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A COMPARATIVE STUDY OF THE GENITAL SEGMENTS AND THEIR APPENDAGES IN MALE TRICHOPTERA

BY

ANKER NIELSEN

København 1957
i kommission hos Ejnar Munksgaard

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Introduction.

Though in Trichoptera the genital segments and their appendages of the ♂♂ play a major role in taxonomy, their morphology has been little known. It is true that there exists a very great number of descriptions which in an excellent way serve their purpose: to provide reliable criteria for distinguishing the various species. From the point of view of comparative morphology, however, they are of little value. They are almost exclusively concerned with structures which can be seen without dissection, and oftener even with structures only which are seen projecting from the posterior end of pinned specimens. The musculature, so important for the understanding of the homologies of the structures in question, has been entirely neglected. In most cases, probably, the descriptions therefore give no clue for estimating the real morphological value of the structures, neither as compared with other insects, nor as compared with other members of the order. SCHMID's valuable and extensive studies of the Limnophilidae (1953, 1954, 1955) to some extent suffer from the same defects. The only attempt giving a comparative morphology of the genitalia of the whole order, so far made, is ZANDER's work (1901). He gives very interesting information about the development of the gonopods and the phallus during metamorphosis. The morphological part of the work, however, is very summary, and his main conclusion, that the order as to the structure of the genitalia falls into two distinct groups, one comprising the Limnophilidae, and another comprising all the remaining families, is far from the truth.

The aim of the present paper is to make good these deficiencies, and also to provide material to elucidate the phylogeny of the order. It is hoped that the work may be followed up with a parallel study of the ♀♀. The following species were examined:

Annulipalpia

Rhyacophilidae	Rhyacophilinae	*Rhyacophila nubila* Zett.
	Glossosomatinae	*Agapetus fuscipes* Curt.
Psychomyidae		*Lype phaeopa* Steph.
		Tinodes waeneri L.
		Psychomyia pusilla Fabr.
Philopotamidae		*Wormaldia occipitalis* Pict.

Polycentropidae	Polycentropinae	*Polycentropus flavomaculatus* Pict.
		Holocentropus dubius Steph.
	Ecnominae	*Ecnomus tenellus Ramb.*
Hydropsychidæ	Hydropsychinae	*Hydropsyche angustipennis* Curt.
Hydroptilidæ	Orthotrichiinae	*Orthotrichia tetensii* Kolbe
	Hydroptilinae	*Agraylea multipunctata* Curt.
		Hydroptila occulta Eat.

Integripalpia

Beraeidae	Sericostomatinae	*Sericostoma pedemontanum* MacL.
	Beraeinae	*Beraea maurus* Curt.
Leptoceridae		*Leptocerus cinereus* Curt.
Molannidae		*Molanna angustata* Curt.
Odontoceridae		*Odontocerum albicorne* Scop.
Lepidostomatinae		*Lasiocephala basalis* Kol.
Brachycentridae		*Oligoplectrum maculatum* Fourcr.
Phryganeidae		*Agrypnia pagetana* Curt.
Limnophilidae	Limnophilinae	*Limnophilus flavicornis* Fabr.
		Stenophylax stellatus Curt.
	Ecclisopteryginae	*Ecclisopteryx guttulata* Pict.
	Apataniinae	*Apatania arctica* Boh.
	Goërinae	*Silo nigricornis* Pict.

These 26 species cover all subfamilies represented in the North European fauna. (Owing to lack of suitable material *Caborius dubius* Steph. was not examined. SCHMID —1955—has transferred this species to the genus *Ironoquia* Bks., which he includes in the subfamily Discomoecinae set up by him. It may be right to transfer *dubius* to this genus, but to me the justification for removing the species from the Limnophilinae seems doubtful). As to those systematic groups which are not represented in Denmark, I have tried to utilize the available descriptions. For reasons mentioned above, this has been possible only to a very limited extent.

The study has been carried out exclusively on material preserved in alcohol. The work was done at the Zoological Museum, Copenhagen. For grants received from the Carlsberg Foundation I wish to express my sincere thanks.

Some remarks on the taxonomy employed in the list above. Like ULMER (1951, pp. 39—40), and for the same reasons I include *Agapetus* Curt. in the Glossosomatinae. The subfamily Ecnominae are oftener included in the Psychomyidae. The immature instars, however, clearly show that *Ecnomus* is a polycentropid, and the genital segments of the ♂, also, are more like those of the Polycentropinae than those of the Psychomyidae. In a previous paper (1943b) I have given evidence, based upon the ontogenetic development, that the Beraeinae and the Sericostomatinae are so closely

related that they ought to be joined in one family. For this I proposed the name Beraeidae in order to avoid confusion with the old, quite unnatural "family" Sericostomatidae. (Cp. p. 94). In the same paper I set up the subfamily Ecclisopteryginae. Later SCHMID (1955) has renamed this subfamily Drusinae. The latter, no doubt, is a more handy name, but according to the rules of priority Ecclisopteryginae must be valid. *Apatania arctica:* SCHMID (1953, pp. 145—46) has shown that the division into the genera *Apatania, Apatidea,* etc., cannot be upheld. Hence, he provisionally considers the species in question as constituting one genus, *Apatania* Kol., though this is very heterogeneous. This point of view is accepted here. Previously (1943b), on the basis of the morphology and biology of the immature instars, I have given evidence that the subfamily Goërinae belongs to the Limnophilidae. The structure of the genital segments of the ♂ (and the ♀) supports this view. (Cp. p. 143).

The posterior abdominal segments successively taper much. Segment VIII is the last typical abdominal segment with separate tergum and sternum. Its posterior border to a greater or less degree overlaps Segment IX, sometimes so much that the latter is partly or entirely concealed. Also in some other respects Segment VIII may be slightly modified, and on some of the preceding segments, too, modifications may be found in the shape of various processes—structures which will not be treated in the present paper.

Segment IX is typically synscleritous, i. e. its sclerotization forms a complete annulus of varying length. Generally the lengths of the dorsal and the ventral side are more or less reduced by indentations from the oral or the anal end, or from both ends. Especially the dorsal side is often so much reduced that it forms only a sclerotic transverse bridge. In rare cases the ventral side is longer than the lateral side. In the Psychomyidæ and the Polycentropinae Segment IX, probably secondarily, is dissclerites, and the reduced dorsal part is so intimately associated with Segment X that Segment IX, to a superficial view, might seem to lack the dorsal side. In *Wormaldia* and *Ecnomus* the much reduced dorsal part of Segment IX has the same association with Segment X, but is still continuous with the lateral part of the segment through a narrow sclerotic bridge. Similar conditions are probably found in *Hydropsyche.*

In many cases a good deal of the oral part of Segment IX has an apodemal character. The apodemal part possibly must be considered a strongly developed antecosta, though also in such cases a marginal thickening of the apodeme may be seen. In rare cases the antecosta is interrupted dorsally or ventrally, or on both these sides. Still rarer is the condition that the ventral side of the segment is partly membranous.

Segment IX is often the site of secondary sutures, most frequently laterodorsal or lateroventral longitudinal sutures. The former are found in the Hydroptilidae (pp. 68, 77, 82), *Sericostoma* (p. 85), *Odontocerum* (p. 101), *Agrypnia* (p. 114), the Limnophilinae (pp. 119, 124) and *Apatania* (p. 133). In *Sericostoma* the laterodorsal suture perhaps is homologous with that of the Hydroptilidae; in both cases the IX/X

muscle (see below) originates dorsally to the suture. In the other Integripalpia mentioned, this muscle, however, originates ventrally to the suture, so the latter is scarcely homologous with that of the Hydroptilidae. On the other hand, it is very likely that there is a mutual homology between these Integripalpia. A lateroventral longitudinal suture occurs in *Agapetus* (p. 20), *Hydropsyche* (p. 65), *Orthotrichia* (p. 68), *Agraylea* (p. 77), *Lasiocephala* (p. 106) and *Silo* (p. 137). It may very well be homologous in all these forms.

The posterior end of Segment IX forms a more or less deep, chiefly membranous depression, the *genital chamber*. From this the following structures arise: dorsally Segment X, ventrally the inferior appendages, and between Segment X and the inferior appendages the copulatory organ, the phallus.

Segment X is so varying in shape that it is difficult to give a general account. It is always much lower, and nearly always much narrower than Segment IX. In most cases the ventral side is more or less concave and partly encloses the phallus. Sometimes the concavity is so pronounced that the segment forms a functional tube. In the literature Segment X is known under the names 'dorsal plate', 'penis-cover', 'upper penis-cover', and 'Rückenschuppe'. The 'intermediate appendages' are processes on Segment X. They are not homologous in all cases.

Segment X may be membranous to a great extent, but the overwhelming rule is that the greater part of the dorsal and lateral sides is sclerotized. In almost all cases the sclerite (or the sclerites) of Segment X is (are) continuous with that of Segment IX. The connection is generally with the lateral side of Segment X through sclerotizations at the bottom of the genital chamber. Sometimes the dorsal sides of the two segments, also, are continuous, and in such cases it may be difficult to draw the boundary between them. The length of Segment X varies much. In extreme cases (Ecclisopteryginae and especially Limnophilinae) it is so much reduced that the sclerites of the segment appears as situated in the bottom of the genital chamber.

Despite the sclerotic connection between the two segments, the dorsal intersegmental musculature is well developed (except in *Hydropsyche*). There is only one muscle (the IX/X muscle; figs. 1 and 2, *6*), which originates laterodorsally on the antecosta of Segment IX. Sometimes the origin spreads over the whole lateral part of the antecosta, or it may shift to a lateroventral position. More rarely (*Agraylea*, *Hydroptila*) it spreads in a dorso-median direction, which may result in the muscle becoming unpaired. In some few cases the origin extends into the surface of Segment IX, and in *Agapetus* it stretches over almost the entire length of this segment. Generally the muscle is inserted to Segment X in such a way as to act as a depressor. The sclerotic parts connecting the two segments by their elasticity constitute an antagonist. In specialized cases the muscle may have other functions. In the Psychomyidae, *Wormaldia*, and the Polycentropinae the intersegmental dorsal musculature between Segments VIII and IX is incorporated in the genital complex.

Segment X carries a pair of movable *superior appendages* (''appendices præanales''). Typically they are large and may even exceed the segment itself in length.

In many cases, however, they are very small, and in about half of the forms they are entirely lacking. (In such cases the term superior appendages sometimes has been applied to other parts of Segment X). The reduction of the appendages, no doubt, has taken place independently in various systematic groups. Sometimes the superior appendages are sclerotically continuous with Segment X itself. They never have any musculature of their own, but in the Polycentropidae the IX/X muscle is attached to the superior appendage.

In *Rhyacophila* (figs. 3 and 4, pp. 16 and 17) the posterior edge of Segment IX is protracted into an unpaired *dorsal process* (*2*), and orally on the dorsal side of Segment X another dorsal process (*3*) arises. The two processes are united, though by membrane only. In *Lype* a dorsal process (fig. 9, *9*, p. 25; 10, *5*, p. 27) is found, which probably is homologous with the dorsal process on Segment X in *Rhyacophila*, and in *Wormaldia* and perhaps *Hydropsyche* such a process is indicated. In some Integripalpia (*Leptocerus*, p. 94; *Oligoplectrum*, p. 111; *Silo*, p. 137) there is a well developed, paired or unpaired dorsal process, which very likely has arisen by fusion of processes on Segments IX and X. In many other Integripalpia (*Molanna?*, p. 99; *Odontocerum*, p. 102; *Lasiocephala*, p. 106; *Agrypnia*, p. 114; *Apatania*, p. 133) a dorsal process is found in a more or less rudimentary state.

More rarely (*Sericostoma*, p. 85) the posterior edge of Segment IX is protracted into an unpaired ventral process, which may be bifurcated (*Mystacides azurea* L.). Generally the lateral side of Segment IX is longer than the dorsal and ventral sides, the posterior edge thus making a lateral bulging. As to the *lateral process* ("intermediate process", "side piece") of the Hydroptilidæ see pp. 68, 77 and 82.

What on the preceding and following pages is called Segment X is a composite structure. Since Venter IX, in all probability, has been obliterated as an external structure by the formation of the ejaculatory duct (Anker Nielsen 1957), the ventral side of this structure in reality belongs to Segment XI. A distinct *Segment XI* comprising epiproct and paraprocts is, however, developed in *Rhyacophila* only (pp. 16—17). In the Polycentropidae (pp. 47, 54 and 62) there are well developed paraprocts carrying accessory copulatory processes. Such processes are seen in *Tinodes vaeneri* (p. 32) also. In other forms the paraprocts have either been reduced or fused with the sclerotization of Segment X s.str. (Cp. also pp. 40 and 151).

Cerci are scarcely present in any Trichopteron ♂, though in *Hydropsyche instabilis* Curt. (p. 63) and *Molanna* (p. 99) there are structures which perhaps might be interpreted as such.

In some forms the *anus* is very distinct. In others it is difficult to localize.

The *inferior appendages* (*gonopods*). In *Rhyacophila*, only, the two appendages are separate from one another, and this condition is probably secondary. Othervise they are mutually united, at least by membrane. In the majority of cases, however, they are also sclerotically united with each other and with an unpaired sclerite (the *basal plate;* figs. 7 D, *6*, p. 22; 51, *4*, p. 92; 63, *5*, p. 112; o.a.) situated at the bottom of the genital chamber between and above the two appendages. (The basal plate of

course must be considered as an integrating part of the inferior appendages). Generally the median sides, also, of the two appendages are sclerotically continuous with each other and with the basal plate. This may be much reduced or entirely lacking. In the latter case the sclerotic connection between the two appendages—if any—is effected in other ways. The posterior edge of Segment IX generally overlaps the bases of the inferior appendages a little. Rarely there is a simple articulation between the posterior edge of Segment IX and the inferior appendages.

The inferior appendages are typically divided into a proximal and a distal joint (*coxopodite* and *harpago*, resp.). In very many forms, however, they are one-jointed. This condition may have arisen in three ways: 1. By reduction of the harpago. Incipient stages are seen in *Beraea* (fig. 51, p. 92), and *Odontocerum* (fig. 57, p. 103). 2. By fusion of the two joints. Incipient stages are seen in *Tinodes* (fig. 16, p. 35), *Leptocerus* (fig. 54, p. 96) and *Lasiocephala* (fig. 60, p. 108). The whole evolution may be followed within the genus *Tinodes*. In *T. waeneri* (p. 34) the two joints are sclerotically continuous on the lateral side. In *T. pallidula* MacL. (KIMMINS 1949) the one-jointed condition is established. The distal end of the appendage in the latter species has approximately the same shape as the harpago in the former. 3. By fusion of the coxopodite with Segment IX. An incipient stage is seen in *Psychomyia* (fig. 19, p. 39), but in no form studied by me this condition is fully established.

Four pairs of extrinsic muscles are attached to the inferior appendages (figs. 1 and 2): *anterior* and *posterior dorsals*, and *anterior* and *posterior ventrals*. The *anterior dorsal muscle* (7) generally originates on the lateroventral part of the antecosta of Segment IX, but the origin may shift more or less in a dorsal direction. It is inserted laterally, laterodorsally, or dorsally on the proximal edge of the coxopodite. The *anterior ventral muscle* (*8*) originates on the ventral part of the antecosta of Segment IX (ventrally to the lateroventral longitudinal suture if this is present), and is inserted proximally on the median side of the appendages. In *Agraylea* and *Hydroptila* this muscle is paired; in all other forms studied by me it is unpaired. In case of the anterior muscles being especially strong, their origins may spread more or less over the surface of Segment IX. The *posterior dorsal muscle* (*9*) originates laterodorsally and anally in Segment IX and is inserted on the basal plate. Its crossing with the anterior dorsal is above the latter. In *Rhyacophila* and the *Beraeidae* the *posterior ventral muscle* (*10*) originates lateroventrally and anally in Segment IX. This was probably the condition in the ancestors of the Trichoptera, but still it is likely that it is secondary in the two groups mentioned. In the vast majority of forms this muscle stretches between the ventroproximal part of the appendage itself and the basal plate. In the Limnophilinae (p. 127) the ventral attachment is partly on the appendage, partly on Segment IX, but this obviously is a secondary condition arisen in connection with the strong reduction of the inferior appendages in this subfamily. In *Lype* and *Wormaldia* the muscle stretches between the dorsal and the ventral side of the coxopodite, and in the Hydroptilidae (pp. 72, 80, and 83) the relations of this muscle are very deviating.

In *Rhyacophila* and the Limnophilidae the posterior ventral muscle has shifted its dorsal (anterior) attachment to the phallus. In *Psychomyia* the insertion of the anterior ventral muscle has shifted to the phallus, and the same perhaps is the case

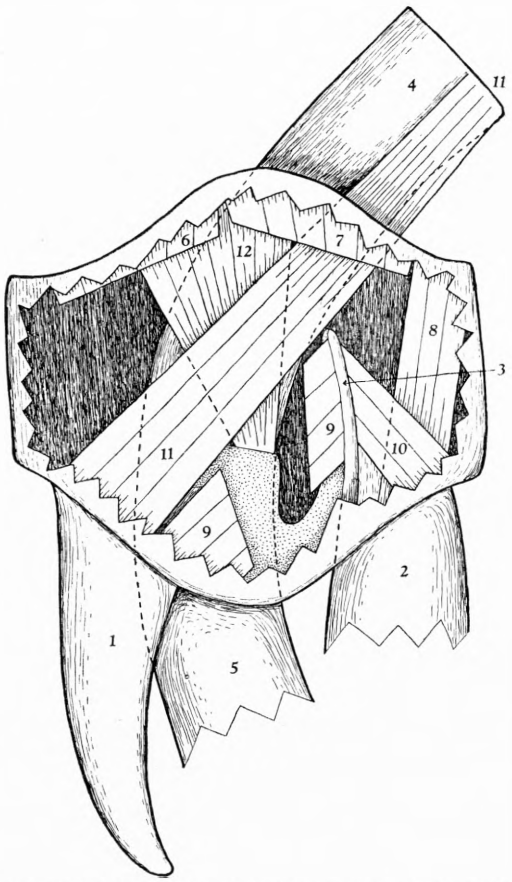

Fig. 1. Diagram showing the musculature of the genital segments, as seen from the right side. The greater part of the right half of Segment IX has been broken off, so that a large "window" is formed. *1:* Segment X ("intermediate appendage"). *2:* right inferior appendage; (its greater part has been broken off). *3:* basal plate of the inferior appendages. *4:* phallic apodeme. *5:* phallus; (its distal part has been broken off). *6:* the IX/X muscle; (only its extreme proximal end is left). *7—10:* muscles of the inferior appendage; *7:* anterior dorsal (only its proximal end is left), *8:* anterior ventral, *9:* posterior dorsal (its middle part is removed), *10:* posterior ventral. *11—12:* phallic muscles; *11:* posterior, *12:* anterior.

with the anterior dorsal muscle in *Apatania* and *Silo*. In *Leptocerus*, finally, the posterior dorsal muscle has shifted its dorsal (proximal) attachment to the phallus.

All four muscles are not present in all forms. In extreme cases (*Limnophilus*, p. 121; *Ecclisopteryx*, p. 131) no muscles at all are inserted on the inferior appendages.

The movements of the inferior appendages are adduction and abduction, levation and depression. The sclerotic connection between the two appendages is generally

of such a sort as to allow the former set of movements. It is often difficult to judge which part the individual muscles take in these movements. Obviously it differs in the various forms. This will be discussed to some extent in the special part. The posterior dorsal muscle must principally act as a depressor by raising the basal plate. By pulling the latter backwards it may act also as an abductor. In the Beraeidae, in which the posterior ventral muscle takes its origin on Segment IX, it may act as a levator and an abductor. In other forms it probably causes movements of the basal plate, through which it may influence the movements of the phallus (cp. below). As mentioned above, this in some cases has resulted in one of the muscle attachments having shifted to the phallus.

Finally, the inferior appendages has an intrinsic *flexor of the harpago*, originating on the lateral side of the coxopodite (generally for the greater part of the length of this joint) and inserted medially and proximally on the harpago. In *Silo* this muscle is divided into two portions. It goes without saying that it is lacking in forms with one-jointed appendages.

The shape of the copulatory organ, the *phallus*, is extremely variable. Generally speaking, it can only be said that it is a tubular organ, as a rule sclerotized to its greater extent. And in some cases even this characterization perhaps is not appropriate. The proximal end of the phallus is lowered into a usually very deep depression, the *phallocrypt*. The relation between this and the basal plate of the inferior appendages varies. In some cases the basal plate is situated on the floor of a small pocket, the entrance of which is separated from that of the phallocrypt. In other cases it is situated on the floor of (the posterior part of) the phallocrypt. In still other cases, in which the basal plate is very small, it simply lies on the floor of the genital chamber outside the entrance to the phallocrypt. In practically all forms a *phallic apodeme* is formed by fusion of the proximal end of the phallus with the anterior part of the wall of the phallocrypt. The apodeme may be partly membranous, but typically it is sclerotized. An unusual form of the phallic apodeme is described by TILLYARD (1925, p. 278) in the genus *Hydrobiosis* MacL., which "have a long, slender penis, coiled up inside the abdomen in the form of a spring" (according to the figure a watch-spring).

In the following the term phallocrypt means only that part which lies beyond the apodeme. It may be entirely membranous, or it may be sclerotized to a greater or smaller extent, and this sclerotization again may be continuous with the inferior appendages (*Hydropsyche, Lasiocephala, Apatania, Silo*) or with Segment X (*Agapetus, Tinodes*—cp., however, below—*Psychomyia*). In *Rhyacophila* there is an articulation between the phallus and the inferior appendage through a sclerite in the wall of the phallocrypt.

No appreciable morphological significance can be attributed to the boundary between the phallic apodeme and the phallocrypt. It simply depends on the extent to which a fusion has taken place. In some cases (e. g. *Limnophilus;* fig. 70, p. 123) the apodeme is only short, whereas the phallocrypt is very deep. In other cases (e. g.

Polycentropus; fig. 25, p. 50) the apodeme is large, but the phallocrypt shallow, possibly reduced to a circular furrow (*Leptocerus;* fig. 55, p. 97) or entirely obliterated (*Tinodes;* fig. 17, p. 36). In the two last-mentioned forms the apodeme as well is much reduced.

In the following the term phallus means that part of the copulatory organ which

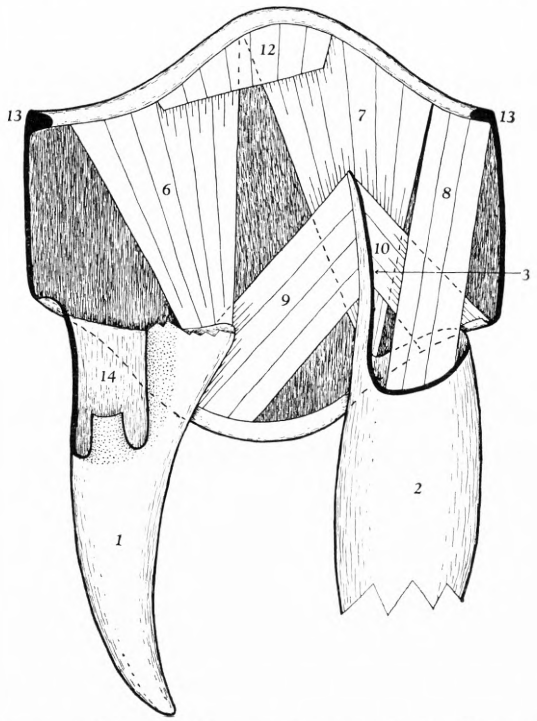

Fig. 2. Diagram showing the musculature of the genital segments. Sagittal section through Segments IX and X; left half as seen from the inside. The phallus and the membranous wall of the genital chamber have been removed. *1:* Segment X ("intermediate appendage"). *2:* left inferior appendage; (its greater part has been broken off). *3:* basal plate of the inferior appendages. *6:* IX/X muscle. *7—10:* muscles of the inferior appendage; *7:* anterior dorsal, *8:* anterior ventral, *9:* posterior dorsal, *10:* posterior ventral. *12:* the posterior phallic muscle; (only its proximal end is left; the whole anterior muscle has been removed together with the phallus). *13—13:* the antecosta of Segment IX. *14:* rectum.

lies beyond the phallic apodeme. In its original shape it was probably divided into a *phallobase* and an *aedeagus*. Among the forms studied here this condition is seen in its typical form only in the Glossosomatinae (fig. 8, p. 23) and the Limnophilidae (fig. 70, p. 123), it is true, but its occurrence in these two distantly related groups indicates that it must be the original one. A typical phallobase is perhaps found also in *Rhyacophila kervillei* Nav. (Schmid 1952, p. 638, fig. 6) and in the genus *Chimarrha* Steph. (Barnard 1934, p. 382). In the two groups mentioned the phallobase is much shorter, but thicker than the aedeagus. Its distal part is invaginated as a membranous *endotheca,* which is almost as long as the phallobase itself, and from the bottom of

which the chiefly sclerotized aedeagus arises. In the Glossosomatinae, the Limnophilinae, and the Ecclisopteryginae the outside of the phallobase (the *phallotheca*), as well is membranous. In *Silo* (fig. 82 B, C, p. 142) the phallotheca is sclerotized proximally, in *Apatania* (fig. 78 B, p. 136) to its greater extent. By means of blood pressure the endotheca can be everted, and the aedeagus thus protracted. The retraction is performed by the *aedeagal retractor muscles*, which originate in the phallic apodeme or (*Apatania*) the phallotheca and is inserted on the aedeagus. — In *Holocentropus dubius* (fig. 29, p. 55) the phallus is divided into two parts, which probably represent the phallobase and the aedeagus, resp., but the latter cannot be withdrawn into the former.

In the majority of the Trichoptera, however, the phallus is undivided. This condition may have arisen in three ways: (1) By a strong development of the phallobase, accompanied by sclerotization of the phallotheca and reduction of the aedeagus. Stages of this development are seen in *Oligoplectrum* (fig. 64, p. 113), *Odontocerum* (fig. 58, p. 105) and *Polycentropus* (fig. 26, p. 51). The final result (figs. 56 F, p. 100, 67, o. a.) is that the copulatory organ is formed by the phallobase, which contains an eversible sac, the endotheca, in the bottom of which the ejaculatory duct opens. This type is seen in *Wormaldia, Ecnomus, Sericostoma, Molanna* and *Agrypnia*, and possibly in *Hydropsyche* also. (2) By obliteration of the endotheca and subsequent fusion of the sclerotized phallotheca with the aedeagus. This process no doubt has taken place in *Lasiocephala* (p. 110), probably in *Rhyacophila* (p. 20), and perhaps in the Psychomyidae (p. 37) and *Leptocerus* (p. 98). In the two latter forms it has been connected with a reduction of the aedeagal retractor. (3) By reduction of the whole phallobase, a direct continuation being established between the phallic apodeme and the aedeagus. An initial stage is probably seen in *Beraea* (p. 94), and the final result (though in a modified form) possibly in the Hydroptilidae (p. 85). This process is accompanied by a reduction of the aedeagal retractor. The undivided phallus of the Psychomyidae and of *Leptocerus* may also have arisen in this way.

The original shape of the aedeagus certainly is that found in the *Rhyacophilidae* (figs. 6, p. 19 and 8, p. 23): it is divided into a dorsal and a ventral branch; the ejaculatory duct opens on the former. In some species of the genus *Chimarrha* Steph., also, the aedeagus seems to have two branches, the ventral in the shape of a "process, which is apically trifid", whereas the dorsal branch appears to be membranous (Barnard 1934, p. 382). In *Stactobia* MacL., too, the aedeagus seems to be divided into a dorsal and a ventral branch (Ulmer 1950, p. 296, fig. 1 a), the former with the opening of the ejaculatory duct, the latter subdivided into 2—4 long spines. (It appears that Vaillant—1951—in this genus has confused Segment X and the phallus). More or less distinct vestiges of such a division is found in the Psychomyidae (p. 37) and in *Polycentropus* (p. 50). It can possibly be traced also in the Hydroptilidae and in many Integripalpia. In the Hydroptilidae the distal end of the aedeagus is hollowed out like a spoon on the dorsal side, and at the bottom of the "spoon" the ejaculatory duct opens on a papilla (*Agraylea*, figs. 43 A, p. 78, 45 C, p. 81; *Hydroptila*) or on a more strongly sclerotized area (*Orthotrichia*, fig. 42, p. 75). The "spoon" probably repre-

sents the ventral branch, the papilla—which in *Orthotrichia* is reduced—the dorsal branch. In *Lasiocephala* (fig. 61 A, p. 109), *Limnophilus* (fig. 70 D, p. 123), and *Silo* (fig. 82 A, p. 142) the ejaculatory duct likewise opens into a spoon-like depression. In *Beraea* (p. 94), *Leptocerus* (p. 98), *Odontocerum* (p. 104), and *Oligoplectrum* (p. 114) the "spoon" has developed into a cavity, the *phallotremal cavity*, at the bottom of which is the opening of the ejaculatory duct surrounded by a *phallotremal sclerite*. In the two first-mentioned forms the aedeagal retractor is lacking, in the two last-mentioned it is inserted on the phallotremal sclerite, and in *Oligoplectrum*, at least, the phallotremal cavity is eversible. It will be seen that in the Hydroptilidae and the Integripalpia it is the dorsal branch which is reduced. In *Psychomyia* (p. 42) and *Holocentropus* (p. 56), on the other hand, it appears that the ventral branch is reduced. In those cases in which the aedeagus on the whole is reduced, the reduction of course has befallen both branches.

In some forms the phallus is provided with appendages which generally are called titillators, but should more appropriately be called *parameres* (cp. Anker Nielsen 1957). In *Agapetus* there is an unpaired, pasively movable appendage (fig. 8, *6*, p. 23) arising from the proximal end of the aedeagus. In *Odontocerum* (fig. 58, p. 105) and the Limnophilidae (fig. 73, p. 128, o. a.) there are paired, passively movable appendages, which arise from the bottom of the endotheca beside the aedeagus or from the proximal end of the latter. In *Rhyacophila* (fig. 6, p. 19), too, there are paired appendages arising from deep, tubular pockets on the undivided phallus, but they are actively movable, the aedeagal retractor being inserted on them. Parameres have been described also in some Philopotamidae (see p. 44). Most probably the parameres are homologous in all the forms mentioned.

In the Hydroptilidae (figs. 37 C, p. 69, 45 A, p. 81) an unpaired, immovable *titillator* is found arising distally to the middle of the undivided phallus (which probably represents the aedeagus only). It is unlikely that it is homologous with the parameres of the other forms. (As to the Hydroptilidae, see also pp. 84—85, 68—69, and 146).

More or less distally the ejaculatory duct—at least fairly often—is surrounded by a packet of close-set unicellular glands. Generally the outermost part of the duct is more or less highly sclerotized.

The intrinsic musculature of the phallus has already been mentioned. There are two pairs of extrinsic muscles (figs. 1 and 2). The *posterior phallic muscle* (*11*) originates laterodorsally or laterally in the posterior part of Segment IX, above the origin of the posterior dorsal muscle of the inferior appendage. In *Polycentropus* the greater part and in Holocentropus the whole of its origin has shifted to Segment X (or, strictly speaking, to Segment XI: the paraprocts). It is inserted on the phallic apodeme or on the anterior part of the phallocrypt. The *anterior phallic muscle* (*12*) originates laterally, lateroventrally, or laterodorsally on the antecosta of Segment IX. Oftener its origin dorsally overlaps a part of the origin of the IX/X muscle and ventrally a part of the origin of the dorsal posterior muscle of the inferior appendages. The phallic muscle then lies medially to the two last-mentioned muscles. It is in-

serted on the phallic apodeme or on sclerotized parts of the phallocrypt. The crossing between the two phallic muscles is such that the anterior lies above the posterior. In *Rhyacophila* and some Limnophilidae there are two pairs of posterior phallic muscles, a dorsal and a ventral pair, the posterior ventral muscle of the inferior appendages having shifted its origin to the phallus. In other Limnophilidae there is only one pair of posterior muscles, but this is the ventral pair; the usual, dorsal pair of muscles is lacking. In *Psychomyia* there are two pairs of anterior phallic muscles, the anterior ventral muscle of the inferior appendage having shifted its insertion and developed into a phallic muscle. In *Leptocerus*, finally, the posterior dorsal muscle of the inferior appendage is attached to the phallus, and the same perhaps is the case with the anterior dorsal in *Apatania* and in *Silo*. — In the Psychomyidae the posterior phallic muscle is lacking, and in *Tinodes* the same is the case with the anterior one. — Generally the posterior muscle is a protractror, the anterior one a retractor, but the two muscles may have other functions.

In this study some weight has been attached to the genital musculature. Nevertheless, in most cases the muscles have been omitted in the figures. This has been done in order not to complicate the drawings too much—or to augment their number too much. It is hoped that the verbal descriptions, as compared with the two diagrams (figs. 1 and 2), will make conditions intelligible.

Like most of the rest of the body the exposed parts of the genitalia are covered with setae, though generally the genital chamber and the phallus are devoid of such. In the special descriptions mention of setae has been made only in those cases where they are remarkable by their size or shape, where they are present on parts normally lacking setae, or, finally, where they lack on parts normally provided with setae. As to current entomological terms the reader is referred to Snodgrass (1935). Here it is only to be pointed out that the term seta always means a seta and nothing else, that setae always are called setae and never spines or the like, and that such terms as spines, spinules, etc., always designate simple cuticular processes and never setae.

As to the figures the following should be noted: With a few exceptions—which are mentioned in the legends—figures seen in dorsal, lateral, or ventral view are orientated so that the anterior end points upwards, figures seen in posterior view so that the dorsal side faces upwards. If anything else is not expressly stated, fine dotting indicates membranous areas.

Special Part.

Rhyacophila nubila.

Segment IX (figs. 3 and 4, *1*). Ventrally the posterior edge has a broad and deep indentation, so that the length in the middle of the ventral side is only a small fraction of that of the lateral side. On the dorsal side the posterior edge is slightly indented, but in the middle of the indentation it is protracted again to a flat, horizontal dorsal process (*2*), which is narrow, with approximately parallel sides and a rounded distal end. Ventrally—along the bases of the inferior appendages— the posterior edge of the segment is sharp. Dorsally it is rounded. On each side of the root of the dorsal process the inflected part of the sclerite is especially strong, and there—as described below—it is continuous with that of Segment X (fig. 5C, *8*).

Orally from the dorsal side of Segment X rises a large, sclerotized dorsal process (figs. 3A and 4A, *3;* fig. 5, *5*), which in a dorsal view entirely conceals the rest of the segment (fig. 4A, *4*). It is scalelike and lies horizontally below the process of Segment IX. Already at its base it is considerably broader than the latter, and the width increases much towards the bilobed distal end. Its dorsal side is connected by membrane with the ventral side of the process of Segment IX. A horizontal section through this membranous part, however, is much narrower and shorter than the dorsal process of Segment IX, so that the margins of the latter overlap the dorsal process of Segment X rather much.

Laterally to the dorsal process of Segment IX, the anterior end of Segment X projects rather far below the posterior margin of Segment IX. At the bottom of the narrow cavity thus formed the sclerite of Segment X is bent sharply in a dorsal direction and is continuous with that of Segment IX (fig. 5C, *8*).

Segment X itself is short and tubular. The dorsal side is sclerotized (fig. 5, *3*), and the sclerite is continuous with the ventral side of the dorsal process. On the connecting, almost vertical part, there are a pair of low, longitudinal keels, and between them a shallow concavity, which is continued, narrower, on Segment X itself. An internal ridge runs along the very descendent lateral margin of the sclerite. On this ridge the IX/X muscle is inserted. It originates dorsally on the antecosta of Segment IX. The most dorsal fibres are almost horizontal, the ventral ones are very descendent. A contraction of this muscle must cause a depression of Segment X. In this movement

the dorsal process of Segment IX no doubt takes part, since the membrane connecting the two dorsal processes is rather close. Hence, the elasticity of the dorsal process of Segment IX possibly is the chief antagonist of the IX/X muscle.

Anally on the dorsal side of Segment X there is a smaller sclerite (fig. 5, *9*), which to its greater extent takes the shape of a pair of backwards directed prongs. The posterior edge of the large sclerite (D, *4*) projects above the unpaired portion of the small

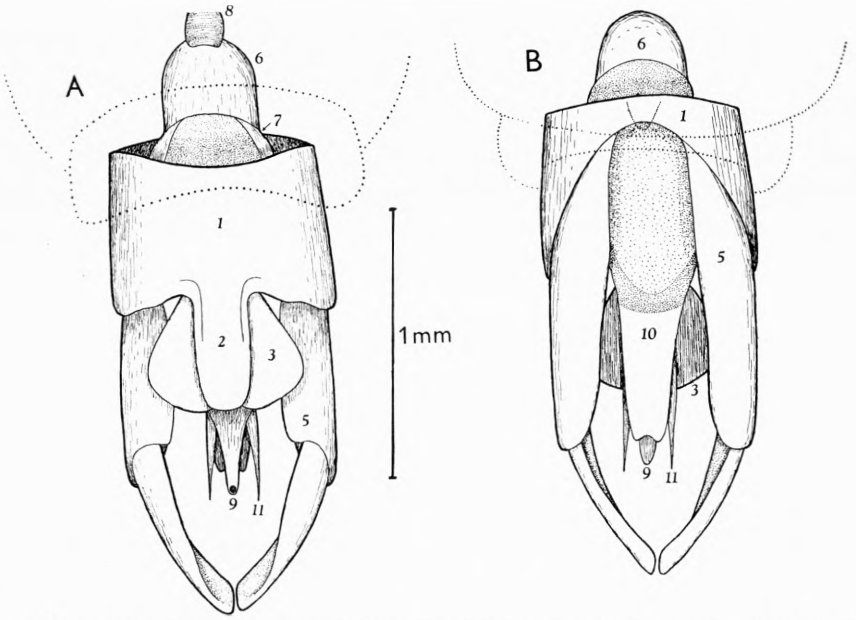

Fig. 3. *Rhyacophila* nubila. Segments IX and X in dorsal (A) and ventral view (B). Coarsely dotted lines: outline of (Segment VII and) Segment VIII. *1:* Segment IX. *2:* dorsal process of Segment IX. *3:* do. of Segment X. *5:* coxopodite. *6:* phallic apodeme. *7:* "horn" issued from the proximal end of the phallus and lying in the wall of the phallocrypt (= fig. 6, *3*). *8:* ejaculatory duct. *9:* dorsal, *10:* ventral branch of phallus. *11:* paramere.

sclerite (*10*). This portion (which like the prongs is very thick-walled) is formed as a narrow and very deep, horizontally lying cup, which may be called a hollow apodeme. It is no doubt justifiable to consider the whole structure (*9* + *10*) as an epiproct. On the dorsal side of the apodeme, muscles (D, 15) are inserted which originate on the dorsal proces of Segment X at the point where the latter joins the sclerite of Segment IX. This part of Segment X may be considered as the antecosta, and the muscles as dorsal intersegmental muscles between Segments X and XI. The very descendent muscles possibly must cause a depression of the prongs of the epiproct.

Lateroventrally Segment X carries a pair of sclerites (*11*), the dorsal edges of which overlap the lateral margins of the (large) dorsal sclerite. The membranous area between the two lateroventral sclerites forms a pair of low longitudinal folds. Anteriorly the two sclerites are united and continued as a narrow sclerotic stripe far into

the phallocrypt, the dorsal wall of which is a direct continuation of the ventral side of Segment X. It is no doubt justifiable to consider these structures (the lateroventral sclerites and the interjacent folds as well as the unpaired sclerotic stripe) as paraprocts.

Rhyacophila thus is remarkable by possessing a distinct Segment XI, comprising both an epiproct and a pair of paraprocts.

The anus is a vertical slit on the descendent membranous area between the epiproct and the paraprocts. From a narrow, transverse area immediately anteriorly

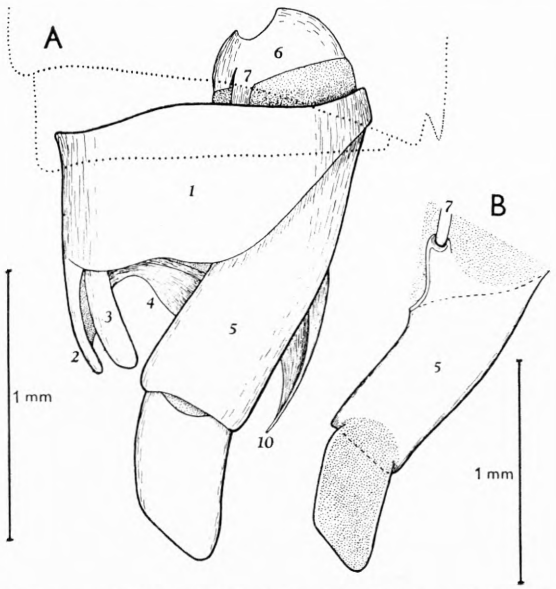

Fig. 4. *Rhyacophila nubila*. A: Segments IX and X in lateral (right) view. B: left inferior appendage in median view. *4:* Segment X itself. Other numbers as in fig. 3.

to the origin of the X/XI muscle, delicate muscle fibres spread out like a fan (*14*) and are inserted on the wall of the rectum. Similar fibres (*16*) stretch between the epiproctal apodeme and the rectum.

Superior appendages are lacking.

The inferior appendages (figs. 3 and 4, *5*) are elongate, sagittally compressed and of a simple shape. They are two-jointed, and the harpago is smaller than the coxopodite. Laterally the distal edge of the latter to some extent overlaps the proximal end of the former. Medially the harpago and the distal end of the coxopodite are membranous. Medio-dorsally the sclerite of the coxopodite projects considerably farther proximally than on the lateral side, and stretches into the wall of the phallocrypt. There it has a simple ginglymus to receive the condylus on the "horn" of the phallus. There is no connection between the two appendages. On the contrary, they are rather widely separate. Dorsally the bases of the appendages are rather much overlapped by the posterior edge of Segment IX. In a ventral direction the overlapping decreases,

and quite ventrally the inferior appendages and Segment IX have fused, though there is a distinct, separating suture.

The strong anterior dorsal muscle originates partly from the surface of Segment IX. It is inserted dorsally on the proximal margin of the coxopodite (a good deal dis-

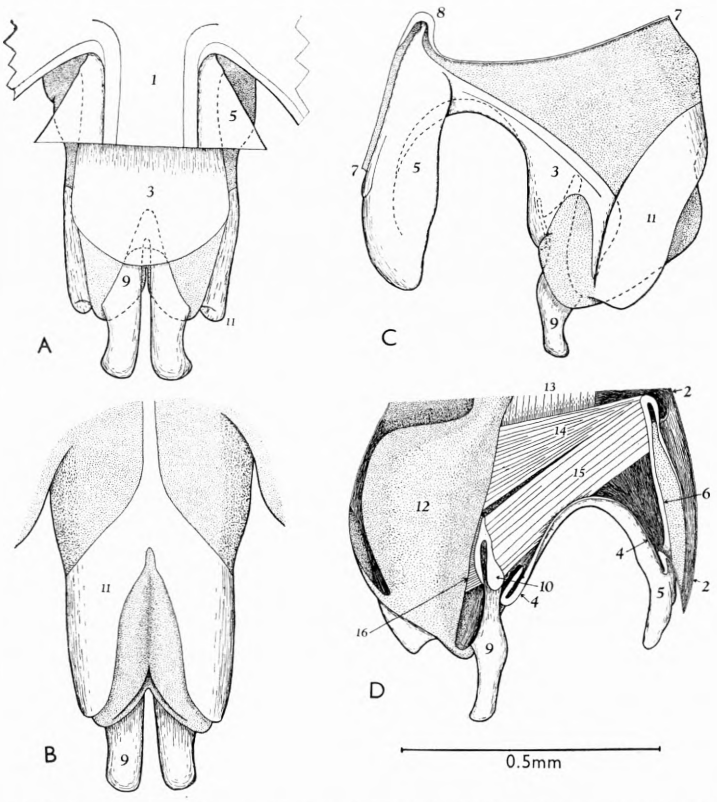

Fig. 5. *Rhyacophila nubila*, Segment X. A: in dorsal view (with the adjacent parts of Segment IX; the distal part of the dorsal processes has been cut off). B: in ventral view. C: in lateral (right) view. D: sagittal section; right half as seen from the inside. *1:* dorsal process of Segment IX. *2:* cut edge through the dorsal side of this process. *3:* Segment X itself. *4:* cut edge through 3. *5:* dorsal process of Segment X. *6:* dorsomedian margin of the sclerite of *5* (not a cut edge; dorsally to *6* the membrane connecting the two dorsal processes is seen). *7—7:* cut edge at the boundary between Segments IX and X. *8:* point of sclerotic connection between Segments IX and X. *9:* epiproct. *10:* cut edge through the unpaired part of *9*. *11:* paraproct. *12:* rectum. *13:* the IX/X muscle. *14:* muscle bands from Segment X to the rectum. *15:* muscle from Segment X to the epiproct. *16:* muscle bands from the epiproct to the rectum.

tally to the ginglymus mentioned). It may cause a levation of the appendage. Its chief function, however, is probably to be an antagonist to the posterior phallic muscle. The posterior ventral muscle has been transformed into a phallic muscle. Other extrinsic muscles are lacking. The flexor of the harpago originates laterally from the dorsal half of the coxopodite and is inserted on the membranous median side of the harpago.

The phallus (fig. 6) is undivided. Including the phallic apodeme, somewhat

more than the proximal half is rather thick, sagittally compressed, and with a feebly marked, dorsal longitudinal keel. The chiefly membranous phallocrypt is rather deep, especially so on the dorsal side. The phallic apodeme (2) is rather strongly sclerotized. Otherwise the proximal, thicker part is feebly sclerotized, or—distally, towards the distal, more slender part—quite membranous. Laterodorsally, on the boundary be-

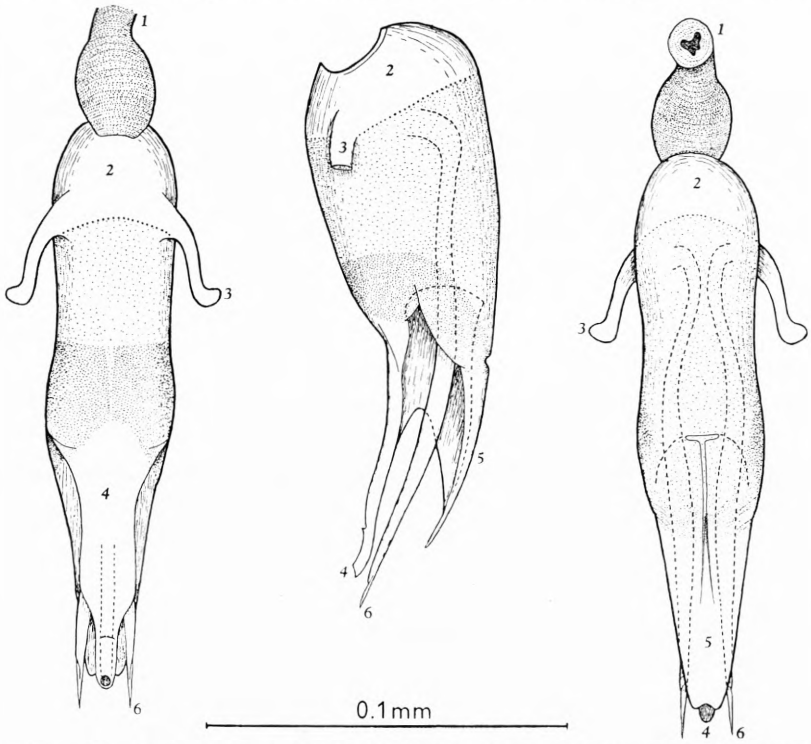

Fig. 6. *Rhyacophila nubila*; phallus in dorsal, lateral (right) and ventral view. *1:* ejaculatory duct. *2:* phallic apodeme. *3:* "horn" issued from proximal end of phallus (= figs. 3 and 4, 7). *4:* dorsal and *5:* ventral branch of phallus. *6:* paramere.

tween the phallic apodeme and the phallus itself a pair of strong, backwards directed "horns" (*3*) rise. These horns (figs. 3 and 4, 7) lie as sclerotic rods in the wall of the phallocrypt. Their distal ends, however, are free processes, articulating with the ginglymi on the coxopodites described above.

There is no anterior phallic muscle. The posterior muscle originates approximately midway between Segment IX and the inferior appendages. It is inserted on the phallic apodeme immediately dorsally to the root of the "horn". In addition there is a much stronger muscle, originating posteriorly and lateroventrally in Segment IX and inserted laterally on the proximal edge of the phallic apodeme. As already mentioned, it is a transformed muscle of the inferior appendage.

The slender distal part of the phallus is divided into a dorsal and a ventral branch, which both are sclerotized. The flattened ventral branch (5) tapers gradually towards

the slightly bilobed distal end. The dorsal branch (*4*), too, is flattened. It falls into a longer and broader proximal part (though narrower than the ventral branch) and a much narrower distal part. Across the dorsal side of the latter there is a sharp ridge, which in a lateral view resembles a forwards projecting tooth. The ejaculatory duct opens dorsally on the distal end of the dorsal branch, which is bent somewhat upwards. The two branches are connected by an unpaired, longitudinal, sclerotic lamella, the distal edge of which is deeply indented. On each side of the lamella there is a depression, from the membranous bottom of which a slender, rod-like, and sharply pointed paramere rises. The proximal part of the paramere is lowered into a deep and narrow, tubular cavity, which stretches to the proximal end of the phallus. Its distal end is flattened and subjected to a torsion of about 90°. The aedeagal retractor originates on the whole phallic apodeme and is inserted on the proximal ends of the paired parameres. The latter can probably be protracted by blood pressure.

The morphology of the phallus. A comparison with *Agapetus* (p. 23) and the Limnophilidae (p. 121) indicates that the origin of the parameres must mark the boundary between the phallobase and the aedeagus. From a morphological point of view the origin of the parameres in *Rhyacophila* is the points from which their tubular sheaths are invaginated. The conclusion is that the thicker proximal part of the phallus represents the phallobase, whereas the slenderer, two-branched distal part represents the aedeagus. Or, more precisely: the proximal, feebly sclerotized part is the phallotheca, the middle membranous part is the permanently everted endotheca, and the two-branched distal part is the aedeagus.

The movements of the phallus. The posterior phallic muscles generally are protractors. In *Rhyacophila*, however, the articulation between the phallus and the inferior appendages does not allow any high degree of protraction. The chief movements possibly are levation and depression, made possible by the two sets of posterior muscles. The axis of these movements is the transverse line between the two articulations. A simultaneous contraction of the ventral phallic muscles and the anterior dorsal ones of the inferior appendages must result in a very strong levation of the phallus. That the latter movement is the more powerful of the two is in good agreement with the fact that the opening of the ejaculatory duct has a dorsal position.

Agapetus fuscipes.

Dorsally as well as ventrally the posterior edge of Segment IX (fig. 7, *3*) is slightly indented. The two concavities are separated by a rounded corner, situated dorsally to the middle of the lateral side, the ventral indentation being considerably broader than the dorsal one. The dorsal side of the segment is somewhat flattened, especially so anally. On the ventral side a pair of longitudinal sutures are seen. They do not reach the posterior border. Anteriorly, bending medially, they unite with the antecostal suture.

As compared with other Trichoptera, Segment X (*4*) is very large. It is somewhat sagittally compressed. The ventral side is very concave, and the edges of the concavity are bent so much inwards that for at large stretch anally to the middle they entirely or almost touch each other. The posterior half or Segment X thus forms a functional tube, enclosing the phallus. Orally to the middle the edges diverge, the tube being reduced to a semitube.

Segment X carries a pair of strong, triangular, lateroventral sclerites. Ventrally they bend round the rather sharp edges of the (semi)tube and continue for a short stretch on the inside of the latter. Their anal corners are produced into upwards curved extensions, the extreme distal ends of which project as free spines. A comparison with *Rhyacophila* makes it possible that these sclerites—at least partly—represent the paraprocts. Orally the two sclerites are connected by a dorsal, transverse bridge. The greater, anal part of the dorsal side, however, is membranous. The anus is found on the very oblique (descendent) posterior end of the segment.

For a little more than the dorsal half the sclerotization of Segment X is continuous with that of Segment IX. Dorsally the two segments are separated merely by a declivity. Laterally the posterior edge of Segment IX projects beyond the anterior end of Segment X, and increasingly so in a ventral direction. A pair of very deep pockets (shown by broken lines in fig. 7 A, C) thus are formed beside Segment X. Dorsally the pockets are sclerotized throughout, ventrally on the median side (belonging to Segment X) only. Ventrally the bottoms of the pockets (i. e. the anterior corners of Segment X) even project further forwards than does the anterior margin of Segment IX. Below Segment X, also, the genital chamber consequently is very deep, forming a horizontal, membranous area.

As mentioned above, the ventral side of Segment X forms a tube. The greater, oral part of the dorsal side of the latter is sclerotized. This "internal" sclerite—which is separated from the external sclerites by rather broad membranous stripes—continues directly in the sclerotic dorsal wall of the phallocrypt (see below).

The firm connection between Segments IX and X would make it probable that the IX/X muscle was lacking. Nevertheless, this muscle is present, though rather feeble. It originates from the dorsal side of Segment IX for almost the entire length of the segment (not from the antecosta), and is inserted on the sclerite of Segment X near the ventro-anterior corner. The muscle is sagittally compressed. In a lateral view its fibres are very descending, almost vertical; in an anterior or posterior view they are converging ventrally. The muscle probably performs a closing movement of the ventral slit on Segment X.

Superior appendages are lacking.

The inferior appendages (fig. 7 A—C, *5*, D) are elongate and one-jointed. In a lateral view their shape is simple, ovate. The median side is concave, so that two toothed edges are formed. Proximally the ventral edge projects further inwards than the dorsal one, distally it is converse. A little proximally to the middle a tooth is seen between the two edges. The median sides of the two appendages are sclerotically con-

tinious at their bases. The basal plate (fig. 7 D, *6*) is a long, slender, spatulate rod, lying in the ventral wall of the genital chamber. The anterior ventral muscle is very strong. It originates to a great extent from the ventral surface of Segment IX, and is inserted on the line where the median sides of the two appendages unite. (There there is an internal, low, but strong, vertical ridge). Since the fibres are ascendent, this

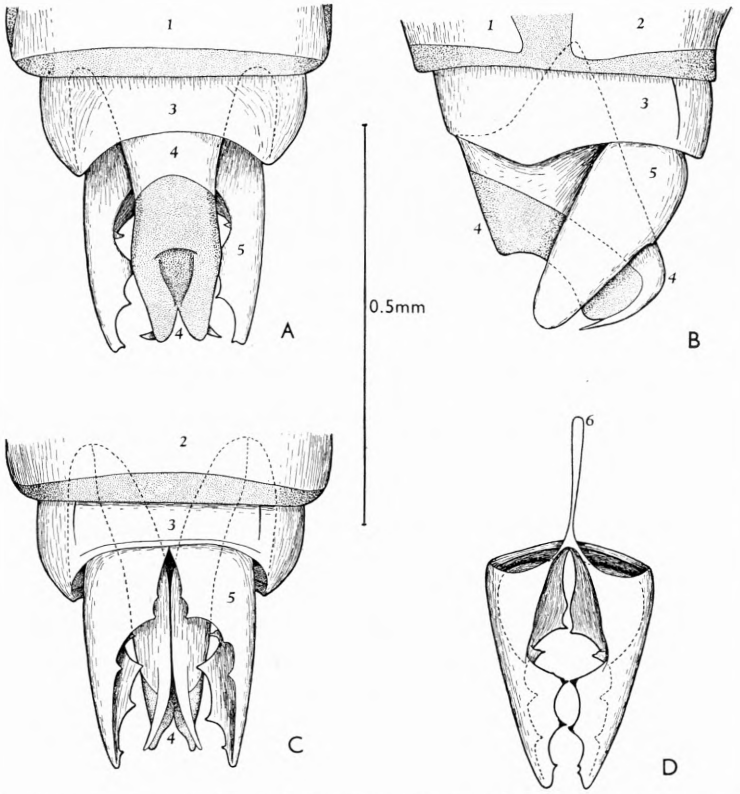

Fig. 7. *Agapetus fuscipes*. A—C: posterior end of abdomen in dorsal (A), lateral (right, B), and ventral view (C). The broken lines indicate the outline of that part of Segment X which is concealed by Segment IX, and in A and C also a horizontal optical section through the sclerotization of the genital chamber. D: inferior appendages in dorsal view. *1:* anal part of Tergum VIII. *2:* anal part of Sternum VIII. *3:* Segment IX. *4:* Segment X. *5:* inferior appendage. *6:* basal plate of the inferior appendages.

muscle probably acts both as a levator and as an adductor. The anterior and posterior dorsal muscles are considerably feebler. They are antagonists to the first-mentioned muscle. The anterior dorsal one is inserted laterally on the proximal edge of the appendage, the posterior one dorsally on the anterior end of the basal plate. They possibly act as an abductor and a depressor, respectively. The posterior ventral muscle is lacking.

The phallus (fig. 8). The phallocrypt is very deep, and the anterior end of the phallic apodeme (*1*) even reaches the oral end of Segment VIII. In the posterior part

of the phallocrypt the dorsal wall is sclerotized, forming a direct continuation of the "interior" sclerite of Segment X. In an anterior direction the sclerite widens and eventually covers the whole wall of the anterior end of the phallocrypt. The phallus is long and slender and curved somewhat downwards. The curvature is most pronounced a little proximally to the middle, i.e. at a point which in the state of repose

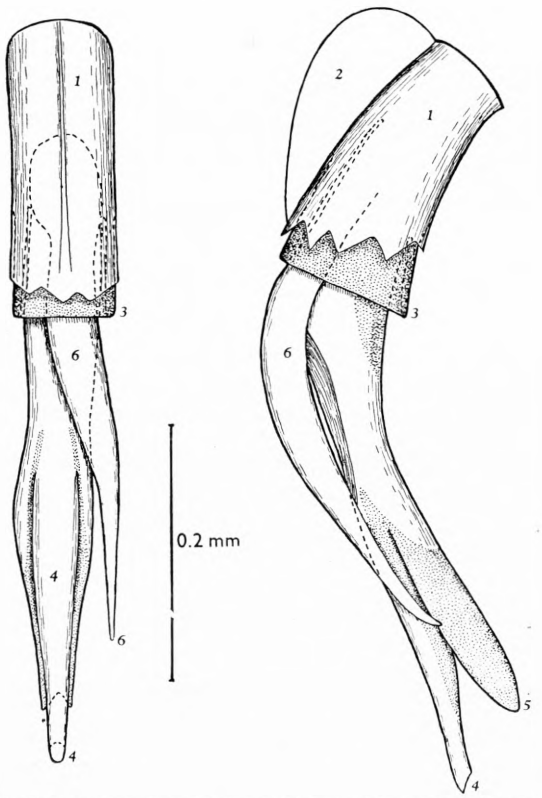

Fig. 8. *Agapetus fuscipes*. Phallus in dorsal and lateral (right) view. *1:* phallic apodeme; (the greater part of the phallocrypt has been broken off). *2:* longitudinal ridge on the phallic apodeme and the phallocrypt. *3:* phallobase. *4:* dorsal and *5:* ventral branch of the aedeagus. *6:* paramere.

is situated at the boundary between the "tube" of Segment X and the phallocrypt. Since the position of the distal part of the phallus is given by the "tube" of Segment X (somewhat descendent), the proximal part of the phallus and the phallocrypt become somewhat ascendent.

The phallus is divided into a short, membranous phallobase (*3*) and a well developed, chiefly sclerotic aedeagus (*4*, *5*). The aedeagal retractor originates in the phallic apodeme and is inserted on the dorsal side of the aedeagus at the point where the curvature is strongest. There is an unpaired, strong, and strongly sclerotized paramere (*6*), which arises dorsally from the base of the aedeagus. (Its ventral side is

much more thick-walled than the dorsal side). The paramere, which is somewhat shorter than the aedeagus, is curved like a sabre in such a way that its distal end comes to lie to the right side of the aedagus. On the dorsal side the latter has an asymmetric impression to receive the paramere. The connection between the paramere and the aedagus is membranous. The former thus is freely (but passively only) movable in relation to the latter.

As in *Rhyacophila* the distal part of the aedeagus is divided into a dorsal (*4*) and a ventral branch (*5*). The ventral branch is membranous, and its thin-walled distal end is slightly bilobed. Proximally its dorsal side is concave and embraces the ventral side of the slenderer and longer dorsal branch. The latter has a membranous ventral side and a sclerotic dorsal side. Quite distally, however, it is wholly sclerotized, and there the opening of the ejaculatory duct is found on the obliquely cut-off distal end. As distinct from conditions in *Rhyacophila*, this opening is directed somewhat downwards.

The posterior phallic muscle is by far the strongest muscle in the genital segments. It is inserted laterally and dorsally on the phallic apodeme and on the anterior part of the phallocrypt. Part of the insertion is on an unpaired, apodemal, dorsal, longitudinal ridge (*2*), which anteriorly is higher and narrower, posteriorly lower and broader. The possible protraction of the phallus must be of a very small extent, since the membranes separating the "internal" and the external sclerite of Segment X scarcely allow any greater movements between these parts. Hence, though the fibres (in a lateral view) run rather parallel to the phallocrypt, there is reason to believe that the chief function of the muscle is to raise the latter (and the phallic apodeme) and thus lower the distal part of the phallus. (In this connection the leverage of the apodemal ridge is probably of some importance). By this movement the phallus is removed from the "tube" of Segment X. During preparation it was seen that this is possible without severing the parts. The opposite movement must be due to elastic forces, since the anterior phallic muscle is lacking.

Lype phaeopa.

Apparently somewhat more than the dorsal half of Segment IX is entirely lacking. The remainder of the segment (figs. 9, *7* and 10 A, *1—3*) is rather long. The posterior edge is slightly indented; the concavity is limited by obtusely angled, though rounded, corners. The anterior edge has a very deep parabolic indentation. In this way the segment gets a pair of lateral forwards directed wings, which to a great extent are of an apodemal character. Owing to the reduction of the dorsal part, Segment IX is not seen from the dorsal side, but Segment X follows immediately behind Segment VIII.

As in *Rhyacophila* Segment X (fig. 9 A, C *8*; fig. 10 A, *4*) has a dorsal process (fig. 9 A, C, *9*; fig. 10 A, *5*). It is much shorter and narrower than the segment itself. Orally it is sagittally compressed, anally it is much flattened dorsoventrally. The

anterior end of Segment X itself has almost the same width as Segment IX. In an anal direction it is tapering, both in a dorsal and in a lateral view. In transverse section it is approximately triangular with a rather sharp dorsal side and a flattened ventral side. The greater, middle part of the latter, however, is very concave, and the edges

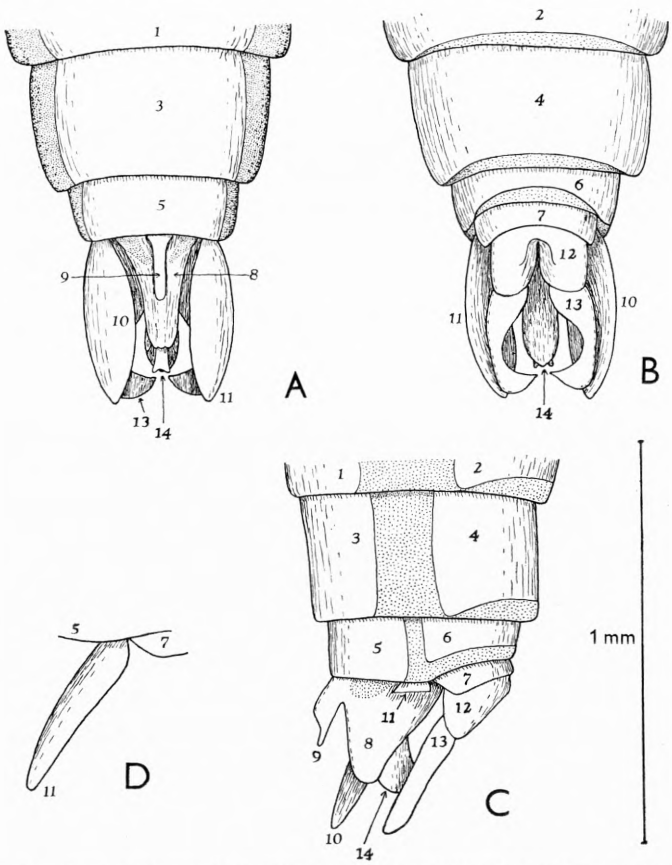

Fig. 9. *Lype phaeopa*. A—C: posterior end of abdomen in dorsal (A), ventral (B), and lateral (right), view (C). D: right superior appendage in lateral view. *1:* anal part of Tergum VI. *2:* anal part of Sternum VI. *3:* Tergum VII. *4:* Sternum VII. *5:* Tergum VIII. *6:* Sternum VIII. *7:* Segment IX. *8:* Segment X. *9:* dorsal process of Segment X. *10:* left superior appendage. *11:* right do. (in C cut off near its base). *12:* coxopodite. *13:* harpago. *14:* phallus.

of the concavity are approached so much (fig. 11 A, *4*) that the segment forms more than half of a tube. Quite orally it even forms a complete tube (see below), enclosing the phallus.

The dorsal process is completely sclerotized. Segment X itself, also, is sclerotized to its greater extent. Orally on the lateral side, however, there is a rather large membranous area. The narrower ventral end of this area overlaps the dorsal edge of Segment IX in the shape of a soft process (figs. 10 A and 11, *6*), carrying the large

superior appendage (fig. 9, *10* and *11;* fig. 11, 7), the shape of which reminds of a hare's ear and which projects far beyond the anal end of Segment X. On the anterior end of the dorsal process there is a transverse internal ridge (figs. 10 A and 11 B, *8*), which continues on a sclerotized stripe along the anterior margin of the membranous area.

On the ventral side the sclerite reaches the anterior end of Segment X. The two sides of the sclerite there are united through a transverse bridge below the entrance to the phallocrypt. Laterally the sclerite is connected with the posterior corner of Segment IX by another short transverse bridge (fig. 11, *9*) lying at the bottom of the genital chamber. In the middle of the latter bridge runs a suture (*10*); bending round the posterior edge of Segment IX it is continued on the lateral side of this segment as a longitudinal suture (fig. 10 A, *11*), which orally joins the antecosta. (On the homologies of this suture see *Tinodes waeneri*, p. 31, and *Psychomyia pusilla*, p. 40).

The phallic sheath formed by Segment X has a membranous dorsal wall. The lateral walls are sclerotized—to the greatest extent orally—and these sclerites are continuous with the external sclerotization of Segment X.

The anus is found on a membranous area on the posterior end of Segment X.

To Segment X the following muscles are attached: (1) A rather feeble muscle, originating from the antecosta of Segment IX at the anterior end of the suture *11* and inserted on the ventral side of the sclerite of Segment X orally to the middle. (2) Also a rather feeble muscle, originating from the anterior end of the dorsal edge of Segment IX and inserted on the lateral (ventral) part of *8*. (3) Muscle bands, originating from the antecosta of Segment VIII and converging posteriorly to their unpaired median insertion on the dorsal side of *8*. — (3), no doubt, is the usual, dorsal intersegmental muscles between Segments VIII and IX. This indicates that 8 in reality is the reduced and (probably secondarily) detached dorsal part of Segment IX, which has been intimately associated with Segment X. Conditions in *Polycentropus* (p. 48) give the key to understanding the muscles (1) and (2). These have the same mutual position as the correspondingly numbered muscles in *Polycentropus* and hence probably are their homologues. This means that (1) is the IX/X muscle, whereas (2) is a muscle originally associated with the paraproct which has shifted its anal insertion to the dorsal part of Segment IX. (It will be seen that it then actually has become an intrasegmental muscle).

As to the functions of the muscles, (1) and (2) probably are antagonists, which may cause a nodding movement of Segment X. The pivot for this movement must be the sclerotic connection between Segment X and the posterior corner of Segment IX. Since this bridge must yield some elastic resistance, it is a little peculiar that the two rather feeble muscles act through short levers only. The muscles (3) act through a much longer lever. These muscles partly may move the IX/X complex as a whole, partly, assisted by the ventral VIII/IX muscles, raise Segment X. This levation possibly is the principal active movement of Segment X. The opposite movement, chiefly

due to elastic forces (the bridge between Segments IX and X) must, of course, be of the same strength.

The inferior appendages (figs. 9A—C, 10A, *12—13*) are two-jointed. The harpago is considerably longer than the coxopodite, especially so dorsally. The distal margin of the latter being indented and the proximal margin of the former correspondingly bulging. In a lateral view the appendages have a very simple shape. In a ventral (or dorsal) view the median side of the harpago is very concave; the claw-

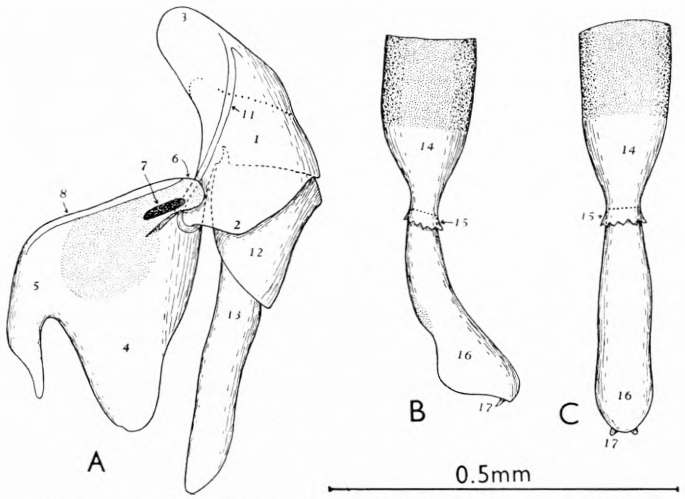

Fig. 10. *Lype phaeopa*. A: Segments IX and X in lateral (right) view; the phallus has been removed. B and C: phallus in lateral (right, B) and ventral view (C). *1:* Segment IX. *4:* body of Segment X. *5:* dorsal process of Segment X. *7:* cicatrice left by removal of superior appendage. *12:* coxopodite. *13:* harpago. *14:* phallic apodeme; (its distal boundary is indicated by a coarsely dotted line). *15:* internal (or anterior) part of phallocrypt; (the external part has been broken off). *16:* phallus. *17* = fig. 12, *3*. Other numbers: see text.

like distal end is curved inwards. Proximally the two appendages have fused to a great extent. On the ventral side that area which surround the cleft between the distal parts of the coxopodites is much impressed. The impression is bounded by a thickened, but sharp ridge in the shape of a U with backwards directed opening.

The anterior ventral muscle is very strong. It originates from the antecosta of Segment IX between the two sutures *11* and is inserted on the bottom of the cleft between the two coxopodites. The posterior dorsal muscle originates in Segment IX at 2 (fig. 10A) and is inserted on a short tonguelike apodeme on the small basal plate. Since abduction and adduction of the coxopodites seem impossible, the two muscles must be a levator and a depressor, respectively. The posterior ventral muscle is formed by bands which run parallel from the dorsal to the ventral side of the coxopodite. Their only possible function seems to be a flattening of the latter, a movement the significance of which is a puzzle to me. The anterior dorsal muscle is lacking. The flexor of the harpago is rather weak.

The phallus (fig. 9A—C, *14*) has a very large apodeme (fig. 10B, C, *14*), almost

as long as and considerably thicker than the phallus itself. It is bottle-shaped and tapers anally towards the collar-like connection with the free part of the phallus. More than the oral part of the apodeme is membranous and very thin-walled. It is entirely filled up by the ejaculatory duct, which has a very strong circular musculature. The phallus (*16*) itself is undivided, slightly clavate, and its distal part is somewhat sagittally compressed. The proximal end is lowered into a very short, sclerotic phallocrypt (*15*).

For about the distal half the dorsal side of the phallus is membranous. On the

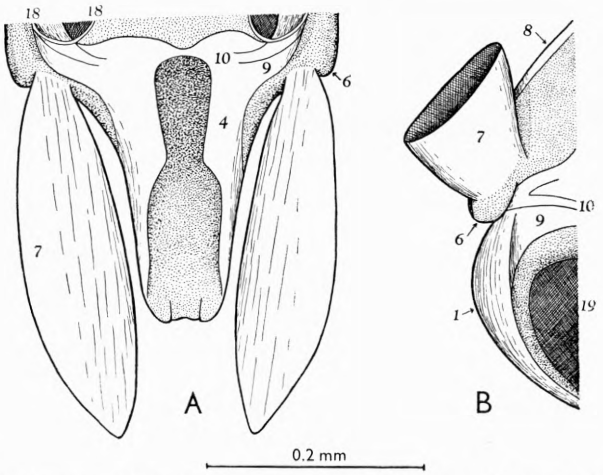

Fig. 11. *Lype phaeopa*. A: Segment X in ventral view. B: the extreme left part of Segments IX and X in posterior view. *1:* Segment IX. *4:* body of Segment X. *7:* superior appendage (in B cut off near its base). *18—18:* cut edge after removal of Segment IX. *19:* cicatrice left by removal of inferior appendage. Other numbers: see text.

thickened distal end (fig. 12) there is a cavity, which opens distally and dorsally. On the lateral and ventral walls of this cavity there is a sclerite, which is broader than long and in transverse section forms approximately three quarters of a circle. The distal margin of the sclerite is protracted backwards as a free fold. Laterodorsally this is low (*1*). In a ventral direction it becomes higher, and on the ventral side it comprises the whole length of the sclerite (and even more than that), a lip (*2*), sclerotized on both sides, thus being formed. In the middle the posterior edge of this lip is protracted into a flattened, backwards directed process (*3*), the upwards bent distal end of which is bilobed (fig. 10 B, C, *17*). Above the base of the lip rises a short, upwards and backwards directed tube (fig. 12, *4*) with the opening of the ejaculatory duct (*5*). The tube is sclerotized ventrally and laterally, but membranous on the greater, distal part of the dorsal side. The strong aedeagal retractor originates on the whole of that part of the dorsal side of the phallus (itself) which is sclerotized, and is inserted dorsally on the proximal end of the tube. It must act as a levator of the tube. Its antagonist is elastic forces: the ventral side of the tube is sclerotically connected with

the lip. (Nor can it be excluded that the lip takes part in the movement. Its membranous connection with the main sclerite of the phallus may make this possible). The ventral side of the tube is protracted forwards as an apodeme, the significance of which is a little doubtful.

The morphology of the phallus will be discussed under *Tinodes waeneri* (p. 37).

The oral half of Segment X entirely encloses the phallus. The distal end of the latter, however, lies below the anal half of Segment X. The two structures resemble the upper and the lower jaw of a beak. The very strong anterior phallic muscle ori-

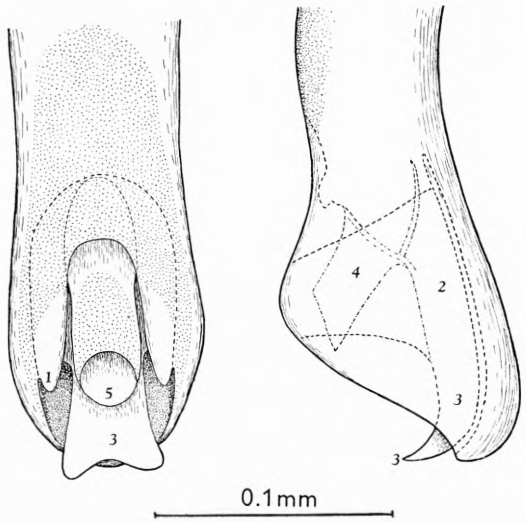

Fig. 12. *Lype phaeopa*. Distal end of phallus in dorsal and lateral (right) view. For explanation see text.

ginates from the antecosta of Segment IX dorsally to the suture *11* (fig. 10 A) and is inserted on the phallocrypt. The (membranous) connection between the latter and the sheath formed by Segment X must limit the extent of a retraction, and hence possibly transform the pull of the muscle into a levation of the distal part of the phallus, moving the two jaws of the "beak" towards each other. (The musculature associated with Segment X also may play some role in this connection). The "beak" possibly is the principal grasping organ in the genital apparatus. There are no posterior phallic muscles.

Tinodes waeneri.

The posterior end of Segment VIII to a great extent overlaps the oral part of the genital segments, especially so dorsally and laterally. The genital chamber is very deep, particularly its dorsal part, which projects forwards as far as the posterior end of Segment VII. The distal part of the phallus has a simpler shape than that of *Lype*. In all other respects conditions in Tinodes are more complicated than in *Lype*.

In Segment IX the same principle is seen as in *Lype:* the reduced dorsal part is entirely detached from the ventral part and intimately associated with Segment X.

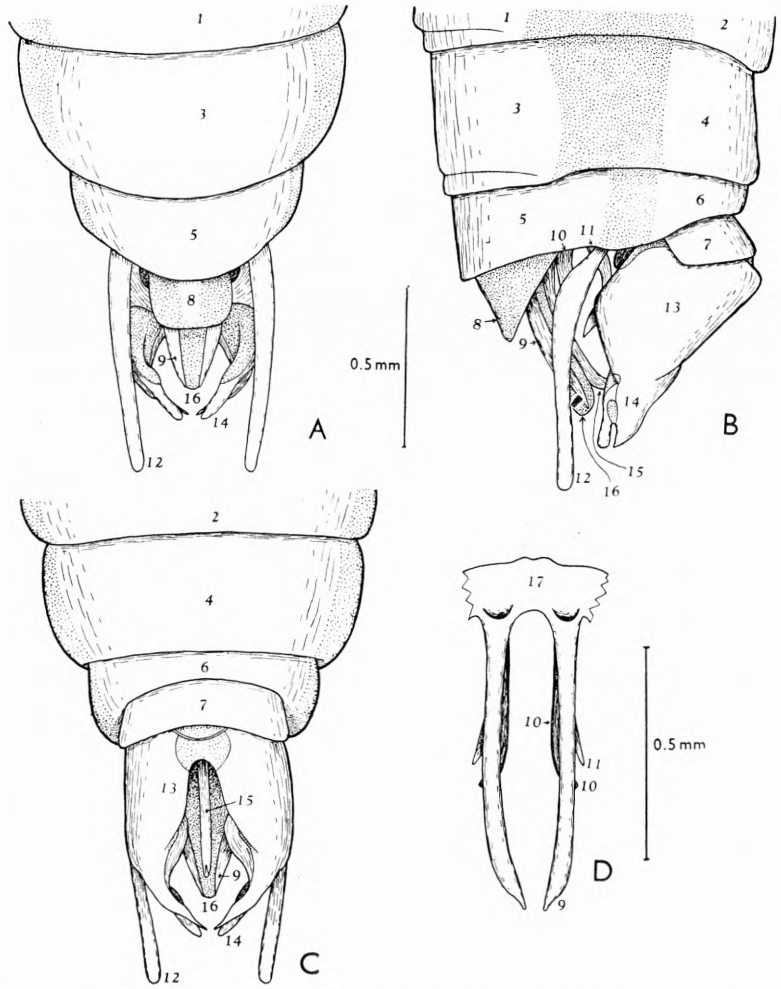

Fig. 13. *Tinodes waeneri.* A—C: posterior end of abdomen in dorsal (A), lateral (right, B), and ventral view (C). D: paraproctal processes in dorsal view. *1:* anal part of Tergum VI. *2:* anal part of Sternum VI. *3:* Tergum VII. *4:* Sternum VII. *5:* Tergum VIII. *6:* Sternum VIII. *7:* Segment IX. *8:* Segment X (fig. 14, *13*). *9—11* branches of paraproctal process (figs. 14 and 15, *14—16*); *9:* dorsal, *10:* intermediate, *11:* ventral branch. *12:* superior appendage (figs. 14 and 15, *17*). *13:* coxopodite. *14:* harpago. *15:* proximal, unpaired process on basal plate of inferior appendages (figs. 14, *22*; 16, *3*). *16:* phallus. *17:* sclerite of the genital chamber (as seen from the haemocoelic side; the lateral parts have been broken off; figs. 14 and 15, *6*).

The structure thus formed takes the shape of a soft "upper lip" (figs. 13A, B, *8;* 14, *13*) of the genital chamber. The lateral margin of the upper lip is steeply ascendent and joins the descendent posterior edge of the ventral part of Segment IX (figs. 13B, C, *7;* 14, *1*) under an approximately right angle. In situ this "mouth angle" is con-

cealed by the overlapping posterior border of Segment VIII (fig. 15 A, 25). Along the anterior margin of the upper lip there is a narrow sclerotic area (fig. 14, 2), probably representing the dorsal part of Segment IX. On the lateral side the sclerite 2 is subjected to a torsion of 90° so that its most lateral part (2 *b*) gets the character of a semicylindrical sclerotization at the bottom of the furrow between Segment VIII and the upper lip. On the dorsal side the sclerite 2 widens to an unpaired sclerotized stripe, which almost reaches the posterior end of the lip.

The rod-like superior appendages (fig. 13, *12;* figs. 14 and 15, *17*) are very long and are that part of the genital apparatus which projects farthest backwards. They rise from the inside of the edge of the genital chamber at the "mouth angle". Their lateral sides are sclerotically continuous with the lateral (or ventral) ends of the sclerite 2.

The ventral part of Segment IX (figs. 13, *7;* 14, *1, 3*) is very long. This is especially so on the ventral side, where the anterior edge is very bulging and stretches a good deal into Segment VII. To its greater extent, however, the ventral part of Segment IX has the character of an apodeme (*3 a*).

At the bottom of the genital chamber there is an unpaired sclerite (figs. 14 and 15, *6*) in the shape of an inverted U, which dorsally encircles the proximal end of the phallus. (It is not, however, directly connected with the latter; see below). The arms of the U are placed very obliquely (descendent) and taper in a ventral direction. The narrow ventral end is a direct continuation of the inflected posterior edge of the ventral part of Segment IX, and is again sclerotically continuous with the median side of the superior appendage. Since the latter, as mentioned above, is continuous with the dorsal part of Segment IX (the sclerite 2), a sclerotic connection between the two parts of the segment thus is established. Both above and below the base of the superior appendage a membranous area is seen. In a dorsal direction the arms of the U widen. Its base (fig. 13 D, *17*) is almost horizontal (though a little ascendent), which means that it lies anteriorly on the ventral side of the upper lip. Along the anterior margin of the arm of the U a suture (fig. 15, *6 a*) runs. It marks the origin of a high, lamella-like apodeme (fig. 14, *3 b*), which forms a direct continuation of the apodeme *3 a*, and which (in a lateral view) is pointed dorsally. The suture *6 a*, no doubt, is homologous with the suture *10* in *Lype* (fig. 11). Like the latter it passes below the base of the superior appendage.

At the boundaries between the base and the arms of the U a pair of large and complicated backwards directed processes issue from the sclerite. Proximally the processes are sagittally compressed, but they very soon become divided into three branches: a dorsal one (figs. 13, *9;* 14 and 15, *14*), an intermediate one (figs. 13, *10;* 14 and 15, *15*) and a ventral one (figs. 13, *11;* 14 and 15, *16*). For some distance the bases of the two latter ones are united. All three branches are curved a little inwards. The dorsal branch, which is by far the longest, is curved somewhat downwards, and applied to the distal part of the phallus. The two dorsal branches form parts of a tripartite phallus-guide, the third part of which is formed by an unpaired process on

the inferior appendages (fig. 13 B, C, *15*). The distal ends of the intermediate and the ventral branch are again curved slightly outwards.

It might perhaps be inferred that the three-branched processes alone represent Segment X, and that the upper lip is formed exclusively of the dorsal part of Segment IX. The fact, however, that the upper lip is penetrated by the rectum shows that it

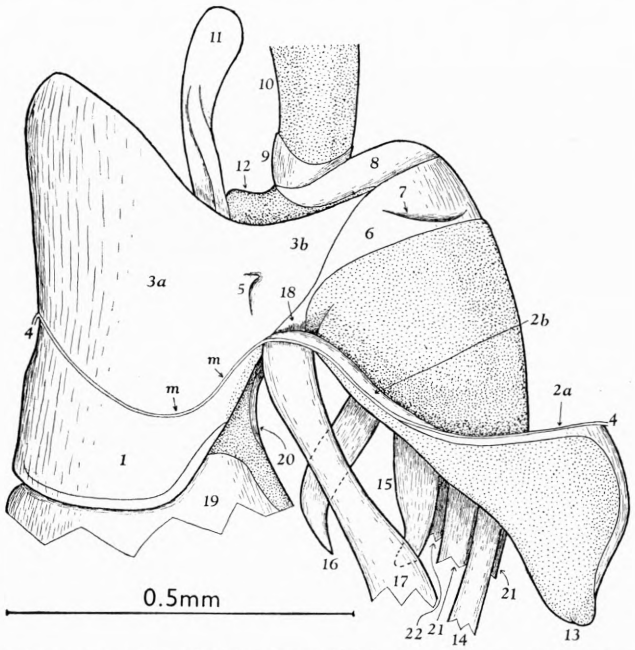

Fig. 14. *Tinodes waeneri*. Segments IX and X in lateral (left) view. *1:* non-apodemal, ventral part of Segment IX. *2:* dorsal part of Segment IX; *a* as seen from the external side, *b* from the haemocoelic side. *3:* apodemal part of Segment IX. *4—4:* cut edge through intersegmental membrane between Segments VIII and IX. *5:* origin of paraproctal muscle. *6:* sclerite of the genital chamber (as seen from the haemocoelic side). *7:* origin of the paraproctal process. *8:* sclerite connecting *6* with the phallus (as seen from the haemocoelic side). *9:* phallic apodeme. *10:* ejaculatory duct. *11:* apodeme on the basal plate of the inferior appendages. *12:* membranous part of the genital chamber (as seen from the haemocoelic side). *13:* Segment X. *14—16:* branches of the paraproctal process (distal part of 14 broken off). *17:* superior appendage (distal part broken off). *18:* origin of the superior appendage (as seen from the haemocoelic side). *19:* coxopodite (distal part broken off). *20:* basal plate of the inferior appendages. *21:* phallus (distal part broken off). *22:* unpaired process on the basal plate of the inferior appendages (distal part broken off). *m—m:* between the arrows the IX/X muscle originates. For further explanation see text.

contains at least the main part of Segment X. The anus is situated on the posterior border of the upper lip. To me it seems justifiable to homologize the processes in *Tinodes* with those of the paraprocts in *Polycentropus* (pp. 46—47). This means that the sclerite shaped like an inverted U represents the fused paraprocts. In *Lype* the latter have fused also with the sclerite of Segment X, and their processes are lost.

Three pairs of muscles are associated with the upper lip: (1) A sagittally compressed muscle originating from the apodeme *3* (fig. 14) between the arrows *m—m*, just anteriorly to the line of union between Segments VIII and IX, and inserted on

the dorsal part of *2b*. This muscle bridges the "mouth angle" and is enclosed in the overlapping fold of Segment VIII (fig. 15A, *25*). (2) A rather small muscle originating from a process (fig. 14, *5*) on the external side of the apodeme *3* and inserted on *2*

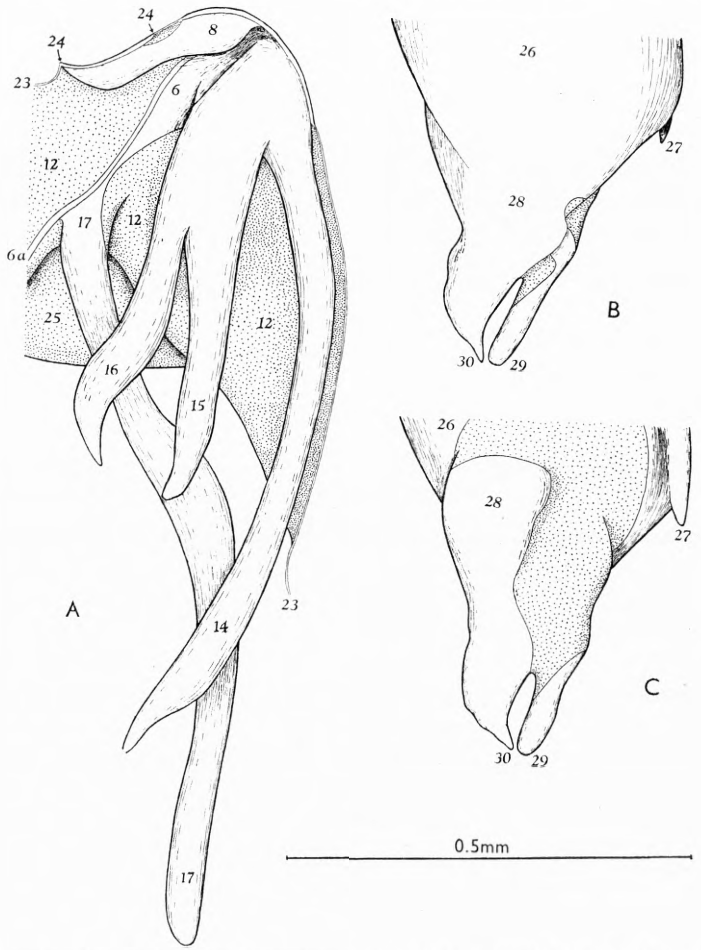

Fig. 15. *Tinodes waeneri*. A: right half of the genital chamber as seen from the inside (median view); the dorsal side of Segment X has been removed. B: distal end of left inferior appendage in lateral view. C: do. of right do. in median view. Numbers as in fig. 14 (*6*, *8*. and *12*, however, are seen from the external side). Further: *6a:* suture on the sclerite of the genital chamber. *23—23:* cut edge arisen by sagittal section through the genital chamber. *24—24:* between the arrows the phallus has been attached. *25:* overlapping posterior border of Segment VIII. *26:* coxopodite. *27:* spine on the dorsal margin of the sclerite of the coxopodite. *28:* harpago. *29* and *30:* dorsal and ventral branch of the latter.

at the boundary between 2a and 2b. (3) the dorsal VIII/IX muscles are inserted on the dorsal part of 2a. The tree pairs of muscles, no doubt, are homologous with those correspondingly numbered in *Lype* (p. 26). In *Tinodes* the muscle (1), also, has shifted its origin to that part of Segment IX which has fused with Segment X. The muscles

(1) and (3) possibly can give the upper lip a nodding movement. In the state of repose the muscle (2) is almost parallel to 2b. During a strong levation of the upper lip, however, it possibly may assist the muscle (3).

The inferior appendages (figs. 13A—C, *13* and *14;* 16) are large and two-jointed. Proximally the two coxopodites are united to a rather great extent, though chiefly by membrane. Quite proximally on the ventral side only, there is a narrow, but strong, sclerotic transverse bridge, which on either side of the membranous area continues as a thickened ridge along the ventral part of the proximal margin of the appendages. Hence, the sclerotic connection is effected chiefly by the large basal plate (figs. 14, *20;* 16A, *1*), which projects far forwards and further is protracted into a long, sagittally compressed and somewhat spoon-like apodeme (fig. 14, *11*). It is connected with the sclerotizations of the appendages themselves by two pairs of narrow bridges only (fig. 16A).

The basal plate is steeply descendent. It carries two unpaired processes. The distal (and ventral) one (fig. 16B, *4*) is short and clumsy and of a rather varying shape. It is provided with a pair of strong, yellow setae (which in fig. 16A are concealed by *3*). The proximal process (figs. 13B, C, *15*; 14, *22*; 16, *3*) takes the shape of a forwards directed, dorsally concave lip, from the anterior edge of which a very long and slender horn arises. Basally the latter is upwards directed, but it soon becomes curved backwards. It forms the ventral part of the phallus-guide. The proximal part of the horn is sagittally compressed. Its downwards curved apex, too, is much sagittally compressed, dagger-shaped, with a sharp anal (or dorsal) edge.

In transverse section the coxopodite is ovate with the broad end dorsally. Except for the bridges mentioned above its median side is membranous. Approximately in the middle of the dorsal margin of the lateral sclerite there is an inwards directed, flattened spine (figs. 16, *6;* 15B, C, *27*), which may be bifurcated or even have a more complicated shape. It may be opposed to the apex of the intermediate branch of the paraproctal process (figs. 14 and 15, *15*).

The harpago (figs. 13, *14;* 15B, C, *28;* 16, *7*) is much smaller than the coxopodite. Its median side is twice as long as the lateral side, but (except quite distally) it is sclerotized in its ventral half only. Distally the harpago is divided into a dorsal (fig. 15, B, C, *29*) and a ventral branch (*30*). The former is finger-like. The stronger ventral branch is claw-like and somewhat concave on the median side. The sclerotic connection between the two branches consists only of a rather narrow, laterodorsal bridge, so they may have some (passive) mutual movement. On the lateral side the sclerites of the coxopodite and the ventral branch of the harpago are continuous.

The anterior dorsal muscle is lacking. The anterior ventral muscle is very strong. It originates on the whole ventral part of the apodeme of Segment IX (fig. 14, *3a*), and also from the anterior end of the non-apodemal part (*1*). Some of the muscle-bands are inserted on the sclerotic part of the median sides of the coxopodites. The vast majority, however, are inserted on the basal plate, from its posterior edge to the base of the process *3* (fig. 16). The posterior dorsal muscle is much smaller, but still

rather strong. It originates from the ventral part of the sclerite (figs. 14 and 15, *6*) in the genital chamber, and is inserted on the oral end of the apodeme of the basal plate (fig. 14, *11*). The posterior ventral muscle originates from the proximal half of the ventral edge of the coxopodite and is inserted on the lateral margin of the basal

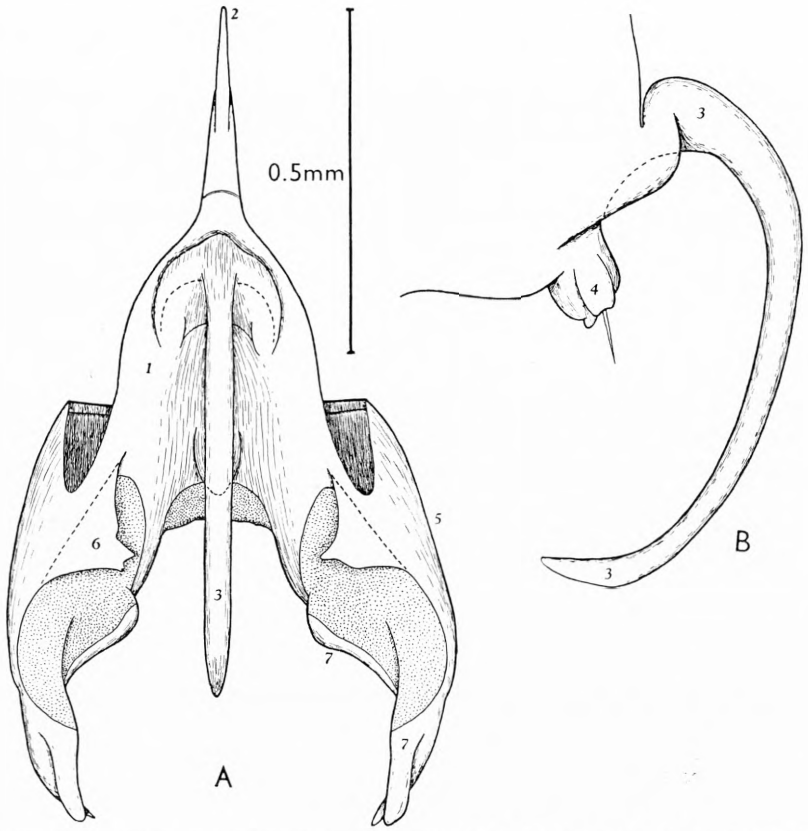

Fig. 16. *Tinodes waeneri*. A: inferior appendages in dorsal view. B: processes of the basal plate in lateral (left) view. *1:* basal plate. *2:* apodeme of the latter. *3* and *4:* proximal and distal process of the basal plate. *5:* coxopodite. *6:* spine on the latter. *7:* harpago.

plate; its fibres are descendent. The flexor of the harpago originates from almost the whole lateral side of the coxopodite and is inserted on the middle of the median side of the harpago, i. e. at the base of the ventral branch of the latter.

A contraction of the anterior ventral muscle must pull the basal plate forwards and thus adduce the two inferior appendages. Considering the small extent of the sclerotic connection between the basal plate and the appendages themselves, the former possibly may perform an independent movement, when the appendages are fixed by grasping the body of the ♀. This movement will be a depression of the oral part of the plate, which again causes a retraction of the base of the horn *3* (fig. 16B) and a

levation of its distal part. The posterior dorsal muscle is the antagonist of the anterior ventral one. Alternating contractions of the two posterior ventral muscles perhaps may give the horn *3* a rocking movement (from side to side).

The undivided phallus (figs. 13, *16;* 14, *21;* 17) is long and slender. From a

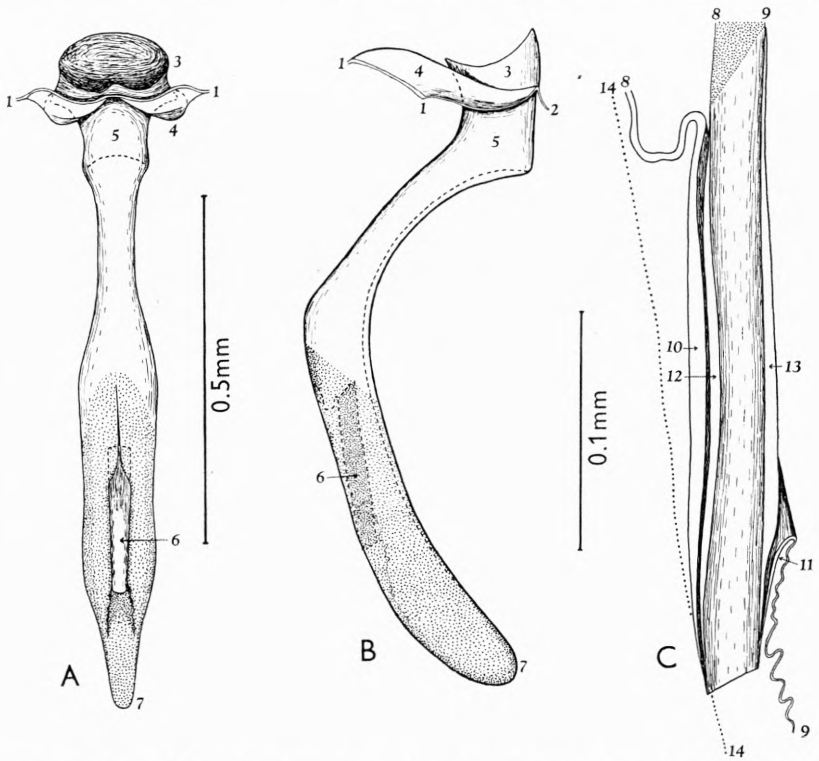

Fig. 17. *Tinodes waeneri.* A: phallus in dorsal view. B: the same in lateral (right) view. C: left half of the dorsal branch as seen from the inside (median view). *1—1:* cut edge along the line of connection between *4* and the sclerite of the genital chamber (figs. 14 and 15, *6*). *1—2:* cut edge through the line of connection between 4 and the membrane of the genital chamber (figs. 14 and 15, *12*). *3:* phallic apodeme. *4:* sclerite connecting the proximal end of the phallus with the sclerite of the genital chamber; in B as seen from the haemocoelic side. *5:* phallus. *6:* dorsal branch of phallus (in B shining through). *7:* ventral branch of phallus. *8—8* and *9—9*: cut edges. *10:* section through upper wall and *11:* section through lower wall of dorsal branch of phallus. *12:* section through upper wall and *13:* section through lower wall of the ejaculatory duct. *14—14* (coarsely dotted line) indicates the position of the upper side of the ventral branch.

purely topographical point of view it may be considered as composed of three parts: (1) A short and comparatively thick proximal part, pointing directly backwards. (2) A very slender, upwards and backwards directed middle part. (3) A thicker, backwards and a little downwards directed distal part, which apically is greatly sagittally compressed. The ventral sides of (2) and (3) form an even curve, congruent with the curve described by the horn of the inferior appendages (figs. 16, *3;* 13, *15;* 14, *22*), and have a concavity, which receives the dorsal side of this horn and proximally is bounded by a sharp edge. As mentioned above, the horn forms the ventral branch

of a tripartite phallus-guide. The dorsal part of the guide is formed by the superior branches (figs. 13, *9;* 14 and 15, *14*) of the paraproctal processes, the distal two thirds of which are applied laterodorsally to the distal part of the phallus.

The proximal and the middle part of the phallus is sclerotized, whereas the distal part chiefly is membranous. On the dorsal side of the distal part there is a longitudinal furrow, in which a sclerotic tube (fig. 17 A, B, *6*) is seen. A closer examination (fig. 17 C) shows that this tube has a double wall. The internal wall (*12, 13*) is the sclerotic distal part of the ejaculatory duct. On the external wall the dorsal side (*10*) is four times as long as and much thicker than the ventral side (*11*).

There is no phallocrypt and the phallic apodeme (figs. 14, *9;* 17, *3*) is very short, especially on the dorsal side. Laterally the base of the phallus is connected with the dorsal part of the sclerite *6* (figs. 14 and 15) by a pair of vertically placed sclerites (*8;* fig. 17, *4*). In transverse (horizontal) section the latter are curved, the convexities facing backwards. For their dorsal two thirds the two sclerites have fused, but are separated by a furrow corresponding to the their curvatures. Between the ventral third of the sclerites and the dorsal side of the phallus there is a triangular (or perhaps rather arrowhead-like) membranous area.

The phallus has no musculature, neither extrinsic, nor intrinsic. Its possible movements are entirely dependent on the musculature of the inferior appendages and Segment X. A levation of the horn of the inferior appendages also means a levation of the phallus. The inferior appendages being fixed by grasping the body of the ♀, the opposite movement may be performed with great power by elastic forces: the sclerites at the base of the phallus and the paraproctal processes.

The tube *6* (fig. 17) might be considered as the aedeagus. This, however, would imply an extraordinary dorsoventral asymmetry of the phallobase. I find it more probable that *6* is homologous with the dorsal branch of the aedagus in *Rhyacophila* (fig. 6, p. *19, 4*), and that part of the phallus (*7*) which projects beyond the base of *6* with the ventral branch in *Rhyacophila* (fig. 6, *5*). The undivided condition would then have arisen in a similar way as in *Rhyacophila:* by obliteration of the endotheca and subsequent fusion of the phallotheca and the aedeagus. In *Lype* the tube *4* (fig. 12, p. 29), no doubt, is homologous with *6* in *Tinodes. 4* (perhaps together with 2 and *3*) then represents the dorsal branch of the aedeagus, whereas the "lower jaw of the beak" in the phallus of *Lype* represents the ventral branch. In *Lype* the aedeagal retractor is inserted on the proximal end of the tube *4*. In *Agapetus* (p. 23) it is inserted on the dorsal side of the aedeagus, i. e. at the base of the dorsal branch.

Psychomyia pusilla.

At a first glance this form is very different from the two other psychomyids. A closer examination, however, reveals the same principle: the reduced and entirely detached dorsal part of Segment IX is intimately associated with Segment X.

The most conspicuous structures are a dorsal pair of large, sclerotic rods (figs.

18, *8—10;* 19, *5—6*), proximally united by a short membranous area, which in situ is concealed by the overlapping posterior border of Segment VIII. The proximal half of the rods is directed backwards, sagittally compressed, and rather high. The distal half is directed upwards and backwards and somewhat flattened. In a lateral view

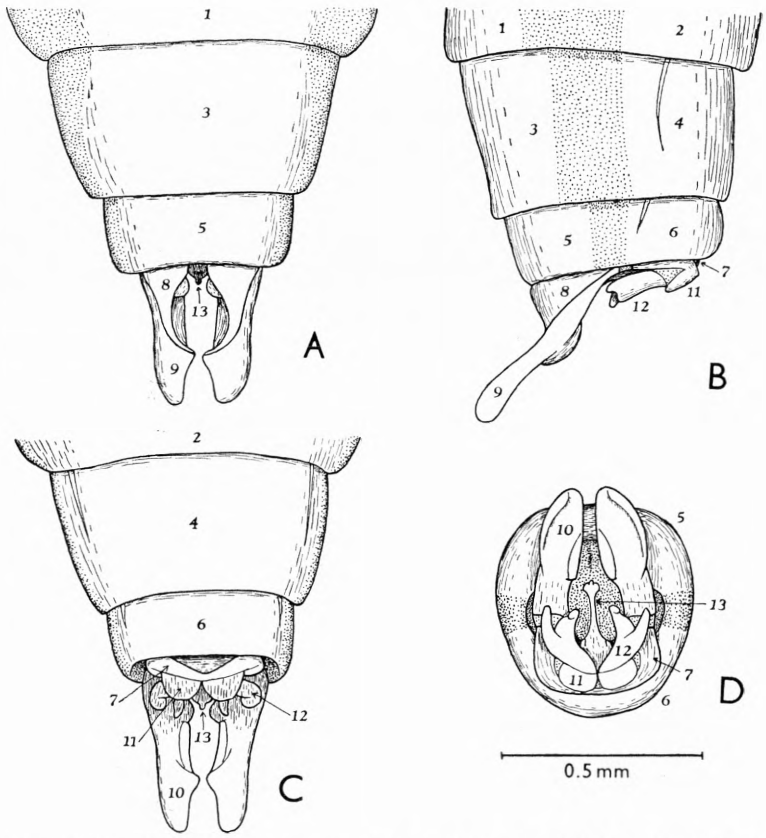

Fig. 18. *Psychomyia pusilla.* A—C: posterior end of abdomen in dorsal (A), lateral (right, B), and ventral view (C). D: Segments VIII—X in posterior view. *1:* anal part of Tergum VI. *2:* anal part of Sternum VI. *3:* Tergum VII. *4:* Sternum VII. *5:* Tergum VIII. *6:* Sternum VIII. *7:* Segment IX. *8:* proximal and *9:* distal part of "dorsal rod", separated by a suture (fig. 19A, *7*). *10:* ventral side of "dorsal rod". *11:* coxopodite. *12:* harpago. *13:* phallus.

a bulge (fig. 19, *8*) is seen in the middle of the rod. It is the brown ventral edge of an oblong, more thick-walled and more strongly sclerotized median area, which is concave; (the concavity faces mediodorsally). Proximally to this area there is, on the median side), a pad-like thickening, densely covered with setae and visible only in a dorsal or a ventral view. The distal end of the rod is spoon-like and more feebly sclerotized.

The sclerotization of the rod is separated from that of the ventral part of Segment IX (figs. 18, *7;* 19, *2*) by a rather broad membranous area. On the ventral side

a suture runs along the proximal margin of the sclerite of the rod. Laterally it makes a rectangular bend and runs, following a slightly sigmoid curve, obliquely backwards across the dorsal side of the rod (fig. 19, 7). It eventually ends on a small projection

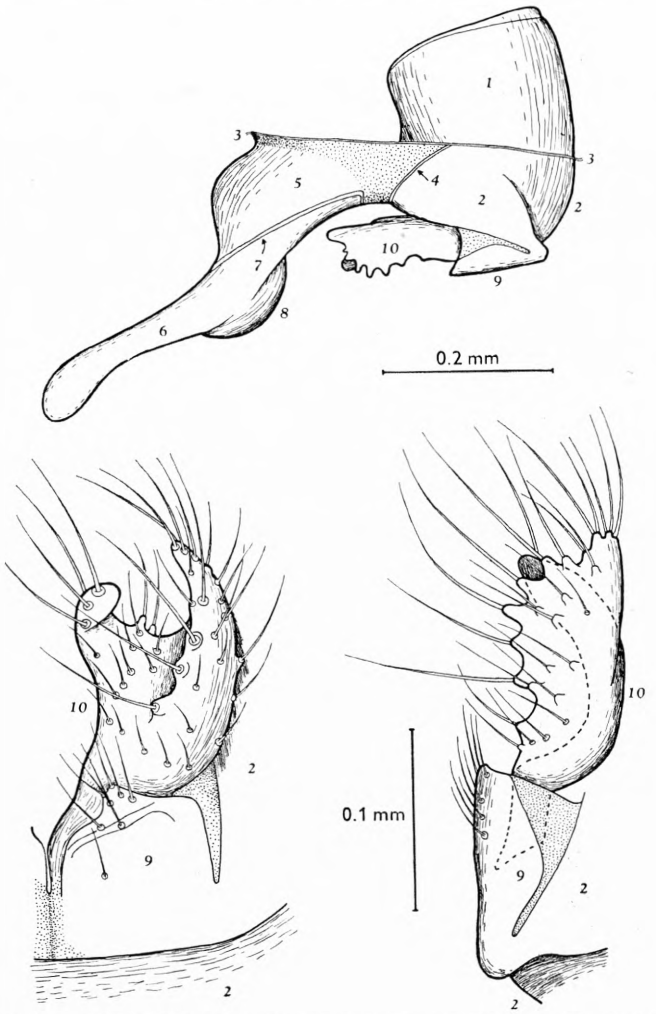

Fig. 19. *Psychomyia pusilla*. Above: Segments IX and X in lateral (right) view. Below: right inferior appendage in posterior and in lateral view; in the last figure the anterior direction is towards the right. *1:* apodemal and *2:* non-apodemal part of Segment IX, separated by *3—3:* cut edge through the intersegmental membrane between Segments VIII and IX. *4:* suture (see text). *5:* proximal and *6:* distal part of "dorsal rod", separated by the suture *7*. *8:* see p. 38. *9:* coxopodite. *10:* harpago.

of the median margin just distally to the cup-like depression described above. It might perhaps be supposed that this suture marks the boundary between Segment X and the dorsal part of Segment IX, the area (figs. 18, *8;* 19, 5) lying proximally (and medially) to the suture belonging to Segment IX, the area (figs. 18, *9;* 19, *6*) lying

distally (and laterally) to the suture to Segment X. The fact, however, that the anus (a vertical slit) is found between the bases of the rods shows that the proximal area contains parts of Segment X as well. The sutures, no doubt, is a secondary strengthening of the rods, and it is impossible to give the boundary between Segments IX and X. The homology of the rods is not entirely clear. They may represent the superior appendages, or they may represent paraproctal processes. I am most inclined to believe in the latter possibility. This view is supported by the fact that the medioventral edge of the rod projects into the phallocrypt and eventually joins the sclerotization of the latter; (cp. conditions in *Tinodes*, p. 37).

The ventral part of Segment IX (figs. 18, *7;* 19, *1—2*) is rather long, but more than its anterior half has an apodemal character (fig. 19, *1*). On the ventral side there is a strong, elevated area along the posterior margin. On the lateral side the sclerite also covers the broadly rounded posterior border of the segment, and at the posterior corner (i. e. quite dorsally) it is protracted as a rod-like sclerite into the phallocrypt. Along the dorsal margin of the non-apodemal part of the sclerite there runs a suture (fig. 19, *4*), which continues for at least some distance on the rod in the phallocrypt. From this suture rises the dorsal, strongly inwards bent part of the apodeme. This part of the apodeme, no doubt, is homologous with *3b* in *Tinodes* (fig. 14, p. 32), which shows that the sutures *4* in *Psychomyia* and *6a* in *Tinodes* (fig. 15) are homologous. In its course the suture *4* in *Psychomyia* shows so a high degree of conformity with the suture *10—11* in *Lype* (figs. 10—11, pp. 27 and 28) that a homology must be considered certain. It is very unlikely that these sutures are homologous with sutures in other families.

The dorsal VIII/IX musculature is divided into two portions. In one portion the bands converge fan-like and are inserted medially on *5* (fig. 19). This portion, which is very strong, must act as a levator and probably also as an adductor of the rods. The other, weaker, portion is inserted laterally and proximally in the rods and probably must act as an abductor. From the inwards bent part of the apodeme of Segment IX originates a strong muscle, which is inserted dorsally and proximally in the rods. It must be a depressor. According to its point of origin it is homologous with the muscle (2) in *Tinodes* (p. 33) and hence is a paraproctal muscle. The IX/X muscle is lacking in *Psychomyia*. Lateroventrally in the non-apodemal part of Segment IX (fig. 19, *2*) originates a muscle which is inserted on the posterior corner of the segment at the point where the latter bends into the phallocrypt. This muscle possibly influences the movements of the phallus and, no doubt, is the posterior ventral muscle of the inferior appendages, which has shifted its insertion.

The inferior appendages (figs. 18, *11—12;* 19, *9—10*) are very small and directed almost straight upwards. A comparison with *Tinodes*, as well as the musculature, seems to show that they have been subjected to a torsion of 90°, so that the backwards directed side represents the morphologically lateral side. (In the following purely topographical designations will be used). The appendage is divided into a shorter coxopodite (figs. 18, *11;* 19, *9*) and a longer harpago (*12*; *10*). The former is sclerotized

on the posterior side only. The two coxopodites are united for rather a long distance, though only by membrane. Proximally (= ventrally) their sclerites have fused with that of Segment IX. The line of union coincides with the elevated ridge along the posterior margin of Segment IX, mentioned above. There is no basal plate. The

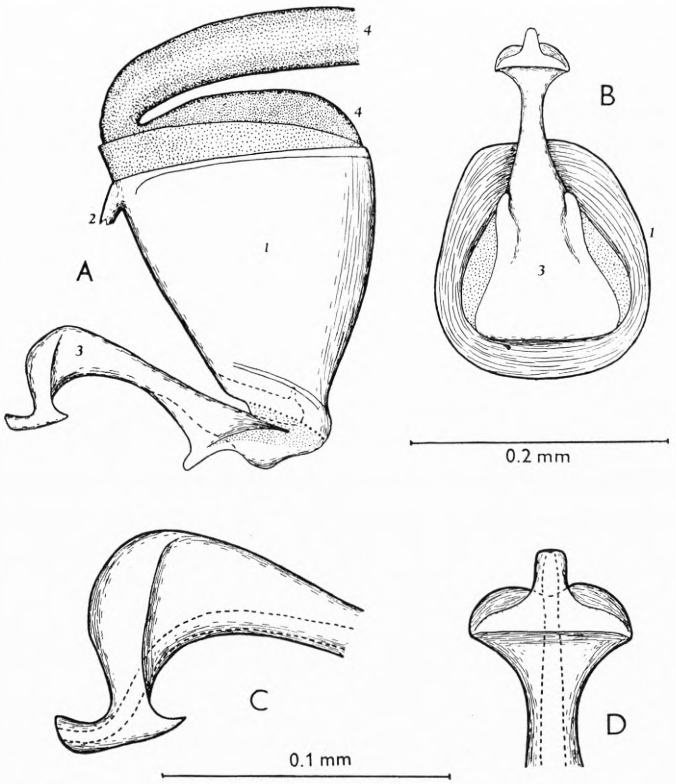

Fig. 20. *Psychomyia pusilla*. A: phallus in lateral (right) view. B: the same in posterior view. C: distal end of phallus in lateral (right) view. D: the same in posterior view. *1:* phallic apodeme. *2:* sclerite in the dorsal wall of the phallocrypt; its posterior part has been broken off. *3:* phallus. *4:* ejaculatory duct; in C and D its distal part is shown shining through. In A the coarsely dotted line indicates the boundary between the phallus and the phallic apodeme.

posterior side of the harpago is somewhat concave. Its distal end is divided into a thicker lateral and a slenderer median branch.

In conformity with the fusion between the coxopodite and Segment IX no muscles are inserted on the former. The two ventral muscles of the inferior appendages have acquired connections with the phallus, the two dorsal ones are lacking. The flexor of the harpago originates from the median margin of the sclerite of the coxopodite. Its bands pass orally and laterally to become inserted laterally and proximally on the anterior side of the harpago. Its function probably is to rotate the harpago, moving the lateral edge of the latter backwards and inwards.

The undivided phallus (figs. 18, *13;* 20) has a very unusual shape. Including the phallic apodeme it falls into two parts: a thick proximal part (fig. 20, *1*) and a slender, upwards directed, hook-like distal part (*3*). The shape of the latter will appear from the pictures better than from descriptions. The proximal part attains its greatest thickness anteriorly and tapers gradually in a posterior direction. In transverse section it is approximately trapezoid (though with much rounded corners) with a narrower dorsal side and a broader ventral side. For the greater part of its circumference the phallocrypt is obliterated, Part *1* being almost exclusively of an apodemal character. Dorsally, only, a pocket stretches forwards almost to the anterior margin of Part *1*. The floor of the pocket is the narrow dorsal side of Part *1*, the roof forms a longitudinal fold. As mentioned above, two pairs of rod-like sclerites (issuing from the dorsal rods and the posterior corners of Segment IX, respectively) stretch into this pocket. Anteriorly they fuse to an unpaired sclerite (*2*), which joins the dorsal wall of the phallus. If the dorsal rods (fig. 19, *6*) are considered as paraproctal processes, it will be seen that in *Psychomyia* there is the same sclerotic connection between the ventral part of Segment IX, the paraprocts, and the phallus as in *Tinodes* (pp. 31 and 37).

The slender, upwards directed distal part (fig. 20, *3*) is very heavily sclerotized. Its broader and flattened base, however, is membranous laterally, but here, also, the dorsal as well as the ventral side is sclerotic. The ejaculatory duct opens distally on the beak-like apex, which — apart from the lumen of the duct—is solid. A large, distal part of the ejaculatory duct is sclerotized. — The distal part (*3*) probably is homologous with the tubes *4* in *Lype* (fig. 12, p. 20) and *6* in *Tinodes* (fig. 17, p. 36), and thus is to be considered a dorsal branch of the aedeagus. This means that the ventral aedeagal branch is entirely reduced.

There are two anterior phallic muscles. One is the ordinary anterior muscle, which originates laterally from the antecosta of Segment IX and is inserted distally and laterodorsally on the phallic apodeme. The other, much stronger, muscle is the anterior ventral muscle of the inferior appendages. It originates from the ventral part of the antecosta and from the greater part of the ventral side of Segment IX and is inserted distally and ventrally on the apodeme. Since the sclerotic connections between the phallus on one side, and Segment IX and the dorsal rods (figs. 18, *8—9;* 19, *5—6*) on the other must exclude any higher degree of retraction, the two muscles probably act as levator and depressor, respectively. As mentioned above, the posterior ventral muscle of the inferior appendage has also been included in the muscular apparatus of the phallus. The posterior phallic muscle and the aedeagal retractor are lacking.

Wormaldia occipitalis.

The same principle is seen as in the Psychomyidae: the dorsal part (approximately the fourth) of Segment IX is much reduced and intimately associated with Segment X. It is still continuous with the ventral part of the segment, however, and appears as an anterior marginal thickening (fig. 22, *2*) of Segment X, forming a dorsal

continuation of the antecosta on the ventral part of Segment IX. *In situ* it is concealed by the overlapping posterior border of Segment VIII.

Lateroventrally Segment IX (figs. 21, *7;* 22, *1*) attains a considerable length and projects into the posterior part of Segment VII. The length of the ventral side is reduced by an oral an anal indentation. The latter, however, is shallow. Owing to the reduction of the dorsal part of the segment a rounded, laterodorsal posterior corner and an upper edge rise.

Segment X (figs. 21, *8;* 22, *3*) has the shape of a thin scale, much attenuated

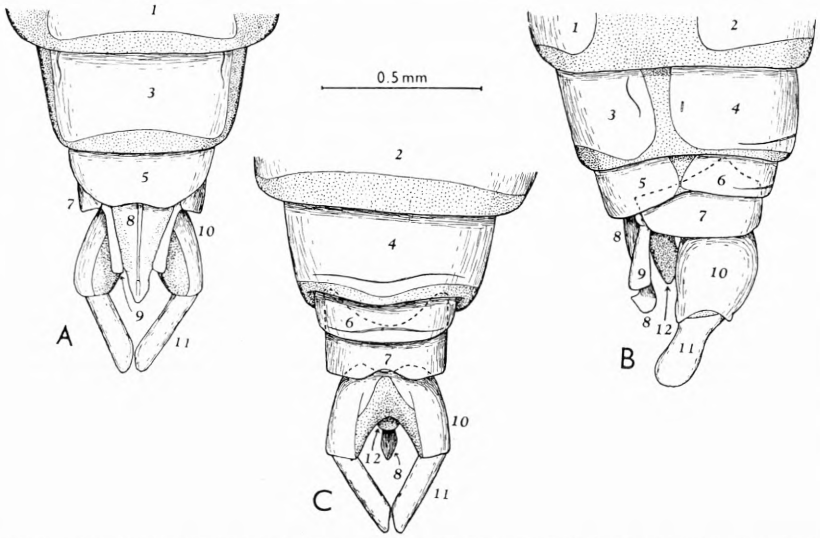

Fig. 21. *Wormaldia occipitalis.* Posterior end of abdomen in dorsal (A), lateral (right, B), and ventral view (C). *1:* anal end of Tergum VI. *2:* anal end of Sternum VI. *3:* Tergum VII. *4:* Sternum VII. *5:* Tergum VIII. *6:* Sternum VIII. *7:* Segment IX; in B and C the outline of its overlapped parts is shown by a broken line. *8:* Segment X. *9:* superior appendage. *10:* coxopodite; in C the ventral outline of its overlapped proximal end is shown by a broken line. *11:* harpago. *12:* phallus.

posteriorly, with a very convex dorsal side and a very concave ventral side. It encloses the phallus dorsally. Apart from the anterior and the posterior end a great, lateral part of the dorsal side is membranous. On the ventral side approximately the posterior half is sclerotized. On the dorsal side a little prominent longitudinal ridge (fig. 22, *4*) is seen. Posteriorly it grows narrower, and quite anally it is raised into a sagittally compressed process. It probably represents a reduced dorsal process.

The superior appendages (figs. 21, *9;* 22, *5*) are large and widened distally; in a lateral view the apex is obliquely cut off. The swollen proximal end medially is continuous with the sclerite of Segment X, so that the appendage is immovable in relation to the latter. On the dorsal side of the proximal end there is a short, broad, rounded longitudinal ridge. The upper edge of Segment IX overlaps the lateral side of this ridge, thus forming a sort of simple articulation.

The rather strong IX/X muscle originates laterally from the antecosta of Segment

IX and is inserted on Segment X at the angle between the segment itself and the superior appendage. The steeply ascendent (more than 45°) muscle must act as a depressor of Segment X (and the superior appendage). Its antagonist probably is the dorsal VIII/IX muscle, which as in *Psychomyia* (p. 40) is divided into two portions. The weaker lateral portion is inserted just anteriorly to the superior appendage. There is no paraproctal muscle.

The inferior appendages (figs. 21, *10—11;* 22 B) are very large, two-jointed and of a simple shape. The coxopodite (fig. 22, *7*) has a sclerotic lateral side and a membranous median side. The two coxopodites are united for approximately half of their length. The union, however, is largely membranous. It is only quite proximally that the common part of the two coxopodites is sclerotized, to the greatest extent dorsally. (The extreme proximal end of the two appendages thus forms an entire, sclerotic ring, the dorsal side of which is longer than the ventral side). The basal plate (*6*) is short and especially narrow. A narrow suture runs along the proximal margin of the appendages. At the posterior end of the basal plate it fuses with a broader, unpaired, longitudinal suture, and the suture thus formed covers the whole basal plate.

The harpago (*8*) is entirely sclerotized and somewhat sagittally compressed. Distally its median side is covered with close-set, short, but relatively very thick setae with rounded apices. Together, at a low magnification, they give the impression of a strong, dark brown thickening.

The anterior dorsal muscle originates lateroventrally from the antecosta (and partly from the surface) of Segment IX, and is inserted dorsally on the proximal margin of the appendage. It is ascendent and must act as a levator. The weaker posterior dorsal muscle acts as a depressor. The anterior ventral muscle, which also is a rather weak muscle, is inserted on the middle of the ventral membranous part of the coxopodites. Laterally to its insertion, but also on the membranous area, other muscle bands are inserted, which originate dorsally from the coxopodite, on the median margin of the sclerite, and which must represent the posterior ventral muscle. Their function—or rather the significance of their function—is obscure to me. The flexor of the harpago originates from the whole lateral side of the coxopodite as well as from the unpaired longitudinal suture of the basal plate and is inserted proximally on the median side of the harpago. It is the strongest muscle of the inferior appendage, and possibly it alone is responsible for their grasping function, since the coxopodites scarcely can be adduced (or abduced).

Including the phallic apodeme the phallus (figs. 21, *12;* 22 C) is composed of a proximal, very thick part (which may be called the bulb; fig. 22, *9*) and a distal, slender, and finger-like part (*10*). The phallocrypt is shallow except on the dorsal side (s. str.), where it is very deep, stretching as a pocket almost to the base of the bulb. (I have been unable to make out the boundaries with absolute certainty). The lateral and the ventral sides of the bulb thus have an apodemal character. In the bulb the ejaculatory duct has a very eccentric position, being shifted towards the dorsal side. It has a very strong musculature, comprising both circular and longitudinal

elements, which entirely fills up the bulb. The muscle layer of course is thickest on the ventral side. The weaker longitudinal muscles lie externally to the circular ones.

The distal, finger-like part of the phallus is membranous to its greatest extent, the extreme basal end, only, being sclerotized. In the state of repose more than the

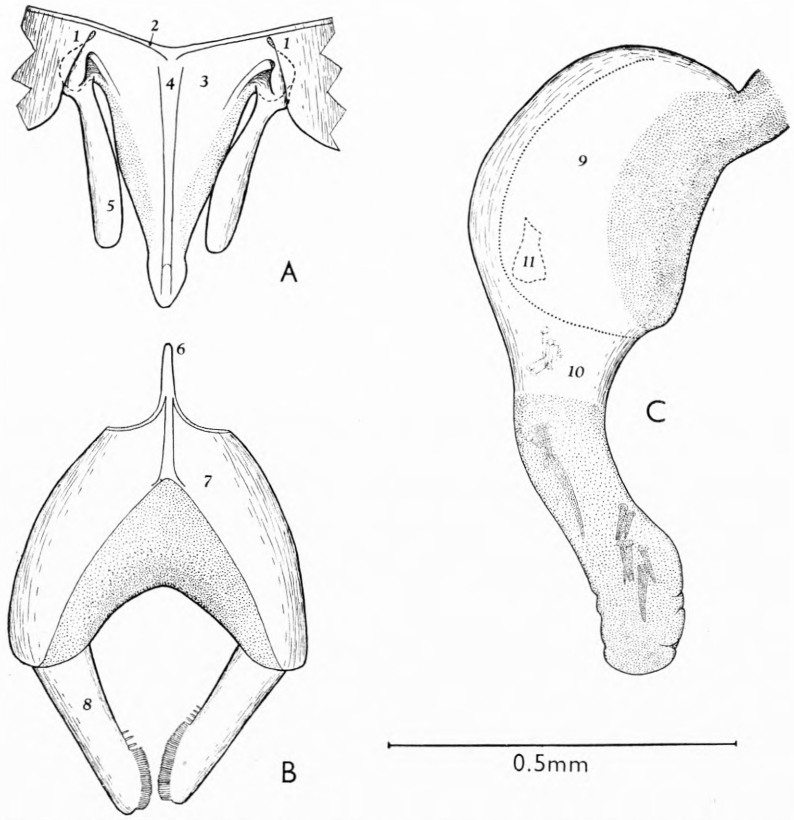

Fig. 22. *Wormaldia occipitalis*. A: Segment X and adjacent parts of Segment IX in dorsal view. B: inferior appendages in dorsal view. C: phallus in lateral (right) view. *1:* (ventral part of) Segment IX. *2:* antecosta, representing the dorsal part of Segment IX. *3:* Segment X and *4:* its dorsal ridge. *5:* superior appendage. *6:* basal plate of inferior appendages. *7:* coxopodite. *8:* harpago. *9:* phallic apodeme. *10:* phallus. The boundary between *9* and *10* is indicated by a coarsely dotted line. *11:* sclerite at the bottom of the endotheca (shining through).

distal half is invaginated into the more proximal part, and must be considered as an endotheca. In all specimens examined this was thrown into quite irregular folds, and hence its outline is not shown in the figure. The ejaculatory duct opens into the bottom of the endotheca, flanked by a pair of small sclerites (*11*), which may be rudiments of the aedeagus, and on which the aedeagal retractor is inserted. This muscle originates on the dorsal side of the bulb and causes an interruption of the circular musculature of the ejaculatory duct (which thus rather should be termed a horseshoe musculature). In (some) species of *Chimarrha* Steph. and *Thylakion* Barn. parameres

have been described (BARNARD 1934, pp. 382—84). The slerites (*11*) mentioned above may, therefore, represent rudimentary parameres (see also p. 12).

On the wall of the endotheca four groups of very strong setae are seen. The number of setae was counted on three specimens. (The group which is seen most anteriorly on the invaginated endotheca is mentioned first):

2—11	1, very large	3—6	1, large
4—10	ca. 6	3—6	1, large

KIMMINS (1953c) has called attention to these setae ("spines") as a means to distinguish the species and subspecies of *Wormaldia*. According to this the Cimbrian subspecies is *W. occipitalis occipitalis* Pict.

The anterior phallic muscle originates from the most dorsal part of the antecosta of Segment IX and on the lateral half of the "antecosta of Segment X" (fig. 22 A, 2). The posterior muscle originates from the rounded posterior corner of Segment IX. The chief function of the two muscles probably is to give the phallus a nodding movement.

Polycentropus flavomaculatus.

In this form, also, the same principle is found as in the Psychomyidae: the dorsal part of Segment IX is much reduced and intimately associated with Segment X.

The ventral part of Segment IX (fig. 23, *5;* in the following simply called Segment IX) is a rather long, sclerotic half-ring. It is longest on the lateral side. On the ventral side a deep, oral indentation reduces the length to less than half of that of the lateral side. Besides an anterior and a posterior edge an almost horizontal dorsal edge is seen. From a morphological point of view the latter is a part of the anterior edge: it is followed by the line of union between Segments VIII and IX, and the antecosta is continued upon it. The greater part of Segment IX is overlapped by Segment VIII, though the segment only to a small extent has an apodemal character.

The structure formed by the union of the dorsal part of Segment IX with Segment X (figs. 23, *6—8;* 24; in the following simply called Segment X) is trilobed. Its most oral part, however, is undivided, and membranous except for a pair of transverse, faintly defined sclerites lying in front of the dorsal (or median) half of the side-lobes (and in fig. 23 concealed by Segment VIII). The dorsal VIII/IX muscles are inserted on these sclerites, which thus, no doubt, represent part of the dorsal side of Segment IX. The muscle in question probably is homologous with the lateral portion of the VIII/IX muscle in *Psychomyia* (p. 40), whereas the median portion is lacking.

The middle lobe (fig. 23, *6*) of Segment X forms a large membranous tube, posteriorly carrying the anus (fig. 24, between the two *3—4*s), the upper lip of which projects much beyond the lower, which is slightly bilobed. On the ventral side of the tube there is a longitudinal pair of strong, rod-like sclerites (fig. 24, *3*). On each

sclerite there is a sharp, longitudinal ridge, which anally projects into a downwards, outwards, and forwards directed hook (figs. 23, *10;* 24, *4*). The sclerites, no doubt, are to be considered the paraprocts (cp. p. 7), and the hooks consequently as paraproctal processes. Accessory copulatory processes on the paraprocts possibly are an old heritage in the Trichoptera. In *Rhyacophila gregoryi* Ulm. Ulmer (1932—33, p. 41) describes "Appendices präanales" in the shape of "S-förmig geschwungene und gedrehte Chitinstäbe, die sich kreuzen." They should probably be interpreted in this way. Something similar is seen in *Rh. montana* Carp. (Ross 1944, p. 33), in *Agapetus cataractae* Ulm. (Ulmer 1951, p. 55), and in some species of *Synagapetus* (Kimmins

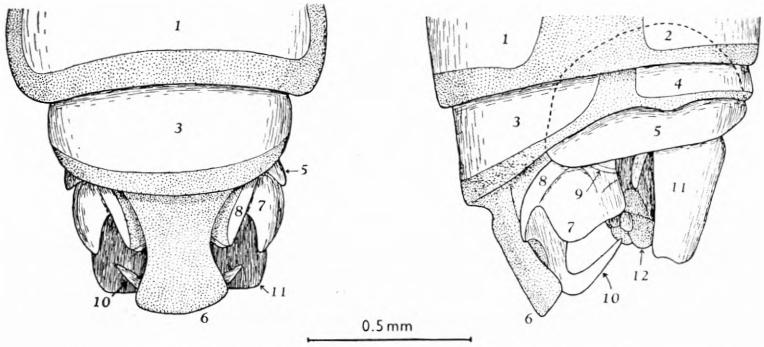

Fig. 23. *Polycentropus flavomaculatus.* Posterior end of abdomen in dorsal and in lateral (right) view. *1:* posterior part of Tergum VII. *2:* posterior part of Sternum VII. *3:* Tergum VIII. *4:* Sternum VIII. *5:* Segment IX. *6:* middle lobe of Segment X. *7:* superior appendage. *8* and *9:* see pp. 47–38. *10:* paraproctal process. *11:* inferior appendage. *12:* phallus.

1953b). In the two latter genera, however, the paraprocts have fused with the sclerite of Segment X (Cp. also p. 21 and pp. 146—47, 150—52). — Between the two sclerites the membranous ventral side is thrown into a longitudinal fold. Their ridges enclose the dorsal side of the phallus.

The side-lobes (figs. 23, 7; 24, *1*) are shorter than the middle lobe. Ventrally (= laterally) their bases are overlapped by the posterior edge of Segment IX. The convex lateral (= dorsal) side is sclerotized, except at the ventroproximal corner and along the dorsal edge, which latter has partly fused with the middle lobe. The strongly concave median side is entirely sclerotized and only by a narrow membranous stripe separated from the paraproctal sclerite (fig. 24, *3*). Proximally the ventral edge of the side-lobe projects below the narrow anterior end of the paraproctal sclerite, though a true articulation is not formed. By a distal notch, which is larger than the notch between the middle lobe and the side lobe, the latter is divided into a narrow dorsal branch and a several times as broad ventral branch. Along the dorsal half of the proximal margin of the side lobe there runs an external ridge (fig. 23, *8*), which continues on the dorsal branch and eventually forms a simple articulation with a process (fig. 24, 5) on the paraproctal sclerite. At the posterior corner Segment IX has an in-

wards directed point, which forms a simple articulation with the ridge *8*, lying anteriorly to the latter. Along the ventral half of the proximal margin there is a suture (figs. 23, *9;* 24, *2*) and a corresponding internal ridge.

The very strong IX/X muscle originates on the whole lateral part of the antecosta of Segment IX and is inserted on the side-lobe, partly—and especially—on the internal ridge corresponding to the suture *9* (fig. 23; fig. 24, 2), partly on the proximal end of the median side. Another, sagittally compressed muscle originates from the antecosta on the dorsal edge of Segment IX and is inserted on the median margin of the paraproctal sclerite. This muscle, no doubt, is an intersegmental muscle stretching between Segments IX and XI (the paraproct). In remote ancestors of the Insecta it probably had its anterior insertion on the antecosta of Sternum X. As a result of the reduction of the latter (p. 7), this insertion must have shifted to Segment IX. An undoubtedly homologous muscle, originating on the sternal region of Segment IX and inserted on the paraproct, is found in *Gryllus* (Snodgrass 1933, p. 69). Examples of intersegmental muscles passing over one or two segments are found also in the anterior end of the abdomen of insects in connection with reduction of terga and sterna.

The IX/X muscle possibly acts as a depressor of Segment X as a whole. Due to the articulation (fig. 24, *5*) between the side-lobe and the paraproct, part of the muscular power is transmitted to the paraprocts causing a rotation of the latter, by which the two hooks *4* (fig. 24) are adduced. This movement is accentuated by the paraproctal muscle. The antagonist to the IX/X muscle probably is the dorsal VIII/IX muscle, which—as mentioned above—has its insertion dorsally to the articulation between Segment IX and the side-lobe.

It seems an obvious conclusion that the side-lobes represent the superior appendages, and probably their ventral branch represents this appendages. A comparison between the origins of the posterior phallic muscle in *Polycentropus* (see below) and in *Holocentropus* (p. 53) indicates that the dorsal branch (fig. 23, *8*) belongs to Segment X itself. In one respect the superior appendage of the Polycentropidae differs very much from those of other Trichoptera: they carry the insertion of the IX/X muscle. An advance towards this condition perhaps is found in *Wormaldia*, in which the insertion of the IX/X muscle is in the angle between Segment X itself and the superior appendage (p. 43).

The inferior appendages (figs. 23, *11;* 24) are one-jointed. The median side is very concave. A distal notch divides the appendages into a dorsal (fig. 24, *7*) and an almost three times as long ventral branch. The dorsal branch has an obliquely cut off and somewhat concave distal edge. The median corner of the latter is protracted into a small, downwards bent tooth, which meets (or almost meets) the apex of another, transverse and lamella-like, tooth on the median side of the ventral branch. Proximally on the ventral side of the upper edge of the appendage there is a molar-like tooth (*8*), which can be opposed to the corresponding structure on the other appendage. Proximally to the "molar" the median side is not concave, but flat, and eventually united with that of the other appendage. The basal plate (*6*) takes the shape

of a small, forwards projecting pocket, on the anterior end of which there is a small, ridge-like, vertical apodeme.

The inferior appendages have only two pairs of extrinsic muscles. The anterior ventral muscle is inserted on the proximal part of the median side. The other is a slender muscle originating anally from Segment IX and inserted on the apodeme of the basal plate. The origin of this muscle is lateroventral, far removed from the origin of the posterior phallic muscle, and it thus might be concluded that it is the posterior ventral one. Since, however, the latter generally originates from the coxopodite, I find it most likely that the posterior muscle present in *Polycentropus* is the dorsal one. The two muscles probably are an adductor and an abductor, respectively, but the possibility also exists that they may act as a levator and a depressor. The flexor of the harpago is of course lacking.

The phallocrypt is very shallow, forming little more than a circular furrow. The phallic apodeme (fig. 25, 2) is large and thick. In a dorsal or ventral view it appears almost globular, in a lateral view it approaches the shape of a vertical cylinder, though with a pronounced, rounded bend on the anterior (morphologically: dorsal) side; for the greater part the phallic apodeme is membranous or at least very slightly sclerotized. It is only the (forwards directed) dorsal side which is (really) sclerotic. By an obtuse-angled bend the phallus is separated from the apodeme. (The bend, however, does not coincide exactly with, but is situated a little distally to, the boundary between apodeme and phallus).

The phallus (figs. 23, *12;* 25) is short and thick, straight, and straight backwards directed. It is formed chiefly by the phallobase (fig. 25, *3*), which is approximately cylindrical, though with a pair of laterodorsal impressions, leaving a proximally broader, distally narrower longitudinal keel, which fits into the interspace

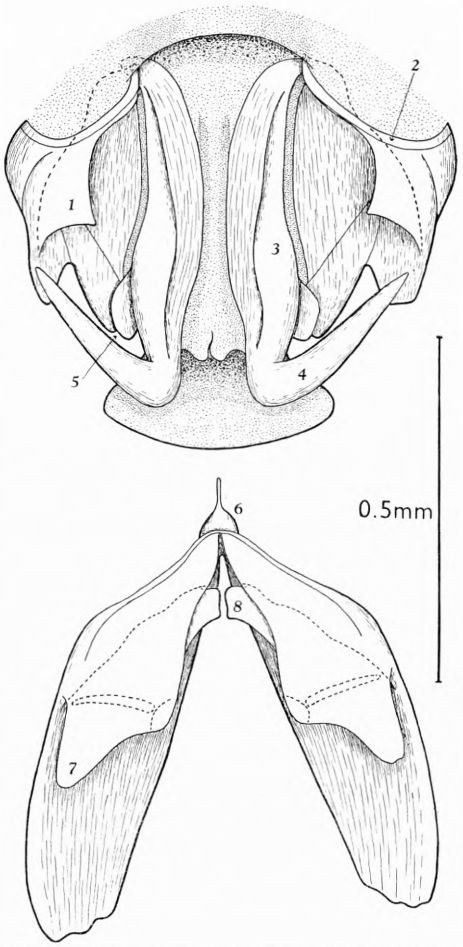

Fig. 24. *Polycentropus flavomaculatus*. Above: Segment X in ventral view. Below: inferior appendages in dorsal view. *1:* ventro-distal corner of superior appendage. *2:* proximal suture on superior appendage (= fig. 23, *9*). *3:* paraproctal sclerites; between their anterior ends the entrance to the phallocrypt, between their posterior ends the anus is seen. *4:* paraproctal process. *5:* articulation between the superior appendage and the paraproctal sclerite. *6:* basal plate of the inferior appendages. *7:* dorsal branch of the inferior appendage. The lamella-like tooth on the median side of this appendage is shown shining through by a broken line. *8:* molar-like tooth on upper edge of the inferior appendage.

between the paraproctal sclerites (fig. 24, *3*). The greater part of the phallotheca is sclerotized, but the sclerite has three distal, membranous indentations: an unpaired dorsal one (= the dorsal lobe described below) and a pair of lateroventral ones (on the ventral lobe described below). The distal end of the phallobase is divided into six lobes: two unpaired ones and two pairs. The unpaired ventral lobe (fig. 26 B, *4*) approximately covers the ventral half of the circumference and contains the lateroventral indentations described above. Dorsally it overlaps the base of the small lateral lobe (A, B, *3*), which is prominent and auricular, and which again overlaps the ventral edge of the laterodorsal lobe (*2*). This lobe in its turn overlaps the lateral edge of the unpaired dorsal lobe (*1*). The latter is entirely membranous (= the dorsal indentation) and has a slightly concave distal edge. The paired lobes are sclerotized on the inside, too.

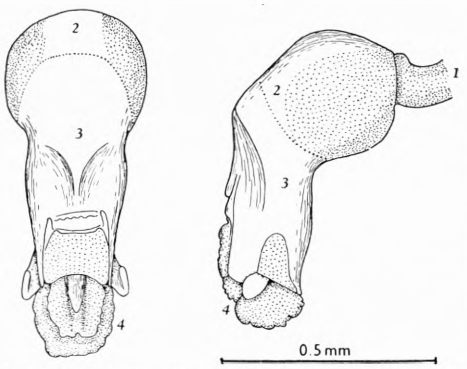

Fig. 25. *Polycentropus flavomaculatus*. Phallus in dorsal and in lateral (right) view. *1:* ejaculatory duct. *2:* phallic apodeme. *3:* phallobase. The boundary between *2* and *3* is indicated by a coarsely dotted line. *4:* aedeagus.

Ventrally the endotheca is very shallow. In a dorsal direction its depth increases rapidly, so that dorsally it is very deep.

The aedeagus (fig. 25, *4*) is much shorter than the phallobase. Those parts which in the state of repose are seen externally are chiefly membranous. By a deep slit the aedeagus is divided into an upper (fig. 26 A, B, *5*) and a lower lip (*6*). The latter is broader and projects farther backwards than the former. Proximally the lateral and the ventral sides of the upper lip (fig. 26 C—E) are sclerotized. The length of the sclerite increases in a ventral direction, and on the middle of the ventral side its posterior margin is produced into a narrow, tongue-like extension (*10*), which reaches the slightly bilobed distal end of the lip. On the ventral side the sclerite has a narrow, but very deep, unpaired, oral indentation. The wing-like parts of the sclerite (*9*) which flank this indentation, may be largely apodemal. Just behind the indentation there is a high and sharp transverse ridge. On the lateral side there runs along the distal margin of the sclerite a deep, descendent furrow, which in transverse section is approximately semicircular. On the ventral side the right and the left furrow are separated by a longitudinal ridge, which together with the transverse ridge mentioned above forms a stellate figure.

The ejaculatory duct opens proximally on the dorsal side of the upper lip. Its distal part has the shape of an elongate pitcher (*7*) and is sclerotized on the lateral and ventral sides as well as proximally on the dorsal side. Ventrally the sclerotization projects posteriorly as a tongue-like sclerite (*8*), which lies in a trough-like depression on the dorsal side of the upper lip. The anterior end of the sclerite *8* is continuous with the sclerite *9*. (This means that the proximal end of the upper lip is encircled by an annular sclerite). On the ventral side of the sclerotization of the

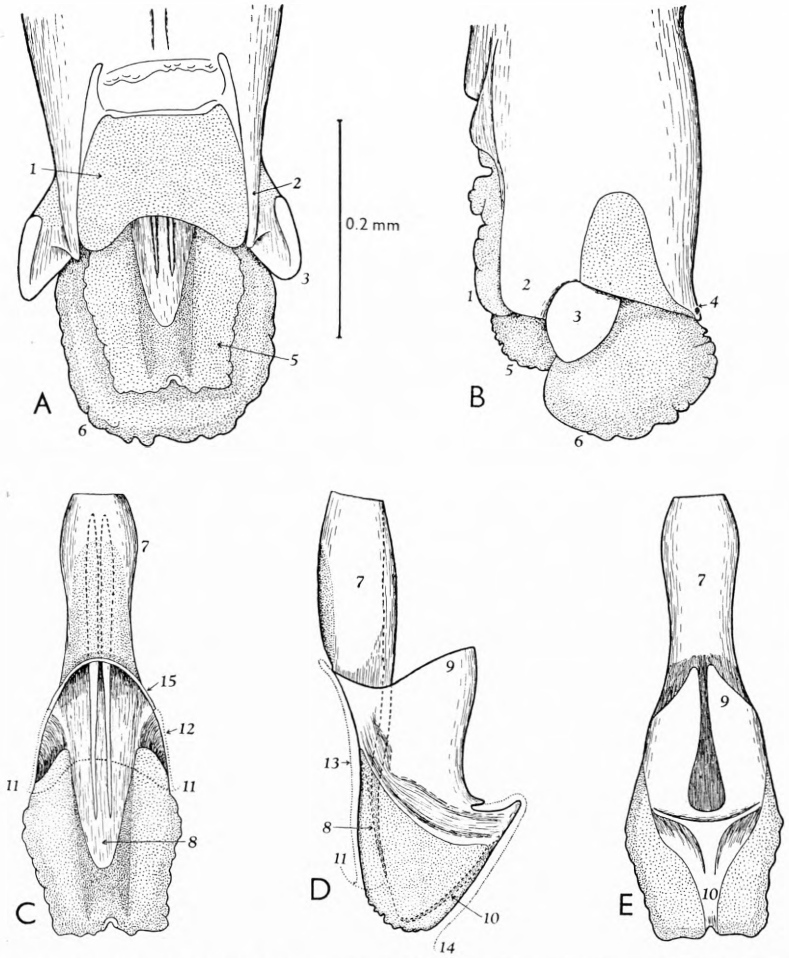

Fig. 26. *Polycentropus flavomaculatus;* phallus. A and B: distal end in dorsal (A) and in lateral (right, B) view. C—E: dorsal branch of the aedeagus in dorsal (C), lateral (right, D), and ventral view (E). *1—4:* distal lobes of phallobase; *1:* dorsal, *2:* latero-dorsal, *3:* lateral, *4:* ventral. *5:* dorsal, and *6:* ventral branch of the aedeagus. In A the aedeagus protrudes more than in B. *7:* distal part of the ejaculatory duct. *8:* distal, tongue-like extension of the sclerite of the ejaculatory duct; (in D shown shining through). *9:* proximal wing of aedeagal sclerite. *10:* ventro-distal end of same; (in D shown shining through). The coarsely dotted lines *11—14* indicate: *11:* distal edge of dorso-distal lobe of phallobase (fig. A, *1*); *12* and *13:* section through dorsal part of endotheca (= inside of dorso-distal lobe); *14:* section through dorsal side of ventral branch of the aedeagus. *15:* cut edge along the line of union between dorso-distal lobe of phallobase and dorsal branch of the aedeagus.

ejaculatory duct there is a pair of strong longitudinal ridges, which continue on the sclerite *8*.

The account of the ejaculatory duct given above perhaps is not quite correct. Within the "pitcher" (*7*) an extremely delicate tube is seen, at its entrance in the "pitcher" covered with long, very slender, backwards directed spinules, which form a sort of weel. Two explanations are possible: Either the delicate internal tube is the

true ejaculatory duct, and the "pitcher" is an apodeme issued from the sclerite of the upper lip. Or the delicate tube is an artefact, due to a delimination of the epicuticle. I am unable to decide between the two possibilities.

The lower lip is entirely membranous and partly encloses the ventral side of the upper lip.

The part of the phallic apodeme (fig. 25, *2*), which lies ventrally to a horizontal plane through the lower side of the phallus is filled up by a strong circular musculature belonging to the ejaculatory duct, whereas the part which lies dorsally to this plane is filled up by the strong aedeagal retractor. The latter muscle is inserted on the sclerite of the upper lip. The upper lip, no doubt, can be entirely everted by blood-pressure, the dorsal, membranous part of the endotheca as well as the cleft between the upper and the lower lip being stretched out.

To me there is little doubt that the upper and the lower lip are homologues of the dorsal and the ventral branch, respectively, of the aedeagus in *Rhyacophilidae* (pp. 19 and 24).

The posterior phallic muscle is very strong. Only a small number of its bands originate from the posterior corner of Segment IX; the vast majority originate from the ridge *8* (fig. 23) on the side-lobe of Segment X. It is inserted on the vertical part of the dorsal side of the phallic apodeme. The weak anterior muscle originates latero-ventrally from the antecosta of Segment IX and is inserted lateroventrally at the boundary between the phallic apodeme and the phallus. Since the shape of the phallic apodeme must prevent any higher degree of protraction, the chief function of the two muscles probably is to give the phallus a nodding movement.

Holocentropus dubius.

The relationship with *Polycentropus* is unmistakable, though there are considerable differences. The terms Segment IX and Segment X will be used in the same sense as in *Polycentropus flavomaculatus.*

The anterior edge of Segment IX (figs. 27, 3; 28, *1—2*) has not the bend seen in *Polycentropus*, but describes an even curve; in a lateral view Segment IX thus tapers gradually towards the rounded dorsal end. Along the whole anterior edge there is a large apodemal area (fig. 28, *1*). The posterior edge is bent inwards.

The membranous middle lobe (figs. 27, *4;* 28, *3*) of Segment X is very much reduced. At a first glance it appears only as small papilla carrying the anus. A closer examination, however, reveals that it stretches as a fine fold, *in situ* concealed by the overlapping posterior border of Segment VIII, to the base of the superior appendage (the side-lobe). The dorsal VIII/IX muscle is inserted on this fold. (Its most lateral bands, however, on Segment IX). Since the fold is very narrow, the muscle, no doubt, acts upon the sclerite in the genital chamber described below.

A very strong, unpaired sclerite lies in the dorsal part of the genital chamber (see fig. 27). It is rather concave, and its ventral edge projects as an elevated keel over

the ventral part of the genital chamber. Dorsally the sclerite has a deep, V-shaped indentation, the entrance to the phallocrypt, which dorsally is limited by the membranous middle lobe of Segment X. The edges of the indentation are bent much backwards, so that there arises a sort of trough (fig. 28, *4*), which—in a ventral view—has a distal V-shaped notch. The corners which flank the indentation are protracted into a pair of slender, entirely sclerotized horns (figs. 27, *7;* 28, *5*), which are backwards directed and downwards curved. The lateral corners of the sclerite are cut off vertically, as it were, leaving small membranous areas, in which the superior appendages are implanted.

The superior appendages (figs. 27, *5;* 28, 7). Almost the proximal half of the

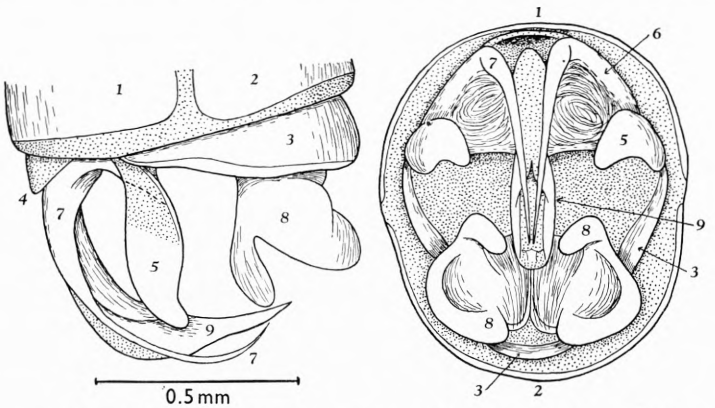

Fig. 27. *Holocentropus dubius*. Posterior end of abdomen in lateral (right) and in posterior view. *1:* posterior end of Tergum VIII. *2:* posterior end of Sternum VIII. *3:* Segment IX. *4:* middle lobe of Segment X. *5:* superior appendage. *6:* external ridge on the sclerite of the genital chamber. *7:* paraproctal process. *8:* inferior appendage. *9:* phallus.

lateral side is membranous. Quite proximally, however, there is a sclerotized stripe, which ventrally, but not dorsally, is continuous with the sclerotization of the median side. The distal part of the lateral side is sclerotic. The greater, distal part of the median side is membranous. Proximally there is a strong sclerotization, which is continuous with the sclerite of the genital chamber.

Between the base of the superior appendage and the horn 7 (fig. 27) the margin of the sclerite in the genital chamber is thickened to an external, rounded ridge (figs. 27 and 28, *6*). On the inside of the sclerite another short, but strong ridge is seen. It is placed lateroventrally at the base of the horn and runs in the direction from medially and dorsally to laterally and ventrally, almost perpendicularly to the entrance to the phallocrypt. From this internal ridge the posterior phallic muscle originates, and the paraproctal muscle is inserted on it (see below).

On the sclerite of the genital chamber the following, less important structures are seen: Lateroventrally on the base of the horn (between the numbers *4* and *5* in fig. 28) a backwards directed, conical, and very slender peg, ca. 60 μ long, distally

carrying a minute (13.5 µ), but relatively thick seta. Just medially to the superior appendages there is a low, ca. 45 µ broad node, which carries 3—5 yellow setae; (in the figs. concealed by the superior appendages).

A narrow suture runs along the posterior edge of Segment IX (see fig. 28, 2). The widened dorsal end of this suture joins the antecostal suture at the boundary of the apodemal part (*1*). (The two sutures enclose a small, triangular, membranous area between them). Eventually the antecosta bends medially and forms a simple

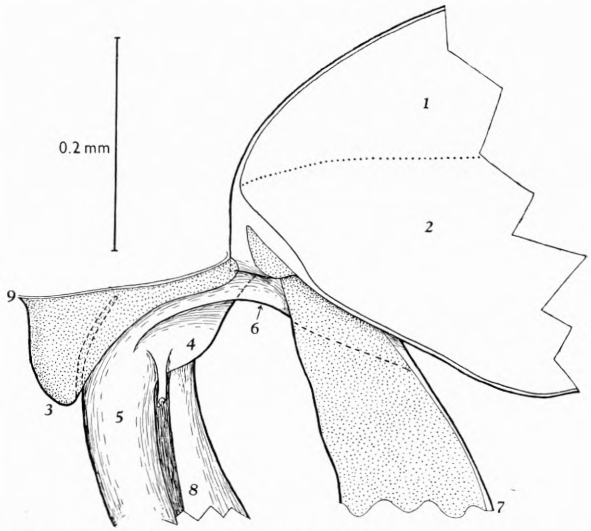

Fig. 28. *Holocentropus dubius*. The figure shows the relations between Segments IX and X; lateral (right) view. *1:* apodemal and *2:* non-apodemal part of Segment IX. *3:* middle lobe of Segment X. *4:* ventral, sclerotized lip of entrance to phallocrypt. *5:* paraproctal process; the greater, distal part has been broken off. *6:* external ridge on sclerite of genital chamber (= fig. 27, *6*). *7:* superior appendage; like *5*. *8:* phallus; like *5*. *9:* cut edge (the connection between Dorsum VIII and the middle lobe of Segment X).

articulation with the sclerite of the genital chamber. The line through the left and the right articulation is the axis of movement for this sclerite.

The very strong IX/X muscle originates from the lateral part of the antecosta of Segment IX and is inserted ventrally on the proximal margin of the superior appendage, partly by means of a leaf-like tendon, to the oral (or dorsal) side of which the muscle bands are attached. Another, weaker, fan-shaped muscle originates from the dorsal part of the antecosta of Segment IX and is inserted on the lateroventral end of the internal ridge on the sclerite of the genital chamber, described above. This muscle has the same position in relation to the IX/X muscle as has the paraproctal muscle in *Polycentropus* (p. 48) and thus, no doubt, is homologous with the latter.

The horns 7 (fig. 27) in *Holocentropus* obviously are homologous with the hooks *4* (fig. 24, p. 49) in *Polycentropus*, and thus are paraproctal processes. The relation between the horns and the sclerite in the genital chamber, as well as the insertion of the paraproctal muscle (see above) and the origin of the posterior phallic muscle (see

above and below), show that the sclerite in question in *Holocentropus* has arisen by fusion of the paraproctal sclerites and the rods *8* (fig. 23, p. 47) in *Polycentropus* into one unpaired sclerite.

The IX/X muscle moves the sclerite of the genital chamber and thus depresses the superior appendage and the horn. Its antagonists are the dorsal VIII/IX muscle and the paraproctal muscle.

As in *Polycentropus* the inferior appendages (fig. 27, *8*) are one-jointed and

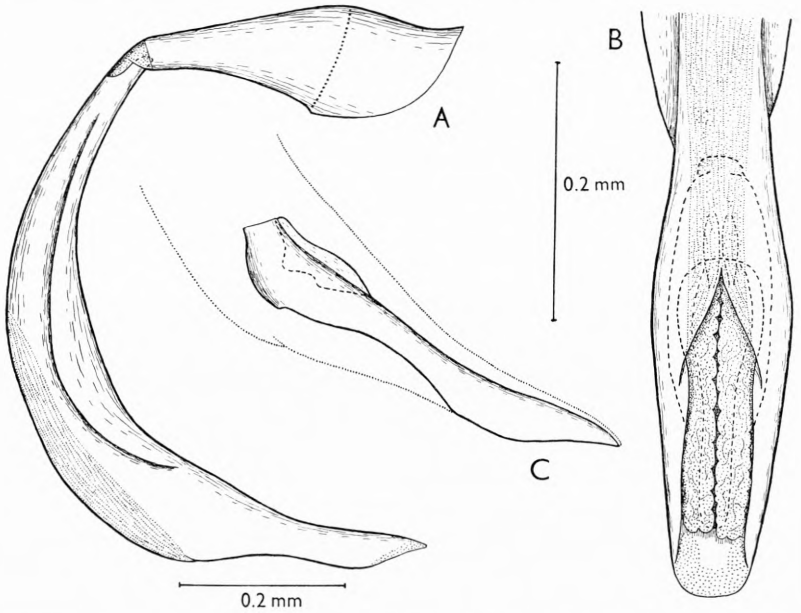

Fig. 29. *Holocentropus dubius*. A: phallus in lateral (right) view. B: distal end of phallus in dorsal view. C: sclerite of the ejaculatory duct and its distal extension in lateral (right) view. Coarsely dotted lines in A indicate the boundary between the phallic apodeme and the phallobase, in C the outline of the distal end of the phallus. Broken lines in B indicate the outline of the sclerite of the ejaculatory duct, in C the dorsal outline of the ventral thickening on this sclerite.

divided into a dorsal and a ventral branch. They have, however, a simpler shape than in *Polycentropus*. Their musculature is developed exactly as in this genus.

The phallus (figs. 27, *9;* 29) is divided into two parts, separated by a membranous articulation. The basal part is conical and very much attenuated towards the distal end. It is completely lowered into the deep phallocrypt, and in situ it has an almost vertical position. (Its longitudinal axis is parallel to the anterior edge of Segment IX). Proximally it continues as a strong phallic apodeme, which dorsally is two and a half times as long as ventrally. The slender distal part is club-shaped and curved rather much downwards. Its thin proximal end lies within the phallocrypt. On the lateral sides there is a pair of sclerotic wings, which together with the dorsal side form a pair of gutters receiving the horns 7 (fig. 27). These horns thus serve as a phallus-

guide. A large, distal part of the dorsal side is membranous with fine longitudinal wrinkles. The distal end itself is formed like a grocer's sugar spoon. The ejaculatory duct opens anteriorly at the bottom of the "spoon". As in *Polycentropus* the distal part of this duct is sclerotic, and as in *Polycentropus* there is a pair of longitudinal ridges on the ventral wall. The sclerite of the ejaculatory duct is produced into a pair of rods lying on the inside of the "spoon" and distally united with the main sclerite of the phallus. Distally the two rods are united also with each other and thus enclose a membranous area at the bottom of the "spoon". A pair of membranous, much wrinkled longitudinal folds rises from this area (in fig. 29 B they conceal the sclerotic rods). The space between these folds functionally continues the ejaculatory duct almost to the apex of the phallus. The extreme distal end of the phallus seems to be membranous or at least very feebly sclerotized, though rigid.

The same picture is seen as in *Polycentropus* (p. 51): Within the sclerotic part of the ejaculatory duct there is an extremely delicate tube, covered with fine, pale spinules. Anteriorly the latter attain their greatest length and form a sort of weel.

The rather weak aedeagal retractor originates from the dorsal side of the basal part and is inserted ventrally on the proximal end of the distal part. The insertion of this muscle shows that the distal part is the aedeagus, and the proximal part the phallobase. The endotheca has been obliterated. The similarity between the aedeagus in *Holocentropus* and the upper aedeagal lip in *Polycentropus* fig. 26 A, B, *5;* C) is so great that the two structures, no doubt, must be considered homologous. This means that the lower lip has been entirely reduced in *Holocentropus.*

As mentioned above, the posterior phallic muscle originates from the internal ridge of the sclerite in the genital chamber. It is inserted on the dorsal side of the phallic apodeme. The anterior muscle originates lateroventrally from the antecosta of Segment IX and is inserted ventrally on the proximal edge of the phallic apodeme. Owing to the shape of the phallobase and of the entrance to the phallocrypt, a protraction is impossible. The two muscles must have the same function, viz. a levation of the phallic apodeme, which will result in a slight protraction of the aedeagus.

Within the phallic apodeme the ejaculatory duct is provided with a strong circular musculature.

Ecnomus tenellus.

The length of Segment VIII is somewhat reduced, especially on the ventral side. In some of the preserved specimens the segment was withdrawn so much into Segment VII that the whole ventral side was concealed, and the dorsal side seen only as a narrow transverse area.

The structure which at a first glance might be supposed to represent Segment IX (figs. 30 and 31, *1—2*) in reality is of a composite nature and has arisen by fusion of Segments IX and X, or Segment IX and parts of Segment X. In the following it will for the sake of simplicity be called Segment IX. It is rather long and somewhat

sagittally compressed. By a pair of deep, longitudinal clefts, stretching anteriorly beyond the posterior margin of Segment VIII, it is divided into an upper (*1*) and a lower lip (*2*), both entirely sclerotized on the external side. Continuing the cleft there is a membranous area, so that the sclerotic connection between the two lips is restricted to a narrow bridge along the anterior margin of the segment. The antecosta continues without interruption from the upper to the lower lip. Orally as well as anally the lower lip projects much beyond the upper lip. There is an oral indentation both on the dorsal and the ventral side. The former is long and broad and evenly curved, the ventral indentation is shorter and narrower, V-shaped.

Anteriorly the ventral edge of the upper lip is very broad and has a broad, rounded longitudinal furrow (fig. 31 B, *8*). It might be supposed that this furrow was destined to receive the dorsal edge of the lower lip. The latter, however, is situated laterally to the former. From the furrow the posterior phallic muscle originates. On the lower lip there is a strong, unpaired longitudinal suture, which on a superficial view makes this lip look like a pair of basal joints of the inferior appendages.

The genital chamber is very deep, its anterior end being situated at the same level as the anterior end of the cleft mentioned above. Owing to the same cleft its wall is incomplete laterally. Quite dorsally in the genital chamber, just below the posterior edge of Segment IX, the anus is found, bounded ventrally by a membranous, bilobed lip. Beneath this, again, on the posterior part of the roof of the genital chamber, there is a pair of rodlike sclerites (figs. 31, *7;* 32 C), each bearing a slender, finger-like, sclerotic process, which points backwards, downwards, and a little outwards. Distally the process carries three short, but strong setae.

The superior appendages (figs. 30 and 31, *3*) are very large. In a lateral view they taper towards the rounded distal end. Dorsally and ventrally the posterior edge of Segment IX overlaps the base of the appendage a little; in the middle the lateral side of the latter is continuous with the upper lip of Segment IX. On the proximal part of the appendage a low keel is seen. Dorsally to this keel the lateral side is slightly concave. Otherwise the appendage forms approximately a quarter of a cylinder, the concavity of which faces downwards and inwards. This shape is especially pronounced distally, where the two superior appendages form a sort of an incomplete sheath for the inferior appendages (*4*). Proximally, however, the median side is somewhat swollen, and there it carries a large node near the ventral edge (fig. 31 B). Like the lateral side the median side of the appendage is sclerotized. The upper part of the proximal edge of the median sclerotization forms a simple articulation with the lateral edge of the sclerite *7* (fig. 31 B), dorsally to the finger-like process. — Distally on the edge of the appendage there is a group of very close-set, short, but extremely strong, medially directed setae. Along the dorsal edge there is a row of more scattered, strong, inwards directed setae, of which the distal ones are the shortest and strongest. On the basal node some few, rather short, but strong setae are seen. The other setae on the appendage are much smaller.

The inferior appendages (figs. 30 and 31, *4;* 32, *6*) are one-jointed. Proximally

the two appendages are connected, though by membrane only: On the ventral side membranous areas are seen both laterally and medially, and on the dorsal side the sclerite of the appendage is connected with the basal plate by a narrow lateral bridge only. (After all there thus is a sclerotic connection between the two appendages

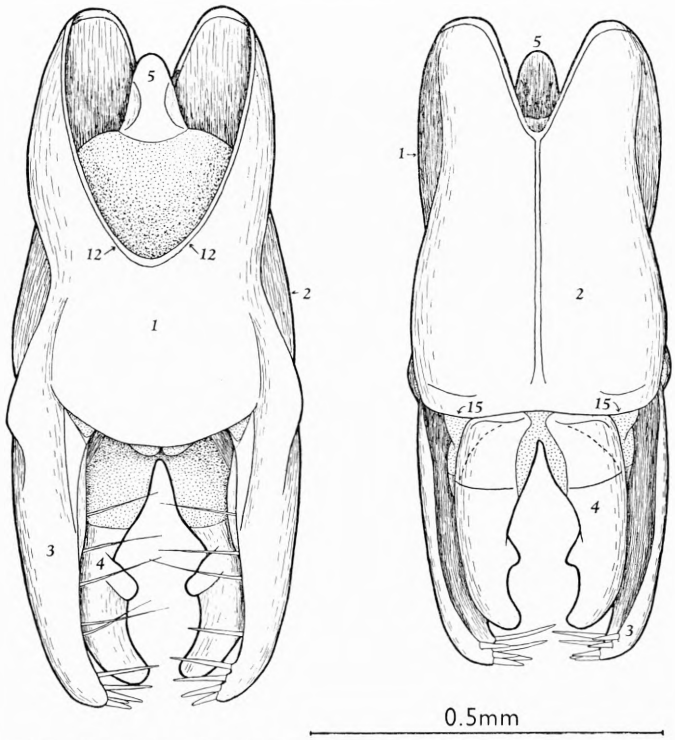

Fig. 30. *Ecnomus tenellus*. Segments IX and X in dorsal and in ventral view. *1:* dorsal lip of the genital segments; in the dorso-oral indentation the membranous roof of the genital chamber is seen from the haemocoelic side. *2:* ventral lip of genital segments. *3:* superior appendage. *4:* inferior appendage. *5:* phallic apodeme; in the figure on the right its proximal opening is seen. *12:* the arrow indicates the dorsal limit to the origin of the IX/X muscle. *15:* the arrow indicates the ventral limit to the origin of the posterior dorsal muscle of the inferior appendage.

via the basal plate). The greater, distal part of the appendage is entirely sclerotized.

The basal plate (fig. 32, 5) is very large. It stretches on the floor of the genital chamber to the anterior end of the latter. Its very strong oral end is continuous with the phallus (see below). In an oral direction the basal plate becomes a little narrower. Near the anterior end the lateral margin has an approximately triangular projection, carrying a strong apodeme, to which muscles are inserted. From the apodeme runs an internal ridge along the anterior part of the lateral margin to the root of the phallus. Anally the basal plate has a triangular indentation, an extension of the membranous area on the dorsal side of the inferior appendages. On the posterior part of

the basal plate, at the same level as the distal end of the phallus (see below) there is a paired group of short, but strong setae.

Each of the two appendages forms approximately a quarter of a cylinder. The concavity, which faces upwards and inwards, is continued on the posterior part of

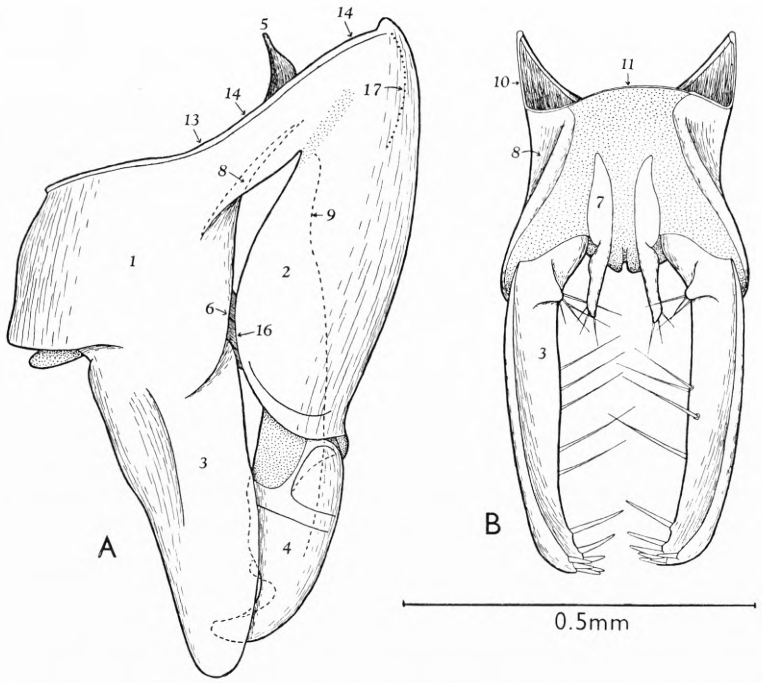

Fig. 31. *Ecnomus tenellus*. A: Segments IX and X in lateral (right) view. B: upper lip of the genital segments in ventral view. *6:* a small part of the phallus seen in the cleft between the upper and the lower lip of the genital segments. *7:* paraproctal sclerite. *8:* furrow on the ventral edge of the upper lip; in A shown by a broken line. *9:* (broken line): optical longitudinal section through the basal plate of the inferior appendages. *10:* cut edge through the sclerotic bridge between the upper and the lower lip. *11:* cut edge through the membranous roof of the genital chamber. *13:* the arrow indicates the ventral limit to the origin of the IX/X muscle. *14—14:* between the arrows the anterior dorsal muscle of the inferior appendages originates. *16:* the arrow indicates the dorsal limit to the origin of the posterior dorsal muscle of the inferior appendage. *17* (coarsely dotted line): origin of the anterior phallic muscle. Other numbers as in fig. 30.

the basal plate, whereas the anterior part of the latter is strongly convex in a transverse section.

On the median side of the appendage, near the dorsal edge, there is a short, finger-like, inwards and backwards directed process, which, no doubt, is homologous with the dorsal branch in *Polycentropus* (p. 48) and *Holocentropus* (p. 55). It is covered with long setae. (*In situ* this process lies far behind the node on the superior appendage). The inferior appendage forms a simple articulation with Segment IX: on the proximal edge of its sclerite there is a transverse furrow receiving a ridge on the posterior edge of Segment IX. On the outer side of the appendage, proximally to the middle, a strong transverse suture is seen. It is connected with a longitudinal suture

(see fig. 31 A), which runs in a proximal direction along the median margin of the lateral membranous area. At the base of the appendage the longitudinal suture is bent medially along the proximal edge. The longitudinal suture has an exceptionally high internal ridge, which unites the distal, more strongly sclerotized part of the appendage with the proximal articulation. The transverse suture might be supposed to

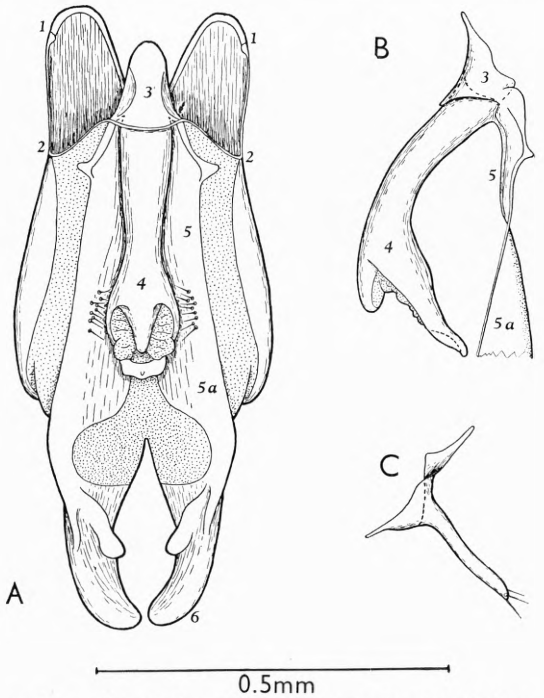

Fig. 32. *Ecnomus tenellus*. A: lower lip of the genital segments in dorsal view. B: phallus and basal plate of inferior appendages in lateral (right) view. C: right paraproct in lateral view. 1—2: cut edge through sclerotic bridge between upper and lower lip. *2—2:* cut edge through the bottom of the genital chamber. *3:* phallic apodeme. *4:* phallus. *5:* basal plate of inferior appendages. *5a:* concave part of basal plate. *6:* inferior appendage.

indicate a segmentation of the appendage. Possibly, however, it is a secondary structure.

The short, downwards curved phallus (figs. 32, *4;* 31 A, *6*) is undivided, formed by the strongly sclerotized phallobase. Its somewhat swollen distal end (fig. 33 A, B) is divided into an upper and a lower "beak", of which the latter is much larger than the former. In the state of repose the upper "beak" is flanked by the processes on the sclerites 7 (fig. 31 B). The distal end of the lower beak is flattened and a little concave on the dorsal side. Between the two lips there is a pair of membranous, much wrinkled longitudinal folds, marking the entrance of the short endotheca, on which the aedeagal retractor is inserted. This muscle originates from a strong apodeme (fig. 33 C, *4*) on the dorsal side of the proximal part of the phallus.

The phallocrypt (fig. 33C, *2*) is developed only dorsally and laterally. On the lateral side it is merely a furrow, and on the dorsal side as well it is very shallow. It is strongly sclerotized. The ventral side of the phallus is continuous with the basal plate of the inferior appendages. Like the phallocrypt the phallic apodeme (figs. 30 and 31, *5;* 32, *3;* 33C, *1*) is very short. It is beak-like, the dorsal side projecting anteriorly far beyond the ventral side.

The musculature of the genital segments is a little atypically developed, and in some instances it may be a bit difficult to decide the homologies of the muscles.

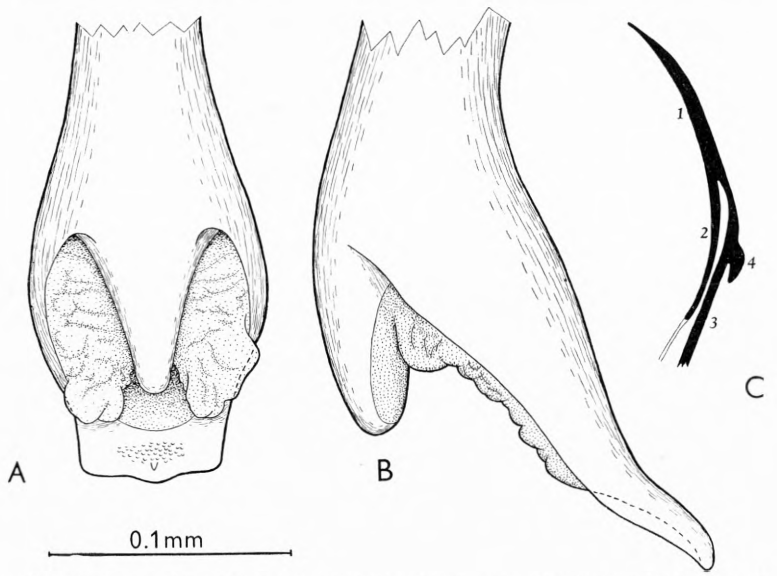

Fig. 33. *Ecnomus tenellus.* A and B: distal end of phallus in dorsal and lateral (right) view. C: optical sagittal section through dorsal side of phallic apodeme and proximal end of phallus. *1:* phallic apodeme. *2:* wall of phallocrypt. *3:* wall of phallus. *4:* transverse apodeme on which the aedeagal retractor originates.

The very strong IX/X muscle originates laterodorsally from the antecosta of Segment IX (figs. 30 and 31, *12—13*) and from the anterior half of the surface of the upper lip. Most of its bands are inserted proximally on the median side of the superior appendage (fig. 31B, *3*). Some of the most median bands, however, are inserted on the lateral margin of the sclerite 7, dorsally to the process. The function of the muscle probably is an adduction of the superior appendage, accompanied by an abduction of the process of the sclerite 7 causing the latter to meet the proximal node on the superior appendage.

The anterior ventral muscle of the inferior appendages is also very strong. It originates from the antecosta of Segment IX along the whole ventrooral indentation and is inserted on the concave part of the basal plate and on the bridges which connect this plate with the appendages themselves. It deviates from the usual picture, partly by being inserted on the basal plate and especially by having paired insertions. The

origin, however, shows that we are concerned with this muscle. It probably acts chiefly as a levator of the inferior appendages, but may be an adductor as well. In various preparations the distance between the apices of the two appendages differs.

The following muscles are weaker than the two already mentioned, but still rather strong. The anterior dorsal muscle of the inferior appendage originates from the antecosta of Segment IX at the lateral part of the dorsooral indentation (fig. 31 A, *14—14*) and is inserted on the anterior side of the apodeme orally on the lateral margin of the basal plate. It may be an accessory levator of the inferior appendages, but it probably also has some relation to the movements of the phallus (cp. the ridge from the apodeme to the root of the phallus). A muscle which originates from the rounded posterior corner of the lower lip (fig. 30, *15*—fig. 31 A, *16*) is inserted on the posterior side of the apodeme just mentioned. It is no doubt the antagonist of the former muscle. It is difficult to decide whether it is the posterior dorsal or the posterior ventral muscle of the inferior appendages. The same arguments which were advanced under *Polycentropus* (p. 49) make it probable that it is the posterior dorsal muscle. The posterior phallic muscle originates from the furrow (fig. 31 B, *8*) on the ventral edge of the upper lip and is inserted on the dorsal side of the phallic apodeme. The anterior muscle has an atypical origin, not from the antecosta, but from the lateral surface of the lower lip (fig. 31 A, *17*). Its bands run upwards and inwards and are inserted on the ventral edge of the phallic apodeme. The two last-mentioned muscles must give the phallus a nodding movement; the connection with the basal plate of the inferior appendages does not allow any independent protraction of the phallus.

At a first glance *Ecnomus* might be considered a more primitive form than the Polycentropinae, in so far as Segment IX forms a complete sclerotic annulus, and its dorsal side seems to be well developed. I find it more likely, however, that conditions in *Ecnomus* are a further specialization of those found in the Polycentropinae, viz. that the upper lip has arisen by sclerotization of a structure homologous with the middle lobe of Segment X in *Polycentropus* (fig. 23, *6*, p. 47), and that this structure secondarily has fused with Segment IX, which latter thus in *Ecnomus* is represented by the lower lip only. (The terms Segment IX and Segment X are used here in the same sense as in *Polycentropus;* p. 46. It is of course also possible—or perhaps likely—that the upper lip never was desclerotized in the ancestors of the Ecnominae). That the middle lobe at least has entered into the formation of the upper lip appears from the following facts: the anus is found immediately below the posterior edge of the upper lip; the superior appendages are sclerotically continuous with the upper lip; the sclerites 7 (fig. 31 B), which beyond any doubt are homologous with the paraproctal sclerites of *Polycentropus* (fig. 24, *3*, p. 49) are situated on the ventral side of the upper lip. A comparison between the origins of the posterior phallic muscle in *Polycentropus* (p. 52) and *Ecnomus* leads to the same conclusion. The origin of the IX/X muscle in *Ecnomus* might suggest that parts of Segment IX have entered into the formation of the upper lip, but it can be explained also by a shifting of the origin subsequently to the fusion

of the middle lobe and Segment IX. In the structure of the genital segments *Ecnomus* perhaps shows affinities to *Hydropsyche*.

As to the IX/X muscle, conditions in *Ecnomus* might be interpreted as an incipient division of this muscle into a IX/X muscle s. str. and a paraproctal muscle. I am more inclined, however, to think that we are concerned with an incipient fusion of the two muscles mentioned. Such a fusion may have taken place also in those (the majority of) Trichoptera in which no paraproctal muscle is seen.

Hydropsyche angustipennis.

The genital apparatus seems to be very simple. In all probability, however, it is a simplicity arisen by specialization.

Segment IX (fig. 34, *1*) forms, at least apparently, a complete, sclerotic annulus, which is shortest ventrally and longest laterally, the posterior edge of the segment having a lateral bulge. The latter is thick and tongue-like and sclerotized on the median side also. Ventrally to the bulge the posterior edge of the sclerite is not bent inwards. Dorsally the segment has a pair of large impressions, so that the middle of the dorsal side is raised as a broad keel (*2*) with a flat upper side.

Segment X (*3*) is a short and thick lobe, which is very feebly sclerotized and entirely membranous on the somewhat concave ventral side. In a lateral view the dorsal side of Segment X is separated from the longitudinal keel of Segment IX by a declivity. Laterally the limit between the two segments is poorly defined. On the oblique posterior end, above the anus, there is an unpaired impression bounded by a pair of rounded, seta-bearing longitudinal folds. In *H. instabilis* Curt. (fig. 35 A) these folds appear as a pair of sharp ridges. In this species the posterior end of Segment X carries a pair of small ventral processes with distal pencils of setae. They may remind of the cerci in the ♀. I find it more probable, however, that they represent rudimentary paraproctal processes. Structures which may be homologous with the paraprocts of the Polycentropidae have been described by Ulmer in some species of the genera *Hydropsyche* (1951, pp. 241 and 46) and *Diplectrona* Westw. (1932—33, pp. 49—52). In *H. angustipennis* there is, on the lateral side of the segment, a low, seta-bearing elevation, which perhaps is homologous with the process in *H. instabilis*. A suture with a corresponding internal ridge runs along somewhat more than the dorsal half of the anterior margin of Segment X. Ventrally (or laterally) it joins a short longitudinal suture, and the two sutures together form a Y-like figure. In *H. instabilis* a very weak muscle is inserted on the branching point of the Y. In *H. angustipennis* I was unable to find this muscle.

Superior appendages are lacking.

As to the morphology of the genital segments, I do not find it improbable that the greater part of the structure which above was termed the dorsal side of Segment IX, in reality is formed by Segment X. The dorsal keel (fig. 34, *2*) may be interpreted as a dorsal process of Segment X (cp. *Lype*, p. 24, and *Wormaldia*, p. 43). According

to this theory the condition in *Hydropsyche* has arisen from one like that in *Ecnomus* (p. 62) by a complete fusion of the upper and the lower lip. What here, in *Hydropsyche*, has been called Segment X may be in part homologous with the bilobed, membranous

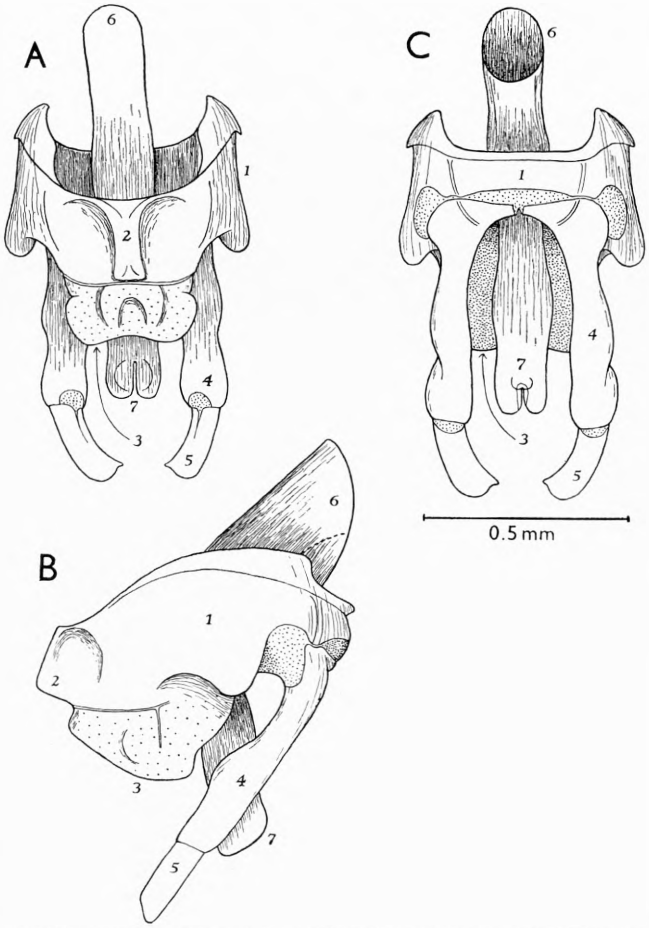

Fig. 34. *Hydropsyche angustipennis*. Segments IX and X in dorsal (A), lateral (right, B), and ventral view (C). *1:* Segment IX. *2:* dorsal keel on Segment IX; (cp., however, p. 63). *3:* Segment X. *4:* coxopodite. *5:* harpago. *6:* phallic apodeme. *7:* phallus.

process below the anus in *Ecnomus*. I am more inclined to interpret the weak muscle found in *H. instabilis* as a paraproctal muscle than as a IX/X muscle.

The inferior appendages (figs. 34, *4—5;* 35 B) are long, slender, and of a simple shape. They are two-jointed, and the coxopodite is about four times as long as the harpago. The coxopodites are united proximally, but for a very short stretch and by membrane only. The sclerites are separated by a narrow, membranous stripe. The latter continues on the middle of the basal plate (fig. 35, *3*), which thus is paired. An indirect sclerotic connection between the two appendages, however, is established

through the phallocrypt (see below). Lateroventrally the inferior appendage forms a simple articulation with the posterior edge of Segment IX. From the point of articulation a longitudinal suture runs to the antecosta of Segment IX. (It is possible that

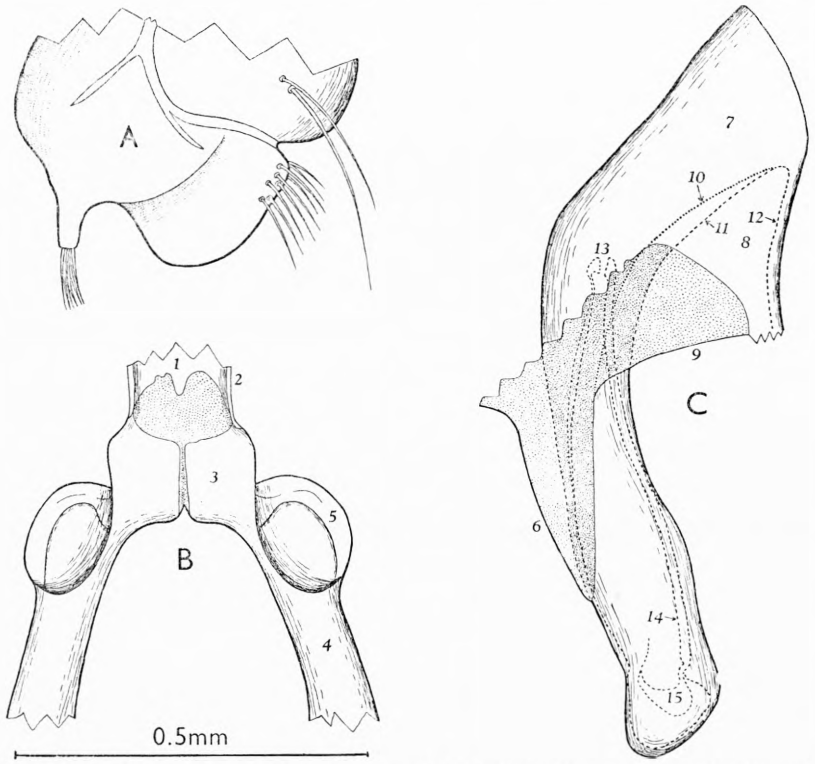

Fig. 35. *Hydropsyche instabilis* (A) and *H. angustipennis* (B, C). A: Segment X and adjacent parts of Segment IX (cp., however, p. 63) in lateral (left) view. B: proximal part of inferior appendages in dorsal view. C: phallus in lateral (right) view. *1:* part of the sclerite in the floor of the phallocrypt. *2:* cut edge through sclerotic wall of phallocrypt. *3:* basal plate of inferior appendages. *4:* coxopodite. *5:* thickening om ventroproximal margin of the latter. *6:* see p. 66. *7:* phallic apodeme. *8:* sclerotic and *9:* membranous wall of phallocrypt, both as seen from the haemocoelic side. *10* (coarsely dotted line): line of union of phallocrypt and phallus. *11—15:* the broken lines indicate: *11:* ventral outline of phallus; *12:* floor of phallocrypt; *13:* proximal end of dilated part of ejaculatory duct. *14:* ventral thickening of this part. *15:* lip at the opening of the ejaculatory duct.

this suture is homologous with the ventral suture in the Hydroptilidae). A corresponding suture runs across the ventral side of the appendage to its median side.

The anterior dorsal muscle originates lateroventrally from the antecosta of Segment IX and is inserted dorsally on the proximal edge of the appendage. It is much stronger than the anterior ventral muscle, which originates ventrally from the antecosta of Segment IX and is inserted proximally and ventrally on the median sides of the appendages. An examination of numerous preserved specimens seems to show that no mutual movement is possible between the two coxopodites, this probably being

prevented by the sclerotic connection with the phallocrypt. The two muscles then are a levator and a depressor, respectively. In the vertical plane the appendages have an exceedingly great motility. The two posterior muscles are lacking. The flexor of the harpago originates from the distal half of the lateral side of the coxopodite and is inserted medially on the proximal edge of the harpago.

The phallic apodeme (figs. 34, *6;* 35C, 7) and the undivided phallus (figs. 34, *7;* 35C) together form a strongly sclerotized tube, which proximally to the middle is bent at an obtuse angle. (The shape of this tube is different in the various species of the genus. In *H. instabilis* its proximal part is bent like the handle of a walking stick,

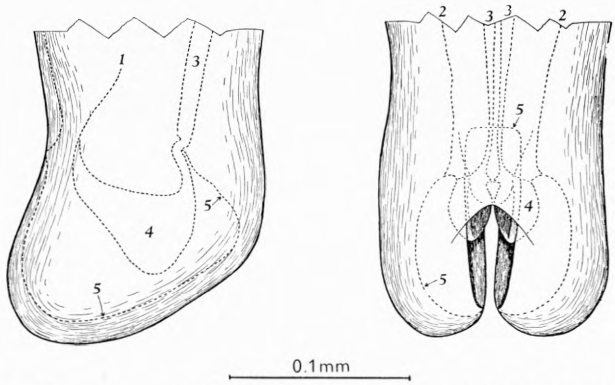

Fig. 36. *Hydropsyche angustipennis.* Apex of phallus in lateral (right) and in ventral view. The broken lines indicate: *1:* dorsal wall of ejaculatory duct. *2:* lateral wall of same. *3:* thickening on ventral wall of same. *4:* lip at the opening of the ejaculatory duct; (the distal ends of the two lips are seen freely exposed in the ventral cleft). *5:* wall of endotheca.

so that the extreme proximal end turns upside down). Ventrally the phallocrypt is very deep, so deep that no apodeme is developed. This part of the phallocrypt forms a spacious, wedge-shaped cavity, which is strongly sclerotized on the ventral side (fig. 35B, *1*) and the ventro-oral half of the lateral side (fig. 35C, *8*), whereas the roof is formed by the proximal part of the phallus. The lateral sclerotizations are connected with the basal plate of the inferior appendages by a pair of strong, sclerotic rods (B, 2). The ventral sclerotization is separated from the basal plate by a membranous area, the anterior margin of which was irregularly sinuous in all specimens examined. In a dorsal direction the depth of the phallocrypt decreases very much. On the dorsal side it even is, so to speak, negative: A tongue-like lobe (C, *6*), which has fused with the dorsal side of the phallus, is issued from the membranous wall of the genital chamber; (the boundary between the phallic apodeme and the phallus thus has an almost longitudinal course). This lobe encloses the anterior phallic muscle, which originates laterodorsally from the antecosta of Segment IX. The much stronger posterior muscle originates from the median side of the lateral, tongue-like bulging of the posterior edge of Segment IX described above. It is inserted proximally on the dorsal side of the phallic apodeme. Since the sclerotic connection with the inferior appendages

exclude any movements of protraction and retraction, the two muscles act as a levator and a depressor, respectively. Despite the sclerotic connection a considerable scissor-like movement is possible between the phallus and the inferior appendages. The chief agents in this movement are the anterior dorsal muscle of the inferior appendages and the posterior phallic muscle.

By a vertical cleft the sclerotic apex of the phallus (fig. 36) is divided into a pair of (external) lips. On the dorsal side the cleft is almost twice as long as, but also considerably narrower than on the ventral side. The lips, which like the rest of the phallus are strongly sclerotized, are very concave on the inside and thus enclose a subspherical cavity (*5*), in which the ejaculatory duct opens. The part of the latter which lies distally to the "knee" of the phallus is very spacious (fig. 35 C, *13—15*). The posterior half of this dilated part is very thin-walled. The anterior half is more thick-walled and sclerotized. Besides, a pair of sclerotic longitudinal ridges (figs. 35 C, *14;* 36, *3*) runs over the whole ventral side of the dilated part. The opening of the ejaculatory duct is narrowed by a pair of folds, the sclerotized distal ends of which project beyond the opening as a pair of internal lips (figs. 35 C, *15;* 36, *4*). Ventrally the two lips are continuous, and their sclerites are continuous with the ventral ridges mentioned above. In detail they have a rather complicated shape. Proximally on the median side there is an almost vertical furrow, semicircular in transverse section, shallower dorsally and deeper ventrally.

The strong aedeagal retractor originates dorsally in the phallic apodeme and runs descendent to the dorsal side of the sclerotic part of the ejaculatory duct, which is a little flattened. I cannot see other explanation of the function of this muscle than that the dilated part of the ejaculatory duct is a sperm pump. The internal lips perhaps may act as a valve, and the same may perhaps be the case with cuticular processes found proximally in the dilated part of the ejaculatory duct.

The morphology of the phallus is not quite clear. The two ventral ridges (figs. 35 C, *14;* 36, *3*) show that the distal, dilated part of the ejaculatory duct (fig. 35 C, *13—15*) is homologous with the distal, sclerotic part in *Polycentropus* (fig. 26, *7*, p. 51) and *Holocentropus* (fig. 29 C, p. 55). The sclerotized, subspherical cavity (fig. 36, *5*) possibly is a reduced, non-eversible endotheca. According to this the copulatory organ is formed by the phallobase.

Orthotrichia tetensii.

The genital structures of this minute form is extremely specialized and much complicated. It is not impossible that I have committed some minor errors in interpreting the structures, which of course had to be made out with the aid of an immersion lens, and the same is true as to the two other hydroptilids treated here. Especially the study of the inferior appendages proved to be a rather difficult task. I feel convinced, however, that the accounts are correct in the main.

Segment VIII, already, is much modified. The tergum (fig. 37, *5*) projects far

backwards and in a dorsal view largely conceals Segment IX. The sternum (*6*), on the other hand, is strongly indented anally, but the venter as a whole is not so much indented as the sternum. In a ventral view about the anterior half of Segment IX is covered by Venter VIII. Anally on Tergum VIII there is a pair of large, pit-like sensilla, probably s. campaniformia.

Segment IX (figs. 37, *7;* 38—41, *1*) is very asymmetrical. On the left side a large, horn-like, somewhat sagittally compressed, entirely sclerotized lateral process (figs. 37—39 and 41, *8*) is seen. On the right side a bipartite lateral process is just indicated (fig. 38). Sinistrally on the dorsal side there is a longitudinal suture, which anteriorly joins the antecosta and posteriorly goes to the base of the lateral process. On the right side but a rudiment of a longitudinal suture is seen quite orally (fig. 40). On this side (fig. 38) there might appear to be an anal transverse suture. This, however, is not the case. The picture is due to the fact that the posterior border of Segment IX, which here is very overlapping, is sclerotized on the lower side as well. Lateroventrally the posterior border of Segment IX to some extent overlaps the base of the inferior appendage, forming a simple articulation with the latter. Here the posterior border of Segment IX is strengthened. Medially to the articulation the strengthening bends forwards and eventually joins the antecosta, which means that Segment IX has a pair of ventral longitudinal sutures. Between these Segment IX and the inferior appendages are separated by a membranous area.

Segment X (figs. 37, *9;* 38—41, *4*) is large and asymmetrical to a still higher degree than Segment IX. The ventral side is very concave, so that the segment may be described as a rather thin lamella which forms more than half of a cylinder, and orally almost a complete cylinder. The ventral opening (fig. 41) is a little asymmetrical, shifted towards the right. In this way Segment X forms a very spacious sheath for the "base" of the phallus. The ventral side of the segment (the inside of the sheath) is membranous (cp., however, below), on the dorsal side there is a large, asymmetrical sclerite (*4a*). It covers the whole left side and a little more than the left half of the dorsal side. The rest of the dorsal side and the whole right side are membranous (*4b*). The dorsal side of the sclerite forms part of a cylinder, the radius of which is smaller than that of the cylinder formed by the segment as a whole. Since, moreover, the sclerite is narrower anteriorly than in the middle, the result is that the oral part of its right margin is steeply descendent. This descendent part of the margin has an internal ridge. On the left half of the dorsal side the sclerite of Segment X merges into that of Segment IX, no boundary between the two segments being visible, and on the left side it is is continuous with the median side of the lateral process of Segment IX through a sclerotization in the genital chamber above the base of the inferior appendage. Anally on the dorsal side the sclerite carries a pair of large spines. The left one (*2*) is very clumsy and bent upwards, the right one (*3*) is slenderer and bent laterally.

Orally on the ventral side of Segment X (the inside of the sheath) a semi-annular sclerite (figs. 38 and 40, *13—13*) is seen. In contrast to the dorsal sclerite, it has been shifted towards the right side. At its left end, i. e. dorsolaterally on the left side of the

segment, it carries two large processes. The left one (*19*) is thick and approximately semiglobular, the right one (*20*) has the shape of a long, slender spine, which almost, but not entirely, reaches the anal end of Segment X; it crosses the phallus, lying dorsally to the latter. A similar structure possibly has been described by ULMER (1951,

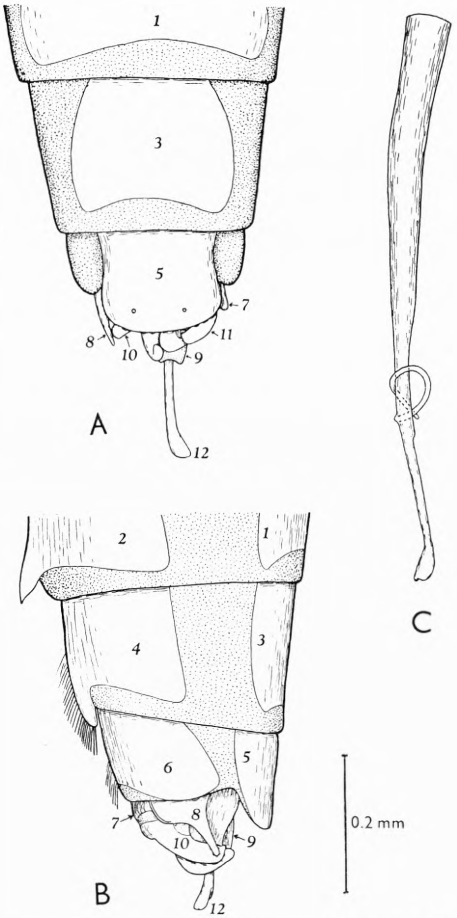

Fig. 37. *Orthotrichia tetensii*. A: posterior end of abdomen in dorsal view. B: the same in lateral (left) view. C: phallus seen from the left side (and a little from the ventral side, too). *1:* anal part of Tergum VI. *2:* anal part of Sternum VI. *3:* Tergum VII. *4:* Sternum VII. *5:* Tergum VIII. *6:* Sternum VIII. *7:* Segment IX. *8:* left lateral process of Segment IX. *9:* Segment X. *10:* left and *11:* right inferior appendage. *12:* phallus.

pp. 76 and 78) in *Javanotrichia* Ulm. as a "Chitingräte", which "überkreuzt in schräger Richtung den Penis", in *Orthotrichiella* Ulm. (l. c., p. 80), and in *Sumatranotrichia* Ulm. (l. c., p. 88); (see also p. 146).

The IX/X muscle is a very strong, unpaired muscle. It originates from the dorsal part of the antecosta of Segment IX. On the left side the origin continues along the longitudinal suture to the posterior end of the segment. Its very asymmetrical insertion

is on the oral, descendent part of the right margin of the sclerite of Segment X (fig. 40, *9*). This muscle perhaps may produce some depression of Segment X, perhaps some rotation towards the right as well.

Superior appendages are lacking.

The one-jointed inferior appendages are very porrect. The right appendage (figs. 37, *11;* 38, 40, 41, *7*) is rather slender, especially in its distal part, which is bent inwards and somewhat backwards above Segment X. The side which faces medially and anally is slightly concave. The left appendage (figs. 37, *10;* 38, 39, 41, *6*) is more robust. Its distal end is divided into two branches. One is directed upwards, the other inwards and touches the sclerite of Segment X (*4a*), which is thickened there. The lateral side of the left appendage is in close contact with the lateral process on Segment IX (*8*). The two appendages are sclerotically continuous on their rounded posterior edge.

On the membranous floor of the genital chamber, immediately in front of the common part of the two inferior appendages, there is a narrow and very deep, funnel-like depression (figs. 40 and 41, *14*). The stalk of the funnel (figs. 39—41, *15*) points forwards. The funnel is sclerotized and thus forms a long apodeme, which projects beyond the anterior margin of Segment IX. As is often the case with large apodemes, it contains a central cavity, at least in its posterior (proximal) part. The musculature associated with the apodeme shows that it must be included under the inferior appendages and represents the basal plate, or rather part of the basal plate. A sclerotic bridge (fig. 41, *12*) connects the left wall of the funnel with the left appendage. The right appendage, however, does not seem to have any direct sclerotic connection with the apodeme.

In front of, above, and a little to the right of the entrance to the apodemal funnel a large, thin-walled, though sclerotized, process (figs. 40 and 41, *5*) is seen. In a dorsal or ventral view it is somewhat clavate, in a lateral view it tapers gradually towards the distal end, which carries a pair of strong setae. The left side of the process is sclerotically continuous with the right wall of the apodemal funnel (*14*). The process is situated just below the anterior end of the ventral cleft in the sheath formed by Segment X. A sclerotic rib (figs. 39—41, *16*), lying in the bottom of the furrow between Segment X and the inferior appendage, is issued from each side of the base of the process. The right rib eventually is continuous with Segment IX (through the inwards bent posterior edge of the latter), the left one with the sclerotization in the genital chamber between Segments IX and X (see above). An approximately parabolic apodeme (*16a*) is issued from each rib. The muscles associated with the latter shows that the rib must be part of the basal plate of the inferior appendages.

The strong anterior dorsal muscle originates from the lateral part of the antecosta of Segment IX and is inserted laterally and dorsally on the proximal margin of the appendage, dorsally to the articulation with the posterior edge of Segment IX. Since there is hardly much mutual motility between the two appendages (the sclerotic connection being rather firm), this muscle possibly acts as a levator. The anterior

ventral muscle, too, is strong. It originates—as usually—from the ventral part of the antecosta of Segment IX. Laterally the origin passes beyond the ventral longitudinal

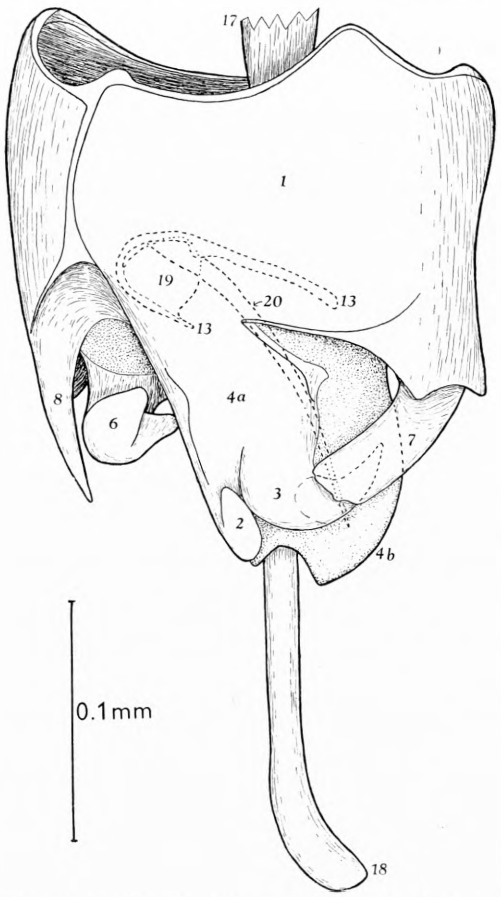

Fig. 38. *Orthotrichia tetensii*. Segments IX and X in dorsal view. In this and the three following figs. the numbers *4*, *5*, *8*, and *14—16* designate structures which probably are homologous with the correspondingly numbered structures in *Agraylea* (figs. 43 and 44) and *Hydroptila* (fig. 46). Legend common to figs. 38—41: *1:* Segment IX. *2:* left and *3:* right spine on Segment X. *4a:* sclerotic and *4b:* membranous part of Segment X. *4c* (fig. 40): membranous inner wall of left side of Segment X. *5:* seta-bearing process (see p. 70); in fig. 41 its distal end is seen freely projecting behind the common part of the two inferior appendages. *6:* left and *7:* right inferior appendage. *8:* left lateral process of Segment IX. *9* (broken line): descendent right margin of the sclerite of Segment X. *10* (broken line): ventral outline of Segment X. *11* (broken line): dorsal outline of proximal part of left inferior appendage. *12:* sclerotic bridge connecting left inferior appendage with funnel-like apodeme. *13:* semi-annular sclerite at the entrance to phallocrypt. *14—15:* funnel-like apodeme (see p. 70). *16:* sclerotic rib in the bottom of the furrow between Segment X and the inferior appendages. *16a:* apodeme issued from this rib. *17:* proximal part of phallus (broken off at different levels in the four figs.). *18:* distal end of phallus. *19:* left and *20:* right process on the semi-annular sclerite *13*.

sutures. It is inserted ventrally on the apodemal funnel *14* (figs. 40 and 41). It possibly —through the sclerotic bridge *12* (fig. 41)—acts as a depressor of the inferior appendages and, no doubt, also exercises some influence upon the process *5*. The strong

posterior ventral muscle originates lateroventrally from the proximal margin of the inferior edge of the appendage, ventrally to the articulation with the posterior edge of Segment IX. It spreads out fan-like and is inserted on the lateral side of the apodeme *16a* (figs. 39—41). Considering the sclerotic connection with the sclerite of Segment IX (and X), the apodeme probably must be the fixed point. The function then will be a depression of the inferior appendage. The posterior dorsal muscle is a weak one, inserted on the anterior end of the apodemal funnel *15* (figs. 39—41). I have been

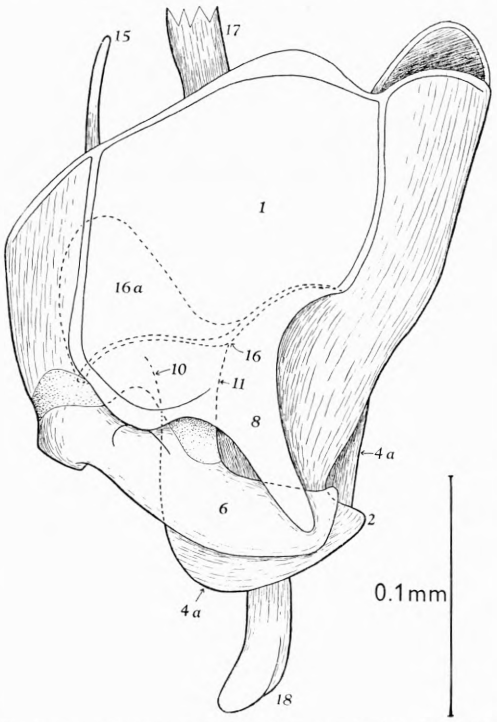

Fig. 39. *Orthotrichia tetensii.* Segments IX and X in lateral (left) view. For explanation see fig. 38.

unable to follow the few muscle bands to their origin, but their direction indicated that this must be in the vicinity of the origin of the posterior phallic muscle. The function possibly is restricted to movements of the process 5 (figs. 40 and 41).

It will be seen that the sclerite of Segment IX, the dorsal sclerite of Segment X, and the inferior appendages are united into a complicated sclerotic framework. Acting together the various muscles possibly can give this framework richly varied movements.

Including the possible apodeme the undivided phallus (fig. 37C) is very long and slender. In all specimens seen by me it seemed to be more or less protracted. In the specimen showing the least degree of protraction its anterior end reached the middle of Segment V. I have been unable to recognize the boundary between the phallus itself and the phallic apodeme, the wall of the phallocrypt being extremely delicate. In

the following the phallus and its apodeme are treated together and simply called the phallus. The phallus can be rotated. Hence it is difficult to say what is the dorsal and what the ventral side. The interpretation given below is that which I find most likely.

In its proximal half the phallus tapers gradually and slightly. The next fourth tapers more strongly. The two distal fourths are separated from one another by an

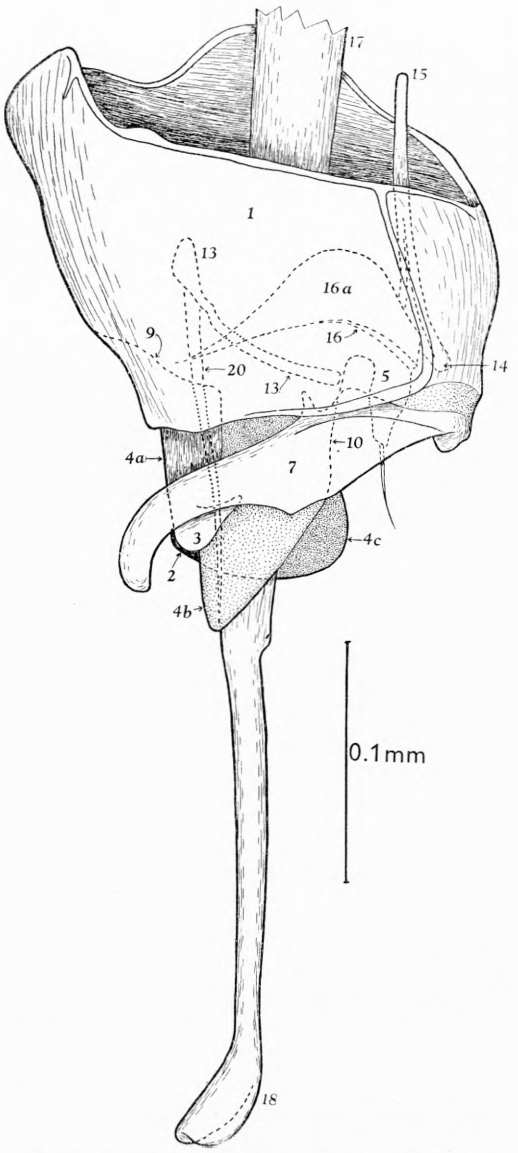

Fig. 40. *Orthotrichia tetensii*. Segments IX and X in lateral (right) view. That this fig. shows a dorsal outline different from that of fig. 39 is due to the fact that it is seen also a little from the ventral side. For explanation see fig. 38.

abrupt decrease in thickness. The distal fourth is extremely slender and almost cylindrical except for the swollen distal end, which is spoon-like excavated on the dorsal side. A little in front of the sudden decrease in thickness an unpaired, slender titillator

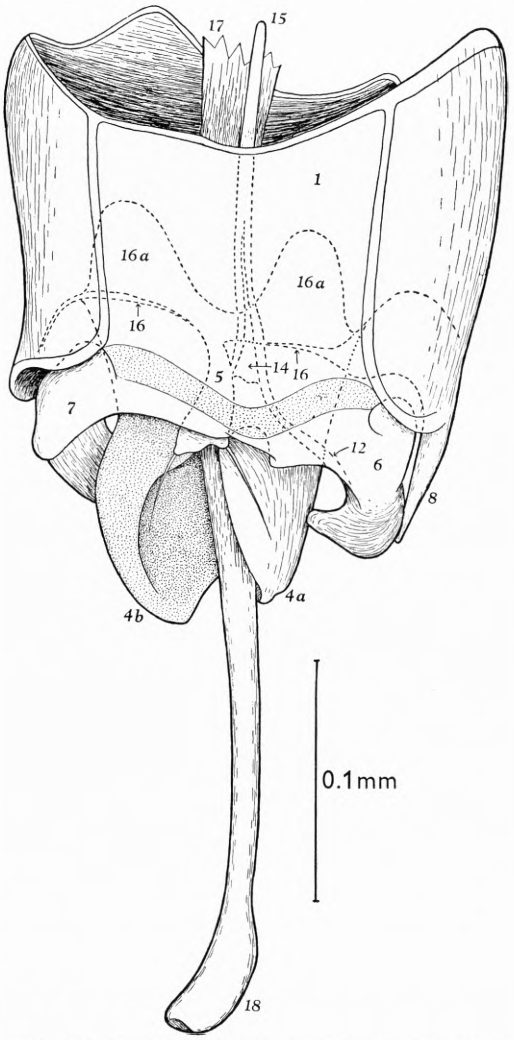

Fig. 41. *Orthotrichia tetensii*. Segments IX and X in ventral view. For explanation see fig. 38.

(fig. 42, 2) rises from the ventral side of the phallus. It is wound once round the phallus, towards the right and anteriorly.

In the greater, proximal part of the phallus the wall is very thin, ca. 1 μ thick, though rigid and thus probably sclerotized. Immediately in front of the abrupt decrease in thickness there is an oblique, annular area (fig. 42, 4), in which the thickness of the wall is somewhat greater, up to a little more than 2 μ. Distally to this area the wall is extremely thin, less than $^1/_2$ μ thick, and soft. The rigidity of the distal, slender part

of the phallus is due to the ejaculatory duct. (That this part of the phallus in fig. 42 is shown with a one-layered wall is due to the fact that it is impossible to distinguish between the two layers in a figure drawn on that scale). In the apical swelling the wall again is a little thicker and rigid.

In the proximal part of the phallus the cuticular wall of the ejaculatory duct (*1*) is particularly thin. A little proximally to the origin of the titillator the duct divides into two branches, one (*6*) entering the distal part of the phallus, the other (*3*) the titillator. In the former branch the thickness of the wall increases rapidly, and in the distal part of the phallus, as mentioned above, it is the ejaculatory duct which forms the skeleton. In the thick wall there are narrow, irregular, greyish annuli, separated by still narrower, yellowish annuli. The greyish colour possibly indicates a stronger sclerotization, and the annular structure allows for some flexibility. The branch entering the titillator has the same appearance, though the thickness of the wall is smaller and decreases again after the branch has entered the titillator. Otherwise the titillator is built in the same way as the distal part of the phallus. There is no indication of a distal opening on the titillator.

On so small an object it may of course be very difficult to make out structures as those described above with absolute certainty. In one of my slide-preparations, however, the ejaculatory duct had been filled with air, and the thread of air was seen very clearly to divide into two branches, one entering the distal part of the phallus, the other the titillator. It is interesting to note that the same branching of the ejaculatory duct occurs in the Lepidoptera (Beirne 1942; there is no titillator in this order), which probably means that this feature is an old heritage in the Trichoptera, though it has been lost in the vast majority of forms. The mechanical use made of it in *Orthotrichia* (see below) possibly is peculiar to this form.

The ejaculatory duct opens at the bottom of the distal spoon-like excavation. The extreme distal part of the duct is especially strongly sclerotized, blackish, and not annulated. Its roof seems to have fused with the bottom of the "spoon", and from this area more strongly sclerotized, brownish "wings" stretch out on the sides of the "spoon".

The anterior phallic muscle may be described as being unpaired and consisting of four portions. (1) originates from the costa corresponding to the left longitudinal suture on the dorsal side, below the IX/X muscle. Its bands, which have a trans-

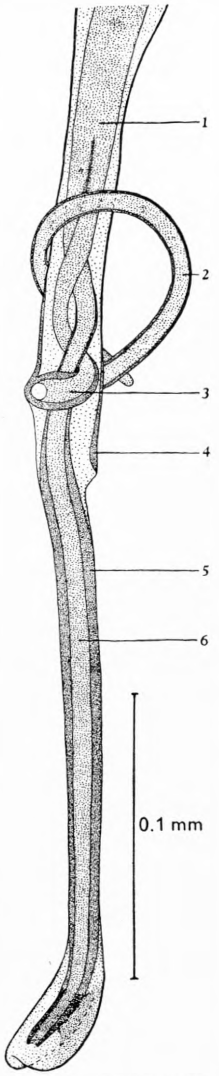

Fig. 42. *Orthotrichia tetensii*. Distal half of phallus as seen from the left and a little from the ventral side. In this fig. varying intensity of dotting indicates different degrees of transparency. *1:* ejaculatory duct just before its bifurcation. *2:* titillator. *3:* branch of ejaculatory duct entering the titillator. *4:* annular thickening of wall of phallus. *5:* thickened wall of ejaculatory duct. *6:* lumen of same.

verse course, cross below the phallus and are then wound round the latter before their insertion. (2) and (3) originate from the antecosta, below the IX/X muscle. (2) (left) crosses from the left side above the phallus and is wound round the latter before its insertion. (3) (right) spreads out rather much in a fan-like fashion, crosses from the right above the phallus, and is wound round the latter before its insertion. (4) also originates from the antecosta, but laterally to the left longitudinal suture. Its bands, which run in a very anterior direction, cross from the left above the phallus and are wound round the latter before their insertion. The insertions on the phallus agree with the numbers given. (1) is inserted most distally (posteriorly), (4) most proximally (anteriorly). The posterior phallic muscle is rather strong. On the left side it originates from the sclerotization in the genital chamber, just dorsomedially to the lateral process. On the right side on the posterior margin of Segment IX, above (and medially to) the rudimentary lateral process. It is inserted quite proximally on the phallus.

The posterior phallic muscle as usually acts as a protractor. The anterior muscle cannot be a retractor. If anything, the portion (4), and partly the the portion (3) as well, act as protractors. No doubt the function of the anterior muscle is to rotate the phallus. The portions (1) and (3) cause a rotation towards the right, (2) and (4) towards the left. In various preparations the phallus is seen at very different visual angles.

Both phallic muscles are inserted on the phallus (or on the ensheathing phallocrypt). As mentioned above, however, the skeleton of the distal part of the phallus is formed by the ejaculatory duct. The branch of the latter entering the titillator provides a means for transmitting the muscular power to the distal part of the duct.

The preserved specimens seen by me showed a very different degree of protraction of the phallus. At the highest degree the origin of the titillator was situated about midway between the anal end of Segment X and the distal end of the phallus. The lowest degree of protraction is shown in fig. 39. Even in this case, however, I think that we are concerned with some degree of protraction. In the living animal the phallus possibly does not project beyond Segment X, and perhaps not beyond the phallocrypt. The musculature indicates that the phallus, once protracted, cannot be retracted again. This means that only one copulation is possible for the ♂. In the genus *Hydroptila* I have made an observation (1948b, p. 127) which may suggest that the phallus is lost as a result of copulation.

The fact that the bands of the anterior muscle are wound round the phallus before their insertion might give an impression that a great part of the latter is surrounded by a circular musculature. Proximally this "circular" musculature almost reaches the basal end of the phallus. The distal limit is marked by the entrance to the phallocrypt, and this without regard to the degree of protraction, which shows that at least part of portion (1) must be inserted on the phallocrypt and not on an apodeme. It is worth noting that the rotations of the phallus exert little or no influence on the position of the semi-annular sclerite (figs. 38 and 40, *13—13*).

A discussion of the morphology of the phallus will be found under *Hydroptila occulta* (p. 84).

Agraylea multipunctata.

Segment VIII has a normal shape. As in *Orthotrichia* a pair of sensilla (possibly s. campaniformia) is seen anally on the tergum. They are, however, much smaller and more close-set than in *Orthotrichia*.

In its dorsal half, Segment IX (figs. 43 and 44) has a very deep anal indentation, so that the length in the middle of the dorsal side is only a small fraction of that of the lateral side. The short dorsal part is flanked by a pair of posteriorly diverging longitudinal sutures (shown as broken lines in fig. 43 A), which, no doubt, are homologous with the dorsal longitudinal suture in *Orthotrichia* (figs. 38 and 39; the homology i. a. appears from the origin of the IX/X muscle). The dorsal VIII/IX muscle is inserted on that part of the antecosta which lies between the two sutures. The areas laterally to the longitudinal sutures project into a pair of flat, tongue-like, sclerotic lobes (*1*), which stretch medially and almost touch each other in the middle line of the segment. The curvature of the outside of the lobes is a direct continuation of that of the lateral side of the segment. Laterally the posterior border of the segment is very bulging, and ventrally to the bulge a short, finger-like, membranous (or at least very slightly sclerotized) process is seen (*2;* in fig. 44 D almost entirely concealed by *13*). A pair of lateroventral longitudinal sutures join the posterior margin at these processes. They possibly are homologous with the ventral sutures in *Orthotrichia* (p. 68). Ventroposteriorly on Segment IX there is a deep, membranous indentation. The entrance to the membranous area, however, is restricted by a pair of medially directed points (*3*), the distal ends of which project as free processes forming articulations with the inferior appendages (*10*). In the middle of the ventral side the antecosta is interrupted.

Segment X has the shape of a broad, membranous lobe (*4*). The IX/X muscle is unpaired as in *Orthotrichia,* but much weaker. It originates partly on the antecosta between the two longitudinal sutures, partly on the anterior part of the latter. The insertion is anally on the dorsal side of Segment X, at the transverse depression seen in fig. 43 A. Whether this depression is the anus or merely a fold produced by the muscle insertion, I cannot tell.

Laterally to Segment X (*4*) the bottom of the genital chamber is sclerotized (*7*). This sclerotization is continuous with that of Segment IX. Ventrally *7* projects into a large, sclerotic process (*8*). This is sagittally compressed, but the distal end is bent inwards, so that in a dorsal or ventral view it is like a large, triangular plate. The two plates almost touch one another in front of the horn *6* (see below). On their ventral side there is a large, approximately semiglobular bulge. The dorsal longitudinal suture continues (fig. 44 D, *9*) along the median margin of *7* to the base of *8*. This relation to the longitudinal suture indicates that *8* is homologous with the lateral process in *Orthotrichia* (figs. 38, 39, 41, *8*).

Segment X (*4*) forms an upper lip for the entrance to the phallocrypt. The lower lip is formed by a lobe (*5*) approximately twice as long, which is membranous on the dorsal side and sclerotized on the lateral and ventral sides. Segment X (*4*) is very

concave ventrally and partly encloses the anterior end of the lower lip (*5*). The part of *5* which projects beyond *4* tapers much posteriorly. Its extreme posterior end projects into a finger-like, downwards and backwards directed, sagittally compressed horn

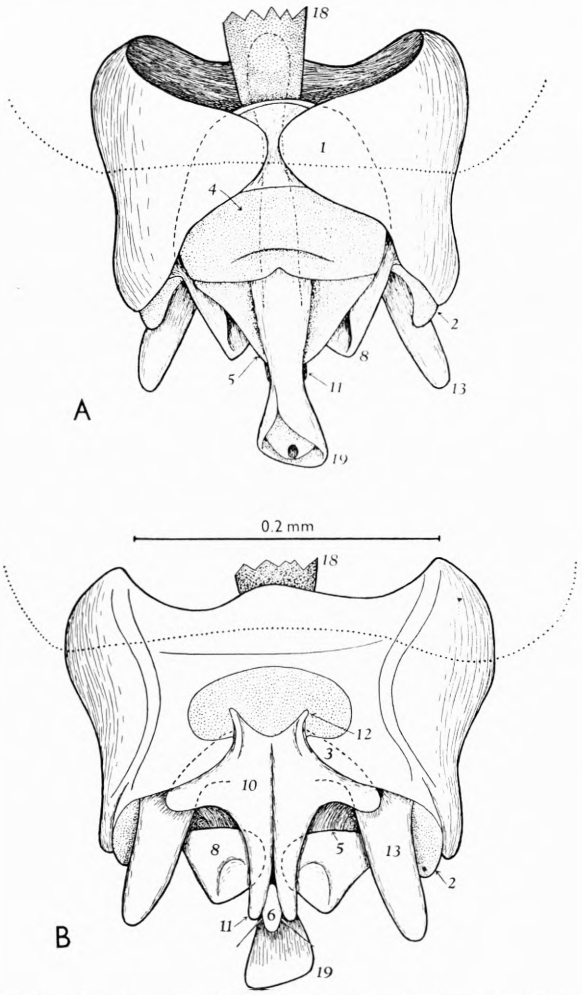

Fig. 43. *Agraylea multipunctata*. Segments IX and X in dorsal and in ventral view. In this and the following fig. the numbers *4*, *5*, *8*, and *14—16* designate structures which probably are homologous with the correspondingly numbered structures in *Orthotrichia* (figs. 38—41) and *Hydroptila* (fig. 46). The coarsely dotted line indicates the posterior border of Segment VIII. *18:* proximal part of phallus (broken off). *19:* distal part of phallus. For further explanation see text.

(*6*), on the base of which a pair of very strong setae is seen. On the ventral side the lower lip (*5*) has a pair of sharp, longitudinal ridges. The concave area between them is produced anteriorly as the sclerotic roof (*14*) of a narrow and deep pocket above the inferior appendages, and farther forwards as an apodeme (*15*), which almost reaches the anterior end of Segment IX.

The margin of the sclerite on the lower lip (*5*) is strengthened. Posteriorly this strengthened part (*16*) encloses the entrance to the phallocrypt like a U. It then runs forwards along the dorsal margin of the sclerite and bends downwards along the anterior margin. The lower end of the vertical part of *16* is interlocked (fig. 45 B)

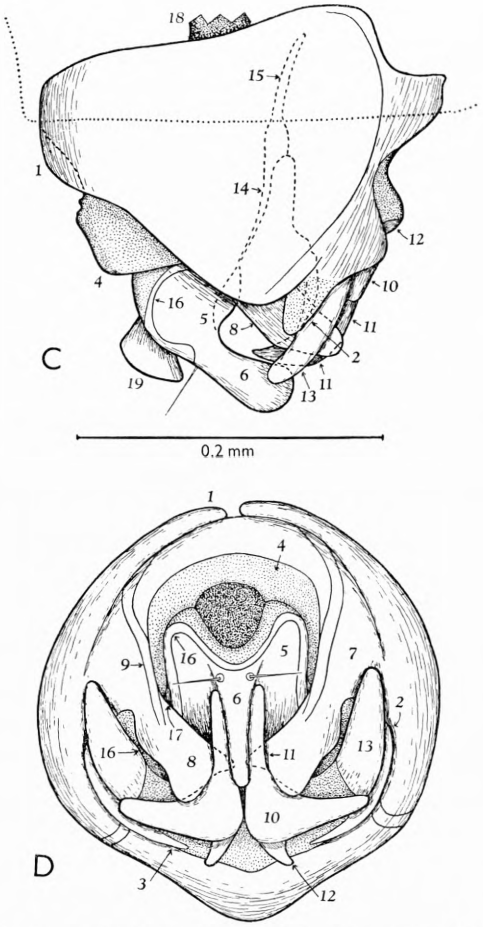

Fig. 44. *Agraylea multipunctata*. Segments IX and X in lateral (right) and in posterior view. In the lower fig. the phallus has been removed; the entrance to the phallocrypt is seen between the numbers *4* and *5*. For explanation see fig. 43.

with an upwards directed, rod-like extension (*17*) of *7*, issued at the base of *8* (fig. 44 D) and lying lateroventrally on the posterior end of Segment X (*4*). From this point *16* continues at the bottom of the genital chamber, running in a curve below the process *8*, and eventually joins the sclerite of Segment IX at the process *2*.

On *14* a pair of strong muscles is inserted, which originates ventrally from the antecosta of Segment IX. The origin covers only a rather small part of the antecosta just medially to the lateroventral longitudinal suture. A pair of weaker muscles origi-

nates on *7* and is inserted on the anterior end of *15*. The two muscles must be considered the anterior ventral and the posterior dorsal muscles, respectively, of the inferior appendages. (The former is unusual by being paired. The lack of the medioventral part of the antecosta of Segment IX has some connection with this fact). This shows that *14* and *15* must be included in the inferior appendages, though they have no sclerotic connection with the appendages themselves. No doubt the structures *5*, *14*, *15*, and *16* are homologous with those designated by the same numbers in *Orthotrichia* (figs. 38—41). The identity of *14* and *15* appears from their connection with the two muscles mentioned above. The identity of *5* partly from its connection with *14*, partly from the fact that as in *Orthotrichia* it carries a pair of strong setae. (*6* in *Agraylea* is a special part of *5*, projecting between these setae). As in *Orthotrichia* *16* forms a sclerotic connection between *5* and the sclerite of Segment IX. — The two muscles described probably act as a depressor and a levator, respectively, of *6*.

The inferior appendage itself (*10—12*) has a short, broad basal piece (*10*), which proximally projects into a small, downwards curved process (*12*), distally into a slender, backwards directed and upwards curved, somewhat sagittally compressed horn (*11*). The right and the left horn are rather closely approached. Quite proximally the two basal pieces (*10*) are sclerotically continuous on the ventral side. Proximally the dorsal side of *10* is membranous. From this area a large, finger-like, sclerotic process (*13*) rises. It possibly represents the harpago, though I have been unable to find any muscles associated with it.

The anterior dorsal muscle of the inferior appendage is very strong. It originates from the antecosta of Segment IX on the whole stretch between the laterodorsal and the lateroventral longitudinal suture, and is inserted laterally and proximally on *11*. The weaker posterior ventral muscle originates from the laterodorsal longitudinal suture of Segment IX and is inserted on *12*. Without knowledge of conditions in *Orthotrichia* (pp. 71—72) it would have been impossible to identify the latter muscle. In *Orthotrichia* it originates from the apodeme *16a* (figs. 39—41). Taking the sclerotic connection between Segment IX and *16* into account, it is not difficult to imagine that the origin may have shifted from *16a* to the dorsal side of Segment IX. — Since one muscle is inserted distally, the other proximally to the articulation with Segment IX (*3*), they act as a levator and a depressor, respectively. The two other muscles of the inferior appendage have already been mentioned.

The mutual position of the parts described above appears from figs. 43 and 44. It is somewhat different in the various preparations. It will be seen that a pair of tongs is formed by *6* and *8* on one side and *11* on the other side. Of those structures which enter into the composition of the tongs *8* is immovable. The process *13* probably has a tactile function.

The phallus (figs. 43 and 44, *18—19*; 45) is very like that of *Orthotrichia*, though it is considerably shorter and thicker. In a fully retracted state it reaches only to the posterior end of Segment VII. A deep constriction divides it into two parts, approximately equal in length. The elongately conical proximal part is considerably more

thin-walled than the slender distal part. A little distally to the constriction an unpaired, slender titillator rises on the ventral side. It is first wound one and a half times round the phallus, towards the right and forwards, and then is directed straight backwards. (Its exact position differs in the various preparations). As in *Orthotrichia* the ejaculatory duct is divided into two branches, one of which enters the titillator. Since this branch is quite thin-walled, the arrangement cannot have the same mechanical function as in *Orthotrichia* (p. 76). Perhaps it serves to prevent a torsion of the ejaculatory duct

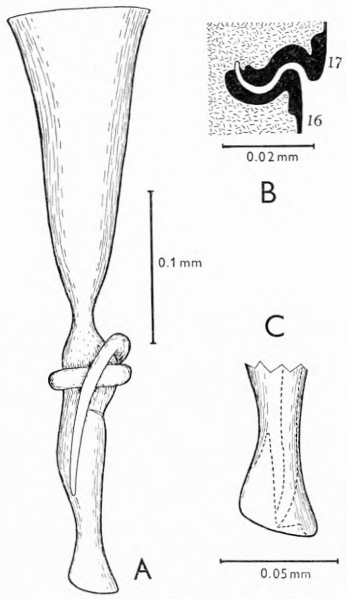

Fig. 45. *Agraylea multipunctata*. A: phallus in lateral (right) view. B shows the interlocking of *16* and *17* (see p. 79); semidiagrammatic horizontal section. C: distal end of phallus in lateral (right) view; the broken lines indicate the ejaculatory duct and the papilla carrying its opening shining through.

during the rotations of the phallus. A little distally to the origin of the titillator a narrow, approximately semicircular, internal ridge is seen on the ventral side of the phallus. (It is better developed on the left than on the right). It is probably homologous with the oblique, thickened annulus in *Orthotrichia* (fig. 42, *4*). The branch of the ejaculatory duct which enters the distal part of the phallus is strongly sclerotized, but its diameter is only a fraction of that of the phallus, and unlike conditions in *Orthotrichia* the skeleton is formed by the wall of the phallus. The somewhat swollen distal end of the phallus is spoon-like excavated on the dorsal side. At the bottom of the "spoon" the ejaculatory duct opens on a low, thick, membranous papilla (fig. 45 C).

The posterior phallic muscle originates from 7 (figs. 43 and 44) and is inserted proximally on the phallus. The anterior muscle originates from the lateral part of the antecosta of Segment IX and behaves in a similar way as in *Orthotrichia*. Two portions can be distinguished, a dorsal one running obliquely in an anal direction, and a ventral one running obliquely in an oral direction. On the left side the former crosses below,

the latter above the phallus, on the right side it is converse. As in *Orthotrichia* the anterior muscle may suggest that the phallus is surrounded by a circular musculature.

A discussion of the morphology of the phallus will be found under *Hydroptila occulta* (p. 84).

Hydroptila occulta.

In a previous paper (1951) I have described the genital segments of this species. Referring to this description, some supplementary information will be given here.

A pair of sensilla (possibly s. campaniformia) is seen posteriorly on Tergum VIII as in *Orthotrichia*. They are, however, much smaller than in this form.

Segment IX. Laterally the anterior margin projects into a long point reaching the middle of Segment VII or the posterior end of Segment VI, according to the state of contraction of the abdomen. (In other species, e. g. *H. cornuta* Mos. and *H. sparsa* Curt., the lateral side is not nearly so long. The anterior margin bulges much, it is true, but it forms an even curve. See Anker Nielsen 1948b, pp. 125—27). Laterodorsally there is a distinct longitudinal suture, which joins the antecosta at an angle of 45° halfway between the centre of the dorsal indentation and the lateral point of the anterior margin. Its relations to the IX/X muscle and the muscles of the inferior appendages indicate that it is homologous with the dorsal longitudinal sutures in *Orthotrichia* (p. 68) and *Agraylea* (p. 77). In *Hydroptila occulta* it extends only over the oral half of the segment, but it points towards the base of the dorsal branch of the lateral process (1951, fig. C). It is possible, therefore, that this branch (fig. 46, *8*) is homologous with the lateral process in *Orthotrichia* (figs. 38, 39, 41, *8*) and the process *8* in *Agraylea* (figs. 43 and 44). The hyaloid process (fig. 46, *2*) no doubt is homologous with the process *2* in *Agraylea*, though it has a more dorsal position than in the latter. The ventral branch of the dorsal process in *H. occulta* then possibly corresponds to the process *3* in *Agraylea;* as will be shown below, the two supposed homologues have similar relations to the inferior appendage.

Segment X. The dorsal side is scarcely entirely membranous, though it is pale and very thin-walled. The two more strongly sclerotized stripes in return are very strong, especially in their oral half. Their anterior ends are bent upwards and backwards like the handle of a walking stick and are continuous with the sclerite of Segment IX. The IX/X muscles are inserted on these rods, just anally to the bend. They originate from the antecosta of Segment IX between the two longitudinal sutures. Unlike conditions in *Orthotrichia* and *Agraylea* the IX/X muscle is paired, though the two origins almost touch each other in the middle of the dorsal side of the antecosta. The function of the muscle is possibly a depression of Segment X.

The inferior appendages. The two appendages not only touch one another medially, but they have also a common, large and thick, membranous part. Whether there is any sclerotic continuity, I do not venture to say; the two sclerites at least are separated by a fine furrow. The anterior dorsal muscle is very strong. It originates from the

antecosta from the longitudinal suture to a point about halfway between the latero-oral point and the middle of the ventral side. It is inserted laterodorsally on the proximal margin of the appendage (i. e. at the distal end of the dark stripe seen in fig. D, 1951). The posterior ventral muscle is weaker and is developed (almost) as in *Agraylea* (pp. 79—80). It originates on the antecosta of Segment IX somewhat dorsally to the longitudinal suture (and of course more distally on the antecosta than the IX/X muscle) and is inserted ventrally on the proximal end of the appendage. The two muscles are

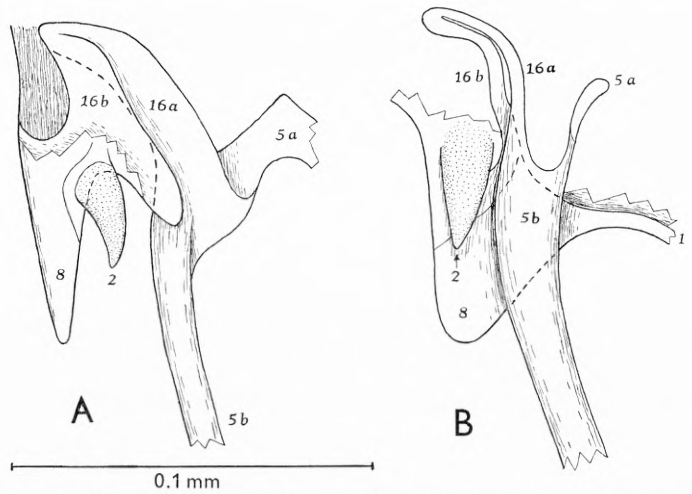

Fig. 46. *Hydroptila occulta*. Showing relations between left "paramere" and Segment IX. A: dorsal view. B: median view. The irregularly serrate lines are (supposed) lines of fracture after severance of sclerites. All membranes—with the exception of that of the process *2*—have been removed. The numbers *2*, *5*, *8*, and *16* designate structures which probably are homologous with the correspondingly numbered structures in *Agraylea* (figs. 43 and 44). *1:* inflected posterior margin of Segment IX. *2:* hyaloid process on the median side of the lateral process. *5a:* "cordate ventral plate" (in B as seen in optical sagittal section). *5b:* left "paramere". *8:* lateral process of Segment IX. *16a* and *16b:* see p. 84; in A *16b* is seen from the haemocoelic side, in B both are seen from the edge.

antagonists (levator and depressor, respectively), the inferior appendage forming a sort of articulation with the ventral branch of the lateral process of Segment IX.

In my previous paper (1951, p. 125) I described "a sheath of the aedeagus" carrying a pair of "parameres". "The sheath" projects rather far backwards (in 1951, fig. B, its distal end is seen between the two inferior appendages) and forms a lower lip for the entrance to the phallocrypt. (The several times longer dorsal lip is formed by Segment X). Proximally the "parameres" (fig. 46, *5b*) are much dilated in a median direction, and quite proximally their sclerites are continuous on the ventral side, thus forming the "cordate ventral plate" (*5a*). The strong seta on the "paramere", alone, indicates that the two "parameres" and their "ventral plate" are homologous with the process *5* in *Orthotrichia* (figs. 40 and 41) and *Agraylea* (figs. 43 and 44; the distal part of the "parameres", beyond the setae, then must be considered homologous with the horn *6* in *Agraylea*). This assumption is confirmed by the fact that the

anterior ventral muscle of the inferior appendage is inserted on the "cordate ventral plate". The "parameres" (and also the "sheath of the aedeagus") thus belong to the inferior appendages, though they are not sclerotically connected with the appendages themselves. The dorsal side of the "paramere" projects anteriorly and laterally into a plate (fig. 46, *16 a*), lying in the floor of a narrow pocket issued from the genital chamber medially to the dorsal branch of the lateral process of Segment IX. Another plate (*16* b), issued from the sclerotic median side of the branch mentioned, lies in the roof of this pocket. At the bottom of the pocket the two plates are continuous. These two plates, which form a sclerotic connection between *5* (the "parameres") and Segment IX, are to be considered homologous with those structures which in *Orthotrichia* (figs. 39—41) and *Agraylea* (figs. 43 and 44) have been marked by the number *16*. (It will be noted that the connection in *Agraylea* as well as in *Hydroptila* passes below the process *2*).

The anterior ventral muscle of the inferior appendages is very strong and approximately cylindrical. As in *Agraylea* it is paired and the origins of the two muscles even are widely separated, being from the very laterooral points of Segment IX (medially to the origin of the anterior dorsal muscle; see above). It is inserted on the proximal margin of the "cordate ventral plate". This muscle acts as a retractor, a depressor, and perhaps also an adductor of the "paramere". The antagonist must be the elastic connection (through *16 a—b*) with Segment IX. The posterior dorsal muscle is lacking.

The phallus is very delicate, but it is not correct to call it membranous. It has the same shape as in *Agraylea*, though it is longer and slenderer. In a fully retracted state (in which condition I have not seen it in any preparation) it will reach to the posterior end or to the middle of Segment V. The titillator rises on the ventral side. It is first directed backwards for a short distance, then it is wound one and a half times round the phallus towards the right and forwards, and eventually it is directed backwards. Distally to the origin of the titillator a fine and rather deep, circular furrow runs in the whole circumference of the phallus; no doubt it is homologous with the semiannular thickening in *Agraylea*. The papilla on which the ejaculatory duct opens is even more prominent than in *Agraylea*.

The lack of an aedeagal retractor makes it difficult to decide in which way the undivided phallus in the Hydroptilidae has arisen. It might be supposed that it was formed by the phallobase, and that the small papilla on which the ejaculatory duct opens in *Agraylea* and *Hydroptila* is the last remnant of the aedeagus. Or that the endotheca had been obliterated, and the phallobase and the aedeagus fused, as is probably the case in *Rhyacophila* (p. 20) and the Psychomyidae (p. 37), and that the boundary between the phallobase and the endotheca should be sought in the vicinity of the origin of the titillator. The exact boundary might be the constriction proximally to the titillator in *Agraylea* and *Hydroptila*, or the circular furrow distally to the titillator in *Hydroptila*.

The last explanation involves that the titillator is homologous with the parameres

in the Rhyacophilidae and the Limnophilidae. I find it likely, however, that the hydroptilid titillator is homologous neither with the paired parameres in *Rhyacophila* and the Limnophilidae nor with the unpaired paramere in the Glossosomatinae. None of these structures contains a branch of the ejaculatory duct. I am inclined to consider the hydroptilid titillator as a secondary structure, which has no homologue in other Trichoptera. In some Hydroptilidae the phallus bears, besides the titillator, various other processes, which have a greater or less resemblance to the titillator (DENNING 1947 a, b, c). In the genus *Oeceotrichia* Ulm., on the other hand, the phallus lacks every sort of processes (ULMER 1951, p. 86).

A third explanation is possible, and this I find the most probable: the copulatory organ represents the aedeagus alone; the phallotheca has been reduced, and the endotheca has been merged entirely in the phallocrypt. What leads me to this conclusion is the semi-annular sclerite at the entrance to the phallocrypt in *Orthotrichia* (figs. 38 and 40, *13—13*). The two processes on this sclerite may be homologous with the parameres in the Rhyacophilidae and the Limnophilidae. This explanation being true, it means that the probable phallic apodeme in the Hydroptilidae is not strictly homologous with that of the other forms, but is an aedeagal apodeme, otherwise not present in the Trichoptera. The "spoon" on the distal end of the phallus possibly represents the ventral branch of the aedeagus, the small papilla at the bottom of the spoon in *Agraylea* and *Hydroptila* the dorsal branch; (this may be true also if the second explanation is preferred).

It must be admitted, however, that the sclerite *13—13* and its processes may be interpreted also as (non-musculated) paraprocts.

Anyway, the hydroptilid phallus is highly specialized. In the genera *Plethus* Hag. (ULMER 1951, pp. 63—65), *Sclerotrichia* Ulm. (l. c., pp. 74—75) and *Protoptila* Bks. (MOSELY 1954), also, the phallus is very much specialized, but in quite another way than in the Danish Hydroptilidae. See also pp. 145—46.

Sericostoma pedemontanum.

Segment IX (fig. 47, *1*) has a deep oral indentation both dorsally and ventrally. Between the indentations the oral margin forms a strong bulge, from the summit of which a slightly descendent longitudinal suture runs backwards. The suture marks the boundary between the origins of the IX/X muscle and the anterior dorsal muscle of the inferior appendages. The anterior phallic muscle, however, has its origin on both sides of the suture. Hence it is uncertain whether the latter can be considered homologous with the dorsal longitudinal suture in the Hydroptilidae (though the posterior dorsal muscle of the inferior appendages originates laterally—or ventrally—to it as in this family). On the ventral side the posterior border of the segment is produced into a broad, triangular ventral process (*2*).

Segment X (*3—4*) is long, tapering posteriorly and bent somewhat downwards. The dorsal and the lateral sides are sclerotized. A deep longitudinal furrow on the

membranous ventral side serves to receive the dorsal side of the phallus. On the dorsal side the sclerite of Segment X is entirely continuous with that of Segment IX, so that it is difficult to state the boundary between the two segments with certainty. An obtusely-angled, rounded bend seen in a lateral view (C) may be considered as the

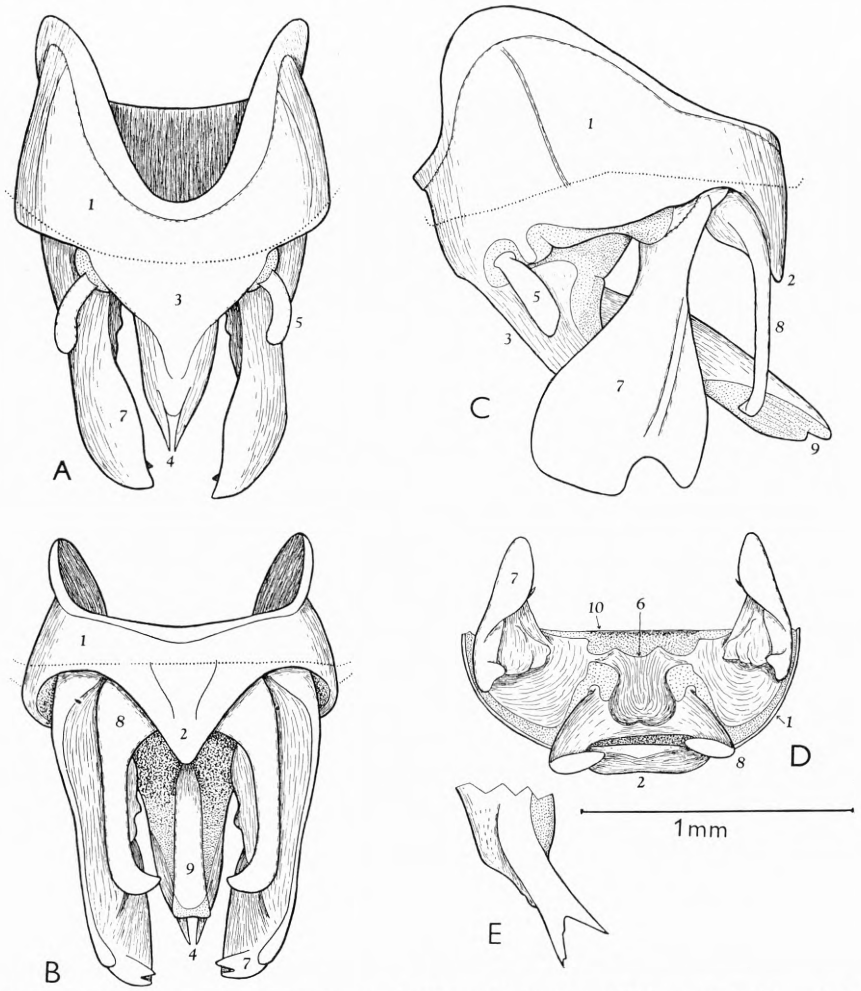

Fig. 47. *Sericostoma pedemontanum*. A—C: Segments IX and X in dorsal (A), ventral (B), and lateral (right, C) view; the coarsely dotted lines indicate the posterior border of Segment VIII. D: inferior appendages in posterior view. E: posterior end of Segment X in lateral (right) view. *1:* Segment IX. *2:* ventral process of Segment IX. *3—4:* Segment X. *5:* superior appendage. *6:* basal plate of inferior appendages. *7:* dorsal and *8:* ventral branch of inferior appendage. *9:* phallus. *10:* cut edge.

boundary, at least from a purely topographical point of view. On the lateral side the two segments are separated by a membranous area, at the dorsal end of which the small superior appendage (5) is implanted. Ventrally to the appendage the posterior margin of Segment IX has a narrow extension, the inwards bent distal end of which almost touches the anterior margin of the sclerite of Segment X. (The extension of Segment IX

lies at a more lateral level than the sclerite of Segment X, so that it does not prevent mutual movements of the two segments). The posterior end of Segment X is divided into three processes (*4*). The median, unpaired one is tongue-like with a strongly concave ventral side. Since it is bent rather much downwards, it in fig. 47 A appears less slender than it really is. The paired lateral processes (E) are sagittally compressed and their distal ends are divided into a dorsal and a ventral branch. (The shape varies a little). The ventral branches form a sort of phallus-guide. The well developed anus is found between the three processes, below the median one; (in B it is concealed by

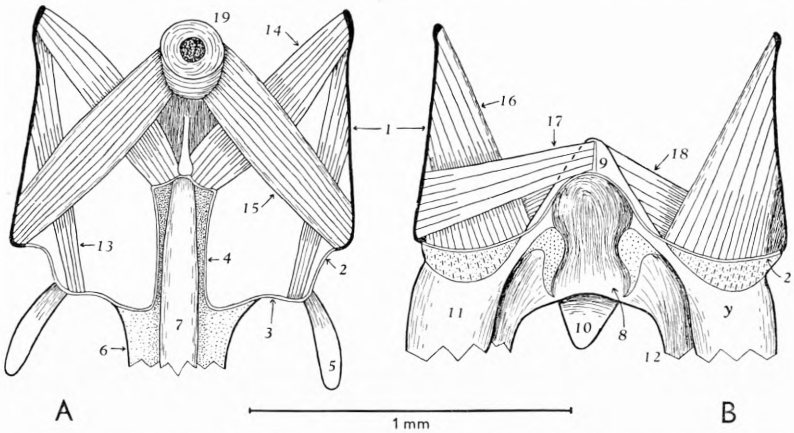

Fig. 48. *Sericostoma pedemontanum*. A shows the IX/X muscle and the phallic muscles in ventral view, B the muscles of the inferior appendages in dorsal view. *1—4:* cut edges, *1* through lateral side of Segment IX, *2* in A through membranous area between Segments IX and X, in B through membranous bottom of genital chamber (= *3* in A), *4* through wall of phallocrypt. *5:* superior appendage. *6:* Segment X (posterior part broken off). *7:* phallus (distal part broken off). *8:* basal plate of inferior appendages. *9:* apodeme on this plate. *10:* ventral process of Segment IX. *11:* dorsal and *12:* ventral branch of inferior appendage (distal parts broken off). *13:* IX/X muscle. *14:* anterior and *15:* posterior phallic muscle. *16—18:* muscles of the inferior appendages; *16:* anterior dorsal; *17:* posterior dorsal (removed on the right side); *18:* posterior ventral (possibly fused with anterior ventral). *19:* ejaculatory duct (cut through). In the pentagonal area between *19*, *14* and *15* the phallic apodeme (much shaded) is seen.

the phallus, *9*). The rather strong IX/X muscle is inserted on the anterior corner of the sclerite of Segment X.

The one-jointed inferior appendages (*7*, *8*) have a much complicated structure. Each appendage is divided into two branches: a smaller ventral (and median) one (figs. 47, *8;* 48 B, *12*) and a larger dorsal (and lateral) one (figs. 47, *7;* 48 B, *11*). The former is very thick-walled and devoid of setae. It is rod-like with an inwards curved and flattened distal end, so that it resembles a miniature golf club. Proximally the two ventral branches are continuous with each other and with the basal plate (figs. 47 D, *6;* 48 B; *8*), which is very concave. Proximally the dorsal branch has a somewhat flattened shaft. (It is flattened, however, in a plane which forms an angle of 45° with the horizontal plane; the median edge of the shaft lies at a more dorsal level than the lateral one). The larger distal part of the branch is much dilated, spoon-like, sagittally compressed and with an asymmetrical distal notch. The edges of the shaft continue as low keels on the median and the lateral side, resp., of the "spoon-

blade". The lateral keel is narrow and little prominent. The median keel soon becomes broad and cushion-like, but does not reach the distal end. Proximally the median side of the dorsal branch is connected with the basal plate by a narrow, sclerotic bridge (figs. 47 D and 48 B). In this way, only, a sclerotic connection is established between the two branches. Along the anterior margin of the bridge and of the basal plate there is a short apodeme (fig. 48 B, *9*), which is provided with a low, unpaired longitudinal ridge on the ventral side.

The very strong anterior dorsal muscle (fig. 48 B, *16*) originates from the oral two thirds of the lateral side of Segment IX (ventrally to the longitudinal suture) and

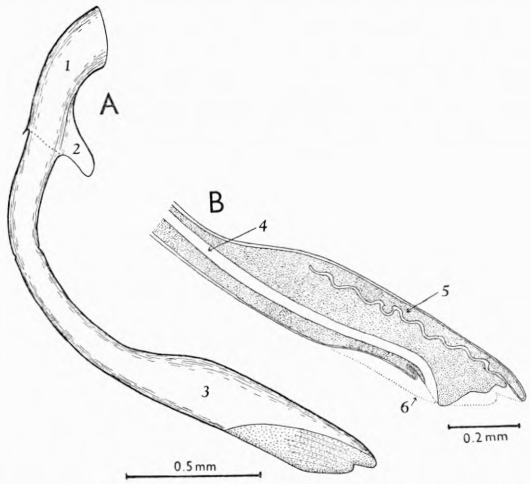

Fig. 49. *Sericostoma pedemontanum*. A: phallus in lateral (right) view. B: sagittal section through distal end of phallus. In B dotting indicates the haemocoele. *1:* phallic apodeme. *2:* ventral process on the latter. *3:* phallobase. The boundary between *1* and *3* is shown by a coarsely dotted line. *4:* ejaculatory duct. *5* (light, sinuous line): endotheca. *6* (dotted line): outline of dorsal longitudinal fold.

is inserted dorsally on the proximal margin of the dorsal branch. The posterior dorsal muscle (*17*) is inserted on the dorsal side of the apodeme *9*. The anterior and the posterior ventral muscles have fused into one very strong muscle (*18*), which originates from the whole ventral side of Segment IX and is inserted on the ventral side of the apodeme *9* and the anterior part of the ventral side of the basal plate. The two last mentioned muscles (*17* and *18*) act as a depressor and a levator, resp. Since *18* is the stronger of the two, the levation is more powerful than the depression. The anterior dorsal muscle is an adductor of the dorsal branches. (The ventral branches probably take no part in this movement). Its antagonist is—at least chiefly—elastic forces.

The phallus (figs. 47, *9;* 48 A, *7;* 49 A) is undivided, long, slender and curved much downwards. The membranous phallocrypt is deep, and there is also a long phallic apodeme (fig. 49 A, *1*). Distally on the ventral side of the latter there is a high, sagittally compressed process (2), the posterior side of which (as far as I can see) lies in the wall of the phallocrypt. The proximal half of the phallus is very slender. The

distal half (*3*) is thickened and sagittally much compressed, and distally its dorsal and lateral sides are membranous. In a lateral view the membranous part is slightly bilobed. The dorsal lip in its whole length (i. e. as far proximally as the membranous area reaches) is divided into two widely separated longitudinal folds, between which a membranous papilla is seen. This papilla is the distal end of an eversible, membranous and thin-walled structure. Or rather, it is that part of this structure which in an invaginated condition lies distally. The furrow which bounds the eversible part is quite low on the dorsal side, but very deep on the ventral side (fig. 49 B, 5). The strong aedeagal retractor, which originates in the phallic apodeme and fills up a great part of the "shaft" of the phallus, is inserted on the eversible structure. The latter probably represents the aedeagus. The phallus then is formed (almost exclusively) of the phallobase. The membranous aedeagus (in the invaginated state) is thrown into numerous folds. Hence I could not with certainty localize the opening of the ejaculatory duct (*4*), but it seems that it will come to lie proximally on the dorsal side of the aedeagus, when the latter is everted. — Proximally in the phallic apodeme the ejaculatory duct is provided with dilator muscles.

The phallic muscles (fig. 48 A), more especially the anterior one, are very strong. Their origins are at either end of the longitudinal suture of Segment IX. The two anterior muscles are inserted on the bottom of the phallocrypt on each side of the process (fig. 49 A, 2) of the phallic apodeme. The posterior muscle is inserted proximally and laterally on the apodeme.

Beraea maurus.

Segment VIII is slightly modified, the sternum being rather short.

Segment IX (fig. 50, *1*) is longest on the lateral side, whereas the length of the dorsal side is reduced by a deep oral indentation, and that of the ventral side by both oral and anal indentations.

Segment X (2) is scale-like, slightly tapering towards the posterior end and with a very concave ventral side. The greater, anterior part of the dorsal side is sclerotized, and this sclerite is continuous with that of Segment IX. The boundary may be stipulated in the same way as in *Sericostoma* (p. 86). The posterior part of the segment forms a hyaloid lamella, so delicate that in microscopic preparations it may be difficult to see its contour. The circular musculature of the rectum can be followed almost as far as the sclerite of the dorsal side goes. I have been unable to make out the exact position of the anus. It must be situated somewhere on the ventral side, and be very small and probably non-functional. On either side of Segment X there is a very deep, membranous indentation, which almost reaches the anterior margin of Segment IX.

Laterally to Segment X there is a pair of long, slender horns (figs. 50, *3;* 51, 2), which project beyond the posterior end of Segment X. Proximally the horn is directed outwards and backwards, but it soon becomes much inwards curved. It is sagittally compressed, and in its greater distal part the median side is slightly concave. In a

lateral view it is seen that the height of the horn proximally increases abruptly. The ventral side of this proximal, higher part is continuous with a triangular sclerite (fig. 51, *3*), which lies on the otherwise membranous ventral side of Segment X, and which —owing to the concavity of this side—is placed almost vertically. The IX/X muscle originates laterodorsally from the antecosta of Segment IX (laterally to the membranous indentation) and is inserted ventrally on the proximal, higher part of the horn. The horn possibly acts as a lever with the posterior border of Segment IX as a pivot, so that the function of the muscles will be to adduce—and perhaps also to some degree to depress—the horns.

The horns might be interpreted as the superior appendages. The fact, however, that they are musculated makes this assumption less probable. I find it most likely that they are homologous with the posterior, paired processes of Segment IX in *Sericostoma* (fig. 47, *4*). The superior appendage—which already in *Sericostoma* is much reduced —then is entirely lacking in *Beraea*, and what above simply has been called Segment X is the homologue of the unpaired median process in *Sericostoma*. (A small node orally on the lateral margin of the sclerite of Segment X may perhaps be considered as a rudiment of the superior appendage. It reminds also, however, of a paired, membranous process in *Molanna;* fig. 56, *4*, p. 100).

As in *Sericostoma* the inferior appendages, which are short and stout, are divided into a ventral (and median) branch (figs. 50, *5;* 51, *8*) and a dorsal (and lateral) branch (figs. 50, *4*; 51, *6*—*7*). The former approaches to the semiglobular shape, though it is longer than thick. On its distal end a small, backwards and inwards directed spine is seen. Quite proximally its sclerite is annular, but otherwise the greater part of the dorsal side is membranous. Distally from the membranous area a short, finger-like, upwards and backwards directed, sclerotic harpago (figs. 50, *6*; 51, *9*) arises. The harpago thus is situated subdistally on the coxopodite. The median side of the sclerite of the ventral branch is produced proximally and is continuous with the basal plate (fig. 51, *4*). Anteriorly the latter carries an unpaired ridge-like apodeme (*5*).

The proximal part of the dorsal branch forms a simple articulation with Segment IX, its lateral side resting in a shallow ginglymus (fig. 51, *10*) on a broad, inwards bent part of the posterior border of Segment IX. The distal part of the dorsal branch again is divided into two branches, of which the clumsy, finger-like dorsal one (*6*) is directed obliquely upwards, whereas the ventral branch (*7*) is bent inwards. The latter branch is much compressed, so that in a dorsal or ventral view it resembles an acute spine, and in a posterior view appears as a rounded plate situated behind the distal end of the ventral main branch of the appendage. (In fig. 50 D the number *6* and the companion arrow are placed on this plate). By a broad, sclerotic bridge the upper side of the dorsal branch is connected with the proximal, annular part of the sclerite of the ventral branch and through this with the basal plate. Besides there is an extensive membranous connection between the two branches.

In *Beraea* as in *Sericostoma* the inferior appendage is composed of two branches. A closer comparison, however, reveals that the position of the branches is the reverse

of that in *Sericostoma:* the dorsolateral branch in *Beraea* (fig. 51, *6—7*) corresponds to the ventromedian branch in *Sericostoma* (figs. 47, *8;* 48B, *12*), the ventromedian branch in *Beraea* (fig. 51, *8—9*) to the dorsolateral branch in *Sericostoma* (figs. 47,

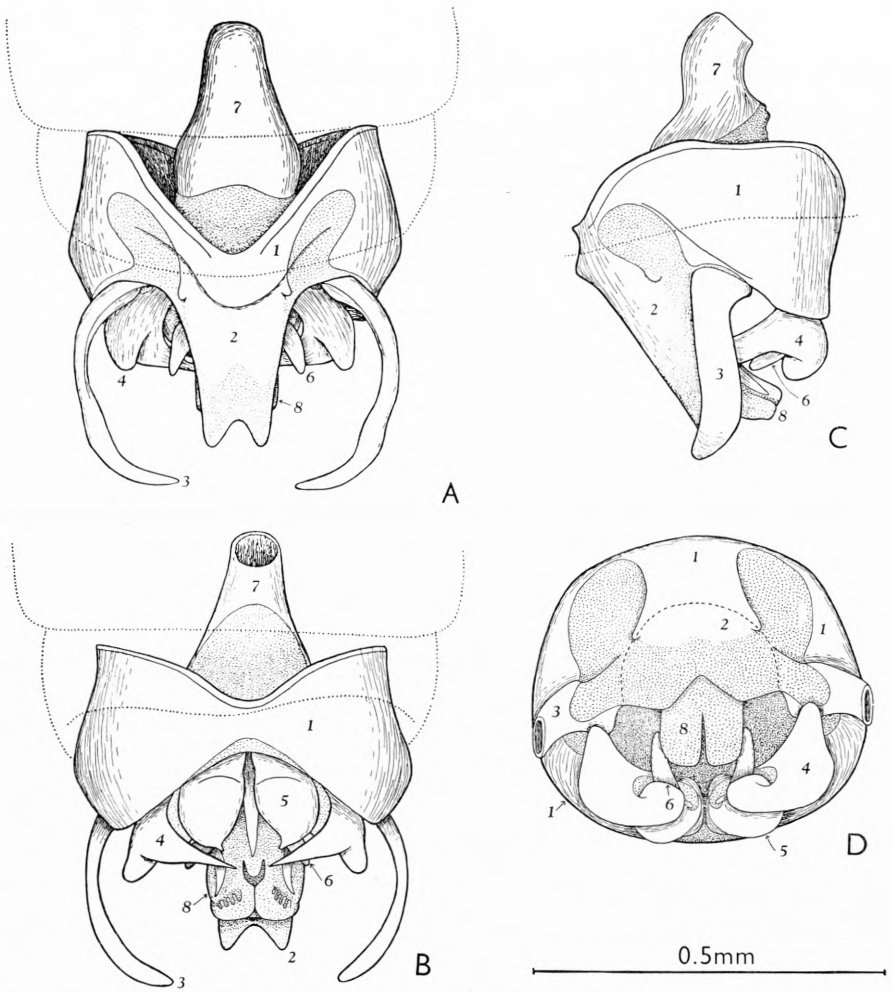

Fig. 50. *Beraea maurus.* Segments IX and X in dorsal (A), ventral (B), lateral (right, C), and posterior view (D). The coarsely dotted lines in A and B indicate the outlines of Segments VII and VIII, in C the posterior border of Segment VIII. The broken line in D indicates an optical transverse section through the ventral side of the anterior part of Segment X (corresponding to the sclerites *3* in fig. 51). *1:* Segment IX. *2:* median part of Segment X. *3:* lateral horn of Segment X (in D cut off near its base). *4:* dorsal branch of coxopodite. *5:* ventral branch of coxopodite. *6:* harpago. *7:* phallic apodeme. *8:* distal end of phallus.

7; 48, *11*). This appears from two facts. First: In *Beraea* it is the ventromedian branch which carries the harpago. In *Sericostoma* both branches are one-jointed, but the structure of the laterodorsal branch makes it probable that it was this branch

which was two-jointed in the ancestors of this genus, and nothing indicates that the medioventral branch has ever been two-jointed. Secondly (and this is more significant): The anterior dorsal muscle in *Sericostoma* is inserted on the dorsolateral branch, in *Beraea* on the ventromedian branch. A comparison with some other Integripalpia in which a more or less rudimentary dorsal branch is present, indicates that the condition in *Beraea* is the original one. The condition in *Sericostoma* may have arisen in

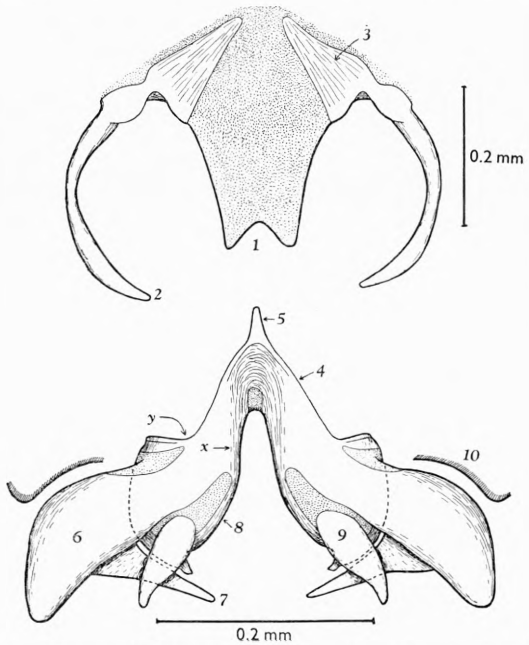

Fig. 51. *Beraea maurus*. Above: Segment X in ventral view. *1:* median part. *2:* lateral horn. *3:* sclerite supporting the latter. Below: Inferior appendages in dorsal view. *4:* basal plate. *5:* apodeme on basal plate. *6:* upper and *7:* lower secondary branch of dorsal branch of coxopodite. *8:* ventral branch of coxopodite. *9:* harpago. *10:* outline of ginglymus on posterior border of Segment IX.

the following way: The area labelled *x* in fig. 51 has been desclerotized, and the dorsal branch (*6*) has been shifted medially and ventrally, moving above the ventral branch. The bridges *y* in figs. 48 B and 51 are homologous.

The musculature of the inferior appendages are normally developed. The strong anterior dorsal muscle is inserted laterally on the proximal margin of the ventral branch (laterally to the arrow *y* in fig. 51). Due to the articulation between the dorsal branch and Segment IX (*6/10*) it must act as an adductor. The same function has the rather feeble anterior ventral muscle, which is inserted proximally on the lower side of the ventral branch. The two posterior muscles are inserted on the apodeme (*5*) of the basal plate. The dorsal one originates on the posterior border of Segment IX at the ginglymus *10* (i.e. rather ventrally). The two posterior muscles are a depressor and a levator, respectively. Acting together they probably also may be antagonists to

the anterior muscles. The flexor of the harpago originates proximally from the lower side of the ventral branch (which there is devoid of setae) and is inserted medially and orally on the proximal margin of the harpago.

The phallus (fig. 50, *8*) together with the phallic apodeme (fig. 52) is composed of two parts separated by a membranous articulation. The proximal part (fig. 52, *1*—*2*) is rather pear-shaped with the thin end proximally. Its dorsal side is more than three times as long as the ventral side. The latter in its whole extent is apodemal, whereas the distal, broader part (*2*) of the dorsal side has the character of a sclerotization in

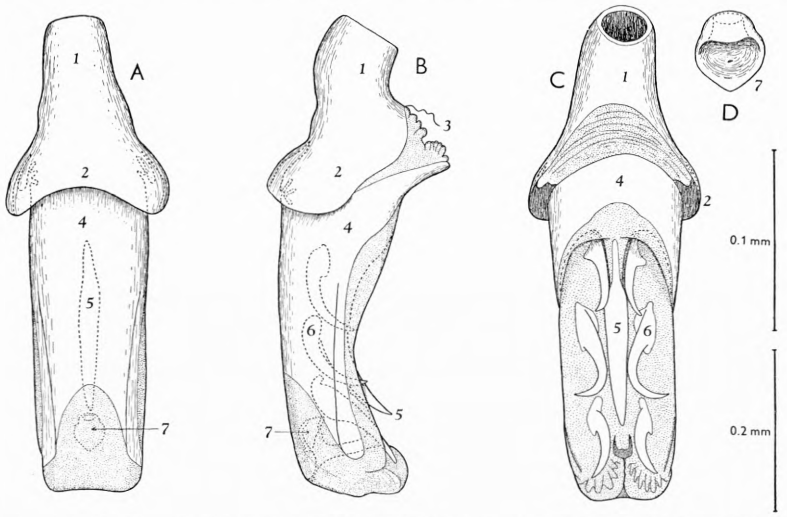

Fig. 52. *Beraea maurus*. A—C: phallus in dorsal (A), lateral (right, B), and ventral view (C). D: phallotremal sclerite (see p. 94) in ventral view. *1:* phallic apodeme. *2:* dorsal wall of phallocrypt (in A and B as seen from the haemocoelic side). *3:* part of ventral wall of same in optical section; in A and C this wall is removed. *4:* phallus. *5:* sclerotic longitudinal fold on ventral side of phallus; in A it is shown shining through (broken line), in B its freely projecting, spine-shaped distal end is seen. *6:* the middle one of the three paired spines. *7:* phallotremal sclerite.

the dorsal wall of the phallocrypt and like a roof projects above the base of the distal part. The distal part (*4*) is almost straight, only slightly downwards bent. Quite basally it is membranous and thrown into several wrinkles, which are much more numerous and more thin-walled on the ventral side than on the dorsal and lateral sides. On the lateral side one (the proximal) of these wrinkles is larger than the others and developed as a backwards directed fold, which is sclerotized (and sclerotically continuous with the proximal part) on the external side. The wrinkles must allow a considerable motility of the phallus, which, however, must be passive, since no muscles are inserted to the distal part. The wrinkles perhaps allow also protraction of the distal part by blood pressure. In this case the retraction also must be passive. After the membranous, wrinkled part there follows a short zone in which the phallus is entirely sclerotized. Ventrally the proximal edge of the sclerite is bent very much downwards. To its greatest extent, however, the distal part is sclerotized only on the dorsal side, which is enclosed

by the very concave lower side of Segment X. The sclerite moreover has a deep, distal indentation, and the extreme apex is entirely membranous. The lateral margin of the sclerite has an internal thickening. The membranous, but thick-walled ventral side is rather concave. Along its middle there runs a light brown, sclerotic longitudinal fold, the distal end of which projects freely as a large, backwards directed and somewhat downwards curved spine (*5*). This structure is flanked by three pairs of black spines (*6*). The proximal and the intermediate spine are curved downwards, the distal spine is curved backwards. The ventral side is much wrinkled, and the black spines to their greatest extent are lowered into membranous pockets (not shown in the figures).

The membranous apex, which is dilated in a ventral direction, is divided into three vertical lips, a pair of larger distal ones and a smaller proximal one. The three lips enclose a vertical U-shaped tube between them. The ventral end of this tube is the functional opening of the ejaculatory duct, which thus is subdistal on the ventral side of the phallus. The morphological opening is at the dorsal end of the U-shaped tube. It is surrounded by a strong, annular sclerite (*7*), the dorsal side of which is considerably longer than the ventral side. No muscles are inserted on this sclerite.

The posterior phallic muscle originates anally and lateroventrally from Segment IX (above the posterior dorsal muscle of the inferior appendage) and is inserted laterally on the proximal edge of the phallic apodeme (*1*). The anterior muscle originates laterally from the antecosta of Segment IX (ventrally to the IX/X muscle) and is inserted laterodorsally and distally on the sclerotic part of the phallocrypt (*2*). In the state of repose this muscle has an almost transverse course. There is no aedeagal retractor. In the phallic apodeme radial muscle bands go to the ejaculatory duct.

The lack of an aedeagal retractor renders it difficult to make out the comparative morphology of the phallus. Quite tentatively I shall suggest that the wrinkled basal portion of the distal part (*4*) is a reduced phallobase, and that the larger, partly sclerotized portion of the distal part represents the aedeagus. The distal, U-shaped tube then may be termed a phallotremal cavity, and the sclerite *7* (fig. 52) a phallotremal sclerite.

The shape of the genital segments is rather different in the Sericostomatinae and the Beraeinae; this is especially true as regards the phallus. The close relationship between the two subfamilies is revealed, however, in the structure of the inferior appendages.

Leptocerus cinereus.

Segment IX (fig. 53, *2—3*) is longest on the ventral side. On the dorsal side the acrotergite (fig. 54 A, *1*) is exceptionally large and very rich in possibly campaniform sensilla. Just behind the antecosta a pair of short, tongue-like, upwards and backwards directed dorsal processes (fig. 53, *6;* cut off in fig. 54 A) is seen. In a dorsal view they cover the posterior part of Segment IX and the anterior end of Segment X.

Segment X (figs. 53, *4;* 54 A, B) is long. Its posterior half is divided into a pair of

entirely sclerotized spines (*5*; *4*), which are a little flattened. In their whole length the two spines are curved slightly inwards, so that their upwards bent points almost touch each other. Although the bases of the two spines are contiguous above the anus (fig. 54 B), a comparison with *Molanna* (p. 99) and *Odontocerum* (pp. 101—02) indicates that they are homologous with the lateral processes in *Sericostoma* (fig. 47, *4*, p. 86). On the anterior half of the segment the dorsal side is much vaulted (transversally), whereas the ventral side is flat or (orally) slightly concave. The segment carries a pair of lateral sclerites, which are continuous with the two anal spines. In the middle of the ventral side the two sclerites almost reach each other (fig. 54 B, *3*), and on the dorsal side they are continuous for a short distance (fig. 54 A, *3*).

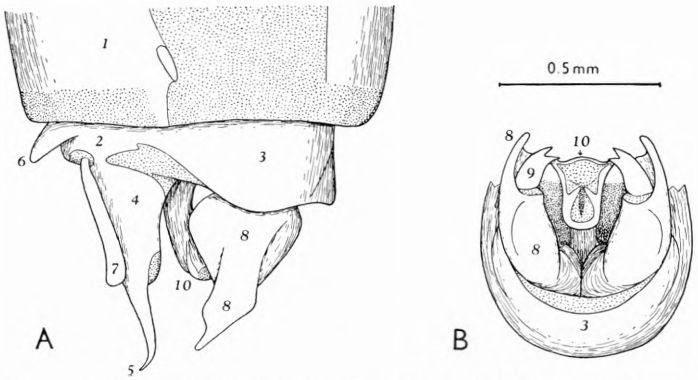

Fig. 53. *Leptocerus cinereus*. A: posterior end of abdomen in lateral (right) view. B: ventral part of Segment IX, inferior appendages and phallus as seen from behind and a little from the ventral side. *1:* Tergum VIII. *2:* dorsal and *3:* ventral part of Segment IX. *4:* Segment X. *5:* posterior spines ("intermediate appendages") of Segment X. *6:* dorsal process. *7:* superior appendage. *8:* coxopodite. *9:* harpago. *10:* phallus.

Laterodorsally the sclerites of Segments IX and X are continuous through a rather narrow bridge. Otherwise they are separated by three membranous areas, an unpaired dorsal one and a pair of laterals. Laterally in the dorsal area the long, slender and slightly clavate superior appendages (figs. 53, *7*; 54, *5*) are implanted. As in other Integripalpia it is difficult to state the boundary between Segments IX and X with certainty. From a purely topographical point of view the membranous areas may be considered as the boundary, but very likely the bases of the dorsal processes mark the true boundary.

The IX/X muscle is inserted on the proximal margin of the sclerite of Segment X ventrally to the bridge which connect this sclerite with that of Segment IX. Its function must be a depression of Segment X, and its antagonist the elasticity of the bridge mentioned; (the dorsal VIII/IX muscles probably move Segment IX + X as a whole).

The inferior appendages (figs. 53, *8—9*; 54 C) are rather long. They are two-jointed, though the harpago (*9*; *10*) is very short. In a lateral view the dorsal side of the coxopodite is strongly convex. The bulge appears as a narrow, sharp ridge, the edge of which is beset with strong, yellow setae. The ventral side, on the other hand,

is broadly rounded. The median side is slightly concave and proximally continuous with that of the other appendage, though a rather sharp furrow is seen between the two coxopodites. Dorsomedially and proximally on the appendage there is an area (fig. 54, 7) which is separated from the rest of the appendage by an approximately rectangular keel. The two areas 7 represent the basal plate which anteriorly is con-

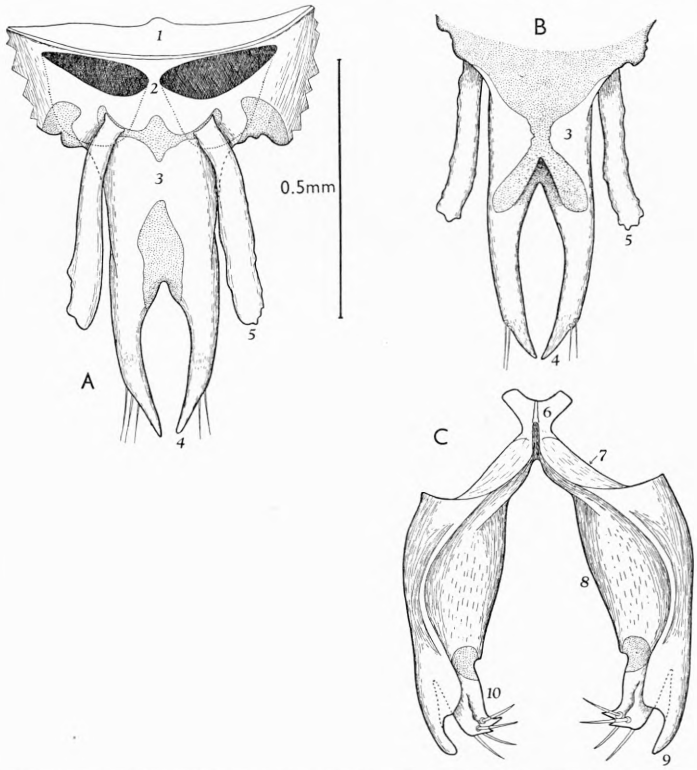

Fig. 54. *Leptocerus cinereus*. A: Segment X and dorsal part of Segment IX in dorsal view. B: Segment X in ventral view. C: inferior appendages in dorsal view. *1:* acrotergite of Segment IX. *2:* tergal region of Segment IX; the number is flanked by the cicatrices after the cut-off dorsal processes, the outlines of which are shown by coarsely dotted lines. *3:* sclerite of Segment X. *4:* posterior spine of Segment X. *5:* superior appendage. *6:* apodeme on *7:* basal plate of inferior appendages. *8:* coxopodite. *9:* distal process of coxopodite. *10:* harpago.

tinued as a Y-like apodeme (*6*), on the ventral side of which there is a longitudinal ridge, a continuation of the furrow separating the two appendages. The lateral side of the coxopodite is protracted into a sagittally compressed and medially concave process (*9*), which projects beyond and in a lateral view entirely conceals the small, claw-like, and bicuspid harpago (*10*). Laterodorsally the coxopodite and the harpago are sclerotically continuous, but the connection probably is flexible.

The anterior dorsal muscle is very strong. It originates from the whole lateral part of the antecosta of Segment IX and is inserted on the lateral half of the proximal margin of the coxopodite. The two ventral muscles are not so strong, but still they

are strong muscles. The anterior one is inserted medioventrally on the proximal margin of the coxopodite. The posterior ventral muscle originates ventrally from the proximal margin of the coxopodite. (The most median part of the origin distally to the insertion of the former muscle). It is inserted on the ventral side of the apodeme *6*. The anterior dorsal muscle and the anterior ventral muscle probably act as an abductor and an adductor, respectively. The posterior ventral muscle, also, may be an

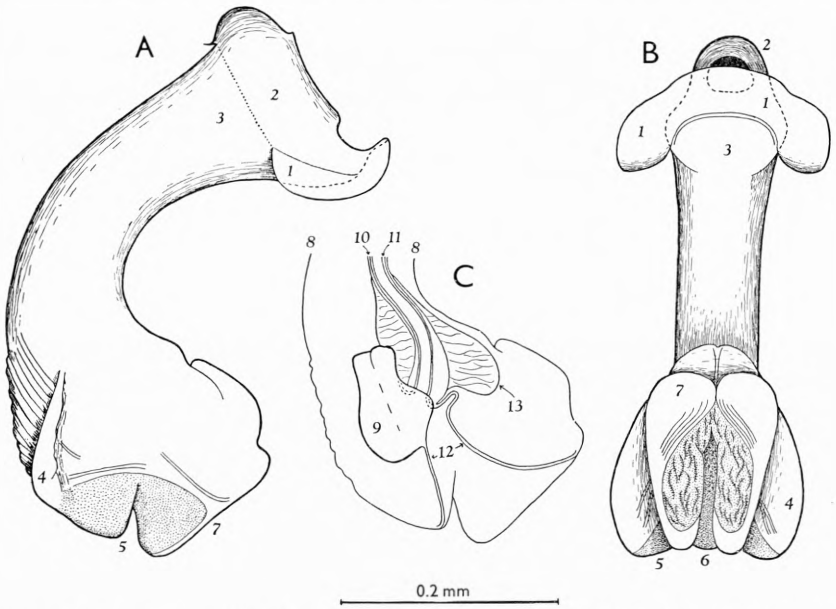

Fig. 55. *Leptocerus cinereus*. A and B: phallus in lateral (right) and ventral view. C: internal structures in distal end of phallus; lateral (right) view. *1:* rim-like sclerite in floor of genital chamber (in A seen from the haemocoelic side). *2:* phallic apodeme. *3:* proximal end of phallus (in A separated from *2* by a coarsely dotted line). *4:* sclerotic wing on distal end of phallus. *5:* lateral and *6:* median lobe of upper lip. *7:* right half of lower lip. *8—8:* outline of phallus. *9:* phallotremal sclerite (see p. 98). *10—13:* optical sagittal sections; *10:* epidermal and *11:* cuticular wall of ejaculatory duct; *12:* wall of phallotremal cavity (see p. 98); *13:* glandular mass.

adductor, but probably it has some relation to the movements of the phallus. The posterior dorsal muscle has been transformed into a phallic muscle (see below). The flexor of the harpago originates from the whole lateral side of the coxopodite and is inserted medially on the proximal margin of the harpago.

The undivided phallus (figs. 53, *10;* 55) is short and stout and sclerotized to its greatest extent. Basally it is directed obliquely upwards, but since it is very much curved its distal end comes to point almost straight downwards. The distal end is dilated and has a complicated structure. Laterodorsally there is a pair of sclerotized wings (fig. 55, *4*). In a lateral view a membranous area is seen below the posterior end of the wings. By a horizontal cleft this area is divided into two lips (*5*, *7*). A ventral view (B) reveals that the upper lip (*5*, *6*) is slightly trilobed, whereas the lower

lip (*7*) is strongly bilobed and sclerotized along the margin. The cleft between the two lips leads into a rather spacious cavity (C, *12*), at the bottom of which the ejaculatory duct (*10, 11*) opens. Above its opening, in the roof of the cavity, there lies a strong sclerite (*9*), a (proximal) part of which perhaps is apodemal. In a dorsal or ventral view the sclerite is broadest towards the proximal end of the phallus. The distal part of the ejaculatory duct is surrounded by a mass of (possibly unicellular) glands.

The phallocrypt is very feebly developed. Dorsally and laterally it appears only as a fine, membranous furrow, ventrally it is quite obliterated. There a crescent-shaped sclerite is developed in the floor of the genital chamber. This sclerite is continuous with that of the phallus and thus appears as a rim (*1*) on the proximal end of the latter (*3*). The greater, median part of the rim is bent forwards into a horizontal pocket between the phallus and the inferior appendages. The basal plate of the latter (fig. 54C, *7*) also is bent into the pocket and closely applied to the rim (*1*). The margins of the rim and of the basal plate are connected by quite a narrow, elastic membrane. The ventroproximal part of the phallus rests on the medioproximal part of the inferior appendages. The phallic apodeme (*2*) is very short.

The phallic musculature is highly specialized. The anterior muscle is lacking. The slender posterior muscle originates lateroventrally from the posterior border of Segment IX, approximately at the middle of the circumference of the inferior appendage. (Its origin thus has been shifted very much in a ventral direction). It is inserted laterodorsally on the phallic apodeme (*2*). Another and feebler muscle originates from the dorsal side of the apodeme of the basal plate of the inferior appendages (fig. 54C, *6*). Its bands spread fan-like and are inserted partly on the lateral side of the phallic apodeme (fig. 55, *2*), partly on the lateral part of the rim *1*. No doubt it is the posterior dorsal muscle of the inferior appendages, which has shifted its origin from the posterior border of Segment IX to the genital chamber (the rim *1*) and in part farther to the phallic apodeme. Initial stages of such a shifting are seen in *Tinodes* (pp. 34—35), *Agraylea* (pp. 79—80), and *Lasiocephala* (p. 109). In all these forms the muscle in question takes its origin from a sclerite in the genital chamber. At least as to the two first-mentioned forms it is a question of analogy only. The two muscles must act as a levator and a depressor, respectively. The depressor muscle is much weaker than the levator, but—owing to the close connection between the basal plate of the inferior appendages (fig. 54, *7*) and the rim *1* (fig. 55)—it probably is assisted by the posterior ventral muscle of the inferior appendage. The aedeagal retractor is lacking.

The latter makes it difficult to say anything with certainty about the comparative morphology of the phallus. I should consider it most likely that in *Leptocerus* we are concerned with a further development of the condition seen in *Lasiocephala* (p. 110), which means that the undivided phallus is formed by a fusion of the phallotheca and the aedeagus. The cavity (fig. 55, *12*) in the distal part of the phallus then is a phallotremal cavity, and the sclerite *7* a phallotremal sclerite. (See *Odontocerum*, p. 104, and *Oligoplectrum*, p. 114). The condition in *Leptocerus* might also be a further development of that in *Beraea* (p. 94), the phallobase having been entirely reduced.

Molanna angustata.

Segment IX (fig. 56, *3*) is short and more or less concealed by the overlapping posterior border of Segment VIII. Especially the dorsal and ventral sides are short, owing to oral indentations. The lateral side has an oral bulge and a lower anal bulge between the superior and the inferior appendage. Dorsally the posterior border projects like a roof above the oral end of Segment X.

Segment X (*5*) has a pair of lateral sclerites, which anally are protracted into a pair of sharply downwards bent processes (*6*), which are much sagittally compressed and sclerotized on both sides. They flank the distal end of the phallus. At the bases of the processes *6* the two sclerites almost touch each other on the dorsal side, being separated only by a narrow membranous stripe. Medio-orally the dorsal side of Segment X is membranous to a great extent. Anteriorly in this membranous area there is a pair of finger-like, membranous processes (*4*), which remind much of a pair of similar processes in the ♀, and which in this sex perhaps may represent cerci. In the ♂, at least, I am more inclined to think that they are homologous with the dorsal processes in *Leptocerus* (fig. 53 A, *6*). The membranous ventral side has in the middle a concavity, which receives the dorsal side of the phallus. The very distinct anus is between and below the bases of the processes *6*, ventrally bordered by a membranous lip, the upper (or inner) side of which in B is seen between the processes. A comparison with *Odontocerum* (pp. 101—02) strongly indicates that the processes *6* in *Molanna* are homologous with the lateral processes (fig. 57, *5*) in *Odontocerum*. This means that the processes mentioned in *Molanna* are homologous with the lateral processes in *Sericostoma* (fig. 47, *4*, p. 86), although they meet or almost meet above the anus. (Cp. also *Leptocerus*, p. 95).

The sclerites of Segment X are continuous with that of Segment IX through a pair of sclerotizations lying laterodorsally in the genital chamber. In these sclerotizations there is a pair of membranous "windows", ventrally in which the large, but rather feebly sclerotized superior appendages (*7*) are implanted. On the ventral edge the sclerite of the superior appendage is continuous with that of the genital chamber.

The IX/X muscle originates laterodorsally on the antecosta of Segment IX and is inserted medially on the ventral margin (at the arrow *9;* C) of the sclerite in the genital chamber. Its function probably is a depression and perhaps also an adduction of the processes *6*.

The large and much inwards curved inferior appendages (*12*) are one-jointed and of a very simple shape. The proximal half of the appendage is thicker than the distal half, sagittally compressed and with a concave median side. The distal half is approximately circular in a transverse section. Proximally and dorsally on the median side there is a spoon-like process (E, *11*), which is much flattened, has a slightly concave ventral side and is bent a little downwards. In all probability it is homologous with the dorsal branch in *Beraea* (and the ventral branch in *Sericostoma;* pp. 90—92). Proximally the two appendages are united, but chiefly by membrane. The

only sclerotic connection is through the basal plate (E, *10*), which lies in the floor of the phallocrypt; its anterior margin is separated from the phallus only by a quite narrow, membranous stripe.

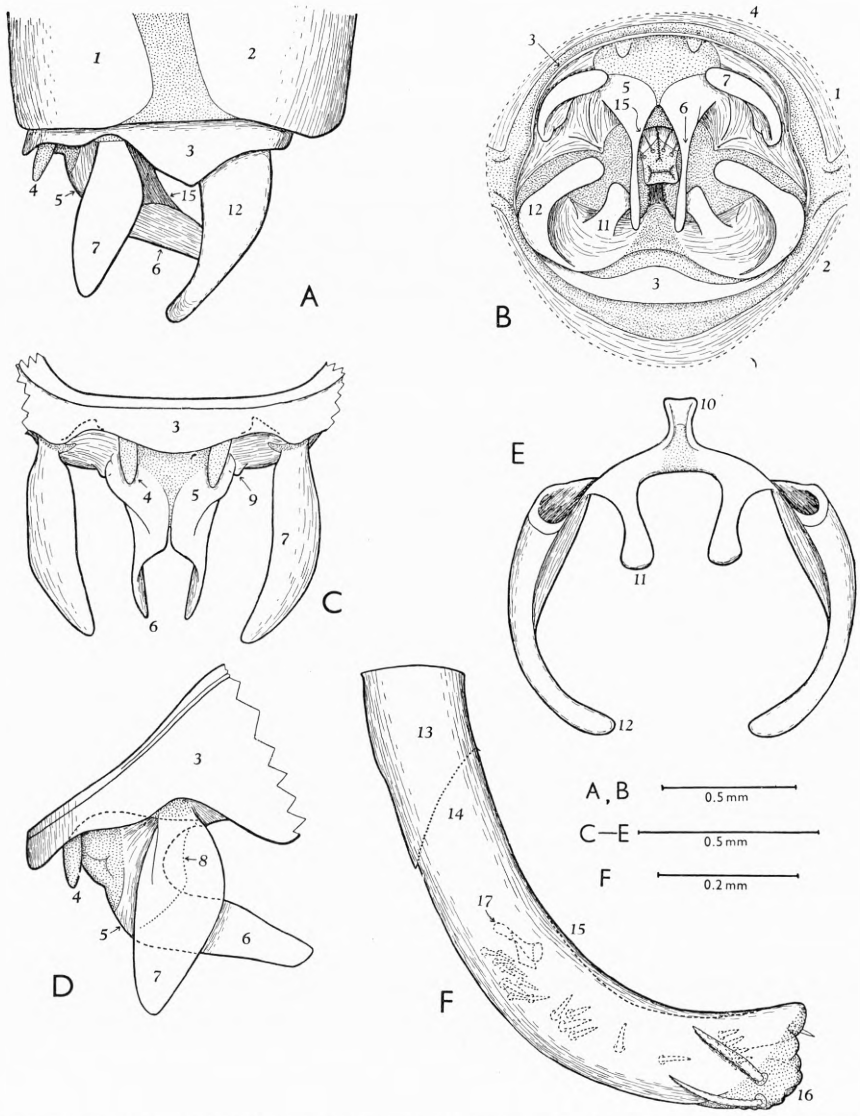

Fig. 56. *Molanna angustata*. A and B: posterior end of abdomen in lateral (right) and in posterior view. C and D: Segment X and dorsal part of Segment IX in dorsal and in lateral (right) view. E: inferior appendages in dorsal view. F: phallus in lateral (right) view. *1:* Tergum VIII. *2:* Sternum VIII. *3:* Segment IX. *4:* dorsal process (see p. 99; by a mistake an arrow pointing towards „S.W." has been omitted in B). *5:* sclerite of Segment X. *6:* posterior process of Segment X. *7:* superior appendage. *8:* (dotted line) outline of membranous ventral side of Segment X. *9:* point of insertion of the IX/X muscle. *10:* basal plate of inferior appendages. *11:* dorsal and *12:* ventral branch of inferior appendage. *13:* phallic apodeme. *14:* proximal, *15:* middle, and *16:* distal part of phallus; the setae of the endotheca are shown shining through. *17:* aedeagal sclerite (shining through; see p. 101).

The anterior dorsal muscle originates lateroventrally from the antecosta of Segment IX and is inserted laterally and dorsally on the proximal margin of the appendage. The anterior ventral muscle is inserted medially and ventrally on the proximal margin of the appendages. The two muscles probably act as a levator and a depressor, respectively. The two posterior muscles are lacking.

The slender and much downwards curved phallus (A, *15;* F) is formed by the phallobase. Except for the extreme distal end (*16*), which carries two pairs of very strong setae, it is sclerotized. Proximally the phallus is circular in a transverse section, more distally the ventral side is slightly concave; the concavity is bounded by a pair of broad, rounded longitudinal keels, which proximally are confluent. In the same region the dorsal side has a sharp and narrow longitudinal furrow. From the membranous distal end the (no doubt eversible) endotheca stretches approximately to the middle of the phallus (the phallic apodeme included). The endotheca is provided with short and thick setae, which are asymmetrically arranged (in fig. F the setae of both sides are shown shining through), and at the bottom of it there is an approximately saucer-like sclerite (*17*), on which the aedeagal retractor is inserted, and in the middle of which the ejaculatory duct opens on a high, tubular spout. It is difficult to say whether this sclerite represents a phallotremal sclerite as in *Odontocerum* (p. 104) and *Oligoplectrum* (p. 114), or it represents the whole aedeagus.

The phallocrypt is shallow, more especially so dorsally. Ventrally it is somewhat deeper, and as mentioned above, its floor is formed by the basal plate of the inferior appendages. There is a well-developed phallic apodeme (*13*).

The posterior phallic muscle originates from the posterior border of Segment IX, approximately in the middle of the lateral side, i. e. at the summit of the latero-anal bulge. It is inserted laterally and posteriorly on the phallic apodeme. The anterior muscle originates from the antecosta of Segment IX, approximately in the middle of the lateral side, i. e. at the summit of the latero-oral bulging. It is inserted laterodorsally on more than the distal half of the phallic apodeme.

Odontocerum albicorne.

Segment IX (fig. 57, *1*). The dorsal side is much reduced in length owing to an oral and an anal indentation. The former is rather evenly curved, the latter is approximately rectangular. At the boundary between the shorter dorsal part and the longer lateral part a distinct longitudinal suture is seen. The ventral side also is somewhat reduced in length by an oral indentation. Between the dorsooral and the ventrooral indentation the anterior margin makes a tongue-like bulge, on which the antecosta is very strongly developed. In the middle of the ventral side the posterior margin has a small, membranous indentation.

The rather large Segment X (figs. 57, *3—5;* 58 B) is sagittally compressed. The membranous ventral side is strongly concave, so that the segment forms a sort of bivalve sheath for the distal part of the phallus. The lateral sides of the segment are

sclerotized, and the sclerites (fig. 57, *3*) are produced posteriorly as a pair of much sagittally compressed processes (figs. 57, *5;* 58B, *2*), which are sclerotized on both sides. Dorsally, between these processes, there is an unpaired. finger-like, but much sagittally compressed process (*4; 1*), which is sclerotized on the dorsal side and distally on the ventral side, too. No doubt the three processes are homologous with the corresponding structures in *Sericostoma* (fig. 47, *4*, p. 86). The anus is found between the lateral processes and below the median one. Ventrally it is bounded by a membranous, slightly bilobed lip (fig. 58B). The sclerite on the median process (fig. 57, *4*) is connected with the lateral sclerites by narrow, sclerotic bridges (B). Furthermore, it is connected with the sclerite of Segment IX by a high and broad longitudinal keel (*2*), which probably represents a dorsal process homologous with the paired dorsal processes in *Leptocerus* (fig. 53A, *6*, p. 95) and the unpaired one in *Silo* (fig. 79, *7*, p. 139). The keel *2* and the narrow bridges mentioned form the only sclerotic connection between the sclerites of Segments IX and X. Otherwise they are separated by membranous areas, laterally in which the large superior appendages (figs. 57, *7, 8;* 58B, *6*) are implanted. The latter are leaf-like with a slightly convex lateral side and a slightly concave median side.

On the external side of the lateral processes (*5; 2*) a high and narrow longitudinal ridge is seen. It is highest orally, where it is protracted into a small, forwards directed spine (fig. 58, *3*). Another, backwards directed spine (*4*) is seen orally, near the ventral margin of the sclerite of Segment X. (The two spines thus are not situated at the same level, but the oral one considerably more ventrally than the anal one). Anteriorly to the last-mentioned spine the sclerite of Segment X is bent outwards as a "wing" (figs. 57, *6;* 58B, *5*), which lies at the bottom of the genital chamber, and the somewhat pointed lateral end of which is contiguous—but not continuous—with an inwards bent extension of the posterior margin of the sclerite of Segment IX. This extension flanks the dorsoanal indentation of the sclerite. The base of the superior appendage is, so to speak, wedged in between the dorsal margin of the "wing" and the posterior margin of Segment IX.

The strong IX/X muscle originates laterodorsally from the antecosta of Segment IX on the stretch between the summit of the laterooral bulge and the laterodorsal longitudinal suture. It is inserted on the ventral margin of the sclerite of Segment X at the median end of the "wing" (*6; 5*). The IX/X muscles must be able to depress and adduce the processes *5* (fig. 57) and probably at the same time cause some movement of the superior appendages.

The inferior appendages (fig. 57, *9—12*) have a large, slender coxopodite (*10*), which is almost circular in a transverse section. Basally it is directed much outwards, but since it is curved, the distal end comes to point almost straight backwards. The harpago (*12*) is small and finger-like. Together with a shorter, medioventral process (*11*) on the distal end of the coxopodite it forms a sort of chelicer. Proximally the median sides of the two appendages are continuous mutually and with the peculiar basal plate. The latter has the shape of a pot-like depression (*9*), the

length (= depth) of which is about twice the width. The "pot" is somewhat streamlined with the greatest width in the middle. On the dorsal side (which is an internal surface) there is a weak longitudinal ridge, on which muscles are inserted. Radiating

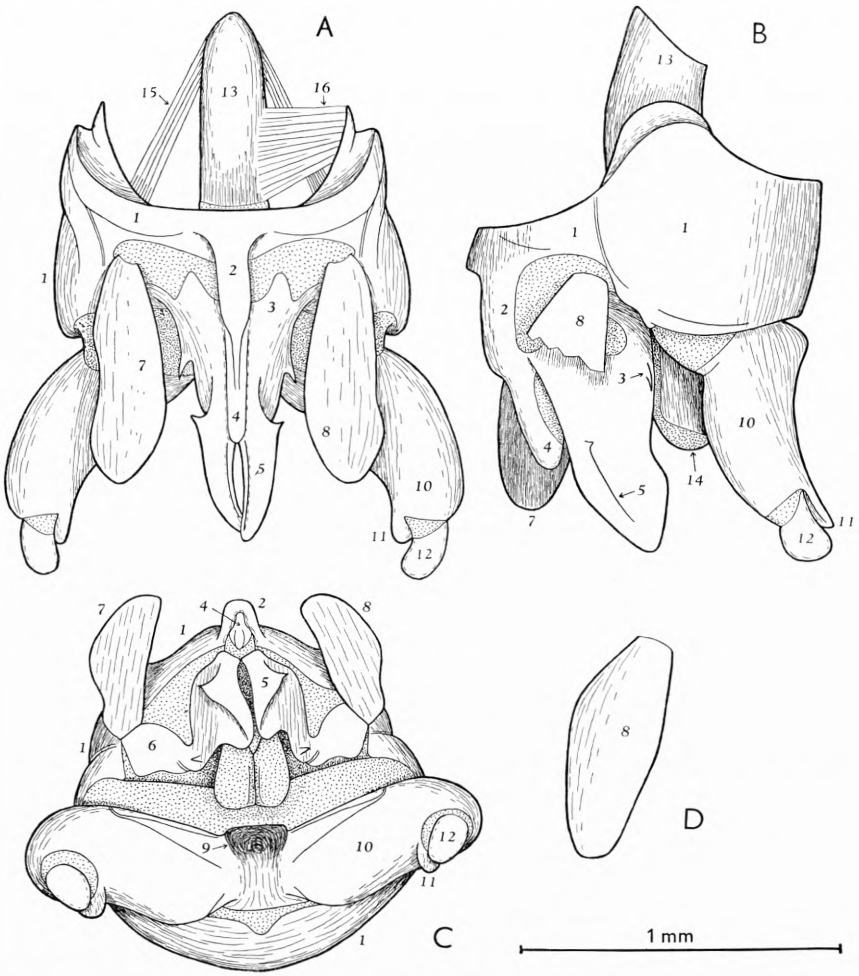

Fig. 57. *Odontocerum albicorne*. A—C: Segments IX and X in dorsal (A), lateral (right, B), and posterior view (C). D: right superior appendage in lateral view. *1:* Segment IX. *2:* dorsal process (see p. 102). *3:* oral part of sclerite of Segment X; in B the arrow points at the spine mentioned on p. 102 (= fig. 58 B, *4*). *4:* median and *5:* lateral process of Segment X; in B the arrow *5* points towards the longitudinal ridge mentioned on p. 102; in C the distal end of the phallus is seen below the two lateral processes. *6:* anterior "wing" of sclerite of Segment X (see p. 102). *7:* left and *8:* right superior appendage; in B the latter has been broken off near its base. *9:* basal plate of inferior appendages; the number is placed on the wedge-shaped area mentioned on p. 103. *10:* coxopodite and *11:* its distal process. *12:* harpago. *13:* phallic apodeme. *14:* distal end of phallus. *15:* posterior and *16:* anterior phallic muscle.

from the entrance to the "pot" there is dorsally on the median side of the coxopodite a wedge-shaped area, in which the cuticle is lighter and possibly also thinner; (in fig. 57 C the number *9* is placed in this wedge). The point of the wedge is bent dorsally

and continues as a narrow, irregularly winding stripe across the dorsal side of the appendage, approximately in the middle of the coxopodite.

The strong anterior dorsal muscle originates lateroventrally from the antecosta of Segment IX and is inserted dorsally on the proximal margin of the coxopodite. The likewise rather strong anterior ventral muscle is inserted on the median sides of the coxopodites ventrally to the entrance to the "pot" *9* (fig. 57 C). The posterior dorsal muscle is rather weak. It originates from the inwards bent extension of the posterior margin of Segment IX (at the lateral end of the "wing" *6:* fig. 57 C) and is inserted on the dorsal longitudinal ridge on the "pot" *9*. The posterior ventral muscle is stronger. It is inserted lateroventrally on the "pot". At least the majority of its bands originate from the proximal end of the ventral side of the coxopodite. An examination of the inferior appendages gives an impression that there is no motility between the two coxopodites. The movements then are levation (the anterior dorsal) and depression (the anterior ventral and the posterior dorsal). The function of the posterior ventral muscle is a puzzle to me, but perhaps the weaker area of the cuticle (the "wedge" described above) has something to do with it. The flexor of the harpago originates from almost the whole lateral side of the coxopodite.

Together with the phallic apodeme (fig. 57, *13*) the phallus (*14*) forms a rather regular, slightly downwards curved tube (fig. 58 A). The phallic apodeme (*7*) constitutes almost half of the length of this tube (when the aedeagus does not protrude). Since there is also a well-developed, though not very deep phallocrypt, the freely projecting part of the phallus is rather short. The phallus is divided into a phallobase (*9*) and an aedeagus (*10*). The latter is longer than the former, but that part of it which normally projects beyond the endotheca is shorter than the phallotheca. Proximally the phallotheca is entirely sclerotized, and the ventral side is sclerotized to the distal end, whereas the greater part of the dorsal side is membranous.

The aedeagus (fig. 58 C) has a sclerotic ventral side and a membranous dorsal side. That part of it which normally is withdrawn into the phallobase is almost semi-cylindrical. On the freely projecting part the membranous dorsal side is dilated so much that this part of the aedeagus is just as high as the phallobase. By a longitudinal furrow this cushion-like thickening is divided into two lips with almost contiguous edges. Proximally a much smaller, unpaired lip is wedged in between the two larger lips. These three lips enclose a cavity. On the floor of this cavity there lies a sclerite (fig. 58, *13*), in the middle of which the sclerotized distal end of the ejaculatory duct opens. From the proximal (anterior) end of the sclerite issues a pair of horn-like extensions, which are curved in semicircles so that their distal ends, lying on the lower side of the unpaired lip, come to point backwards. The strong aedeagal retractor, which originates from the proximal part of the phallic apodeme, is inserted on the sclerite. Since the latter is entirely separated from the sclerite on the external side of the aedeagus, I have decided to term it a phallotremal sclerite and the cavity which contains it a phallotremal cavity.

Proximally on the aedeagus two pairs of plate-like, strongly sclerotized para-

meres arise (*11*, *12*). Both pairs are short and normally do not project beyond the phallobase. The ventral pair (*12*) is the shorter and broader, triangular with acute points. The dorsal pair (*11*) is longer and narrower and has rounded points (fig. 58C;

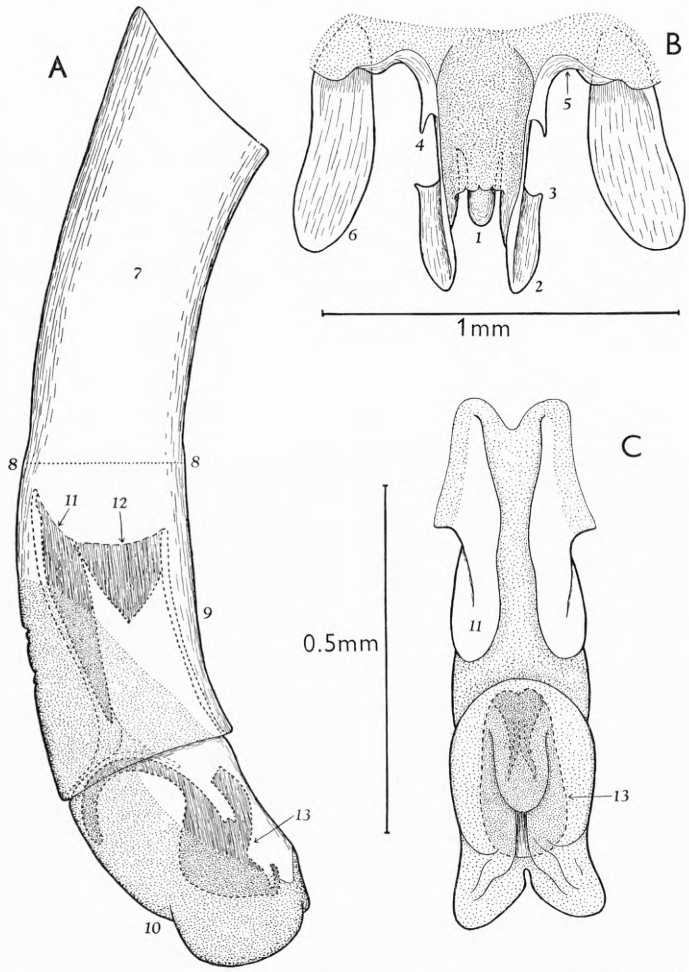

Fig. 58. *Odontocerum albicorne*. A: phallus in lateraï (right) view. B: Segment X in ventral view. C: aedeagus in dorsal view. *1:* median and *2:* lateral process of Segment X. *3* and *4:* the two spines mentioned on p. 102. *5:* the anterior "wing" of sclerite of Segment X (see p. 102). *6:* superior appendage. *7:* phallic apodeme. *8—8* (coarsely dotted line) indicates the boundary between *7* and *9:* phallobase; the broken lines are the outlines of the withdrawn part of the aedeagus and of the parameres. *10:* aedeagus. *11:* dorsal and *12:* ventral paramere (in A shining through). *13:* phallotremal sclerite (shining through).

in fig. B the dorsal paramere is seen from the edge and hence seems to be acutely pointed). Basally the two ventral parameres almost touch each other on the ventral side of the aedeagus, whereas the two dorsal ones are widely separated. Very likely the two pairs of parameres have arisen by division of one pair.

The anterior phallic muscle (fig. 57A, *16*) originates from the antecosta of Seg-

ment IX at the summit of the laterooral bulge, and is inserted laterally on more than the distal half of the phallic apodeme (*13*). In the state of repose this muscle has an almost tranversal course. The weaker posterior muscle (*15*) originates from the inwards bent extension of the posterior margin of the sclerite of Segment IX, just above the origin of the posterior dorsal muscle of the inferior appendage, and is inserted lateroventrally on the proximal end of the phallic apodeme.

Lasiocephala basalis.

Segment IX (fig. 59, *5*, *6*) is short, especially on the dorsal side, which is more or less completely concealed by the overlapping posterior border of Segment VIII. The length decreases gradually from the ventral side to the dorsal side, so that no distinct indentations are seen, except in the middle of the dorsal side, where there is a shallow anal indentation (fig. 60 B). Just in this place, however, it is difficult to state the boundary between Segments IX and X. On the ventral side there is a large, semicircular, membranous area, which almost reaches the anterior margin of the segment. Laterally to this area a pair of longitudinal sutures is seen. At the posterior end of the suture the edge of the sclerite has a slightly prominent, very much sclerotized node, which forms a simple articulation with the proximal margin of the inferior appendage.

Segment X (figs. 59, *8;* 60 B, *3*) is rather small. Its posterior half is divided into a pair of sagittally compressed processes, which are sclerotized on the lateral as well as on the slightly concave median side. The two processes, which probably are homologous with the lateral processes in *Odontocerum* (fig. 57, *5*), flank the subdistal part of the phallus. They are directed obliquely downwards and backwards; their pointed apices are bent upwards. In a posterior view (fig. 59 D, *8*) they converge dorsally. On the lateral side the sclerotization proceeds to the anterior margin of the segment and is continuous with that of Segment IX by a sclerotization lying in the genital chamber (fig. 59 D). On the dorsal side the sclerites of Segments IX and X are separated by a membranous—or at least very slightly sclerotized—area, which is raised into a pair of incompletely separated, cushion-like thickenings (figs. 59, *7;* 60 B, *2*). A comparison with *Oligoplectrum* (p. 111) indicates that we are concerned with a bipartite, much reduced dorsal process, homologous with the dorsal processes in *Leptocerus* (fig. 53 A, *6*, p. 95). Unlike (the rest of) Segment X the thickenings are covered with setae. Orally to the posterior processes the ventral side is membranous and concave. The small anus is found between the bases of the processes. Its ventral edge is deeply indented.

The IX/X muscle originates laterodorsally from the antecosta and adjoining parts of the surface of Segment IX, and is inserted on the ventral margin of the sclerite of Segment X, which there has a wedge-shaped, brown thickening. The muscle, which is not particularly strong, has almost parallel, steeply descendent bands. It can

adduce the posterior process. (In some preserved specimens the dorsomedian edges of the two processes touch each other).

Superior appendages are lacking.

The slender and apparently one-jointed inferior appendages (figs. 59, *10—11;* 60 A) are curved a little inwards and in their usual position directed somewhat up-

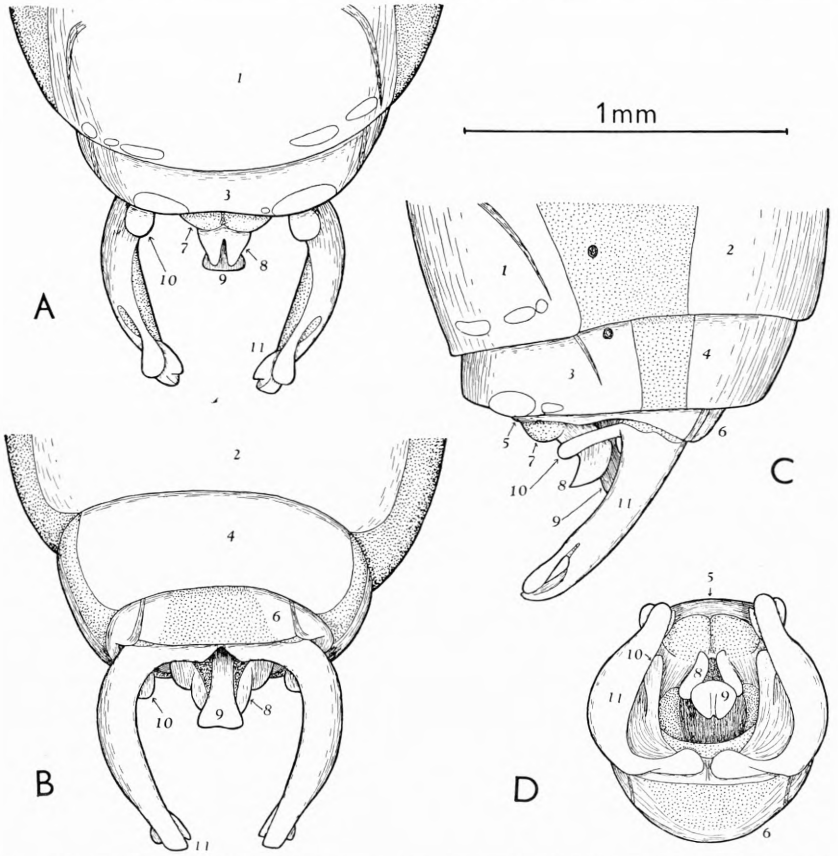

Fig. 59. *Lasiocephala basalis.* A—C: posterior end of abdomen in dorsal (A), ventral (B), and lateral (right) view (C). D: Segments IX and X in posterior view. *1:* Tergum VII. *2:* Sternum VII. *3:* Tergum VIII. *4:* Sternum VIII. *5:* dorsal and *6:* ventral part of Segment IX. *7:* dorsal process. *8:* lateral process of Segment X. *9:* distal end of phallus. In D the much shaded area below *8* and *9* is the proximal, broader part of the phallus. *10:* dorsal and *11:* ventral branch of inferior appendage.

wards. The apex is bifurcated. The dorsal prong (fig. 60 A, 7) is pear-shaped and much flattened. Proximally to it there is on the dorsal side a low, rounded keel, which is separated from the lateral side by a narrow, membranous area. The ventral prong is thicker and is again partly divided into two prongs. Except for the bifurcated apex the greater, distal part of the median side of the appendage is membranous. Dorsally from the proximal, sclerotized and slightly concave part of the median side issues an upwards and backwards directed branch (5), which is club-shaped and slightly

flattened. This structure, no doubt, is homologous with the dorsal branch in *Beraea* (fig. 51, *6*, p. 92). Proximally the median sides of the two appendages are united, though a vertical furrow is seen between them. The latter, however, is sclerotized and forms an internal ridge. The appendages moreover are connected with the basal plate (*4*), though this connection consists only of a pair of very narrow, but strong bridges issued from the bases of the dorsal branches (*5*). In continuation of these

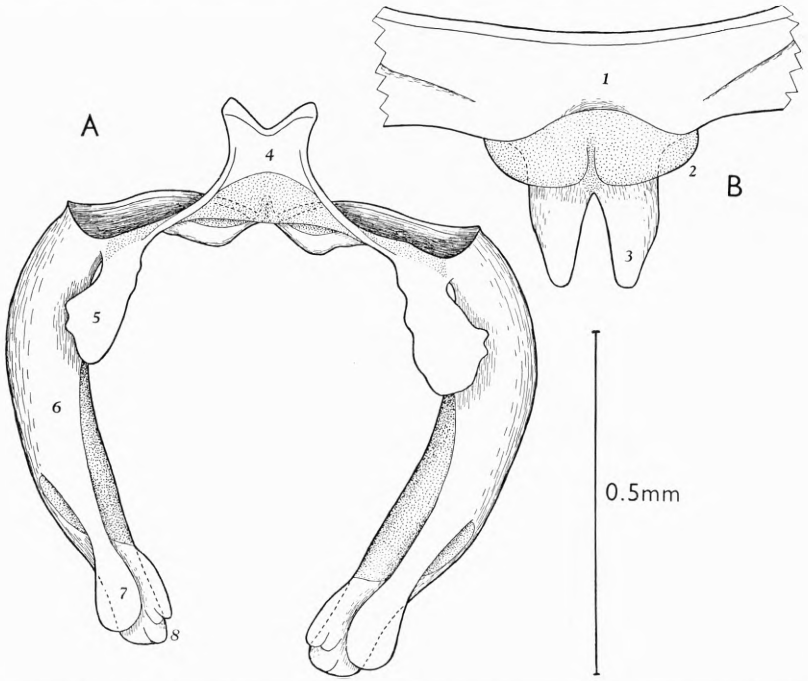

Fig. 60. *Lasiocephala basalis*. A: inferior appendages in dorsal view. B: Segment X and adjacent parts of Segment IX in dorsal view. *1:* dorsal part of Segment IX. *2:* dorsal process. *3:* lateral process of Segment X. *4:* basal plate of inferior appendages. *5:* dorsal and *6:* ventral branch of coxopodite. *7:* distal projection of same. *8:* harpago.

bridges the posterior half of the lateral margin of the basal plate is thickened internally. The concave anterior margin, also, is thickened. Between the posterior margin of the basal plate and the median sides of the inferior appendages a rather large membranous area is seen.

The strong anterior dorsal muscle originates lateroventrally from the antecosta of Segment IX and is inserted dorsally on the proximal margin of the appendage. The insertion stretches from the base of the branch 5 to the middle of the bridge connecting the latter with the basal plate. The anterior ventral muscle is still stronger. The majority of its bands are inserted ventrally on the median two thirds of the proximal margin, the rest on the vertical, internal ridge between the two appendages. The origins of the two anterior muscles are separated by the ventrolateral longitudinal

suture of Segment IX. The posterior dorsal muscle originates from the sclerite in the genital chamber (which connects the sclerites of Segments IX and X). Its converging bands are inserted on the anterior corner of the basal plate. The strong posterior ventral muscles stretch between the lower side of the basal plate and the appendage itself. From the basal plate its bands converge towards their insertion laterally on the proximal margin of the appendage. Possibly there are only a slight ab- and ad-

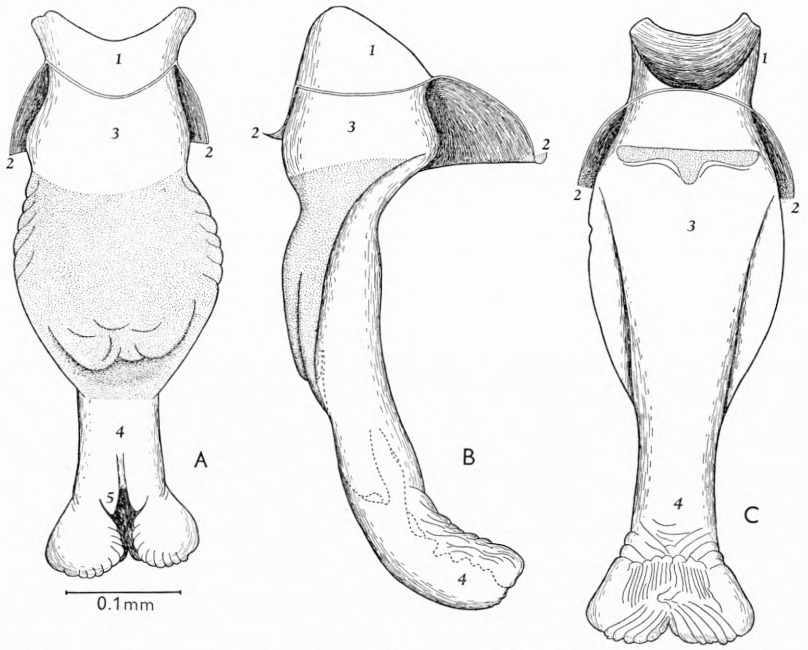

Fig. 61. *Lasiocephala basalis*. Phallus and phallocrypt in dorsal (A), lateral (right, B), and ventral view (C). In A the the dorsal, in B the right, and in C the ventral part of the phallocrypt is removed. *1:* phallic apodeme. *2—2:* cut edge through wall of phallocrypt. *3:* proximal and *4:* distal part of phallus. *5:* lip flanking the opening of the ejaculatory duct.

duction, if any at all. The anterior muscles then are a levator and a depressor, respectively. The posterior muscles perhaps may cause an independent movement of the branch *5* (provided that the connection with *6* is flexible), or they may be included in the mechanism of the phallus.

Although the appendage apparently is one-jointed, there is a well-developed and even very strong flexor of the harpago, which originates from more than the proximal half of the lateral side and is inserted medially on the proximal margin of the sclerotization of the ventral prong (*8*). This shows that the ventral prong represents the harpago, though not the slightest suggestion of an articulation is seen on the lateral side. (On the median side the harpago is bounded proximally by the membranous part of this side). The strong flexor indicates that the prong *8* must be capable of some movement.

The phallus (figs. 59, *9;* 61) is highly specialized. It is undivided; as will be

shown below, this condition has arisen by obliteration of the endotheca and subsequent fusion of the phallotheca and the aedeagus. From a purely topographical point of view the phallus may be described as consisting of two parts. The larger, proximal part (fig. 61, *3*) is—in a dorsal or ventral view—approximately ovoid and rather much flattened, being provided with large, thin, lateral wings. The ventral side of this part is sclerotized, though with a transverse, membranous area near the proximal end. The dorsal side is sclerotized proximally, but its larger part is membranous. The distal part of the phallus (*4*) is entirely sclerotized, and on the ventral side its sclerite is continuous with that of the proximal part. It consists of an approximately cylindrical shaft and a dilated, somewhat flattened, much downwards curved and slightly bilobed apex. The dorsal side of the latter is spoon-like excavated, but the edges of the "spoon" very much approach to each other. Anteriorly at the bottom of the "spoon" the ejaculatory duct opens, flanked by a pair of sclerotic, immovable lips (*5*). In the distal part of the ejaculatory duct (which is surrounded by a thick glandular mass) a small sclerite is seen on the ventral side. The strong aedeagal retractor originates proximally and dorsally in the phallus and is inserted dorsally on the proximal end of the shaft of *4*. It must be able to give some levation of the distal part. A transverse fold distally on the dorsal membranous area probably has some connection with this movement, the pivot of which perhaps is the proximal membranous area on the ventral side.

The insertion of the aedeagal retractor shows that at least the distal part (*4*) belongs to the aedeagus. Since this muscle generally is not inserted proximally in the aedeagus, the latter probably includes also part of *3*. The transverse membranous area on the ventral side perhaps mark the boundary between the phallobase and the aedeagus. The spoon-like depression on the distal end then is a phallotremal cavity (cp. *Odontocerum*, p. 104, and *Oligoplectrum*, p. 114), and very likely it is homologous also with the "spoon" in the Hydroptilidae (figs. 42, p. 75; 43 A, p. 78; 45, p. 81).

The phallocrypt (*2*—*2*) is sclerotized proximally. On the dorsal side the sclerite covers about the proximal half, on the ventral side, where the phallocrypt is deeper and very spacious, it reaches the entrance except in the very middle. Lateroventral extensions of the sclerite are bent downwards and forwards; they come to lie in the roof of a pocket, the floor of which is formed by the basal plate of the inferior appendages, and eventually they fuse with the anterior corners of the latter. The phallic apodeme (*1*) is short, especially so ventrally; in the middle of the ventral side its length is reduced to nil.

The posterior phallic muscle originates from the sclerotization in the genital chamber just above the posterior dorsal muscle of the inferior appendages; in its whole course it is rather closely applied to this muscle. It is inserted on the lateral side of the apodeme. The anterior muscle originates from the antecosta of Segment IX, a little ventrally to the middle of the lateral side, and is inserted dorsally, partly on the phallic apodeme, partly on the sclerotic part of the phallocrypt. The two muscles possibly act as a depressor and a levator, respectively.

Oligoplectrum maculatum.

Segment IX (fig. 62, *1*), which largely is withdrawn into Segment VIII, is short. Especially dorsally and lateroventrally the length is much reduced by deep oral indentations. Between the two lateroventral indentations the anterior margin makes a large ventral bulge. This would have given the ventral side a considerable length, if the posterior margin had not been deeply indented. Between the lateroventral and the dorsal indentation the anterior margin forms a broader and lower bulge. On the lateral side the posterior border of the segment has a broad and low bulge. This is sclerotized on the lateral as well as on the median side, and dorsally on the median side the sclerite is continuous with that of Segment X.

Segment X (figs. 62, *3;* 63) is short, very broad anteriorly and much attenuated towards the slightly bilobed posterior end. It is somewhat flattened and has a very concave ventral side. The dorsal and the ventral side are membranous. The lateral side is sclerotized, and this sclerite is continuous with that of Segment IX, partly—as mentioned above—through the latero-anal bulge of Segment IX, partly through a narrow bridge between this bulge and the dorsal process. The latter (figs. 62, *2;* 63, *3*), which arises between Segments IX and X, is large, broad, and much flattened (with a convex dorsal side); it has a deep anal notch, so that a pair of triangular lobes is formed. These lobes are sclerotized on the dorsal side, whereas the medio-oral area

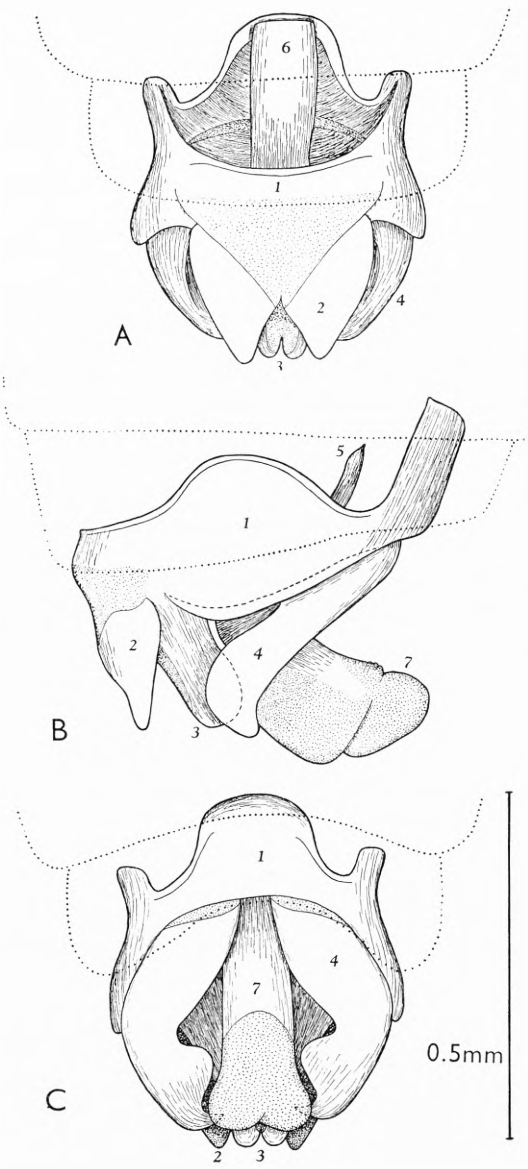

Fig. 62. *Oligoplectrum maculatum*. Segments IX and X in dorsal (A), lateral (right, B), and ventral view (C). The coarsely dotted lines indicate the outlines of Segment VIII and of the posterior end of Segment VII. *1:* Segment IX. *2:* dorsal process. *3:* Segment X. *4:* inferior appendage. *5:* basal plate of inferior appendages. *6:* phallic apodeme (not seen in B, since the phallus there is much protracted). *7:* phallus. The much shaded area which in B is seen between *1* and *4* is part of the phallus. In C the much shaded area between *4* and *7* is the broadly rounded ventral edge of Segment X.

of the dorsal side of the process as well as its whole ventral ventral side are membranous. The dorsal process in *Oligoplectrum*, no doubt, is homologous with the paired dorsal processes in *Leptocerus* (p. 94).

The small anus is situated in the furrow between the dorsal process and Segment X. This clearly shows that the processes *4* (fig. 63) are homologous with the lateral processes in *Sericostoma* (fig. 47, *4*, p. 86), since it is impossible that the median process in the latter form can shift its position in relation to the anus. They certainly are homologous also with the processes *3* in *Lasiocephala* (fig. 60 B).

The IX/X muscle originates laterodorsally from the antecosta of Segment IX, i. e. on the dorsal side of the lateral bulge of the anterior margin, and is inserted

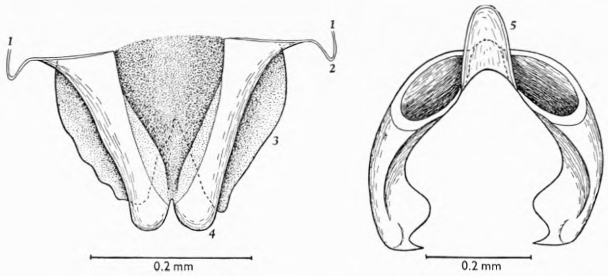

Fig. 63. *Oligoplectrum maculatum*. Segment X in ventral view and inferior appendages in dorsal view. *1:* cut edge through lateral part of Segment IX and through the sclerotic bridge connecting Segments IX and X (see p. 111). *2:* posterior edge of lateral part of Segment IX. *3:* dorsal process. *4:* Segment X. *5:* basal plate of inferior appendages.

orally on the ventral margin of the sclerite of Segment X. It has an almost horizontal course. I do not venture to make any statement on the function of this muscle.

Superior appendages are lacking.

The inferior appendages (figs. 62, *4;* 63) are short, strong and one-jointed. In their usual position they are much upwards directed. In a lateral view the apex again is bent downwards; it terminates in a strong, inwards directed spine. The median side of the appendage is very concave. The lower edge of the concavity on a whole is more prominent than the upper edge, and just proximally to the apex it moreover has an approximately semi-circular bulge. By movements of the inferior appendages (and of Segment X?) the anal end of Segment X may be brought to rest in the cavity between this bulge and the upper edge. Proximally the median sides of the two appendages are continuous mutually and with the basal plate (fig. 63, 5), which forms the floor of a pocket between the inferior appendages and the phallocrypt.

The strong anterior dorsal muscle originates lateroventrally from the antecosta of Segment IX, i. e. ventrally from the lateral bulge of the anterior margin. Its descendent bands are inserted dorsally on the proximal margin of the appendage. The still stronger anterior ventral muscle originates from the ventral part of the antecosta of Segment IX (the ventral bulge of the anterior margin) and is inserted ventrally on the proximal parts of the median sides of the appendages. The origins

of the two anterior muscles are separated by the lateroventral indentation of the anterior margin. The rather weak posterior dorsal muscle originates laterodorsally from the posterior border of Segment IX and is inserted on the anterior margin of the basal

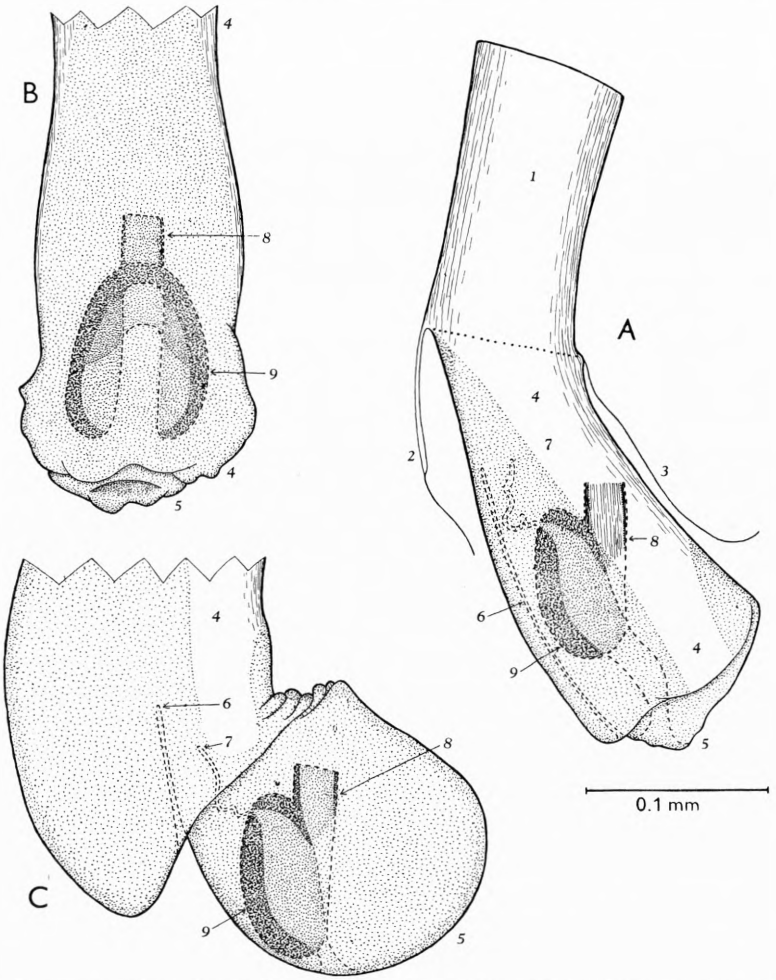

Fig. 64. *Oligoplectrum maculatum*. A: phallic apodeme and phallus in lateral (right) view. B and C: (distal part of) phallus in dorsal and in lateral (right) view. In A and B the aedeagus is retracted, in C it protrudes (but possibly not maximally). *1:* phallic apodeme. *2* and *3:* optical sagittal sections through dorsal and ventral wall of phallocrypt. *4:* phallobase. *5:* aedeagus. *6* (broken line): endotheca. *7* (broken line): blind end of phallotremal cavity. *8:* distal end of ejaculatory duct. *9:* phallotremal sclerite.

plate. The posterior ventral muscle stretches between the lateral margin of the basal plate and the lateral part of the proximal margin of the appendages. The most important movements of the inferior appendages possibly are levation and depression, though some abduction and adduction perhaps also may take place.

The phallocrypt (fig. 64 A, *2—3*) is deep. Its dorsal side is sclerotized proximally.

The cylindrical phallic apodeme (figs. 62, *6*; 64 A, *1*) also is of a considerable length. The phallus (*7*; *4*—*5*), on the other hand, is rather short. It is divided into a phallobase (fig. 64, *4*) and an aedeagus (*5*). At the extreme proximal end the phallotheca is entirely sclerotized. Otherwise the dorsal side is membranous, and the ventral side sclerotized. The latter, however, has a distal, membranous indentation, so that the sclerite reaches the distal end of the phallotheca on the lateral side only. The aedeagus is entirely membranous and in the state of repose completely, or almost completely, withdrawn into the endotheca. Dorsally the endotheca (*6*) is deep; in a ventral direction the depth decreases, and quite ventrally the endotheca is wholly obliterated. When the aedeagus is protruded by blood pressure, a strong bend therefore arises between it and the phallobase. The aedeagus contains a deep, eversible phallotremal cavity (cp. *Odontocerum*, p. 104). The latter to its greatest extent is membranous, but near (not at) the bottom it has a strong, annular sclerotization (*9*), a phallotremal sclerite, which has two distal indentations: a deep and narrow dorsal one and a broad and shallower ventral one. (The phallotremal sclerite has some resemblance to the gaping shells of a bivalve. Proximally it forms a pot-like cavity, though with a fine opening, through which the phallotremal cavity continues as a membranous cul de sac). The ejaculatory duct (*8*), the distal end of which is sclerotized, opens in the ventral indentation. The phallotremal sclerite of course delimits the degree of eversion of the phallotremal cavity. The aedeagal retractor originates proximally from the phallic apodeme. It is strong and fills up most of the lumen of the phallus. It is inserted—at least chiefly—on the phallotremal sclerite.

The posterior phallic muscle originates laterodorsally and anally from Segment IX and is inserted laterally and proximally on the phallic apodeme. The weaker anterior muscle originates from the antecosta of Segment IX at the summit of the lateral bulge and is inserted on the sclerotized part of the dorsal side of the phallocrypt.

Agrypnia pagetana.

Segment IX (fig. 65, *3*—*4*) is rather short. In the figure it is to a great extent concealed by the overlapping posterior border of Segment VIII (*1*—*2*). The segment is longest lateroventrally. The length of the ventral side is reduced by shallow oral and anal indentations, that of the dorsal side by a deep oral indentation. On the other hand, about the dorsal fourth of the posterior border is protracted into a short and very broad, tongue-like dorsal process (*3*), which is sclerotized on the upper as well as on the lower side, and the posterior edge of which is closely beset with long and strong, backwards directed, yellow setae. (The belt of setae is about three "rows" broad. In A the setae have been cut off near their bases, in B they have been omitted). The part of the segment which carries the dorsal process is separated from the lateral part by a longitudinal suture, which anteriorly joins the antecosta at an approximately right angle. The relation of this suture to the IX/X muscle (see below) makes it very unlikely that it is homologous with the dorsal longitudinal suture in the Hydroptilidae

(p. 82). Between the dorsal process and the point of greatest length (lateroventrally) the posterior border of the segment has a broad and deep indentation.

Segment X (figs. 65, *5;* 66 A, B) tapers much posteriorly. The very concave ventral side is membranous to its greatest extent, whereas the roof-like dorsal side is sclerotized. The sclerite continues around the lateral edge of the segment for some distance into the ventral side (fig. 66, *1;* broken line). The ventral part of the sclerite projects forwards (*2*), and on this extension the IX/X muscle is inserted. It originates from the antecosta of Segment IX laterally to the longitudinal suture. It is somewhat descendent, and possibly acts as a depressor. A comparison between various preserved specimens gives the impression that it may be able also to alter the slope of the "roof". Anteriorly the sclerite of Segment X widens into a plate, which covers the dorsal part of the genital chamber, and in which the small superior appendages (figs. 65, *6;* 66, *4*) are implanted in a pair of membranous "windows". The margin of the plate almost touches that of the sclerite of Segment IX, but it is continuous with the latter only for a very short distance at the lateral end of the dorsal process. The connection has the character of a strong sclerotization (fig. 66, *3*), which lies at the bottom of the furrow between the dorsal process and Segment X and continues on the surface of Segment IX as the longitudinal suture mentioned above.

The posterior end of Segment X is cleft into a pair of flat, laterally sloping processes, below the bases of which the anus is found. The latter is bounded ventrally by a thick, membranous lip, which does not project so far backwards that it is seen in the notch between the two processes. I am unable to decide whether the processes are homologous with the paired, lateral process in *Sericostoma* (fig. 47, *4*, p. 86) or with the median unpaired process in this form. I am most inclined, however, to believe in the latter possibility. In *Beraea*, also, the median process (fig. 50 A, *2*) is slightly bilobed. (Cp. also the Limnophilidae, p. 138).

For most of their length the inferior appendages (figs. 65, *7—9;* 66 C) are divided into an upper (*9*) and a lower branch (*8*). The latter in its greater, proximal part is somewhat sagittally compressed, with a rounded ventral and a sharp dorsal edge. The longer and slenderer upper branch is a little club-shaped and in its distal half slightly flattened. The appendages are curved inwards, so that their apices almost—or on the lower branches entirely—touch each other. A closer examination reveals that the upper branch is connected with the basal part (*7*) by a membranous articulation. A small muscle originates lateroventrally from the basal part and is inserted medially to the proximal end of the upper branch. This muscle is the flexor of the harpago. The upper branch thus represents the harpago and not—as might have been supposed—a dorsal branch as seen in *Beraea*. Proximally the median sides of the two appendages are continuous mutually and with the approximately triangular basal plate (fig. 66 C, *5*). Between the two appendages there is, however, a deep, vertical, sclerotized furrow, the origin of a plate-like apodeme (*6*), which is connected with the basal plate also.

The anterior dorsal muscle originates lateroventrally from the antecosta of

Segment IX and is inserted dorsally on the proximal margin of the appendage. The anterior ventral muscle is inserted on the furrow between the two appendages. Both of these muscles are strong. The weaker posterior ventral muscle stretches between the anterior end of the basal plate and the proximal end of the ventral side of the

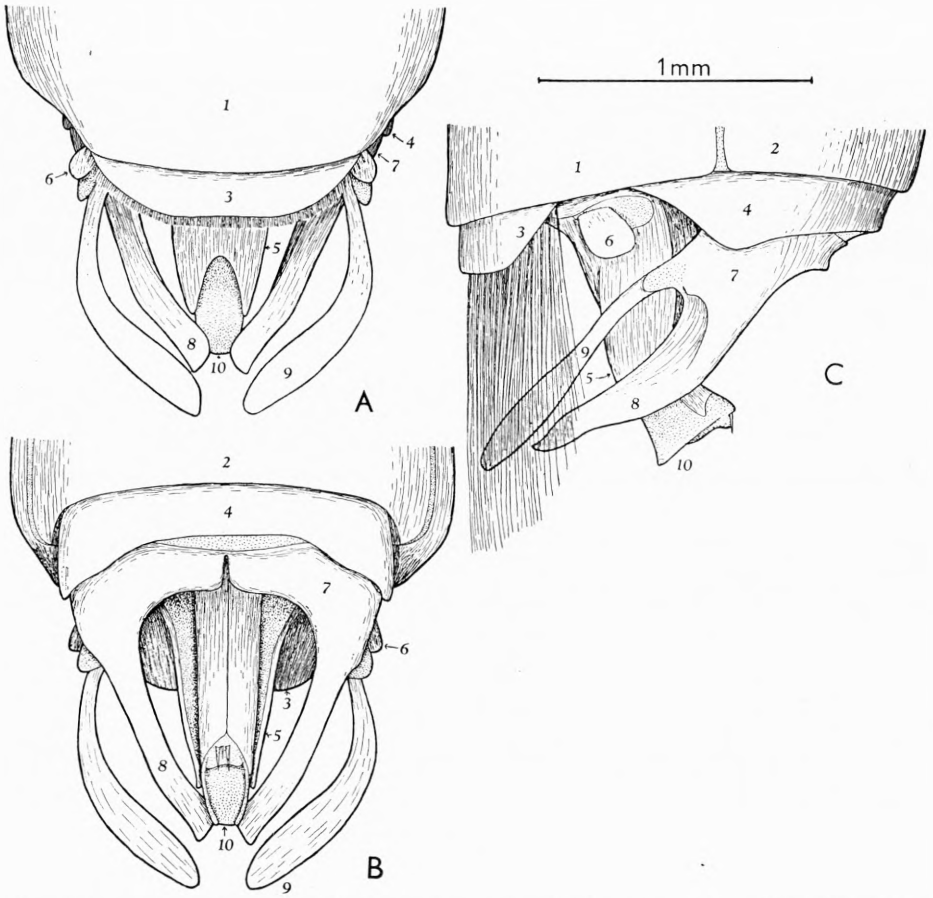

Fig. 65. *Agrypnia pagetana*. Posterior end of abdomen in dorsal (A), ventral (B), and lateral (right) view (C). *1:* Tergum VIII. *2:* Sternum VIII. *3:* dorsal process; (its setae are shown in their full length only in C). *4:* ventral part of Segment IX. *5:* Segment X. *6:* superior appendage. *7:* coxopodite. *8:* distal projection of coxopodite. *9:* harpago. *10:* phallus.

appendage. (The latter insertion is proximal to the origin of the flexor of the harpago). The posterior dorsal muscle is lacking. The positions in which the inferior appendages are seen in various preserved specimens show that the movements are both levation and depression and—at least some—abduction and adduction.

The undivided phallus (fig. 65, *10;* 67) is formed by the phallobase (fig. 67, *4—4*). It is almost straight, only slightly downwards curved, and almost entirely

sclerotized. The dorsal side is rounded, whereas the ventral side has a rather sharp longitudinal keel. Distally the sclerite is indented both dorsally and ventrally; the dorsal indentation is the deeper. The sagittally compressed, slightly axe-shaped distal end therefore is chiefly membranous. The entrance to the endotheca, which in the

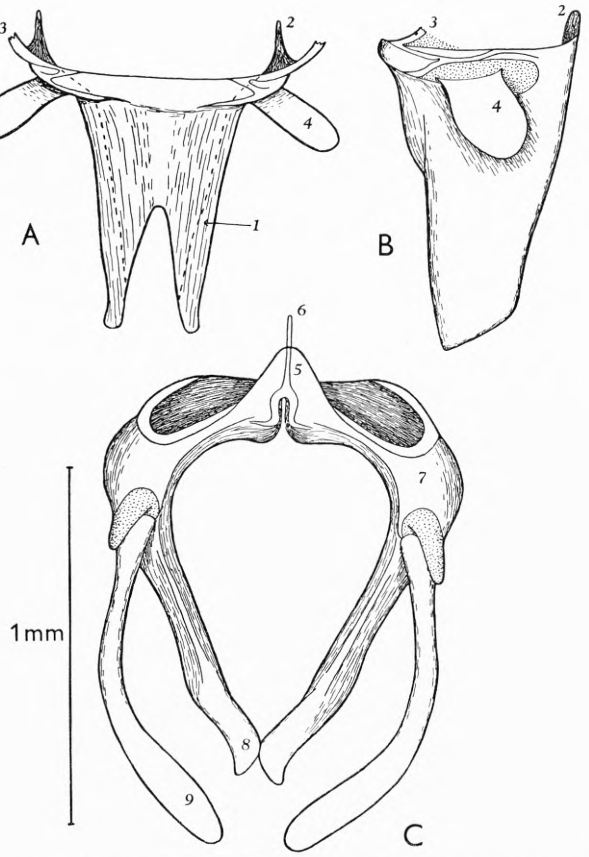

Fig. 66. *Agrypnia pagetana*. A and B: Segment X in dorsal and in lateral (right) view. C: inferior appendages in dorsal view. *1* and *2:* see p. 115. *3:* sclerotic bar connecting the sclerites of Segments IX and X. *4:* superior appendage. *5:* basal plate of inferior appendages and *6:* its apodeme. *7:* coxopodite and *8:* its distal projection. *9:* harpago.

inverted state almost reaches the proximal end of the phallobase, is ventrally at the distal end. When the endotheca is entirely inverted, the distal end of the phallus is slightly bilobed (fig. 67 A. B shows an initial stage of eversion). At the bottom of the endotheca there is a small sclerite (*6*), carrying a rather high process, on the apex of which the ejaculatory duct (*5*) opens. The strong aedeagal retractor originates proximally in the phallic apodeme (*1*), and is inserted on the sclerite *6*. It is difficult —or rather impossible—to decide whether this sclerite represents the whole aedeagus or is only a phallotremal sclerite. The distal part of the ejaculatory duct (*5*) is

sclerotized and surrounded by glandular tissue. In the endotheca three groups of spines (not setae) are seen. The group nearest to the entrance (*9*) contains the fewest spines. In most preparations seen by me they were freely exposed as shown in fig. 67 B; (in A they are concealed by the spines *8*). The next group (*8*) forms a dense pencil near the entrance to the inverted endotheca. On the everted endotheca it must form

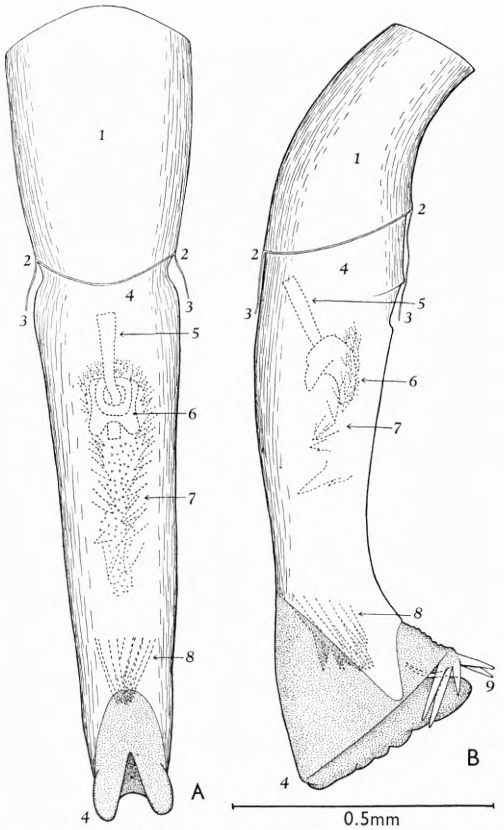

Fig. 67. *Agrypnia pagetana*. Phallus in dorsal (A) and in lateral (right) view (B). *1:* phallic apodeme. *2—2:* cut edge (boundary between phallic apodeme and phallus). *2—3:* optical section through wall of proximal part of phallocrypt. *4:* phallobase. *5:* distal part of ejaculatory duct (shining through). *6:* aedeagal sclerite (shining through; see p. 117). *6—8:* the three groups of spines on the endotheca (see p. 118).

a subproximal ring of spines. In the last group (*7*; in B the spines of the right side only are shown), the spines are more scattered and restricted to the ventral side, whereas the dorsal side is covered with pointed nodules. The spines gives the endotheca a certain resemblance to that of *Molanna* (fig. 56 F, p. 100). This similarity, however, is quite superficial, since in *Molanna* we are concerned with setae and in *Agrypnia* with cuticular processes, two entirely different sorts of structures.

The phallocrypt is deep and entirely membranous. The phallic apodeme (*1*) also is large. It is somewhat flattened and downwards curved. The anterior phallic

muscle originates from the antecosta of Segment IX in the middle of the lateral side and is inserted distally and laterodorsally on the phallic apodeme (and in part on the phallocrypt also). The posterior muscle originates laterally on the posterior border of segment IX and is inserted proximally and lateroventrally on the apodeme. Both muscles have an almost horizontal course. They certainly act as a retractor and a protractor, respectively.

Limnophilus flavicornis.

Segment IX (figs. 68 and 69, *4*) like the preceding segments is rather much sagittally compressed. It is longest dorsolaterally. The length of the ventral side is reduced by broad oral and anal indentations. The former is quite shallow, the latter very deep. For approximately the dorsal fourth the segment—or at least its sclerite—is reduced to an extremely narrow, sclerotic bridge, which in the middle does not comprise much more than the antecostal suture. (This part of Segment IX is entirely concealed by the overlapping, membranous posterior border of Segment VIII). The reduction is due chiefly to a very deep anal indentation, which is bounded by distinct, rounded posterior corners. Continuing the dorsal edge of the posterior corner a short longitudinal suture runs forwards and eventually joins the antecostal suture. It is probably homologous with the laterodorsal longitudinal suture in *Agrypnia* (p. 114). Immediately below the corner mentioned the posterior margin of Segment IX is bent inwards, forming an approximately rectangular, though rounded point. In this way the dorsal edge of the long, laterodorsal part of Segment IX embraces the base of the "superior appendage" (*8*).

Dorsally at the bottom of the genital chamber there is an unpaired, approximately vertical sclerotization (*5*), which is continuous with the dorsal, transverse bridge of Segment IX. Laterally this sclerotization has a pair of deep indentations, in which the "superior appendages" are implanted. The indentations are much larger than the bases of the appendages. Between the indentations the sclerotization, which here almost touches the sclerites of Segment X, is strongly convex in a horizontal section. This bulge perhaps represents a rudimentary dorsal process.

Segment X is so short that it can scarcely be regarded as an independent structure. It forms the steeply descendent floor of a depression, the anterior wall of which is formed by the sclerotization (*5*) described above, whereas overlapping parts of Segment VIII form the roof and the lateral walls. Segment X is provided with a pair of small sclerites (*6*), which are approximately triangular with an oral (or dorsal), a lateroanal (or -ventral) and a medioanal (or -ventral) margin. Anteriorly (dorsally) the two sclerites almost touch each other, posteriorly (ventrally) they are more widely separated. Along their medioanal margin two pairs of processes arise. The anterior processes (*7;* "intermediate appendages") are very strong. They are divergent, directed backwards and upwards, sagittally compressed and tapering greatly towards the almost black apex. The posterior processes (*12*) are much smaller, short and

finger-like. From the furrow between the anterior and the posterior process a suture runs to the lateral corner of the sclerite. The anus is a longitudinal slit in the membranous area between the two anterior processes. Below it there is an unpaired, tongue-like lobe (*13*), which is chiefly membranous, though the lateral sides are very slightly sclerotized.

The backwards and somewhat upwards directed "superior appendage" is very

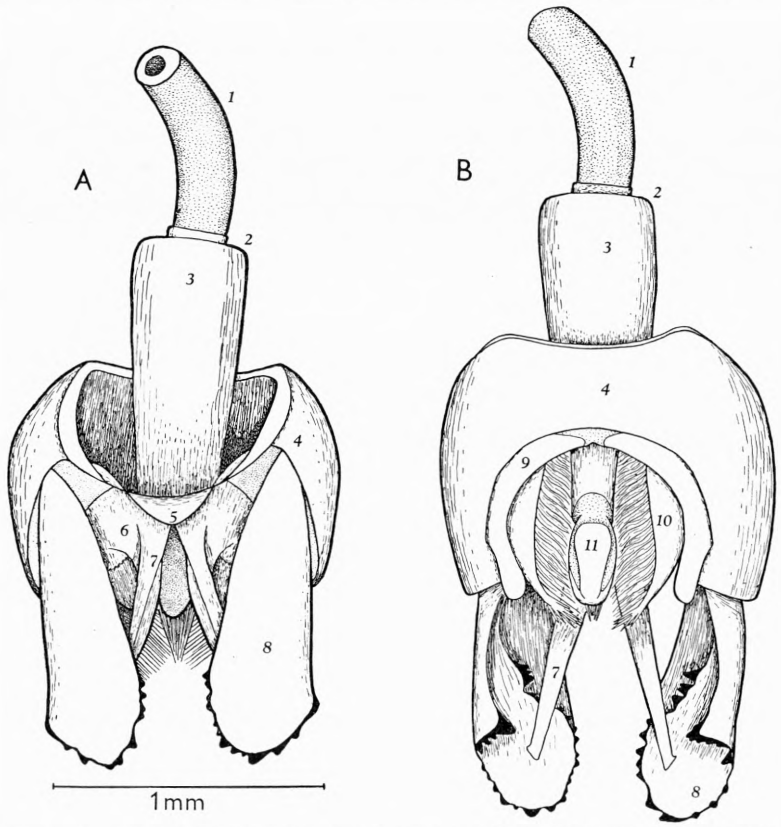

Fig. 68. *Limnophilus flavicornis*. Segments IX and X in dorsal (A) and in ventral view (B). *1:* ejaculatory duct. *2:* phallic apodeme. *3:* phallocrypt (as seen from the haemocoelic side). *4:* Segment IX. *5:* dorsal sclerotization in the genital chamber. *6:* sclerite of Segment X. *7:* anterior process ("intermediate appendage") on this sclerite. Between the two anterior processes in A the subanal lobe of Segment X (dotted) is seen anteriorly, the cuticular processes of the parameres posteriorly. *8:* laterol process ("superior appendage") of segment X. *9:* inferior appendage. *10:* paramere. *11:* distal end of aedeagus.

large. As mentioned above, its base is laterally embraced by the dorsal edge of the lateral part of Segment IX; medially it touches the lateral corner of the sclerite (*6*) of Segment X. In a lateral view the appendage has almost parallel sides and a concave distal edge. Distally the median side is strongly excavated, and the concavity thus formed is encircled by a row of black teeth, which, however, is incomplete ventrally. The greater, proximal part of the median side is flat (though the concavity proceeds

proximally through the gap in the row of teeth as a gutter along the ventral edge). Quite proximally the median side even is bulging and overlaps the lateral corner of the sclerite (*6*) of Segment X to a great extent.

The strong IX/X muscle originates on the lateral part of the antecosta of Segment IX; the longitudinal suture marks the dorsal boundary of the origin. It is inserted on the lateral corner of the sclerite (*6*) of Segment X. Its action is probably as follows: By the contraction of the muscle the sclerite *6* turns on an axis along its medioanal margin, and thus the "intermediate appendage" is moved outwards and upwards. At the same time the "superior appendage" is moved inwards and downwards. In this way the two appendages form a pair of pincers, the chief—and probably only—clasping device of the genital apparatus.

A discussion of the morphology of Segment X will be found under *Silo nigricornis* (p. 138).

The inferior appendage (*9*) has a very broad base, but is extremely short, appearing only as a rounded keel along the posterior margin of Segment IX. Quite dorsally, only, it projects as a small, sagittally compressed process. The latter is entirely sclerotized; otherwise the median side of the appendage is membranous. The two appendages are mutually united, but only by membrane. There is no basal plate. Quite ventrally the sclerite of the inferior appendage is separated from that of Segment IX by a very narrow, membranous stripe. Otherwise the sharp posterior edge of Segment IX overlaps the base of the appendage a little. The posterior ventral muscle is attached to the phallus, and the other muscles are lacking. The inferior appendage thus is not musculated.

The approximately cylindrical phallocrypt (figs. 68 and 69, *3;* 70, *2*) is very deep and projects far into Segment VIII. The phallic apodeme (*2; 1*), in return, is very short. It is shaped like a bowl with an asymmetrically placed foot. The "foot" is only slightly sclerotized. The anterior three fourths of the phallocrypt is faintly sclerotized, and on this part of the phallocrypt the phallic muscles are inserted. The latter are developed almost as in *Stenophylax* (p. 127), though the dorsal one of the two posterior muscles is lacking in *Limnophilus*.

The phallus (figs. 68 and 69, *11;* 70) is divided into a membranous phallobase (fig. 70, *3*) and a slender, almost entirely sclerotized aedeagus (*4—7*). The latter again is divided into two parts, separated by a membranous articulation and constituting three fourths and one fourth, respectively, of the aedeagus. The proximal part (*4—6*) is straight, the distal part (*7*) is bent slightly upwards. There is a pair of complicated parameres (figs. 68 and 69, *10;* 70, *9—11*), which originate laterodorsally at the bottom of the endotheca and are of the same length as the aedeagus. On the dorsal side of the proximal half of the latter there is a pair of longitudinal impressions, which partly receive the basal part of the parameres. The central keel (fig. 70, *4*) thus formed has a sharp longitudinal furrow in the middle. Proximally it is raised into a hump, which projects between the bases of the parameres. On the ventral side of the proximal part of the aedeagus there is a pair of sharp longitudinal furrows, which divide this

side into three rounded keels (*5*, *6*). Distally to the middle the central keel is much dilated.

The distal part of the aedeagus (*7*) is somewhat flattened. On the ventral side of this part also there is a pair of longitudinal furrows separating three folds. The lateral

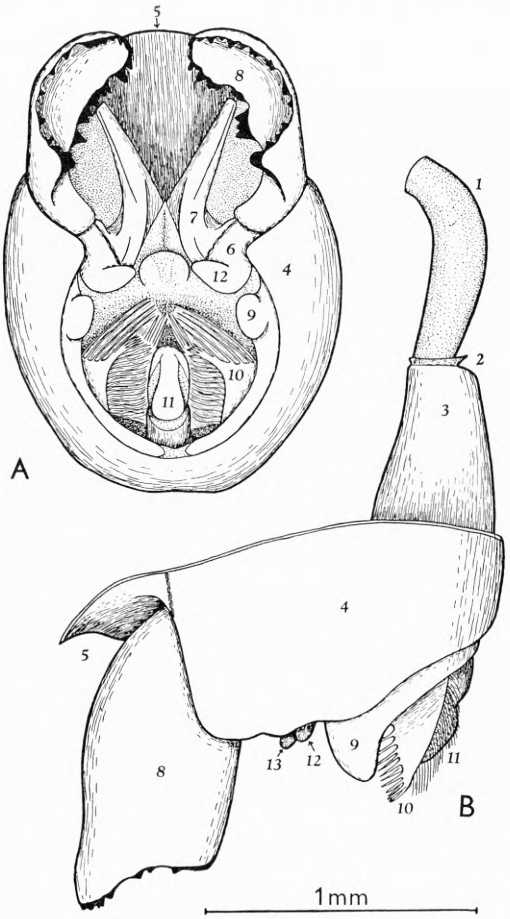

Fig. 69. *Limnophilus flavicornis*. Segments IX and X in posterior (A) and in lateral (right) view (B). *12:* posterior process on sclerite of Segment X. *13:* subanal lobe of Segment X; (in A it is seen between the two posterior processes. Other numbers as in fig. 68.

folds have sharp edges and are membranous on their median sides. The median fold is much broader than the lateral ones; its sole-like proximal end is especially strongly sclerotized and raised above the surroundings. Apically the sclerite of the median fold is continuous with that of the rest of the distal part of the aedeagus. For more than its posterior half the distal part of the aedeagus is spoon-like excavated on the dorsal side. Laterally the cavity is bounded by sharp edges. At its bottom the trumpet-like opening of the ejaculatory duct (*8*) is seen. The "spoon" can probably be re-

garded as a phallotremal cavity homologous with those of *Odontocerum* (p. 104) and *Oligoplectrum* (p. 114). The distal part of the ejaculatory duct is sclerotized and surrounded by a thin layer of glandular tissue.

The parameres have a sagittally compressed shaft (*9*) and a much dilated

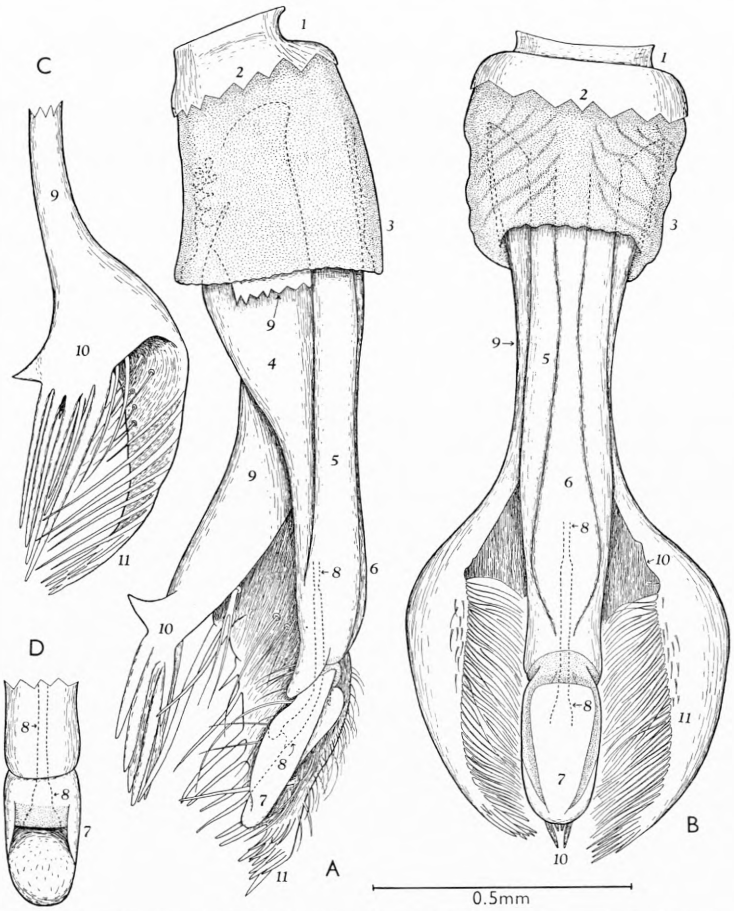

Fig. 70. *Limnophilus flavicornis*. A and B: phallus in lateral (right) and in ventral view; in A the right paramere has been broken off near the edge of the phallocrypt. C: distal end of right paramere in dorsal view; the cuticular processes of the ventral edge have been omitted. D: distal end of aedeagus in dorsal view. *1:* phallic apodeme. *2:* phallocrypt as seen from the haemocoelic side (the greater, distal part broken off). *3:* phallobase. *4:* dorsal, *5:* lateral, and *6:* ventral keel on proximal part of aedeagus. *7:* distal part of aedeagus. *8* (broken line): outline of ejaculatory duct. *9:* shaft, *10:* dorsal, *11:* ventral branch of paramere.

terminal part, which is divided into a smaller and stronger dorsal branch (*10*) and a larger and more delicate ventral (or lateral) branch (*11*). The former is flattened and directed somewhat medially. It terminates in a strong, inwards and upwards directed tooth and carries on its distal edge a row of long, strong, backwards directed spines. The teeth of the two dorsal branches are in contact with each other. The

ventral branch is placed vertically, convex on the lateral side and concave on the median side. On the dorsal edge there is a row of medially and distally directed spines, which are slenderer than those on the dorsal branch. (Such spines may be found singly on the median side, too). Distally—on the pointed distal end of the branch—the spines are shorter and close-set, forming a tuft. The spines of the two branches together form a grating above the distal part of the aedeagus. On the lower edge of the ventral branch there is a dense belt of hair-like spines, which fill in the interval between this edge and the aedeagus. Finally there is a varying—but always small—number of setae on the median side of the ventral branch. These setae, which especially are found proximally, are often bifurcated.

The aedeagal retractor is not particularly strong and fills only a rather small part of the lumen of the phallus. It originates laterally in the phallic apodeme and is inserted laterally in the phallus, proximally to the middle.

Stenophylax stellatus.

The genital segments are largely built as in *Limnophilus*, though distinct differences are seen.

Segment VIII is slightly modified. The tergum (fig. 71, 3) is a little broader than the preceding terga. At a short distance from the anterior corner the antecostal suture is bent backwards and runs subparallel to the lateral margin. (The same is the case on the preceding terga). At its anal end the posterior margin has a tongue-like extension. The large, anal, membranous area of Dorsum VIII is densely covered with minute, but comparatively thick, brown setae. Sternum VIII (*4*) is more feebly sclerotized than the preceding sterna.

Segment IX (figs. 71 and 72, *5*) is longest laterally. The length of the ventral side is reduced by an oral as well as by an anal indentation, and the dorsal side is reduced to a very narrow, transverse bridge, which comprises little more than the antecostal suture, and which is entirely concealed by the much overlapping posterior border of Segment VIII. Unlike conditions in *Limnophilus* the reduction of the dorsal side is due almost exclusively to a deep oral indentation. Quite laterally on the transverse bridge a pair of low, tongue-like, entirely sclerotized processes (fig. 72, *7*) are seen. These processes, on which the strong dorsal VIII/IX muscles are inserted, must be considered bulgings of the acrotergite and thus cannot be homologized with dorsal processes in other forms. In a lateral view the middle of the posterior margin of the segment is protracted into a sharp, backwards directed point, from which a suture runs forwards and downwards. This suture, which is far from reaching the antecostal suture, is possibly homologous with the laterodorsal longitudinal suture in *Limnophilus* (p. 119). In a posterior view it is seen that the point is bent inwards at a right angle and—placed at the bottom of the genital chamber—forms an efficient articulation with the sclerite of Segment X.

Segment X (figs. 71, *6—7;* 72, *8—12*) is not clearly defined as an independent structure. On the other hand it is much larger than in *Limnophilus*, but it is chiefly membranous and can be withdrawn very much. Maximally protruding, as shown in figs. 71 and 72 A, it has a horizontal dorsal side and a vertical posterior side, whereas it has no ventral side, or—perhaps more correctly—the ventral side forms part of the roof of the phallocrypt. The sclerites (fig. 72, *8*) of Segment X, which have almost the same shape as in *Limnophilus*, are situated on the posterior side of the segment, and are widely separated. The rounded ventral corner does not carry any process like that in *Limnophilus* (fig. 69, *12*). This corner is bent a little into the entrance of the

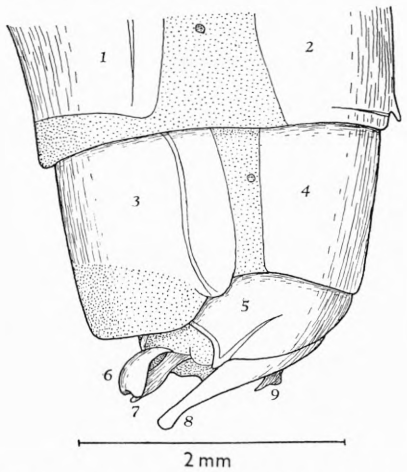

Fig. 71. *Stenophylax stellatus*. Posterior end of abdomen in lateral (right) view. *1:* Tergum VII. *2:* Sternum VII. *3:* Tergum VIII. *4:* Sternum VIII. *5:* Segment IX. *6:* lateral and *7:* median process of Segment X. *8:* inferior appendage. *9:* distal end of aedeagus.

phallocrypt. In the middle the lateroventral edge of the sclerite to a great extent overlaps the inwards directed point on the posterior margin of Segment IX described above. This is the pivot for the movements of the sclerite of Segment X. Along the margin this sclerite has a strong internal thickening, so that a small rounded "window" arises in the middle.

The "intermediate appendage" (figs. 71, *7;* 72, *9*) is directed upwards and backwards. It is much compressed sagittally. The ventral edge is almost twice as long as the dorsal edge. The base of the latter is connected with an elevated, sclerotic rib (fig. 72, *11*), which runs in a laterally concave curve on the dorsal side of Segment X towards the posterior margin of Segment IX. The rib is at a lower level than the dorso-posterior margin of Segment IX, so we are not concerned with a true articulation.

The "superior appendages" (figs. 71, *6;* 72, *10*) are much smaller than in *Limnophilus flavicornis*, directed much upwards and so placed that the homologue of the median side in *Limnophilus* faces backwards. The medioproximal corner of the appendage is in close contact (but not fused) with the base of the dorsal edge of

the "intermediate appendage". Otherwise the superior appendage is widely separated from the sclerite of Segment X. The posterior side is very concave, and the distal edge is deeply indented. The dark-coloured median one is the stronger of the two lobes

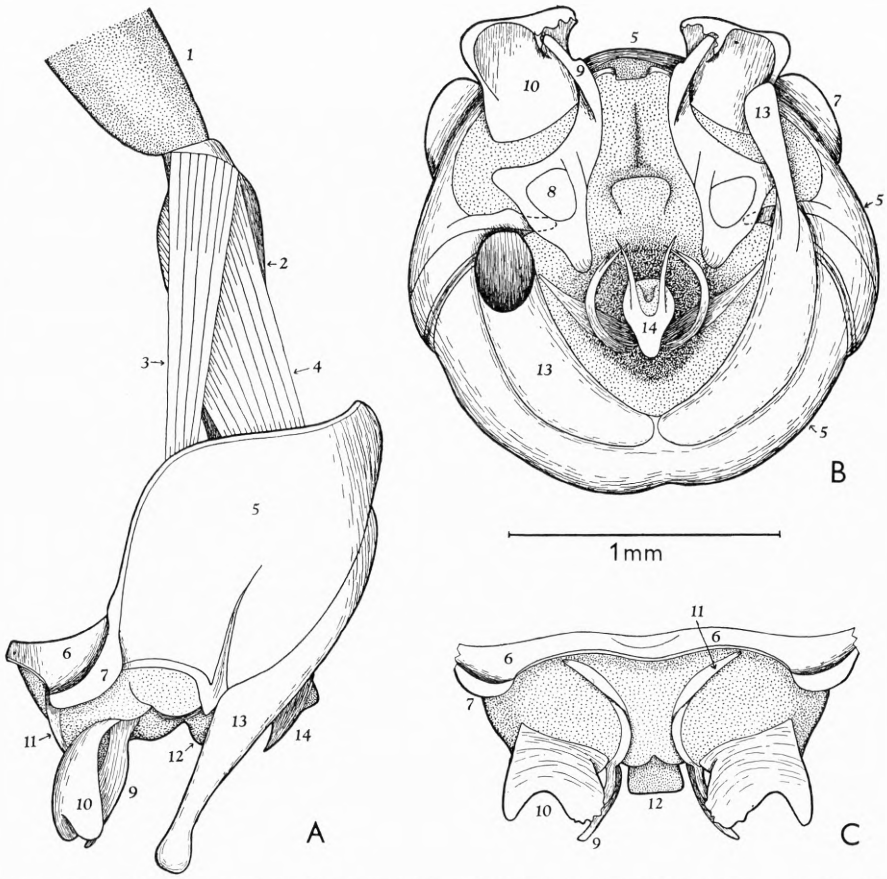

Fig. 72. *Stenophylax stellatus*. A and B: Segments IX and X in lateral (right) and in posterior view. C: Segment X and dorsal part of Segment IX in dorsal view. *1:* ejaculatory duct. *2:* phallocrypt as seen from the haemocoelic side. *3:* posterior phallic muscle. *4:* posterior ventral muscle of inferior appendage (transformed into a phallic muscle). *5:* Segment IX. *6:* dorsal part of antecosta of Segment IX. *7:* tongue-like process on which the VIII/IX muscle is inserted. *8:* sclerite of Segment X. *9:* median process ("intermediate appendage") and *10:* lateral process ("superior appendage") of Segment X. *11:* sclerotic rib on dorsal side of Segment X (seen—but not labelled—also in B). *12:* subanal lobe of Segment X. *13:* inferior appendage; in B the freely projecting part of the left appendage has been cut off. *14:* distal end of aedeagus. (In B *14* is seen projecting from the phallocrypt, flanked by the parameres. The extensions of the sclerotization of the phallocrypt are also seen. Above the phallocrypt the subanal lobe of Segment X, and above this again the anus).

thus formed. It has a concavity of its own, the edges of which are toothed, and which serves to receive the apex of the "intermediate appendage" (see below).

The very strong IX/X muscle originates on almost the whole lateral part of the antecosta of Segment IX, and is inserted on the lateral corner of the sclerite of Seg-

ment X (fig. 72 B, *8*). By the contraction of the muscle this sclerite turns on the inwards directed point of Segment IX and assumes a horizontal position. This implies a shortening of the dorsal side of Segment X and an increase of the curvature of the rib *11*. (The ribs *11* thus are the antagonists of the IX/X muscles). The "superior appendage" becomes adpressed to the bottom of the genital chamber (so that it can be seen only in a posterior view). The apex of the "intermediate appendage" is moved forwards and together with the median lobe of the "superior appendage" acts as a pair of pincers. — Pinned specimens will often be preserved with the IX/X muscles in a state of contraction, so that the "superior appendages" are not seen in a lateral view, and the same may be the case with specimens preserved in fluid.

The anus is a vertical slit between the two sclerites of Segment X. As in *Limnophilus* an unpaired, membranous lobe (12) is seen below the anus.

A discussion of Segment X will be found under *Silo nigricornis* (p. 138).

The inferior appendages (figs. 71, *8;* 72, *13*) have a similar shape as in *Limnophilus flavicornis*. Their dorsal processes, however, are considerably longer, much upwards directed, slender, conical with a knob-like thickened distal end. The rest of the appendage takes the shape of a rather thick, rounded fold along the posterior margin of Segment IX. This fold is sclerotized on the outside as well as on the inside, and—likewise opposite conditions in *Limnophilus flavicornis*—the two appendages are sclerotically continuous. For almost its whole extent the base of the inferior appendage has fused with the sclerite of Segment IX. Ventrally the fusion has left only slight traces; otherwise a distinct separating suture is seen. As in *Limnophilus* the posterior ventral muscle is attached to the phallus, but unlike conditions in *Limnophilus* the inferior appendages have also a musculature of their own. It is composed, however, only of the anterior ventral muscle, which is not particularly strong. It may possibly cause some depression of the processes of the appendages.

The phallocrypt (fig. 72, *2*) is rather spacious, especially so posteriorly, where it is somewhat funnel-shaped. Its greater, anterior part is sclerotized. Laterodorsally the margin of the sclerotization is protracted into a pair of long, rod-like, tapering extensions, the pointed distal ends of which almost touch the margin of the inferior appendages. The phallic apodeme (fig. 73, *1*) is considerably longer than in *Limnophilus flavicornis*.

The phallus has two pairs of posterior muscles. The dorsal pair (fig. 72 A, *3*), which is the weaker, originates on the posterior border of Segment IX just laterally (or ventrally) to the process *7* and is inserted proximally on the lateral side of the phallic apodeme. The stronger ventral pair (*4*) originates lateroventrally on the posterior border of Segment IX and partly also on the inferior appendages. It has a more diffuse insertion than the former pair, laterally and dorsally on the phallic apodeme and especially on the phallocrypt. It represents the posterior ventral muscle of the inferior appendages. The anterior phallic muscle, too, is strong. Like the IX/X muscle it originates on almost the whole lateral part of the antecosta of Segment IX. Its origin is more distally (medially) on the antecosta than that of the former muscle,

which in a median view is almost entirely concealed by the phallic muscle. It is inserted on the posterior extension of the sclerite of the phallocrypt mentioned above.

The phallus (figs. 71, *9;* 72, *14;* 73) is divided into a phallobase (fig. 73, *3*) and an aedeagus (*4*). That part of the latter which in the state of repose is withdrawn into the endotheca is comparatively thick; dorsally it is entirely membranous, laterally

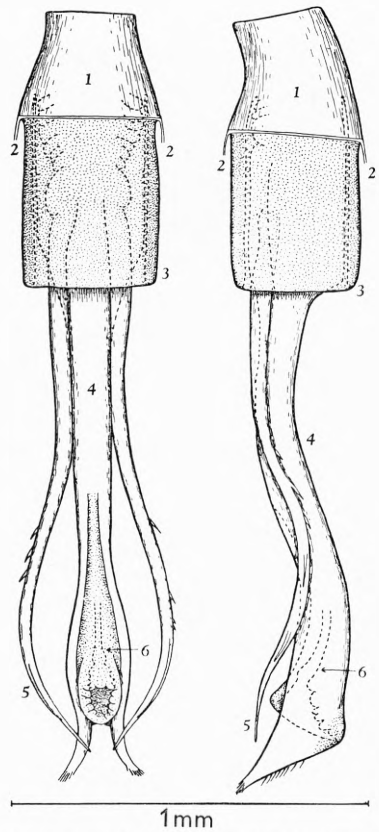

Fig. 73. *Stenophylax stellatus.* Phallus in dorsal and in lateral (right) view. *1:* phallic apodeme. *2—2:* cut edge (boundary between phallic apodeme and phallobase). *3:* phallobase. *4:* aedeagus. *5:* paramere. *6:* (broken line): outline of ejaculatory duct.

and ventrally it is only feebly sclerotized and thrown into numerous, irregular longitudinal folds. The part of the aedeagus which is free of the phallobase is very slender and slightly sigmoid. About the distal third of the dorsal side is membranous. The membranous area is bounded laterally by a pair of sharp, sclerotic ridges, which distally are protracted into a pair of triangular, vertical lamellae. Apically the lamellae carry a tuft of fine spinules and on their ventroposterior edge a row of minute setae. Still smaller setae are found scattered over the rest of the aedeagus. Distally on the ventral side there is a shallow membranous indentation. The ejaculatory duct (*6*),

the distal part of which is sclerotized, opens in a funnel-like depression (a phallotremal cavity) on the membranous part between the two sclerotic lamellae.

The parameres (*5*) are almost as long as the aedeagus. They are extremely slender and slightly sigmoid. Their proximal ends are implanted in pocket-like longitudinal furrows latero-dorsally on the thick basal part of the aedeagus. They are sparsely covered with fine spines.

The aedeagal retractor muscle is strong and fills more than the ventral half of the thick basal part of the aedeagus. The majority of the bands is inserted at the boundary between the thick and the slender part of the aedeagus, but some bands proceed rather far distally, where they are inserted ventrally.

Slide preparations were made of three phalli. On one of these a large (300 μ long) seta was seen on the edge of the left paramere-pocket.

Ecclisopteryx guttulata.

Segment VIII is slightly modified. The tergum (fig. 74, *3*) is broader than the preceding terga. In the middle it is protracted into an unpaired, anal extension (*5*), which is bent downwards on the exceptionally thick and otherwise membranous posterior border of the segment, and which is very densely covered by very short, but also very thick, black setae. In a lateral view (B) it is seen that this extension has a broad, rectangular transverse furrow, so that the posterior border of the segment descends, as it were, by two stages.

Segment IX (*6*) is short. It is longest laterally, where both the oral and the anal margin are bulging. Ventrally there are an oral and an anal indentation, so that the ventral side is very short. In the very middle this side is membranous. The dorsal side is reduced to a sclerotic transverse bridge, which comprises only the antecostal suture (fig. 75, *2*) and the acrotergite (*1;* which latter here, in return, is comparatively long). In the middle of the dorsal side the antecosta is interrupted. Dorsally to the inferior appendages the bottom of the genital chamber is provided with a pair of crescent-shaped, strong, lateral sclerotizations (*4*), which are continuous with the sclerite of Segment IX, though separated from it by a sharp edge. Medially the sclerite *4* is continuous with that of Segment X. The sclerotic bridge thus formed between Segments IX and X is strengthened by two high external ridges, between which a deep furrow (*5*) is seen.

Segment X (figs. 74 and 75, *7—9*) is somewhat better developed than in the Limnophilinae. It takes the shape of quite a short process, the anal end of which is cut off obliquely, descendent and lying in a plane almost parallel to the dorsolateral parts of the posterior margin of Segment IX. In a transverse section the process is coarsely triangular; the ventral base is smaller than the height. The sclerite of Segment X (figs. 74, *8;* 75, *8—9*) is annular. On the very short ventral side (fig. 75, *9*) a longtudinal furrow is seen. Lateroventrally the sclerite of Segment X is continuous with the sclerite in the genital chamber and through this with that of Segment IX.

Each half of the sclerite of Segment X is homologous with the triangular sclerite in the Limnophilinae (figs. 69A, *6;* 72B, *8*). Unlike conditions in this subfamily it does not carry processes of any kind. The rather small, but strong, rounded "superior appendage" (figs. 74 and 75, *7*) is continuous with the lateral side of the sclerite of Segment X. Between these two structures there is a deep, sclerotic concavity. The anus

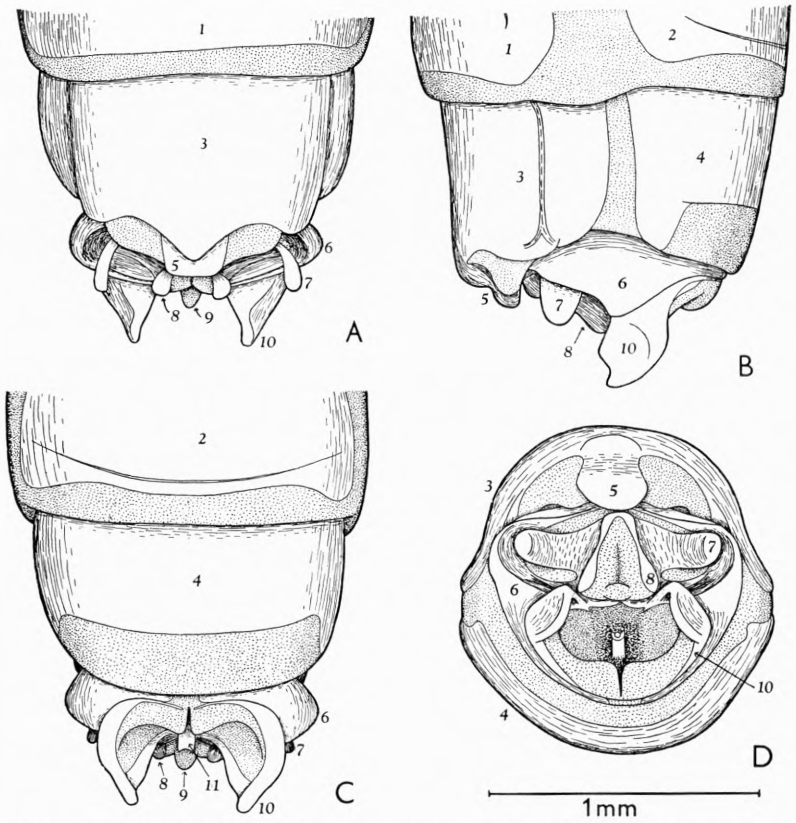

Fig. 74. *Ecclisopteryx guttulata*. Posterior end of abdomen in dorsal (A), lateral (right, B), ventral (C), and posterior view (D). *1:* anal part of Tergum VII. *2:* anal part of Sternum VII. *3:* Tergum VIII. *4:* Sternum VIII. *5:* anal extension of Tergum VIII. *6:* Segment IX. *7:* lateral process ("superior appendage"), *8:* median part, *9:* subanal lobe of Segment X. *10:* inferior appendage. *11:* distal end of aedeagus (in D seen projecting from the phallocrypt between the two inferior appendages).

is situated on the membranous posterior side of the segment. It is a vertical slit, below which a small, membranous process (fig. 74, *9*) is seen.

The very strong IX/X muscle originates on the laterodorsal part of the antecosta of Segment IX and is inserted on the sclerite in the genital chamber at the very point where the latter joins the sclerite of Segment X (at the median number *6* in fig. 75).

A discussion of Segment X will be found under *Silo nigricornis* (p. 138).

The inferior appendages (fig. 74, *10*) are very like those of the Limnophilinae. They have very broad bases, but are extremely short except dorsally, where they are

protracted into processes (fig. 76, *9*). In a transverse section the latter are approximately triangular with a slightly convex dorsal side, a slightly concave lateral side and a flat medioventral side. The process is entirely sclerotized, and its apex is rough with short, strong spinules. Otherwise the sclerotization of the inferior appendage is restricted to a narrow stripe (fig. 76, *8*) proximally on the external side. In a ventral direction the width of this stripe decreases, and quite ventrally the appendage is entirely membranous. The two appendages are continuous with each other, though there is a deep and narrow notch in the part common to them, so that the ventral ends of the appendages form a bilobed lower lip of the entrance to the phallocrypt (fig. 74C—D). The sclerite of the appendage is continuous with that of Segment IX, though separated from it by a distinct suture. The dorsal side of the process is like-

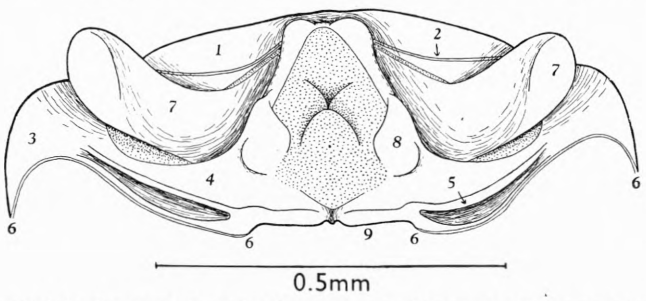

Fig. 75. *Ecclisopteryx guttulata*. Segment X and adjacent area of Segment IX as seen from behind and partly from below. *1:* dorsal side of Segment IX (the number is placed on the acrotergite). *2:* antecostal suture of Segment IX. *3:* lateral part of Segment IX. *4:* sclerite in the genital chamber. 5: see p. 129. *6—6:* cut edge through Segment IX and the sclerite of the genital chamber near the union of the latter with the inferior appendage; the insertion of the IX/X muscle is at the median number *6*. *7:* lateral, *8:* median, *9:* ventral part of Segment X.

wise continuous with the sclerite in the genital chamber (fig. 76, *6*). This union also is marked by a distinct suture. As in the Limnophilinae the posterior ventral muscle has been transformed into a phallic muscle, and the other muscles of the inferior appendages are lacking.

The clasping apparatus is very highly specialized. Its only muscle is the IX/X muscle. It acts on a lever, the sclerite in the genital chamber, which—as mentioned above—is strengthened by external ridges. The median end of the lever is pulled forwards, and owing to the continuity of the various sclerites the result is that both the "superior appendage" and the inferior appendage are bent inwards. Together the two pairs of appendages thus form a pair of tongs with bifurcated jaws. The movement involves a deformation of Segments IX and X. This is facilitated by the following structures: The dorsal transverse bridge of Segment IX is placed in a vertical plane, and the antecosta is interrupted in the middle. The middle of the ventral side is membranous. The longitudinal furrow on the ventral side of Segment X. (It is worth noting that in the Limnophilinae also the IX/X muscle is the only muscle of the clasping apparatus; see pp. 121 and 126—27). In preserved—and especially in pinned —specimens the IX/X muscle will often be fixed in different degrees of contraction.

This explains the difference which is seen in various pictures of the genital segments of *Ecclisopteryx guttulata*. In a fully relaxed condition the processes of the inferior appendages point almost straight backwards.

The phallus (figs. 74, *11;* 76) is largely built like that of the Limnophilinae.

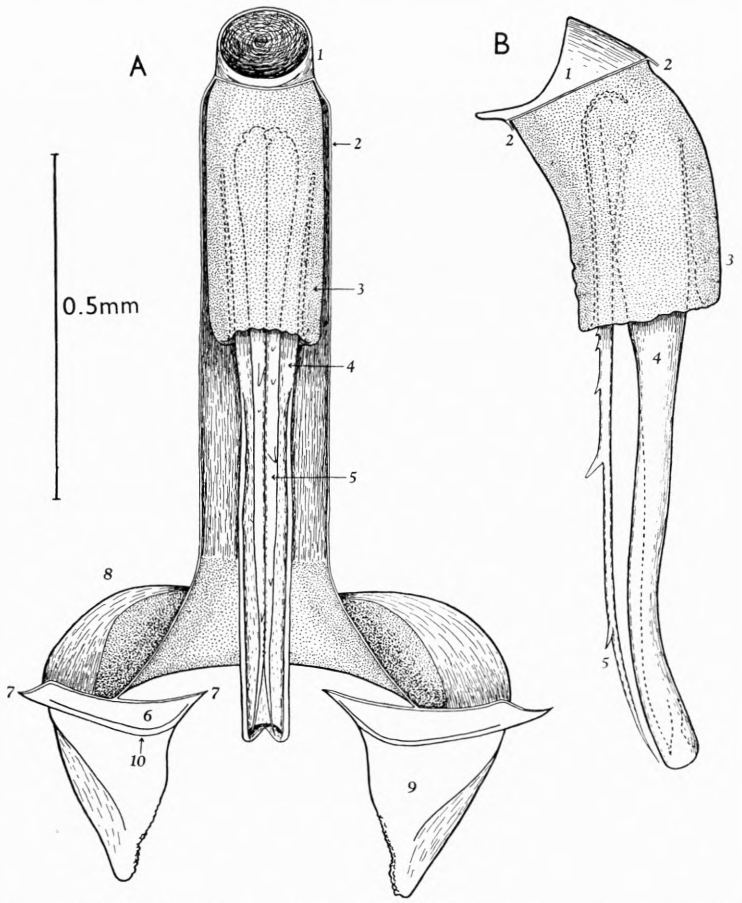

Fig. 76. *Ecclisopteryx guttulata*. A: inferior appendages, phallocrypt, and phallus in dorsal view; the dorsal wall of the phallocrypt has been removed. B: phallus in lateral (right) view. *1:* phallic apodeme. *2:* phallocrypt. *3:* phallobase. *4:* aedeagus. *5:* paramere. *6:* sclerite of the genital chamber. *7—7:* cut edge through this sclerite and Segment IX. *8:* sclerite of inferior appendage as seen from the haemocoelic side. *9:* freely projecting part of inferior appendage. *10:* suture separating this part from the sclerite of the genital chamber.

The phallocrypt (fig. 76, *2*) is sclerotized to its greatest extent. The phallic apodeme (*1*) is short. The phallic muscles are slender. As in *Stenophylax* two pairs of posterior muscles are present. The dorsal one originates laterodorsally on the posterior border of Segment IX and is inserted on the dorsal side of the phallocrypt somewhat anteriorly to the middle of the latter. The ventral posterior muscle originates in the inferior appendage, just ventrally to the process of the latter, and is inserted laterodorsally

on the middle of the phallocrypt. (As mentioned above, it represents the posterior ventral muscle of the inferior appendage). The anterior phallic muscle originates approximately in the middle of the lateral side of the antecosta of Segment IX and is inserted latero dorsally and posteriorly on the sclerotic part of the phallocrypt. The phallus being retracted, the anterior muscle takes an almost transverse course. It acts as a retractor, the posterior muscles as protractors.

The aedeagus (fig. 76, *4*) is extremely slender. The part which in the state of repose is enclosed by the phallobase (*3*) is a little thicker and has a membranous dorsal side. The aedeagus is almost straight, the distal end only is bent a little downwards. On the part which projects from the phallobase, the dorsal side is concave for most of its length. The apex is slightly bilobed. The ejaculatory duct opens apically. Its distal part is sclerotized almost as far as the thicker, basal region of the aedeagus. The very slender and sharply pointed parameres (*5*) carry some few spines on their dorsal sides. Their thicker proximal ends lie close against each other, lowered a little into a depression proximally on the dorsal side of the aedeagus. A peculiar asymmetry is noted: near its base the ventral side of the left paramere carries a strong seta ($55\times 4\ \mu$) on a process ($15\times 9\ \mu$). The aedeagal retractor muscle originates in the phallic apodeme. It almost entirely fills up the thick part of the aedeagus.

Apatania arctica.

In a previous paper (1943a, pp. 22—24; cp. 1950a, p. 400) I have given a description of the genital segments of this species. Here some supplementary information, especially concerning the musculature, will be given.

Segment IX. The length of the dorsal side is reduced to one fourth of that of the ventral side by an oral and an anal indentation. The former is trapezoidal. As in *Silo* (p. 137) the anterior part of the lateral side is apodemal. In *Apatania*, however, the length of the apodemal part is only one fifth of that of the whole lateral side. On the dorsal and the lateral sides, between the bases of the inferior appendages, a suture runs along the posterior margin of the segment. On the dorsal side it is connected with the antecostal suture by a pair of strong longitudinal sutures. The distance between the two latter is a little smaller than that between the two superior appendages, and is like the width of the bottom of the oral, trapezoidal indentation. (The longitudinal sutures probably are homologous with those of *Limnophilus;* p. 119). In the middle of the dorsal side there is thus an approximately rectangular area embraced by sutures (the antecostal suture, the posterior suture and the longitudinal sutures). This area is a little bulging and protracted backwards, so that a rudimentary dorsal process (fig. 77, *3*) is formed. In a dorsal view the latter conceals the median part of the posterior suture. In the middle of the ventral side of the segment there is a small, anal, membranous indentation.

Segment X to its greatest extent is strongly sclerotized, only the ventral side of the oral, undivided part being membranous. There the anus is found, ventrally

bounded by a slightly bilobed, membranous lip. Between the bases of the laterodorsal horns (*5*) the dorsal side is very concave. On the vertical lateral side the anterior margin of the sclerite is bent outwards as a narrow rim. The anterior corners of the sclerite are produced forwards as rod-like extensions (*7*), which, lying horizontally in the roof of the posterior part of the phallocrypt, converge anteriorly. Laterally on the dorsal side (in front of the superior appendages) the sclerites of Segments X and IX are continuous. The boundary between the two segments, however, appears distinctly, partly by Segment X having a considerably lighter brown colour than Seg-

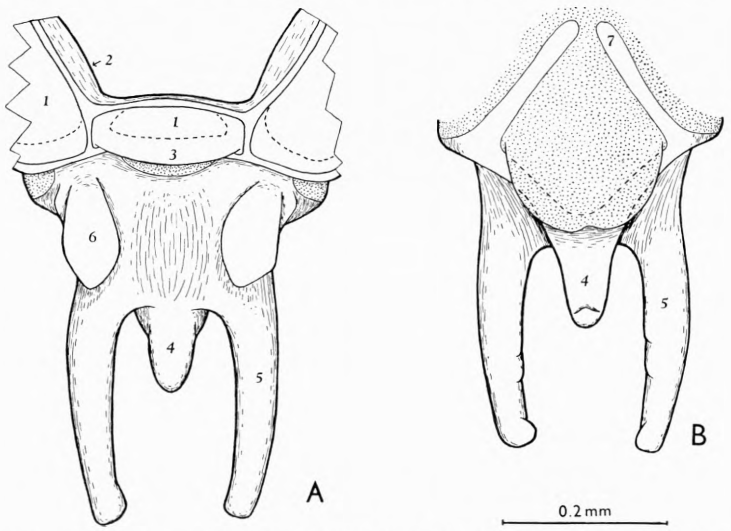

Fig. 77. *Apatania arctica*. Segment X in dorsal (A) and in ventral view (B); in A the adjacent parts of Segment IX is seen. Broken lines indicate in A edges of internal ridges shining through, in B sclerotic parts covered by the subanal lobe of Segment X. *1:* Segment IX. *2:* antecosta of Segment IX. *3:* dorsal process. *4:* median and *5:* lateral process of Segment X. *6:* superior appendage. *7:* anterior extension of ventroanterior corner of Segment X.

ment IX, partly by Segment X being at a lower level than Segment IX, and finally by the posterior suture of Segment IX mentioned above. On the greater median part of the dorsal side as well as on the lateral sides the two segments are separated by membrane.

The small superior appendages (*6*) are sclerotically continuous with the sclerite of Segment X.

The IX/X muscle is very strong and originates on the whole lateral part of the antecosta of Segment IX. Dorsally the origin is bounded by the longitudinal suture. It is inserted on the proximal margin of the sclerite of Segment X on the ventral half of the lateral side, and on the posterior half of the rod *7* (fig. 77 B). It must act as a depressor of Segment X.

A discussion of Segment X will be found under *Silo nigricornis* (p. 138).

The inferior appendages (fig. 78 A). The median side of the coxopodite (*9*)

is slightly concave. Ventrally the concavity is bounded by a broadly rounded edge, dorsally by a sharp edge which continues the dorsal edge of the distal projection (*10*). Proximally the median sides of the two coxopodites merge evenly into each other. In this way a sclerotic semitube (*8*) is formed, which proceeds forwards for some distance on the floor of the phallocrypt, and which represents the basal plate of the appendages. In the middle the posterior edge of the semitube is broadly rounded, but is not seen in a ventral view, since the posterior border of Segment IX overlaps the bases of the inferior appendages rather much. On the ventral side of the appendages there is an unpaired, lenticular, membranous indentation, corresponding to the membranous indentation in the posterior margin of the sclerite of Segment IX. The tongue-like distal processes (*10*) of the two coxopodites are situated in planes which converge posteriorly and dorsally. The harpago is implanted in a small, membranous area, and laterally it is lowered rather much into the coxopodite. It is divided into a larger upper (*11*) and a smaller lower lip (*12*).

The inferior appendages have only one extrinsic muscle, the anterior ventral muscle, which originates on the ventral part of the antecosta of Segment IX. Its bands converge posteriorly and are inserted on the ventral side of the part common to the two appendages. This muscle possibly acts as a depressor. The posterior ventral muscle is developed as a phallic muscle, and the two other muscles are entirely lacking, or perhaps the anterior dorsal has fused with the anterior phallic muscle. The flexor of the harpago is very strong. It originates from more than half of the lateral side of the coxopodite and is inserted medio ventrally on the proximal margin of the harpago. By its contraction it must rotate the latter in such a way that the apex of its upper lip (*11*) meets the apex of the distal process (*10*) of the coxopodite, a pair of pincers thus being formed.

The spacious phallocrypt (*2—4*) stretches into the posterior part of Segment VII. Its dorsal half is entirely membranous except for the rods (fig. 77 B, *7*) issued from the anterior corners of Segment X. Ventrally about the anterior half is sclerotized (fig. 78 A, *2*), and the posterior part of the floor is formed by the above-mentioned semitube (*8*), which is continuous with the inferior appendages. These two sclerotizations are separated by a large membranous area. Their dorsal margins, however, are connected by a pair of rod-like, somewhat ascendent sclerotizations (*3—4*), the posterior part of which (*4*) is colourless and hyaloid (though distinctly defined) and no doubt flexible and elastic. The ventral, membranous area between the two rods bulges into the lumen of the phallocrypt as a valve, which both orally and anally overlaps the sclerotized areas to a great extent. The phallic apodeme (fig. 78 B, *1*) is short and thin.

There are two pairs of posterior phallic muscles. The dorsal muscle, which is very strong, originates dorsally in Segment IX, just laterally to the longitudinal suture and on the whole area between the antecostal suture and the posterior suture. It is inserted on the phallic apodeme in the entire circumference of the latter: both dorsally and ventrally the insertions of the two muscles meet. The ventral muscle is

considerably weaker. It originates lateroventrally on the proximal margin of the coxopodite, and the insertion extends over the oral sclerotized part (*2*) of the floor of the phallocrypt. The two pairs of posterior muscles are protractors. Their antagonist is probably the elasticity of the hyaloid part (*4*) of the rod *3*—*4*. The membranous valve in the floor of the phallocrypt is a feature which allows the movements of protraction and retraction. The rather weak anterior phallic muscle originates lateroventrally on the antecosta of Segment IX and is inserted on the dorsal margin of the anal sclerotization (*8*) in the floor of the phallocrypt. Perhaps it has an antagonistic relation to the anterior ventral muscle of the inferior appendage. In a

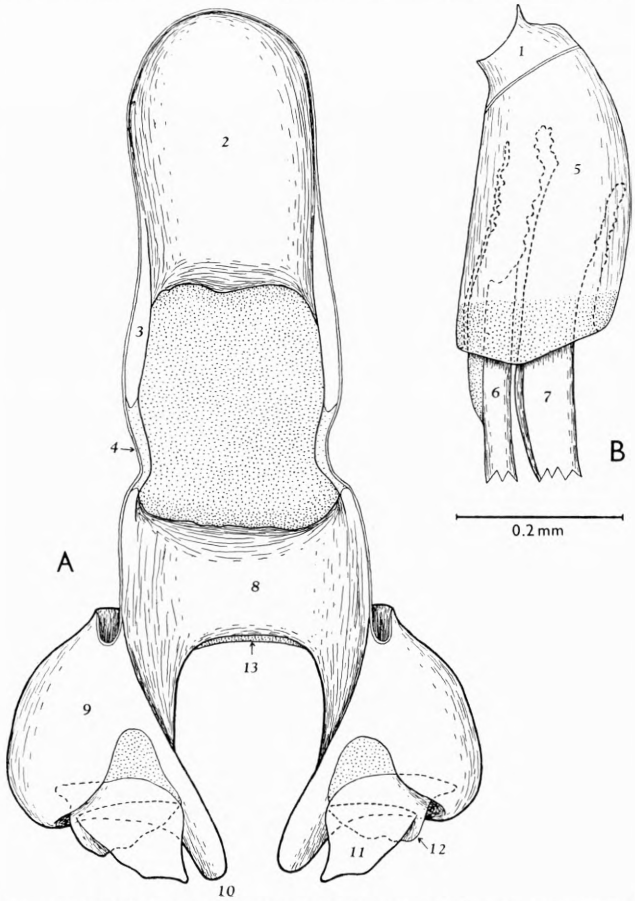

Fig. 78. *Apatania arctica*. A: inferior appendages and phallocrypt in dorsal view; the dorsal wall of the phallocrypt has been removed together with the phallus. B: proximal part of the phallus in lateral (right) view. *1:* phallic apodeme. *2:* sclerotic part of ventral wall of phallocrypt. *3:* rod-like sclerite connecting this part with the basal plate of the inferior appendages. *4:* flexible part of this rod. *5:* phallobase. *6:* paramere (distal part broken off). *7:* aedeagus (distal part broken off). *8:* basal plate of inferior appendages. *9:* coxopodite and *10:* its distal projection. *11:* upper and *12:* lower lip of harpago. *13:* membranous posterior border of Segment IX.

median view the anterior phallic muscle conceals the ventral part of the IX/X muscle.

The phallobase (fig. 78 B, *5*) is well developed. It tapers proximally, so that the short phallic apodeme (*1*) is considerably thinner than the phallobase. The phallotheca is slightly sclerotized except quite distally. The aedeagus (*7*) is somewhat flattened. On its proximal, broader part the dorsal side is flat, though with a pair of shallow longitudinal furrows, impressions after the parameres (*6*), whereas the ventral side forms a feebly defined, rounded longitudinal keel. In the distal half of the aedeagus the ejaculatory duct is sclerotized, and just proximally to this part it is surrounded by glandular tissue. The "spurs" on the distal end of the aedeagus are not setae, but spines, i. e. simple cuticular processes. The parameres, which proximally are united by membrane, are thin-walled. The aedeagal retractor originates proximally on the ventral side of the phallotheca and is inserted distally and laterally on the broad part of the aedeagus.

Silo nigricornis.

Segment IX (figs. 79 and 80, *6*) is very short and entirely concealed by the overlapping posterior border of Segment VIII. It is longest on the lateral side, where there is a large oral bulge, which to a great extent has the character of an apodeme (*6 a*). The dorsal as well as the ventral side are much reduced in length. In the middle the former is developed only as quite a narrow transverse bridge. Ventrally on the lateral side there is a longitudinal suture, which anteriorly joins the antecosta. The relation between this suture and the IX/X muscle makes it doubtful that it should be homologous with the longitudinal suture in *Apatania* (p. 133) and the Limnophilinae (p. 119), whereas it may be homologous with the lateroventral suture in various other forms; (see pp. 5—6). In the middle of the ventral side the antecosta of Segment IX is interrupted.

Segment X is broad anteriorly and tapers much posteriorly. The dorsal and the lateral sides are sclerotized, whereas the greater, median part of the ventral side is membranous. For more than the posterior half Segment X is cleft into a pair of strongly and entirely sclerotized processes (figs. 79—81, *9*). Basally the latter are sagittally compressed, but their dorsal edges are twisted inwards, so that the distal part of the processes becomes dorsoventrally flattened. This part is applied to the dorsal side of the aedeagus. The anus is between the two processes. Orally and laterally Segment X carries a pair of ear-shaped "superior appendages" (*8*), which are sclerotically continuous with the segment itself. Anteriorly on Segment X there is an unpaired, elongate, tongue-like, and entirely sclerotized dorsal process (*7*). The dorsal sides of this process and of Segment IX are connected by a narrow, sclerotic longitudinal bridge. The latter, the width of which is only a small fraction of that of the process, constitutes the only sclerotic connection between Segments IX and X. The unpaired dorsal process in *Silo* is probably homologous with the paired dorsal pro-

cesses in *Leptocerus* (fig. 53, *6*, p. 95) and *Oligoplectrum* (fig. 62, *2*, p. 111) a. o. The IX/X muscle is very strong. It originates from the whole apodemal part of Segment IX (*6a*) and is inserted on the prominent ventro-anterior corner of Segment X (see fig. 81).

A comparison between *Ecclisopteryx*, *Apatania*, and *Silo* gives strong evidence that the "superior appendages" in *Ecclisopteryx* (figs. 74 and 75, *7*) and *Silo* (figs. 79 and 80, *8*) are homologous with the lateral horns in *Apatania* (fig. 77, *5*). In *Apatania* these structures certainly are not superior appendages, since such (fig. 77, *6*) are present at the same time. The inference is that the "superior appendages" in *Ecclisopteryx* and *Silo* do not justly bear this name, but are structures homologous with the lateral processes in *Sericostoma* (fig. 47, *4*, p. 86) and *Beraea* (fig. 50, *3*, p. 91). The same of course is the case with the lateral horns in *Apatania*. The median horn in this genus (fig. 77, *4*) then is homologous with the median, unpaired process in *Sericostoma*, and the processes *9* in *Silo* (figs. 79 and 80) no doubt are homologous with the median horn in *Apatania*. In *Silo* the median process of Segment X thus is bifurcated, a condition which possibly finds its parallel in *Agrypnia* (p. 115) and to some extent in *Beraea* (fig. 50, *2*, p. 91) also. A comparison between the Limnophilinae and the Ecclisopteryginae strongly indicates that the "superior appendages" in these two subfamilies are homologous. The "superior appendages" of the Limnophilinae then are lateral processes of Segment X and not true superior appendages. The latter are lacking in all the Limnophilidae studied here with the exception of *Apatania*, in which they are present in a rudimentary state. The "intermediate appendages" in the Limnophilinae (figs. 68 and 69, *7*) is the median process of Segment X, bifurcated as in *Silo* (fig. 79, *9*). In *Ecclisopteryx* this process is lacking. It is a feature peculiar to the Limnophilinae that the sclerite of Segment X is divided into a right and a left half. An analogy is found i. a. in *Molanna* (p. 99). It is a much higher degree of specialization, however, that the lateral and the median processes are separated by an articulation and movable against each other. The lobes *13* in *Limnophilus* (fig. 69), *12* in *Stenophylax* (fig. 72), and *9* in *Ecclisopteryx* (fig. 74) are obviously homologous with each other and with the membranous lower lip of the anus in *Apatania* (Anker Nielsen 1943a, p. 25, fig. 4A). Such a lower lip is found more or less distinctly developed also in other Integripalpia.

Schmid (1955, p. 10) also considers the "superior appendages" of the Limnophilinae and the Eccolisopteryginae as parts ("branches externes") of Segment X itself. He calls the median process(es) "branches internes". He further recognizes a pair of "branches inferieures". In *Limnophilus* the latter are represented by the processes *12* (fig. 69). In my opinion, however, they are structures of only secondary importance and may in some cases have arisen by a subdivision of the median processes, in others perhaps by a subdivision of the lateral processes; in many Apataniinae the latter are bifurcated (Schmid 1953, 1954). Schmid calls the membranous parts of Segment X "corps de Xme segment". Expecially in some Apataniinae it may be produced into rather complicated lobes. I think, however, that secondary importance only can be attributed to these lobes.

The two-jointed inferior appendages are large and directed almost straight backwards. The coxopodite (figs. 79, 80 and 82 A, *10*) is semicircular in a transverse section; the dorsal side is membranous. Proximally the two coxopodites are contiguous and quite proximally the median sides of their sclerites are continuous, but a basal plate is not developed. From the proximal half of the laterodorsal margin of the sclerite a strong and rather broad, sclerotic rod (fig. 82 A, *6*) is issued, which proceeds

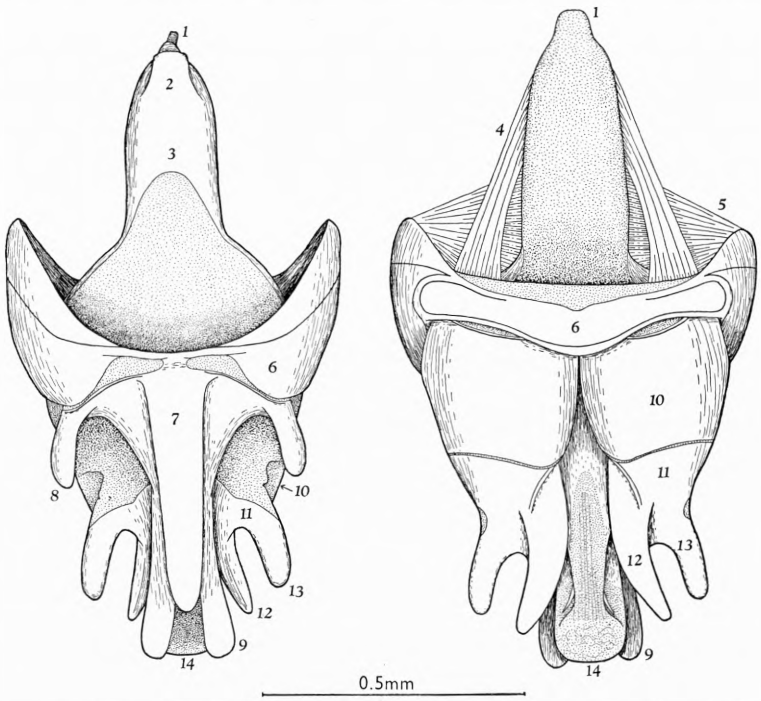

Fig. 79. *Silo nigricornis*. Segments IX and X in dorsal and in ventral view. *1* = *1* in fig. 80. *2:* phallic apodeme. *3:* sclerotic part of dorsal wall of phallocrypt as seen from the haemocoelic side. *4:* posterior ventral muscle of inferior appendage, transformed into a phallic muscle. *5:* anterior phallic muscle. *6:* Segment IX. *7:* dorsal process. *8:* lateral process ("superior appendage") and *9:* median process of Segment X. *10:* coxopodite. *11:* harpago. *12:* median and *13:* lateral branch of the latter. *14:* distal end of aedeagus.

into the phallocrypt, where it—being subjected to a torsion—comes to lie on the lateral wall of the latter; eventually it joins the sclerotization of the phallocrypt. The ventral side of the harpago (*11*) is much longer than the dorsal side. Distally the harpago is divided into two branches: one median (and a little ventral; *12*), the other lateral (and a little dorsal; *13*). The latter is finger-like. The former is flattened, and its dorsal side faces a little medially; proximally on its ventral side a sharp, elevated keel is seen. The dorsal sides (of the median branches) are more or less closely applied to the aedeagus and thus completes the aedeagus-guide, the rest of which is formed by the median processes of Segment X. The inferior appendages and Segment X together enclose the middle part of the aedeagus in such a way that only the distal end of the latter (fig. 80, *14*) is seen in a lateral view.

The rather weak anterior ventral muscle is inserted on the sclerotized furrow between the two coxopodites. The posterior ventral muscle is developed as a phallic muscle. The posterior dorsal muscle is lacking, whereas it is possible that the anterior dorsal muscle has fused with the anterior phallic muscle. The flexor of the harpago is divided into two portions. One is very strong. It originates on the ventral side of the coxopodite and is inserted proximally on the dorsal side of the harpago. The other

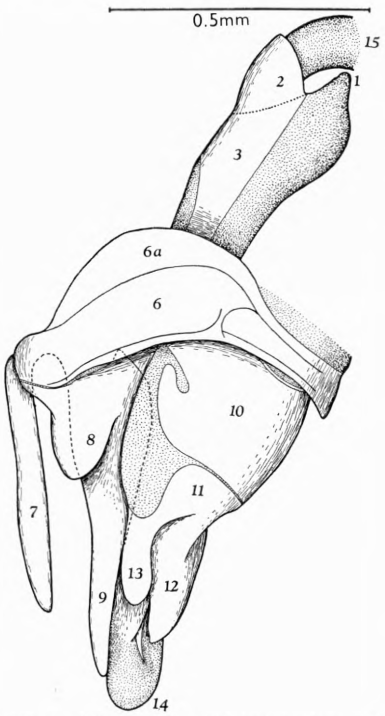

Fig. 80. *Silo nigricornis*. Segments IX and X in lateral (right) view. *6a:* apodemal part of lateral side of Segment IX. *15:* ejaculatory duct. Other numbers as in fig. 79.

portion is weaker, but still rather strong. It originates on the median side of the coxopodite and is inserted on the ventral side of the harpago, rather distally, between the bases of the two branches. It can hardly act as an antagonist to the former portion, but perhaps plays a role in the rather complicated movements of the harpago: By the contraction of the flexor the harpago is bent upwards, and the ventroproximal, undivided part of its sclerite comes to be placed as a lid on the distal end of the coxopodite. The distal branches, however, are bent downwards in relation to the rest of the harpago and hence continue to point obliquely backwards. During this movement the the median branch is removed from the aedeagus and together with the "superior appendage" forms a pair of tongs.

The phallocrypt (figs. 79, 80 and 82·A, *1* and *3*) is very deep. In a lateral view its anterior end is bilobed. The upper, beak-like lobe (2) is sclerotized, and through

its open ventral side the ejaculatory duct (*15*) enters the phallus. This "beak"alone represents the phallic apodeme. The inferior lobe (*1*) is membranous. The ventral side and the distal part of the dorsal side of the phallocrypt are membranous. Proximally the dorsal side is sclerotized (*3*), and the posterior corners of the sclerite are protracted backwards into the above-mentioned rods (fig. 82 A, *6*), which unite it with the inferior appendages.

The phallus consists of a short phallobase (fig. 82, 5) and a long, slender aedeagus (figs. 79 and 80, *14;* 82, 7). The distal end of the phallobase is cut off very obliquely; the ventral side is longer than the dorsal side, but nevertheless the latter

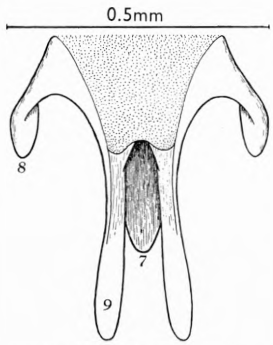

Fig. 81. *Silo nigricornis.* Segment X in ventral view. For explanation see fig. 79.

projects farther backwards than the former. Proximally the lateral and the ventral sides of the phallotheca are sclerotized, but the phallobase is membranous to its greatest extent.

The proximal half of the aedeagus is somewhat flattened, whereas the distal half approaches the cylindrical shape and hence, in a lateral view, appears swollen. The part of the aedeagus which in the state of repose is concealed in the endotheca, is membranous, and on the dorsal side the membrane stretches over the proximal two fifths of the organ. The apex is membranous, too; on the dorsal and especially on the ventral side the membrane proceeds farther proximally than on the lateral side. Distally a great part of the dorsal side is excavated spoon-like. The anterior part of the bottom of the "spoon" is sclerotized and very thick-walled, and there, rather far removed from the distal end of the aedeagus, the opening of the ejaculatory duct is found. The "spoon" may be considered as a phallotremal cavity (see pp. 12—13). Lateroventrally on the aedeagus there is a pair of deep and narrow depressions, which serve to receive the parameres (fig. 82, *8—9*). The latter are very slender and slightly sigmoid. They arise close together at the bottom of the endotheca, ventrally to the aedeagus.

The phallus has no posterior muscle of its own, but as mentioned above, the posterior ventral muscle of the inferior appendage is associated with the phallus. It originates on the lateroventral part of the proximal margin of the coxopodite and is

inserted on the phallic apodeme (*2*). The anterior muscle is very strong, stronger than the posterior one. It originates on the lateral side of Segment IX in front of the origin of the IX/X muscle. Its insertion extends in a horizontal, or rather slightly descendent, plane. The posterior half is on the rod (fig. 82 A, *6* a) connecting the inferior appendage with the sclerite of the phallocrypt (*3*), the anterior half on this

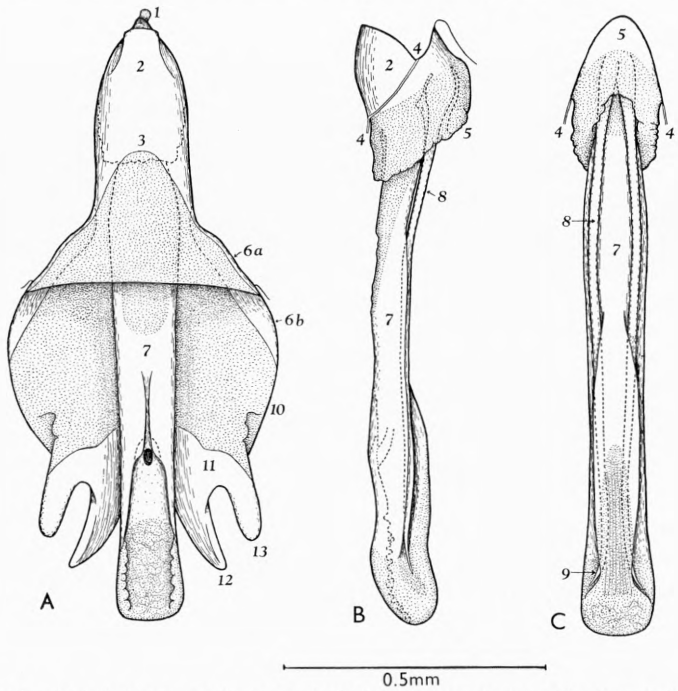

Fig. 82. *Silo nigricornis*. A: inferior appendages and phallus in dorsal view; the dorsal side of the phallocrypt is seen from the haemocoelic side. B and C: phallus in lateral (right) and in ventral view. *1* = *1* in fig. 80. *2:* phallic apodeme. *3:* sclerotic part of dorsal side of phallocrypt. *4—4:* cut edge through wall of phallocrypt (boundary between phallic apodeme and phallobase). *5:* phallobase. *6:* rod-like sclerite connecting inferior appendage with sclerite of phallocrypt; *6a* is seen partly from the haemocoelic side, partly shining through (broken line). *7:* aedeagus; in A the opening of the ejaculatory duct is seen in the middle of the freely projecting part. *8:* paramere. *9:* distal end of the latter. *10:* coxopodite. *11:* harpago. *12:* median and *13:* lateral branch of the latter.

sclerite. In the state of repose the most posterior muscle bands go a little backwards, the most anterior ones much forwards. The relation to the inferior appendage does not exclude the possibility that the muscle has arisen by a fusion of the anterior dorsal muscle of this appendage and the anterior phallic muscle, but nothing can be said with certainty about this. The function of the two muscles is not clear to me. If the posterior muscle acts as protractor, the elasticity of the rod *6* must be a very powerful antagonist. The strong development of the retractor (the anterior muscle) then is difficult to understand. Possibly the two muscles perform some other functions than protraction and retraction. The aedeagal retractor is rather weak.

The structure of the genital segments of *Silo* shows that the Goërinae are true

members of the family of Limnophilidae, and especially closely related to the Apataniinae. There is a great similarity between the two subfamilies as regards the stucture of Segment X, and the similarity becomes still greater if other forms of the Apataniinae are included in the comparison. In species of the genera *Radema* Hag. and *Thamastes* Hag., and also in some species referred to the genus *Apatania* Kol., there is a dorsal process of the same shape as that in *Silo*, and the median process of Segment X is bifurcated as in the latter (SCHMID 1953, 1954). In the development of the inferior appendages there are important points of resemblance between the Apataniinae and the Goërinae. It is especially noted that the harpago is bifurcated and that a sclerotic bridge connects the coxopodite with a sclerotization in the anterior part of the phallocrypt. (The rod-like extension of the sclerite of the phallocrypt which in *Stenophylax* —p. 127—almost reaches the inferior appendage may perhaps be homologous with the bridge mentioned. This being the case, it means that conditions in the Apataniinae are the original ones within the Limnophilidae, and those in Limnophilinae and Ecclisopteryginae due to a reduction). In the development of the musculature of the inferior appendages the Goërinae show affinities not only to the Apataniinae, but also to the Limnophilinae and the Ecclisopteryginae: The only extrinsic muscle associated with the appendages is the anterior ventral one; the posterior ventral muscle is developed as a phallic muscle, and the two other muscles are lacking. In the Apataniinae and the Goërinae, however, there is some evidence that the anterior dorsal muscle has fused with the anterior phallic muscle, and the same of course may be the case in the Limnophilinae and the Ecclisopteryginae. Finally, the phallus in *Silo* is decidedly of a limnophilid type.

In a previous paper (1943b, pp. 106—16) I have discussed the phylogeny of the Limnophilidae. In this paper I advanced the theory that within this family two main lines of evolution may be distinguished, one comprising the Apataniinae, the Goërinae and the Ecclisopteryginae, the other the Limnophilinae. The chief arguments were the facts that the Ecclisoptryginae like the Apataniinae, but unlike the Limnophilinae, lay their eggs below water, and that the mouth-parts of the Ecclisopteryginae larvae show similar adaptations to torrential life as do those of the Apataniinae and the Goërinae. Based upon a study of the imagines this theory has been criticized by SCHMID (1955, p. 116), who considers the Ecclisopteryginae more closely related to the Limnophilinae than to the Apataniinae. The structure of the genital segments, and more particularly of the inferior appendages and the phallocrypt, may indicate that SCHMID is right. This being the case, however, the two above-mentioned and several other points of similarity in the morphology and biology of the developmental stages of the Ecclisopteryginae on the one hand and the Apataniinae and the Goërinae on the other must be explained as convergencies. The aquatic egg-deposition of the Ecclisopteryginae undoubtedly is more primitive than the terrestrial egg-deposition of the Limnophilinae. The safest which at present can be said on the question of the systematic position of the Ecclisopteryginae is perhaps that it still is open to discussion.

Concluding Remarks.

An important purpose of the present study has been to throw some light upon the phylogeny of the Trichoptera. Before entering this subject it will not, perhaps, be superfluous to say some few words on phylogenetic considerations in general, though very likely others have expressed similar thoughts.

It goes without saying that no recent systematic group can be the ancestors of any other recent systematic group. Nor is it to be expected that any group has a very great similarity to the hypothetical, common ancestral form. Since the very beginning of Life on Earth the organisms have been subjected to the pressure of natural selection. Those, only, which in one or another direction became specialized were able to survive. Hence truly primitive animals (or plants) do not exist. The specializations have followed many different paths, which is the cause of the variety of Life. It seems that the specialization generally has comprised the vast majority of features. But it also seems that various features may be specialized to very different degrees: whereas some are highly specialized, others have remained comparatively primitive. And, finally, it seems that in various groups it is not the same features which have remained primitive. Comparative studies therefore give us a possibility of judging what condition is to be considered the original one. It is that which recurs in several forms which for other reasons must be considered distantly related. It then turns out that in some forms the specialization has comprised only comparatively few features (which in return more often are very highly specialized), whereas most features have remained comparatively primitive. Such forms are called generalized, primitive or "low"—though in some respects they may be very highly specialized. The more features the specialization comprises, the more specialized or "higher" the form is said to be.

From the above it will appear that when in the following mention is made of primitive forms, intermediate forms, etc., these terms must be taken *cum grano salis*. Their meaning is just that the forms in question are suited to give us some idea of what the true primitive or intermediate forms were like.

In a previous paper (1948a, pp. 177—91) I have advanced the theory that the Glossosomatinae are intermediate between the Rhyacophilinae and the Hydroptilidae, and that the latter again are intermediate between the Glossosomatinae and the Integripalpia. In a paper not yet published I am going to advance another theory, viz.

that the Psychomyidae are intermediate between the Rhyacophilinae and the families with net-spinning larvae (Philopotamidae, Polycentropidae and Hydropsychidae). The last-mentioned theory has already been published in popular form (ANKER NIELSEN 1950b; in Danish). It is now interesting to see whether the two theories are compatible with the facts about the structure of the male genital segments.

Both theories imply that the genus *Rhyacophila* Pict. is the most primitive among recent Trichoptera. This point of view (on which most trichopterologists agree) is supported by the fact that *Rhyacophila* is the only one among the forms studied here in which a distinct Segment XI comprising both an epiproct and a pair of paraprocts is found (pp. 16—17). The dorsal processes on Segments IX and X probably also represent a primitive condition (p. 7). In the stucture of the inferior appendages and the phallus the two Danish species of *Rhyacophila* are rather specialized. As to the former we are to some degree concerned with a specialization by reduction. (Cp. also p. 47: *Rh. gregoryi*).

In its original shape the first mentioned theory, that of the evolution of the Integripalpia, involved that the recent (Danish) Hydroptilidae had a diphyletic origin, the Orthotrichiinae and the Hydroptilinae representing two independent side-branches on the main stem between the Glossosomatinae and the Integripalpia. This cannot be upheld. The two subfamilies have too many features in common for that. Some of these, especially the structure of the inferior appendages, might perhaps be explained as very original features, but the phallus very obviously is highly specialized and that in the same direction in the two subfamilies. The Orthotrichiinae and the Hydroptilinae thus, no doubt, represent one line of evolution which later on has bifurcated. With this modification I think that the theory can be upheld.

Three things might seem to speak against the theory: 1. Superior appendages are lacking in *Rhyacophila*, *Agapetus fuscipes* and most Hydroptilidae, whereas they are present in the Psychomyidae and the Polycentropidae as well as in most Integripalpia. 2. The inferior appendages are two-jointed in *Rhyacophila* and most Integripalpia, but one-jointed in *Agapetus* and most Hydroptilidae. 3. Provided that the titillator of the Hydroptilidae is homologous with the parameres of other Trichoptera, *Agapetus* and the Hydroptilidae agree in having an unpaired paramere, but differ in this respect from both *Rhyacophila* and the Integripalpia.

Much weight cannot be attributed to the two first points. Both the reduction of the superior appendages and the establishment of a one-jointed condition in the inferior appendages no doubt have taken place independently in various systematic groups (pp. 6—7 and 8). Moreover, structures which probably are superior appendages have been described in many *Agapetus* species (ULMER 1930a, p. 375, 1951, pp. 53 and 55; DENNING 1941, p. 201, 1950, p. 117; ROSS 1944, p. 40; KIMMINS & DENNING 1951; KIMMINS 1953b), in *Synagapetus* MacL. (ULMER & KRAWANY 1938, pp. 307—08; KIMMINS 1953b) and in *Pseudagapetus moselyi* ULM. (ULMER & KRAWANY 1938, p. 310). The hydroptilid *Paduniella semarangensis* Ulm. also seems to have superior appendages (ULMER 1912, pp. 81—82. The procss 2 in Agraylea and Hydroptila—fig. 43, 44

and 46, pp. 78, 79 and 83—perhaps may be interpreted as a superior appandage; cp. pp. 146—47). Among the Hydroptilidae the inferior appendages probably are two-jointed in *Agraylea* and in *Baliotrichia* Ulm. In the latter genus Ulmer (1951, pp. 89—90) besides the inferior appendages describes three pairs of cylindrical rods. I interpret the three rods, one of which carries a strong seta, as the dorsal branch of the inferior appendage (see below), the harpago and a paired paramere (see below).

The third objection might seem more serious. I find it unlikely, however, that the hydroptilid titillator is homologous with the paramere of *Agapetus* (pp. 84—85), and the unpaired condition of the paramere may very well be a development special to the Glossosomatinae. Paired parameres are found in *Glossosoma confluens* Kimm. (Kimmins 1953b, pp. 169—70) and probably also in *Myspoleo murinus* Barn. (Glossosomatinae; Barnard 1934, p. 390). In the genus *Himalopsyche* Bks. (Rhyacophilinae) some species have two, others only one paramere (Kimmins 1952). Furthermore, structures which are homologous with the paired parameres in other Trichoptera are possibly found in *Orthotrichia* (p. 85), and similar structures seem to be present in the hydroptilid genera *Protoptila* Bks. (Ross 1944, pp. 41—44), *Baliotrichia* (see above), a. o. (see p. 69).

In several other respects features which support the theory, may be pointed out.

In Integripalpia the posterior part of Segment X is divided into three processes: a pair of lateral ones and an unpaired median one, which latter may be bifurcated. This feature is particularly typically developed in *Beraea* (p. 89) and the Limnophilidae (p. 138), but can also be traced in the other Integripalpia, though the median process often is suppressed. (In some few cases—*Agrypnia*, p. 115—it is perhaps the lateral processes which are suppressed). The processes *8* in *Agraylea* (figs. 43, p. 78; 44, p. 79) remind very much of the lateral processes in the Integripalpia. As mentioned above (pp. 77 and 82), the processes *8* in *Agraylea* possibly are homologous with the processes *8* in *Orthotrichia* (figs. 38, p. 71; 39, p. 72; 41, p. 74) and *Hydroptila* (fig. 46, p. 83), which implies that the lateral processes of Segment IX in the last-mentioned genera are homologous with the lateral processes of Segment X in the Integripalpia. This theory is not so improbable as it might seem at a first glance. In a great number of Integripalpia Segments IX and X have fused to such a degree that the boundary cannot be given with any degree of certainty; (e. g. *Sericostoma*, p. 86; *Beraea*, p. 89; *Leptocerus*, p. 95). And in those cases in which the boundary seems distinct, it may very well be secondary and not the true boundary between the two segments. The same applies to the Hydroptilidae (cp. *Orthotrichia*, p. 68). The inference is that Segment IX in *Orthotrichia* and *Hydroptila* is a composite structure, which includes parts of Segment X—or perhaps rather of Segment XI (see below). A condition like that in *Agraylea* seems to occur in the hydroptilid *Microptila bejela* Mos. (Mosely 1948, p. 85): Segment X is tripartite, and its median process is membranous.

To me the two following assumptions seem reasonable: 1: That the lateral processes of Segment X in the Integripalpia, the processes *8* in the Hydroptilidae and the posterior parts of the sclerites of Segment X in *Agapetus* (p. 21) are homologous and

represent the paraprocts, which have fused with the sclerite of Segment X. On p. 47 it was pointed out that accessory copulatory processes on the paraprocts possibly are an old heritage in the Trichoptera. The fact that structures which seem to represent such processes are present in some Glossosomatinae supports this assumption. *Beraea* (pp. 89—90) might be supposed to represent an original stage, the paraprocts having not yet fused with the sclerite of Segment X. I am more inclined, however, to think that in *Beraea* this condition is secondary. 2. That the median process of Segment X in the Integripalpia represents the epiproct, which like the paraprocts has fused with the sclerite of Segment X. In *Agapetus* and the Hydroptilidae the epiproct has either been suppressed or been subjected to a desclerotization, though in *Orthotrichia* (p. 68) it may be represented by the spines 2 and 3. It is worth noting that the median process of Segment X in some Integripalpia is bifurcated like the epiproct in *Rhyacophila* (p. 16).

Another common feature of the Integripalpia is that the coxopodite is divided into a dorsal and a ventral branch, the latter carrying the harpago. This is seen particularly distinctly in the Beraeidae (pp. 87 and 90—92), but in a somewhat rudimentary condition the dorsal branch is present also in *Molanna* (p. 99) and *Lasiocephala* (p. 107), and it seems that it is found also in some limnophilid genera, viz. *Halesochila* Bks., *Chianophylax* Schmid, *Ecclisomyia* Bks. and *Farula* Milne (Schmid 1950, p. 59; 1951, pp. 58 and 60; 1955, pp. 57—58, fig. 33 and pp. 71—72, fig. 46). The dorsal branches are present also in the Hydroptilidae, though it seems in a rather specialized condition, represented by the structures labelled *5* in figs. 39, p. 72; 40, p. 73; 41, p. 74; 43, p. 78; 44, p. 79; 46, p. 83; (and *6* in figs. 43 and 44). Especially the "parameres" in *Hydroptila occulta* (p. 83) remind very much of the dorsal branches in *Beraea*. Structures of the same sort as the "parameres" in *H. occulta* are found also in some other species of the genus (Betten 1934, p. 513; Schmid 1947; Mosely 1948). They further occur in the following genera, though being much shorter (and with the setae placed distally), and thus having a still greater resemblance to the dorsal branches in *Beraea: Javanotrichia* Ulm. (Ulmer 1951, pp. 76 and 78), *Orthotrichiella* Ulm. (l. c., p. 81) and *Baliotrichia* Ulm. (l. c., pp. 89—90). The similarity to the dorsal branches in *Beraea*, however, is particularly great in the genera *Stactobia* MacL. (Ulmer 1950, p. 296; described as "obere Anhänge"; in this genus Vaillant—1951—seems to have confused these structures with the phallus), *Plethus* Hag. (Ulmer 1951, pp. 63—65; described as "Appendices präanales") and *Oeceotrichia* Ulm. (l. c., p. 86; each provided with a seta). In *Pasirotrichia* Ulm. they have the shape of a pair of hook-like rods (l. c., p. 91).—In *Sumatranotrichia* Ulm. there is an unpaired structure, which has some resemblance to the process *5* in *Orthotrichia*, though it is much longer (l. c., p. 88).

In this connection it should be mentioned that there also is some likeness between the structures mentioned in the Hydroptilidae and the processes on the basal plate in *Tinodes* (fig. 16, p. 35). Especially the process *5* in the Hydroptilidae reminds of the process *4* in *Tinodes*, both being provided with a pair of strong setae,

In species of the genera *Psychomyia* Pict. and *Psychomyiella* Ulm. ULMER (1951, pp. 163, 165, 166 and 168) describes "3 starke Chitingräten" which perhaps may be homologous with the processes of the basal plate in *Tinodes*. This indicates that the two-branched condition of the coxopodite is a very original feature in the Trichoptera, which now has been lost in most Annulipalpia.

In most Integripalpia with two-jointed inferior appendages the harpago arises subdistally on the coxopodite, so that the latter has a distal projection beyond the base of the former. This condition is seen most distinctly in *Agrypnia* (fig. 66, p. 117), but among the forms treated here it is only in *Silo* that the harpago arises distally, and in the closely related *Goëra pilosa* Fabr. it has a subdistal origin. In the Hydroptilidae the inferior appendages generally are one-jointed, but if the process *13* in *Agraylea* (figs. 43, p. 78 and 44, p. 79) really is a harpago—which seems very likely—it means that this joint in the Hydroptilidae also has a subdistal position; (cp. also *Baliotrichia*, p. 146). (In *Rhyacophila gregoryi* Ulm.—ULMER 1932—33, p. 42—the harpago is likewise placed subdistally. This, however, is possibly a development particular to this species and arisen in connection with a strong reduction of the harpago).

The hydroptilid phallus is very much specialized. Nevertheless, the shape of its distal end foreshadows conditions in the Integripalpia (cp. pp. 12—13).

As to the second theory, the evolution of the families with net-spinning larvae, some features may be pointed out in which these families resemble each other and the Psychomyidae, but differ from other systematic groups of Trichoptera. As the morphology and the biology of the developmental stages show, the families Psychomyidae, Philopotamidae, Polycentropidae, and Hydropsychidae are natural units. Hence, features which are common to these families must have evolved before their ways parted, and if such a feature is lacking in a member of one of the families, this lack must be due to a reduction. This means that the apparent simplicity in the structure of the genital segments in *Lype* and probably also in *Wormaldia* (see below) has arisen by reduction.

In the Psychomyidae (pp. 24—26, 30—31 and 37—40) and the Polycentropinae (pp. 46—48 and 52—55) the reduced dorsal part of Segment IX is detached from the ventral part and intimately associated with Segment X. In *Wormaldia* (pp. 42—44) conditions are very similar, though the two parts of Segment IX are sclerotically continuous; this latter, however, is possibly secondary. *Tinodes* and *Psychomyia* resemble the Polycentropinae in that Segment X is (at least chiefly) membranous. This, however, is probably due to parallel evolution in the two groups. In *Lype* Segment X is sclerotized like that of *Wormaldia* and provided with a dorsal process. The latter, no doubt, is a primitive feature, and since it is difficult to imagine a dorsal process in connection with a membranous Segment X, the sclerotic condition must be considered the original one in the family Psychomyidae.

The Polycentropidae are exceptional in that the IX/X muscle is inserted on the superior appendage (pp. 48, 54, 61). This condition may have evolved from that

in *Wormaldia*, in which the superior appendage is sclerotically continuous with Segment X, and the muscle inserted in the angle between the segment itself and the appendage (pp. 43—44).

As mentioned above (pp. 46—47), paraprocts with accessory copulatory processes are possibly an old heritage in the Trichoptera. Well developed, musculated paraprocts are found in the Polycentropidae (pp. 46—47, 54—55, and 62). The processes *14—16* in *Tinodes* (figs. 14 and 15), no doubt, belong to the paraprocts (p. 32), and the same is possibly the case with the rods *5—6* in *Psychomyia* (fig. 19; cp. p. 40). In both of these genera the paraproctal muscle is present (pp. 33 and 40), though in *Tinodes* it has shifted its insertion to a part of Segment X which, strictly speaking, belongs to Segment IX. In *Lype* (pp. 24—26) the paraprocts are reduced, but the paraproctal muscle is still found and has a similar insertion as in *Tinodes*.

In *Wormaldia* (pp. 43—44) the paraprocts are likewise reduced, and the paraproctal muscle either is lacking or has fused with the IX/X muscle. It seems, however, that the typical genital equipment of the Philopotamidae comprises paraproctal processes. Structures which may be interpreted as such are found in *Philopotamus* Leach. (Since I had only dried material of this genus at my disposal, I was unable to decide the question with certainty). Similar structures have been described in other philopotamids, viz. many species of the genus *Chimarrha* Steph. (Ulmer 1916; 1930b, p. 481. Barnard 1941, p. 106. Denning 1952), in *Vigarrha tibialis* Nav. (Ulmer 1930a, p. 377) and in *Thylakion* Barn. (Barnard 1934, p. 384).

On pp. 62—63 and 63—64 it has been accounted for how the genital segments of *Ecnomus* and *Hydropsyche* may have evolved from a polycentropine type.

Judging from MacFarlane's descriptions (1951) the rhyacophilid subfamily Hydrobiosinae approaches the family group in question: The dorsal part of Segment IX is much reduced. Both "superior" and "intermediate appendages" are described. The latter quite obviously are the true superior appendages; the former may be paraproctal processes.

Due to the intimate association of the dorsal part of Segment IX with Segment X the dorsal VIII/IX muscle is incorporated in the genital system. In *Psychomyia* (p. 40) and *Wormaldia* (p. 44) this muscle is divided into two portions, one the bands of which converge towards an unpaired median insertion, and another inserted laterally. In *Lype* and *Tinodes* the lateral, in the Polycentropidae and the Hydropsychidae the median portion is lacking.

In *Tinodes* (p. 34) and *Psychomyia* (pp. 40—41) the harpago is bifurcated, and the same is the case in *Philopotamus* Leach. The simple shape exhibited by *Lype* (p. 27) and *Wormaldia* (p. 44) therefore must be considered secondary. In the Polycentropidae (pp. 48, 55 and 59) the distal end of the inferior appendage is divided into two branches (the dorsal one much smaller than the ventral one). If the one-jointed appendage in this family has arisen by fusion of the coxopodite and the harpago—which is most probable—this indicates that the harpago was bifurcated. In *Ecnomus furcatus* Ulm. (Ulmer 1930a, p. 430) the bifurcation is very strongly pronounced, so

that the appendage has no small resemblance to that of *Tinodes pallidula* (p. 8). As in *Lype* and *Wormaldia* the simple shape of the harpago in *Hydropsyche* is possibly secondary.

A bifurcation of the harpago also occurs in some Integripalpia. It is especially distinct in the Apataniinae (p. 135) and the Goërinae (p. 139), but traces of this condition are found also in *Leptocerus* (p. 96) and *Lasiocephala* (pp. 107—09). The dorsal branch of the inferior appendage in *Sericostoma* (p. 87) probably includes the harpago (pp. 90—92). Its distal notch indicates that the harpago was bifurcated. A bifurcation of the harpago thus seems to be a very old feature in the Trichoptera. It is also seen in many species of *Rhyacophila* (Betten 1934, p. 506; Ross 1944, p. 33; Banks 1947, fig. 10; Schmid 1952, pp. 636 and 46; Kimmins 1953a).

The shape of the phallus varies much within the four families in question. Still, its proximal part (including the apodeme) shows a striking resemblance in *Lype* (pp. 27—28), *Psychomyia* (p. 42), *Wormaldia* (p. 44), *Polycentropus* (p. 49) and *Holocentropus* (p. 55).

Below a table is given of the development of the musculature of the inferior appendages and the phallus:

	Inferior appendage				Phallus	
	anterior dorsal	anterior ventral	posterior dorsal	posterior ventral	anterior	posterior
Lype	−	+	+	+	+	−
Tinodes	−	+	+	+	−	−
Psychomyia	−	+	−	+	+	−
Wormaldia	+	+	+	+	+	+
Polycentropus	−	+	+	−	+	+
Holocentropus	−	+	+	−	+	+
Ecnomus	+	+	+	−	+	+
Hydropsyche	+	+	−	−	+	+

The posterior ventral muscle of the inferior appendage has a similar and unusual development in *Lype* (p. 27), *Tinodes* (p. 35) and *Wormaldia* (p. 44). In *Psychomyia* (p. 40) this muscle is very highly specialized; in the Polycentropidae (pp. 49, 55 and 62) it probably and in *Hydropsyche* (pp. 65—66) it certainly is lacking. Since there can be no doubt that the Polycentropinae are more closely related to *Ecnomus* than to the Psychomyidae, the lack of the anterior dorsal muscle in both the Psychomyidae and the Polycentropinae must be due to parallel evolution. On the other hand, it is possible that the lack of the posterior ventral muscle in both the Polycentropidae and the Hydropsychidae is a sign of closer affinities.

It should now be possible to give an outline of the male genital segments of the hypothetical primeval Trichopteron: Segment IX was synscleritous; its posterior border was protracted into an unpaired dorsal process, and perhaps a similar ventral

process was found. The dorsal side of Segment X was sclerotized and anteriorly carried an unpaired dorsal process and a pair of passively movable superior appendages. Very likely the dorsal processes of Segments IX and X were united by membrane as is seen in *Rhyacophila* (p. 15). On the ventral side of Segment X (cp. p. 7) there was a pair of paraprocts, each carrying an accessory copulatory process, and above the anus an epiproct, perhaps divided into a right and a left prong, occurred. The epiproct was movable by a pair of muscles originating on the antecosta of Segment X (p. 16), the paraprocts by another pair originating in Segment IX (p. 48). The inferior appendage was two-jointed; the coxopodite was divided into a dorsal and a ventral branch, the latter carrying the harpago, which again was bifurcated; proximally the two coxopodites were sclerotically continuous with each other and with an unpaired basal plate. The phallus, the proximal end of which was lowered into a phallocrypt, was divided into a phallobase and an aedeagus; the distal part of the latter was cleft into a dorsal and a ventral branch; the opening of the ejaculatory duct, the phallotreme, was on the dorsal branch; at the bottom of the endotheca, beside the aedeagus, a pair of parameres took their origin. Finally, it must be mentioned that the ejaculatory duct probably was bifurcated as in the Lepidoptera (Beirne 1942); in recent Trichoptera this condition seems to be preserved only in the Hydroptilidae (p. 75). The specializations within the order have to a varying degree been accompanied by simplifications of the ground-plan described above.

Two main lines of evolution can be traced; (cp. pp. 144—45). 1: Rhyacophilinae — Glossosomatinae — Hydroptilidae — Integripalpia. 2: Rhyacophilinae — Psychomyidae — Philopotamidae, Polycentropidae, Hydropsychidae.

In Group 1 the dorsal processes of Segments IX and X have united into a single structure, which may be paired. It is rarely, however, well developed (*Leptocerus*, p. 94; *Oligoplectrum*, p. 111; *Silo*, p. 137). More frequently it is rudimentary to a greater or less degree, and in about half of the forms treated here it is entirely reduced. In Group 2 the dorsal process of Segment IX is lacking, but that of Segment X may be retained (*Lype*, p. 24; partly in *Wormaldialdia*, p. 43; possibly in *Hydropsyche*, p. 63). A most striking feature in this group is the fact that the sclerite of Segment IX is secondarily divided into a dorsal and ventral part, the former being intimately associated with Segment X.

In Group 1 the epiproct and the paraprocts have united with the sclerite of Segment X; in this way the tripartite structure of Segment X typical of the Integripalpia has arisen. The median process may be considered the epiproct, the lateral ones the (somewhat reduced) copulatory processes of the paraprocts. In Group 2 the epiproct is entirely reduced, whereas the paraprocts are often retained in a primitive condition.

Originally Segments IX and X were connected by two pairs of muscles, the IX/X muscle and the paraproctal muscle. This condition is preserved in *Lype* (p. 26), *Tinodes* (pp. 32—34) and the Polycentropidae (pp. 48, 54, 59 and 61), but in the vast majority of Trichoptera there is only one pair of muscles between the two segments.

The question then is whether it is the IX/X muscle or the paraproctal muscle which is preserved. In *Psychomyia* (p. 40) there is evidence that it is the paraproctal muscle, and it is perhaps also this muscle which is found in *Hydropsyche instabilis* (pp. 63 and 64). In *Rhyacophila* (p. 15), on the other hand, the paraproctal muscle seems to be reduced. In most cases, however, I am inclined to think that the single muscle has arisen by a fusion of the IX/X muscle and the paraproctal muscle. Among recent Trichoptera an epiproctal (dorsal X/XI) muscle is found only in *Rhyacophila*.

The dorsal branch of the coxopodite is retained in a rather primitive shape in the Beraeidae, and in a more or less rudimentary state in some other Integripalpia. It is retained also in the Hydroptilidae, but in this family it is oftener highly specialized. In Group 2 it is found (in a specialized condition) only in some Psychomyidae.

The phallus is perhaps that part of the genital structures which shows the richest variation. It may be very different even in forms which for other reasons must be considered closely related. In general, however, it may be pointed out that in Group 1 there is a tendency towards reduction of the dorsal branch of the aedeagus, whereas in Group 2 there is a tendency towards reduction of the ventral branch (pp. 12—13).

To sum up, it can be said that nothing in the structure of the male genital segments speaks definitely against the two theories, whereas some things speak in their favour. It will probably be better not to enter further into a phylogenetic discussion until more facts (i. a. a study of the female genital segments) are available.

Summary.

Segment VIII is the last typical abdominal segment with a separate tergum and sternum, though even this segment may be slightly modified. Its posterior border to a greater or less degree overlaps Segment IX, sometimes so much that the latter is partly or entirely concealed. Segment IX is typically synscleritous, forming a strong annulus. More often the dorsal part of the annulus is shorter than the other parts, and in extreme cases it is reduced to a narrow transverse bridge. Sometimes the sclerite has an anal membranous indentation on the ventral side, and rarely the ventral side is entirely interrupted by a membrane. The posterior end of Segment IX is a mainly membranous depression, the genital chamber. From this depression the following structures arise: Segment X dorsally, the inferior appendages ventrally, and between Segment X and the inferior appendages the copulatory organ, the phallus.

Except for the paraprocts, mentioned below, Segment X may be entirely membranous or very slightly sclerotized. Oftener, however, it is provided with a dorsal, sometimes paired sclerite. The latter varies greatly, and the shape of the segment as a whole is also extremely variable. In extreme cases (Ecclisopteryginae and especially Limnophilinae) its length is reduced so much that the sclerites of the segment appear as situated at the bottom of the genital chamber. The ventral side of Segment X is generally more or less concave, and part of the dorsal side of the phallus lies in this concavity. In some cases the edges of the concavity approach each other so much that the base of the phallus becomes enclosed in a functional tube. The segment typically carries a pair of superior appendages, which vary greatly in size and very often are lacking.

Segment X is a composite structure. It also comprises Segment XI. A distinct Segment XI, however, is developed only in the Rhyacophilinae, but in most other forms traces of it can be found. In nearly all forms there is some sort of sclerotic connection between Segments IX and X, and in many Hydroptilidae and Integripalpia the boundary between the two segments cannot be stated with any degree of certainty. In those forms in which there seems to be a distinct boundary it is most likely a secondary one. In the Psychomyidae and the Polycentropinae the reduced dorsal part of Segment IX is secondarily detached from the rest of the segment and intimately associated with Segment X. In *Wormaldia* conditions are very similar, though the two

parts of Segment IX are sclerotically continuous; this latter, however, is possibly secondary. The apparently more primitive condition in the Ecnominae and the Hydropsychidae probably has arisen by fusion of the secondary Segments IX and X of the Polycentropinae.

In *Hydropsyche instabilis* Curt. (p. 63) and *Molanna* (p. 99) structures which perhaps might be interpreted as cerci are found, though I find other interpretations more likely.

The inferior appendages, the gonopods, typically are divided into a proximal and a distal joint, coxopodite and harpago, respectively. In very many forms, however, they are one-jointed. This condition may have arisen in three ways: 1. By reduction of the harpago. 2. By fusion of the two joints. 3. By fusion of the coxopodite with Segment IX. In most cases the two coxopodites are sclerotically united with each other and with an unpaired basal plate situated at the bottom of the genital chamber between and above the two appendages. In some few forms they are connected by membrane only. This is, no doubt, a secondary condition, and the same is true in *Rhyacophila*, in which there is no connection between the appendages. The inferior appendages generally form the chief clasping apparatus. In some few forms, however, they are much reduced. This is especially the case in the Limnophilinae, in which subfamily they may be non-musculated. In the Ecclisopteryginae also the inferior appendages are much reduced, but still play an important rôle in the clasping apparatus.

The base of the phallus is lowered into a tubular depression, the phallocrypt, which generally is very deep, but may be almost entirely obliterated. In practically all forms a phallic apodeme is formed by fusion of the proximal end of the phallus with the anterior part of the phallocrypt. The length of this apodeme is extremely variable. The relation between the phallocrypt and the basal plate of the inferior appendages varies. In some cases the basal plate is situated on the floor of a small pocket, the entrance of which is separated from that of the phallocrypt. In other cases it is situated on the floor of the phallocrypt. In still other cases, in which the basal plate is very small, it simply lies on the floor of the genital chamber outside the entrance to the phallocrypt. In a rather large number of forms there is a sclerotic connection between the basal plate and the root of the phallus.

The phallus is probably that part of the genital apparatus which is most varying. In its original shape it was divided into a (probably membranous) phallobase and a mainly sclerotized aedeagus, which latter arises from an eversible depression, the endotheca, on the apex of the phallobase. In the majority of the Trichoptera, however, the phallus is undivided. This condition may have arisen in three ways: 1. By a strong development of the phallobase accompanied by a sclerotization of its external wall, the phallotheca, and a reduction of the aedeagus. The final result is that the copulatory organ is formed of the phallobase, which contains an eversible sac, the endotheca, at the bottom of which the ejaculatory duct opens. 2. By obliteration of the endotheca and subsequent fusion of the sclerotized phallotheca with the

aedeagus, or 3. By reduction of the whole phallobase, a direct continuation being established between the phallic apodeme and the aedeagus. The highly specialized phallus of the (Danish) Hydroptilidae possibly represents the final result of this process, though in a modified form. In detail the variations of the shape of the phallus are so numerous that they cannot be enumerated here.

By comparison of recent forms it is possible to give an outline of the male genital segments of the hypothetical primeval Trichopteron.

The posterior border of the synscleritous Segment IX was protracted backwards into an unpaired dorsal process. The sclerotized dorsal side of Segment X anteriorly carried a similar dorsal process. In *Rhyacophila* both processes are present, connected by membrane. In some Integripalpia a dorsal process is found, which may be paired, and which probably has arisen by fusion of the processes of Segments IX and X, and in some Annulipalpia the dorsal process of Segment X is retained. In most Trichoptera, however, dorsal processes are lacking. Segment IX perhaps was provided also with a ventral process. Such a process is found in *Sericostoma* and *Mystacides.*

Segment XI had the structure typical of primitive Pterygota: On the ventral side of Segment X, below the anus, there was a pair of paraprocts, each carrying an accessory copulatory process, and above the anus there was an unpaired, but perhaps bifurcated epiproct. Among recent forms a distinct Segment XI is found in *Rhyacophila* only (though in the Danish species the paraprocts lack copulatory processes), but well-developed paraprocts with copulatory processes are found in the Polycentropidae, no doubt in *Tinodes* also, and possibly in *Psychomyia.* In the Integripalpia the epiproct and the paraprocts have united with the sclerite of Segment X; in this way the tripartite structure of Segment X typical of the Integripalpia (and especially clearly shown by the Apataniinae and the Goërinae) has arisen. The median process may be considered the epiproct, the lateral ones as the (somewhat reduced) copulatory processes of the paraprocts. Very often the median process, more rarely the lateral ones are reduced; or all the three processes may be reduced in size (e.g. *Sericostoma*). In the Hydroptilidae Segment X has a similar structure. Owing to the intimate association between Segments IX and X the lateral processes in some hydroptilid genera appear as processes of the former segment. Segment X of the Glossosomatinae seems to be of the Integripalpia type with reduced median process.

In the Limnophilinae Segment X is highly specialized. In this subfamily the segment has no sclerotic connection with Segment IX, and its sclerite is paired. Moreover, the ear-like lateral process and the paired median process are detached from each other and together form a pair of pincers, which is the chief (or only) clasping apparatus. The lateral process has wrongly been termed "superior appendage". In *Ecclisopteryx* another specilization is found: the right and the left half of Segment IX can be moved in relation to each other, by which movement the lateral processes of Segment X (the "superior appendages") and the one-jointed inferior appendages together act as a pair to tongs with bifurcated jaws.

The coxopodite was divided into a dorsal and a ventral branch. The former is retained in a rather primitive shape in the Beraeidae, and in a more or less rudimentary state in some other Integripalpia. Furthermore, it is retained in *Hydroptila occulta* Eat. It is found also in other hydroptilids, but there the right and the left dorsal branch have fused into an unpaired, highly specialized structure. A similar condition is seen in some Psychomyidae. The ventral branch carried the harpago subdistally, which position it still has in most Integripalpia. Probably the harpago was bifurcated like the coxopodite.

The aedeagus was divided into a dorsal and a ventral branch, the former with the opening of the ejaculatory duct distally. This condition is found in the Rhyacophilidae, and more or less distinct traces of it are left in the Psychomyidae and in *Polycentropus*. In most recent Trichoptera, however, the aedeagus (when present) is undivided. In the Hydroptilidae and in the Integripalpia it seems that it is the dorsal branch which is reduced. The result of this is that the ejaculatory duct opens at the bottom of a spoon-like depression on the dorsal side of the undivided aedeagus. This spoon may develop into a distinct phallotremal cavity, at the bottom of which the opening of the ejaculatory duct is found surrounded by a phallotremal sclerite. In the Annulipalpia, on the other hand, there seems to be a tendency towards reduction of the ventral branch.

At the bottom of the endotheca, beside the aedeagus, a pair of parameres took their origin. In most recent Trichoptera they are lacking. The unpaired titillator, which in the Hydroptilidae arises distally to the middle of the undivided phallus, is scarcely homologous with the parameres of other forms.

It is interesting to note that in the Hydroptilidae the distal part of the ejaculatory duct is bifurcated, which is the case also in the Lepidoptera.

The specializations within the order have to a varying degree been accompanied by simplifications of the ground-plan described above.

The copulatory apparatus is provided with the following muscles: A dorsal IX/X muscle connects Segments IX and X. Another muscle originates in Segment IX and is inserted in the paraproct. Both of these muscles are well developed in *Lype*, *Tinodes*, and the Polycentropidae. In most Trichoptera, however, there is only one pair of muscles between Segments IX and X. In *Psychomyia* and perhaps in *Hydropsyche instabilis* Curt. there is evidence that it is the paraproctal muscle, in *Rhyacophila* that it is the IX/X muscle. In most cases I think that the single muscle has arisen by fusion of the IX/X muscle and the paraproctal muscle. A dorsal X/XI muscle, inserted in the epiproct, among recent Trichoptera is found only in *Rhyacophila*. The inferior appendages have four pairs of extrinsic muscles: anterior and posterior dorsal ones, and anterior and posterior ventral ones. Except in some Hydroptilidae the two anterior ventral muscles have fused to an unpaired muscle. Furthermore, there is an intrinsic flexor of the harpago; in *Silo* it is divided into two. The superior appendages have no musculature of their own, but in the Polycentropidae the IX/X muscle is attached to the superior appendage. The phallus has two pairs of extrinsic muscles, an anterior

and a posterior one, and an intrinsic retractor of the aedeagus. The latter originates in the phallic apodeme or in the phallotheca and is inserted in the aedeagus; in *Rhyacophila*, however, it is inserted on the bases of the parameres. All the muscles mentioned above are not present in all forms, and in many forms the genital musculature becomes very highly specialized. In the Psychomyidae, Philopotamidae, and Polycentropinae the dorsal VIII/IX muscles have been incorporated into the genital system.

The author has previously advanced the theory that within the order Trichoptera two main lines of evolution may be traced, viz. Rhyacophilinae-Glossosomatinae-Hydroptilidae-Integripalpia and Rhyacophilinae-Psychomyidae-Philopotamidae, Polycentropidae, Hydropsychidae. It seems to me that nothing in the structure of the male genital segments speaks definitely against the theory, whereas some things speak in its favour.

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