EVIDENCE OF THE TAXONOMIC RELATIONS OF THE TRICHOPTERA

BASED ON A STUDY OF THE SKELETAL MUSCULATURE

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PREFACE

It is scarcely necessary to emphasize the importance of correct identification of species and anatomical parts in biological work on insects. Such identification, however, is still a difficult matter for the biologist who has not had a great deal of experience or training in morphology or taxonomy. This is in part due to the fact that taxonomists have failed to modify their classification schemes as new and more acceptable ideas on phylogeny appear. The trivial characters used in the keys involve considerable error even in the hands of specialists; but the task of eliminating the use of such characters requires more understanding than a mere knowledge of the external appearance of the animal. Those who no longer consider it a misdemeanor in taxonomy to look inside of a bug find new and valuable support for their opinions. Those who use additional evidence from embryology, paleontology, and physiology enjoy still more advantage over those who do not. The burden of rendering prompt identifications, however, rests so heavily upon the taxonomist that he has little time for investigation in these fields. The physiologist, too, has little time for original work on the identification of organs, tissues, or cells with which he works. It is the business of the morphologist to interpret the anatomical details which are not readily understandable. The vast number of such details, however, makes it difficult

to keep track of them except as they may be classified in a unified
system. Immediate need of opinion necessitated the improvision
of a system even though some of the facts were wanting. With each
contribution in morphology, then, the system may be substantiated
or revised. Work on special groups thus has a two-fold purpose;
first, to prepare the way for a more reliable and workable
classification of the group itself; and second, to verify (or
modify) our conception of the hexapod makeup with specific facts
which the general morphologist may have overlooked or had not
time to investigate. There is need of such work on several groups
of insects, particularly the Plecoptera, Mecoptera, and Trichoptera,
for which orders there is no published account of the musculature.
It is in recognition of this need that the present studies have
been undertaken. It is hoped that the facts and conclusions herein
presented will not only lead to a sound taxonomic treatment of the
order, but will also aid in the solving of problems concerning
related orders.

INTRODUCTION

Our present conception of the skeletal mechanism of insects
is largely due to comparatively recent studies based upon relation-
ships, particularly those concerning the muscles. In the English
language the various publications of Snodgrass are the most
acceptable; in the German, those of Weber. In their studies the
acceptable ideas of other workers were brought together and
clarified and the new information resulting from original work
sufficiently filled in the gaps to allow postulation of the
origin and relationships of the various sclerites and muscles.
To expect the occurrence of a species which exhibits these
relationships in the primitive condition throughout its entire
make-up, however, would be to presume one of three improbabilities:
(1) that there exists an environment exactly like that in which
the ancestral form lived;(2) that evolution has not occurred in
that species; or(3) that there has been no correlation between
environment and evolution. But whether environmental change in
some way effects structural change, or whether a modification in
structure induces the organism to seek a new environment the
reality of adaptation is nevertheless generally accepted. In a
group of animals wherein the different body regions are not all
suited to the same purpose it is therefore not supprizing to find
in a species which shows primitive conditions in one of these

regions some rather striking specializations in others. The practice of formulating hypothetical schemes when none of the known forms exhibits a plan of structure from which the others may be derived thus has its merits.

To denounce such a practice in a storm of criticsm seems unfair unless one can offer a more logical interpretation of the conditions involved, or at least give evidence of having thoroughly reviewed the argument advanced. In the following pages, therefore, some references will be made to such hypothetical schemes as well as to species in other orders, particularly the stonefly Perla, which, in the opinion of the writer, represents the nearest approach to the hypothetical pterygote.

In the selection of representative material the writer is strictly in sympathy with the practice of using the most primitive species, but in the light of our present knowledge the search for a trichopteron representing an approach to the ancestral form of the order seems fruitless. Comstock has cited Rhyacophila as a primitive form on the basis of wing venation, but Krafka contends that campodeoid larvae (of which the larva of this genus is an example) are not primitive. Furthermore the male and female genital segments show considerable specialization. But while Krafka admits independence of evolutionary trends between larvae and adults, he goes on to select the Leptoceridae as the stem form of the order in spite of obvious specialization in the adults.

Argument might be advanced for considering the limnephilids

the most generalized on the basis that only in this family

is the female genital opening located before the ninth abdominal

sternum; but here again we deal with a group rather specialized

in other respects, particularly in regard to the male genitalia

and the entire lack of mandibles in the adult. For each unit

discussed in the following pages, therefore, that species will be

cited which the writer considers most generalized in that unit

Many of the illustrations, however, will necessarily be based

upon other species because of convenience regarding availability

and ease of manipulation. The dissections were made under a

binoccular with specimens preserved in 80% alcohol. The figures

were made with the aid of a camera-lucida.

THE CADDISFLY HEAD

In a previous dissertation on the morphology of the head of
Platyphylax designatus conclusions were drawn on the basis of
muscle relationships. Further investigation based upon comparative
studies has added little to modify those conclusions except in
minor respects. The basal part of the labium in the larva, for
example, shows a high degree of specialization in the Limnephilidae
which is not characteristic of the entire order. In Leptoceridae
and Brachycentrinae the conditions of the labium are more primitive.
An account of relationships in Brachycentrus incanus is here given
in support of the hypothesis prviously offered to explain the
origin of the specialized condition.

Larval Head of Brachycentrus

Except in the ventero-posterior region the head of
Brachycentrus is much like that of Platyphylax designatus.
During ecdysis the head capsule separates along the coronal and
frontal sutures into three principal areas: the frons-clypeus
and the parietals. The labrum remains attached to the frons-
clypeus, while the mandibles and the labio-maxillary complex
become free.

The frons-clypeus is facial in position, lying between the
frontal sutures. An epistomal suture is lacking and there is no

differentiation of frons and clypeus except internally: the
buccal muscles (stomodeal muscles which lie anterior to the
frontal ganglion) arise anterior to the tentorial arms, while
the pharyngeal muscles and the retractors of the labrum arise
near the posterior end of the plate and decidedly behind the
tentorial arms. Externally these regions usually are indicated
by a medial swerving of the frontal sutures*, at which points
the anterior tentorial pits are located.

The parietals, which together constitute the larger part of
the head capsule, bear the eyes and antennae**, but are other-
wise undifferentiated except along the ventral and posterior
borders where they are strengthened by internal ridges. The
grooves marking the origin of these ridges usually are obliterated,
but in Brachycentrus incanus Hagen they are still evident where
they mark off the subgena, the hypostoma, and the postocciput.
The latter is not always distinct throughout its entire length
but is sometimes largely inflected with the postoccipital ridge.

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* Except in Leptoceridae.

** Rhyacophilinae, Philopotamidae, Polycentropidae, and Hydropsych-
idae are not known to possess antennae in the larval stage.

The labrum usually is ~~quite~~ generalized, but occasionally
is very broad and weakly sclerotized (chimarrha). It hinges
to the frons-clypeus by means of a flexible membrane which may
be somewhat hardened to form a preclypeus (Rhyacophila) but the
latter has no muscles attached to it.

The muscles in the head of Brachycentrus are essentially
the same as those of Platyphylax and need not be discussed here.

Larval Thorax

A typical relationship between a primitive thoraeis leg
and its segment is well shown in the caddisworm. The segmental
dorsum and venter vary considerably in degree of sclerotization,
but there is always a simple pleuron associated with the basal
part of the leg. The pleural suture is a prominent groove
dividing the plate into an episternum (anterior) and an
epimeron. The pleural coxal process at its lower end is the
sole point of articulation between the free part of the leg and
the body. The most important division of the leg is the
dicondylic joint between coxa and trochanter as Snodgrass has
pointed out. It marks the differentiation of the original limb
base (which has further differentiated into coxa and pleuron) and
the telopodite (which has differentiated into trochanter, femur,
tibia, tarsus, and pretarsus). It allows movement of the
telopodite in a somewhat dorso-ventral plane. The other
dicondylic joint of the leg is that with which the tibia hinges
to the femur. On it the tibia may swing toward or away from the
axis of the body, movements which are termed respectively
adduction and abduction. It is obviously the most important
joint of the telopodite. The tarsus and pretarsus hinge respective-
ly to the tibia and the tarsus by means of monocondylic joints,
which permit them to swing toward or away from the axis of the body.

The remaining joint of the telopodite occurs between the trochanter

and the femur. It is unique in that it permits the femur to swing

forward and back, which movements are spoken of as production and

reduction. An apparent division of the trochanter is sometimes

rather prominent, especially in the Leptoceridae. The distal part

of the trochanter of the metathoracic leg has frequently been

referred to as a part of the femur, probably because it is very

long and the femur is relatively short. Between it and the femur,

however, is a typical trochantero-femoral joint, the musculature

of which can leave no doubt regarding its identity. The

morphological significance of the line which superficially divides

the trochanter is not well understood. Snodgrass has described

the double condition of the trochanter in Odonata, the muscles of

which indicate that the two parts possibly represent two originally

separate trochanteral segments. In the prothoracic leg of larval

Trichoptera, however, some of the fibers of the reductor muscle

of the femur may arise in either part, a circumstance which throws

doubt upon a similar origin for the condition in this order. In

some cases the possibility that it represents a weakened place

in the cuticula to facilitate breaking off the leg in case of need

is suggested. In Rhyacophila fuscula there is a perceptible ridge

which one might regard as a basicostal strenghening of the rim,

but in all of the other larvae examined such a ridge is lacking.

The musculature of the telopodite closely approximates the

hypothetical scheme which Snodgrass describes in his work on the
thoracic mechanism of a grasshopper. There are no muscles
within the tarsus, but running through it to the basal rim of
the pretarsus if a tendon upon which are inserted muscles having
origin in the femur and the tibia (Pl. IV D, Ad Ap). An apodeme
located ventrally on the basal rim of the tarsus bears the
insertion of a group of muscle fibers (Pl. IV, 30) which arise
dorsally on the anterior and posterior walls of the tibia.
Muscular contraction, then, can cause only adduction of the tarsus
and pretarsus; abduction is probably due to elasticity in the
joint. On the basal rim of the tibia, however, two muscles are
inserted which oppose each other in function. The abductor,
(Pl. IV, 31), serving to swing the tibia outward and away from
the longitudinal axis of the body, takes origin on the dorsal
wall of the femur and inserts on a process between the two
condyles of the joint. The adductor consists of two branches, one
(Pl. IV, 32) arising on the anterior wall of the trochanter, the
other (Pl. IV, 33) arising on the dorsal wall of the femur. Both
insert on an apodeme located ventrally on the basal rim of the
tibia. Between the femur and trochanter there is but a single
muscle, (Pl. IV, 34) the reductor muscle of the femur. In the
prothoracic trochanter some of its fibers arise in the first
part of the trochanter while the remaining fibers arise in the
second; but in the meso and metathoracic legs they all arise in

the second. As previously indicated, the movements of the entire
telopodite are levation and depression. The muscles inserting on
the basal rim of the trochanter are therefore spoken of as the
levator and the depressor of the telopodite, (Pl. IV, C, 35 & 36).
The former of these (Pl. IV, 35) arises anteriorly on the outer
wall of the coxa and inserts dorsally between the two condyles.
The depressor muscle (Pl. IV, 36) consists of two main branches,
one arising on the sternum, and the other on the mesal wall of
the coxa; both insert on the apodeme of the ventral rim of the
trochanter.

The musculature of the basal part of the appendage is
represented by the coxal muscles and the pleuro-tergal muscles.
A two branched promotor of the coxa (Pl. IV, 37) arises on the
tergum and inserts in the membranous area at the anterior basal
rim of the coxa. Laterally a muscle (Pl. IV, 38) arising on the
dorsal margin of the episternum inserts on the base of the coxa
just in front of the pleural-coxal process. In a few limnephilids
(e.g., Stenophylax limbatus Banks) there is a corresponding muscle
from the posterior basal rim of the coxa to the dorsal margin of
the epimeron, but in the majority of caddisworms it is lacking.
The tergal remotor arises posteriorly on the tergum and inserts
on the posterior basal rim of the coxa. Two coxo-sternal muscles
are present. One of these (Pl. 3 fig. B, 40) arises on a
sclerotized area near the intersegmental line between the mesothorax

and metathorax and inserts on the outer rim of the coxa behind
the pleuralcoxal process. The other (Pl. III, 41) has its origin
near the anterior margin of the sternum and inserts on the anterior
rim of the coxa. There are two groups of pleuro-tergal muscles.
One of these (Pl. III, 42) consists of two bands of fibers inserted
on the margin of the pleuron at the dorsal end of the pleural
ridge. One of the bands extends forward, (Pl. III, 42a), the other
dorsally (Pl. III, 42b) to origins in the tergum. The other group
consists of small bands located a slight distance interior to the
dorsal group. A pleuro-sternal muscle (Pl. III, 43) arises on a
'scleratized spot along with the posterior, coxo-sternal muscle
(Pl, III, 40) and inserts on the pleural ridge.

Many of the muscles of the body of the segment assume such
diagonal and criss-cross positions that they are not easily
identified with those of the abdomen or with those of the adult
thorax (Pl. 3, fig. B). Three principal groups of them,
however, may be distinguished. The dorsal group (Pl.III, 44)
probably represents the internal and external dorsals and the
paratergal muscle. The ventral group (Pl. III, 45) occurs
in much the same manner as those of the abdomen, consisting of
internal and external bands of fibers. The lateral group
(Pl. III 46) consists of many bands radiating from a small
sclerotized area near the intersegmental line on the lateral
margin of the venter. Some of them evidently correspond to the

internal lateral muscles of the abdomen, but it is doubtful that they all do.

In the prothorax (Pl. I, fig. D) the change in position of some of the muscles has been carried on still further, and some of the lateral group seem to have disappeared altogether. The anterior end of a band which appears to be the lateral internal dorsal muscle (Pl. III, 47) has shifted to a ventral position, inserting with the ventral internal muscle on the neck membrane near the tentorial arm. The dorsal muscles (Pl. III, 48,49,50) insert on the neck membrane bordering the postocciput along with two other muscles of uncertain identity. The latter (Pl. III, 51 & 52) arise near the anterior ventral angle of the pleuron. That they are homologues of muscles which in the adult arise on the cervical sclerits is uncertain, but the appearance and function are very similar. Muscle (Pl. III, 53) inserting the neck membrane near the postocciput and arising on the intersegments line between the pro- and mesothorax appears to have been derived from the ventral longitudinal group.

Adult Thorax

External features of the adult thorax have been considered
in a general way in various publications for comparison with
representatives of other orders. Some of the parts have not been
examined thoroughly; some have been the subject of controversy;
none of them has been studied with reference to muscle attach-
ments. In considering the muscular relationships, then, it is
necessary to begin with a review of the skeletal features. The
differences existing among representatives of the various families
are fundamentally so minor that the selection of a species for
an example is largely a matter of preference. A limnephilid
is therefore chosen because its large size redners dissection
less difficult.

Prothorax. Our knowledge concerning the prothorax and the
nature of the insect neck is based largely upon comparative external
anatomy and on the musculature of Orthoptera, Hemiptera, and
Coleoptera --- orders in which these regions are not particularly
generalized. A comparative study of the musculature of the
prothorax and neck region is still needed to verify the conclus-
ions of authors relative to these regions, or to modify them
according to whatever new facts may be disclosed. For this
reason the present discussion of the trichopterous prothorax is
supplemented with comparative notes on the Plecoptera, Neuroptera,

and Mecoptera.

In the larger caddisflies, as exemplified in Stenophylax and Platyphylax, the pronotum is a simple plate slightly overlapping each pleuron by means of a membranous fold (Pl. III, A). The pleuron exhibits a prominent pleural groove, (Pls) but the episternum (Epm) and particularly the epimeron (Epm) differentiated by it are neither well sclerotized nor well differentiated from the membranous areas bordering them. The sternum (Pl. II D) is a narrow plate exhibiting internally a low vertical longitudinal plate and two long apodemes directed toward the upper margins of the pleura with which they fuse. On each side of the neck occurs a cervical plate (Pl. II A, cv) which articulates anteriorly with a condyle on the postocciput of the head, and posteriorly with the episternum; it fuses ventrally with the cervical plate of the opposite side. Weber regards the cervical plates as remnants of the labial sternum which correspond to the "post-sternites" of thoracic segments, but the arguments advanced in favor of this view are not very convincing.

The prothoracic leg of the adult (Pl. II B) exhibits nothing of unusual interest. The coxa hinges to the pleural coxal process (CxP) at the lower end of the pleural suture, but otherwise it is bordered by a membranous area which allows it considerable variety of movement. The remainder of the joints and leg segments are similar to those of other pterygote insects. The series

of spines and particularly the spurs or <u>calcaria</u> (Spr) of the

tibiae vary sufficiently among the taxonomic groups to be used

as identification characters. The difficulty of naming the

prothoracic muscles is in part due to uncertainty regarding

their original identity, in part to uncertainty regarding their

individual functions. Future studies may be able to establish

their identity on the basis of comparative anatomy or on that

of innervation. At present it seems most advisable to describe

them according to location and attachments. (Pl. III, II).

The muscles which appear to belong to the dorsal longitudinal

group are three in number:

55. A horizontal muscle from the postocciput to the first

phragma.

56. An oblique muscle from the postocciput to the tergum.

57. An oblique muscle from the phragma to the tergum.

The ventral group consists of four principal muscles:

58. A horizontal muscle from the base of the posterior

tentorial arm to the base of the furcal apodeme.

59. A horizontal muscle from the ventral end of the cervical

plate to the base of the furcal apodeme.

60. An oblique muscle from the postocciput to the base of the

furcal apodeme .

78. Furca to spina.

Three muscles of uncertain origin are attached to the cervical

plate:

61. An oblique muscle to the phragma (This muscle appears to correspond with a dorsal longitudinal muscle of the larva in which it has apparently shifted its anterior attachment ventrally; it is evidently lacking in insects having incomplete metamorphosis.)

62. A tergal muscle of the cervical plate extends from the anterior end of the plate to its attachment near the lateral border of the tergum.

63. A head muscle of the cervical plate extends obliquely from the ventral end of the plate to its attachment on the postocciput.

Muscles obviously derived from the original limb region consist of the leg muscles and the pleurotergal muscles. There are three of the latter:

64. An anterior pleuro-tergal muscle extending from the dorsal margin of the pleuron to its attachment somewhat anteriorly and medially on the tergum. (Pl. III, F).

65. A posterior pleurotergal muscle extending laterally and posteriorly from the dorsal margin of the pleuron to the latero-posterior margin of the tergum (a region which overlaps the pleuron).

66. Anterior margin to the lateral margin of the tergum.

The leg muscles which arise in the prothorax consist of

coxo-pleural, coxo-sternal, and coxo tergal muscles, and a

branch of the depressor of the telopodite. The first group

(Pl. III, 6 a ^{a} ^{b} b) consis s of two muscles inserting on the

basal rim of the coxa in front of the pleural-coxal process

and arising on the median vertical plate of the sternum, **the**

other (Pl. III,69) inserting on the posterior basal rim of

the coxa and arising on the first spina. The coxo-tergal

muscle (Pl. III,70) inserts on the posterior basal rim of the

coxa, and arises in the posterior region of the ter um. The

depressor muscle of the telopodite consists of three branches

inserting on the apodeme located on the medial basal rim of

the trochanter: one (Pl. III, 71) arises on the epimeron near

the upper margin, another (Pl. III, 72) arises on the furcal

apodeme, and the third arises on the lateral wall of the coxa.

Two muscles not accounted for in the above groups are:

(Pl. III, 73) a muscle from the tentorium to the tergum; and

(Pl. III, 74) an oblique intersegmental muscle (Pl. III, 75)

from the base of the furcal apodeme to the mesothoracic

epi sternum. The latter muscle is obviously repeated in the

two succeeding thoracic segments.

For convenience in comparison the muscles in the stonefly

Perla are numbered as they are in the caddisfly. Several

outstanding differences occur, however, which make it inadvisable

to attempt generalizations without extensive comparative

studies with other groups. These differences may be sum-marized as follows:

1. The coxo-tergal muscle (Pl.III,A, 37) is present in Plecoptera, but lacking in the Trichoptera.

2. The oblique muscle from the cervical plate to the phragma is present in Trichoptera, but lacking in the Plecoptera.

3. A pair of diagonal muscles (Pl.III, 76) in the Plecoptera;each crosses the prothorax to extend from one attachment on the episternum near the coxal margin to the other attachment on the cervical plate of the opposite side. They are lacking in the Trichoptera.

4. A muscle (Pl. III, 77) from the dorsal part of the episternum to the medial side of the basal rim of the coxa is present in the Plecoptera, but absent in the Trichoptera.

5. The anterior coxo-sternal muscle (Pl. III, 68) in Plecoptera arises on the furcal arm; in Trichoptera it arises on the median vertical plate.

6. The posterior pleuro-tergal muscle in Trichoptera is not represented in Plecoptera; the anterior pleuro-tergal muscle in Plecoptera is not represented in the Limnephilidae, but it is present in Hydropsyche (Pl.III,66)

Preliminary investigations on the prothorax of Neuroptera (Chauliodes), Mecoptera (Panorpa nuptialis) , and Lepidoptera (Danaus) indicate close similarity of structure among these

ord rs nd Trichoptera. The Plecoptera, on the otherhand,
more nearly resemble the Orthoptera, except that in the latter
the pleuro-tergal muscles are absent, a circumstance which is
not surprising, considering the cryptopleurous condition in
Orthoptera.

Mesothorax

The mesothorax is usually considered the most typical
thoracic segment because it has maintained its identity more
completely than has either of the other two segments. That
the neck region has obscured the segmental limits of the
prothorax has already been pointed out; and it will be seen
later that the abdomen has had a somewhat parallel influence
on the metathorax. In most insects the greater part of the
burden of flight has fallen upon the mesothorax, and as a
consequence the specializations necessary for flight are more
pronounced in this segment. The metathoracic wings are broader,
it is true, but since they move synchronously with the fore
wings the two function as a single unit. It is a well known
principle of aeronautics that the greater lifting power lies
in the anterior half of a plane (or wing), a principle which
explains the fact that a long narrow wing has greater lifting
power than a short wing of equal area. One can expect, then,
to find in the mesothorax larger muscles, more complete and
distinct strengthening ridges, and a more highly developed
pleuron.

In the mesothoracic tergum one may easily distinguish two
primary regions which Snodgrass has termed the notum and postnotum.
The latter, as Snodgrass points out is merely a rather broad

precosta which, as a functional unit, has reestablished itself
in the segment from which it was originally derived by the
development of overlapping terga. The notum is a much larger
region concerned primarily with regulation of wing movements.
Laterally it exhibits an anterior and a posterior wing process
and a peculiar notch which is associated with a part of the first
axillary sclerite. It has long been known that elevation of
this part of the notum is the principal cause of depression of
the wings, a process accomplished by contraction of the long-
itudinal muscles. Efficiency has been increased by the develop-
ment of certain internal ridges. Their external grooves
differentiate definite areas on the notum. In the caddisfly
there are three such ridges, one of which, is the familiar V-ridge
marking off the scutellum. One of the others is the median notal
ridge dividing the scutum into two lateral areas, and the other
is the prescutal ridge marking off a narrow prescutum. Laterally
the prescutum continues on each side as the prealare ("Tergal arm"
of Weber), the distal end of which rests upon the episternum.
The grooves are so uniform among the Trichoptera that they are
of little use in distinguishing species except as land-marks for
describing the location of callosities and setae.

Weber has already pointed out the principal modifications of
the sternum in connection with the development of sternal points
of articulation of the coxae and the shifting of the latter toward

the median ventral line. Briefly considered, the modifications

result principally from the medial inflection of the greater part

of the sternum to form a median internal plate situated in a

vertical plane. Toward its posterior end the plate bears the

sternal apophyses. They consist of the usual furcal arms which

have muscular connections with the pleural ridge and two

secondary arms which extend laterally to and fuse with the posterior

margin of the epimeron. Weber mentions this feature, but apparently

he regards it as being of little significance. It is present in

the Neuroptera and Lepidoptera as well, but is never present in

the metathorax. It is to be recalled that a spina frequently

occurs between the two segments of the pterothorax, but is

never present between the thorax and abdomen. Aside from the

similarity of segmental distribution, however, evidence is lacking

that these apophyses represent the spina. On either side of the

inflected part the sternum extends ventrally from the bases of the

furcal arms to the inner basal rim of the coxa where it bears

the sternal point of aritculation. Weber desiguates this plate

the "sterno-coxale". Its individuality, however, is not

traceable to primitive subdivision of the coxa, but rather to

secondary development adding strength to the weakly sclerotized

medial surface of this limb segment. Its identity as a part

of the coxa is established by muscular connections to be described

later. Continuing across the sternocoxale the inflected ridge

proceeds posteriorly a short distance,_then swerves ventrally and
around the coxa to an upward course, terminating at the coxal
junction wilk the pleural coxal process. At this point it is
considerably thickened, providing the necessary strength for such
a point of articulation. The ridge is not continuous with the
pleural ridge, however, for although its course is in line with the
latter it turns abruptly forward to continue as the marginal
flange described above. That part of the coxa lying behind this
ridge is known as the meron(Mn). It was once thought to have
been derived from the pleuron, but its identity as a part of the
basicoxite (that part of the coxa basal to the strengthening ridge
or basicosta) has been thoroughly established by Snodgrass. The
remainder of the leg (the telopodite) differs little from that of
the prothorax. Anteriorly the sternum broadens and apparently
extends for considerable distance along the front border of the
episternum. Weber is of the opinion that this strip is not entirely
sternal in origin, but has in it a part of the original subcoxa.
There is no definite line of demarcation but the strip is usually
designated   the precoxal bridge. The coxa in the mesothorax
differs considerably from that of the prothorax. The basal rim
in front of the pleural-coxal process is inflected to provide
greater muscle attachment surface. The anterior lateral angle
of the basal rim is capped by the broadened tip of the trochantin,
a mechanism which Crampton has pointed out as a lifting point,

rather than a point of articulation. Proceeding from this point

the flange-like inflection abruptly turns ventrally to a small

plate with which the coxa articulates on the sternal-coxal process.

The mesothoracic pleuron is well differentiated by the usual

pleural suture into an episternum (anterior) and an epimeron. The

latter is typically developed, exhibiting the usual junction dorsally

with the postnotum. Between this junction and the pleural suture

is a large membranous area in which the basalar sclerite is imbedded.

The relationship between the latter and the second axillary sclerite

is an important one in connection with wing movement. Ventrally a

narrow membranous strip separates the epimeron from the meron of

the coxa. The episternum, on the other hand, exhibits some

specializations which are characteristic of Trichoptera and related

orders. An irregular quadrangular plate which Weber designates

"Pleurotrochantin" is marked off in the region adjacent to the

coxa by the development of internal ridges. At its ventral end

it bears a narrow strip which broadens to fit over the anterior

lateral angle of the coxa where it furnishes attachment forthe

tergal promotor muscle. This muscular connection establishes

the identity of the strip as a part of the trochantin, S. st.,

but the manner by which it has altered its basal connection is

not well understood. In the neuropteron Sialis Weber describes

a cleft which partly divides the pleurotrochantin into an upper

and a lower strip. The latter, he thinks, represents the

trochantin, S. st., but he does not suggest that in Trichoptera
the cleft has merely been obliterated. There is still the
possibility that the neuropteron cleft is itself a secondary
development. The upper region of the episternum is very irregular
in its dorsal margin. Anteriorly this margin is inflected to form
a lobe which bears internally the attachments of several muscles.
A narrow strip along its posterior border is continued dorsally
along with the pleural ridge to furnish support for the wing.
Poorly defined grooves partially mark out two small plates on
this strip. In the Mecoptera these plates are more distinct,
but Snodgrass has shown that they lack muscle attachments and
therefore cannot represent the basalare. Issiki, disregarding
this criterion, has designated them as the basalare as though they
were the homologues of true basalare plates in the Orthoptera.
The writer deems it safer to accept a conclusion based upon clear-
cut relationships than one based solely upon appearances.

Except in regard to setae and callosities the taxonomic
importance of the thorax apparently has not been investigated.
The use of thoracic characters, however, would require material
preserved in fluids because of shrinkage and distortion in dried
specimens. A further objection to their use is that the differences
concern relative size and shape of the sclerites rather than more
fundamental relationships.

Since the work of Snodgrass on the thoracic mechanism of a

grasshopper there has been little original work on the thoracic musculature of insects. Nevertheless the changes in musculature which presumably accompanied the development of wings are not thoroughly understood. It now appears that certain pleuro-tergal muscles which were given but scant attention in hypothetical schemes are more important than was supposed. Their full significance, however, can hardly be appraised without more complete information on their presence in the _Apterygota_.

With a specimen of _Platyphylax designatus_ cut into longitudinal halves (Pl.II,F; Pl.III,A) the muscles may be identified as they are individually removed from their attachments. They occur as follows, beginning medially and anteriorly:

80. Internal dorsal muscles --- thick longitudinal muscles extending from phragma to phragma)shown by interrupted line in the figure).

81. External dorsal muscle (?) --- A small muscle extending from the second phragma to the posterior face of the V-ridge; it is also present in the _Sialidae_ and Plecoptera.

82. Oblique dorsal muscle --- extends from the lateral edge of the phragma to the scutum just in front of the V-ridge.

83. Ventral longitudinal muscle --- extends from the mesothoracic furca to the metathoracic furca.

84. A muscle extending from the spina to the mesothoracic furca.

85. Tergo sternal muscles --- two muscles extending side by side from the anterior part of the sternum to the anterior part of the scutum.

86. Tergal promotor of the coxa --- insertion of the expanded tip of the trochantin which caps the anterior angle of the coxa; origin laterad of the tergo sternal muscles.

87. Tergal branch of the depressor of the telopodite --- insertion with other branches on the apodeme in the membrane of the coxo-trochanteral joint; origin just posterior to that of the tergo sternals on the scutum.

88. Tergal remotor of the coxa --- insertion on the basicostal suture just behind the sternocoxale; origin on the posterior part of the scutum.

89. The pleural branch of the depressor of the telopodite --- insertion with 87 on the depressor apodeme; origin on the basalar lobe.

90. Coxo pleural muscle --- insertion on the basicosta in front of the pleuro coxal process; origin laterad of 89 on the basalar lobe.

(Note: two small muscles from the basicosta to the episternum in the stonefly are absent in the Trichoptera.)

93. Basalar episternal muscles --- two branches: one on the ridge which marks off the pleurotrochantin (93b); one to the upper plate of the episternum (93a).

94. Posterior coxo pleural muscle --- insertion on the meron; origin on the subalare.

95. Subalar epimeral muscle --- extends from the subalare to the point of fusion of the secondary apodeme (Fua) with the episternum.

96. Oblique intersegmental muscle --- extends from the second-ary furcal arm to the lower edges of the phragma; it is possibly serially homologous with one of the lateral muscles of the abdomen.

97. Tergo pleural muscle --- extends from the lateral margin of the scutum to the pleural ridge; it is lacking in some Rhyacophila species; it is present in Plecoptera, Neuroptera, and Mecoptera.

98. Prealar pleural muscle --- extends from the anterior face of the pleural ridge just below the pleural wing process to the prealare.

99. Basalar tergal muscle --- extends from the basalare to the prescutum.

100. Basalar tergal muscle --- extends from basalare to lateral margin of scutum.

101. Wing flexor --- consists of two branches inserted on the third axillary; one arises on the episternum, one on the pleural ridge.

102. Three fan-like bands (a, b, and c); two extend from the furcal arm to the basicosta between the meron and the lower part of the coxa.

103. Anterior rotator of the coxa --- extends from basicosta below the trochantinal attachment to the inflected sternal plate (SR).

104. Posterior rotator of the coxa —— insertion just behind the sternocoxale; origin on the inflected plate of the sternum.

105. Sternal branch of the depressor of the telopodite ——— insertion on the depressor apodeme; origin on the inflected plate of the sternum.

106. Coxal branch of the depressor of the telopodite ——— insertion on the depressor apodeme; origin on the anterior wall of the coxa.

107. Levator of the telopodite —— insertion on the outer basal rim of the trochanter; origin on the outer wall of the coxa and the ventral face of the basicosta.

108. Second levator of the telopodite ——— insertion on the outer basal rim of the trochanter; origin on the sternocoxale.

The metathorax differs so little from the mesothorax that
discussion may be restricted to the points of difference which have
not already been mentioned. The precoxal bridge and the
pleurotrochantin are less strongly developed. The distal end of
the coxa is twisted so that the telopodite is directed posteriorly.
The femur is much longer. The relative lengths of these leg segments
in the thoracic   segments has not been investigated for
taxonomic values. They vary considerably, however, with the
families.

Larval Abdomen

In external features the abdomen differs considerably in the two principal groups of caddisworms. In the eruciform group (i. e., the case-builders) it is rather straight and cylindrical and the constrictions between the segments are not very prominent. The tracheal gills may be branhced or simple, located singly or in groups; but they are distributed variously throughout the first eight segments. A lateral line consisting of a fringe of dark setae extending along each side of the abdomen from the second to the eighth segment marks the dorso-pleural line separating the dorsum of the abdomen from the region of limb attachment. The tenth segment is distinct and the pygopods are rather small and laterally placed. In the net-spinners, et al, (the so-called campodeoid forms) the constrictions between the segments are prominent; the lateral line is absent; ; the gills if present are located ventrally; and the pygopods are long and terminally located. The musculature of the larval abdomen is of particular interest from two standpoints: first, if exhibits one of the simplest plans to be found among larvae; the second, there is a great deal of similarity between the larval musculature and that of the adult.

Since there is little difference in the musculature of the various families the limnephilids are here used as an example

because of their availability and the ease with which they may
be dissected. The muscles may be considered according to the four
groups which Snodgrass has outlined in his work on the insect
abdomen. The internal dorsals and ventrals (Pl.rIII, E, di & vi)
occur as very heavy bands of fibers which show a tendency to
continue from one segment into another. The external dorsals
and ventrals are much more slender and they are disposed in
diagonal positions. The internal lateral muscles (Pl. III, li)
consist of bands diverging from a small area of attachment on
the lateral margin of the sternum near the intersegmental line.
The external laterals (Pl., III, le) are three rather heavy
bands located in a dorso-ventral position in the segment. Whether
they correspond to appendicular muscles of the thorax is not
known, but if they do not, they have no counterparts in the
caddisworm thorax.

Krafka has discussed the external features of the pypogods
from a phylogenetic point of view, but his conclusions are open
to question on the basis that his figures show an obvious mis-
understanding of fundamental relationships of the sclerites.
In his figure 12 (a species of Rhyacophila from Colorado) he
designates as plate "A" a dorsal sclerite which is clearly not
the homologue of "plate A" in his figures of eruciforms. It will
be shown directly that in R. fuscula (a species closely resembling
Krafka's Colorado species) there is a ventral plate which correspond

to the "plate A" of eruciform larvae.

In his work on the insect abdomen Snodgrass considered the musculature of *Platyphylax* *designatus* and a species of *Hydropsyche* and found it difficult to homologize the various muscles of the two types of larvae which they represent. Subsequent investigation of several species of each type has failed to show any closer relationship than Snodgrass has indicated, and the writer is inclined to regard the two types of pygopods as a sound basis for separating the Trichoptera into two distinct sub-orders.

To supplement Snodgrass' studies dissections of *Neuronia* *postica* (eruciform) and *Rhyacophila* *fuscula* and *Macronema* *zebrata* are here figured and compared. Designation of the muscles and plates has been copied from Snodgrass for convenience in comparison.

Neuronia shows essentially the same fundamental plan as the limnephilid *Platyphylax*, but one of the muscles inserted on the ventral plate arises in the anterior part of the ninth segment in a manner similar to that of muscle 3 *Hydropsyche*. The pygopod of *Macronema* strongly resembles that of *Hydropsyche*, but the dorsal muscle inserted on the membrane at the base of the drag-hook consists of two branches, one of which arises on the base of the plate b of the appendage. This branch is apparently lacking in *Hydropsyche*, but since it more nearly resembles the branches la and lb of the eruciforms it is thus designated in the figure and the long muscle is designated lc. *Rhyacophila* exhibits a plan

of musculature similar to that of <u>Macronema</u>, but the sclerites are very different in shape. The dorsal plate is provided with strengthening ridges which are externally indicated by grooves (sutures). A small area thus marked off at the dorsal base of the drag-hook was mistaken by Krafka for the plate $\underline{c}$ (which he labelled $\underline{A}$ in his figures). Plate $\underline{c}$, however, occurs at the ventral base of the drag-hook where it exhibits the usual muscle attachments.

Authors have been inclined to regard the pygopods as appendages of the tenth segment in the segmental series of appendages. The adult socii are likewise regarded as appendages of this segment, but it should be borne in mind 1) that the adult socii are not provided with muscles, and 2) that the groups in which the pygopods show the highest development usually do not exhibit socii.

The Adult Abdomen

The similarity of the musculature of the pregenital segments of the adult and larval abdomen has already been mentioned. The relative size of the muscles, however, differs, and there are in-dications that some of the muscles disappear after the adult instar has been attained. The possibility of similar modifications in the head has already been discussed with reference to the mandibular muscles. To demonstrate conclusively that such a thing actually takes place would be difficult, for it would require the rearing of suitable species (preferably limnephilids or phryganeids) in order to obtain adults of known ages.

The principal modifications of the larval musculature to produce that of the adult chiefly concerns the size and number of bands of fibers in the respective groups as already indicated. The dorsal and the ventral longitudinal muscles are considerably reduced. The external lateral group consists only of a single band. The internal lateral group is represented by a single band which at first glance appears to correspond with the oblique intersegmental muscle of the thorax. It is to be noted, however, that in the thorax the ventral attachment of the muscle is on the sternal pophysis. To regard it as the same muscle one must presume an extensive migration of this attachment.

Numerous workers have sought to homologize the various parts
of the copulatory organs of male holometabolous insects. The most
generally accepted idea is that the gonapophyses of segment nine
combine with the original penis to form the definitive intromittant
organ, the aedeagus, and that the remainder of the gonopod becomes
the clasper. Whether this hypothesis is correct, it is still not
adequately supported by morphological facts. There is ample evidence
that many of the structures,and the muscles associated with them
are secondary developments which are not necessarily homologous
in the different orders. It is unfortunate that it is at
present impossible to determine with reasonable assurance the
exact identity of the various parts, for in many cases the male
genitalia are the sole means of distinguishing species.

Taxonomists dealing with Trichoptera generally describe
"superior, inferior, and intermediate appendages" in the male
without regard to the relative significance of the structures
involved. The practice has led to confusion in many cases, especially
in the Limnephilidae. Among members of this family the blade-
like processes appearing on either side of the anus on the terminal
segment are sometimes regarded as the "intermediate appendages",
but more frequently the lateral branches of the aedeagus are so
regarded. Likewise, the "superior appendages" are sometimes the
socii, sometimes other processes on the ninth or the tenth segment.
Unfortunately, confusion of this sort will continue as long as

taxonomists consider only the external appearance of the exoskeleton.

Zander distinguishes two principal types of male genitalia in Trichoptera, one represented by the limnephilids, the other by the remaining families. The differences, he thinks, are sufficient to warrant dividing the order into two suborders, but it hardly seems reasonable to place so much phylogenetic importance on structures which are obviously specialized to extremes. It is interesting to note, however, that the female limnephilids are also unique in certain features of the genital segments --- they alone have the genital opening situated in front of the ninth sternum. Undoubtedly, the family comprises a very distinct and natural group of genera and species, but differences among the remaining families are equally as great, although they are not always so apparent externally. To the writer it would seem more rational to postpone rearrangement of the present taxonomic scheme until many features of internal anatomy have been thoroughly considered.

According to Zander the male limnephilids possess an aedeagus which is sclerotized at its distal end but membranous at its base where it is surrounded by a sclerotized sheath of the narrow pocket in which it is deeply retracted. Males of the remaining families each possess a sclerotized aedeagus in which a membranous tip is retracted; the shallow pouch which it occupies is membranous throughout. This second group itself shows extreme variation in

the sclerotic parts of the aedeagus. In Polycentropus it is a simple decurved sclerotized tube, but in Rhyacophila it exhibits complex secondary developments which vary considerably among the species. How closely these various types correspond to a fundamental plan is a question yet to be settled, but one which will require extensive comparative studies on forms which are as yet imperfectly known.

The "inferior appendages" or "pedes genitales" of taxonomists are the only male clappers which are probably appendicular. Two principal types may be recognized; the one type, as exemplified in Hydropsychidae, Rhyacophilinae, Phryganeidae, and certain sub-families of other groups consist of a basal part, or coxopodite, and a distal part, or stylus. Whether the latter corresponds to the stylus of the abdominal appendages of apterygote insects is not definitely established and many writers prefer the use of the noncommital term harpe. The harpe is provided by a group of muscle fibers inserting on its base and arising in the coxopodite. The movement occasioned by these fibers is one of adduction, and the muscle is therefore designated as the adductor of the harpe. Abduction seems to be due to the elasticity of the joint. The coxopodite hinges in a latero-ventral position upon the posterior margin of the ninth segment. Usually it is capable of four movememts; levation, depression, adduction, and abduction. In Neuronia there are three muscles inserted on the basal rim of the coxopodite.

The depressor inserts ventrally on the lateral margin and arises ventrally in the anterior margin of the sternum. The levator inserts dorsally on the lateral margin and arises laterally on the anterior margin of the ninth segment. The adductor inserts somewhat dorsally on the medial basal margin of the coxopodite and arises laterally and somewhat ventrally on the posterior margin of the ninth segment. Just how abduction is brought about is obscure, but it may be due to elasticity, or it may be occasioned by the simultaneous contraction of both levator and depressor.

The other type of appendage consists of but a single segment, but that it represents the fused harpe and coxopodite, or that it represents either one of them alone if difficult to establish. In Polycentropus a peculiar blade-like hook might easily be mistaken for the harpe, but it is not provided with muscles, nor is there any other evidence that it is anything but an apophysis. The three muscles which insert on the base of the appendage strongly suggest community of origin with those of Neuronia and that the clasper represents the coxopodite, either alone, or fused with the harpe. The movement of the clasper has not been observed, but it is probable that it takes place in a manner similar to that of Neuronia. In the limnephilids these appendages seem to have fused with the segment which bears them, and there are no muscles attached directly to the remnants. The "Superior

appendages" known as socii are well developed but they, too, lack muscle insertions. Movement of them has not been observed, but if it occurs it must be accomplished indirectly by the pull of muscles on surrounding areas. For distinguishing species the terminal abdominal segments of the female are far less valuable than those of the male. For differentiating the larger taxonomic groups, however, the characters of these segments may be found useful. Limnephilidae, for example, are distinguished by the position of the genital opening (Pl. IV, K, ·Gpr). between the eighth and ninth segments. In all other groups the opening is behind the ninth sternum, or it occurs with the anal operning in a common chamber associated with the tenth segment. (Pl. IV , J, ·Clo). The number of taxonomic groups in this latter category has not been determined, but it now seems probable that it includes all of those in which the larvae are campodeoid, and possibly some of the others In Rhyacophila and certain genera of the families Polycentropidae, Philopotamidae, and Psychomyidae the terminal part of the abdomen may be withdrawn almost completely into the eigth segment or extended for considerable length, presumably as an ovipositor. The fact that the females of a given family vary in the nature of the terminal segments has led to the view that the above characters are not of phylogentic importance. It has not been shown, however, that the distinguishing features of the families as now recognized are phylogenetically important.

The subject is one which needs further investigation, but it is inadvisable to suggest a revision of the families without sufficient representative material from other continents.

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LIST OF ABBREVIATIONS USED IN FIGURES

A --------anal veins

Ab -------abdomen

AdAp ---- apodeme of pretarsus

Aed ----- aedeagus

An ------ anus

Ant ----- antenna

Ap ------ apodeme

Ax ------ axillary sclerite

Ba ------ basalare

Bc ------ basicosta of coxa

C ------- costal vein of wing

Cd ------ cardo

Clo------ cloaca; combined genital and anal opening

cv ------ cervical sclerite

Cx ------ coxa

CxP ----- pleural coxal prosess

Cxpd ---- coxopodite

CxS ----- sternal coxal process

FrClp --- frons-clypeus

Fu ------ furca

Fua ----- secondary arm of furca

Ge ------ gena

Gpr ----- female genital opening

Hphy ------ hypopharynx

Lb -------- labium

M --------- Median vein of wing

Mr -------- meron

N --------- notum

O --------- ocellus

Osc------- occular sclerite

PcxB ----- precoxal bridge

Pl -------- pleuron

PlR ------ pleural ridge

Pls ------ pleural suture

PN ------- postnotum

Poc ------ postocciput

pos ------ postoccipital suture

pra ------ prealare

Ptr ------ pretarsus

s --------- spiracle

Sct ------ scutum

Scl ------ scutellum

Spn ------ spina

Spr ------ tibial spur

Stcx ----- sternocoxale

tar ------ tarsus

tb ------- tibia

EXPLANATION OF FIGURES

Plate I

A. Perla species, adult head and prothorax, median section.

B. Perla species, muscles of the basal part of the prothoracic leg.

C. Perla species, outer muscles of prothoracic leg.

D. Stenophylax divergens, adult head and prothorax, median section.

E. Hydropsyche species, adult head and prothorax, median section.

F. Hydropsyche species, prothorax with some of the median muscles.

Plate II.

A. Stenophylax, head and prothorax, exterior view.

B. Stenophylax, prothoracic leg.

C. Stenophylax, mesothorax, dorsal view.

D. Platyphylax, mesothorax with left coxa, pleuron, and tergum
    removed, posterio-lateral view.

E. Platyphylax, mesothorax and metathorax, lateral view.

F. Platyphylax, mesothorax and metathorax and first two abdominal
    segments, median section.

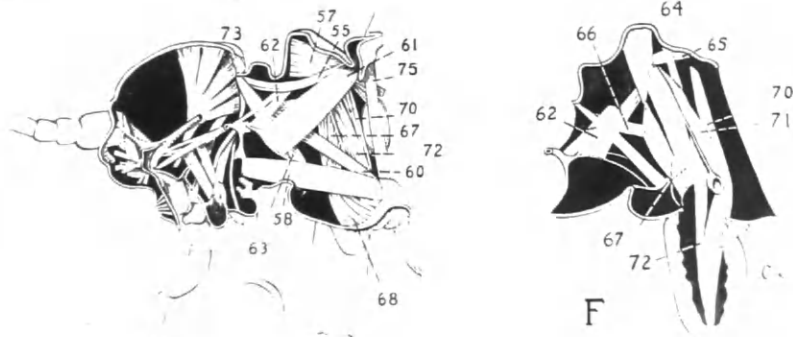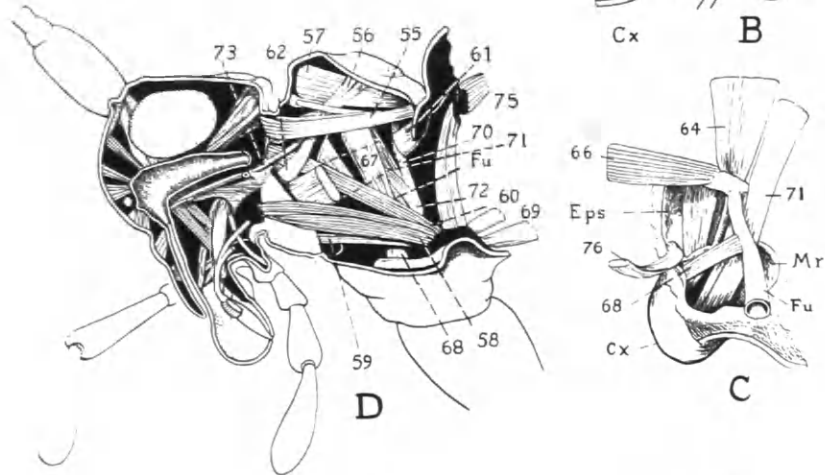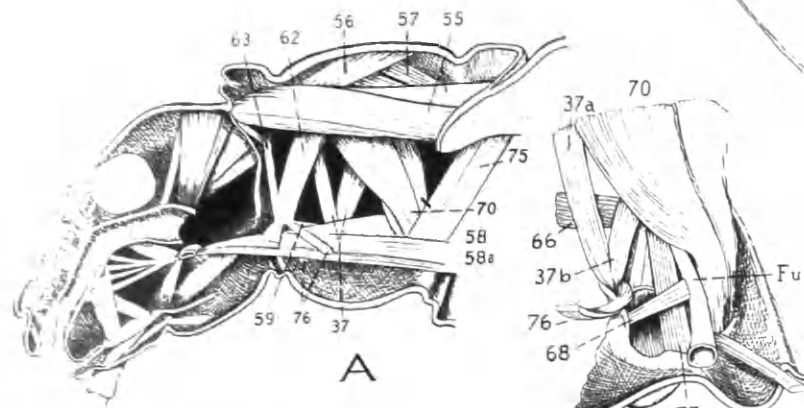G. Platyphylax, muscles inserted on the base of the mesothoracic
    trochanter.

Plate III.

A. Platyphylax, outer muscles of mesothorax.

B. Stenophylax, larval mesothorax and metathorax, median section.

C. Stenophylax, larval mesothoracic right leg, posterior view.

D. Stenophylax, larval prothoracic right leg, posterior view.

E. Stenophylax, larval abdominal segments IV and V.

F. Platyphylax, adult abdominal segments II-V.

Plate IV.

A. Rhyacophila fuscula, pygopod, inner view.

B. Rhyacophila fuscula, pygopod, exterior view.

C. Macronema zebrata, pygopod, inner view.

D. Neuronia postica, pygopod, inner view of terminal part.

E. Polycentropus, male abdomen, muscles of clasper and terminal segment.

F. Polycentropus, male abdomen, terminal segments, exterior view.

G. Polycentropus, male, aedeagus.

H. Stenophylax, male abdomen, terminal section, median section.

I. Neuronia postica, male, clasper.

J. Dolophilus major, female abdomen, terminal segments, ventral view.

K. Platyphylax designatus, female abdomen, terminal segments, exterior view, ventral.

PLATE I.

PLATE II.

PLATE III.

PLATE IV.