

# The Abdominal Morphology of *Povilla adusta* Navas (Polymitarcidae) and of Ephemeroptera in General

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Ent. scand. 2. 1971. 139-160.

## Abstract

The morphology of the abdomen of the mayfly, *Povilla adusta* Navas (Polymitarcidae) has been studied from dissections of muscles and nerves in male and female imagines and in a female nymph and a number of apparently very primitive traits

have been disclosed. The findings have been compared to similar structures in other mayflies and, as a result, a revised interpretation of the genital and postgenital segments of Ephemeroptera is proposed.

## I Introduction

Ephemeroptera is one of the oldest known groups of recent insects—types morphologically similar to the recent ones are known from as early as Upper Carboniferous—and hence the order is of special interest in connection with any morphological or anatomical survey.

During a study of the male insect genitalia in general a number of African Ephemeroptera were dissected, and in no case were any traits found which were inconsistent with previously published accounts of these structures, with the single exception of *Povilla adusta* Navas, which showed many, apparently primitive, features and for that reason was made the subject of some further studies.

## II Ephemeroptera in general (as previously published)

### (1) Ontogeny

The embryological development of Ephemeroptera was first carefully studied by Heymons in *Ephemera vulgata*. He not only figured eleven abdominal segments, but also realized that the cerci were the appendages of the last of these (Heymons, 1896 b, c), and that at a certain stage, all the abdominal segments carried rudiments of appendages (Heymons, 1896 a: 85: "Es bilden sich bei *Ephemera* 11 Paar kleiner, flacher Extremitätenanlagen am Abdomen . . ."); but unfortunately he did not follow the development on the penultimate

segment further. In the imagines, however, most authors at that time had recognized only nine (Pictet, 1843) or ten abdominal segments (Hagen, 1863; Lubbock, 1863; Vassière, 1882; Eaton, 1888); only Packard (1883) mentions ten abdominal segments and remains of an eleventh one, a view which has been shared by most later students. A single publication (Snodgrass, 1931: 28) mentions a supra-anal lobe in the young stages as the remains of the twelfth segment or telson.

The post-embryonic development of the male genitalia of Ephemeroptera has been followed by Qadri (1940), who states, that the penes first appear as two well separated dermal outgrowths well caudally of the ninth sternum, in the membranous area; later they may fuse more or less completely. The appendages of the ninth segment are present as gonocoxites on the caudal edge of the ninth sternum, separated in some genera such as *Ephemera*, *Callibaëtis* and *Baëtis* (Michener, 1944) but fused in most others; each gonocoxite carries distally a stylus, which may be secondarily segmented. The so-called "parameres" and other processes on the penes originate as mere outgrowths on these at a relatively late stage.

### (2) Anatomy

A detailed description of the pre-genital musculature of a number of nymphs and imagines of several species are given by Dürken (1907). A diagram of the ventral musculature in the apical half of a generalized female

Ephemeroptera is figured by Brinck (1956), and, even if simplified, it agrees very well with Dürken's detailed figures of *Ephemerella ignata* (Dürken, 1907: tab. XXIV, 1 & tab. XXVI, 4).

Both authors agree—even if neither of them mentions it directly—that the ventro-longitudinal musculature comprises two sets of muscles, viz. an internal one, from one antecosta to the antecosta of the following segment, and a second set of external muscles, from somewhere on the internal surface of the sternum to the frontal edge of the following sternum.

Relative to the male genital appendages, the styliiger plate has (as mentioned under ontogeny) been considered the gonocoxae of the ninth segment, still separate in *Ephemerella*, *Calibaëtis* and *Baëtis*, but fused in most others, (Michener, 1944) and accordingly the arthro-styli ("genostyli", "styli") have been considered the homologues of gonostyli in other insects. The penes are developed from the membrane caudally of sternum IX, and are generally considered derivatives of the tenth segment, the penial bars (penial basal arms) being the remains of sternum X (Snodgrass, 1936; Qadri, 1940; Brinck, 1956).

The musculature of the male genital appendages has been studied by various authors (Snodgrass, 1936; Levy, 1948; Brinck, 1956; Grandi, 1960). It consists of a more or less mid-ventral muscle from sternum IX to the styliiger plate and a—sometimes very small—muscle from the styliiger plate to the arthro-stylus. The "penial bar" is connected by a muscle to sternum IX, and by another one to tergum IX (Grandi, 1960), further, in some species, a muscle connects the "penial bar" with the "penis" (Grandi, 1960).

The male gonopores are situated caudally on venter IX, but several authors maintain, that originally the gonopores were situated on venter X, and that they secondarily have moved frontad (Snodgrass, 1936; Qadri, 1940; Brinck, 1956); recently this view has been opposed by Smith (1969: 1074).

### III *Povilla adusta* Navas

#### Material

The material of imagines was kindly put at my disposal by my colleague prof. A. Tjønn-

land, who had caught it in a mercury vapour light trap at Lake Koka, Ethiopia. In spite of a severe draught and a water level ten feet below the normal one, the writer managed to secure a single nymph at the same locality the following year (1966). All material was fixed in 70% alcohol and dissected under microscope (for technic vide: Birket-Smith, 1965: 150).

#### Biology

The purely tropical genus *Povilla* (Polymirtarcidae) is only a small, but highly specialized one. The immature stages stay by day in a silk-lined burrows excavated by themselves in—even hard—wood. They feed on plankton which is obtained by filtering the water through a highly specialized filter apparatus formed by the legs, which are armed with long bristles (Hardland-Rove, 1958), even if it has been suggested that an Indian species *P. cf. corporaali* (Lestage) actually eat the material excavated from the burrows (Vejabhongse, 1937).

As with many other species of mayflies, the imagines swarm in huge crowds at rather regular intervals, where the species is common (Hardland-Rove, 1958; Tjønneland, 1960).

#### A. Anatomy of the abdomen of imagines

The following description of the morphology and anatomy of the abdomen of *Povilla adusta* applies only to the male unless otherwise stated.

##### (1) Integument

Externally, the morphology of the abdomen is very similar to that of other mayflies (fig. 1 A). The first segment is partly fused to metathorax. The segments II to IX each have a thin and weakly sclerotized, but well defined tergum and sternum. The pleural areas are weakly sclerotized as well, but the sclerotized areas are irregular and rather indistinctly defined, forming no distinct pleuron. The pleural areas of segments II to VII are almost identical: the shape is rather broad and rounded at the frontal end, tapering caudally; the dorsal edge is marked by a distinct, nearly straight fold with a peculiar vortex, *wl*, at the caudal third-point, while the ventral edge is deeply

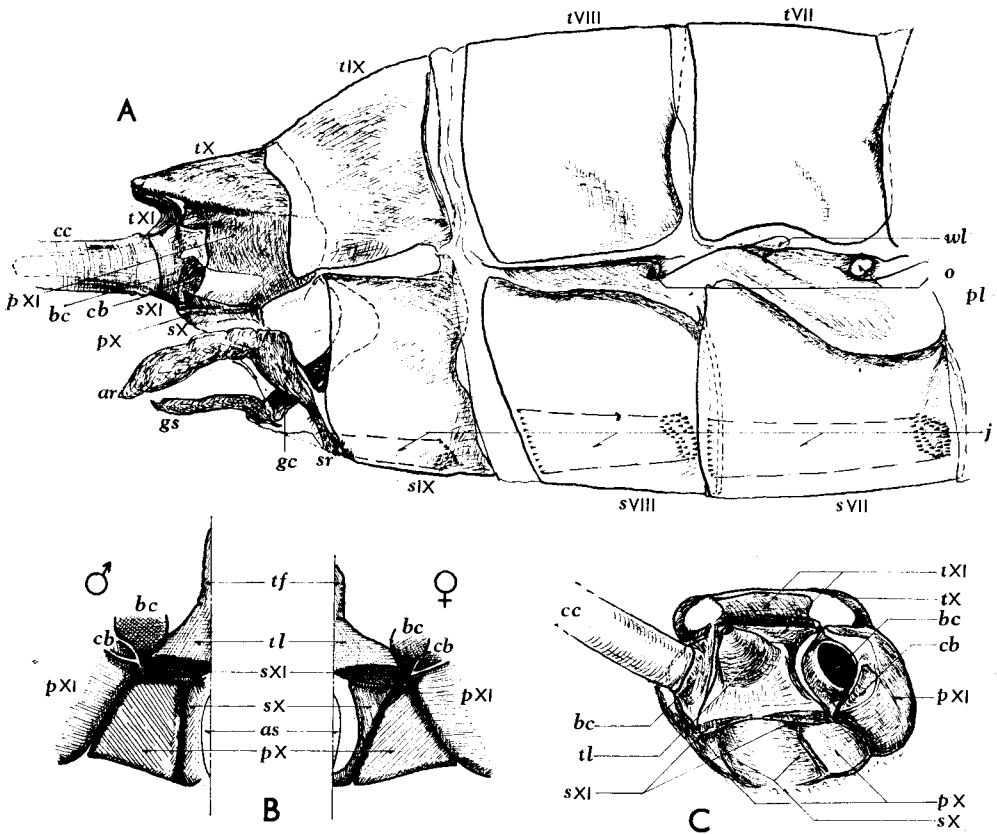


Fig. 1. *Povilla adusta* Navas, terminal abdominal sclerites; A, segments VII to X of male in right lateral view; B, ventral view of post-genital segments of male and female; C, oblique ventro-caudal view of post-genital segments of male.

S-curved and smooth. The spiracle is relatively large and situated in the dorsal fold near its anterior end. The pleural area in segment VIII is somewhat narrower, the dorsal fold without a vortex and the ventral edge only slightly S-curved. The area between tergum and sternum in segment IX is very narrow, completely deprived of folds and sclerotizations and without any spiracle. (In females the pleural areas are almost identical, except in segment IX, where the pleural area is considerably larger than in the males, and have a distinct dorsal fold, but no spiracle). Along the middle of the caudal edge of st. IX is a narrow transverse plate, the styliger plate, *sr*, hinged to the sternum by a narrow membrane and laterally terminating in long, pointed, cylindrical and weakly sclerotized processes, the arthrotyli, *ar*.

The intersegmental membrane caudally of st. IX is very wide. In this membrane is a large, sickle-shaped sclerite, *gc*, its "point" attached by a narrow tough membrane to the dorso-caudal corner of st. IX, (and thus forming the medial side of a frontad directed fold inside the dorsal part of the caudal edge of st. IX). The ventro-caudal end of this sclerite, *gc*, is freely protruding and rounded cylindrically; on its medial surface, which nearly touches its opposite number, it carries the male gonopore, *de* (fig. 3 A); distally a pointed, cylindrical and bent process, *gs*, is attached by a pair of condyles.

The postgenital segments form a partly fused relatively strongly sclerotized unit (fig. 1 A, B, C). The tenth tergum, *tX*, is approximately semi-circular and protudes porch-roof

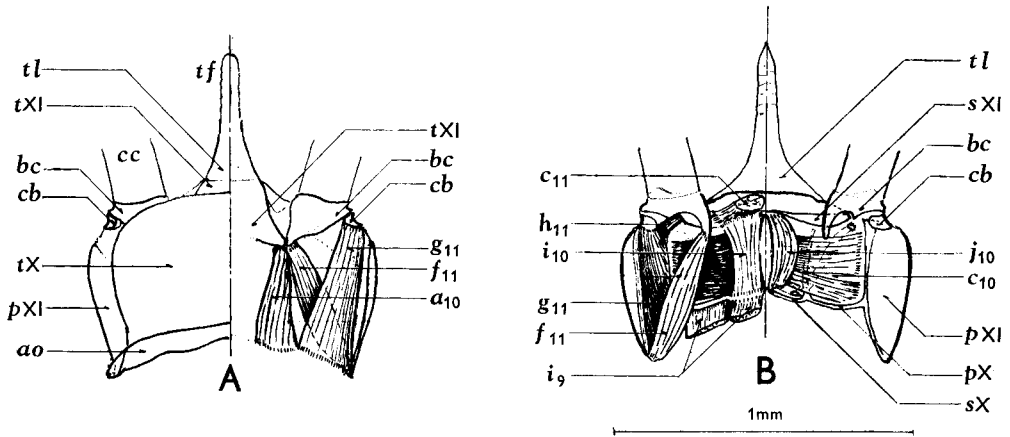


Fig. 2. *Povilla adusta* Navas, dorsal views of post-genital segments of male; A, in the left side of the figure an external view, in the right side the tenth tergum,  $tX$ , is removed; B, the more ventrally placed muscles; in the right side of the figure the muscles  $i_9$ ,  $f_{11}$ ,  $g_{11}$ ,  $h_{11}$  and  $i_{10}$  are removed.

fashion over the end of the abdomen; the acrotergite is bent sharply dorsad. Laterally the tenth tergum is fused to the lateral plates,  $pXI$ ; the line of fusion is caudally distinct as a seam, and frontally it is indicated by a shallow, but distinct notch just at the end of the acrotergite. Ventrally these lateral plates,  $pXI$ , are fused along a distinct seam to a pair of irregularly tetragonal, weak sclerites,  $pX$ , which again along their ventral edges are fused to a weak midventral sclerite,  $sX$ , which is completely interrupted in the midventral line where the anus,  $as$ , is situated. (In the female the ventro-lateral sclerites,  $pX$ , are irregularly triangular, and the midventral sclerite,  $sX$ , is U-shaped, its caudal side having a deep incision for the anus. While in the male the midventral sclerite,  $sX$  is nearly flat, it is strongly folded in the female, the frontal connection between the two lateral parts being invaginated towards the anus, which thus is situated in the bottom of a depression.)

The terminal segment consists of a dorsal plate,  $tXI$ , the frontal part of which, the acrotergite, is very wide and bent sharply dorsad. Vento-caudally this dorsal plate,  $tXI$ , is connected along a slightly depressed line to a sclerotized cone,  $tl$ , which at its apex carries the terminal filament,  $tf$ . Ventrally this cone,  $tl$ , is widened and its ventral edge is lined by a

pair of thick, wedge-shaped sclerites,  $sXI$ . The cerci,  $cc$ , have each a distinct basis cerci,  $bc$ , the medial side of which is connected to the lateral sides of the dorsal plate,  $tXI$ , and the sclerotized cone,  $tl$ , by a wide membrane; dorsally and ventrally the basis cerci,  $bc$ , carries a condyle, which fit into ginglymi at the dorso-caudal and ventro-caudal corners of the lateral plates,  $pXI$ ; a small oblong sclerite,  $cb$ , is intercalated ventrally between the basis cerci,  $bc$ , and the lateral plate,  $pXI$ , flexibly connected to both by narrow strips of membrane. While the terminal filament,  $tf$ , is rather short, the cerci,  $cc$ , are very long, in the male about three times the entire length of the body, in the female about as long as the diameter of the abdomen. It might be added that the extensions of the various sclerotizations seem to vary to some extent from one individual to another.

## (2) Musculature of the pregenital segments

Before going into details concerning the muscles, it might be useful to go through a generalized abdominal segment (figs. 3, 5 A). The interior dorso-longitudinal muscle,  $a$ , is very broad and runs from the antecosta of one segment to the antecosta of the following one; it appears, especially dorsally, to have two

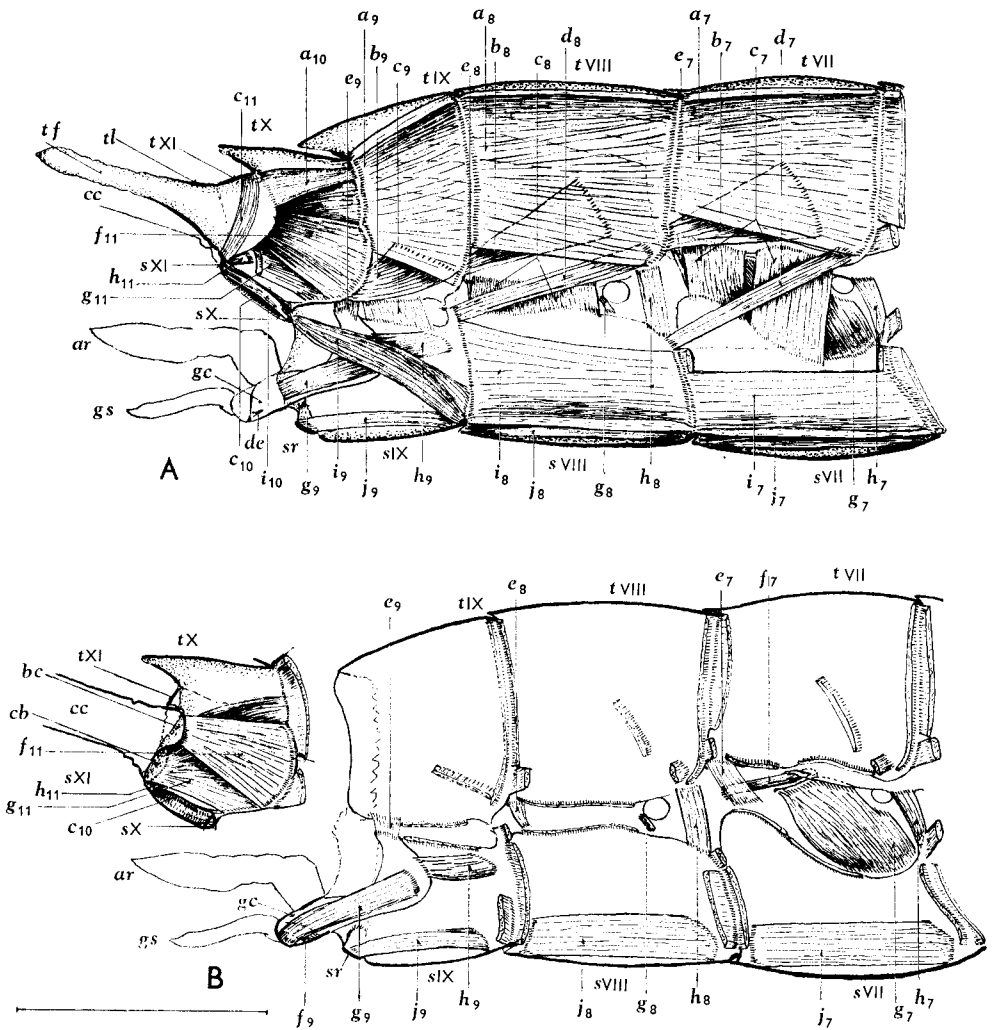


Fig. 3. *Povilla adusta* Navas, left lateral halves of seventh to terminal segments of male in right lateral view;  
 A, intestine, gonads etc. removed, only muscles left;  
 B, internal longitudinal and oblique muscles, viz. mm *a, b, c, d* and *i*, removed in the seventh to the tenth segments.

layers, with caudally ascending fibers in the outer one and caudally descending fibers in the inner one, but it is not possible to separate the two layers. The exterior dorso-longitudinal muscle, *b*, is attached laterally on one tergum just before the middle, the fibers descending and converging towards the insertion on the lateral part of the antecosta of the following tergum.

In the interior ventro-longitudinal muscle, *i*, all fibers are parallel or nearly so; but the muscle is divided by a longitudinal cleft (exaggerated in fig. 5 A) into a usually broader lateral part, *i<sub>l</sub>*, and a smaller medial part, *i<sub>m</sub>*; it runs from the antecosta of one sternum to the antecosta of the following sternum. The exterior ventro-longitudinal muscle, *j*, is situated near the midventral line, and runs from

well behind the antecosta of one sternum to the caudal edge of the same one, both insertions usually being more or less covered by the internal ventro-longitudinal muscle. While the functions of the previously mentioned muscles, *a*, *b*, and *i*, are evident, the function of the external ventro-longitudinal ventral muscle, *j*, may be less clear; a contraction of this muscle will cause the sternum to bend in a longitudinal plane, and hence to flatten itself in a transverse plane and in this way it will flatten the entire transverse section of the abdomen; since nearly the entire transverse section—at least, of segment II to VIII—are filled out by the air-filled lumen of the intestine, a flattening of one or more of the transverse sections of the abdomen will cause a longitudinal extension of the entire abdomen, and thus the external ventro-longitudinal muscle, *j*, in a way, is the antagonist of the internal longitudinal muscles, at least as long as no air is released from the lumen of the intestine and presumably even if the lumen is in open connection with the exterior. The extension of the abdomen will be intensified by a contraction of the exterior dorso-longitudinal muscle, *b*, simultaneous with the contraction of the ventral one, *j*. It should be noted, that while the actions of the external longitudinal muscles are too weak to cause any noticeable under-pressure in the gut, the relative strength of the internal longitudinal muscles suggest that they are able to cause a certain compression of the air in the gut. (In the females the external ventro-longitudinal muscles have completely vanished in segments II to VI—which are kept continuously extended by the egg masses—and in segment VIII; the internal ventro-longitudinal muscles are relatively weaker than in the males.)

The dorso-ventral muscle, *c*, is a thick sheet of vertical fibers connecting about two-thirds of the lateral edge of tergum to a similar part of the lateral edge of sternum of the same segment; it is often divided by a more or less conspicuous cleft into an anterior and a posterior part. The oblique dorso-ventral muscle, *d*, runs from well behind the lateral end of antecosta of tergum to the lateral end of the antecosta of sternum of the following segment; it passes internally of the dorso-ventral muscle, *c*. The function of this muscle seems to be antagonistic to the exterior longitudinal muscle, *b*, when a sole contraction of this muscle has caused a flexion between the terga.

The dorso-pleural muscle, *e*, is a relatively small muscle from caudally on the lateral edge of tergum—this insertion more or less covered by the dorso-ventral muscle, *c*—to near the ventral edge of the pleural area, the fibers not quite vertical, but sloping frontad.

The ventro-pleural muscle, *h*, is of a similar size, from frontally on the lateral edge of sternum to the dorso-pleural fold just in front of the spiracle; it appears that this muscle may act as a closing muscle for the spiracle.

Two intrinsic pleural muscles are present: the posterior muscle, *f*, a small muscle from caudally on the pleural area—this insertion covered by the dorso-pleural muscle, *e*—to the dorso-frontal part of the vortex, *wl*, on the dorsal, pleural fold. The anterior pleural muscle, *g*, is a very strong muscle from the ventro-frontal extension of the pleural area, partly to the ventro-caudal part of the vortex, *wl*, of the dorsal pleural fold—some fibers often inserted under the posterior pleural muscle, *f*,—and partly to the dorsal pleural fold in front of the vortex.

### (3) *Innervation in the pregenital segments* (fig. 5 A, comp. fig. 4)

The ventral nerve cord is double in the front of the segmental ganglions, but caudally of the ganglions the two cords appear more or less fused. From the ganglions (in segments II to VI) two somatic nerves arise. The anterior segmental nerve arises near the frontal end of the ganglion; it is immediately divided into two branches, one of which will continue internally across the medial part of the internal ventro-longitudinal muscle, *i<sub>m</sub>*, dive out through the longitudinal cleft between the two parts of this muscle, and then continue laterad, exteriorly of the lateral part of the internal ventro-longitudinal muscle, *i<sub>i</sub>*; while passing this muscle, the branches innervating both the lateral and the medial part of it, *i<sub>i</sub>* and *i<sub>m</sub>* respectively, arise on the caudal side of the main stem; in some cases these two branches will originate from the same point, rarely, they will originate as one branch which is soon forked. Just free of the ventro-longitudinal muscles, the main trunk will give off a frontad directed branch, which partly innervates the ventro-pleural muscle, *h*, and partly appears to carry sensory threads to the sur-

roundings of the spiracle. The branch innervating the dorso-ventral muscle, *c*, is given off immediately after, usually from the caudal side of the main stem. The main stem of the nerve continues dorsad, internally of all muscles and gives off branches innervating the oblique dorso-ventral muscle, *d*, and the two dorso-longitudinal muscles, *b* and *a*.

The other branch of the anterior segmental nerve will extend caudad and then continue externally of the internal ventro-longitudinal muscle, *i<sub>m</sub>* and *i<sub>i</sub>*, but internally of the external ventro-longitudinal muscle, *j*, go through the ventral part of the dorso-ventral muscle, *c*, and then fork to innervate the two pleural muscles, *f* and *g*.

The posterior segmental nerve from the ganglion is considerably smaller than the anterior one, arises ventro-laterally on the ganglion and innervates only the exterior ventro-longitudinal muscle, *j*, (but contains, apparently, some sensitive threads as well). The innervation of a typical segment could thus be written in the shape of a formula. (gf) *i<sub>m</sub>* *i<sub>i</sub>* hcdba + *j*, or but rarely (gf) (*i<sub>m</sub>* *i<sub>i</sub>*) hcdba + *j*.

It has not been possible, in imagines, to trace the innervation of the dorso-pleural muscle, *e*.

As already mentioned, the air-filled gut occupies most of the abdominal segments II to VII; the walls are here only a thin membrane lying closely against the dorsal and ventral muscles of the body wall, to which it is attached only by fine sheet-like ligaments to the antecosta. (In the females, the intestine in the pre-genital segments is collapsed and atrofied, but fills nearly the entire lumen of the abdomen in the complete postgenital segments.) From segment VIII and onwards, the intestine narrows, and its wall thickens and becomes free of the abdominal wall. The suspensory ligaments of this "free" part of the intestine is combined with dilatory muscles, *m*, which, however, are not inserted on the antecosta as are the ligaments (apparently there is no room for them) but the insertions are on the latero-caudal parts of the preceding sternum, between the oblique dorso-ventral muscle, *d*, and the internal ventro-longitudinal muscle, *i<sub>i</sub>*. (It is remarkable, that even if the air-filled intestine seems to occupy the entire lumen of the eighth and ninth abdominal segments of the females, there are still small dilator muscles present in these segments.)

The dilator muscles are innervated by sepa-

rate nerves from the central nervous system. The median nerve gives off a pair of lateral branches in each segment in front of the ganglion of this segment, but the neurocytes of these lateral branches are situated in the ganglion of the preceeding segment (Snodgrass, 1935). The lateral branches in most of the pregenital segments bend frontad and then they follow the intestinal ligament to the level of the pleural area, where they bend caudad, giving off branches to the reproductive organs and tracheae etc. The median nerve as well as its branches appear to be of a structure different from the double nerve cord and the other segmental nerves, since the former retain certain stains (Picric Acid—Acid Fuchsin, Hansen's Hematoxyline, Indigo Carmine etc.) far better than the latter.

Apart from the practical point of making the two types of nerves readily distinguishable, these differences in staining ability confirm the assumption of a fundamental difference between the median and the double nerve cord and their respective derivatives (Escherich, 1903; Snodgrass, 1935.)

In segment VII the median nerve gives off two pairs of lateral branches; the first pair is in all respects similar to the preceeding ones. The second pair is given off near the caudal edge of the segment and is obviously the one belonging to segment VIII, since the two branches bend caudad to proceed dorsad along the antecosta of this segment (from about the cleft between *i<sub>m</sub>* and *i<sub>i</sub>*, figs. 4, 5 A). In segment VIII,—the first segment with dilator muscles,—two thin nerves of staining qualities similar to the ones characteristic of the median nerve, originate from the dorsal surface of the terminal ganglion (gl 8, fig 4); these nerves *m<sub>IX</sub>* innervate the dilator muscle inserted on st. VIII, and give off two branches each which proceed to the succeeding segment, one branch, *n<sub>IX</sub>*, terminating along the tracheae etc. in the pleural area. It must therefore be concluded that these nerves are segmentally homologous with the lateral branches of the median nerve in the previous segments, and that they are the ones belonging to segment IX; accordingly the position of the dilator muscle, *m*, is a secondary one, its lateral insertion having been translocated frontad. (It might be added, that the introduction of the dilator muscle, *m*, in the "generalized segment", fig. 5 A, is somewhat of a disingenuousness, since dilator muscles are

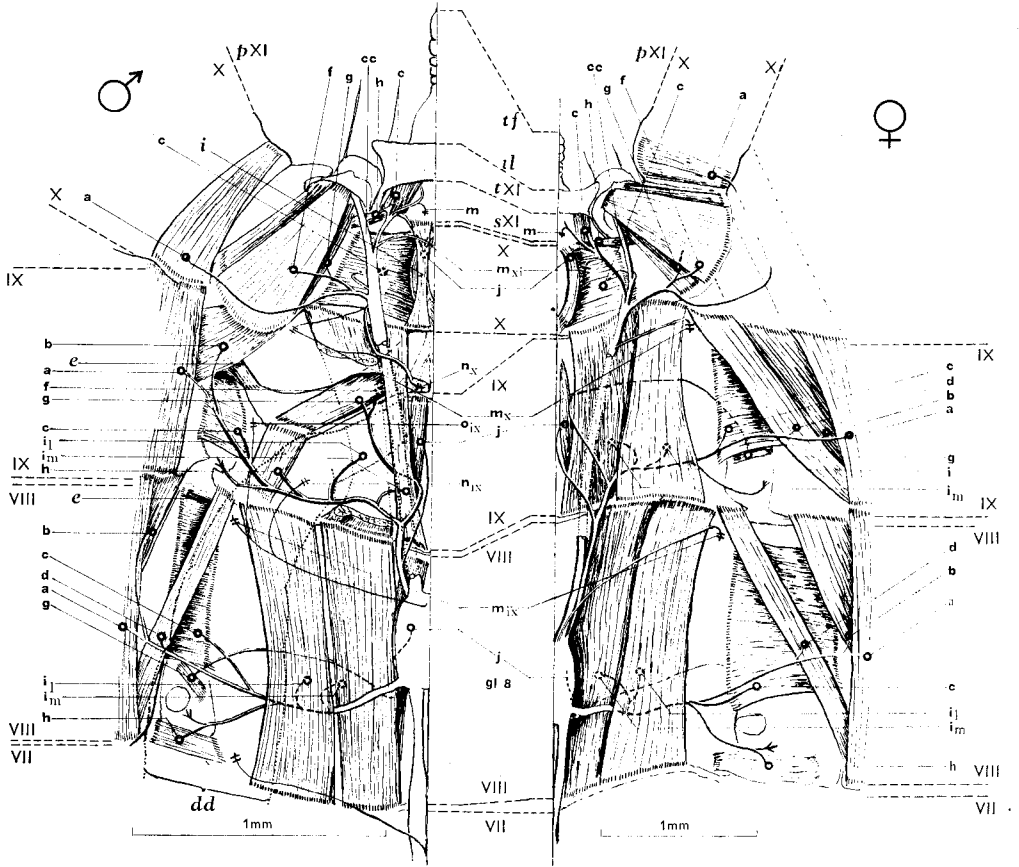


Fig. 4. *Povilla adusta* Navas, ventral parts of segments VIII to X, slightly flattened, showing the muscles and their innervations; the left side of the figure shows the male, the right side the female.

only found in the specialized segment VIII and in the following ones.)

(4) *Musculature of the genital segments*

From segment VIII a certain specialization sets in, even in the female (figs. 2, 3, 4). In segment VIII the pleural area is somewhat reduced; the posterior pleural muscle, *f*, has completely disappeared, even if the pleural area here is considerably wider than in the males.

In segment IX the internal dorso-longitudinal muscle, *a*<sub>9</sub>, is normal; the external dorso-longitudinal muscle, *b*<sub>9</sub>, is caudally inserted on the lateral sclerites, *pXI*. The internal ventro-

longitudinal muscle, *i*<sub>m9</sub>, is for the largest part caudally inserted on the frontal edge of the ventro-lateral sclerite, *pX*, only a minor part is inserted on the remains of the midventral sclerite, *sX*. The dorso-ventral muscle, *c*<sub>9</sub>, has the usual appearance, spanning across the very narrow area between tergum and sternum. A narrow muscle, *j*<sub>9</sub>, is frontally inserted on sternum, *sIX*, near its frontal edge; caudally it is inserted on the styliger plate, *sr*. No other muscle has been found on the styliger plate, *sr*. The sickle-shaped sclerite, *gc*, is connected by a small muscle, *e*<sub>9</sub>, to the ventro-caudal corner of tergum, *tIX*, and by a strong muscle, *h*<sub>9</sub>, to the sternum, *sIX*, near its dorso-frontal corner. The sickle-shaped sclerite, *gc*, has two intrinsic



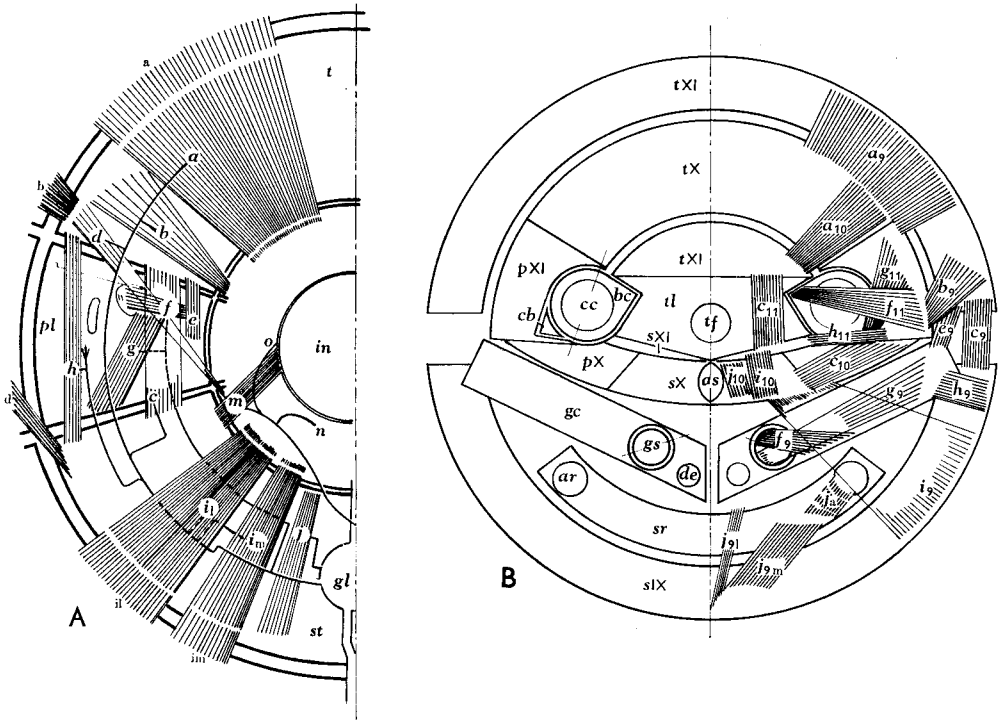


Fig. 5. *Povilla adusta* Navas, diagrams of musculature in axial projection in frontal view; A, the right half of a generalized abdominal segment, showing the muscles and their innervations; B, the male genital and post-genital segments, the left side of the figure showing the sclerites, the right side the muscles.

muscles inserted on it: a strong one,  $g_9$ , from near the insertion of the muscle  $h_9$  to the medial side of the base of the process,  $g_5$ ; the other muscle,  $f_9$ , (fig. 3 B) is very small; proximally it is inserted medio-ventrally in the distally protruding cylindrical part of the sickel-shaped sclerite,  $g_c$ , distally it is inserted on the fronto-lateral side of the base of the process,  $g_s$ .

(In the females the internal and external dorso-longitudinal muscle,  $a_9$ , and  $b_9$ , the dorso-ventral muscle,  $c_9$ , and the internal ventro-longitudinal muscle,  $i_9$ , are developed very much as in the males. Further, it appears, that segment IX is the first segment in the females, in which an external ventro-longitudinal muscle,  $j_9$ , is present. A small, but distinct anterior pleural muscle,  $g_9$ , is present, and the oblique dorso-ventral muscle,  $d_9$ , is larger than in the preceding segments.)

##### (5) Innervation in the genital segments and discussion of homologies

The innervations of the somatic muscles in segment VIII is as in the preceding segments and the median nervous system in this segment has been mentioned. The innervation of the ninth segment must obviously be deviating, since the terminal ganglion is situated in segment VIII, but the deviations are very small, at least as far as the innervations of the somatic muscles are concerned. From the caudal end of the terminal ganglion two pairs of nerve trunks arise, the dorsal one innervating the post-genital segments, the ventral one solely innervating the ninth segment, and the genital appendages. In the females (fig. 4) the nervous system in the ninth segment only differ from that in the males by the common emergence from the ganglion of the nerve for the external ventro-longitudinal muscle,  $j_9$ , to-

gether with the nerves for the remaining somatic muscles,  $a_9-i_9$ ; from a direct comparison to the male (fig. 4) it seems justified to homologize the two nerves,  $j_9$ , and accordingly the styli muscle,  $j_9$ , is segmentally (metamerically) homologous with the external ventro-longitudinal muscles,  $j_8, j_7$ , etc. of the preceding segments. The branches  $i_m i h c b a$  in the male and  $i_m i c b d a$  in the female have identical courses and shapes, except that there is no oblique dorso-ventral muscle,  $d_9$ , in the ninth segment of the male, and no ventro-pleural muscle,  $h_9$ , in the female. These branches may therefore be considered homologous with the similar branches in the preceding segments; consequently, the muscle,  $h_9$ , from the ninth sternum,  $sIX$ , to the sickel-shaped sclerite,  $gc$ , might be considered segmentally homologous with the ventro-pleural muscles,  $h_8, h_7$ , etc. in the preceding segments, even if the nerve for it branches off from the main stem separate from the (presumably) sensory branch, which usually accompanies it.

Considering the absence of a ventro-pleural muscle in segment IX of the female, the question may arise, whether the muscle  $h_9$  in the male is homologous with the oblique ventro-dorsal muscle,  $d_9$ , in the female; however, in this case the frontal insertion should have shifted from tergum to sternum, to exactly the place, where in the preceding segment the ventro-pleural muscles are inserted.

The nerve branch to the pleural muscles,  $g_9$ , in the ninth segment of the female has a course identical with the branches to the pleural muscles,  $f$  and  $g$ , in the preceding segments and may thus be considered segmentally homologous with them. The branch,  $fg$ , to the two muscles,  $f_9$  and  $g_9$  on the sickel-shaped sclerite,  $gc$ , in the ninth segment of the male has further an identical course, diving between the exterior and interior ventro-longitudinal muscles, and this nerve is therefore considered homologous with the branch  $fg$ , to the pleural muscles in the preceding segments. Consequently, the muscles  $f_9$  and  $g_9$  are considered segmentally homologous with the intrinsic pleural muscle,  $f$  and  $g$ , in the preceding segments; a confirmation of this assumption may be found in the mutually crossing fibers in the muscles  $f_9$  and  $g_9$  as compared to the marked tendency of mutual crossing found in any pair of pleural muscles  $f$  and  $g$ . The

logical consequence of the above interpretation must be, that the sickel-shaped sclerite,  $gc$ , is the sclerotized and translocated pleural area of segment IX; a further confirmation of this assumption may be found in the presence of the muscle  $e_9$ , from the ventro-caudal corner of the ninth tergum,  $tIX$ , to the sickel-shaped sclerite,  $gc$ , originating on the ninth tergum in the same place as the dorso-pleural muscles,  $e$ , originate on the terga of the preceding segments. This interpretation further brings to mind the earlier view of the abdominal pleurites being derivatives of bases of primitive abdominal appendages (Snodgrass, 1931, 1935), viz. primary coxopodites. The muscles  $f_9$  and  $g_9$  are distally inserted in the pointed process,  $gs$ ; in the preceding segments the pleural muscles,  $f$  and  $g$ , are inserted on or near the vortex,  $wl$ , on the dorsal fold of the pleural area; hence it is close at hand to suggest, that both are derivatives of the distal segment of the primitive abdominal appendages, the telopodite or styli, in segment IX adapted for sexual purposes as true gnostyli,  $gs$ , carried on modified coxopodites, as true gonocoxae, while in the pregenital segments the primitive abdominal appendages only remain in an abortative condition as the vortex,  $wl$ , on the dorsal fold of the pleural area. (About the nymphs, see later.)

The styli muscle,  $sr$ , is only moved by one muscle,  $j_9$ , inserted on the ninth sternum,  $sIX$ , for this reason the styli muscle,  $sr$ , cannot be regarded as a true segment (since such a one will normally be moved by a pair of antagonistic muscles). Taking the segmental homologies of the styli muscle,  $j_9$ , and the external ventro-longitudinal muscles  $j_8, j_7$ , etc., into consideration, the styli muscle must be regarded as a mere part of the ninth sternum,  $sIX$ ; or as a special poststernal structure (see later). The function of the styli muscle,  $j_9$ , will then be an adduction of the styli muscle,  $sr$ , including the arthrostyles,  $ar$ , and not, as for the external ventro-longitudinal muscles in the preceding segments, as an antagonist to the internal ventro-longitudinal muscles, which anyway in the ninth segment IX have a function different from that in the pregenital segments. The lateral processes, the arthrostyles,  $ar$ , of the styli muscle,  $sr$ , are immovably connected to the latter, insofar as there is nothing

like a joint between them; still, a certain movement is possible, due to the flexibility of the weakly sclerotized arthrostyles, *ar*, which is heightened by the irregular transverse depressions in the surfaces of the arthrostyles, (but which cannot be termed "false segmentation", since there appears to be no difference in the degree of sclerotization throughout the entire length of the arthrostyles). It should again be emphasized, that no muscles have been found connecting the arthrostylus, *ar*, to the styliiger plate, *sr*.

It remains to account for the median nervous system in the genital or ninth segment, *sIX*. In analogy with the condition in the pregenital segments, a branch from the median nerve should be given off in segment IX, and this branch should then innervate the dilator muscle(s) inserted caudo-laterally on sternum IX—if such muscles were present—and further, the intestinal wall and/or the tracheal stems in segment X as well as the genital duct in this segment. A thin nerve, of staining qualities similar to the preceding branches of the median nervous system, arises from the common postgenital nerve trunk just where it passes the caudal insertion of the interior ventro-longitudinal muscle, *j<sub>9</sub>*. This nerve divides itself immediately, and by far the largest part of it, *n<sub>x</sub>*, bending frontad and ventrad to end at the genital duct, near the gonopore; a second, thin branch, *m<sub>x</sub>*, is extended laterad and ends at the base of the dilator muscle, which appears to be inserted in the intersegmental membrane between the insertions of the exterior dorso-longitudinal muscle, *b<sub>9</sub>*, and that one of the interior ventro-longitudinal muscle, *i<sub>9</sub>*; a tiny branch (not drawn) is bent ventro-caudad towards the anus, its end being uncertain. (In the female a similar nerve originates slightly more frontad from the common postgenital nerve trunk, but is, as far as could be ascertained, unbranched and ends at the lateral insertion of the dilator muscle, *m<sub>x</sub>*.)

(6) *The muscles of the post-genital segments and their affinities*

Of the postgenital segments the tenth tergum, *tX*, has one pair of muscles, *a<sub>10</sub>*, which presumably, since it is inserted on the antecosta of the tenth tergum, is the interior dorso-longitudinal muscle. The large lateral

sclerite, *pXI*, has the insertions of the two large muscles moving the cerci, *cc*; the external one of these *g<sub>11</sub>*, is distally inserted on the medial side of basis cerci, *cb*. The cerci are, as shown from embryological evidence (Heymons, 1896 a, b) formed from the abdominal appendices of the eleventh segment. The muscles moving the cerci, *f<sub>11</sub>* and *g<sub>11</sub>*, should therefore be segmentally homologous with the intrinsic pleural muscles, *f* and *g* of the preceding segments, according to the above conditions. It is considered significant that their fibers exhibit a tendency to mutual crossing, but it should be added, that the structures have been so much distorted, as to make it impossible to ascertain which of them is homologous with the anterior, and which one with the posterior pleural muscle. The lateral sclerite or pleurite XI, *pXI*, is further connected to the wedge-shaped sclerite, *sXI*, by a small muscle, *h<sub>11</sub>*; further the wedge-shaped sclerite *sXI*, is connected to the sclerite, *tXI*, by a relatively strong muscle, *c<sub>11</sub>*. Since the dorsal sclerite, *tXI*, must be the eleventh tergum (epiproct), the wedge-shaped sclerite, *sXI*, connected to it by dorso-ventral muscle, *c<sub>11</sub>*, is assumed to be the eleventh sternite, (paraproct); and the dorso-ventral muscle, *c<sub>11</sub>*, segmentally homologous with the dorso-ventral muscles *c*, of the preceding segments, while the muscle, *h<sub>11</sub>*, is assumed to be segmentally homologous with the ventro-pleural muscles, *h*, of the preceding segments. (The musculature of the females is identical, only it is relatively weaker.)

It remains to decide on the homologies of the sclerites surrounding the anus, the latero-ventral sclerite, *pX*, and the ventral sclerite, *sX* (figs. 1 B, C & 2 B). The latero-ventral sclerite, *pX*, is internally covered by a sheet of transverse muscle fibers, *c<sub>10</sub>*, laterally inserted on the lateral edge of this sclerite, medially inserted along the lateral edge of the ventral sclerite, *sX*. At the frontal edge of the latero-ventral sclerite is further inserted the greater part of the internal ventro-longitudinal muscle, *i<sub>9</sub>*, from the ninth sternum, *sIX*; the remainder of this muscle is inserted along the frontal edge of the ventral sclerite, *sX*.

The frontal edge of the ventral sclerite, *sX*, is connected to the wedge-shaped sclerite on the eleventh sternum (paraproct), *sXI*, by a very thin muscle, *i<sub>10</sub>*. Further, a crescent-shaped muscle, *j<sub>10</sub>*, is connecting the frontal

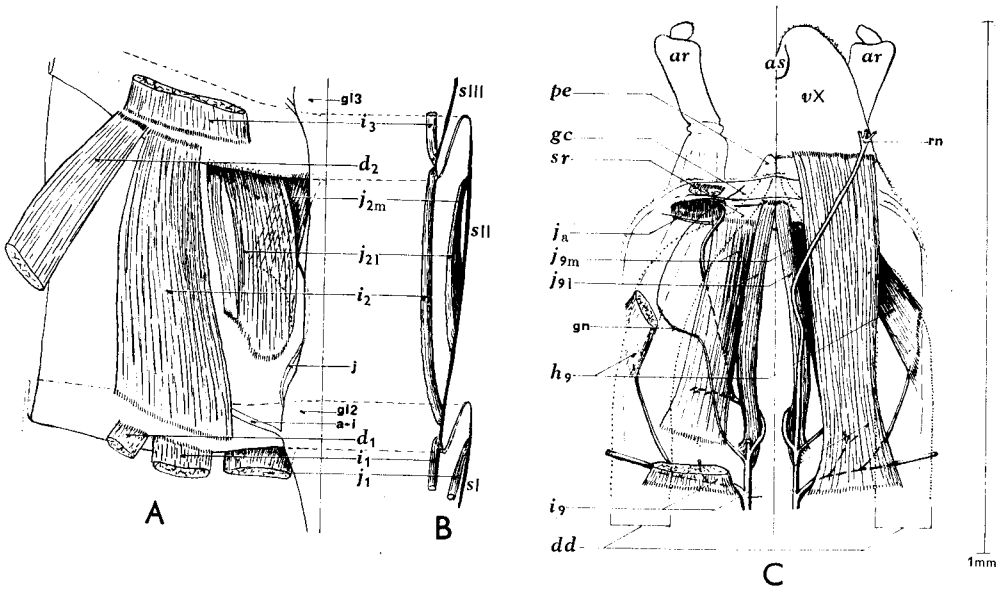


Fig. 6. *Centropitulum falcatum* Cras., the ventro-longitudinal muscles and their innervation;

A, the right half of the second sternum in dorsal view;

B, the same in optical longitudinal section;

C, the ninth sternum and the styliger plate of the male; in the right side of the figure in toto, in the left side the internal muscles are removed.

and the caudal edges of the ventral sclerite; it must be emphasized, that this muscle,  $j_{10}$ , even if close to the wall of the intestine and to a certain extent enveloped in connective tissues from the intestinal wall (and presumably acting as a sphincter ani), still is definitely inserted on the ventral sclerite,  $sX$ , and can be separated from the weak muscles of the intestinal wall. (Probably the antagonist of this muscle is  $i_{10}$ .) From the position of the ventral sclerite,  $sX$ , it appears that it is the tenth sternum, even if in a somewhat reduced condition. Assuming this, the muscles  $i_{10}$  and  $j_{10}$ , would be the internal and external ventro-longitudinal muscles respectively, homologous with the muscles  $i$  and  $j$  in the preceding segments, their insertions on the tenth sternum X similar to the insertions of the homologous muscles on their respective segments.

The latero-ventral sclerite,  $pX$ , might then, from its position, be the tenth pleurite, and in agreement with this assumption, it is covered by a dorso-ventral muscle,  $c_{10}$ , homologous with the dorso-ventral muscles,  $c$ , in the pre-

ceding segments, the only difference being that the dorsal insertion of the dorso-ventral muscle in the tenth segment has been translocated from the ventral edge of the tenth tergum,  $tX$ , to the dorsal edge of the tenth pleurite,  $pX$ , a translocation which might be explained by the presence of two strong cercal muscles,  $f_{11}$  and  $g_{11}$ .

(In the females the musculature is identical, except that it has not been possible to demonstrate the muscle  $i_{10}$ , the reason for which probably is to be found in the fact that the ventral sclerite, the tenth sternum,  $sX$ , here is in one piece, even if deeply incised caudally, and hence the muscle could effect no movement whatsoever.)

#### (7) Innervation in the post-genital segments

The postgenital nerve trunk continues from the terminal ganglion out into the cercus in an unbroken, almost straight line, giving off various branches along its course. Since no muscles are found in the cerci, the cercal

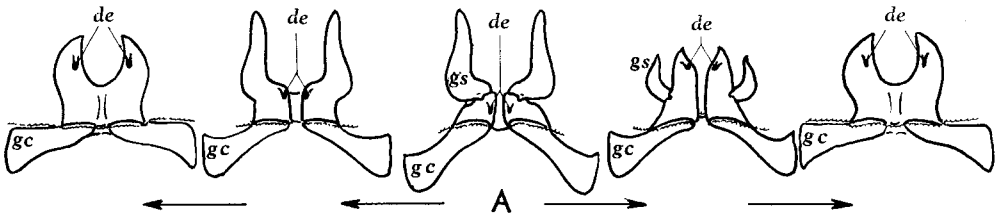


Fig. 7

Fig. 7. Two possible lines of development of the "penes" of usual Ephemeropteran type from the type found in *Povilla adusta*, viz. A-B-C and A-D-E.

nerve, cc, presumably consists of sensory fibres; nevertheless these seem to constitute more than half of the bulk of the postgenital nerve trunk. (In the female, with its short cerci, the cercal nerve, cc, is considerably smaller, but is still the thickest one of the branches.)

The first branch given off is, as mentioned, the branch of the median nerve system in segment IX, to segment X. Just caudal of this branch, a dorso-lateral branch is given off, which soon divides into a long, thin dorsad directed branch, a, for the dorso-longitudinal muscle,  $a_{10}$ , and into a forked branch, fg, for the cercal muscles,  $f_{11}$  and  $g_{11}$ . (While in the male the root of the branch a+ (f+g) appear to be one nerve, in the females, this root is clearly two nerves in a common envelope, and in some—2 out of 9—specimens, the branch, a, was given off from the main trunk near the root of the branch, m, to the dilator muscle inserted caudally on sternum IX.)

A small branch, c, originates on the ventral side of the main trunk near the root of the branch a+ (f+g), and dives immediately into the muscle  $c_{10}$ , where it ends; a very fine branch of it emerges from the dorsal surface of the muscle, but it has not been possible to ascertain, whether this branch innervates the muscle,  $i_{10}$ , even if it has direction towards this muscle.

Near the caudal edge of the muscle  $c_{10}$ , the nerve trunk divides; what appears to be the main trunk, cc, continues into the cercus, while a smaller, medial branch bends into the terminal segment, giving off branches right and left (naturally this last branch should morphologically be considered the main trunk).

The first branch given off is a thin mediad directed and very strongly staining branch, terminating in the intestinal wall, obviously a branch of the median nervous system, and the branch in segment X for segment XI. Just above the wedge-shaped sclerite, sternum XI (paraproct),  $s_{XI}$ , the nerve is trifurcated; the medial branch, j, ends in the external ventro-longitudinal muscle,  $j_{10}$ ; the lateral branch is immediately forked into the branches h and c, which innervate the muscles  $h_{11}$  and  $c_{11}$ ; the median branch of the tri-furcation continues into the terminal segment and the terminal filament; just as it passes the dorso-ventral muscle,  $c_{11}$  it gives off a tiny medio-ventral branch, which appear to have staining qualities similar to the preceding branches of the median nerve system, but due to its small size this is difficult to ascertain; it might be the median nerve branch in segment XI for segment XII. It ends, apparently, blind, near the ventral part of the cone-shaped sclerite,  $tl$ . (In the females there are only minor differences, viz. near the caudal edge on the sternum IX,  $s_{IX}$ , the main trunk is trifurcated and forming a small swelling; the dorso-lateral branch a+ (f+g) has been mentioned; the median branch, c+cc, continues to the cercus, cc, giving off the branch innervating the muscle  $c_{10}$ ; the ventro-medial branch continues to the terminal filament, giving off the branches  $m_x$ , h, c, h, and  $m_{XI}$  in this sequence.)

#### (8) Discussion of imagines

From the above description it might have appeared that *Povilla adusta* have several very primitive anatomical and morphological traits

as compared to other Ephemeroptera. The terminal ganglion is situated in segment VIII, as in a "generalized mayfly" (Brinck, 1956); a still more primitive trait is that the entire nerves to segment IX leave the terminal ganglion as one separate nerve stem contrary to the conditions in *Ephemer* and *Siphonurus* (vide: Brinck, 1956). Further, that a true gonostylus, *gs*, maybe what is usually termed "penis" (see further below) is connected to the gonocoxa, *gc*, by double condyles and two antagonistic muscles, *f<sub>9</sub>* and *g<sub>9</sub>*, with an innervation identical to the innervation of the pleural muscles. The gonopore, *de*, is situated on the gonocoxa, *gc*, and not on the gonostylus, *gs*. In most species the "penis" is continuous with the "penial bar", and carries the gonopore (Comp. e.g. Levy, 1948; Brinck, 1956; Grandi, 1960).

In a number of species the "penial bar" is moved by two muscles one to tergum and one to sternum; a fewer species have a single intrinsic penial muscle, but in only one species (*Rhithrogena semicolorata* Curt., Heptogeniidae) two intrinsic penial muscles have been described (Grandi, 1960); but from no species has been reported a true joint between the "penis" and the "penial bar" (or "penial basal arm").

It will have appeared to the reader, that the conception of the male genitalia and the post-genital segments as outlined above, is a somewhat singular one.

It is not an uncommon opinion among taxonomists that the "penial bar" and the "penis" belong to the ninth segment, but since this opinion is based on superficial assumptions rather than anatomical studies, much weight cannot be attached to it. The general opinion to-day among morphologists is, that the gonopore and the "penis" belong to segment X, the "penial bars" being the last remains of the tenth sternum, while the styliiger plate and the arthrotyli are the gonocoxae and gonostyli, belonging to the ninth segment, an opinion derived solely from anatomical studies of palaeartic species less primitive than *Povilla adusta*. The, so far greatest, insect morphologist also quoted the above interpretation with all kinds of reservations (Snodgrass, 1936: 74 ff.) reservations, which later, unfortunately, have largely been ignored or forgotten.

Ontogenetically the "penis" and the "penial bars" arise from the intersegmental area be-

tween sternum IX and sternum X; and from this point of view they could be derived from either segment. That the gonopore and the terminal parts of the genital ducts belong to segment X as earlier suggested (Snodgrass, 1936; Qadri, 1940; Levy, 1948; Brinck, 1956; but opposed by Smith, 1969: 1074) is confirmed in the present case of *P. adusta*, by the termination of the median nerve branch, *n*, at the outermost part of the genital duct (fig. 4).

The innervation of the musculature connected with the "penial bars" in *Povilla adusta* will, as originating from the nerve trunk which besides contains all the nerves to the ninth segment and as having the course of each nerve identical with the similar ones in the preceding segments, strongly suggest that the "penial bars" of this species belong to segment IX—unless one will suggest a highly complicated analogous development. It remains to consider, that the "penial bars" of other species are not homologous with the gonocoxae, *gc*, in *Povilla adusta*; but this is most improbable, since the latter species then by all characters except the genitalia should belong to the order Ephemeroptera. The homology of the "penes" of the other mayflies and of the true gonostyli, *gs*, of *Povilla adusta*, is less certain. Several lines of development from a type as found in *Povilla* to the one usually seen in mayflies may be envisaged (fig. 7). One line could be (fig. 7 A—B—C) an elongation and modification of the caudal end of the gonocoxa, *gc*, combined with simultaneous atrophy of the true gonostylus, *gs*; another line (fig. 7 A—D—E) might be the fixation of the true gonostylus, *gs*, on the gonocoxa, *gc*, followed by a distad translocation of the gonopore, *de*. It has not been possible to find any support for either of these theories.

The styliiger plate has earlier been considered homologous with the tenth sternum (Eaton, 1883–88; Morgan, 1913), but is now usually regarded as the gonocoxae of the ninth segment. If the gonocoxae, *gc*, of *Povilla* are homologous with the "penial bars" as assumed above, the styliiger plate, *sr*, of this species must, from the relative positions of the various parts, be homologous with the styliiger plate in other species. Accordingly, the segmentation of the arthrotylus, *ar*, (usually termed "stylus") as seen in many species must be a

secondary feature, a so-called "false segmentation". A few problems will then arise in connection with the musculature.

Regarding the ventro-longitudinal musculature a small difference is evident between *Povilla* and the "generalized mayfly" as described by Brinck (1956); the exterior ventro-longitudinal muscle, *j*, in *Povilla* seem to be homologous with the "medial outer sternal muscle, mostm", in the "generalized mayfly" (Brinck, 1956, fig. 2), and the lateral part of the interior ventro-longitudinal muscle, *il*, seem to correspond to the "inner sternal muscle, istm", in the "generalized mayfly" (Brinck, 1956, fig. 2); but the medial part of the interior ventro-longitudinal muscle, *im*, in *Povilla* does not seem to have any counterpart in the "generalized mayfly", no more than a counterpart of the "lateral outer sternal muscle, lostm", of the "generalized mayfly" (Brinck, 1956, fig. 2) is found in *Povilla*. However, from the course of the anterior segmental nerve, it might be assumed the "lateral outer sternal muscle" in the "generalized mayfly" is the counterpart of the medial part of the internal ventro-longitudinal muscle, *im*, in *Povilla*, its frontal insertion in the former having shifted dorsad; all of the ventro-longitudinal muscles in the "generalized mayfly" in Brinck's diagrammatical figure appear to be caudally inserted on antecosta of the following segment. The alternative seems to be, that the medial part of the ventro-longitudinal muscle, *im*, in *Povilla* has no counterpart in the "generalized mayfly" and that the "outer longitudinal sternal muscle" here is split in two parts, a medial and a lateral one. Two things speak in favour of the last assumption, viz. the course of the segmental nerves would still be as indicated in Brinck's figure (1956, fig. 2), and in various mayflies (fig. 6 A, B) the external ventro-longitudinal muscle is incompletely split into a lateral and a medial part, the caudal insertion of both parts being slightly in front of the antecosta of the following segment. There appears to be no doubt (see above) that *Povilla* has the styliger plate muscle, *j<sub>9</sub>* (figs. 3 and 4), segmentally homologous with the exterior ventro-longitudinal muscles, *j*, of the preceding segments; since the "medial outer sternal muscle, mostm" in Brinck's "generalized mayfly" never is present in segment IX, but on the other hand the styliger plate always is, (Brinck, 1956: 5) it might be justified to con-

sider the styliger muscle segmentally homologous with the "medial inner sternal muscles" in the "generalized mayfly".

In many mayflies a second muscle is present, connecting the styliger plate with the proximal part of the arthrostylus ("stylus", "genostyle"), but since no such muscle is present in *Povilla*, the above description gives no hint as to the origin of this muscle. A few other species in which this muscle is well developed have therefore been dissected with the innervation of the arthrostylus in mind (fig. 6 C); in all specimens examined, this nerve arose as a branch of the nerve innervating the styliger plate muscle, and passed ventrally and/or laterally of any other muscle or nerve, before it passed the arthrostylus muscle medially in order to enter it from the external side, exactly as is the case for the innervation of the styliger plate muscle. Hence it may be assumed that the arthrostylus muscle, *ja*, (as well as the "medial outer sternal muscles" in the preceding segments) is a derivative of the styliger muscle, *j<sub>9</sub>*. (Compare the innervation of the intrinsic pleural muscles, *f* and *g*, which are always by a separate nerve, while the anterior ventropleural muscles, *h*, are innervated from a nerve trunk in common with the greater part of the somatic muscles.)

The opinions as to the interpretation of the postgenital segments have varied in the course of time. From studies on the embryology of mayflies, it is evident that the abdomen consists of eleven complete and a twelfth incomplete segment, the telson (Heymons, 1896 a, b). The same condition was accepted for the imaginal abdomen (Snodgrass, 1931); but this view has later been abandoned (Snodgrass, 1936 ff.; Qadri, 1940; Levy, 1948; Brinck, 1956), mainly on the grounds that its acceptance meant that the anus would have moved frontad, splitting the tenth sternum into two parts. Instead of the earlier mentioned theory another one was promoted, according to which the eleventh sternum had extended frontad, while the tenth sternum remained only as the "penial bar" (which in many species must be considered hemisternites, since they are unconnected midventrally), and this seems to be the generally accepted view to-day.

The conditions in *Povilla adusta* seem difficult, if not impossible to explain according to this theory without resorting to absurdities.

Assuming the above theory to be correct,

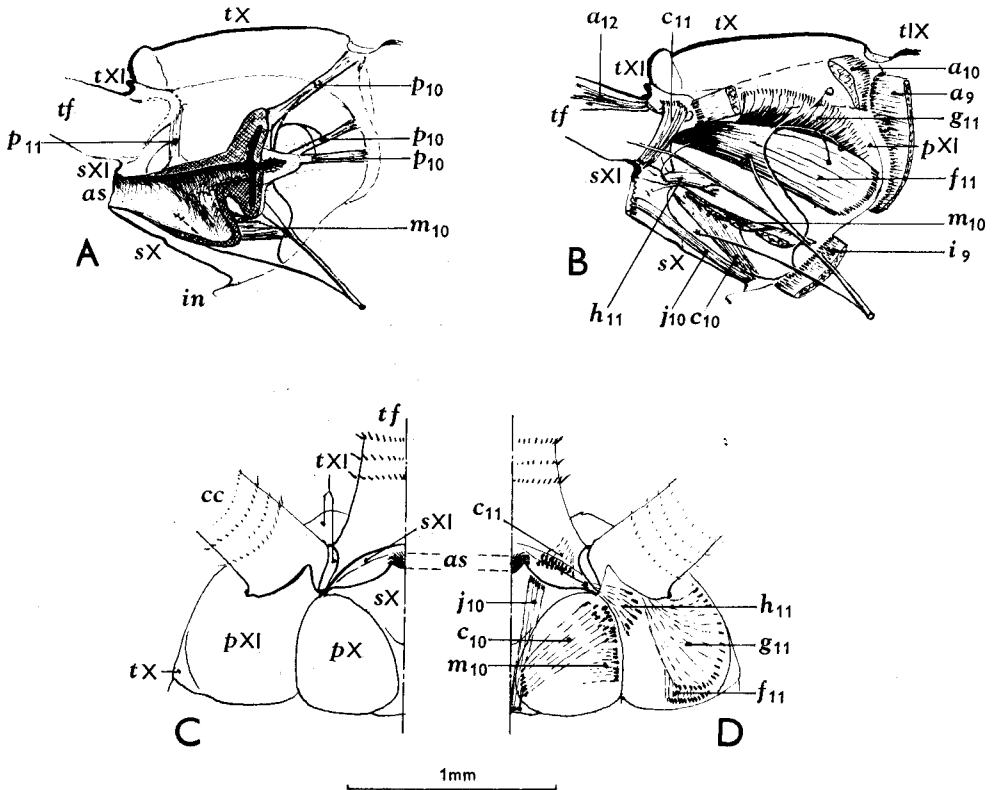


Fig. 8. *Povilla adusta* Navas, juv., the post-genital segments of a 17 mm long female nymph;

A, medio-longitudinal section showing end of intestine and anus in right median view;

B, same, but intestine removed in order to show the musculature;

C, ventral (external) view of left half showing sclerites;

D, ventral view of the right half showing the muscles as seen through the sclerites.

the ventro-lateral and the ventral sclerites,  $pX$  and  $sX$  respectively, surrounding the anus in *Povilla adusta* should be the eleventh sternum, the paraprocts. We therefore have, firstly, the unique condition of an entire, even if deeply incised, sternum XI, or the paraprocts being fused frontally in the female *Povilla adusta*. Secondly, the eleventh sternum, the paraprocts, have been sub-divided in a manner rather unusual for a mayfly sternum. Thirdly, there are the wedge-shaped sclerites,  $sXI$ , to consider; either they are supernumerary sclerites, with a musculature of their own, evolved as a substitute for the eliminated sternum X; or they are true sclerites of a true segment, in which case they must either be the post-anal segment XII, telson, which has been trans-

located ventrad, having retained a unique musculature,  $c_{11}$  to the eleventh tergum,  $i_{10}$  to the eleventh sternum and  $h_{11}$  to the pleural area of the eleventh segment; the other alternative being, that they are parts of sternum XI, in which case the eleventh segment will either have two dorso-ventral muscles,  $c_{10}$  and  $c_{11}$ , of which the former has shifted both of its insertions ventrad, turning into an intrasternal muscle, or, if the muscle,  $c_{10}$ , is considered the ventro-pleural muscle, two ventro-pleural muscles are present in the eleventh segment, viz.  $c_{10}$  and  $h_{11}$ ; further, if the wedge-shaped sclerites are considered parts of the eleventh sternum, both the ventro-longitudinal muscles,  $i_{10}$  and  $j_{10}$  have changed into intrasternal muscles, and it is difficult to see any



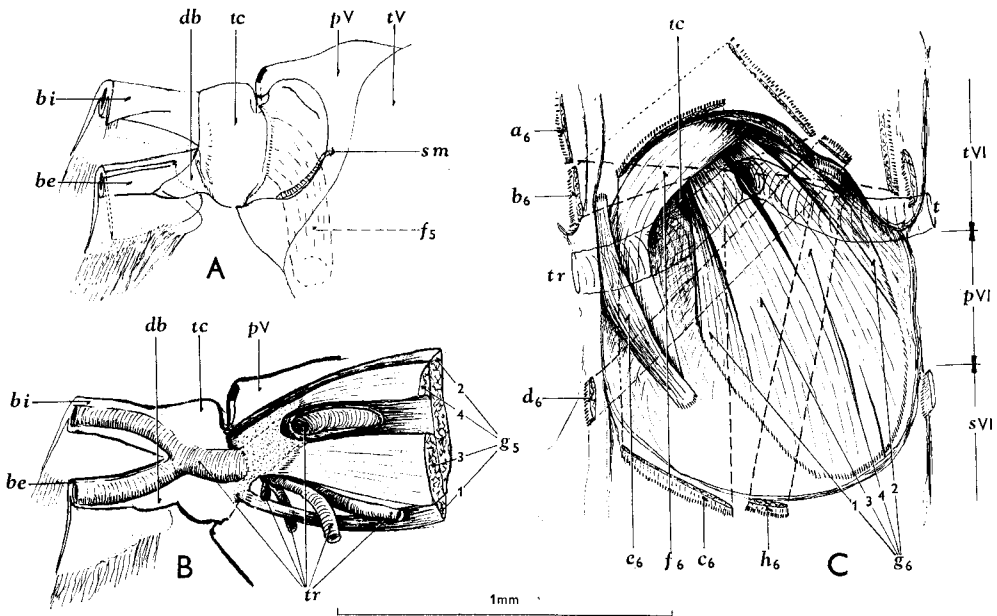


Fig. 9. *Povilla adusta* Navas, juv., abdominal gill of 17 mm long female nymph; A, base of the left gill of the fifth abdominal segment in dorso-caudal (external) view; B, same, in nearly vertical section, showing muscles and tracheal stems; C, left pleural area and base of gill of the sixth abdominal segment in medial (internal) view; the dorso-ventral muscles,  $c_6$ ,  $d_6$  and  $h_6$ , and the dorso-longitudinal muscles,  $a_6$  and  $b_6$  removed, the tracheae drawn transparent.

differences between their functions. The assumption of the theory will further imply that the "penial bars" in *P. adusta*, here called the gonocoxae,  $gc$ , are derivations from the tenth sternum, which again implies the assumption of true appendices attached to, and probably evolved from a sternum and innervated by nerves from the preceding segment. Since the above interpretation appear untenable to the writer, he is inclined to lean on the early opinion of Snodgrass (1931), and maintain the designations of the various parts as mentioned above (and as indicated by the symbols on the figures).

A theory as the above, however, cannot be exclusive to one species, but must comprise, at least all other species of the same order.

There seems to be only one serious objection to the interpretation of the various parts in other Ephemeroptera as has been applied here to *Povilla adusta*, viz. the splitting of the tenth sternum in two hemisternites caused by a frontad translocation of the anus. (If the

"penial bars" represent the tenth sternum, as assumed by the said theory, its adherents will still have to accept a tenth sternum split into two hemisternites, since, as mentioned, the two "penial bars" are separate in many species.) Further, if the gonopore has moved frontad from the tenth (primary) segment, then at least parts of the tenth sternum, viz. the antecosta X, must have split, and then it is difficult to see any principal objections to a similar—and probably subsequent—splitting of the same sternum, caused by an analogous frontad translocation of the anus. On the other hand the writer is aware of the necessity of abundantly substantiating a view, which is contrary to the opinion of so many distinguished scholars. For this reason the dissection of a 17 mm long female nymph (one of the last nymphal instars) is included (figs. 8, 9), but only the differences between this and the female imago shall be mentioned here.

## B. Anatomy of the abdomen in nymphs

### (1) *Terminal segments, X-XI*

The tenth tergum, *tX* (fig. 8), is superficially similar to the one in the imago, but is by a distinct seam separated from the lateral sclerite, *pXI*—here assumed to be the eleventh pleuron—and is fronto-laterally elongated into a sickle-shaped extension, which embraces the most of the frontal edge of the lateral sclerite, *pXI*, and on which the dorso-longitudinal muscle, *a<sub>9</sub>*, is inserted.

The anus, *as*, is situated behind the mid-ventral sclerite, *sX*, of the tenth abdominal segment, in the membranous area caudally of this sclerite and between the two small sclerites, *sXI*. The posterior part of the proctodeum is not anywhere connected to the mid-ventral sclerite, *sX*, but the narrow space between the two is filled with an adipose tissue of a type identical to the one found everywhere else in the abdomen.

The exterior ventro-longitudinal muscles, *j<sub>10</sub>*, are well developed, originating on the frontal edge of the midventral sclerite, *sX*, caudally diverging and inserted on the caudal edge of this sclerite, a movement which is facilitated by a slight transverse fold in the thin integument. The anatomy of the tenth segment of the female nymphs thus seem to confirm the interpretation of the morphology of the female imago, in which the midventral sclerite, *sX*, is regarded as the tenth sternum.

The latero-ventral sclerites, *pX*, are defined towards the adjoining sclerites, *sX* and *pXI*, by definite seams. The transverse muscle, *c<sub>10</sub>*, of this sclerite, which is very well developed in the imago, is only present as a somewhat oblique, irregular and apparently non-functional fibers in this nymph. (Too regular in fig. 8 D.)

The muscle, *h<sub>11</sub>*, from the lateral sclerite, *pXI*, to the paraproct, *sXI*, is considerably larger than in the imago, and so is the dorso-ventral muscle, *c<sub>11</sub>*, from the eleventh tergum, *tXI*, to the paraproct, *sXI*. An especially interesting feature are the two small dorso-lateral bundles of muscle fibers *a<sub>12</sub>*, originating latero-dorsally on the antecosta of the eleventh tergum—near the dorsal insertion of *c<sub>11</sub>*—and inserted latero-dorsally in the base of the terminal filament, *tf*. These two bundles of

fibers do not form regular muscles; even if they at their origin are united, they soon separate into single fibers and these are inserted singly over an indefinite area in the terminal filament. It has not been possible in the nymph to distinguish a separate basal part of the terminal filament, similar to its base, *tl*, in the imago.

### (2) *Pre-terminal segments, I-IX*

The preterminal segments of the female nymph (the first to ninth abdominal segments) are very similar to the corresponding segments in the adult female. Superficially the most striking difference between these segments in nymph and imago is the presence of lateral gill appendages on the first seven abdominal segments of the former; a pair of single, simple and apparently abortive ones on the first segment; a pair of single, plumose ones on the second, and a pair of double, plumose appendages of the third to the seventh segments.

While the powerful thoracal legs are used for crawling and clinging to the substratum, as well as, thanks to their elaborate systems of long setae, for "sifting" plankton, the abdominal gill appendages are the sole organs used for swimming (and the nymphs are actually, both active and able swimmers). But in spite of the abdominal gill appendages being active locomoter organs, no differences in principle exist between the musculature of the nymphs and the imagines. The differences found are only relative ones, the most conspicuous ones in the gill bearing segments being as follows (fig. 9):

The dorso-ventral muscle, *c*, is smaller and less conspicuously divided into two portions, if divided at all.

The dorso-pleural muscle, *e*, is considerably stronger in the nymph than in the imago, both longer and thicker, and somewhat spindle-shaped. Its innervation is easily traced as a relatively thick nerve originating from the nerve stem, *ab*, just basally of the root of the nerve for the exterior dorso-longitudinal muscle, *b*, and running caudad exteriorly along the ventral edge of this muscle.

As could be expected, the intrinsic pleural muscles, *f* and *g*, are, since inserted on the gill appendage, the ones which are most different from their homologues in the imago.

The posterior pleural muscle (M. abductor branchialis), *f*, is considerably longer and stronger than in the imago. It originates caudally on the pleuron, just dorsally of the dorso-pleural muscle, *e*, and in medial view the origin is covered by this muscle; from its origin it goes dorsad and then bends frontad around the big tracheal stem. It is inserted on the dorsal edge of the base of the gill appendage.

The anterior pleural muscle, *g*, (M. abductor branchialis), is also considerably bigger than in the imago, even if it here appeared to be one of the strongest muscles. Further, while its origin, which occupies most of the ventral part of the pleura, is entire, the muscle is distally split up into four bundles, each having its own insertion, directly or indirectly, on the ventral part of the gill appendage. (These four bundles of the anterior pleural muscle, *g*, may be identical or homologous with the four muscles, which have—in general—been regarded as separate muscles connected to the base of the gill appendage (vide i. a. Dürken, 1907, taf. XXVI; Snodgrass, 1935, 1 b, 2 b, 3 b and 4 b in fig. 150). It should, however, be emphasized, that these four bundles (1, 2, 3, 4) are here considered parts of one and the same muscle, since 1.) they all four originate from one undivided area; 2.) they are innervated from one nerve which splits up inside the muscle in a large number of subequal branches; 3.) the splitting into four bundles is irregular, fibers passing from one bundle to the next, and 4.) a contraction of either bundle will have the same effect, viz. an adaxial swing of the gill appendage (which is the forward driving strike while swimming). The splitting of the anterior pleural muscle, *g*, into four bundles appears to be in order to make room for the large tracheal stems, which pass between any two bundles (fig. 9 B). Of the four bundles of the anterior pleural muscle, *g*, the ventral bundle (2) is the largest and inserted directly on the ventral edge of the base of the gill appendage. The other three bundles (1, 3, 4) are inserted in the tough connective tissue surrounding the tracheal stem to the gill appendage and firmly fastened to the ventral internal surface of the base of the gill appendage.

It is interesting to note, that a relatively thick trachea ends in a thickened spot, *sm*, on the dorso-frontal cuticle of the somewhat

semiglobular pleuron; this spot, *sm*, both from its position, and particularly as the blind end of an else unmotivated trachea, must be assumed to be a closed spiracle, thus indicating, that primitively also the juvenile Ephemeroptera were air-breathing terrestrial animals, and the present adaption to life in water is a secondary one.

The gill appendage itself consists of a basal segment, *tc*, from which the exterior (or posterior) branchia originates, and a smaller distal segment, *db*, from which the exterior (or posterior) branchia originates. The basal segment, *tc*, is hinged to the pleural sclerite by a very strong condyle on the latter, marked by a black spot on the frontal side of socket for the branchial appendage, and another, far weaker condyle on the caudal side of the basal segment. The axis of the movement of the branchial appendage pass through its basal segment, somewhat dorsally of its middle and just dorsally of the tracheal stem, and is more or less slanting anteriorly.

From a comparison between the pleural areas of the nymph and the imago it appears that the vortex, *wl*, in the imago is the remain of the now nearly obliterated gill appendage, and since the intrinsic pleural muscles, *f* and *c*, appear to be metamericly homologous with the muscles *f*<sub>9</sub> and *g*<sub>9</sub> of the process *gs* of the male, the gonostylus, this must itself be homologous with at least some part of the gill appendages of the preceding segments. It seems to be a generally accepted view, that the abdominal gill appendages of Ephemeroptera are true segmental appendages (or legs: Snodgrass, 1935; Imms, 1957); further the branchia themselves, *bi* & *be*, have been regarded as styli, homologous with telepodites (Snodgrass, 1935). However, the writer is more inclined to consider the two branchiae, *bi* & *be*, as exites, the only part of the gill appendage homologous with the telopodite of the generalized insect leg being the two small basal segments, *tc* & *db*. The cuticle of these segments is similar in texture to the cuticle on the body, but quite different from the integument of the branchiae, and a distinct seam is visible between them and the branchiae; the proximal one of the two basal segments, *tc*, might possibly be a basipodite, or a first (or a first and second) trochanter, while the distal of these segments might be one or more of the following segments, in the latter case all of them being

completely fused and reduced. Since, the two basal segments, *tc* & *db*, are completely fused with no trace of a true seam, only a shallow depression separating them and no muscles have been found connected to either of them; it has not been possible to offer more than a mere suggestion as to their identity.

It might further be noted, that the exterior ventro-longitudinal muscle, *j*, is present in all segments, even if it is smaller than in the imago, and that it is innervated by a separate nerve as in the imago; the nerve innervating the intrinsic pleural muscles, *f* and *g*, is branched off from the main stem of the general segmental nerve at the very base of this, and it actually runs caudad along the surface of the ganglion for a short distance, before it bends laterad.

All things considered it must be concluded, that the anatomy of the nymph confirms the interpretation of the structures in the imago.

#### IV Conclusions

The interpretation of the various structures in *Povilla adusta* will, when extended to comprise all Ephemeroptera, introduce an intersexual and metameric consistency in the designations of muscles and nerves, which includes the genital and post-genital segments. The secondary modifications will in this case only amount to disappearance and reduplication of muscles—in the latter case, muscles with parallel fibers and common innervation—while the nerve paths are identical in males and females. Otherwise the traits, which must be considered secondary modifications would be very remarkable indeed, viz. a nerve path for the appendages of the tenth segment in males, which are identical with the nerve path for the ninth pleural area in the females.

Further the present interpretation implies, that the reduction of the abdominal segment in Ephemeroptera has taken place in regular succession from behind, in accordance with what seems to be the rule in other arthropods (Trilobita, Crustacea etc.).

An objection to the present views may arise from the fact, that the male gonopores are considered to be situated on the gonocoxae. It has been suggested, that primitively the gonopores were situated on the leg bases (Gustafson, 1950), and thus a, usually latent, gene

for this may be present in Arthropoda (for further discussion vide: Sharov, 1966; Smith, 1969). Whether this view is accepted or not, it is indisputable, that gonopores situated on the coxae are known from several other, only remotely related groups of arthropods (i.e. Pycnogonida, Crustacea, Diplopoda). If the objection should be based on the sheer magnitude of difference between the male copulatory organs of Ephemeroptera and Neoptera, it should be kept in mind, that the only other recent order of Palaeoptera, viz. Odonata, in this respect is still more diverging.

As final conclusions should shortly be lined out:

(i) that the male appendices, usually termed "penes" are evolved from the ninth segment as true gonostyli and are—at least in parts—homologous with, at least parts of the abdominal gill appendices, which again are generally considered telopodites (or styli) of true abdominal appendages.

(ii) that the "penial basal arms" or "penial bars" are true gonocoxae, homologous with the pleural plates carrying the gill appendages, which again are generally considered true coxae, or probably more correctly: coxopodites, of abdominal appendages.

(iii) that the two muscles connecting the gonostyli to the gonocoxae are metamERICALLY homologous with the two intrinsic pleural muscles of the pregenital segments in imagines, which again are homologous with the two muscles moving the gills (in the widest sense of the word) of the nymphs. In all cases these two muscles are mutually skew (i.e. crossing in different planes), and they are innervated by a common nerve trunk, which originates from the main segmental nerve, just proximally of the branch(es) for the internal ventro-longitudinal muscle(s), and which passes ventrally of this/these muscle(s).

(iv) that the styliiger plate, often termed "gonocoxae", is a derivative of the ninth venter, and its musculature is metamERICALLY homologous with the external ventro-longitudinal muscles, which is differing from all the other muscles by being innervated by a nerve originating directly from the segmental ganglion, the origin being situated more ventrally on the ganglion, than the common segmental nerve stem.

(v) that the arthrostyli, often termed "gonostyli" or "styli" are secondary modifications of

the stylicher plate, pertaining to the ninth venter, and their muscles, if any, are derivatives from the muscles of the stylicher plate.

(vi) that there has been found no sign of any splitting of the male appendages, viz. the appendices of the gonocoxae, the gonostyli, into a lateral and a mesal part, so as to form additional "gonapophyses". Further,

(vii) that the presence of an abortative, closed spiracle on the gill bases of the nymph, indicates, that Ephemeroptera also in the immature stages, originally were air-breathing and terrestrial, and that the present adaptations for aquatic life are secondary modifications.

*Explanation of letters and symbols used in the figures.*

Letters in italic:

Single letters followed by a roman numeral:

<i>p</i> pleura	<i>t</i> tergum
<i>s</i> sternum	<i>v</i> venter

while the numeral refer to the relevant segment.

Single letters, alone or with arabic indices, signify muscles; see the relevant text.

Double letters signify morphological or anatomical structures as indicated below:

<i>ac</i> acrotergite	<i>gs</i> gonostylus
<i>ar</i> arthrostylus	<i>in</i> intestine
<i>as</i> anus	<i>pe</i> penis
<i>bc</i> basis cerci	<i>pl</i> pleura in general
<i>be</i> branchia externa	<i>sm</i> spiracle mark
<i>bi</i> branchia interna	<i>so</i> spiracle, open
<i>cb</i> cercal base	<i>sr</i> stylicher plate
<i>cc</i> cercus	<i>tc</i> proximal branchial base
<i>db</i> distal branchial base	<i>tf</i> terminal filament
<i>dd</i> all genital ducts	<i>tl</i> terminal dorsal sclerite
<i>de</i> gonopore	<i>tr</i> trachea
<i>gc</i> gonocoxa	<i>wl</i> vortex in pleural fold

Letters in bold face:

Letters in bold face signify parts of the nervous system, viz. ganglions marked **gl**, and nerves, which are marked with the same letter(s) as the structure they innervate; an additional number or index, in roman or arabic numerals, indicate the relevant abdominal segment.

Erratum: fig. 5 B uppermost, for tXI read tIX.

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Manuscript received June 18, 1970.