Reproductive system and mating in Ephemeroptera[1]

BY

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Preface

When I worked on the same topic in Plecoptera, it was often found desirable to make comparisons with other primitive pterygote insects. As regards Orthoptera this was usually easily performed, as there are thorough studies on the morphology as well as embryology of their genital organs. For other primitive groups such investigations are few, and the details obtainable are mostly scattered in short papers in various journals. This deficiency was especially regrettable regarding Ephemeroptera, as these insects apparently represent a basic scheme of considerable importance from a general point of view. The most useful general paper on mayfly genitalia is still the classic by J. A. Palmén (1884), in spite of the fact that it was written long before comparative insect anatomy and morphology developed.

It is true that after Swammerdam's Ephemeri vita (1675) many data have been gathered on certain parts of the topic, as mating and mating flight. But a review of the literature showed that regarding this phenomenon too, the general features of which are well-known to most people and described by poets as well as scientists in a very extensive literature, there are thorough controversies. This is easily accounted for: mayfly mating occurs at dusk, usually in the air beyond the scientist's reach, and it is momentary.

I had collected various material for investigation but observations on the mating flight of mayflies had revealed no more than previous studies of swarms and netting of disturbed pairs. That was where things stood, when on the 26th of July, 1955, I was driving from Tromsö in Norway to Karesuando in Sweden along the Finnish border, via the military road constructed in 1944. This is wild and magnificent country, with numerous untamed rivers and streams, and I seized the opportunity of studying certain peculiar northern species of Plecoptera which had not been included in a first paper on mating conditions of this group. I was skilfully assisted by my companions, professor K. G. Wingstrand, Copenhagen, and Mr. L. Cederholm, Lund. At nine p. m. we stopped at a tributary of the large Köngämä River, about 45 miles W.S.W. of Karesuando. When leaving the car we were immediately surrounded by dense clouds of mosquitoes, simuliids and ceratopogonids. Only a few Plecoptera and Ephemeroptera were seen. But suddenly swarms of the mayfly *Parameletus chelifer* Bengts. arose from the river banks. Males gathered above the stream but numerous females were coming in from many directions and were caught by the males. Scattered pairs started mating in the air, but a great many flew on to stones, willow-bushes or to a bridge where they could be studied and even photographed for the few seconds mating lasted. This initiated the following paper.

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[1] Reprints were published in November 1956.

Introduction

With regard to the reproductive system there is no great variation in the Ephemeroptera. Compared to the stoneflies the mayflies exhibit an astonishing uniformity in most details. So far as known, the diversity of the internal sexual organs means rather inconsiderable modifications of the same simple basic type. The external organs are more varied, but never depart from a common generalized scheme, even where considerable reductions occur.

Because of this, I find it pointless to describe in detail a series of species, chosen among the various families, but have preferred to deal with the organs or groups of organs separately, in each case discussing previous or personal results as far as necessary for the analyses.

1. The segmentation of the mayfly abdomen

The authors of the nineteenth century presented different conceptions of the number of segments present in the mayfly abdomen: Pictet (1843) gives nine joints, several authors ten (Hagen 1863, Lubbock 1863, Eaton 1888, Packard 1883, Vayssière 1882, and Heymons 1896) and one counts eleven segments (Hayek 1881).

More recent authors claim that there are ten distinct segments, followed by a reduced eleventh. Sometimes even traces of a twelfth are said to occur (Snodgrass 1931, p. 28). The interpretation of the postgenital segments varies, however. Taxonomists agree that there are ten well-developed segments, the last of which forms the terminal segment of the body and carries the long cerci. This means that the eleventh segment is very reduced: the epiproct is fused to the paracercus (terminal filament) and the paraprocts are united with the bases of the cerci. This opinion was accepted by Snodgrass in 1931 (p. 21), in spite of the fact that it meant that the anal opening would have been displaced forward and split the 10th segment into two hemisternites and further that the paraprocts would have disappeared almost completely. Later (1936, p. 77), however, he abandoned this opinion. The hemisternites were regarded as the paraprocts which had extended forward following the reduction of the tenth sternum. The only sternal part which might be referred to the tenth segment was the transverse basal plate (or arms) of the penes. This was accepted by Qadri (1940, p. 126).

Embryological data put forward by Heymons (1896 a, p. 85 and 1896 b, p. 29) show that the abdomen consists primarily of 11 segments (plus telson with the proctodaeum), which are provided with 11 pairs of "Extremitätenanlagen". The last pair forms the cerci while the paracercus is developed from the tergal part of segment 11.

Already in the fresh first-stage larva there is a reduction of the number of complete segments. The abdominal tergum of the unmodified larva is morphologically similar to that of the adults. There are ten well-developed tergal plates, the last of which is more or less produced hindwards, so that it covers an underlying plate (the epiproct of the 11th segment) which carries the paracercus. Thus, it agrees principally with other primitive pterygote insect groups.

The abdominal sternum of the unmodified ephemerid larva is also similar to that of the adults. The anterior nine segments are easily recognized. A normal tenth sternum is lacking, however. Behind the ninth sternum of the

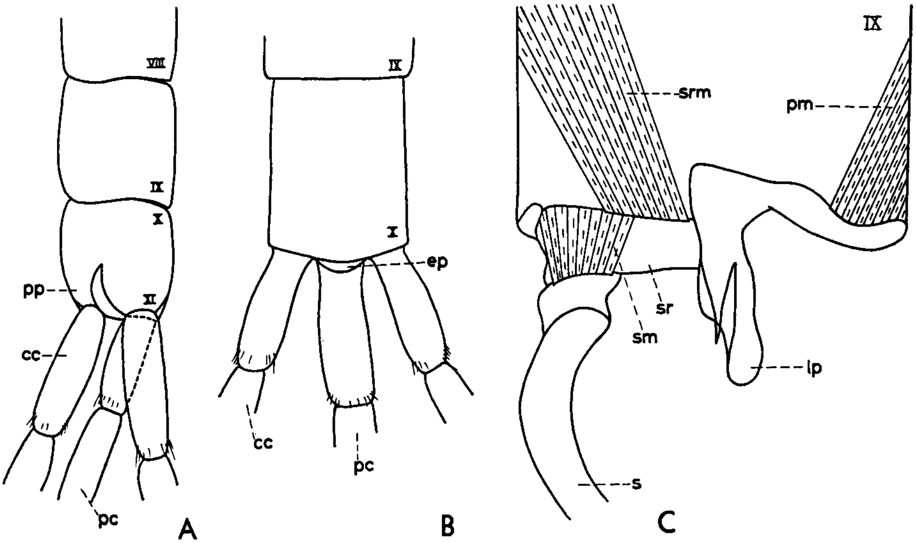

Fig. 1. A—B. Apical part of abdomen of first stage larva (0,8 mm long) of *Ephemera vulgata* L. A. Ventro-lateral view. B. Dorsal view. (cc=cercus, ep=epiproct, pc=paracercus, pp=paraproct. Roman figures=numbers of segments.) — C. The musclature of the male genital structures of *Ephemera vulgata* L. Ventral view. Right penis and penial arm removed, as is also the left part of the styliger plate with attached stylus. (lp=left penis, pm=muscle of penial arm, s=stylus, sm=stylus muscle, sr=styliger, srm=styliger muscle.)

male follows a transverse bar carrying the penes and succeeded by a pair of plates, covering the cercal bases. In the females there are no structures separating the ninth sternum from the last-mentioned pair of plates.

I have examined first-stage larvae of various species of mayflies but never found any traces of a separate tenth sternal plate, lying in front of the terminal pair of plates. The general appearance has been as shown in fig. 1 A—B: behind the ninth sternum there is a fairly broad annulus the ventral part of which is medially cleft in the posterior third or half. The absence of a separate tenth sternal plate already in the first larval stage is of no phyletic significance, however, as even in other primitive groups it is usual that the tenth sternum is reduced very early. In the following stages the anterior annulus is reduced ventrally by forward extension of the lobiform posterior plate.

There seems to be no doubt that the complete tenth annulus (of the first-stage larva) represents the tenth abdominal segment, while the lobiform plates are the extending ventral parts of the 11th segment (the paraprocts). Besides the embryological evidence mentioned above, this is proved by the following facts: the cerci occur as appendages of the terminal plates and furthermore these plates are innervated by the abdominal segmental nerve No. 11 while penes plus penial bar (and the persisting dorsal part of the annulus) are innervated by nerve No. 10 (for details vide below).

As mentioned above, Snodgrass supposed the penial bar to be the remains

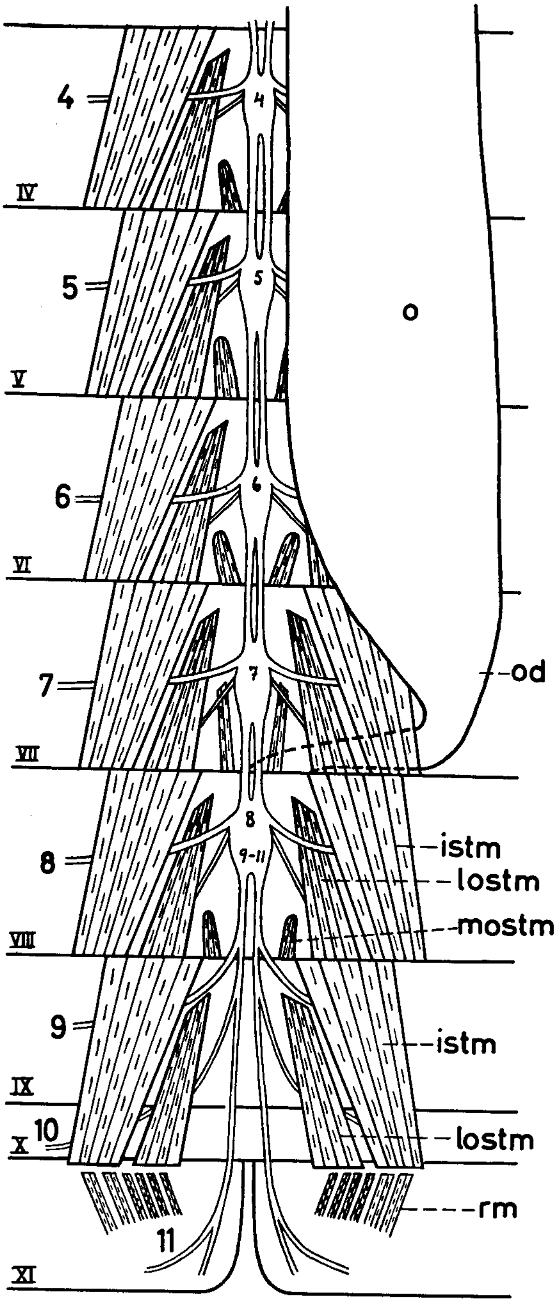

Fig. 2. Apical half of female abdomen of generalized mayfly, demonstrating the ventral musculature in relation to the segmental nerves and genital ducts. Dorsal view. Only right ovary+oviduct figured. (istm = inner sternal muscle, lostm=lateral outer sternal muscle, mostm=medial outer sternal muscle, o=ovary, od=oviduct, rm=rectal muscles. Roman figures = numbers of the resp. abdominal segments. Arabian figures=numbers of the resp. segmental nerves and corresponding ganglia.)

of the tenth sternum. Embryologically, it arises from the intersegmental area behind the ninth sternum, and from this point of view there is nothing supporting the taxonomists' theory that it should belong to the latter sternum.

Snodgrass' opinion is also supported by the fact that it is innervated by a branch of the penial nerve (segm. nerve No. 10; vide fig. 4). Because of this it seems probable that the derivation of the musculature of the penial bar is a secondary modification.

As seen in fig. 2 the ventral abdominal musculature of the mayflies is fairly schematic. There is a broad internal sternal muscle which is always well developed in the anterior segments. In certain species (like *Ephemera vulgata* L.) this muscle is very weak in segments 6—7 in mature specimens, while in the nymphs it is well present, as in quite fresh specimens. Its medial part is well developed in segments 8—9. There are two outer sternal muscles: the median one is absent in the last segments; the lateral one is present through the abdomen. This normal scheme is independent of sexual modifications of the abdomen. The genital sclerites are situated below the intersegmental muscles running from the ninth to the eleventh segments. As is evident from fig. 1 C the muscles of the penial basal plate form part of the lateral section of the sternocoxal musculature of the ninth segment; its medial part inserts on the styliger. In the latter arise muscles inserting on the basal joint of the stylus. The peripheral joints contain no muscles.

In the prosopistomids there is a secondary contraction and fusion of the anterior abdominal segments with the thorax.

It seems that the present general type of abdominal segmentation was established very early. When reviewing Permian Ephemeroptera Carpenter says (1933, p. 490): "Ten segments are visible in the abdomen from above; the terminal filaments were present in both sexes and in the male were at least as long as the abdomen, containing upwards of 40 segments; the genital claspers of the male were very much like those in existing species".

2. The position of the gonopore

Most previous authors dealing with mayfly genitalia agree that the male genital opening lies behind the ninth segment, while the female vulva opens behind the seventh segment. As regards the female genital aperture, its position does not give rise to any doubt regarding to what segment it belongs, although it can be discussed whether this position is primary or secondary, as has been done by Walker (1919).

Based on embryological and morphological data, Snodgrass (1937, p. 77) and Qadri (1940, p. 126) suppose that the penes (and the male gonopore) belong to the tenth segment (and not the ninth as usually accepted).

Below I have discussed the gonopore with special regard to its primary position, which is of great interest with respect to the conditions in other primitive groups of insects. For this purpose I have examined the relations between muscles, nerves and genital organs in the posterior abdominal segments.

In the generalized mayfly there are eight abdominal ganglia. Nos. 1—7 are simple, while No. 8 consists of the united embryonal ganglia 8—11. The first abdominal ganglion has moved forward and is more or less intimately connected to the metathoracal ganglion. Ganglia 2 to 7 are situated in the respective normal segments. The composite ganglion 8 lies in the eighth segment.

Each ganglion gives rise to two pairs of principal nerves. The anterior one is large. These nerves run dorsally of the lateral outer sternal muscles (vide

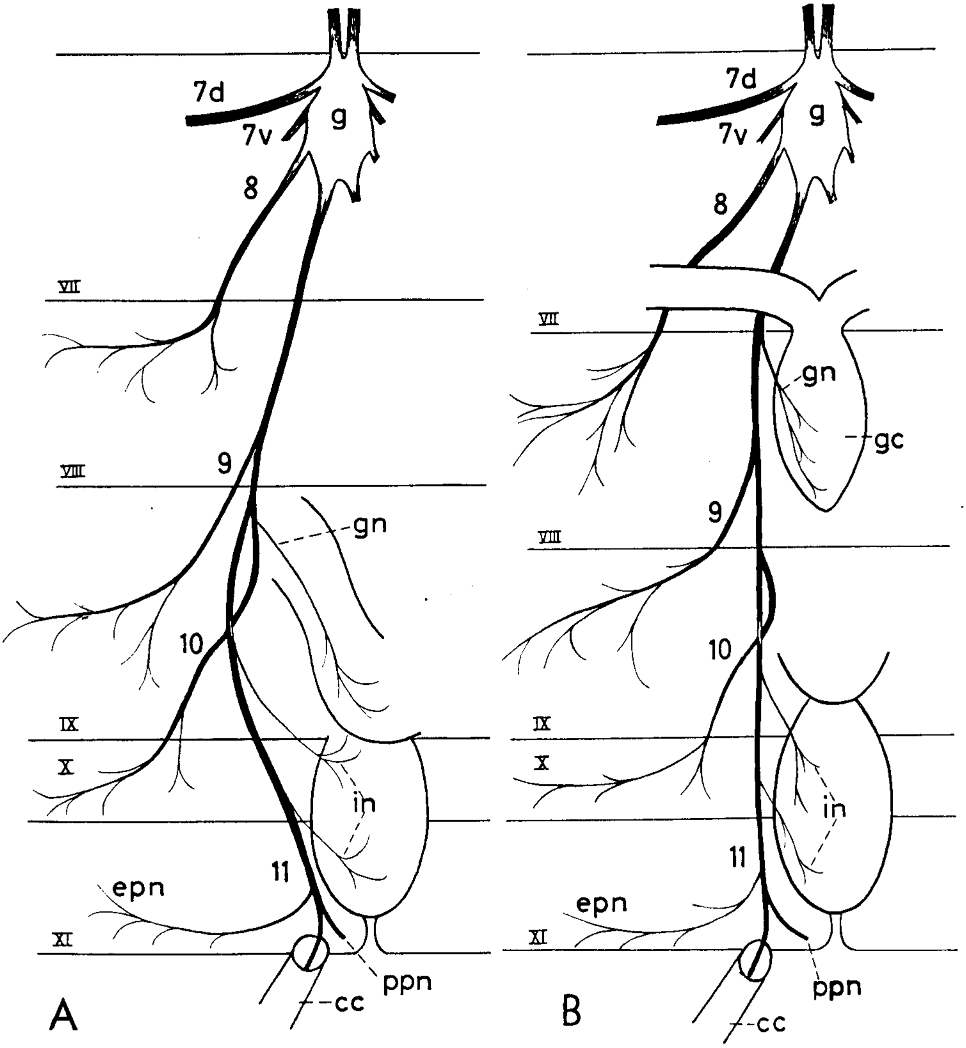

Fig. 3. The nervous system of the last abdominal segments in the male (A) and female (B) of the Plecopteron *Diura bicaudata* L. Ventral view of right half. (cc=cercus, d=dorsal branch, epn=epiproctal nerve, g=last abdominal ganglion, gc=genital cavity, gn=genital nerve, in=nerves to colon and rectum, ppn=paraproctal nerve, v=ventral branch. Roman figures=the numbers of the resp. abdominal segments. Arabian figures=the numbers of the resp. segmental nerve trunks.)

figs. 2 and 7) and then dive below the internal sternal muscles. The posterior pair of nerves pass ventrally of the lateral outer sternal muscles as well as the internal sternal muscles. In the siphlonurids and relatives these posterior (ventral) nerves are comparatively large and their origin is more posterior, so

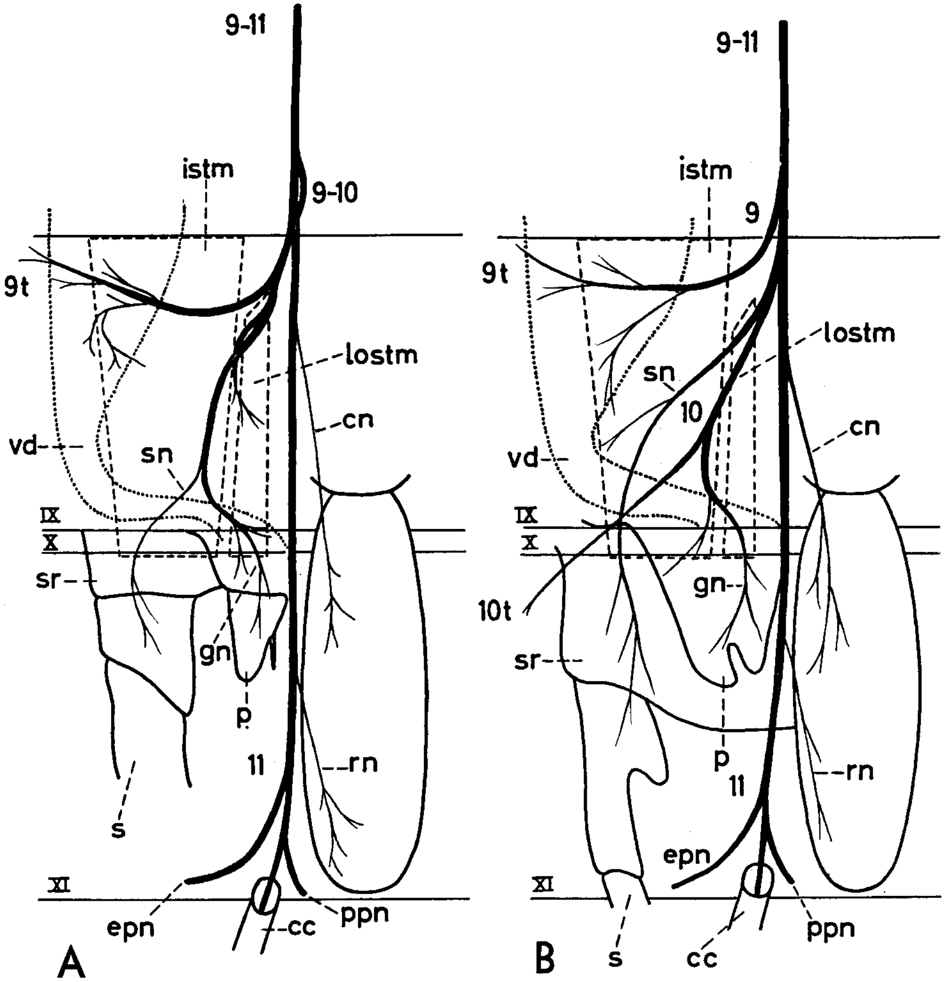

Fig. 4. The distribution of the segmental nerves in the last abdominal segments of A. male *Ephemera danica* Müll., B. male *Siphlonurus aestivalis* Etn. Semi-diagrammatic ventral view of right half. Vas deferens dotted. Sternal muscles of 9th segment indicated with broken lines. (cc=cercus, cn=colon nerve, epn=epiproctal nerve, gn=genital nerve, istm=inner sternal muscle, lostm=lateral outer sternal muscle, p=penis, ppn=paraproctal nerve, rn=rectal nerve, sr=styliger, t=branch of segmental nerve running to the tergal part of the segment, vd=vas deferens. Roman figures=the numbers of the resp. abdominal segments. Arabian figures=the numbers of the resp. segmental nerves.)

they are fairly easily observed. In the ephemerids, however, they are very small and rise only slightly behind the large anterior nerves.

From the posteriormost part of ganglion 8 arises an additional pair of large nerves which extend hindwards and successively give rise to lateral branches to the posterior abdominal segments. At the first sections for investigation of their extension, I used specimens of the genus *Ephemera.* It was found that in males as well as females there is no separate 10th segmental nerve and the tracing of the muscles and organs innervated by the various branches of the 9th stem was fairly difficult. Section of various material revealed that these conditions are certainly derivative. Among the siphlonurids more generalized conditions were met with and because of the general importance for the understanding of the genital segments and related organs, the cases will be dealt with in more detail.

For illustration of primitive conditions, I have figured the primary abdominal nerves of a generalized Plecopteron, viz. *Diura bicaudata* L. (vide fig. 3). From the complex last ganglion two posterior pairs of nerves run hindwards: the anterior one to the eighth segment, the posterior one to posterior segments. The latter stem branches off the following important nerves: in the 8th segment the 9th segmental nerve, in the 9th segment the 10th segmental nerve, and in the 11th segment the nerves to the paraproct, epiproct. and cercus. The lateral part of each segmental nerve also innervates the pleura and the dorsum of the segment. From the stem of nerve No. 11 branch off the posterior intestinal nerves, and finally in the male the genital nerve branches off from the base of No. 10, while in the female the (ectodermal) genital cavity is innervated by a branch from the general stem, in front of No. 9. The run of No. 10 is especially important. At least among generalized insects, investigated by me, it usually persists, if the 10th sternum is reduced, passing to the dorsal parts of the segment. As the paraprocts are always innervated by a branch of the 11th segmental nerve, the run of these nerves makes possible a decision as to the numbering of the last segments, the sternal parts of which are frequently reduced or modified.

In the siphlonurids the distribution of the segmental nerves in the posterior abdominal segments is as follows (cf. figs. 4, 5). In the male the 9th nerve branches off from the common stem (9—11) in the 8th segment; its appearance and run are normal. No. 10 originates in the anterior part of the 9th segment and is soon cleft into two branches: the lateral one passes to the ventral part of the segment and innervates the styliger plate, while the medial part divides into an upper branch which runs to the tenth tergum and an inner branch which innervates penis and penial plate. Segmental nerve No. 11 is as usual. — In the female the branching of the 9th and 10th nerves is similar except that the styliger nerve is lacking and the genital branch is reduced to a small nerve which runs to part of the outer sternal muscles.

In the ephemerids the 9th and 10th nerves have a common root (cf. figs. 4, 5). This branches off in the 8th segment and divides in the anterior part of the 9th segment, giving rise to an anterior branch (which is a homologue of the separate 9th nerve of the siphlonurids) passing to the 9th dorsum and a posterior part (the homologue of the separate 10th nerve of the siphlonurids) which gives rise to a styliger branch and a genital branch. The 11th nerve is as usual. — In the female the basic scheme agrees with that found in the male, although the posterior branch of the 9th stem (i. e. the 10th nerve) is poorly developed.

Connected with the ventral nerve cord there is a very fine unpaired median nerve which gives rise to a pair of lateral branches in front of each abdominal ganglion (vide fig. 7). Although well developed, this posterior "sympathetic"

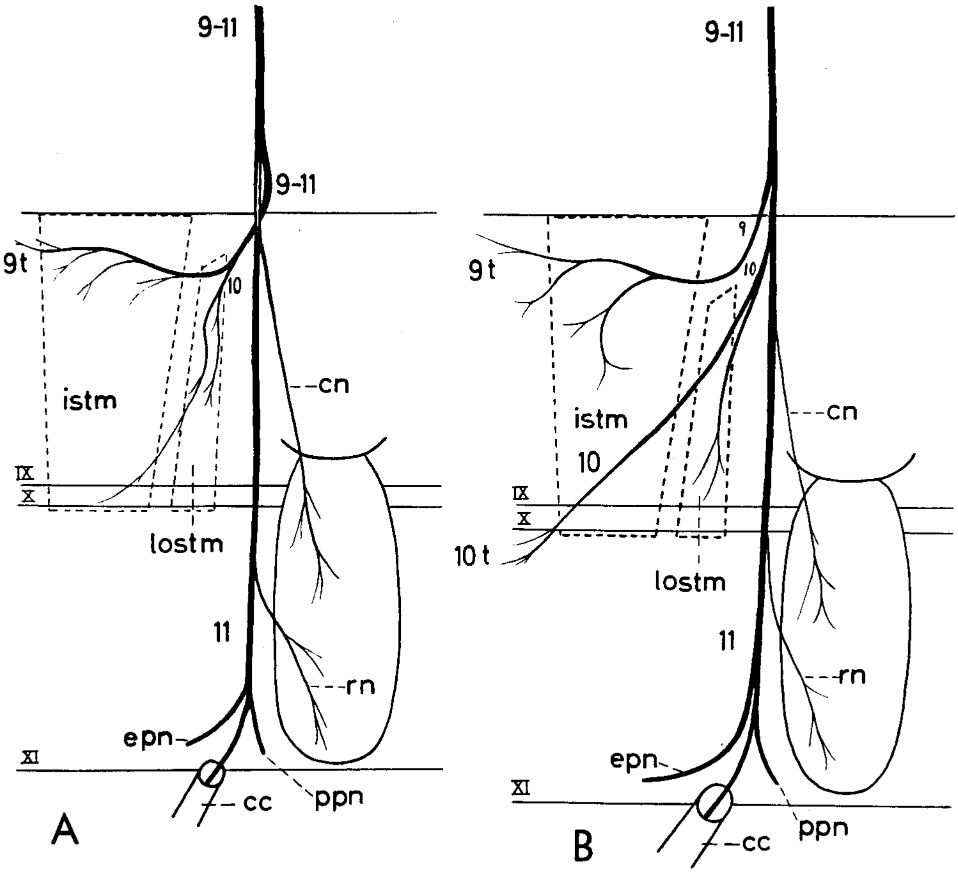

Fig. 5. The distribution of the segmental nerves in the last abdominal segments of A. female *Ephemera danica* Müll., B. female *Siphlonurus aestivalis* Etn. Semi-diagrammatic ventral view of right half. Sternal muscles of 9th segment indicated with broken lines. Legend vide fig. 4.

system is only very vaguely mentioned by those few authors who have observed it (Vayssière 1882, p. 125, and Drenkelfort 1910, p. 600).

In modified genera the abdominal nerve cord is more or less contracted. In the derivative prosopistomids and baetiscids there is a strong concentration of the cord: the thoracic and abdominal ganglia are fused to a single mass (cf. Vayssière 1890 and 1934).

Like in previous diagrams showing the relations between nerves, muscles and genital ducts in Plecoptera, I have used the position of the principal segmental nerves for illustration of the conditions. At the dissections, I noticed that the relations between the segmental nerves and the sternal muscles are rather different, compared to the corresponding conditions among stoneflies, and although it has no influence upon the run of the genital ducts I find it worth description. I seize the opportunity to describe these matters also

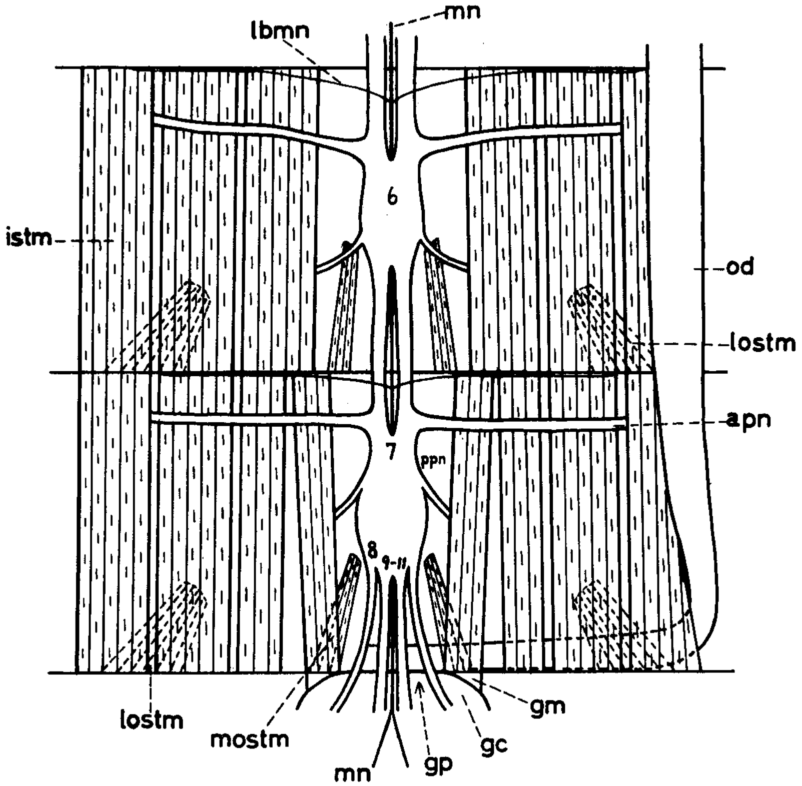

Fig. 6. The relations between nerves, ventral muscles and gonoducts in the 6th and 7th abdominal segments of the Plecopteron *Diura bicaudata* L. Dorsal view. Only right oviduct figured. (apn = anterior principal nerve = dorsal branch of the 7th segmental nerve, gc = genital cavity, gm = genital muscle = medial half of the first bundle of the internal sternal muscle, gp = gonopore, istm = inner sternal muscle, lbmn = lateral branch of median nerve, lostm = lateral outer sternal muscle, mn = median nerve, mostm = medial outer sternal muscle, od = oviduct, ppn = posterior principal nerve = ventral branch of 7th segmental nerve. Arabian figures = the numbers of the resp. ganglia and segmental nerves.)

regarding Plecoptera, thus completing previous anatomical data (cf. Brinck 1956, p. 97 ff.).

The conditions in the Plecoptera (*Diura bicaudata* L.) have been illustrated in fig. 6. The internal sternal muscles are very well developed and in perfectly preserved specimens they occur as three bundles. Close to the nerve cord there is a small, slightly oblique medial outer sternal muscle and below the lateral bundles of the internal muscle there is an oblique and short lateral outer sternal muscle. In the 7th segment the medial bundle of the internal sternal muscle is cleft and its inner part inserts on the anterior wall of the genital cavity, apparently serving as a retractoral muscle. As in the mayflies there is an anterior large nerve in each segment. This does not rise from the respective ganglion, however, but usually more or less in front of it. It runs

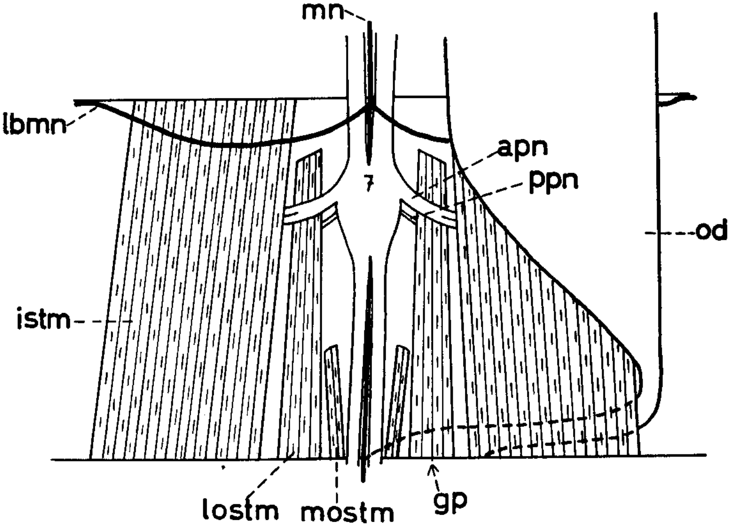

Fig. 7. The relations between nerves, ventral muscles and gonoducts in the 7th abdominal segment of *Ephemera danica* Müll. Dorsal view. Only right oviduct figured. Legend vide fig. 6.

dorsally of the first two bundles of the internal sternal muscle and then dives below the third (outer) bundle. Further, each ganglion gives rise to a posterior pair of small (ventral) nerves which pass above the medial outer sternal muscle but dive below the internal sternal muscles. Finally, there is a well developed unpaired median nerve, branching off a pair of lateral nerves before each ganglion.

The conditions in the Ephemeroptera have been illustrated in fig. 7. The sternal musculature, the ventral cord and its nerves have been described above.

A comparison between the Plecopteron and the Ephemeropteron shows that there are no thorough differences as regards the musculature. The internal sternal muscle is well developed in both groups, and the medial outer sternal muscle is short and narrow. In the Plecoptera there is, however, a very oblique and short lateral outer muscle which differs from the corresponding muscle in the mayflies; this originates in the anterior part of the segment and inserts near the median line of the following segment. With regard to the run of the nerves it would seem that the latter muscle corresponded to the medial parts of the internal sternal muscles of the Plecoptera. In *Diura* the anterior principal nerve passes above the inner bundles of this large muscle and then dives below the outer bundle, while the posterior principal nerve passes above the medial outer muscle and dives below all the internal muscle. In *Ephemera* (and other mayflies investigated) the anterior nerve passes above the lateral outer muscle and then dives below the internal muscle, while the posterior nerve runs below the lateral outer muscle, too. It is hardly possible, however, to homologize the muscles on the present material, as the run of the anterior nerve in relation to the internal musculature may be secondary.

The male gonopore

According to the investigations by J. A. Palmén (1884) and Qadri (1940) the mesodermic vasa deferentia during their ontogeny end in a pair of hollow ampullae, each lying at the base of the corresponding penial anlage. In the early instars the primitive penial lobes are solid. During succeeding stages the ejaculatory ducts arise as ectodermal invaginations on the dorsal surface of the apices of the penial lobes. Although the penes (when present) are partly hidden by the posterior margin of the 9th segment (frequently forming the styliger plate) and so are situated in a fold, formed by the intersegmental membrane, this ectodermic pouch does not form a separate genital cavity. During its ontogeny as well as in the adult male the gonopore is associated with the posterior margin of the ninth segment.

Snodgrass (1937, p. 77) refers to embryological evidence brought forward by Heymons (1895 and 1897) and Wheeler (1893), indicating that the primary genital ducts of male insects opened originally on the tenth abdominal segment, and based on this evidence he supposes that the ephemeropteran penes belong to the tenth segment, the sternal part of which is reduced very early during the ontogeny (vide above). Qadri (l. c.) was "inclined to accept that view and regard the penes of the mayflies as the appendicular outgrowths of the tenth abdominal segment". As is seen from my discussion of the same conditions among Plecoptera, this opinion is strongly supported by recent embryological investigations by Else (1934), Rawat (1939), Roonwal (1937) and Sharif (1937) (vide Brinck 1956, p. 100).

It would of course be of some value if further facts supporting this opinion could be found in the Ephemeroptera. And as a matter of fact they are furnished by the relation between the muscles and nerves of the posterior abdominal segments.

From the testes the vasa deferentia in the mayflies extend posteriorly to the ninth segment, pass below the intersegmental sternal muscles of segments IX—XI and run medially to the ejaculatory ducts (penes). During this run each seminal duct passes above all segmental nerves except the last one (No. 11) which is passed after the duct has dived below the intersegmental muscles of segments IX—XI. Cf. fig. 4.

The same conditions have been described for Plecoptera previously (Brinck 1956, p. 99—100) and the interpretation presented on that occasion is valid also for the mayflies. Thus, it is evident that the diving of the seminal duct below the muscles running from the ninth segment to the paraprocts is secondary and caused by the disappearance of the posterior insertion point of musc. sternalis IX (following the complete reduction of sternum X) and its junction with musc. sternalis X, inserting on the paraprocts. The fact that the duct passes between the tenth segmental nerve and the eleventh segmental nerve cannot be interpreted in any other way than that also primarily the duct has passed by this way to an opening on the tenth sternum.

The female gonopore

According to Qadri (1940, p. 123) the mesodermal oviducts during their ontogeny extend to the posterior margin of the seventh segment where they end in a pair of hollow ampullae. The vestibule and possible copulatory and spermathecal sacs develop as ectodermal invaginations at the posterior margin of the seventh segment. The paired oviducts usually open separately into the vestibule (vide below).

Walker (1919, p. 308) claims that the present position of the genital aperture of female Ephemeroptera is secondary, based on the opinion that the vulva "of a typical generalized Pterygote insect" should be "situated at or near the posterior end of the eighth abdominal sternum" (l. c., p. 274).

In the Ephemeroptera the lateral oviducts turn medially in the seventh segment, passing below the internal as well as the outer sternal muscles to the opening(s) at the posterior margin of the segment. Each oviduct runs above the sternal muscles of all anterior segments. In the same way it passes above all principal segmental nerves, including the seventh, but lies below the connectives which connect ganglia Nos. 7 and 8. Cf. figs. 2 and 7.

Based on the argumentation in my previous paper on these conditions in Plecoptera (1956, p. 102), the above relation between the genital ducts and the segmental nerves and muscles is accepted as giving the primary position of the ducts and the gonopore(s). It should be noted that in generalized mayflies primitive conditions have been kept, so far as can be imagined agreeing with the position of the gonopores (and the female genital apertures) in ancient pterygote insects and their ancestors. After all, the development of an (ectodermal) genital cavity penetrating the 8th segment is a derivative condition, and not vice versa as supposed by Walker (l. c.), although such modifications are widely distributed among the insects.

3. The male organs of reproduction

Testes and efferent ducts

So far as is known the paired testes are always separate. They consist of numerous testicular follicles which are arranged on the dorso-lateral part of the testicular duct (figs. 8 A, 9 F). The follicles are rounded and cover the duct from the anteriormost part of the abdomen to the fifth or sixth segment. The follicles are contained in a peritoneal sheath.

The aspect and arrangement of the mature testis are best studied in the nymphal instars. Already before the subimaginal stage the follicles empty their contents into the deferential duct and in the imago they have all collapsed, so that they are difficult to observe. This fact has caused the widespread erroneous statement (from Swammerdam 1752 and onwards) that the sac-shaped upper parts of the vasa deferentia are the testes.

The vasa deferentia are simple and tubiform. Their shape is rather variable, dependant on the amount of sperm present in their various parts: in the imago they are successively emptied and their anterior parts collapse early. They are never convoluted and thus form no "epididymis". There are no separate seminal vesicles but the sperm is stored in the deferential ducts, particularly in their posterior parts. The ducts open into the separate ejaculatory ducts. These are ectodermal, lined with a sclerotized intima. It is peculiar that Palmén's statement (1884) that the male genital ducts are mesodermal down to the exit, is to be found in a great many text-books and special articles on mayflies, in spite of the fact that it was corrected by Wheeler as early as 1893. Recently Qadri (1940, p. 128) has emphasized that the ejaculatory ducts are ectodermal invaginations.

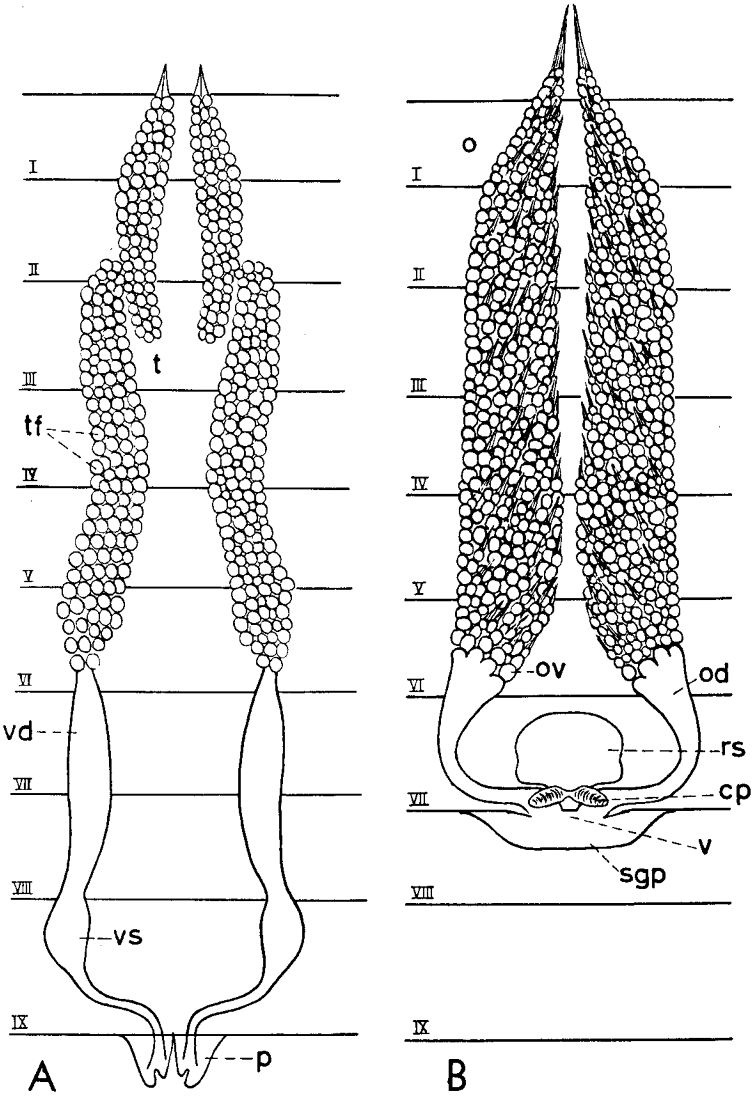

Fig. 8. *Siphlonurus* sp. A. Male genitalia. — B. Female genitalia. Dorsal view. (cp=copulatory pouch, o=ovary, od=oviduct, ov=ovariole, p=penis, rs=seminal receptacle, sgp=subgenital plate, t=testis, tf=testicular follicle, v=vestibule, vd=vas deferens, vs=sac-shaped extension of the efferent duct, primitive vesicle. Roman figures=the numbers of the resp. abdominal segments.)

In all species of mayflies examined the efferent ducts remain separate, except that in *Polymitarcys virgo* Oliv. there is an anastomosis just in front of the penial bases (Palmén 1884, p. 45). It is probable, however, that such conditions will be found also in other species, thus functioning as primitive accessory seminal vesicles.

The above conditions have been checked for several genera: *Ephemera* L., *Leptophlebia* Westw., *Ephemerella* Walsh, *Baetis* Leach, *Cloëon* Leach, *Siphlonurus* Etn., *Parameletus* Bengts., and *Heptagenia* Walsh. Other genera have been examined by Palmén (1884), viz. *Oligoneuriella* Ulmer (sub nom. *Oligoneuria*), *Polymitarcys* Etn. (cf. above), *Palingenia* Burm., *Potamanthus* Pict., *Caenis* Steph., *Ecdyonurus* Etn. and *Rithrogena* Etn. (both sub nom. *Heptagenia* spp.). Further Heiner (1915) described inter alia *Habrophlebia* Etn., and Vayssière (1934) investigated *Baetisca* Walsh.

Accessory glands do not occur. Old authors (e. g. Swammerdam, 1752) figure a pair of elongate bodies which are attached to the efferent ducts, but they must have been Malpighian tubules or parts of the fat body.

Penes and accessory structures assisting copulation

As concluded in the above discussion of the position of the male gonopore there can be no doubt that the paired penis of the mayflies belongs to the tenth abdominal segment. The same seems to apply to the penial bar, supporting the penes (vide pp. 4—5).

In not too small nymphs the primary penial lobes usually appear as ectodermal outgrowths in the intersegmental area behind sternum IX (cf. fig. 9C). These anlages are primarily always separate. In the adult they evolve in various ways and sometimes unite to form a single organ, in which the ejaculatory ducts remain separate. The protean mayfly penes are described and illustrated in many taxonomic papers, to which I refer. It should be mentioned, however, that the penes may be reduced (e. g. Baetidae).

The penial anlages are simple and during the ontogeny they never divide or split into different parts. In the adults there may be secondary penial immovable outgrowths which have been termed parameres by Walker (1922, p. 3), as accepted by e. g. Imms (1951). Spieth (1933, p. 78) has distinguished two types of such outgrowths, viz. parameres and spurs. Needham, Traver and Hsu (1935) further differentiated the spurs into spurs and reflex spurs. These structures are all of the same superficial nature. Therefore it is unfortunate that certain types of processes have been called parameres as they are not homologous with the parameres of other pterygote insect groups. In the latter the parameres arise by division of the penial anlages during an early stage of the ontogeny.

Basally, the penes are supported by a sclerotic bar which is more or less well developed. In *Ephemera* it appears as a pair of arms which laterally attach to the lower angles of the ninth tergal plate (figs. 9 D, E). In other genera these basal arms may be united to a single plate, sometimes appearing as lateral prolongations of the (united) penes only.

An important structure of the male external genitalia is formed by the claspers (forceps). They arise from the posterior margin of the ninth sternum (vide fig. 9 C) and develop into more or less jointed appendages (figs. 9 and 10) which assist the copulation by grasping the female abdomen. Several authors (Crampton 1919, 1920; Walker 1919, 122; Snodgrass 1936, and Qadri 1940) have compared them with the abdominal appendages of the Thysanura and Odonata and, although the homologies cannot be proved, present data support them.

The forceps consists of two parts: a distal stylus and a proximal coxite

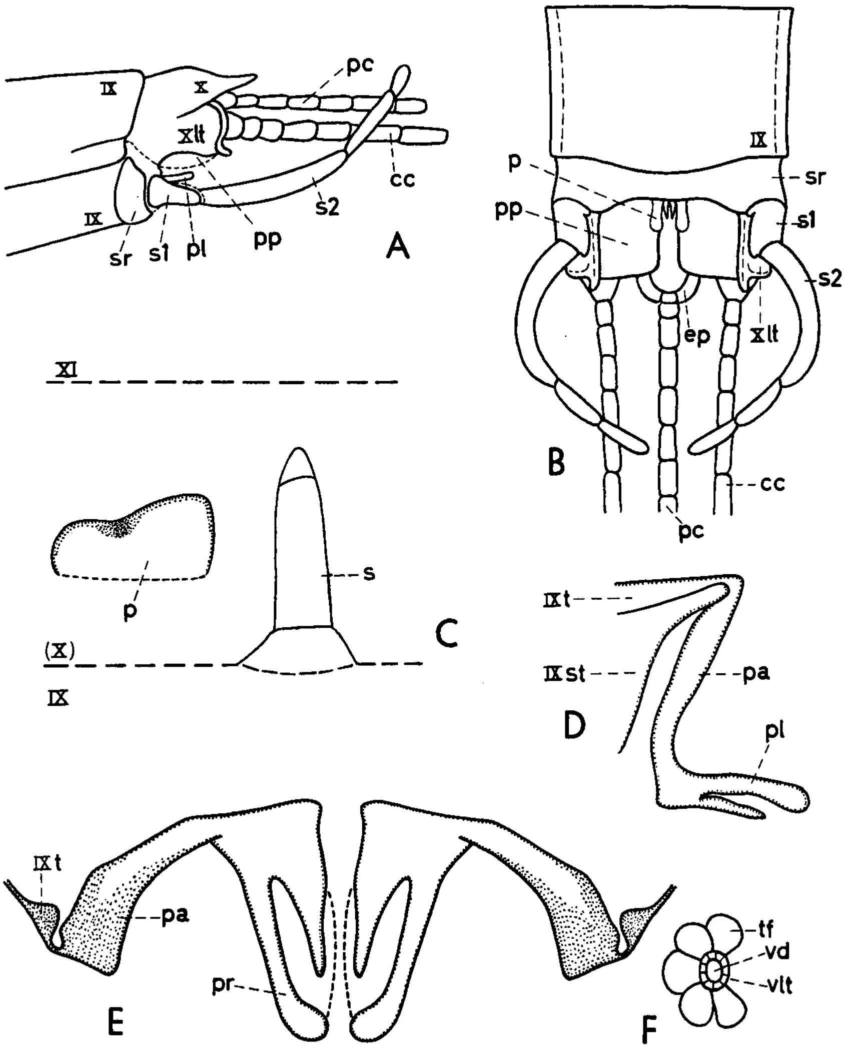

Fig. 9. A. Left side of abdominal apex of male *Ephemera vulgata* L. — B. Ventral view of abdominal apex of same. — C. The intersegmental area behind the 9th sternum of larva of *Ephemera vulgata* L. (length 9 mm, excl. antennae and cerci). — D. Lateral view of the *Ephemera*-penis and its supporting structures. — E. Ventral view of the *Ephemera*-penes and their supporting structures. — F. Transverse section of mature testis of *Siphlonurus* sp. (cc=cercus, ep=epiproct, lt=dorso-lateral part of tergum, p=penis, pa=penial arm, pc=paracercus, pl=left penis, pp=paraproct, pr=right penis, s=stylus, s1=first joint of stylus, s2=second joint of stylus, sr=styliger, st=sternum, t=tergum, tf=testicular follicle, vd=vas deferens, vlt=ventro-lateral surface of testicular duct, resting on the intestines.)

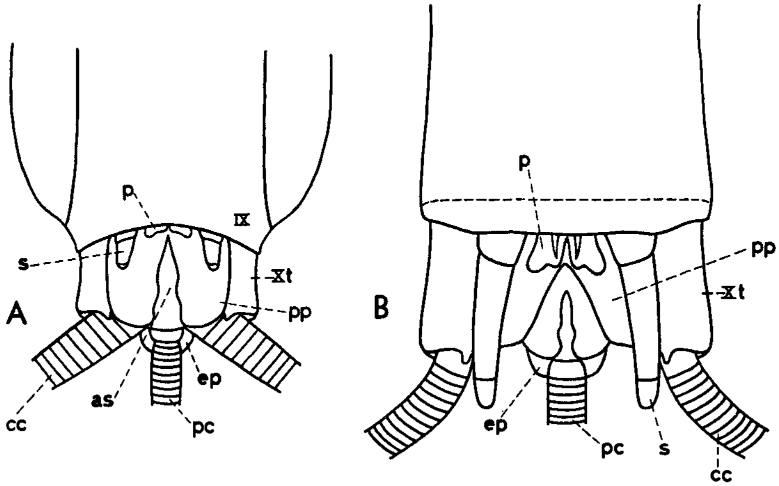

Fig. 10. *Ephemera vulgata* L. A. Apex of abdomen of halfgrown nymph (length 10 mm, excl. antennae and cerci). Ventral view. — B. Apex of abdomen of fullgrown nymph (length 18 mm, excl. antennae and cerci). Ventral view. (as=anal slit, cc=cercus, ep=epiproct, p=penis, pc=paracercus, s=stylus, Xt=ventro-lateral part of 10th tergum).

(coxopodite). The latter is usually absorbed in a plate (called styliger plate) which attaches to the posterior margin of the ninth sternum. Sometimes it is (partly) free and may be superficially very similar to a basal joint of the stylus.

The nymphal stylus is unsegmented or contains few segments, the number always being less than in the adult stage. A proximal joint is easily observed in several genera (like *Ephemera,* fig. 10), and in these genera there is also usually an apical segment which is more or less delimited. In certain derivative genera the forceps and adjoining structures are not formed until in the last nymphal instar (e. g. Baetidae, excl. its comparatively primitive genus *Callibaetis* in which a tiny nymphal forceps is retained; cf. Spieth 1933, p. 76). This retarded development of imaginal structures in the baetids is of considerable general phyletic interest.

In the adult mayfly the stylus is always present, 1- to 4-jointed, in *Palingenia* even 5- to 6-jointed. It has been supposed (e. g. by Needham, Traver and Hsu 1935) that the division of the stylus into several segments is a primitive condition, but it is hardly so, as the segmentation of the styli seems to be secondary.

The primitive stylus (as in Thysanura) is always 1-jointed. In its basal part inserts a stylus muscle which arises on the coxite. In the Ephemeroptera with more than one segment in the forceps only the first segment is provided with muscles (vide fig. 1 C). In generalized genera these muscles arise on the lateral parts of the broad styliger plate, behind the ninth sternum. Apparently this plate corresponds to the above coxites. It is attached to the ninth sternum and is moved by muscles which should be sternocoxal, in accordance with the above theory that the claspers are comparable with Thysanuran abdominal appendages. In certain genera the styliger is divided so that the coxites become partly free (e.g. the primitive *Ephoron* Will. and the derivative Baetidae), but this seems to be secondary, as also in these cases medial parts of the coxites remain united with the sternum, although the lateral parts (containing the stylus muscles) are freely movable. Ontogenetically the styliger always seems to develop as a plate, very closely associated with the posterior margin of the ninth sternum. Therefore the innervation of the styliger by a branch of the 10th segmental nerve seems to be secondary (cf. above p. 8); presumably the styliger nerves originate from the primary ninth abdominal ganglion.

The styliger with attached styli exhibits great diversity of form and is of considerable taxonomic importance. Various types have been described and discussed by Spieth (1933, p. 72 ff.) and Snodgrass (1936, p. 76).

According to Needham, Traver and Hsu (1935, p. 111; cf. fig. 18) male as well as female nymphs of the North American genus "*Pentagenia* shows a vestigial pair of styli on the tenth segment [sc. 11th] in a position corresponding to the forceps of the ninth". These appendicular outgrowths, however, are hardly true styli. Appendices of the paraprocts have also been described for Odonata and tridactyloid Orthoptera. In the Odonata they are membranous lobiform outgrowths not even comparable to styli. In the tridactylids, however, they are styliform and were regarded by Crampton (1918, fig. 48) as true styli. Walker (1919, p. 287), Snodgrass (1931, p. 107) and Ander (1934, p. 11) opposed this, claiming that they are secondary outgrowths. There is no doubt that the same applies to the paraproctal "styli" of *Pentagenia*.

Finally, it should be mentioned that the male cerci assist copulation by loosely fixing the female body in the mating position (vide below).

4. The female organs of reproduction

The ovaries are always paired and separate. They contain a considerable number of panoistic ovarioles (cf. Brandt 1878 and Palmén 1884) which are arranged on the dorsolateral part of the oviduct (fig. 8 B). The nymphal ovarioles cover the oviducts to the sixth or seventh segment, while anteriorly they extend to the first abdominal segments. Successively, the eggs collect in the oviducts, and in the subimago and adult the latter form a pair of large sacs which are greatly extended by the large amount of mature eggs. These sacs fill up the abdomen to the seventh or eighth segment and may even penetrate through the thorax (e. g. in *Caenis*). The oviduct is a short tube, retaining this shape because of the pressure of the sternal internal muscles of segment VII.

After the eggs have passed into the oviducts, the ovarioles collapse and occur as membranous rudiments which are easily overlooked. This is probably the reason for several statements (mainly in the literature of the 19th century) that the mayfly ovary is simply sac-shaped.

The tubiform oviducts pass laterally in the seventh segment, until they turn medially and dive below the sternal musculature (fig. 2). The openings of the ducts (the gonopores) are always situated in the posterior part of the seventh segment. The surroundings, however, may be modified in various ways. The following types can be recognized:

1. The gonopores open to the exterior in a non-modified intersegmental area. The seventh sternum is not produced posteriorly or only slightly so. Represented by Baetidae, Ephemeridae and related families.
2. The posterior margin of the seventh sternum is produced to a subgenital plate, forming a chamber into which the gonopores open. This space is unmodified. Primitive Ecdyonuridae.
3. A subgenital plate covering a vestibulum. An invagination from the vestibulum forms a sac-shaped seminal receptacle which is more or less modified and part of which may serve as copulatory pouches. — Various modifications are widespread in Ecdyonuridae, Siphlonuridae and Ephemerellidae.
4. A short subgenital plate covers a pouch-like vestibulum which is somewhat constricted towards the opening. No seminal receptacles occur. *Oligoneuriella rhenana* Imh., described by Grandi (1955, p. 28).
5. Subgenital plate lacking or moderately developed. The vestibulum forms a pouch with a more or less narrow opening, in certain genera corresponding to a more or less prominent sclerotization of the 8th sternum which is important for oviposition. Leptophlebiid genera e. g. *Habrophlebia* subg. *Habroleptoides* Schoenemund, vide Pleskot (1953).
6. Subgenital plate well developed. The lateral oviducts open into a common oviduct which continues posteriorly to the apex of the subgenital plate. The apical part of the latter is tubiform with terminal gonopore. In the American *Hagenulus caligatus* Etn. the subgenital plate is strongly produced hindwards and the gonopore has moved dorsad (cf. Morrison 1919). Leptophlebiid genera.

As the above conditions have been investigated by previous authors I refer to their articles, viz. Palmén (1884), Morgan (1913), Heiner (1915), Morrison (1919), Ulmer (1924), Needham & Murphy (1924), Pleskot (1953) and M. Grandi (1947 and 1955). The latter author gives an interesting survey of a series of genera and species.

It is evident that there is a trend to evolution and modification of the surroundings of the primary female gonopores, thus better serving various purposes, as copulation, reception and storage of the sperms, and oviposition — for which there are no special arrangements in the generalized mayfly. This evolution has advanced considerably in the family Leptophlebiidae, ranging from the primitive *Choroterpes* Etn. (genitalia almost as simple as in the Baetids) to the strongly modified *Hagenulus* Etn. and *Hagenulopsis* Ulm.

Evidently, the differentiation starts by formation of a more or less well developed subgenital plate of the 7th sternum which covers a small chamber, mainly consisting of the extended intersegmental area. A positive modification follows, involving a median invagination between the oviducts: primarily this means formation of a more or less specialized vestibulum (vide Qadri 1940; this modification is called Genitalbulbus by Pleskot, 1953, in *Habroleptoides*) and from this may be derived a median seminal receptacle. The opening of this pouch lies slightly above the oviductal apertures, and there is a protruding membranous lip which separates the openings from each other. In siphlonurids a small, posterior part of the median sac is distinguished from the large anterior (the seminal receptacle) and forms a transverse chamber (which is often constricted medially) which receives the penes during copulation. The walls of this sac are often strongly and characteristically sclerotized; this applies particularly to the ventral wall. The sacs were studied in Ecdyonurids by Palmén (1884) who claimed their function as bursae copulatrices, demonstrating that the apices of the penes exactly fit into the sacs. When examining mating pairs of *Parameletus chelifer* Bengts., I was able to confirm his opinion. The apical parts of the penes penetrate into the sacs and the ejaculated sperm is pressed into the anterior pouch, serving as receptaculum seminis.

Since the terminology of the above authors is very variable, as are also their interpretations of the various cases, a few words on the basic conditions may be justified.

The mesodermal oviducts are paired and terminate in a pair of ampullae near the posterior margin of the seventh sternum. The development of a vestibulum (finally a common oviduct) and copulatory sacs and seminal receptacles occurs by simple invagination from the posterior margin of sternum VII and these structures are all ectodermal.

Following Snodgrass (1935, 1936) I have accepted the term vestibulum for the invaginations from behind the seventh sternum (thus restricting "genital cavity" to invaginations from behind the eighth sternum). This is also justified by the simplicity of the above arrangements, compared to the complicated conditions which usually arise by invagination from the eighth sternum.

There are no principal differences between the shallow vestibulum without sperm sacs and the comparatively closed chamber with sacs. As shown by the genera of Leptophlebiidae the formation of a common oviduct can easily be connected with the transformation of the sac-shaped vestibulum and the ontogeny proves that they are both developed in the same way.

Some authors call the produced subgenital plate ovipositor. From a morphological point of view, however, this term should be used for structures formed of the gonopods of the eighth and ninth abdominal segments. Such structures are completely lacking in the Ephemeroptera and the plate under discussion is certainly an extended part of the seventh sternum. In a functional meaning, ovipositor has been accepted for the egg-laying tube formed by the terminal abdominal segments of certain advanced insect groups, like Diptera, and for (paired) sclerites formed by the modified 9th sternum, like Coleoptera, but such conditions do not prevail in Ephemeroptera.

Also in the female genitalia are accessory glands absent.

5. **The mating habits**

The great aerial performances given by many species of mayflies must have been long known to man. In native folklore as well as modern poetry the "smoke of the river" or "snowstorm in midsummer" form the picturesque background of many a tale. Only comparatively lately, however, was it realized that the flight of the mayflies is a sort of wedding-dance, and there is still much controversy about the copulation and its execution. As intimated above the reasons are that mating usually occurs in the air in twilight and lasts for some 10 or 20 seconds only.

A first scientific description of a mayfly and its habits was presented by Swammerdam in 1675, in his Ephemeri vita. Swammerdam studied the insect (*Palingenia longicauda* Oliv.) in 1667 at a branch of the Rhine, passing the

Dutch town Kuylemburg. His descriptions and figures of 1675 were included in the famous Biblia Naturae (1737—38, 1752), although stripped of the lengthy religious contemplations which had made the edition of the first work possible.

The mating conditions are dealt with on p. 126—127 in Ephemeri vita and again in the various editions of the Biblia Naturae. In the German version (1752, p. 112) the concluding paragraph runs as follows: "The Hafft [adult mayfly] zeugt weder in den Busen des Wassers, noch auf dem Lande, noch in der Luft, sondern das Weibgen schiest seine Eyer auf die Fläche des Wassers hin, und das Männgen stürzt seinen Rogen darüber aus." The opinion that there was no real copulation between the males and females of *Palingenia* is explained at some length in the following paragraphs.

In May and June 1745, Ch. de Geer studied the mating flight of the Ephemerids at his estate Leufsta in central Sweden and in a letter of the 7th of May, 1746, to R. de Réaumur he describes his observations. Part of the letter was published in 1755 (p. 461—469). The paragraph dealing with the mating is as follows:

"J'ai été très-attentif à observer les soirs où les éphémères voloient, si elles s'accouploient, & je les ai vûes plusieurs fois s'accoupler véritablement. J'en ai vû souvent attachées ensemble, qui voloient dans l'air sans se quitter. J'ai vû au milieu de l'air dans une assemblée d'éphémères, un male se saisir d'une femelle, & rester attaché à elle; elles s'envolèrent toutes deux vers le haut d'un mur, où elles se posèrent sans se quitter l'une l'autre ... Enfin nous savons du moins par cette observation, bien qu'imparfaite, que les éphémères s'accouplent véritablement, comme tous les autres insectes ...".

Thus the first step in the right direction had been taken: it was a fact that mating occurred.

De Geer continued his studies (on *Ephemera vulgata* L.) in 1748 (cf. 1771, p. 644 ff.):

"Cette année ... était très-abondante en Ephémères. Je m'amusai les soirées à contempler leurs assemblées aëriennes, composées uniquement de mâles, comme elles le sont presque toujours, et je remarquai que dès qu'une femelle se rendoit en volant dans la mêlée, ce qui arrivait fort souvent, ceux-ci se mettoient dabord à la poursuivre et sembloient se disputer deux ou trois à la fois sa conquête, jusqu'à-ce qu'enfin l'un d'entre eux parvenoit à s'envoler seul avec la femelle. Ordinairement le couple amoreux gagne les airs & va se placer ou au haut d'une muraille, ou à la cime d'un arbre, pour y chever l'ouvrage; mais deux ou trois couples se placerent heureusement sur les feuilles d'un buisson où ils furent à portée de mes yeux. Je vis alors que le mâle s'étant placé en dessous de la femelle, qu'il avoit saisie par le même endroit du corps, il recourboit son ventre par en-haut & qu'il en appliquoit l'extrémité contre l'ouverture qui se trouve au ventre de la femelle entre le septième & huitième anneau ... L'affaire fut achevée dans un instant, après quoi le mâle s'envola ..."

As a matter of fact this first description of mating flight and copulation in Ephemeroptera is very good. It is true that it is imperfect but it does the author great credit that the missing details were not substituted by suppositions, as has been the case with many later descripions. At the end of the observation, De Geer says: "Il restoit à observer comment il s'étoit saisi en l'air du corps de la femelle avec ses longues pattes antérieures: car je soupçonne cet usage. Il faudroit encore avoir vû, comment il embrassoit le ventre de sa femelle au moyen des deux crochets qu'il porte au derrière." Thus, the observations of these details were left to following naturalists.

De Geer's descriptions, however, remained unknown to most authors on mayfly mating who based their work on Swammerdam.

An interesting contribution was made by Cornelius in 1848. Cornelius studied *Palingenia longicauda* on the Lippe, a German tributary to the Rhine. In June the species occurred in enormous numbers and Cornelius observed mating: "Sie geschieht in der That vielleicht eben so häufig auf dem Wasser, als in der Luft ..." (p. 32). Because of the dusk no details could be observed on flying specimens but on the water mating is described to occur as follows: "Die Weibchen lassen sich vom Wasser treiben und erwarten den Besuch der Männchen, die über dem Wasser dahinfliegen. Jetzt setzt sich ein Männchen auf das Weibchen ... Sobald nun beide in Ruhe gekommen sind weiss das Männchen zur rechten Seite des Weibchens sich so hinab zu senken und zu wenden, dass es fast ganz under das letztere zu liegen kommt. Der Hinterleib des Männchens steht dabei unter dem des Weibchens weit hervor. Das Männchen krümmt jetzt den Hinterleib so weit aufwärts nach vorn, dass es die Hinterleibsspitze des Weibchens erreicht, und die Begattung wird vollzogen. Dies Alles geht äusserst rasch — vielleicht binnen einer Viertelminute vor sich. Dass Männchen erhebt sich darauf wieder in die Luft ..."

Tümpel (1901, p. 75) accepts Cornelius's observations without any objections and Eaton (1888) presents a picturesque story telling that "the male of *Palingenia* has very short fore legs; and he is mated, not in mid air, but upon the river amidst crowds of rivals, who pile themselves up upon him and his surroundings until he is overwhelmed by a large struggling mass of them floating down the stream like a heap of foam" (p. 10).

Drenkelfort (1910) has pointed out that as regards *Palingenia longicauda* the above description seems to be erroneous. The morphology of the male indicates mating in the air, as was also observed by Cornelius. It is most probable that mating on the water surface is an exception, or perhaps the observations are based on specimens which dropped to the surface after or during copulation; this seems possible as mating pairs always lower themselves during copulation until they almost reach the water.

In 1907 a second type of mating was described for Ephemeroptera. Bernhard investigated *Cloëon dipterum* L. and describes the mating flight as follows:

"Ab und zu steigt eines der Weibchen in schräg aufwärts gerichtetem Flug über den Schwarm der tanzenden Männchen hinweg in die Höhe. Sofort stürzen sich diese in grösserer Anzahl auf das Weibchen und suchen zur Kopulation zu gelangen. Schlesslich gelingt es einem Männchen den Thorax des über ihm befindlichen Weibchens mit den langen Vorderbeinen zu umklammern und durch Aufwärtskrümmen des Abdomens seinen doppelten Penis in die getrennt mündenden Ovidukte (vagina) einzuführen. Das Pährchen erhebt sich darauf in der Stellung, wie es Fig. 1 zeigt, hoch in die Lüfte und entschwindet gewöhnlich dem Auge. Etwa nach 10 Minuten, solange bleiben Männchen und Weibchen in Copula, steigt das Pärchen hernieder und trennt sich voneinander." (p. 468).

Fig. 1 shows a mating pair arranged with the ventral sides towards each other! Cf. fig. 11 B. This is certainly wrong as are several other details in this paper (cf. Heiner 1915). Bernhard's description was accepted, however, and is found in many textbooks and special papers, e. g. Ulmer (1924), Weber (1933) and quite recently in von Buddenbrock's comprehensive book on "Das Liebesleben der Tiere" (1954). Certain authors (e. g. Wesenberg-Lund 1915, p. 38, and 1943, p. 47) also said that they had been able to confirm Bernhard's observation.

In the meantime S. Bengtsson opposed those opinions on mayfly mating. In a review of 1916 he emphasizes that Bernhard's description must be erroneous, and in 1926 he sums up his experience from several years' studies on these insects. In this way two previous errors were corrected: the position of the male in relation to the female (below the female with his back facing her ventral side) and the application of the male claspers (round the 8th or 9th abdominal segment). In previous descriptions the claspers are said to clutch the 7th segment, in spite of the fact that this means that the female genitalia would have been closed (cf. Eaton 1888, p. 10).

Bengtsson's short notes on mayfly mating are in Swedish and were noticed by few authors on these subjects. Further, it is evident from the articles that his observations were done on netted specimens which are of course disturbed, and this might be the reason why Wesenberg-Lund would not abandon the results obtained by him with field-glasses and supporting Bernhard's observations.

In 1913, a fairly correct though imperfect description of mayfly mating had been presented by A. H. Morgan, based on a couple of *Baetis* examined in the field: "The male flew up and attached himself beneath a female, pressed the dorsal side of his head against the ventral side of her thorax and extended his fore-legs upward, in order to clutch her prothorax . . . The position of the abdomen could not be clearly seen . . ." Apparently similar observations were made by Needham, and in Needham, Traver, Hsu (1935, p. 105) there is a diagram showing the main features of the copulatory position of a pair of mayflies in flight. This diagram (or modifications) has been reproduced in some text-books, e. g. Despax (1949) and Bertrand (1954). Cf. fig. 11 C. A similar description and figure was published by H. G. Cooke (1940, p. 12) based on observations on the North American species *Stenonema vicarium* (cf. fig. 11 A).

As mentioned in the preface, I had recently an opportunity to study the mating of *Parameletus chelifer* Bengts. during very favourable conditions. This made it possible for me not only to decide as to the general copulatory position but also to observe several interesting details, e. g. the position of the front legs and the cerci (cf. fig. 12).

Parameletus chelifer swarms in the evening or early night like most other mayflies and this would at a southern latitude make observations as difficult as usual. In northernmost Scandinavia, however, the midnight sun provides sufficient light for detailed studies during these hours.

As mentioned above the observations were made on a tributary to the Köngämä River, about 45 miles W. S. W. of Karesuando, on July 26th, at nine p. m. Swarms of the mayfly gathered irregularly over the stream. At first there was an abundance of males, but soon numerous females mixed with the swarms. Many couples mated in the air and could be examined when hovering close to a bridge. Several specimens, however, males as well as females, dropped on to the bridge. The males were comparatively active and

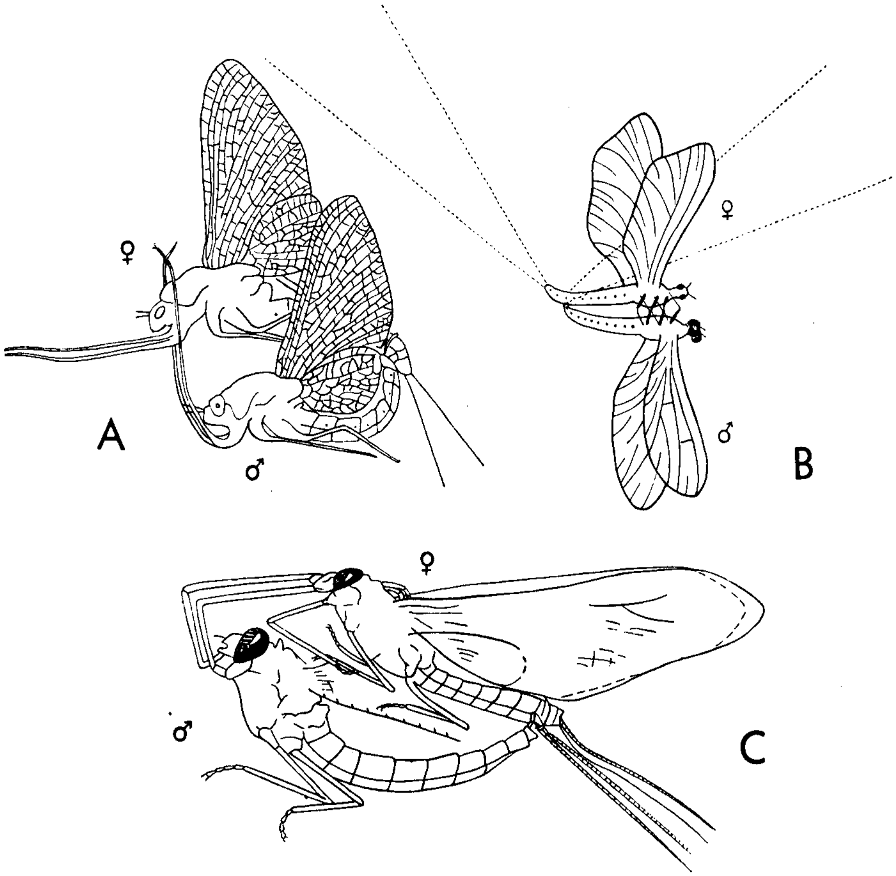

Fig. 11. Previous illustrations of mayfly mating. A. *Stenonema vicarium*, acc. to H. G. Cooke (1940). — B. *Cloëon dipterum*, acc. to C. Bernhard (1907). — C. *Rhitrogena* (*Cinygmula*) *minus*, acc. to Needham (after Despax 1949).

crept to the females, immediately trying to copulate. The male pressed himself under the female abdomen und stretched the front legs forwards and upward along the sides of her body, until they reached the prothorax. Then the tarses were bent so that each clasped round a wing-base (cf. fig. 12 B). At the same time the abdomen was curved and the forceps grasped the 8th or 9th abdominal segment (cf. fig. 13 B). The female abdomen was usually held like an S so that the penes were easily pressed into the vestibulum. The male cerci were stretched forward, fixing the female abdomen at the same vertical plane as the male abdomen. The female cerci were directed obliquely hindward. Vide also plate 1. The copulation lasted about 20 seconds and then the male took off, soon followed by the female.

In flight the male flew on to a female from below, stretched the anterior legs upward and forward and curved the tarses so that they caught the female wing-bases. At the same time the forceps grasped the abdominal apex

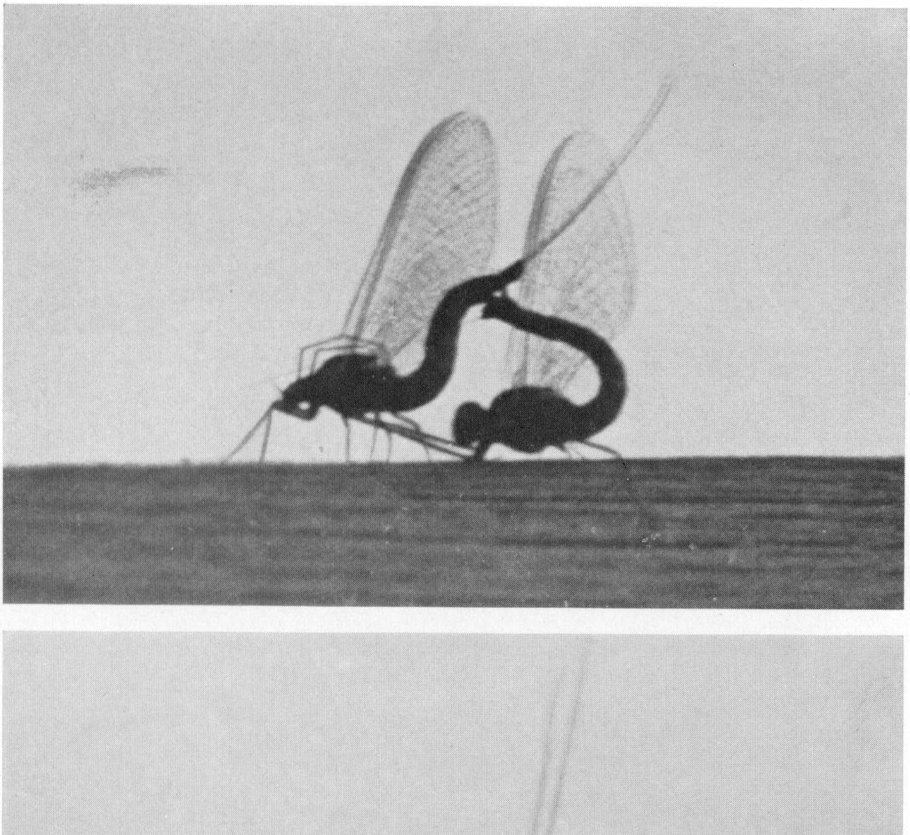

Plate 1. Two mating couples of *Parameletus chelifer* Bengts. (Lapland: on tributary to the Köngämä River, July 26th, 1955. K. G. Wingstrand phot.)

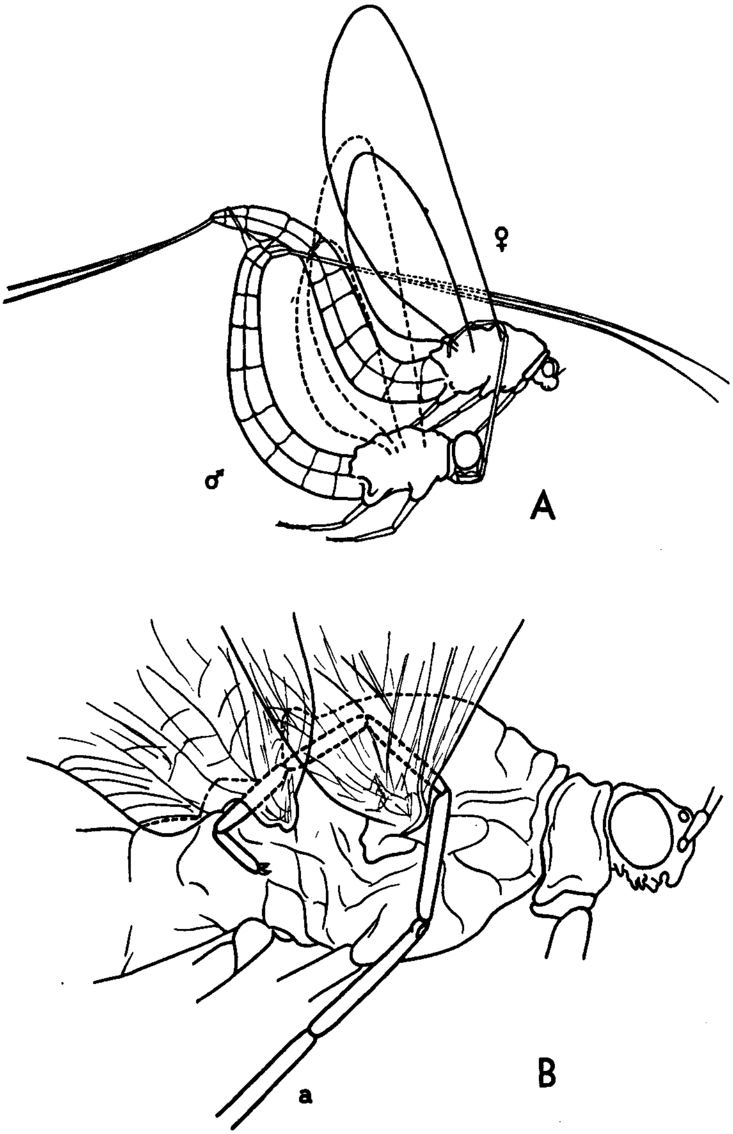

Fig. 12. *Parameletus chelifer* Bengts. A. Mating couple in flight. (Female cerci abbreviated. Male wings indicated with broken lines.) — B. Lateral view of anterior part of female in copula, demonstrating the clasping of the male anterior tarsus (a) round the female wing-base.

of the female which curved her abdomen so that the penes were easily inserted. The male cerci were held at the sides of the female body and wings, while the female cerci were stretched hindward. While mating the couple slowly lost height but always separated before it reached the ground or the water surface.

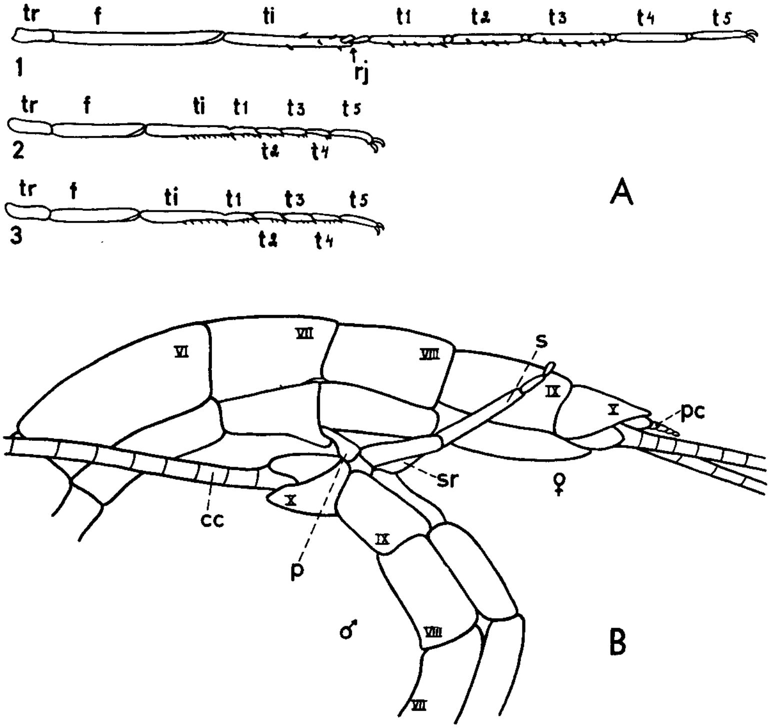

Fig. 13. *Parameletus chelifer* Bengts. A. Left side legs. 1=anterior leg, 2=middle leg, 3=posterior leg. (f=femur, rj=reversible joint, t1, t2, t3, t4, t5=the resp. tarsal segment, ti==tibia, tr=trochanter.) (Note that in the middle and hind legs the first tarsal joint is partially fused with the tibia.) — B. Lateral view of male and female abdominal apices in copula. Carnoy-fixation. (cc=cercus, p=penis, pc=paracercus, s=stylus, sr=styliger. Roman figures=the numbers of the resp. abdominal segments.)

The suspension of the male body in the anterior legs and the forceps is certainly very safe. As seen from various descriptions and diagrammatic figures (cf. fig. 11), it has been supposed that the male attached himself to the female by folding the anterior legs round her head, neck or prothorax, but this would be a comparatively loose suspension.

The backward bent of the tarses, necessary for the suspension, is made possible by a reversible joint at their bases (vide fig. 13 A).

It is most probable that the above type of male suspension in anterior tarses and forceps is a characteristic of this insect group. This is indicated by the presence of the forceps in all males investigated and lengthened male front legs in practically all species known.

The brief life of the mayflies above the water and the fact that most of the species are as adults independent of *terra firma* (after emergence they mate, oviposite and soon die) has caused strange mutations, that would be lethal under other conditions, to be established. Most remarkable is the stump-legged American genus *Campsurus*, the adults of which are entirely dependent upon

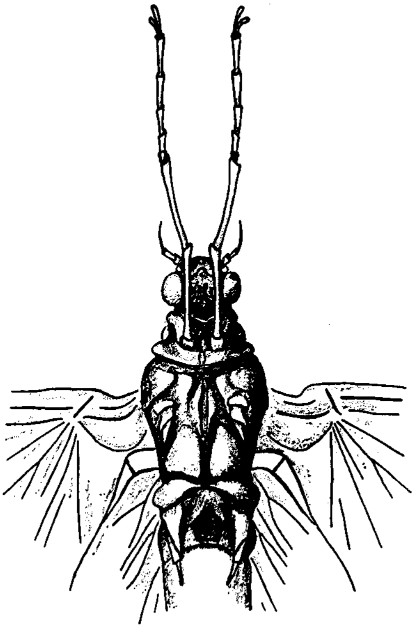

Fig. 14. *Campsurus segnis* Needham. Ventral view of adult male (left) and female (right). Note that the legs are vestigial, except the male front legs which are necessary for copulation. (After Morgan, 1929.)

their wings for existence (cf. Morgan 1929). In the male the middle and hind legs are vestigial, while the front legs are well developed and lengthened as in related genera. In the female all pairs of legs are aborted stumps. Vide fig. 14. With regard to the fact that even the adult mouthparts are reduced, it is strange to state that although the adults are free-living all pairs of legs and their derivations are rudimentary in the female, while in the male two have been kept, viz. the front legs and the forceps, both absolutely necessary for mating.

A further peculiar specialization is the strong development of the eyes in the males of certain genera, which is especially obvious in the divided eyes of the baetids. It has been supposed that the upper turbinate portion functions at the mating flights, thus enabling the males to see females coming in above them. Cooke (1940), who studied *Stenonema vicarium*, states that if a male be approached by a female from below, she will be completely ignored, but if she is above him, she is immediately seized.

It is peculiar that a considerable part of the population at the tributary to the Köngämä River mated on the ground, as the general morphology and behaviour of the species indicates aerial copulation. It should be noted that weather conditions seemed to be optimal: there was no wind and temperature was comparatively high. It seems probable, however, that certain species at least may be able to mate out of the air. As mentioned above De Geer (1771) observed another such case. Eaton (1888, p. 10) says that the adults of a New Guinean species (*Plethogenesia papuana*) mate on the surface of the water whence they emerge, in the same way as Cornelius stated for part of the Central European *Palingenia*. But in the former species it may be normal, as according to Eaton the anterior legs of the males are not lengthened, and thus unable to suspend the males in the way described above.

6. A review of the terms used for Ephemeropteran external genitalia

The external genitalia of the mayflies are comparatively unitary from a general point of view. This is not matched by a similar simple terminology. As a matter of fact an astonishing amount of terms has been produced for the structures involved in mayfly mating.

Below I have gathered them (so far as I know of them) in a table, completed with definitions. As the table has been compiled for taxonomists, the sense of "external genitalia" is very wide, including any morphological structure of the abdominal apex involved in copulation.

Principally, this table is arranged in the same way as that presented for Plecoptera in a previous article (cf. Brinck 1956, p. 114 ff.). Thus, for each structure in question, I have chosen an English term which is defined in a few words. Under a special heading synonymous terms in English, French, German, Italian and Latin are given. As in English, there is often in German and French an assortment of terms covering each definition. I have not selected German or French versions adequate to the English terms, but usually such equivalents are easily found.

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(Cont. p. 34.)

Table 1. *Terminology of the*

Term	Definition	
		English
Cercus ♂+♀	Many-jointed, setiform appendages arising from the paraprocts	abdominal filaments (Stephens 1835) caudal filaments (Berner 1950) caudal setae (Eaton 1888) cercopoda (Packard 1883) lateral caudal setae (Uéno 1931) lateral tails (Needham, Traver, Hsu 1935) outer caudal setae (Phillips 1930) setae (auct. var.)
Egg guide ♀	Prominent, basal sclerotization of the 8th sternum (Leptophlebiidae)	egg guide (Morrison 1919) egg valve (Berner 1950)
Epiproct ♂+♀	Dorsal portion of the 11th abdominal segment	epiproct (Crampton 1918) pygidium (Crampton 1917) supra-anal plate (auct. var.) sur-anal plate (Crampton 1917) tenth tergum (auct. var.)
Forceps ♂	A pair of movable, appendicular claspers, arising from the posterior margin of the 9th abdominal segment and consisting of a proximal coxite and a distal stylus.	arthrostyli (Crampton 1918) clasper (Snodgrass 1936; Phillips 1930) forceps (Eaton 1888) forceps-limbs (plus forceps-basis) (Eaton 1888; Uéno 1931) genital styles (Crass 1947) gonopods (Tiensuu 1935) harpagones (Snodgrass 1936) lower rhabdopoda (Packard 1883) outer rhabdites (Packard 1883) styli (Crampton 1918)
Genital opening or vulva ♀	External orifice of the vestibulum	—
Gonopore ♂+♀	Aperture of the gonoducts (usually to the exterior; in females sometimes to a vestibulum)	—
Paracercus or cercoid ♂+♀	Un-paried appendage of the epiproct, usually cerciform, rarely reduced or absent	cerciform appendage (Walker 1922) intermediate seta (Tiensuu 1935) median caudal filament (Imms 1951) median caudal seta (Eaton 1888) median filament (Berner 1950)

external genitalia in Ephemeroptera.

Synonyms		
French	German	Italian and Latin
cercus (Despax 1949) cerques latéraux (M. L. Verrier 1949) soies latérales (Despax 1949)	Cerci (Handlirsch 1928) Seitenborsten (Bengtsson 1909) seitliche Schwanzborsten (Ulmer 1929)	cerci (Grandi, op. plur.) setae caudales (Palmén 1884)
—	Eiführung (Pleskot 1953)	inspessimento dell' ottavo urosterno (Grandi 1955)
épiproct (Bertrand 1954)	Dorsalklappe des Telson (Handlirsch 1928)	—
coxite+style (Bertrand 1954) crochets (De Geer 1771; Pictet 1845; Bertrand 1954) forceps (Bertrand 1954) forcipule (Lestage 1924) genostyle (M. L. Verrier 1949) gonopodes (Despax 1949) styles sous-génitaux (Peytoureaux 1895)	Appendices (Hagen 1888) Forceps (Palmén 1884) Genitalfüsse (Klapálek 1909; Ulmer 1929) Gonopoden (Klapálek 1904; Weber 1933) Haltezange (Heiner 1915) sichelförmige Haken (Cornelius 1848) Zange (Palmén 1884)	coxopodite+stili (Grandi 1943) forceps (Palmén 1884) stiligero+stili (Grandi op. plur.)
—	—	—
—	—	—
cerque impair (Bertrand 1954) cerque médian (M. L. Verrier 1949) filum terminale (Bertrand 1954) mésocerque (Bertrand 1954) soie médiane (Despax 1949)	Mittelborste (Klapálek 1909) mittlere Schwanzborste (Bengtsson 1909) Terminalfilum (Handlirsch 1928)	appendix dorsalis (Eaton 1888; Tillyard 1923) filamento mediano (Grandi 1941)

Synonyms		
French	German	Italian and Latin
plaque subgénitale (Bertrand 1954)	Eiklappe (Bengtsson 1909) Ovipositor (Pleskot 1953) Subgenitalplatte (Klapálek 1909; Bengtsson 1928)	lamina subgenitale (Grandi 1955) ovi-valvula (Palmén 1884)
—	Genitalbulbus (Pleskot 1953)	vestibolo (Grandi 1955)

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