized, with a 4 μ thick cuticle and a 10.5 μ wide lumen. Near the 31 μ broad opening the latter is funnel-like dilated.

The whole surface of sternum V, except for the areas laterally to the longitudinal sutures and a posterior, pale area, has a sculpture of irregularly hexagonal, 12–20 μ broad “scales”, each no doubt corresponding to an epidermal cell. Each “scale” carries on the posterior margin 5–6 ca. 8 μ long and relatively thick microtrichia,

Fig. 92. *Ecclisopteryx dalecarlica*. Posterior end of abdomen in a dorsal view (A), as seen from the right side (B), in a ventral (C) and a posterior view (D). E: Processus spermathecae as seen from the right side.



and on the surfaces of the “scales” microtrichia are just as close-set. They are found also on the other terga and sterna, but here the hexagonal pattern is lacking.

Tergum VIII (fig. 92 A, B) is a little broader than tergum VII, and the longitudinal suture—which has about the same length as on tergum VII—hence farther removed from the lateral margin. A postero-mesal area, which on the preceding terga is pale, is on tergum VIII narrower, but more sharply delimited and membranous. In its middle the sclerite has again a low, triangular extension.

The rather flat sternum (fig. 92 B, C) has the

same width as sternum VII and, excluding the “vulvar scale”, the same length as tergum VIII. For the greater part of its width the anterior margin has a shallow, slightly sclerotized or entirely membranous indentation. The antecostal suture is developed only laterally to this indentation and other sutures are not seen. The posterior margin has a large membranous indentation, in which the base of the “vulvar scale” is situated. The latter has no sclerotic connection with sternum VIII. Quite on the contrary, the indentation of the posterior margin of the latter is especially deep in front of the “vulvar scale”.

Segments IX and X (fig. 92) are so intimately

united that the boundary cannot be stated with any degree of certainty. Together they are very short and narrow. As in *Potamophylax* a dorsal and a ventral lobe can be distinguished, though in *Ecclisopteryx* they are contiguous and in part continuous.

The dorsal lobe (IXa-c) is a little widened at the anterior end. In a transverse section it is approximately semicircular. It is sclerotized on the dorsal and lateral sides. At the anterior end the dorsal lobe is continuous (by membrane; see below) with the ventral lobe; hence only the posterior part of the former has a ventral side. This side is strongly concave, so that the posterior part of the dorsal lobe roughly forms a half-cylinder, which is sclerotized on both sides (fig. 92 D). The posterior margin has a shallow indentation, the shape of which will appear from fig. 92 A; a pair of sagittally compressed processes (IXc) thus is formed. In the bottom of the half-cylinder a transverse and vertical, membranous area (Xa) is found. The anus, in the shape of a vertical cleft, is situated on this area.

In a lateral view it is seen that the descendent upper side of the dorsal lobe, in front of the posterior indentation, is divided into two humps by a shallow, but broad, rounded furrow.

The anterior part of the dorsal lobe is considerably darker than the posterior part, and the boundary between the two colours is sharp. This colour difference, however, hardly can be attributed any morphological significance.

The ventral lobe (Xc-e), which is shorter and a little narrower than the dorsal lobe, can best be described as a very thick, in a posterior direction strongly tapering tongue with a flat dorsal side. By a broad and rounded, transverse and horizontal furrow its posterior end is divided into an upper (Xc) and a lower part (Xd-e). The rounded hind end of the latter projects farther backward than the former, the hind end of which is an approximately semicircular, horizontal, rounded keel below the membranous anal area (Xa; fig. 92 D). On the lateral side the lower

margin of the dorsal lobe overlaps the upper margin of the ventral lobe a little as a thin fold. In the bottom of the narrow furrow thus formed the two lobes are continuous, though not by sclerite.

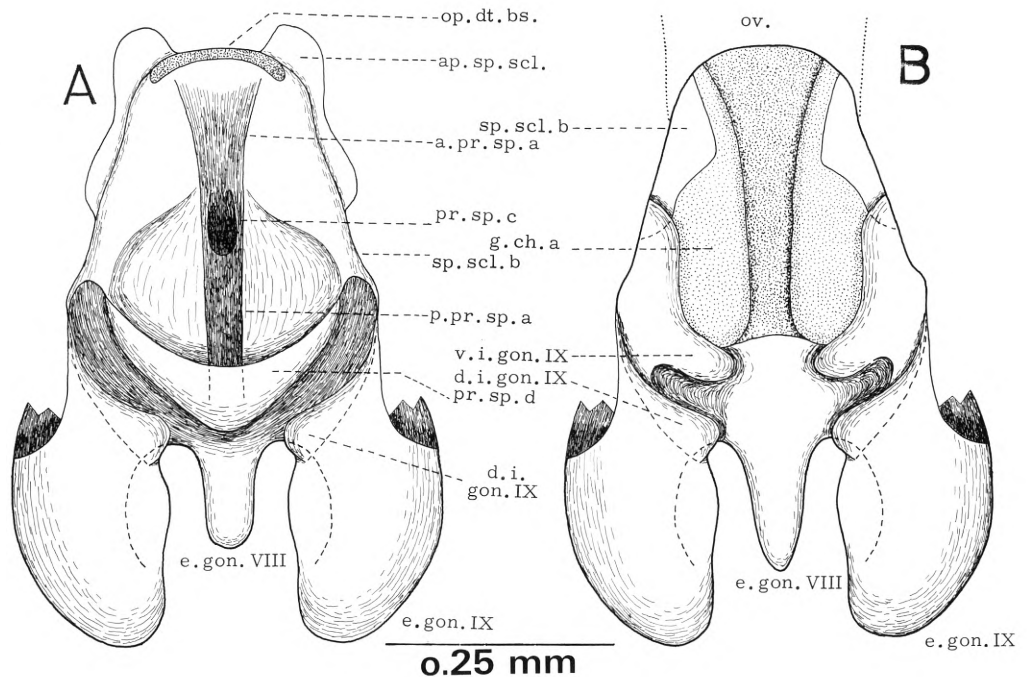
On the lateral side of the ventral lobe a distinct suture is seen at some distance from the upper margin (fig. 92 D). Below the greater, anterior part of this suture the lateral side of the ventral lobe is membranous. Otherwise this lobe is weakly sclerotized and pale. The mesal part of its ventral side, which has a slight, rounded longitudinal keel, forms the upper lip of the genital opening.

As mentioned above the lateral side of the ventral lobe is membranous to a great extent. In a lateral view (fig. 92 B), however, this membranous area is concealed by a large, but short, rounded process (IXd), which no doubt is homologous with the process so labelled in *Limnephilus flavicornis*. The lateral, dorsal and mesal sides of the process, as well as its apex, are sclerotized. Its membranous ventral side is connected with the membranous area in front of the "vulvar scale" by a thick, membranous fold. The ventral lobe as well as the mesal sides of the processes IXd are devoid of setae and microtrichia.

The "vulvar scale" (fig. 92 B-D, e.gon.VIII, e.gon.IX) is, as in the limnephilines, trilobed. The very small middle lobe is peg-like and somewhat varying in shape (cp. fig. 93 A and 93 B). In a lateral view the side lobes are somewhat tapering toward the rounded distal end. They are very high and sagittally compressed. The concave mesal side faces a little downward (fig. 92 C). The "vulvar scale" is sclerotized also on the dorsal side (fig. 93). It is devoid of setae, but richly provided with microtrichia.

The *genital chamber* is short, extending only to the middle of sternum VIII. In its greater, anterior part three sections of the dorsal side can be distinguished, though they by no means are sharply delimited. The anterior one (1) is almost horizontal, though slightly concave in a longitu-

Fig. 93. *Ecclisopteryx dalecarlica*. A: The sclerites in the genital chamber in a dorsal view. B: Same after removal of the processus spermathecae.



dinal direction. The next one (2) is ascendent in a dorsally convex curve. The last one (3) is steeply ascendent in an antero-dorsally concave curve. The most posterior part of the dorsal wall (4) is steeply, though not vertically, descendent.

The three first sections of the dorsal wall is covered by the spermathecal sclerite (figs. 92 E and 93 A). In section one this sclerite, apart from the keel (pr.sp.a) mentioned below, is rather flat, in sections 2 and 3 it bulges, for most of its width, into the lumen as a large and plump tongue (pr.sp.d), the rounded posterior end of which almost touches section 4 of the dorsal wall. The upper side of pr.sp.d is transversely convex; it is much shorter than the ventral side, and its anterior margin is strongly concave. Except for the keel mentioned below, the ventral side is slightly concave.

For almost its whole length the mesal part of the spermathecal sclerite is raised into a high, but relatively narrow, though at the front end somewhat broader keel (pr.sp.a). In front its

ventral side bends upward into the vertical anterior end. The latter proceeds for a short distance onto the dorsal (or posterior) side of the ductus bursae as a sclerotic, tongue-like extension (sp.scl.c). Laterally to the anterior end of the keel the spermathecal sclerite sends a pair of small extensions (sp.scl.d) onto the otherwise membranous lip between the ductus bursae and the common oviduct. This thick lip proceeds forward for some distance as an unpaired longitudinal fold (fig. 92 E, ov.a) on the dorsal side of the oviduct.

The opening of the ductus bursae is on the narrower anterior end of the spermathecal sclerite (fig. 93 A), in front of the keel pr.sp.a, in the shape of a narrow, transverse and curved, posteriorly concave, cleft for most of the width of the sclerite. The greater, mesal part of the anterior side of the cleft is not sclerotized.

Approximately in the middle of the ventral side of the keel pr.sp.a a slender, backward directed "spout" (pr.sp.c) issues; it does not

project nearly as far backward as pr.sp.a itself. The opening of the ductus spermathecae is found on the obliquely cut off posterior end of the "spout". Behind the latter pr.sp.a is lower. Here it forms, together with pr.sp.d, an even curve.

Along its lateral side the spermathecal sclerite is downward bent. In section I this part of the sclerite forms a wing-like apodeme (ap.sp.scl.), the shape of which will appear from figs. 92 E and 93 A. It will be seen that it projects farther forward than the spermathecal sclerite itself.

For about its anterior three fourths the ventral side of the genital chamber is membranous and raised into a pair of thick folds (fig. 93 B, g.ch.a) flanking the keel pr.sp.a on the spermathecal sclerite. At the anterior end the dorsal side of this fold is partly sclerotized, and the sclerite (sp.scl.b) is continuous with the base of the apodeme ap.sp.scl. mentioned above. The posterior end of the fold is distinct, though rounded.

For about the posterior two thirds of the genital chamber two pairs of successive, descendent, rounded sclerotic folds (fig. 93 B, v.i.gon.IX and d.i.gon.IX) lie on the lateral side. The anterior and higher of these folds (v.i.gon.IX) lies above the posterior half of the fold g.ch.a. Antero-dorsally it is continuous with the base of the apodeme (ap.sp.scl.) on the spermathecal sclerite (fig. 92 E).

In both pairs the right and the left fold are far from reaching each other on the ventral side of the genital chamber, but their postero-mesal (or postero-ventral) ends form low, rounded processes; that of the posterior fold (d.i.gon.IX) is situated proximally on the narrow dorsal side of the side lobe of the "vulvar scale". The rounded furrow between the anterior and the posterior fold is sclerotized.

The sclerite on the dorsal side of the "vulvar scale" proceeds forward until the posterior end of the folds g.ch.a. It is continuous with the sclerites of the folds v.i.gon.IX and d.i.gon.IX.

The opening of the colleterial duct is above

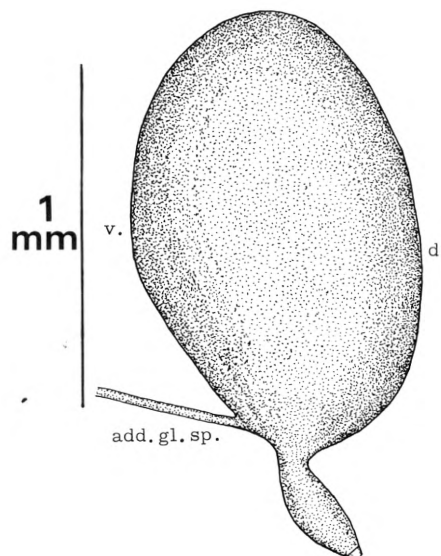


Fig. 94. *Ecclisopteryx dalecarlica*. Spermatheca as seen from the right side; only the most proximal part of the additional gland is shown.

the process pr.sp.d, flanked by a pair of membranous processes (g.ch.b; not shown in the figs.). The basal parts of the latter are apposed to the lateral sides of pr.sp.d, their distal parts lie in the furrows between the folds v.i.gon.IX and d.i.gon. IX. They also touch each other and thus almost occlude the lumen of the genital chamber.

Behind the opening of the colleterial duct the dorsal wall of the genital chamber, as mentioned above, is steeply descendent. Here it is sclerotized, and the sclerite is continuous with that on the tongue Xd-e (fig 92 A-D), but rather widely separated from those on the folds v.i.gon.IX and d.i.gon.IX.

The bursa copulatrix is very much like those of *Limnephilus flavicornis* (p. 163) and *Potamophylax latipennis* (p. 171).

The spermatheca (fig. 94) is divided into two parts, separated by a distinct constriction. The

proximal is very small, slender and fusiform. It opens into the ductus spermathecae through a sclerotic funnel. In some of the dissected specimens it was filled with an amorphous substance. In one specimen it contained the remains of a "spermatophore".

The many times as large distal part is a large, ellipsoidal sac, provided with a rather feeble circular musculature. An additional gland opens subproximally in this part. I was unable to ascertain its length.

The ductus spermathecae has a short and slender distal part and a longer and thicker proximal part, which is knee-like bent. The glandula spermathecae opens into the latter. The proximal part of this gland is thick and straight, whereas its distal part is slender, very long and tightly curved.

The colleterial glands are plurilobed with both anterior and posterior branches. I was, however, unable to make out their shape in detail. The colleterial duct is funnel-like.

Musculature. My dissections of the musculature were not successful, but notes were made on some few muscles which perhaps may aid in homologization. The muscle dvm_4 is still present in segment VIII.

A muscle, which probably is $gonm_1$, originates laterally and approximately in the middle of sternum VIII and is inserted to the anterior corner of the "vulvar scale".

Two muscles originate in the process IXd (fig. 92), proximally on the lateral side and distally on the mesal side, resp. They seem to have relations to the posterior part of the genital chamber. The former probably is $gonm_3$, the latter a IX-X muscle (cp. *Limnephilus flavicornis*, p. 165, and *Potamophylax latipennis*, p. 173).

The muscle $gchm$, originating on sternum VIII, is inclined toward the mesal plane, and in a lateral view it is vertical.

Fine transverse muscle bands seem to be present in the anterior indentation of the dorsal side of the process $pr.sp.d$ (fig. 93 A).

Apatania zonella Zett.

(*A. arctica* Boh.)

Previously (1943) I have given a brief description of the genital segments of this species, though wrongly identified. I then believed *A. zonella* to be exclusively parthenogenetic, Moseley's description of the male (1930) having escaped my attention, and since the percentage of males in the locality of provenience was rather high, I thought that the specimens could not belong to *A. zonella*. (Later I have found males at lake Gjuvvatn, about 1900 m above sea level, in southern Norway). I have given also (1950, cp. 1969) a description of *A. muliebris* McL. These descriptions are badly in need of supplements and corrections.

For comparison I have given a "translation" of the lettering used in the 1943 paper to that used in the present paper.

1943, fig. 3, above: IX = IXaa; X = Xab; 8 = IXd. Fig. 3, middle: IX = IXaa; X = IXc; 8 = IXd; 9 = e.gon.VIII. Fig. 3, below: X = Xc-e; 8 = IXd; 9 = e.gon.VIII.

1943, fig. 5: 1 = ov. 2 = dt.bs. 3 = dt.sp. 4 = op.dt.sp. 5 = pr.sp. 6 = v.i.gon.IX; 7 = g.ch.a; 9 = i.gon.VIII.

Pregenital segments. In addition to lateral longitudinal sutures there is, on the terga, a pair of quite short, mesal longitudinal sutures. On sternum VII a transverse suture, found on the preceding segments, is lacking. On the posterior segments both the terga and the sterna have a postero-mesal, pale and at least very weakly sclerotized indentation. On the sterna it is most sharply delimited on segment VII.

The gland on sternum V is developed approximately as in *Ecclisopteryx dalecarlica* (p. 173), and this sternum has the same hexagonal sculpture.

Segment VIII. The tergum is broader than tergum VII, so that the pleural membrane is much narrower. The extreme anterior end only of the lateral suture is developed. In return there is, near the lateral margin and approximately in the middle of the tergum a small depressi-

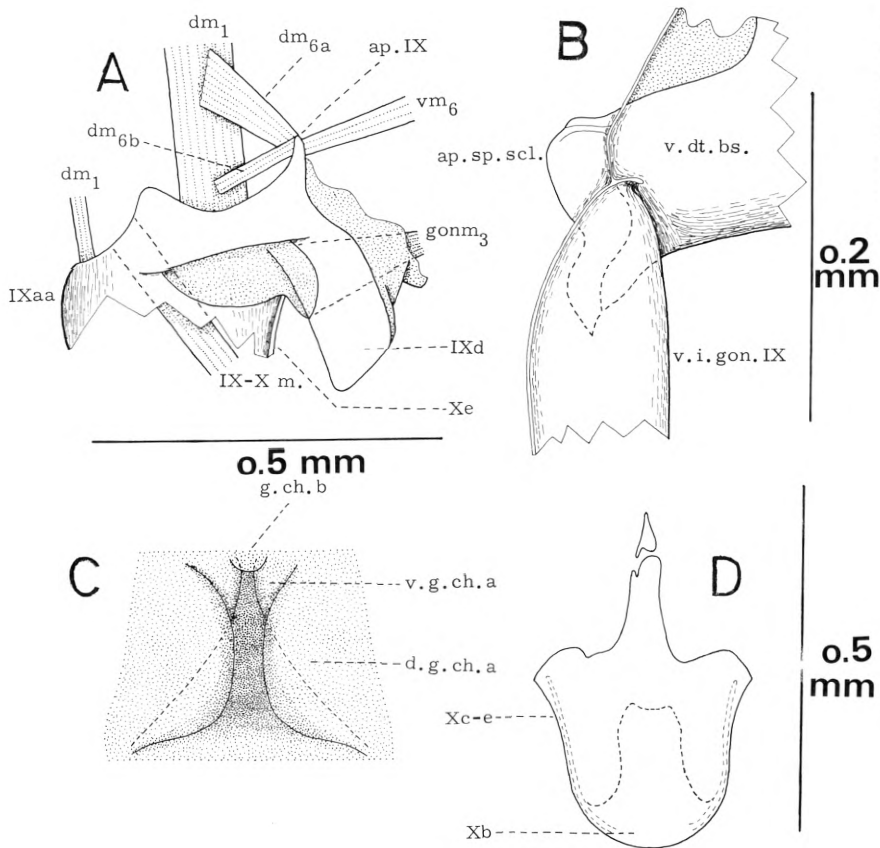


Fig. 95. *Apatania zonella*. A: Anterior part of segments IX and X as seen from the right side. B: The relations between bursa copulatrix and gonopod IX; left side in a dorsal view. C: Anterior part of the floor of the genital chamber in a dorsal view. D: "Supragenital plate"; Xb is shown by a broken line.

on. There are no mesal longitudinal sutures. The postero-mesal indentation is more sharply delimited than on the preceding terga and membranous.

The rather flat sternum is as broad as sternum VII and a little shorter than tergum VIII. There is, however, compensated for this difference in length by the presence of a posterior, membranous part of the venter. The sternum has at least no distinct antecosta, nor traces of other sutures, but near the lateral margin and approximately in the middle there is an oblong depression, which is more pronounced than the corresponding depression on the tergum.

Segments IX and X (figs. 95 A, 96 A) are so intimately united that the boundary cannot be stated with any degree of certainty. In my

previous paper (1943) I have considered the declivity on the combined segment as the boundary between segments IX and X, but this no doubt is a misinterpretation. It seems reasonable to consider the area laterally (or ventrally) to the longitudinal part of the declivity (apart from the "supragenital plate"; see below) as homologous with the process IXc in *Limnephilus flavicornis* (p. 158), and the same probably is true for the "broad but little prominent corner" in *muliebris* (1950, p. 386). In this respect *A. zonella* has some resemblance to *Potamophylax* (p. 168) and *Ecclisopteryx* (p. 175), which may indicate that in the genus *Apatania* conditions in *zonella* are the more primitive, and that conditions in *Potamophylax* and *Ecclisopteryx* are more primitive than in *Limnephilus flavicornis*.

That part of the combined segment which lies behind the transverse part of the declivity might be considered homologous with the dorsal side of the "tubular piece" in *Limnephilus flavicornis* (p. 159). The musculature, however, suggests that the dorsal side of segment X has been turned upside down and is concealed in the "tubular piece", the dorsal side of which (IXab) thus is formed by segment IX. Hence the "tubular piece" in *A. zonella* is not homologous with that in *Limnephilus flavicornis*. In *A. muliebris*, however, the short ventral side of the "tubular piece" probably is homologous with that in *L. flavicornis* (Xc).

In *A. zonella* the inside of the "tubular piece", in the bottom of which the true anus is found, is membranous except for the ventral side. The latter is partly covered by a very strong sclerite, the subanal plate (figs. 95 D, 96 A, Xb), which is descendent in a dorsally convex arch. Its posterior margin is continuous with that of the supragenital plate, forming a sharp edge. The supragenital plate obviously is homologous with the tongue Xe in *L. flavicornis*.

The sclerite Xb is present also in *A. muliebris*, but here it is not united with the supragenital plate, but separated from the latter by a sclerotized area. The condition in *muliebris*, the subanal and the supragenital plate being separate structures, probably is the plesiomorphic one. The greater size of the supragenital plate in *zonella*, as compared with *muliebris*, is due to the fact that it has coalesced with the ventral side of the "tubular piece" or, as it were, replaced the latter.

The anterior margin of the sclerite on segment IX (fig. 95 A) has three broad, but shallow indentations, an unpaired mesal one and a pair of laterals, separated by obtuse-angled and rounded corners. In the figure previously given (1943, fig. 3) this is concealed by the overlapping posterior margin of dorsum VIII. The anterior margin of the sclerite joins the antero-ventral margin of the "sidelobe" (see below) at a right angle. This corner, however, is produced into a

narrow extension (ap.IX), which at least in part is apodemal.

What previously (1943) has been called the "side lobe" in *A. zonella* to all probability is not homologous with the side lobe of the "vulvar scale" in *Limnephilus flavicornis*, but with the process IXd in this species (p. 160). The muscle gonm₃ proves that it is homologous with the process IXd in *Ecclisopteryx* (pp. 175 and 178). This explanation is substantiated—apart from the connection with the sclerite of segment IX—also by the fact that the "side lobe" is clothed with setae on the lateral (but not the mesal) side, which true side lobes are not, as well as by its relations to the folds of the genital chamber. The more or less acute "posterior corner of segment IX" (1950, p. 386) in *muliebris* probably also is homologous with this process. In this respect *zonella* seems to represent the plesiomorphic condition. (See also below: the "vulvar scale"). In *A. zonella* the "side lobes" are somewhat sagittally compressed and sclerotized on both the lateral and the mesal sides.

The "vulvar scale" thus is represented only by the middle lobe, though the process IXd perhaps may contain parts which are homologous with the side lobe in *Limnephilus*; like the latter it has relation to the fold d.i.gn.IX in the genital chamber. (Cp. also *Silo*, pp. 188–89). Otherwise the external parts of the gonopods IX are represented only by the membranous areas flanking the middle lobe. The latter is united with sternum VIII by a bridge, which is broad and broadest in the middle. It is devoid of setae.

The "false side lobes" in *A. muliebris* (1950, p. 387) are not homologous with the side lobes in the Limnephilinae and the Drusinae. They are posterior extensions of the folds v.i.gon.IX (1943, fig 5 B, 6) and have no relations to the folds d.i.gon.IX.

The genital chamber (fig. 96) is in front divided into a long dorsal and a much shorter ventral branch. The point of branching is situated somewhat in front of the middle of venter VIII.

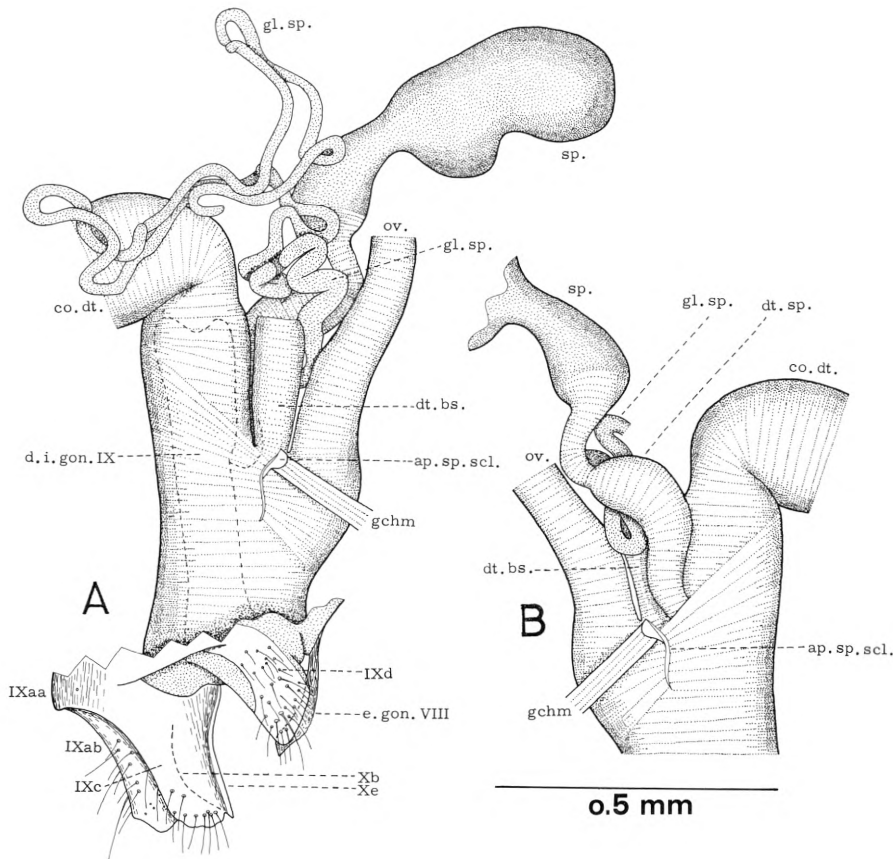


Fig. 96. *Apatania zonella*. A: The genital chamber etc. as seen from the right side. B: Part of A as seen from the left side.

The colleterial duct opens into the anterior end of the dorsal branch, the common oviduct and the ductus bursae into the front end of the ventral branch.

The greater, mesal part of the lip between the dorsal branch and the ductus bursae projects backward as a sclerotized tongue, described in my previous paper (1943, p. 26). It is a part of the processus spermathecae, which is unusually long and slender. The ventral side of the tongue is considerably longer than the dorsal side, and longer than shown in 1943, fig. 5. It extends far onto the dorsal wall of the ductus bursae, even farther than the sclerite on the ventral wall of the latter (see below).

The rather thick lip (fig. 95 B, v.dt.bs.) between the ductus bursae and the common ovi-

duct is sclerotized and fits, as formerly mentioned (1943), into the furrow between the "heel" of the "foot-shaped piece" and the processus spermathecae s.str. Ventrally the sclerite covers only the curvature of the lip, dorsally it extends far onto the ventral side of the ductus bursae. At the hind end of this duct the dorsal and the ventral sclerite are continuous across the lateral wall.

A comparison with the Limnephilinae and the Drusinae (*Ecclisopteryx*) shows that the sclerotized lip (v.dt.bs.) between the ductus bursae and the oviduct is a part of the spermathecal sclerite. The relations between this lip and the fold 6 (v.i.gon.IX) is not described correctly in my previous paper (1943). The lower and narrower anterior end of this fold extends onto the

posterior half of the lateral sclerotization in the ductus bursae (fig. 95 B), where its base of course is continuous with both the dorsal and the ventral sclerotization of the duct. (The former is the ventral side of the processus spermathecae s.str.). From the latter it is separated only by a narrow cleft, which continues in a lateral direction as a platelike apodeme (ap.sp.scl.), which proceeds forward for the whole length of the ventral sclerotization of the duct. In an anterior direction it becomes broader, somewhat downward bent and provided with a transverse, rod-like reinforcement near the front margin.

Nor is the basal boundary of the sclerite on the fold 6 (v.i.gon.IX) described correctly. Behind the base of the processus spermathecae it proceeds in a dorsal direction beyond the fold and is continuous with the sclerite on the latero-dorsal fold (d.i.gon.IX) described below.

In my previous paper (1943) I described two pairs of sclerotic rods lying on the lateral walls of the dorsal branch of the genital chamber. A closer examination, however, discloses that they are the dorsal and the ventral bases, resp., of a pair of sclerotic folds (fig. 96 A, d.i.gon.IX), which proceeds backward for the whole length of the genital chamber. The anterior part of this fold covers the whole lateral side of the dorsal branch. In the undivided part of the genital chamber it is a little narrower and lies dorsally on the lateral side. In a transverse section the fold is triangular, though with a narrowly rounded mesal edge. The fold d.i.gon.IX has about the same height as v.i.gon.IX, and thus the two folds, right and left, are very far from reaching each other in the middle of the genital chamber. At the posterior end the sclerite on the ventral half of the fold d.i.gon.IX is continuous with that mesally on the "side lobe" (IXd). The base of the processus spermathecae s.str. is wedged in between the folds d.i.gon.IX and v.i.gon.IX.

There is no sclerotic connection between the folds in the genital chamber and the "vulvar

scale". Quite on the contrary, the posterior, membranous part of the ventral wall of the genital chamber forms a rather thick fold above the base of the "vulvar scale".

The membranous fold 7 (fig. 95 C, d.g.ch.a) in front of the "spout" 8 (i.gon.VIII) is quite short. Below it there is another mesally directed fold (v.g.ch.a). The posterior end of the latter is very low. In an anterior direction it becomes so high that the two folds, right and left, almost touch each other. Above their anterior ends a small, unpaired upper lip (g.ch.b) of the opening of the common oviduct is seen.

The supragenital plate (Xe) sends a small extension onto the dorsal side of the genital chamber. The anterior end of this sclerite, the width of which is only a small fraction of that of the plate itself, may be broken up in one or some few small, irregular sclerites (fig. 95 D).

In my previous paper I, following the example of Stitz (1904), have reversed the terms bursa copulatrix and spermatheca.

The bursa copulatrix is a small, thin-walled sac. At its opening the muscular duct (fig. 96 A) is funnel-like dilated, but flattened. Then, in a distal direction, it is shifted toward the right and lies at the right side of the ductus spermathecae. Both ducts lie between the dorsal and the ventral branch of the genital chamber.

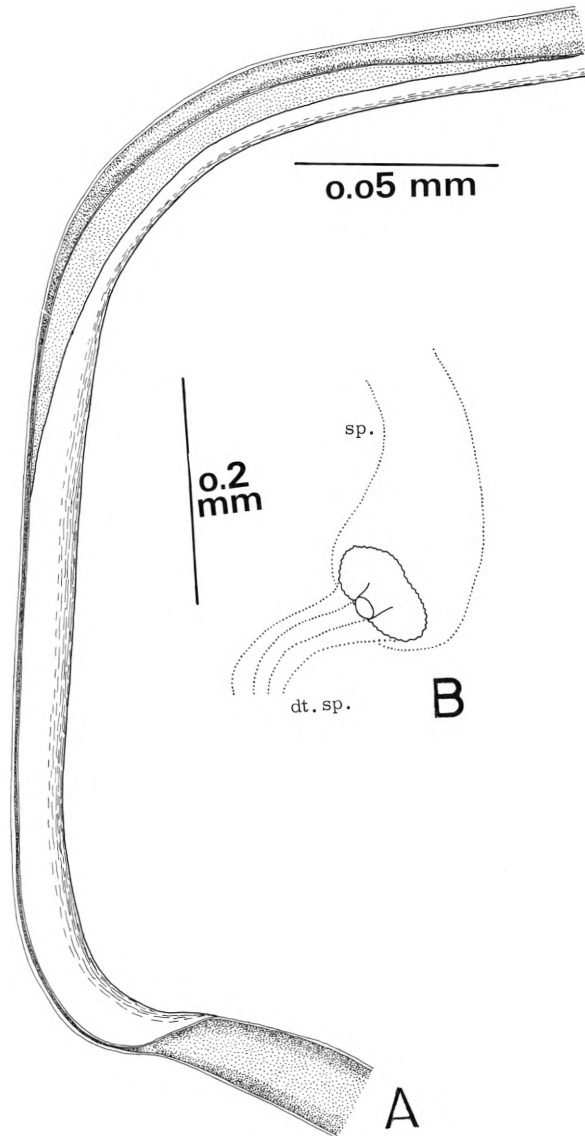
The spermatheca (fig. 96) is composed of a more slender proximal part and a larger, sac-like distal part. There is, however, no distinct boundary between the two parts. In the proximal part there is, at the inner opening of the ductus spermathecae, a funnel-like structure which, however, has another shape than in the *Limnephilinae* and the *Drusinae*, rather as a miniature dinner-plate with a small, tube-like "spout" in the middle (fig. 97 B).

The short ductus spermathecae is rather sharply divided into a proximal and a distal part, which both are muscular. The former is much the longer. In a distal direction it increases, due to the musculature, in thickness, forming a bulb,

and then rather abruptly decreases toward the slender distal part.

In the latter a valve apparatus is seen (fig. 97

Fig. 97. *Apatania zonella*. A: Sagittal section through the ductus spermathecae (including most distal part of the bulb, but excluding most distal part of the duct); left side as seen from the inside; cuticular parts only. B: Transition between the ductus spermathecae and the spermatheca (p. 271).



A). In a proximal direction (i.e. away from the spermatheca) the cuticle of the ventral side is gradually and strongly thickened, so that in the proximal half of this part the lumen is almost occluded, being much dorso-ventrally flattened; the breadth also decreases. The outer diameter of the cuticular tube, however, remains the same. In the thick dorsal wall there is from the outside (i.e. from the epithelial side) a deep and broad furrow, which almost reaches the lumen and is flanked by a pair of thick, longitudinal folds (cp. *Silo nigricornis*, fig. 100 C, p. 188). In the region where the width of the lumen decreases these folds are sclerotized in their dorsal part, (which nearest to the spermatheca means throughout), and in the region where the lumen is most narrow they are entirely sclerotized. By contraction of the circular musculature this mechanism no doubt allows for a total closure of the lumen of the duct. At the opening into the bulb of the proximal part of the duct the width of the lumen increases rather abruptly.

The circular musculature of the duct proceeds for a short distance onto the spermatheca itself.

For the greater part of its length the ductus spermathecae is shifted toward the left, lying to the left side of the ductus bursae.

The glandula spermathecae opens into the right side of the bulb of the duct. It is long, slender and tightly coiled up. There is no accessory gland opening into the spermatheca itself.

The colleterial glands. Each gland is divided into only two branches, a longer anterior one and a shorter posterior one. The funnel-like duct is almost vertical, though a little ascendent. Its short stalk bends backward at a right angle and opens ventrally into the anterior end of the dorsal branch of the genital chamber (fig. 96).

Musculature (fig. 95 A). My dissections of the musculature were far from successful, but some few details, which may be of some value in homologizations, can be given.

The external ventral VII-VIII muscle is divi-

ded into two portions. One is rather strong and has its anterior attachment approximately in the middle of each half of sternum VII, behind the antecosta. It converges in a posterior direction, and the right and the left muscle have their posterior attachment close together on sternum VIII, behind the antero-mesal indentation. The other and weaker muscle has its anterior attachment postero-laterally to the former muscle. It diverges in a posterior direction and is inserted to the anterior corner of sternum VIII. I did not find an internal muscle, but it may very well be present.

Among the dorso-ventral muscles at least dvm_4 is present in segment VIII.

Among the dorsal VIII–IX muscles the longitudinal dm_1 is divided into two widely separated portions. The lateral and rather broad portion has its posterior attachment dorsally to the middle of the latero-anterior indentation in the sclerite of segment IX. The mesal portion is more slender.

Three muscles are inserted on the apodeme at the anterior corner of segment IX (ap.IX). Two are interpreted as portions of dm_6 . One, dm_{6a} , originates approximately on the middle of tergum VIII, superficially to the lateral portion of dm_1 . It is ca. 45° descendent, and its bands converge toward their insertion mesally on the apodeme. The other, dm_{6b} , is very slender. It originates near the hind end of tergum VIII, just laterally to the posterior indentation (p. 179). It is steeply ascendent and inserted to the dorsal side of the apodeme. The third muscle, interpreted as vm_6 , is also slender, though a little stronger than dm_{6b} . It originates on sternum VIII behind the depression mentioned above (p. 179), is steeply ascendent, almost vertical, and inserted to the ventral side of the apodeme.

A muscle which originates dorsally in the “side lobe”, is very steeply ascendent, almost vertical, and inserted rather mesally to the posterior part of the bridge connecting the “vulvar scale” with sternum VIII, has by comparison with *Ecclisopte-*

ryx been interpreted as $gonm_3$, though it might seem rather to be associated with gonopod VIII.

A layer of muscle bands originates along a longitudinal line extending for almost the whole length of sternum VIII, just mesally to the depression on the latter. They pass inward and a little backward and are inserted rather mesally on what here is called sternum VIII; the insertions on the right and the left side, however, are clearly separated. They may represent either $gonm_1$ or a transverse musculature (cp. p. 25).

The muscle $gchm$ (fig. 96 A) originates on the anterior corner of sternum VIII and is inserted to the anterior part of the apodeme (ap.sp.scl.) of the spermathecal sclerite.

This apodeme divides the circular musculature of the genital chamber into halves. The anterior dorsal halves and the posterior ventral halves are very oblique, descendent. The former pass over the upper side of the dorsal branch of the genital chamber, here forming an outer muscle layer. They conceal parts of the ductus bursae and the ductus spermathecae. The posterior ventral halves likewise form an outer muscle layer.

The dorsal and the ventral branch of the genital chamber each has a circular musculature of its own. There is a weak transverse musculature in the base of the tongue of the processus spermathecae. Finally, internal longitudinal bands are inserted to the posterior side of the tongue between the ductus bursae and the common oviduct.

Silo nigricornis Pict.

Pregenital segments. Both the terga and the sterna have, for almost their whole width, a paler and possibly more weakly sclerotized posterior indentation. On sternum VII (fig. 98 B, C), however, it is quite the opposite: in this segment the posterior margin of the sternum is convex, so that it in the middle reaches the hind end of the segment, whereas its very broadly rounded

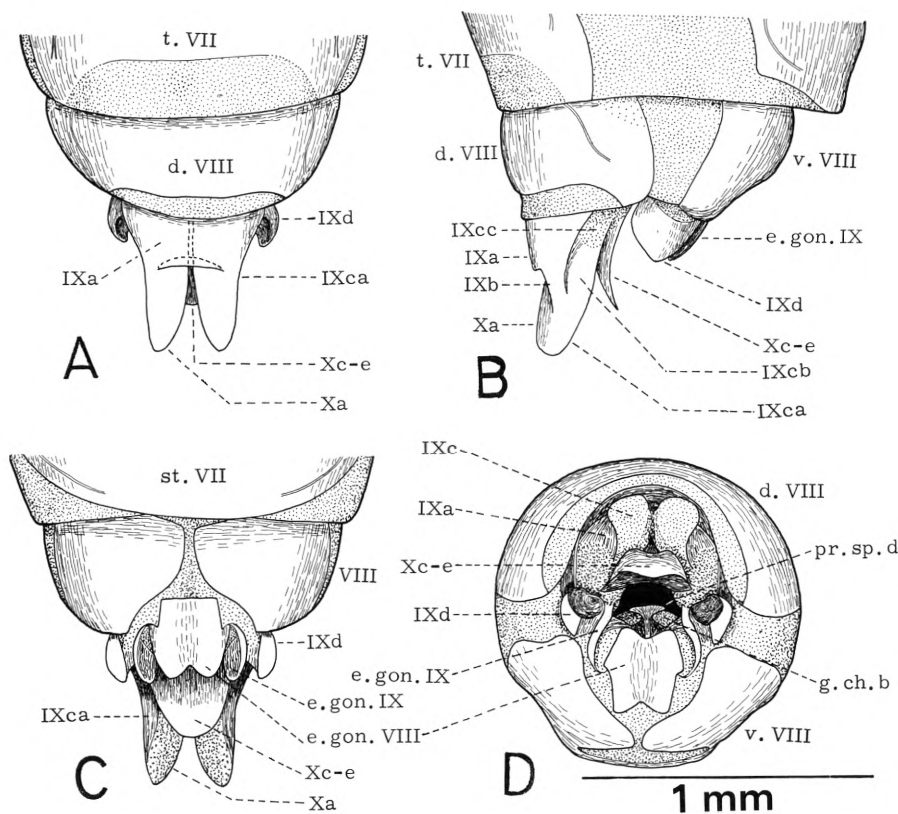


Fig. 98. *Silo nigricornis*. Posterior end of abdomen in a dorsal view (A), as seen from the right side (B), in a ventral (C) and a posterior view (D).

posterior corners are removed from the hind end of the segment.

The lateral, longer part of the acrotergite differs from the rest of the tergum by having a darker colour and being rather densely covered with tiny sensilla campaniformia. The area thus distinguished proceeds onto the tongue-like extension of the anterior corner. In segment II the antecostal suture extends along the whole hind margin of this extension, in the other segments only along its mesal half. The longitudinal sutures extend for most of the length of the tergum. There is, in addition, though not on tergum II, a pair of short mesal longitudinal sutures. In a posterior direction they become longer, and extend on segment VII for almost one third of the length of the segment.

On the anterior part of the sternum condi-

tions are very much like those on the tergum, though no colour difference is seen, the tiny sensilla campaniformia are distributed over the whole acrosternite, and the antecosta does not proceed onto the latero-anterior tongue, which is broader than on the tergum. The posterior ends of the two longitudinal sutures are connected by a transverse suture, which curves a little forward. On sternum VII only the lateral parts of this suture are developed. They appear as mesally directed continuations of the lateral sutures.

There is no gland on segment V.

Segment VIII (fig. 98). Tergum is broader than tergum VII, and hence the longitudinal suture is farther removed from the lateral margin. On this tergum it forms a direct, backward bent continuation of the antecostal suture, which

thus does not proceed laterally to the anterior end of the longitudinal suture. This probably has some connection with the fact that at the anterior corner of tergum VIII there is a weakly sclerotized, almost entirely membranous area.

There is the same dark-coloured extension of the acrotergite as on the preceding terga. It reaches, however, only half-way onto the weakly sclerotized area. The posterior indentation is more sharply delimited than on the preceding terga.

The sternum is approximately as long as the tergum and as broad as sternum VII. As in the other *Limnephilidae* it has a postero-mesal membranous indentation in which the "vulvar scale" is situated. In *Silo* (fig. 98 C, D) the indentation proceeds forward as a narrow membranous middle stripe, which bisects the sternum, but does not quite reach the anterior margin of the sclerite. In front this membranous stripe is strongly widened, thus being T-like (fig. 99 C). The rather broad cross bar of the T occupies more than half the width of the sternum, which bulges forward in front of the cross bar, whereas the latter is flanked by a pair of rounded indentations.

The narrow bridge in front of the cross bar of the T is entirely occupied by a well developed antecostal suture. Laterally to the cross bar this suture goes, in a slight curve and gradually less distinct, backward and outward, and eventually onto the slightly produced anterior corner of the sternum. In front of the lateral parts of the antecostal suture the acrosternite thus is rather broad. It has here a dense clothing of small sensilla campaniformia.

Laterally to the postero-mesal indentation with the "vulvar scale" the hind corners of the sternum are bent upward onto the otherwise membranous posterior margin of the segment. Hence, in a lateral view (fig. 98 B) one might get the impression that the posterior part of the sternum is broader than the anterior part.

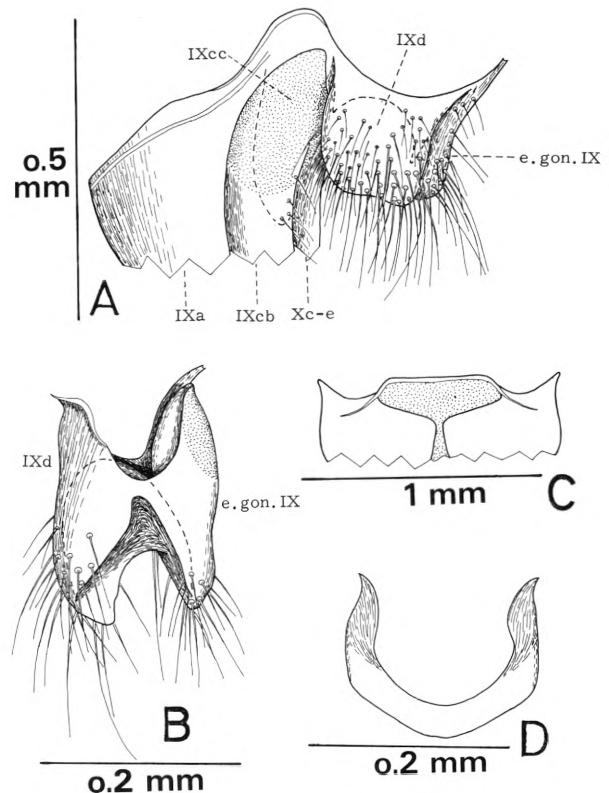
Behind and laterally to the middle of the

sternum there is, on each side, a pale spot with 7-8 especially large setae.

Segments IX and X (fig. 98) are so intimately united that the boundary cannot be stated with any degree of certainty. Together they form a structure which is about as long, but only half as broad as tergum VIII; it is sclerotized to its greatest extent. On the dorsal side the sclerite has a shallow and broadly rounded, anterior indentation, which in fig. 98 A and B is concealed by the overlapping posterior margin of segment VIII.

There is a well developed antecosta, which runs at a rather great distance from the anterior

Fig. 99. *Silo nigricornis*. A: Anterior part of segments IX and X as seen from the right side. B: The process IXd + e.gon.IX in a dorsal view. C: Anterior end of venter VIII. D: The U-shaped sclerite in g.ch.c (p. 189).



margin of the sclerite (fig. 99 A). Hence the acrotergite is unusually broad (or long), especially so latero-dorsally. Approximately in the middle of the lateral side the here otherwise very short sclerite IXa forms a forward directed tongue. The latter is longer than will appear from fig. 99 A, since it also is bent outward, so that its external side faces outward, backward and in part downward. The antecosta proceeds only to the most dorsal part of the tongue, but in return the anterior margin of the latter is reinforced. As mentioned below, the tongue ventrally is connected with the sclerite on the process IXd.

For about its posterior half the structure formed of segments IX and X is divided into two processes (IXca, Xa). The lateral part of the process (IXca), together with the areas IXcb and IXcc, no doubt is homologous with the process IXc in *Limnephilus flavicornis* (p. 158). The muscle IX-X₁ (p. 195), however, proves that the mesal part of the process must belong to segment X. Proximally (or in front) the process is roughly triangular in a cross section, with a dorsal, a latero-ventral and a meso-ventral side. The two former are sclerotized, the latter membranous. Approximately the mesal two thirds of the dorsal side is slightly concave, and the concavity is delimited toward the undivided part of the combined segment (IXa) by a backward directed ridge, which is continuous on the two sides of the body. The lateral third of the dorsal side is separated from the concavity by a keel (IXb), which appear as a sharply backward bent continuation of the transverse ridge and is especially conspicuous in a lateral view.

The latero-ventral side of the process is strongly concave. The concavity proceeds forward (IXcb) on the undivided part of the combined segment, and here it is even more pronounced; its most anterior part is membranous (IXcc).

The latero-ventral concavity on IXca, as well as IXcb and IXcc, dorsally is bounded by a very

sharp ridge which, however, becomes somewhat more rounded in a posterior direction. In front (in fig. 98 B concealed by the posterior margin of segment VIII) this ridge bends downward and backward, merging with the lateral margin of the tongue Xc-e described below.

The distal part of the process IXca + Xa is compressed, though rather thick, with a dorso-lateral and a ventro-mesal side. The latter is membranous, and the membrane extends to the anterior end of segment IX. Hence the undivided part of the combined segment contains an, in a transverse section triangular, cavity with membranous walls, through which the anus opens. The floor of the cavity is formed of the tongue Xc-e described below.

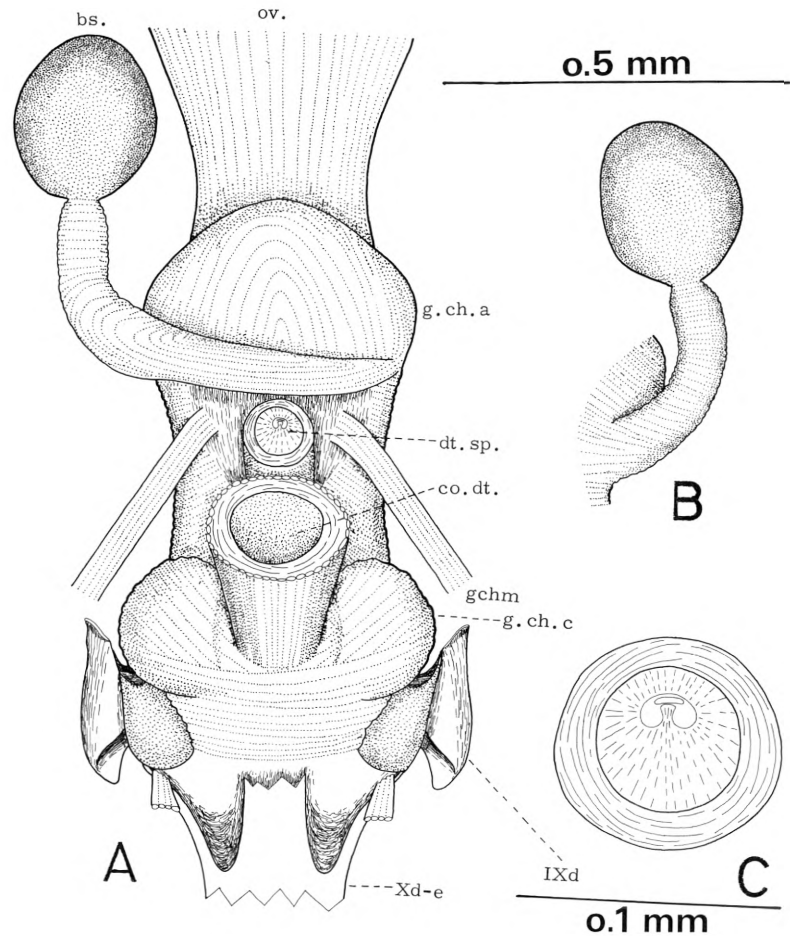
This tongue, which extends approximately to the middle of the processes IXca + Xa, are a little narrower than these two processes together. It has sharp margins, a concave ventral side and a convex dorsal side. The whole ventral side and the posterior part of the dorsal side are sclerotized. The anterior part of the dorsal side is membranous and laterally united with the ventro-mesal side of the process IXa + Xa; in fig. 99 A the line of union is shown by a broken line.

The tongue Xc-e forms the upper lip of the genital opening. The anus is found in the bottom of the cavity between this tongue and the processes Xa.

The sclerotized parts of the process IXca + Xa, like most of the surface of the body, is clothed with small setae. Distally on the latero-dorsal side the setae are very short (ca. 20 μ), but at the same time very thick (ca. 4 μ). The ventro-mesal side of the process, as well as the whole of the tongue Xc-e, is devoid of setae.

The "vulvar scale" (fig. 98 C-D, e.gon.VIII), which is rather broad, is undivided, but has a bilobed distal end. It is sclerotized on both sides, but on the dorsal side the sclerite does not proceed so far forward as on the ventral side. The latter is concave in a transverse direction,

Fig. 100. *Silo nigricornis*. A: The genital chamber etc. in a dorsal view. B: bursa copulatrix, ductus bursae etc. as seen from the left side. C: Transverse section of ductus spermathecae.



and this concavity proceeds forward on venter VIII. Hence the membranous middle stripe of the latter is situated in a flat, V-like furrow. Quite distally the ventral side of the “vulvar scale” is clothed with setae.

Laterally to the “vulvar scale”, flanking the genital opening, a pair of very complicated processes (figs. 98 C-D, 99 A, e.gon.IX + IXd) is seen. Each of these processes (fig. 99 B) is short, but thick, with a strongly convex lateral side and a slightly concave mesal side. The distal end of the process is pot-like depressed for almost three fourths of the length of the process. The mesal side of the “pot” is several times as thick as the rather thinwalled lateral side. Both dorsally and

ventrally the margin of the pot is indented, dorsally for two thirds, ventrally for scarcely one third of the length of the process. Since the dorsal and ventral sides of the sclerite of the process also have proximal indentations, the sclerite on the dorsal side is almost entirely bisected. The “pot” probably receives some part of the male genitalia during copulation.

Proximally to the distal indentation the ventral side of the process is transversely concave, two longitudinal ridges thus arising. The mesal ridge is continuous with the sclerite on the “vulvar scale” through an extremely narrow, hook-like bridge, running on the otherwise membranous posterior margin of venter VIII.

The mesal side of the process also is connected with the lateral edge of the free part of the "vulvar scale" by a horizontal lamella. This lamella, which in a ventral view goes outward and forward from the "vulvar scale", is largely membranous, though the sclerite on the "vulvar scale" proceeds for a smaller or greater distance onto the lamella (fig. 98 C).

On the dorsal side of the process also there is a slight and indistinct transverse concavity. The keel mesally to this concavity is by a narrow bridge connected with the lateral tongue of the sclerite on segment IX, i.e. with the acrotergite IX (fig. 99 A).

The process described above to all probability is a composite structure, formed of parts which are homologous with the side lobe of the "vulvar scale" and the process IXd in *Limnephilus flavicornis* (p. 160). The membranous area above its base is homologous with the similarly situated area in *Apatania zonella* (Anker Nielsen 1943, fig. 3). In *A. muliebris* (Anker Nielsen 1950, fig. 2) this area is sclerotized. (Cp. also *Apatania zonella*, p. 180).

The process is clothed with setae on the lateral side, as well as distally on the dorsal, mesal and ventral sides. In the pot-like depression of the distal end setae are found only quite distally on the mesal side.

The genital chamber (figs. 100 A, 101, 102, 103), which extends to the boundary between segments VII and VIII, has a rather unusual shape. In a cross section it is almost circular, though with a slight tendency to be triangular. On the dorsal side it has, for its whole width, two large bulges, one at the anterior end (g.ch.a), the other at the posterior end (g.ch.c).

The anterior bulge, between the openings of the ductus bursae and the common oviduct, is approximately semiglobular and pushes forward above the common oviduct. The opening of the latter into the genital chamber has the shape of a very low, circular valve (fig. 102).

At the ventral entrance to the anterior bulge

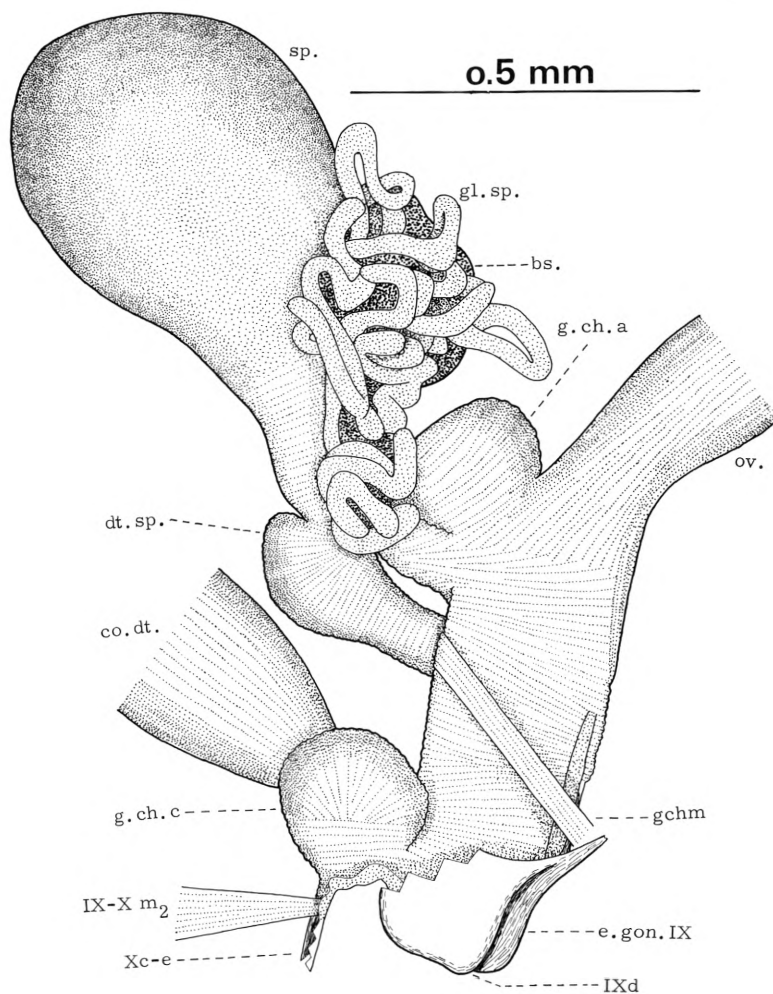
(g.ch.a) there is, on the lateral wall of the genital chamber, a pair of ascendent, longitudinal folds (fig. 103 A, g.ch.ab), which have sharp mesal edges and are membranous or, especially at the hind ends, slightly sclerotized. In front the two folds, right and left, are not far from touching each other, in a posterior direction they diverge, becoming much lower. Moreover, the dorsal wall of g.ch.a bulges into the lumen as an unpaired lobe (figs. 102, 103 A, g.ch.aa), which together with the folds g.ch.ab almost entirely obstructs its lumen.

The posterior bulge (g.ch.c), which is a little broader than the genital chamber itself, has the shape of a thick upward and forward directed tongue. In a dorsal view (fig. 100 A) it is roughly cordate, its distal (or anterior) end being divided into three parts. The narrower and unpaired middle part receives the opening of the colleterial duct. The lateral parts, which each is both broader and thicker than the mesal part, form a pair of hyaloid vesicles flanking the proximal part of the colleterial duct.

In the bottom of the bulge g.ch.c there is a sclerite (fig 102, g.ch.d) in the shape of a U with a rounded bottom and short legs (fig. 99 D) and with the opening facing forward. The bottom of the U lies on the middle part of g.ch.c, behind the opening of the colleterial duct. The legs of the U are situated on the mesal sides of the two hyaloid vesicles. At the boundaries between the bottom and the legs the sclerite is subjected to a torsion of ninety degrees. The anterior end of the sclerite on the tongue Xc-e bends upward and almost touches the U-like sclerite; the two sclerites, however, are separated by a distinct membranous stripe (fig. 102).

Two sclerites are situated on the dorsal side of the genital chamber between the bulges g.ch.a and g.ch.c (figs. 103 A, 104), together representing the spermathecal sclerite. The anterior and larger of the sclerites (sp.scl.a) is roughly triangular with slightly S-like curved sides. This shape conforms to the fact that the dorsal wall of

Fig. 101. *Silo nigricornis*. The genital chamber etc. as seen from the right side.



the genital chamber, between the two bulges, first tapers in an anterior direction and then widens again. The broad front margin of the sclerite is deeply indented, conforming to the shape of the opening of the ductus bursae. The margins have strong reinforcements.

The mesal part of the anterior sclerite, in the rear for the whole width of the sclerite, bulges into the lumen of the genital chamber as a rather high processus spermathecae (pr.sp.a; see also fig. 102), the posterior end of which is much sagittally compressed. In front the ventral side of this process bends upward in an even curve

and continues, vertically, for some distance on the posterior (or dorsal) side of the ductus bursae. This part of the sclerite (fig. 104 B, sp.scl.c) proceeds also forward (sp.scl.d) onto the oblique part of the ductus bursae (see below), where it carries a pair of small, ventral, freely into the lumen of the genital chamber projecting lamellae (sp.scl.f), which postero-mesally are supported on the processus spermathecae. The sclerite on the ductus bursae (sp.scl.d) proceeds farther forward on the lateral sides of the bulge g.ch.a as a pair of rods (sp.scl.g) which eventually almost, but not entirely, reach each other on

the anterior side of the bulge. In a lateral view these rods, which lie above the folds g.ch.ab, appear slightly curved with a ventral concavity.

For the greater, posterior part of its length the processus spermathecae has a broad longitudinal keel (pr.sp.b) on the ventral side. At the posterior end the lateral sides of this keel and of the processus itself are flush. Except for its base the keel is largely membranous. In lateral view this membranous area is divided into three sections: an anterior, short, descendent and slightly convex one, a middle horizontal one, and a posterior ascendent one; the two last mentioned sections are about equal in length. On the middle section there is a sclerite, in a ventral view resembling a horse-shoe, the posterior ends of which almost touch each other. In a

lateral view (fig. 104 B) it is broadest in the middle. The sclerite encloses a drop-like membranous area, in the posterior part of which the egg-like opening of the ductus spermathecae is found.

The posterior sclerite (sp.scl.h) is much smaller than sp.scl.a and has a more complicated structure. Its basal part is the sclerotized lip below the entrance to the middle part of the bulge g.ch.c. On the ventral and posterior sides of this lip a high, but relatively narrow keel rises; it is broadest at the rounded anterior end. In the rear it is produced into hammer-like structure (pr.sp.d) with a short shaft. The latter is high, but narrow, much sagittally compressed. The lateral sides of the "shaft" and of the greater, posterior part of the keel itself are strongly

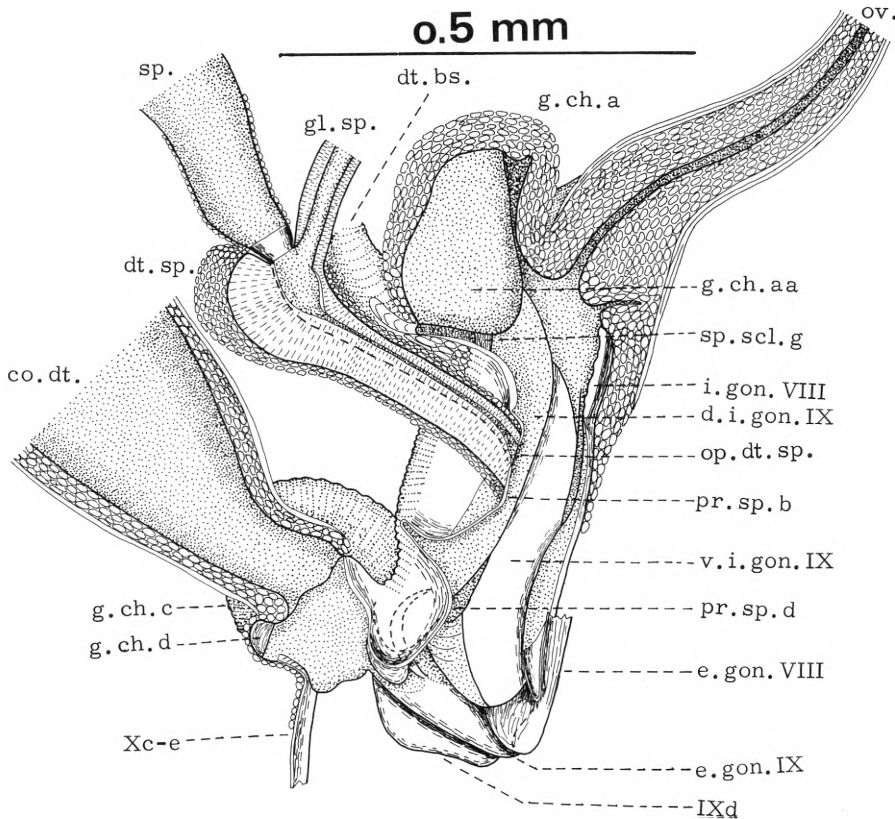
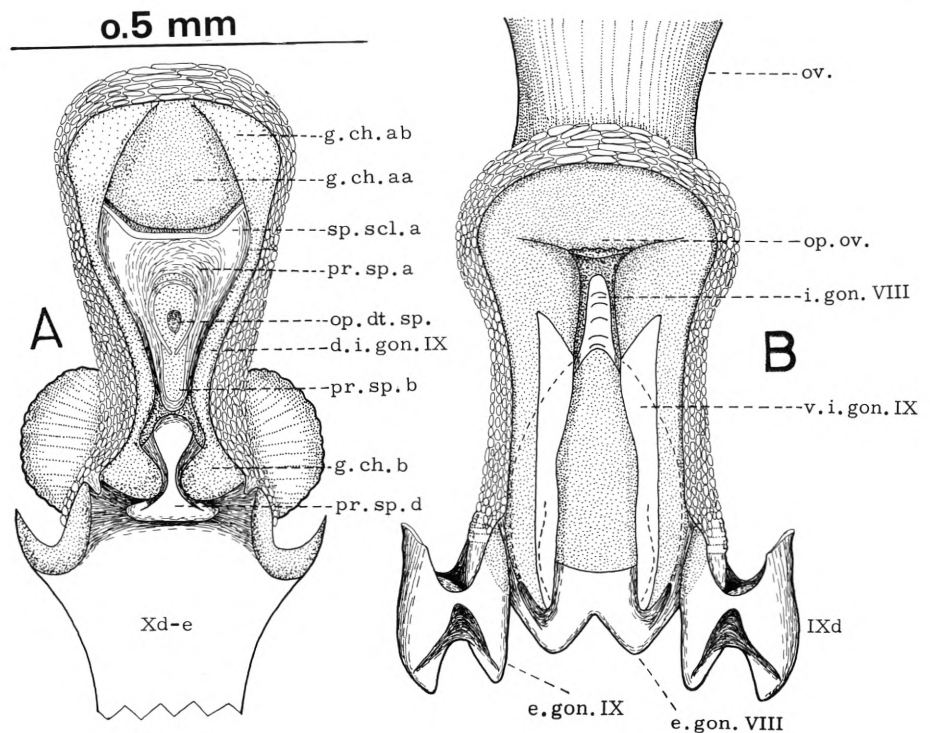


Fig. 102 *Silo nigricornis*. Sagittal section through the genital chamber; left side as seen from the inside.

Fig. 103. *Silo nigricornis*. A: Upper wall of the genital chamber etc. in a ventral view. B: Lower wall of the genital chamber etc. in a dorsal view.



concave. Ventrally, and on the “shaft” dorsally too, the concavity is delimited by sharp edges. The ventral side of the “shaft” is much narrower than the dorsal side.

The sclerites *sp.scl.a* and *sp.scl.h* are closely apposed, though separated by a short, steeply descendent, membranous area.

Ventrally on the lateral side of the genital chamber, for almost its entire length and for about half the height of the lumen, there is a pair of longitudinal folds (figs. 102, 103 B, *v.i.gon.IX*), which become broader in an anterior direction. Their posterior ends, projecting as a pair of short processes (probably homologous with the “false side lobes” in *Apatania muliebris*) above the “vulvar scale”, are far removed from each other, their anterior ends approach, but do not reach each other. In front the folds end abruptly and are closely apposed to the lateral parts of the circular valve surrounding the opening of the oviduct. Apart from the

anterior part the fold is sclerotized mesally, to the greatest extent on the ventral side, where the sclerite is continuous with that on the dorsal side of the “vulvar scale”. The sclerotization proceeds farthest forward, however, on the dorsal side.

In the posterior part of the fold *v.i.gon.IX* its mesal side is broader than its base and concave. At the extreme posterior end of the fold, however, the base is dilated and proceeds dorsally as a narrow, vertical, membranous fold behind the process *g.ch.b* described below.

As mentioned above the ventral side of the “vulvar scale” is transversely concave, and conforming to this its dorsal side is transversely convex. This convexity proceeds forward onto the floor of the genital chamber as a quite low, unpaired fold between the two *v.i.gon.IX*. In an anterior direction it becomes still lower and narrower, as the distance between the folds *v.i.gon.IX* decreases. Quite in front, below the dorsal bulge (*g.ch.a*), the fold carries a strong

sclerite (i.gon.VIII), which is slightly transversely wrinkled. The posterior margin of this sclerite is deeply indented, and the corners of the indentation are produced into narrow rods, which diverge in a posterior direction and eventually are united with the sclerite on the dorsal side of the "vulvar scale".

Finally there is, for most of the length of the genital chamber, a pair of membranous folds (figs. 102, 103 A, d.i.gon.IX). In front they are connected with the folds g.ch.ab described above, though the connecting stretch is rather indistinct. For most of their length they are only low, but their posterior ends project as a pair of short, finger-like, slightly sclerotized, inward bent processes (g.ch.b) in front of the entrances to the side lobes of the bulge g.ch.c; they fill the spaces between the "shaft" and the "head" of the "hammer" pr.ps.d. The structures g.ch.b and pr.sp.d thus together form a trilobed lower lip of the entrance to the bulge g.ch.c. The process g.ch.b no doubt is homologous with those so designated in *Limnephilus* (p. 162), *Potamophylax* (p. 170) and *Ecclisopteryx* (p. 177).

The bursa copulatrix (figs. 100 A, B; 101) is a small, slightly oblong sac, which has an asymmetrical position, shifted to the left. The short, muscular duct is bent downward and toward the right. It is strongly transversely dilated toward the opening, which is just behind the dorsal bulge g.ch.a of the genital chamber. The opening, which in the rear is bordered by the spermathecal sclerite (fig. 104 A), has the shape of a narrow cleft with a transverse middle part and lateral parts, which diverge ca. 45° in an anterior direction. The concavity of the cleft thus faces forward, which is unusual. In front it is delimited by the fold g.ch.aa (fig. 102).

The spermatheca (fig. 101) is a large, pear-like sac. At the opening of the slender "stalk" into the ductus there is a funnel-like sclerite (fig. 102). The short, almost vertical ductus spermathecae is developed, for its whole length, as a bulbus, which is due more to the epithelium

than to the musculature, the latter, which proceeds for some distance onto the spermatheca itself, being rather feebly developed. The epithelium—and quite distally the musculature too—is several times thicker on the posterior (or dorsal) side than the anterior side.

The extreme distal part of the lumen is bottle-like dilated (fig. 102) and receives, on the anterior side, the opening of the glandula spermatheca. This gland, which is very long and much coiled, has a rather wide lumen and an epithelium, which is about as thick as that on the anterior side of the duct. There is no additional gland opening into the spermatheca itself.

In one of the dissected specimens a "spermatophore" was found. The remainder and larger part of the spermatheca was filled with an amorphous substance.

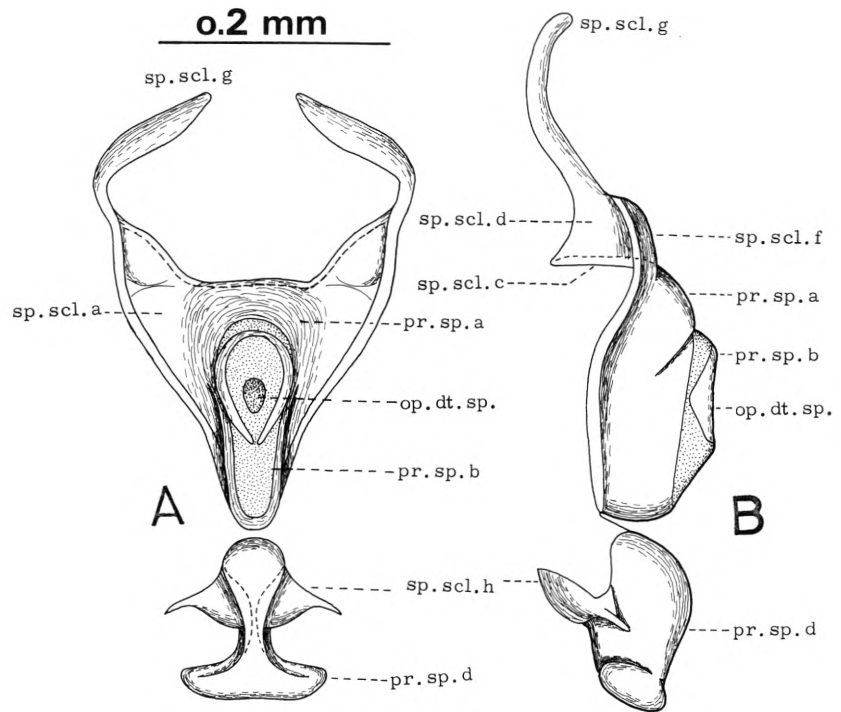
For most of its length the lumen of the ductus spermathecae is narrow. On the anterior (or ventral) side the cuticle is many times as thick as on the posterior side (fig. 100 C). It has, however, from the haemocoelic side, a broad longitudinal furrow, which almost reaches the lumen, flanked by a pair of thick folds. This is highly reminiscent of conditions in *Apatania* (p. 183) and—among many other things—a proof of the close relationship between the *Apataniinae* and the *Goërinae*. By constriction of the circular musculature this structure no doubt allows for an entire closing of the lumen of the ductus spermathecae.

The colleterial glands. Each is divided into three branches, a longer anterior one and two shorter posterior ones, the latter being dorsal and ventral, resp. The funnel-like duct has a small opening in the middle section of the postero-dorsal bulge (g.ch.c) of the genital chamber (figs 101, 102).

Musculature. My dissections were not successful, but some notes were made.

The external of the ventral VII–VIII muscles is divided into two portions, both consisting of numerous fine bands. One originates on a little

Fig. 104: *Silo nigricornis*. Processus spermathecae etc. in a ventral view (A) and as seen from the right side (B).



less than the lateral half (of each half) of the antecosta of sternum VII. The two muscles, right and left, as well as their bands converge toward their insertion on the antecosta of sternum VIII, at the corner of its anterior bulge (fig. 99 C). The other portion originates on the posterior part of the lateral margin of sternum VII, has an almost transverse course and is inserted superficially to the former muscle. The internal muscle is narrower, but more compact. It originates quite mesally on the antecosta of sternum VII, diverges in a posterior direction and is inserted laterally to the antecosta of sternum VIII.

In segment VIII the muscle dvm_4 can be followed to the posterior end of the lateral margin of the sternum.

I found three VIII-IX muscles, which I have interpreted as dm_1 , dm_4 , and dm_6 . The first mentioned is a strong muscle, originating on the

whole antecosta of tergum VIII and inserted to approximately the dorsal half of the antecosta of segment IX. The second is an oblique muscle composed of fine bands. It originates in the middle of each half of the antecosta of tergum VIII, superficially to the former muscle, and is inserted quite laterally to the antecosta of segment IX. Finally, dm_6 originates at the posterior corner of tergum VIII and converges fan-like toward its insertion on the anterior reinforcement on the lateral tongue of the sclerite on segment IX (p. 277; fig. 99 A).

There is only one muscle associated with the gonopods, $gonm_1$. It originates along a longitudinal line on a little more than the anterior half of sternum VIII and converges fan-like toward the small insertion on the mesal edge of the same sclerite (fig. 98 C) at the level of the anterior corner of the "vulvar scale". Even the most posterior bands go a little backward. This

muscle might perhaps also be considered as a transverse muscle (pp. 26–40).

There are three IX–X muscles. IX–X₁ originates mesally on the antecosta of segment IX (though the origins of the right and the left muscle are clearly separated) and is inserted just behind the ridge separating the process IXc from IXa. IX–X₂ originates somewhat behind the antecosta of segment IX; the steeply ascendent, almost vertical muscle (fig. 101) passes laterally to IX–X₁ and is inserted to the ventral side of the tongue Xc-e. IX–X₃ originates just dorsally to the sharp edge which delimits the area IXcc from IXa (figs. 98 B, 99 A). By IX–X₂ it is divided into two portions, passing in front and behind this muscle, resp., and inserted to the anal tube.

The rather slender muscle gchm (fig. 101) originates on the upward bent posterior corner of sternum VIII. It passes inward and much forward and is inserted to the anterior corner of the spermathecal sclerite.

The genital chamber (figs. 101, 102) has the usual circular musculature, but only the most anterior bands, which dorsally encompasses the proximal part of the ductus bursae, are complete. Farther behind the rings are incomplete dorsally, bending into the cavities of pr.sp.a and

the keel on sp.scl.h (fig. 104). Still farther behind the bands are interrupted also ventrally, having their ventral attachments to the posterior halves of the folds v.i.gon.IX (fig. 103). In the anterior part of this stretch, however, there is a ventral transverse musculature uniting the two rods issued from the corners of the sclerite i.gon.VIII.

In the hindmost part of the genital chamber, behind the bulge g.ch.c, the circular musculature is complete dorsally, but not ventrally. The most posterior bands are attached to the folds v.i.gon.IX and pass through the membranous folds connecting IXcc with Xc-e (fig. 99 A).

The bulges g.ch.a and g.ch.c have their own, rather feeble musculature, the arrangement of which will appear from figs 101 and 102. That of g.ch.a conceals the entrance to the fold g.ch.aa.

Both the common oviduct and the colleterial duct have externally to the strong circular musculature a weak longitudinal musculature. Latero-dorsally that of the common oviduct proceeds onto the base of the bulge g.ch.a, mingling with the circular musculature of the latter. Ventrally the longitudinal musculature of the oviduct proceeds rather far backward on the ventral side of the genital chamber.

Concluding Remarks

The present study has shown that on a family and subfamily level the female genitalia of Trichoptera are still more varying than those of the males, and that there in this respect may be very great differences between genera of the same subfamily (Tinodes–Lype–Psychomyia, Polycentropus–Holocentropus, Agraylea–Hydroptila, Limnephilus–Potamophylax).

The plesiomorphic condition will appear to be that segments VIII–XI are strongly modified, and often segment VII, too, somewhat, exceptionally even much modified. In many cases, however, and just in families which are considered more advanced, segment VIII does not seem so much modified. There is good evidence, though, that this condition is secondary. In Annulipalpia a distinct boundary apparently is seen between segments IX and X, but there is evidence that this, too, is secondary. In Integripalpia the boundary between these two segments cannot be stated with any degree of certainty. The combined segment, which is larger than in Annulipalpia, may attain a very elaborate shape. In Anulipalpia there is a pair of small appendages which probably are cerci, but otherwise segment XI cannot be recognized as a separate entity.

Ephemeroptera have paired, though close-set gonopores between segments VII and VIII. In Thysanura the unpaired gonopore has, from a morphological point of view, the same position, but the functional gonopore has shifted backward, to the posterior margin of segment VIII. In all other insect orders the morphological gonopore has at least shifted thus far backward. Based upon conditions in Thysanura and upon the fact that in Trichoptera the ventral VII–VIII

musculature differs distinctly from that in the preceding segments, the theory is put forward that this shift has been accomplished by the limbs of segment VII having united with each other and with segment VIII.

It is generally stated that in four orders, Mecoptera, Trichoptera, Lepidoptera and Coleoptera, the gonopore is situated between segments IX and X. Evidence, corroborated by a study of the musculature, is here represented to the effect that at least in Trichoptera the apparent ventral side of segment IX actually is the gonopods VIII and IX.

In the Trichopteron *Ecnomus* the morphological gonopore definitely is situated just behind segment VIII, bordered ventrally by a tongue, which to all probability is the united distal ends of gonopods VIII. Though I have not observed the egg-laying, I have reason to believe that the functional gonopore is near the tip of the abdomen.

From conditions in *Ecnomus* three or four trends of development can be followed, though they do not necessarily represent phylogenetic lines.

In the Psychomyidae the morphological gonopore has moved backward, though not so far backward as the functional one. This is due to the fact that the homologue of the tongue in *Ecnomus*, mentioned above, has united with the anterior ends of the margins of a cleft in the ventral side of segment IX, which margins to all probability represent parts of the gonopods of this segment.

In *Wormaldia* the morphological gonopore has moved still farther backward, and in *Rhyacophila*, *Agapetus* and the hydroptilids it is situa-

ted very near the posterior end of the abdomen, i.e. the morphological and the functional gonopore are identical.

Due in part to invaginations an elaborate atrium has been formed in the polycentropines and *Hydropsyche*. In *Holocentropus* the backward shift of the gonopore has not been quite achieved, in *Polycentropus* and *Hydropsyche* it has.

In some families of Integripalpia conditions to a certain degree are similar to those in e.g. *Rhyacophila*, though the externally visible parts of the gonopods are larger, forming an apparent, longitudinal subdivided sternum IX. In the more advanced families they are again reduced in size, or at least in length, and firmly united with (the secondary) sternum VIII, so that the gonopore seems to be located behind the latter, bordered ventrally by MacLachlan's "vulvar scale". It is true that the small "vulvar scale" in the Limnephilidae is separated from sternum VIII (though not so distinctly in *Apatania*) but this may be secondary. In the most advanced groups of Integripalpia the relations between segments IX, X and the gonopods are so complicated that only comparisons, including the musculature, can give a clue as to which part of the body some structures belong.

The conclusion is that the apparent ventral side of segment IX actually is formed by the gonopods VIII and IX, which also form the lateral and ventral walls of the genital chamber, the latter thus being a secondary structure in Trichoptera. I think that the same holds true for the three other orders mentioned above.

As to the Mecoptera this view has been expressed by Mickoleit (1973–76). In *Boreus* (Stitz 1908, Mickoleit) the gonopods VIII are united for about the anterior two thirds of their length, but not with the gonopods IX, which are united with the lateral parts of segment IX itself. In *Panorpa* (Grell 1942) the union between segment IX itself and its gonopods is not complete, the posterior part of the genital chamber being open laterally.

In Lepidoptera (Verson & Bisson 1896, Aman 1954, Brumold 1957, Leclercq-Smekens

1976) the surroundings of the secondary gonopore are formed by two pairs of imaginal discs, belonging to segments VIII and IX, and no doubt homologous with those imaginal discs which in Hymenoptera form the ovipositor (Dewitz 1874, 1877). Verson & Bisson think that they are derived from embryonic limb rudiments. The ditrysian condition may have arisen by a "failure" of the basal parts of gonopods VIII to unite. In the psychid *Fumea casta* Dallas the opening for egg-laying is surrounded by two pairs of lobes, which perhaps may be interpreted as the distal ends of the gonopods.

Böving (1913) has given beautiful descriptions and figures of the female genitalia in Noteridae and a number of Dytiscidae. In my opinion they can easily be interpreted as a much modified—and in some cases perhaps not so very much modified—ovipositor, though the author himself considered them as secondary structures. Burmeister (1975, 1976), however, considers the surroundings of the gonopore in Dytiscidae and other Hydradephaga (including Gyridae) as formed by the gonopods. A similar opinion has been expressed for other systematic groups by Blackwelder (1936: Staphylinidae), Evans (1961: the tiny cryptophagid *Atomaria ruficornis* Marsh.) and Doyen (1966. *Tenebrio*)—and for beetles in general by Verhoeff (1902).

In *Rhyacophila*, *Agapetus*, *Wormaldia* and the hydroptilids the genital segments as in Mecoptera (except Bittacidae and Boreidae) and some Lepidoptera form an extensile and retractile "Legeröhre" with a pair of long apodemes on both segment VIII and segment IX. This may be considered a plesiomorphic condition, a hypothesis which perhaps is substantiated by the fact that the apodemes, and especially those of segment IX, show a tendency to persist, though in a very much reduced form, in other families. If it is a plesiomorphy, it probably is an heritage from ancestors with terrestrial metamorphosis, since in principle there is no difference between the egg-masses of e.g. *Rhyacophila* with and *Hydropsyche* without a "Legeröhre".

The idea of a "Legeröhre" as a plesiomorphic character might seem to be in conflict with that of considering the position of the gonopore in *Ecnomus* as a plesiomorphy. However, conditions in *Wormaldia* show that it need not be so.

Most *Tinodes* species (Fisher 1977) and *Lype* have some sort of non-extensile and non-retractile "Legeröhre". On this matter Fisher writes: "The long ovipositor of most *Tinodes* species is associated with the laying of eggs in cracks and crevices of the substratum." In *Lype* it may be associated with the fact that the larvae are borers in decaying and waterlogged wood, as first shown by Hickin (1950).

According to Riek's figures (1976) the marine caddisfly family Chathamiidae has a similar, though not identical "Legeröhre". The females of this family have the peculiar habit of laying their eggs in the coelomic cavities of starfishes (Anderson & Lawson-Kerr 1977).

In a few Integripalpia the abdomen is much contracted during egg-laying, and the posterior segments retracted, so that on the posterior end of the abdomen a cavity is formed, in which a ball of eggs may be carried, in a Plecoptera-like fashion, before deposition in the water. This has been directly observed in *Oligoplectrum* and must be supposed in *Molanna* and *Odontocerum*.

As mentioned above the lateral and ventral walls of the genital chamber are formed by the gonopods VIII and IX. Its dorsal wall is the true ventral side of segment IX together with part of segment X. Sometimes so much of the latter segment is included that the anus is situated in the genital chamber, a cloaca thus being formed.

The shape of the genital chamber varies to a high degree, but in most forms it is extremely complex, no doubt unrivalled among insects. It may be noted that most Trichoptera have a bursa copulatrix, to all probability homologous with those in Mecoptera (Grell 1942) and Lepidoptera.

It is tempting to speculate about the relations between the female and the male genitalia. To tell the truth, I have only in some very few cases, e.g. *Rhyacophila*, *Psychomyia* and *Apatania*, been able to see a little of this relation. Statzner (1974) has described the copulation in *Cheumatopsyche*, Fisher (1977) in *Tinodes*.

The typical outfit of Trichoptera comprises a pair of small glands, opening near the anterior corners of sternum V, though they are lacking in about half the forms here studied. In some few forms special glands are found in segment VIII, IX or X.

A comparison of female genital structures no doubt can contribute to elucidate the phylogeny of the order. To me, at present, the picture seems a bit confusing. Before drawing any conclusion I think it will be better to await studies on non-European systematic groups, which may fill in some gaps in the present study. Only a small point shall be made here: The subfamily Ecnominae sometimes is included in the Psychomyiidae. However, the posterior end of the abdomen clearly shows that they are polycentropids, as do the morphology and biology of the larvae. On the other hand, the female genital structures show a distinct affinity to the Psychomyiidae.

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