# THE ADULT MUSCULATURE OF THE ANISOPTEROUS DRAGONFLY THORAX (ODONATA, ANISOPTERA)

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SEVEN FIGURES

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## INTRODUCTION

Experiments on the correlation of wing atrophy and wing-muscle atrophy in Odonata (which gave negative results), led me to a review of the morphological accounts of the dragonfly musculature for the last hundred-odd years, since the most recent accounts by Maloeuf ('35), and Maki ('38), did not agree with my own findings. Tabulation of the various accounts, listing the names given each muscle by the various investigators, gave rise to a rather unwieldy table, which showed the discrepancies between the accounts in the number of muscles, and in the nomenclature. Table 1, given below, is a condensed version of the table constructed. (The names may be found in the Appendix.) The various investigators are listed across the top, in chronological order. The symbols III and II, under each name, indicate a muscle reported in the metathorax (III), in the mesothorax (II), which corresponds to a muscle listed in the last, or author's, column. The abbreviations I have listed in the last column will be explained

TABLE 1

*Muscle pairs of the pterothorax of the adult dragonfly, as reported by various investigators, stigma muscles excluded*

| CHABRIER 1820–1822 | POLETAIEW 1879–1881 | LENDENFELD 1881 | LUKS 1883 | AMANS 1883–4–5 | CALVERT 1893 | BERLESE 1909 | TILLYARD 1917 | CREMER 1934 | MALOEUF 1935 | MAKI 1938 | CLARK (WRITER) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| III | III | | III | III | III | I Ab | III | | III | III | $IIIvlm_1$ |
| | | | | | III | III | III | | III | IAb | $IIIvlm_2$ |
| II | III–II | | | III–II | | II | II | | II | II | $dlm_1$ |
| III | III | | | III | III | III | III | | III | III | $IIIism_1$ |
| III–II | III–II | III–II | III–II | III–II | III–II | III–II | III–II | III–II | III–II | III–II | $dvm_1$ |
| | III–II | | | | | | | | | III–II | $dvm_2$ |
| III–II | III–II | III–II | III–II | III–II | III–II | III–II | III–II | III–II | III–II | III–II | $dvm_3$ |
| III–II | III–II | III–II | III–II | III–II | III–II | III–II | III–II | III–II | III–II | III–II | $dvm_4$ |
| III–II | III–II | ? — ? | ? — ? | III–II | III–II | III | III | III–II | | III–II | $dvm_5$ |
| III–II | III–II | III–II | ? — ? | III–II | III–II | III–II | III–II | III–II | III–II | III–II | $dvm_6$ |
| III–II | III–II | III–II | ? — ? | III–II | III–II | III–II | III–II | III–II | III–II | III–II | $dvm_7$ |
| III–II | III–II | III–II | III–II | III–II | III–II | III–II | III–II | III–II | III–II | III–II | $pm_1$ |
| III–II | III–II | III–II | III–II | III–II | III–II | III–II | III–II | III–II | III–II | III–II | $pm_2$ |
| III–II | III–II | | ? — ? | III–II | III–II | III–II | III–II | III–II | III–II | III–II | $pm_3$ |
| III–II | | III–II | | III–II | III–II | III–II | III–II | III–II | III–II | III–II | $pm_{4a}$ |
| | | | | | | | | | III–II | | $pm_{4b}$ |
| III–II | | | | III–II | III–II | | | III–II | III–II | III–II | $pm_5$ |
| | | | | | | ? — ? | ? — ? | | III–II | III–II | $pm_6$ |
| | | | | | | | ? — ? | | III–II | III–II | $pm_7$ |
| | | | | | | ? — ? | ? — ? | | III–II | III–II * | $bm_1$ |
| | | | | | | ? — ? | ? — ? | | III–II | III–II | $bm_2$ |
| III—13, II—12 | III—13, II—11 | III—9, II—9 | III–9 or 10 II 8 or 9 | III—14, II—12 | III—14, II—11 | III—14, II—12 | III—17, II—14 | III—11, II—11 | III—18, II—16 | III—18 II—20 see note | III—21 II—18 |

I Ab., reported as a muscle of the first abdominal segment.
? Imperfectly described, or misprint on figure, table.
III, reported in metathorax; II, reported in mesothorax.
Blanks in columns signify, no report.

Muscles in the last column without prefix III are reported as homologues in the meso- and metathorax.
* Maki splits my $bm_1$ into two muscles in the mesothorax.
Maki also reports a muscle 23, first anterior tergosternal of the mesothorax, not seen by me.
Maki's muscle 22 has been seen by me in larvae only.



later. Muscles in the last column without the prefix III indicate homologues in the meso- and metathorax. Muscles with the prefix III are metathoracic muscles only. Blanks in the columns indicate no report.

Tabulation of the synthoracic muscles brought out the following facts: (1) There is general agreement in the reports for muscles $dvm_1$, $dvm_3$ to $pm_4$.

These muscles are wing muscles, with which all the investigators, excepting Berlese, were primarily concerned, up to Maloeuf ('35). The present writer at the time of the wing-muscle atrophy experiments did not have access to Maloeuf's paper, then in process of publication, and sought to establish a standard for musculature with Berlese's paper, which proved imperfect. Thus a physiological investigation became purely morphological. The differences between Maloeuf and the present writer led to a wider investigation of twelve genera. The investigation was complete when Maki's paper appeared, and the differences persisted, although much diminished. A standard is still needed for the musculature of the dragonfly.

(2) The nomenclature of the dragonfly musculature was found to be vague, confusing, and misleading. Some of the muscles bore as many as twelve different names, others bore numbers only. There is a need for pure positional nomenclature, as favored by Berlese, Snodgrass, Weber, and attained in part by Maki.

The discrepancies found in table 1 led to the construction of table 2, below, for the prothoracic muscles. The disagreement persisted. It was found that the prothoracic muscles were not completely illustrated, and not satisfactorily described. The present writer attempts, in this paper, to completely illustrate, describe, and name by positional nomenclature, the muscles found in twelve genera, about 100 specimens, of the dragonfly adult, with regard to the synthorax and prothorax only.

It may be mentioned in passing, that there are several muscles reported by Berlese and Maki that have not been confirmed. They are: (1) the fourth intersegmental muscle of the prothorax, reported in Diplax by Berlese and included in Tillyard's translation, (2) Maki's muscle 22, anterior transverse muscle of the mesothorax, seen by me in larvae only, (3) Maki's muscle 23, first anterior tergosternal muscle of

TABLE 2

*Muscle pairs of the prothorax of the adult anisopterous dragonfly, as described by various investigators*

| CLARK, WRITER | BERLESE ('09) | MALOEUF ('35) | MAKI ('38) |
|---|---|---|---|
| 1-$Ovlm_1$ | | | (14) |
| 2-$Ovlm_2$ | | (11) | (4) |
| 3-$Ivlm_1$ | 105–106 | (41)[1] | (21)[1] |
| 4-$Ivlm_2$ | 105–106 ? | | |
| 5-$Ivlm_3$ | | | (43)[2] |
| 6-$Odlm_1$ | | (1) | (3) |
| 7-$Idlm_1$ | | (2) | (2) |
| 8-$Idlm_2$-(not constant!) | | | (1) |
| 9-$Oism_1$ | | (8) | |
| 10-$Oism_2$ | | (4) | (6) |
| 11-$Oism_3$ | | (5) | (7) |
| 12-$Idvm_1$ | 144a | (7) | (8) |
| 13-$Idvm_2$ | 120 | (13A–B) | (12) |
| 14-$Idvm_3$ | | (13A–B) | (13) |
| 15-$Idvm_4$ | CXXI | (14) | (16) |
| 16-$Ipm_1$ | | (12) | (10) |
| 17-$Ipm_2$ | 117 | (18) | (18) |
| 18-$Ibm_1$ | | | (15) |
| 19-$Ibm_2$ | | (19) | (19) |
| 20-$Ibm_3$ | ? fig. 475 | (16) | (17) |
| 21-$Izm_1$ | | | (11) |
| | | | (5) |
| | | | (9) |

? Imperfectly described.
[1] Reported in mesothorax.
[2] Reported in metathorax.

the mesothorax, (4) Maki's muscle 5, ventral transverse muscle, of the prothorax, (5) Maki's muscle 9, anterior prothoracic tergopleural muscle.

## MATERIAL AND METHODS

Each muscle has been checked at least ten times, in as wide a range of species as was obtainable. Adult dragonflies were fixed in hot 95% alcohol, and preserved in 70% alcohol.



In abbreviations for the skeletal parts, the subscripts 1, 2, 3, stand for pro, meso, metathoracic, respectively. In abbreviations for the muscles, the prefixes O, I, II, III, stand for head, pro, meso, metathoracic, respectively; subscripts are series within classes, explained under the beginning of the annotated list of the muscles.

## ABBREVIATIONS (ADAPTED FROM SNODGRASS)

Ab, abdomen, preceded by I, II, Iab, first abdominal, IIab, second
ac, antecosta
acro-S., acrosternite
An, alinotum
ap., apodeme
Aph., prophragmal substitutes, Apha, anterior, Aphb, posterior Aph
apn, anterior part of pronotum
art.pl., prothoracic articulating plate
axc., axillary cord
Axp., axillary process or plate
Ba., basalar region, epipleural plates may be cap-tendons $dvm_{3-4}$, invaginated
bm., "Beinmuskeln," sternal leg muscles
C, costal wing vein
c, carina
Cu., cubital 5th wing vein
Cv., neck or cervix
Cvm, neck membrane
Cx., coxa
d.ao.m., dorsal aorta muscle
dlm., dorsal longitudinal muscle
dvm., dorsoventral muscle
epm., epimeron
eps., episternum
F., furca, sternal apophysis, apodeme
g., ganglia, ganglion
HP., humeral process or plate
I-II, abdominal segments when followed by Ab
ism., intersegmental sternodorsal muscle
ismsppr., intersegmental sternopleural process
ism. sut., intersegmental suture
j.cup., jugular process cup
j.pr., jugular process, internal sternal infolding of the lateral cervical sclerite
L., left side
l.c., lateral cervical sclerite
l.s., lateral suture
m., membranes
mdc., mid-dorsal carina of $eps_2$
Me., meron of coxa, posterior basicoxal plate
Mph., middle phragmal substitute, Mpha, appears to be true middle phragma;
Mphb, metatergal invagination
N., notum; AN, alinotum, PN, postnotum, acrotergite
n.m., neck membranes
n.s., neck spur
pcfr., posterior cephalic foramen rim; pcfs, pcfr sternite; pcft, pcfr tergite
Ph, phragmal substitute, or phragma
pm., pleural muscles
PN, postnotum
pn-epms, pronotal-epimeral suture
Pphr., postphragma, antecosta of 1st abdominal tergite
R, right side
S, sternum
Sa, subalar region; epipleural sclerites may be invaginated as cap-tendons of $pm_{1-2}$
Sp., spiracle
Sp.d., spiracular dorsum, a bridge connecting mesothoracic spiracles
sut., suture
t., tergum, tergal, tergite
Tn, tentorium
tn, tendon (followed by muscle abbreviation)
Tr., trochanter
tr, ap., trochanteral apodeme
V., ventral
vlc, ventrolateral carina, $epm_3$
vlm, ventral longitudinal muscle
WP, wing or fulcral process
zm, "Zwischenmuskel," sternopleural muscle

Some were fixed in Carl's formalin fluid (Tillyard, '17). Some were purchased, preserved in wood alcohol. Some were examined fresh. The alcoholic specimens seemed best. The following species were examined: 1 Gomphus villosipes, 1 Gomphus exilis, 4 Dythemis sterilis, 1 Didymops transversa, 2 Aeschna umbrosa, 1 Epiaeschna heros, 8 Anax junius, 27 Plathemis lydia, 26 Pachydiplax longipennis, 2 Sympetrum vicinum, 1 Sympetrum rubicundulum, 20 Erythemis (Mesothemis) simplicicollis, 4 Libellula pulchella. The dissections were made in water with the aid of fine needles, a binocular dissecting microscope, and a spotlight. Records were kept of each muscle removed or observed in frontal and sagittal sections.

## SOME REMARKS ON THE ANISOPTEROUS ODONATE SKELETON

The somewhat aberrant dragonfly thoracic skeleton—with the very mobile prothorax tending to remain rather small, the synthorax hugely developed, as a fusion of the meso- and metathorax, with the mesepisterna meeting on the dorsal mid-line, and the metepimera meeting on the ventral mid-line—has been studied by Berlese, Snodgrass, and Sargent.

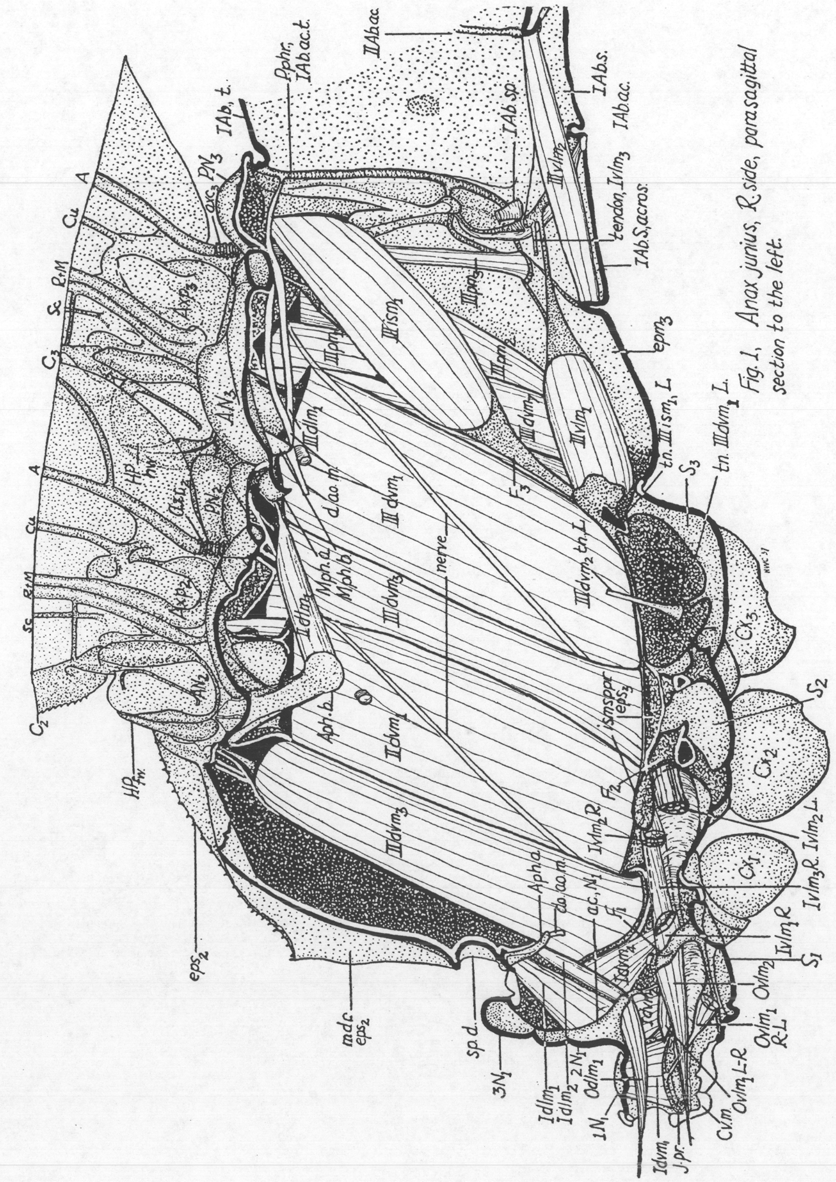
Snodgrass ('27, p. 71) finds that there is a seeming lack of the usual phragmas and tergal longitudinal muscles. The writer would like to point out, that the postphragma (fig. 1, Pphr), or antecosta of the first abdominal segment, serves as

Figures 1, 2, 3, 4 and 5 each have been obtained by composite of eight camera-lucida outline drawings. The details were filled in free-hand. Figures 6, 7, are single camera-lucida outline drawings, detailed in free-hand. All elements excepting muscles and skeleton have been removed, but for a few fragments. Figures 1 to 5 were also compared with photographs of the dissections, for proportions.

Fig. 1 Thorax of Anax junius, internal view of right side, parasagittal section, slightly to the left.

The drawing shows the more median synthoracic, and some of the prothoracic, muscles undisturbed. Note the phragmal substitutes, AcN$_1$, Apha-b, median tergal invaginations, and the true phragmas, Mpha, Pphr, and the median metatergal phragmal substitute, Mphb. Left side structures shown are: ismsppr, intersegmental sternopleural (episternal) invagination, to the midline, fusing anteriorly with the mesosternal infolding, posteriorly with the metasternal infolding, and also with its fellow of the right side; note anterior portion affording attachment for Ivlm$_1$. Note also the left mesofurca, F$_2$, the right metafurca, F$_3$, and the tendons of the left IIIdvm$_{1-2}$ as stalked metasternal apodemes (tn. IIIdvm$_{1,2}$). The tendon of Ivlm$_3$ is cut near insertion, for the right side.





an attachment for the dorsal longitudinal muscle $IIIdlm_1$, when this muscle is present. The middle phragma (fig. 1, Mpha), serves as an attachment for the dorsal longitudinal muscle $IIdlm_1$. Both notal muscles attach anteriorly to median tergal invaginations (Aphb, Mphb) which, if not phragmas, are at least phragmal substitutes, since the muscles in the larva are not at all unusual. It happens that Snodgrass' source for Odonata in 1927 was Lendenfeld, who did not report notal muscles. The fate of the larval prophragma, which disappears in the adult, is yet to be worked out. Phragmal substitutes in the adult are the median process Aphb, the spiracular dorsum Sp.d, and the median protergal process $AcN_1$ (see fig. 1), which serve as points of attachment for the tergal longitudinals $IIdlm_1$, $Idlm_{1-2}$, $Odlm_1$.

Snodgrass ('35, p. 230) states "the dorsal muscles . . . . are reduced in the strong-flying Odonata," but just how much, he does not state, nor is the phragma question clarified. This matter is discussed more completely later.

Another peculiar feature which the writer would like to discuss is the apparent fusion of the meso- and metafurcae into a single piece (see figs. 1, 5). This plastron-like structure is vaguely referred to in the literature as meso- or metafurca, depending upon the apparent location in the thorax. The apparent plastron is divided into three parts: anteriorly, it is the mesosternum folded dorsad, fused with the true larval mesofurcae which may be identified by the posterior attachments of muscle $Ivlm_2$. There is also fusion with the metepisternal invagination ismsppr (intersegmental sterno-pleural process) (figs. 1, 5), the anterior tip of which extends into the mesothorax and affords posterior attachment for the ventral muscle $Ivlm_1$. The process ismsppr is fused posteriorly with the metasternum, which has folded dorsad, enveloping the nerve cord. Posteriorly, I have identified the tendon of attachment of muscle III $ism_1$ as the true metafurca, which is quite distinctly separate from the process ismsppr in the larvae I have studied. In the larva the intersegmental sternopleural process is joined with its fellow of the opposite side by a transverse muscle (absent in the adult, due to fusion of the skeletal parts), and is entirely freed from the sternum. There is a similar process occurring in the mesothorax which does not quite go to completion, but affords in the adult the ventral attachments of muscles $IIdvm_{3-4}$. The transverse muscles disappear, leaving a space, in the adults I have examined, but Maki has seen the transverse muscle in the adults of Crocothemis servilia.



## ANNOTATED LIST OF THE THORACIC MUSCLES OF THE DRAGONFLY ADULT, STIGMA MUSCLES EXCLUDED

While some of the muscles have been described many times, the writer feels that all should be included in this new report on the adult dragonfly. The annotations of the following lists follow Voss ('05) in abbreviations, and description.

For each segment of the thorax, the muscles are considered in the following order: (1) Intersegmental muscles, (a) vlm, ventral longitudinal muscles, (b) dlm, dorsal longitudinal muscles, (c) ism, intersegmental dorsoventral muscles; (2) Segmental muscles, (a) dvm, dorsoventral segmental muscles, (b) pm, pleural segmental muscles, (c) bm, "Beinmuskeln," (leg muscles), from sternum to coxa, trochanter, (d) zm, "Zwischenmuskeln," pleurosternal muscles.

Longitudinal muscles are designated as having origin in the more anterior segment, and are preceded by Roman numerals for the segment of origin, thus, I, prothoracic, II, mesothoracic, III, metathoracic, O, muscles attaching to the head. Segmental muscles are prefixed O, head, I, pro-, II, meso-, III, metathoracic. Muscles of the same class, to be distinguished from each other, carry an arabic numeral subscript, as $Idvm_1$, $Idvm_2$, etc. The system used here differs from Voss, in that there are no broken series of subscripts; the muscles are considered as they exist, not with the idea of homologization of the muscles of one segment with those of another, although for the synthorax this is actually the case, but not in the prothorax.

The reader is referred to tables 1 and 2, given above, for the sequence in the following annotated list. All of the muscles occur in pairs in the body.

## SYNTHORACIC MUSCLES

### *Intersegmental*

(*a*) *Ventral.* IIIvlm$_1$, Lateral thoracico-abdominal. Calvert (1893) (figs. 1, 3, 5). "Manifesto in alcune forme col 1° urosternite distinto, manca in Ortotteri," Berlese, page 398. An intersegmental, ventral, longitudinal, mesolateral muscle. Flat and heavy, the muscle has its origin by fleshy fibers from the posterior part of the metathoracic sternal infolding, extends posteriorly to insert on both sides of a flat tendon which extends posteriorly, becoming rounded and thin, inserting in turn on the antecosta of the first abdominal sternite, laterad to IIIvlm$_2$, mesad to the tendon of Ivlm$_3$. The muscle protracts the first abdominal sternum.

IIIvlm$_2$, Submedian ventral thoracico-abdominal, Calvert (1893) (figs. 1, 5). "Non trova alcun omologo," Berlese, page 406. My homology, Voss' Musculus metasterni II, III, IV or V. An intersegmental, ventral, longitudinal, submedian muscle. Flat, long and powerful, the muscle has its origin from a ridge between the ventral floor formed by the metepimeron, and a posterior semicircular plate, designated by me as the acrosternite of the first abdominal sternum. The muscle extends posteriorly, inserting into the antecosta of the second abdominal sternum. Function: protractor of the second abdominal sternum.

There are no mesothoracic ventral intersegmental muscles.

(*b*) *Dorsal muscles.* III-IIdlm$_1$, Metanotal, mesonotal (figs. 1, 3, 4). Positional name from Luks, Voss. Homologues, M. metanoti, mesonoti, I, II, Voss, muscle A, Snodgrass ('10, '27, '35). Of the IIIdlm$_1$, Berlese states, "manca in Libellulidi," page 400. Of IIdlm$_1$, Berlese states, "non ha correspondenti in altri insetti," page 429. The notal muscles are very common.

In the adult dragonfly, the notal muscles are intersegmental, dorsal, longitudinal, median (anteriorly), lateral (posteriorly), long, thin muscles. IIIdlm$_1$ is quite small, and ribbon-like, well-formed in Aeschna (fig. 4), but more ribbon-like and reduced in Anax (fig. 1), and it is absent in the higher genera (Libellulidae). The presence in some genera and the absence in others has led to the divergent reports. IIdlm$_1$ is a medium-sized, powerful, rounded, longer muscle, quite active and present in all genera. Both notal muscles have their origins by fleshy fibers from a median invagination of the anterior part of the alinotum. The mesonotal invagination Aphb is more pronounced than the metanotal invagination Mphb. The muscle IIdlm$_1$ inserts by a small tendon on the true middle phragma Mpha; the muscle IIIdlm$_1$ when present inserts on the post-phragma Pphr. Both insertions are lateral.

Function: when present and active, the notal muscles are indirect wing depressors, assisting the depressors to restore the shape of the notum after it has been buckled down by the elevators.

(*c*) *Dorsoventral muscles.* IIIism$_1$, Intersegmental sternodorsal (figs. 1, 3, 4, 5). Combined name, Poletaiew and Berlese. M. intersegmentalis metathoracis, Voss, is the cricket homologue. Muscle F, lateral intersegmental muscle, Snodgrass ('35).

An intersegmental, metepimeral, dorsoventral muscle, very heavy, strong and flat. The origin is from the true metafurca, a flat triangular tendon; the muscle extends dorso-laterad and posteriorly, to insert into a cup-like process which appears to be drawn out from the postphragma, antecosta of the first abdominal tergum. The muscle is a powerful wing depressor, restoring the shape of the notum after it has been buckled down by the elevators; it also may protract the first abdominal tergum.

There are no ism muscles of the mesothorax.

### 2. *Segmental muscles of the metathorax*

(*a*) *Dorsoventral.* III-IIdvm$_1$, First tergosternal, principal elevator, large head, wing elevator (figs. 1, 3, 4, 5). Named by Berlese, page 401. "Elevator dell'ala, Strauss-Dürckheim ed altri,'' lacking in Gryllus, Blattidae, Vespa, Diptera, present in Acrididae, Cicada, Lepidoptera (Berlese). Muscle C, Snodgrass ('35, p. 188).

A segmental, dorsoventral, tergosternal, submedian, large, powerful wing muscle, ovoid in cross section, flattened on the mesal side. The origin is a stalked cup from the basisternum anterior to the coxa (figs. 1, 5); the insertion is into a flat, cup-like tergal apodeme (squame) (figs. 1, 4), which appears to be drawn out from the lateral edge of the alinotum. Function: as named above.

III-IIdvm$_2$, Second tergosternal, principal elevator, short head, wing elevator (figs. 1, 3, 4). Name adapted from Berlese, reported first by Poletaiew. Berlese describes a muscle in Cicada, M. tergosternale secondo, resembling dvm$_2$, page 401. A derivative of muscle C, Snodgrass ('35).

A segmental, dorsoventral, tergosternal, very small, pyramidoidal wing muscle (fig. 3). The origin (fig. 1) is by a very long, thin transparent tendon rising from the sternal cup-tendon of dvm$_1$. The tendon passes between the fasciculi of dvm$_1$, emerging from this muscle near its dorsal part (fig. 3), where it becomes the small dvm$_2$, which inserts on the lateral middle edge of the squame of dvm$_1$. Function: as named, assisting dvm$_1$.

III-IIdvm$_3$, First basalar, anterior depressor of the wing (figs. 1, 2, 4, 5). Name adapted from Snodgrass, Maki. Berlese classes the muscle as a tergosternal derivative, page 401. Very common, and variable, Snodgrass ('35). His 1E' closely resembles dvm$_3$ (pp. 188, 231, '35).

A segmental, dorsoventral, lateral, episternal, basalar wing muscle, large, and rectangular in cross section. IIIdvm$_3$ has its origin (figs. 1, 5) from the intersegmental sternopleural process, ismsppr (furcal bridge, Sargent, sternopleural region, Maloeuf, prefurca of metasternum, Berlese). The muscle inserts into a large cap-tendon which may be the basalar plate invaginated into the body cavity (fig. 2); the cap-tendon inserts into the anterior edge of the humeral wing process. IIdvm$_3$ has a larger episternal plate of origin (figs. 1, 5), which



does not quite meet its fellow at the midline of the body. Function: as named, described in full under the wing mechanism, below.

III-IIdvm$_4$, Second basalar, accessory anterior depressor of the wing (figs. 2, 4, 5). Name adapted as for dvm$_3$. In Vespa, not in others, Berlese. Derivative of muscle E' of Snodgrass ('35).

A segmental, dorsoventral, lateral, episternal, small, flat wing muscle, laterad to dvm$_3$ (fig. 2). IIIdvm$_4$ is fusiform, composed of parallel bundles; the origin is by a cap tendon rising from the intersegmental ridge between the meso- and

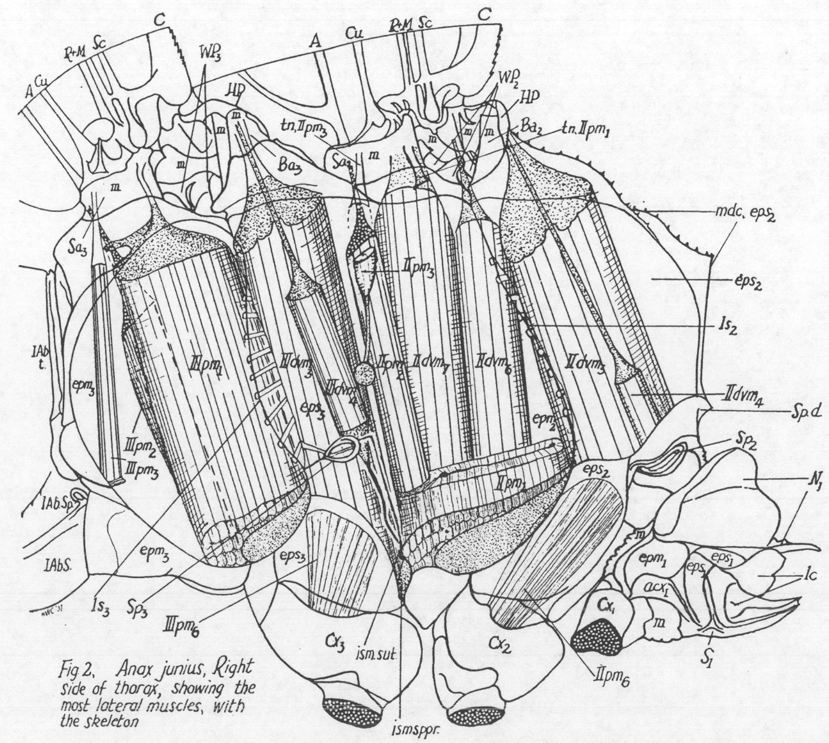



Fig. 2 Thorax of Anax junius, right side, lateral view. The more lateral muscles may be seen, with relation to the skeletal outline. Muscle IIpm$_1$ has been cut near the ventral pleural attachment, and removed to the point of insertion, showing IIpm$_2$, IIdvm$_{6-7}$. IIpm$_3$ is cut near its middle belly and near the tergal tendon, to show the cap-tendon of IIpm$_2$.

metathorax. The dorsal cap-tendon of insertion inserts into the humeral process of the wing, near the tendon of $dvm_3$. $IIdvm_4$ is more rounded, and rises from the same ventral episternal plate with $IIdvm_3$, not a cap-tendon like $IIIdvm_4$. Function: See $dvm_3$.

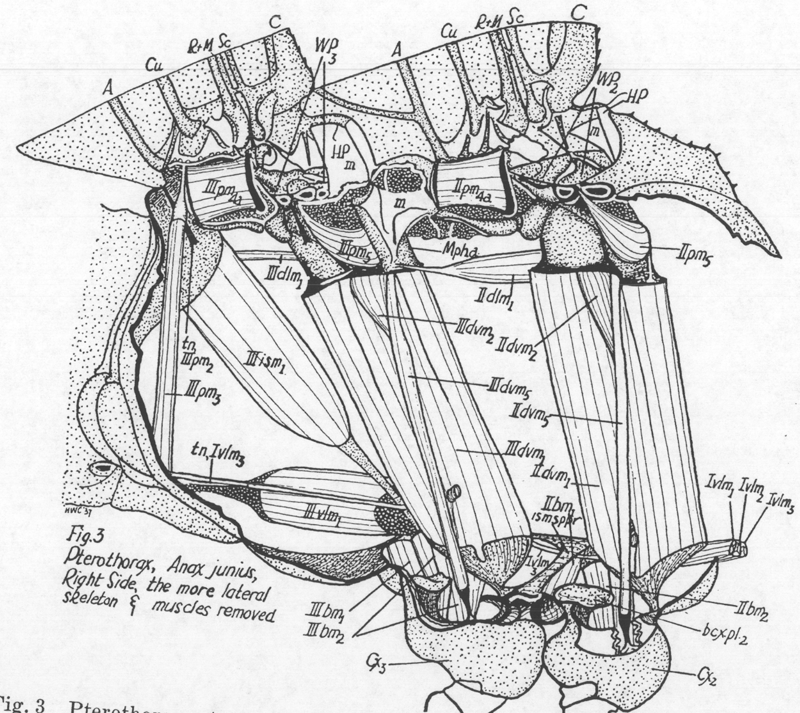



Fig. 3 Pterothorax, Anax junius, right side, lateral view, the more lateral skeleton and muscles removed. Compare with figure 2. The drawing shows the lateral side of $dvm_1$, with $dvm_{2-5}$, the leg muscles $bm_{1-2}$ the wing muscles $pm_{4a,5}$, and the lateral insertion of $dlm_1$.

III-IIdvm$_5$. Notocoxal (figs. 3, 5). Named by Berlese. Homologues: Voss, M. dorsoventralis I or VI, elevator coxae. Muscle I, tergal promotor of the leg, Snodgrass (p. 189, '35).

A segmental, dorsoventral, notocoxal, long, thin, lateral, leg-wing muscle. The dorsal attachment (origin ?), is from the lateral edge of the notal squame of $dvm_1$, just anterior to the insertion of $dvm_2$ (fig. 3). $Dvm_5$ lies against $dvm_1$ and



the anterior edge of $dvm_2$, passes ventrad laterally to $dvm_1$ through a notch in the stalked ventral cup-tendon of $dvm_1$, to insert into a small cap-tendon which in turn inserts into the latero-anterior edge of the basicoxa of the leg. The function is problematical, but it is most likely a leg muscle more than a wing muscle, and abducts the third leg, promotes the second leg.

III-IIdvm$_6$, Anterior coxoalar, anterior accessory wing elevator (figs. 2, 4, 5). Name original, positional. Homologues in other insects, none. Sub-homologue, Voss, M. dorsoventralis quartus. Subalar muscle 3 E″ of Snodgrass (p. 232, '35), has the same origin, but not the same insertion or function. Peculiar to Odonata, Maki, page 313.

A segmental, dorsoventral, lateral, coxoalar, epimeral, leg-wing muscle. The fusiform muscle (fig. 2), has its ventral attachment on the anterior part of the meron of the coxa (fig. 5), and extends dorsad to the dorsal attachment, a cap-tendon which inserts into a semi-detached notal plate (sclerite a, Snodgrass ('35) p. 220, fig. 123 B). Function: denoted by the name. There is some possible leg action, and if so, it is remotion for the second leg, adduction for the third leg.

III-IIdvm$_7$, Posterior coxoalar, posterior accessory wing elevator (figs. 2, 4, 5). Positional name original. Homologue in the cricket, M. dorsoventralis II or III, Voss. In Cicada, Coleoptera, Lepidoptera, Berlese. See $dvm_6$. Peculiar to Odonata, Maki.

A segmental, dorsoventral, lateral, epimeral, coxoalar, leg-wing muscle. The fusiform muscle (fig. 2), is flat, heavier than $dvm_6$, has its ventral attachment on the meron of the coxa posterior to $dvm_6$, and extends dorsad into both sides of a flat, transparent tendon which is the dorsal attachment, inserting into a notal plate attached to the posterior-lateral part of the alinotum, between the notum and the anterior part of the axillary plate (fig. 4). Since there are two distinct fasciculi, the muscle may be regarded by some as a double muscle, lying between $dvm_1$ and $pm_1$, posterior to $dvm_6$. Function: See $dvm_6$.

(*b*) *Pleural muscles.* III-IIpm$_1$, Pleuroradial, posterior depressor of the wing (figs. 2, 4, 5). Named by Berlese. No homologue, but subhomologue of seventh and eighth laterals of Voss, Berlese, page 404. Exact homologue of Snodgrass' 1E″, epimeral subalar (p. 232, '35).

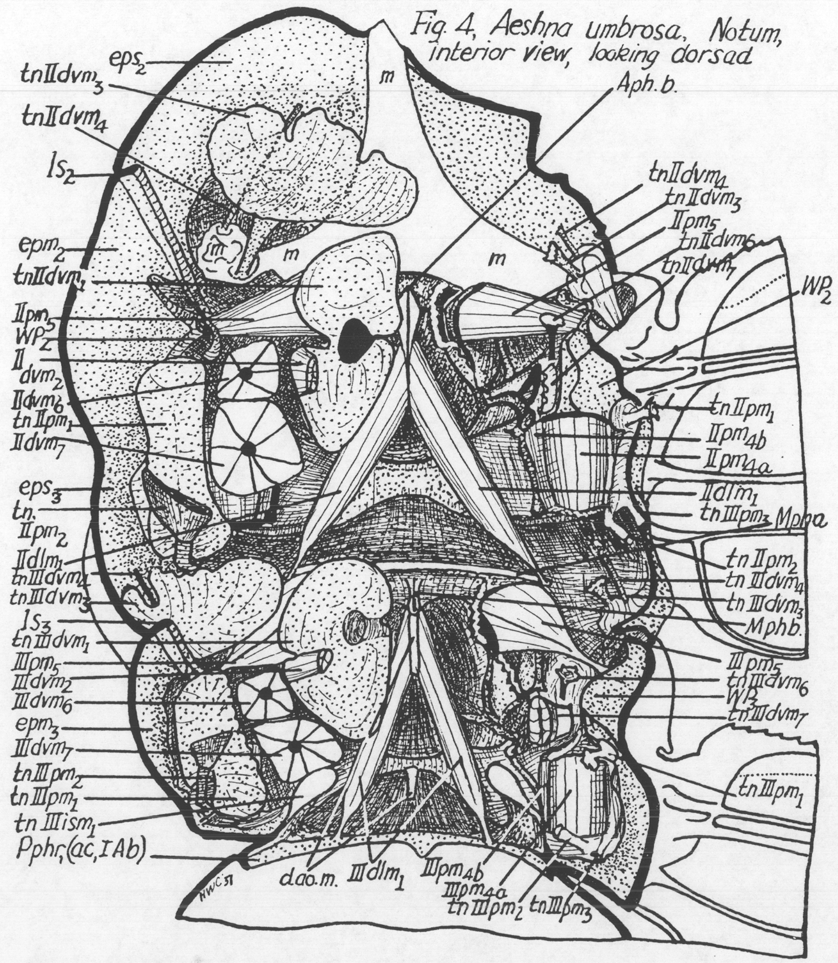



Fig. 4 Pterothorax, Aeschna umbrosa, notum, interior view, looking dorsad. For the appearance before dissection, see the right side of figure 5. On the left side of figure 4, the cap-tendons have been left intact. On the right side, they have been removed, but the stumps may be seen. The drawing shows the dorsal muscles intact.



A segmental, dorsoventral, pleurotergal, lateral, epimeral, subalar, large and powerful muscle (fig. 2). The origin is by fleshy fibers from the ventral region of the epimeron, which is heavily sclerotized. Pm$_1$ extends dorsad and slightly posteriorly, to insert into a large cap-tendon, which in turn inserts into the basal wing membrane, axillary region, just beneath the wing veins Sc and R-M (region radiale, Berlese). Function: the muscle depresses the posterior portion of the hind wing. Further analysis is given below, under muscle mechanism.

III-IIpm$_2$, Pleuroaxillary, anterior accessory of the posterior depressor. Named topographically, for attachment near axillary region. Homologues: See under pm$_1$ (figs. 2, 3, 4, 5).

A segmental, dorsoventral, pleurotergal, lateral, epimeral, subalar, large wing muscle (fig. 2), originating posterior and mesad to pm$_1$, from the heavy sclerotization of the ventral part of the epimeron. The muscle extends dorsad in the same direction as pm$_1$, mesad and posterior to pm$_1$, inserting in a cap-tendon which inserts in turn into the basal wing membrane, near the anal vein. The cap-tendon passes through a notch in the cap-tendon of pm$_1$. Function: See pm$_1$.

III-IIpm$_3$, Pleurocubital, posterior accessory of the posterior depressor (figs. 2, 3, 4, 5). Named topographically, for attachment near cubital wing vein. Homologues: See under pm$_1$.

IIIpm$_3$ is a segmental, dorsoventral, pleurotergal, lateral, epimeral, subalar, small wing muscle (figs. 2, 5), having its origin by fleshy fibers from a distinct apodeme at the posterior ventral edge of the epimeron, just anterior to the antecosta of the first abdominal pleuron. The muscle extends dorsad to insert into a pale elastic tendon attaching to the basal wing membrane, just laterad and slightly anterior to the cap-tendon insertion of pm$_2$, near the cubital wing vein. IIpm$_3$ is much shorter than IIIpm$_3$, and differs in origin (fig. 2). IIpm$_3$ originates from an intersegmental ridge between the meso- and metathorax, just above the metathoracic spiracle, in some genera (Anax), by a short tendon, in other genera

(Pachydiplax), by fleshy fibers from the intersegmental ridge. The function of $pm_3$ is described under $pm_1$.

III-II$pm_{4a, 4b}$. Fulcroalar a, b, depressors of the hind margin of the wing (figs. 3, 4). Name adapted from Chabrier, Berlese. Homologues: one of the three heads of the flexor of the wing, Strauss-Dürckheim, Berlese. M. lateralis XII, Voss; muscle D, Snodgrass (p. 188, '35). Not a wing flexor in Odonata, Anisoptera.

The muscles are segmental, tergopleural, fulcronotal, axillary, lateral, epimeral, wing muscles, very small and intimately associated. $Pm_{4a}$ is ventral, and lateral, to $pm_{4b}$. The origins are a discoidal, short tendon for each muscle, from the posterior apex (subalar arm), of the wing or fulcral process. The very small cylindrical muscles lie just under the axillary plate, between the wing veins R-M and the anal vein. The insertions are small and short, stalked disc-tendons which are attached to the latero-posterior part of the alinotum and involve the axillary plate and the region of the axillary cord. Function: depressors of the hind margin of the wing. A more complete analysis is given later.

III-II$pm_5$, Fulcronotal, wing pronator (figs. 3, 4). Positional name original. Functional name suggested by Snodgrass. Homologues, M. lateralis X, XI, Voss, page 388. Subhomologue, muscle 3B, Snodgrass, a highly variable tergopleural muscle (pp. 187, 188, fig. 103B, '35).

A segmental, tergopleural, episternal, transverse, wing muscle, very small, pyramidoidal in shape. The muscle attaches by a rounded tendon from the wing process at the pleural ridge; it extends mesad to attach by fleshy fibers into a semi-detached notal sclerite, plate a, figure 123B, Snodgrass ('35), which rises from the anterolateral part of the alinotum. Function: The muscle pronates the wing along its long axis.

III-II$pm_6$, Episternocoxal, abductor of the third leg, abductor-promotor of the second leg (figs. 2, 5). Positional name original. Functional name suggested by Snodgrass. Homologues: M. lateralis IV, V, Voss; "manca in Libellulidi," Berlese, page 402; muscle M, Snodgrass (p. 190, '35), abductors of the coxa if the coxa has no sternal articulation, which is the case in Odonata.



A segmental, lateral, episternal, pleurocoxal, leg muscle. The broad, flat, heavy muscle originates (fig. 5), by fleshy fibers from a heavy ridge between the episternum and infraepisternum, and extends ventrad to the lateral coxal base, laterad to $pm_7$, inserting here by a broad flat tendon. Function: see name.

III-II$pm_7$, Episternotrochanteral, abductor of the leg, pleural depressor of the telepodite (fig. 5). Positional name original, functional name suggested by Snodgrass. Homologues: M. lateralis III, meso-metathoracis, Voss. "Nei soli Gryllus," Berlese, page 402; muscle M, Snodgrass (p. 190, '35), abductor of the coxa.

A segmental, lateral, episternal, pleurotrochanteral, leg muscle, pyramidoidal in shape; its origin is by fleshy fibers from the pleural ridge with $pm_6$, mesad to $pm_6$; the muscle tapers ventrad to the trochanter, where it inserts on the trochanteral apodeme with $bm_2$. Function: double, see name.

(*c*) *Sternal muscles of the thorax.* III-II$bm_1$, Sternocoxal, adductor-rotator of the third leg, remotor-adductor-rotator of the second leg (figs. 3, 5). Positional name original; multiple functional name from Snodgrass. Homologues: M. pedalis II, III, IV, Voss, muscles L, N, Snodgrass, rotator-adductor (pp. 189, 190, '35). In the dragonfly, the anterior rotator, the adductor, and the posterior rotator may be combined as this muscle $bm_1$.

A segmental, sternocoxal leg muscle, very heavy and flat, and composed of several bundles which might be resolved into two or even three muscles. This is discussed under the muscle mechanism, below. The origin is by fleshy fibers from the sternal infolding; the insertion is ventrad on a wide area of the posteromesal coxal rim. Muscle $bm_1$ lies under $bm_2$. Function: see discussion under muscle mechanism, below.

III-II$bm_2$, Sternotrochanteral, adductor of the leg, sternal depressor of the telepodite (figs. 3, 5). Positional name original. Functional name from Snodgrass. Homologues, M.

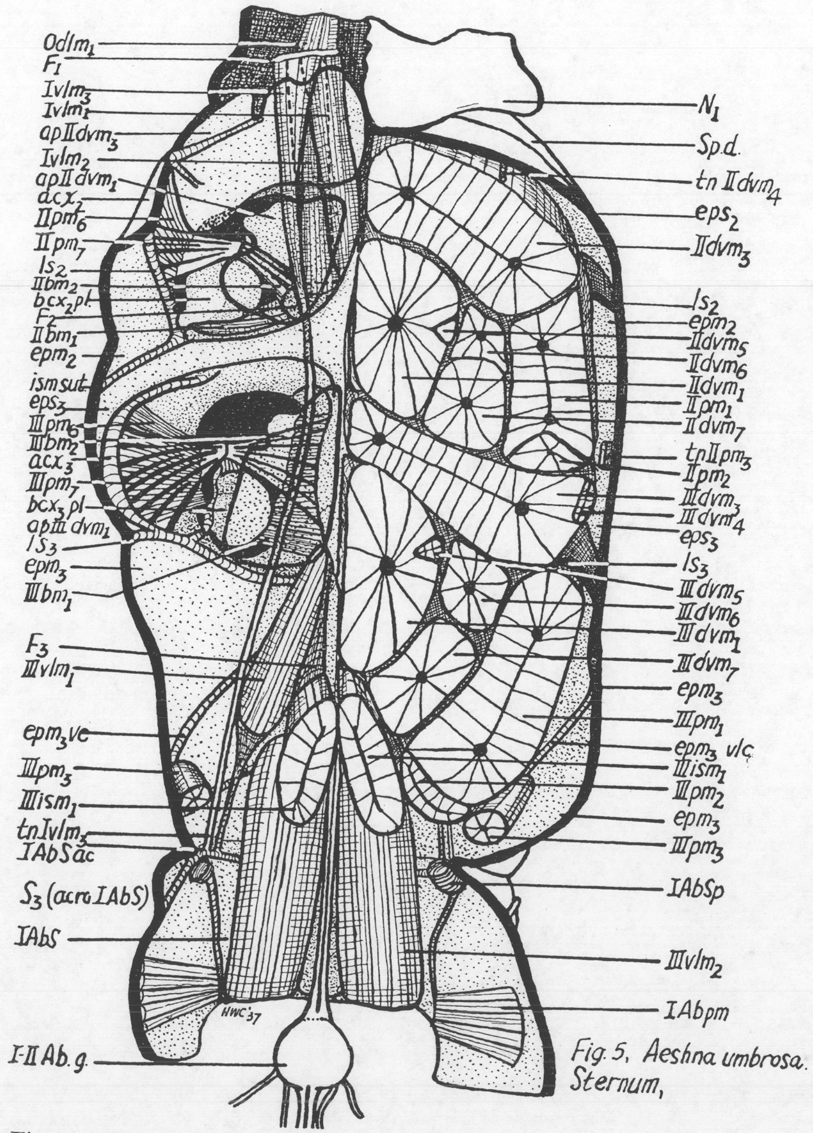



Fig. 5 Sternum, pterothorax, Aeschna umbrosa, interior view, looking ventrad. On the right side, the pterothorax has been cut at about the level of the pleural attachment of $IIIpm_3$, obtaining a frontal section of the sternum and a cross section of most of the dorsoventral and pleural muscles. On the left side, the dorsoventral, pleurotergal, and notocoxal muscles have been removed, with the lateral skeleton down to the level of the infraepisternum. The ventral attachments of $dvm_1$, $IIdvm_3$ have been rendered in outline only, to show the structures beneath them when they are removed. Muscles $Ivlm_{1-2-3}$ are intact, also leg muscles $pm_{6-7}$, $bm_{1-2}$.





pedalis IV, Voss, muscle N, Snodgrass (p. 190, '35), adductor of the coxa.

A segmental, sternotrochanteral, flat, heavy, powerful, pyramidoidal muscle. The origin is by fleshy fibers from the sternal infolding, over $bm_1$; tapering ventrad to the insertion, the muscle inserts with $pm_7$ into the trochanteral apodeme. Function: See name. Discussion is given under muscle mechanism, below.

ANNOTATED LIST OF THE MUSCLES IN TABLE 2, PROTHORAX

*1. Intersegmental muscles*

(*a*) *Ventral.* $Ovlm_1$, Chiasmatic coxojugular (figs. 1, 6, 7). Name suggested in part by P. P. Calvert. Homologues, M. "micro" sterni, II, Voss, page 439. The description of this muscle agrees almost exactly with that of Voss for G. domesticus. An intersegmental, chiasmatic, ventral, paired, longitudinal, small, long, ribbon-like, flat muscle, tapering anteriorly and posteriorly. The origin is by a flat transparent tendon from the middle of the dorso-mesal part of the lateral cervical sclerite, or jugular process. The "untermittel kräftige Muskel" crosses over the nerve cord and its fellow muscle from the opposite side of the body, extending posteriorly to the coxa of the opposite side of the body, where it inserts on the antero-basicoxal rim by a long thin rounded tendon near the point of articulation of coxa and pleuron. The muscle originating left seems to pass over the muscle of the right side origin, in most cases examined. Voss thinks that the muscle might act as a rotator, but suggests that it may play a part in ecdysis, pages 439 to 440.

$Ovlm_2$, Profurcocephalic, depressor capitis (figs. 1, 6, 7). Positional name original; functional name suggested by Luks (Voss, p. 440). Homologues: M. "micro" sterni Voss; "manca in Libellulidi," Berlese, p. 418. He is in error.

An intersegmental, lateral, ventral, longitudinal, long, flat, tapering anteriorly, muscle. The insertion is fleshy fibers from the anterior dorsal face of the profurca; the muscle tapers anteriorly to end in a long thin tendon of origin; rising from the sternal rim of the posterior cephalic foramen, near the point of articulation with the jugular process (fig. 7). The function is expressed in part by the name depressor capitis; other functions appear to be retraction and abduction of the head.

$Ivlm_1$, Internal promesofurcal (figs. 1, 3, 5, 6). Prosternal retractor. Positional name original; functional name suggested by Luks (Voss, p. 419). Homologues: M. prosterni III-IV-V, Voss, page 419.

An intersegmental, longitudinal, ventral, sub-median, flat, thin, ribbon-like muscle. The origin is by fleshy fibers from the posterior, dorsal face of the profurca (fig. 6); the muscle (fig. 5) passes posteriorly beneath the ventral episternal plate of origin of $dvm_{3-4}$, mesad to $Ivlm_{2-3}$, to insert on the point of fusion of the process ismsppr, the mesosternal infolding, and the true mesofurca, which stands out like a cup handle. Function: Retractor of the prothorax, with the synthorax as a fixed point.

$Ivlm_2$, External promesofurcal, prosternal retractor (figs. 1, 3, 5, 6). Positional name original; functional name by Luks. Homologues in other insects, see $Ivlm_1$.

An intersegmental, longitudinal, ventral, lateral, flat, thin, ribbon-like muscle. The origin is the same as $Ivlm_1$ (fig. 6), laterad to $Ivlm_1$; the muscle passes posteriorly, laterad and slightly ventrad to $Ivlm_1$ (fig. 5), to insert on the cup-handle-like mesofurca, the true larval mesofurca fused with the infolded mesosternum. Function: with $Ivlm_1$, retractor of the prothoracic sternum.

$Ivlm_3$, Profurco-abdominal (figs. 1, 3, 5, 6). My positional name agrees with that of Maki, but he lists the muscle as a metathoracic muscle. Homologues: Knox, $vlm_1$, in the mayfly larva, page 155; present in Zygoptera, Maki, page 136.

An intersegmental, longitudinal, ventral, lateral, very small muscle with a very long posterior tendon (fig. 5), the ensemble jumping three segments of the body, which is rather unusual. I regret that I have not been able to work out the larval state of the muscle. The origin is by fleshy fibers from the lateral posterior dorsal face of the profurca (fig. 6); the belly



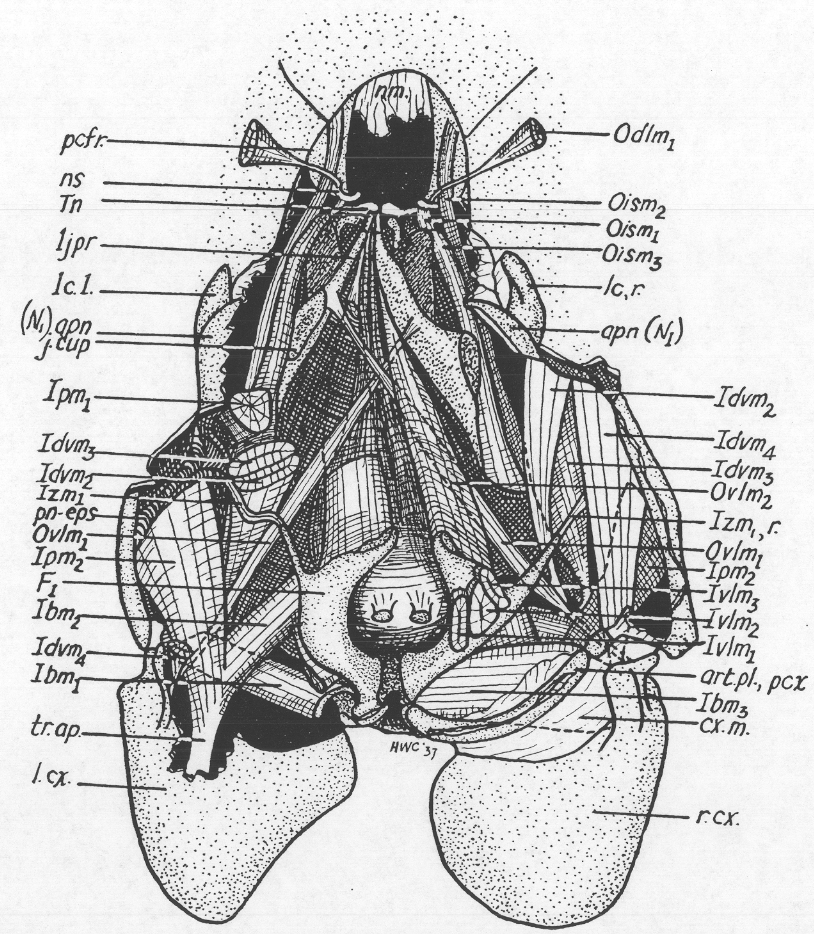



Figure 6, Prosternum, P. lydia.

Fig. 6 Prosternum, Plathemis lydia, looking ventrad and cephalad, interior view. The entire pronotum and the dorsal neck membrane have been removed, with $Odlm_1$, $Idlm_{1-2}$, $Idvm_1$. Note tendon of $Odlm_1$. The left $Ipm_1$ and $Idvm_{2-3}$ are cut near notal insertions; $Idvm_4$ near coxal insertion, $Ibm_3$ near the profurca, and removed, with $Izm_1$, left. The left $Ovlm_2$ is cut near both attachments, to show the cross-over of $Ovlm_1$, left and right. The left coxa is cut away to show the common trochanteral apodeme of $Ipm_2$, $Ibm_2$. $Ivlm_{1-2-3}$ are left as stumps on the right $F_1$.

of the muscle is short, and ends, at the mesofurca (fig. 5), in a thin, transparent, long tendon, which passes over the mesofurca, under the intersegmental sternopleural process, proceeding posteriorly laterad to $IIIvlm_1$, to insert on the antecosta of the first abdominal sternum, laterad to the tendon of $IIIvlm_1$ (figs. 1, 5). The function is problematical, but the muscle $Ivlm_3$ must act in part with III $vlm_1$ as a protractor of the first abdominal sternum, and as a retractor of the prothoracic sternum with $Ivlm_{1-2}$.

(*b*) *Dorsal muscles of the prothorax.* $Odlm_1$, Pronotocephalic, elevator capitis (figs. 1, 6). Positional name original, functional name from Strauss-Dürckheim (Berlese, p. 418), "elevateur de la tete." M. "micro" noti (pronoti) I, Voss, page 441. Many insects have dorsal muscles from the prophragma to the head, from the pronotum to the head, or either or both.

An intersegmental, dorsal, longitudinal, long, powerful, muscle, which tapers anteriorly (fig. 1). The insertion is fleshy fibers from the antecosta of the pronotum ($AcN_1$) a median process which assumes various shapes in the different genera. The tendon of origin (fig. 7), is a thin, rounded tendon which inserts into the latero-tergal posterior cephalic foramen rim, near the tentorial-occipital junction, the axis for the movements of the head. Functions assigned to homologues of the muscle are retraction, rotation, elevation. Contraction of one side would seem to abduct the head, contraction of the left and right together would seem to retract the head; the muscle may also help rotate the head. Elevation is effected largely by $Oism_2$ assisted by $Odlm_1$.

$Idlm_{1-2}$, Pro-mesonotals, pronotal retractors (fig. 1). Positional name original. Functional name in part from Burmeister, Luks (Voss, p. 422). Homologues: M. pronoti III, b, Voss, page 422. Many insects have one or more pro-mesonotal muscles.

$Idlm_1$ is the external promesonotal muscle, intersegmental, dorsal, longitudinal, thick, flat, and heavy. The origin is by fleshy fibers from the lateral side of the pronotal median



antecostal process, $AcN_1$; the muscle connects the pro- and mesothorax by inserting into the ventral lip of the spiracular dorsum, and the lateral sides of the median process Apha.

$Idlm_2$, the internal promesonotal muscle, is not constant, and may be, in instances observed, a larval rudiment, not yet

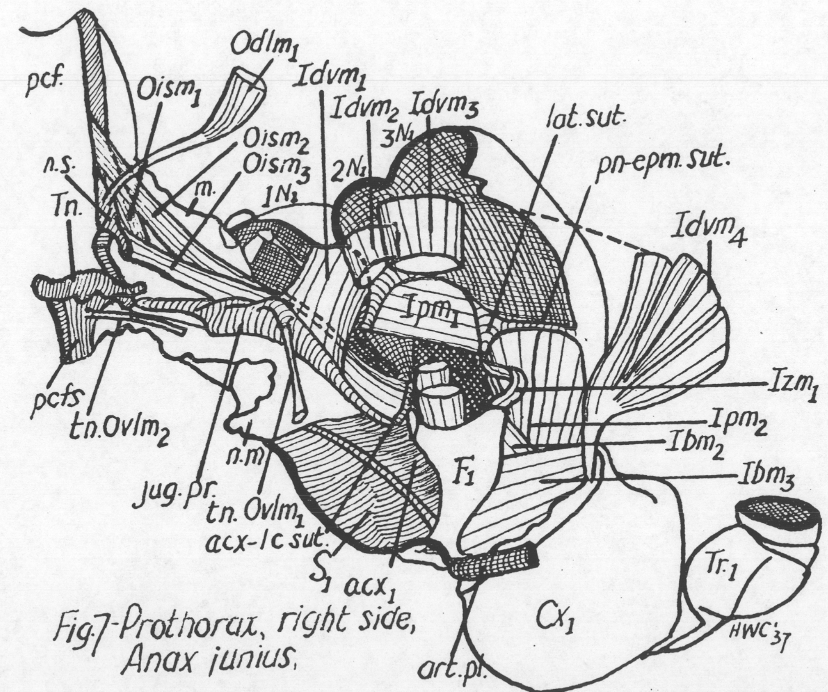



Fig. 7 Prothorax, Anax junius, right side, interior view, looking laterad and cephalad. The prosternum and the ventral neck-membrane have been cut along the mid-line to the head. The pronotum and the dorsal neck membrane have been cut more laterally, to show the lateral prothoracic muscles. Compare with figure 6. $Odlm_1$, $Idlm_{1-2}$ have been removed. Muscles $Ovlm_2$, and $Ovlm_1$ are in fragments. $Idvm_{2-3}$ have been cut and removed to show $Ipm_1$. $Idvm_4$ is intact, but laid aside to show $Ipm_2$. Note the sternal attachments of $Oism_{2-3}$.

resorbed. It is an intersegmental, dorsal, longitudinal, submedian, muscle pair extending between the processes Apha, $AcN_1$, as a thin ribbon-like band. Observed by me in two Anax out of eight; seen by Maki in Crocothemis servilia. Function: with the pterothorax as a fixed point, $Idlm_{1-2}$ retract the pronotum. $Idlm_1$ may also afford some slight prothoracic rotation.

(*c*) *Dorsoventral muscles of the prothorax.* $Oism_1$, Jugular-cephalic, rotator capitis (figs. 6, 7). Positional name in part from Berlese. Functional name from Luks (Voss, p. 445). Homologues: M. dorsoventralis II, III, IV, "micro" thoracis, Voss; "molto constante e comune, manca in Vespa," Berlese, page 421.

An intersegmental, (?) dorsoventral, lateral, short, flat, ribbon-like, very small muscle, first reported by Maloeuf. The writer, in checking Maloeuf, found that the muscle varies in origin and insertion. In Anax (fig. 7), the muscle rises from a raphe on the lateral surface of $Oism_3$, near its anterior end, which contains a plate which may be a displaced neck-plate. In Plathemis lydia (fig. 6), the origin is from a neck-plate embedded in the neck membrane, and forms the anterior attachment of $Oism_3$. The neckplate here is closely associated with the jugular process (internal process of the lateral cervical sclerite). The head attachment is likewise variable. In Anax (fig. 7) the muscle passes dorsally to the posterior cephalic foramen rim, to insert (?) with $Oism_2$. In Plathemis lydia (fig. 6) the muscle passes dorsally and inserts (?) on the neck-spur of the rim, appearing to the causal observer as the continuation of $Oism_3$. $Oism_1$ may be completely absent in some genera, and present in some, and absent in other, specimens of the same species. The terms origin and insertion are questioned, since the muscle connects between the head and the sternum. The intersegmental nature is questioned, since the line of demarcation between head and prothorax is imaginary. The muscle plays a part in the complex action of rotation of the head.

$Oism_2$, External precoxal-cephalic, elevator-rotator-abductor-retractor capitis (figs. 6, 7). Positional name original, multiple functional name in part from Luks (Voss, p. 444). Homologues: M. rotator capitis externus II, Voss, page 442; present in all orders, Maki, table XIX, page 313.



An intersegmental, dorsoventral, lateral, long, flat, slender, powerful, neck muscle. The prothoracic attachment (figs. 6, 7) is by fleshy fibers from a ridge between the precoxa of the first leg, and the lateral cervical sclerite. The muscle extends dorsad and cephalad, to attach by fleshy fibers into the latero-tergal posterior cephalic foramen rim, and lies just beneath the neck-membrane for a great part of the length of the muscle. The principal function of the muscle, when acting with its mate of the opposite side, seems to be that of elevation. Secondary functions: retraction, acting with $Odlm_1$, $Ovlm_2$, $Oism_3$ (all pairs acting in unison); rotation, acting with $Oism_{1-3}$; abduction, with $Odlm_1$, $Ovlm_2$, $Oism_3$, one side acting only. The muscle is an important neck muscle.

$Oism_3$, internal precoxal-cephalic, abductor-rotator-retractor-capitis (figs. 6, 7). Positional name original; functional name in part from Luks (Voss, p. 445). Homologues: M. dorsoventralis II "micro" thoracis, or III, "micro" thoracis, Voss, page 445. Present in all orders, Maki, page 313.

An intersegmental, dorsoventral, lateral, long, flat, slender, powerful, neck muscle. The origin (figs. 6, 7) is the same as, but mesad, to $Oism_2$. In Anax (fig. 7), the head attachment is by fleshy fibers to the neck-spur on the tergal posterior cephalic foramen rim, near the tentorial junction. The term origin is doubtful, since the muscle may originate in the head, but there is also the ventral attachment. In Plathemis lydia (fig. 6), the head attachment is on the neck-plate which gives rise to $Oism_1$. In Crocothemis Maki finds $Oism_3$ arising on the upper side of $Oism_2$. $Oism_3$ lies mesad and parallel to $Oism_2$ for the greater part of its length. Function: Complex, like $Oism_2$; acting alone, it may abduct the head to one side, pulling on the neck-spur in Anax, pulling on the neck-membrane in Plathemis. Rotation, a complex action, occurs when it acts with $Oism_{1-2}$; retraction occurs when $Oism_3$ acts with its mate of the opposite side in unison with other retractors. $Oism_3$ is an important, complex, neck muscle.

### 2. *Segmental muscles of the prothorax*

(*a*) *Dorsoventral.* $Idvm_1$, Pronotal-jugular, rotator capitis (?) (figs. 1, 6, 7). Positional name original; functional name in part from Luks (Voss, p. 444). Homologues: M. intersegmentalis "Micro" thoracis, Voss, page 444; present in all orders, Maki, page 313.

A segmental, dorsoventral, lateral, thick, heavy, flat muscle. The origin (fig. 7) is by fleshy fibers from the jugular process, the insertion is by fleshy fibers into the lateral part of the anterior lobe of the pronotum. The term segmental is doubtful, since the imaginary line between head and prothorax is not defined. Function: Rotation of the head, but just how, is not known.

$Idvm_{2-3}$, Anterior notocoxal, muscles a-b, promotors of the coxa of the first leg (figs. 6, 7). Name adapted from Berlese, notocoxal, in the synthorax. Functional name from Snodgrass. Homologues: M. lateralis IV, V, prothoracis, Voss, page 426; muscle I, sometimes double, tergal promotor of the leg, Snodgrass (pp. 189, 201, '35). Present in all but Neur., Mec., Trich., Lepid., Diptera, Maki, p. 313.

The muscles are segmental, dorsoventral, fan-shaped, powerful, notocoxal, leg muscles. The origins are by fleshy fibers from the second and part of the third pronotal lobes, laterally, muscle *a* mesad to muscle *b*. The muscles narrow into tendons ventrally, and insert into the latero-anterior basicoxa, muscle *a* anterior to muscle *b*. Functions: the muscles pull the coxa up, anteriorly, promoting the first leg.

$Idvm_4$, Posterior notocoxal, remotor of the coxa of the first leg (figs. 1, 6, 7). Name from Berlese, see $Idvm_{2-3}$. Functional name, from Snodgrass. Homologues: M. dorsoventralis II prothoracis, Voss, page 424, VII, page 425; muscle J, a single or group of muscles, tergal remotor(s) of the leg, Snodgrass (pp. 189, 202, '35). Present in all but Diptera, Maki, page 314.

A segmental, dorsoventral, notocoxal, lateral, composite, fan-shaped, powerful, leg muscle. The origin is by fleshy fibers from the posterior (third) lobe of the pronotum, posterior and mesad to $Idvm_3$. The tripartite muscle extends ventrad, mesad to $Idvm_3$, to insert by a heavy tendon into the posterior lateral basicoxal rim. The muscle(s) pull the coxa up and posteriorly, remoting the first leg.



(*b*) *Pleural muscles.* $Ipm_1$, Pronotal-episternal (fig. 7). Positional name original, there is no apparent function. Homologues: M. lateralis XII prothoracis, Voss, page 429; present in all insects excepting Thysanoptera, Maki, page 314.

A segmental, lateral, pleural (episternal) short, thick, stumpy muscle, extending between the episterno-notal suture and the prothoracic pleural ridge, inserting at both ends by fleshy fibers. Function: Maloeuf believes that "there is no apparent function other than the offering of skeletal substantiality," page 100. A possible function is the pulling-in of the hypodermis during ecdysis.

$Ipm_2$, Proepimeral-trochanteral, abductor of the first leg, tergo-pleural depressor of the telepodite (figs. 6, 7). Positional name original. Functional name from Snodgrass. Homologues: Musculus dorsoventralis VIII prothoracis, Voss, page 425; a modification of muscle M, functional abductor, muscle 133c, body branch of the depressor of the trochanter, Snodgrass (pp. 202, 205, '35). Present in all but Plec., Psoc., Neuroptera, Maki, page 314.

A segmental, tergopleural-trochanteral, epimeral, lateral, fan-shaped, powerful, doubly-functioning leg muscle. The origin (figs. 6, 7) is by fleshy fibers from a ridge between the third prothoracic notal lobe, and the proepimeron; the muscle extends ventrad, tapering into the common trochanteral apodeme which arises from the ventral trochanteral lip, in common with $Ibm_2$ (fig. 6). Function: see functional name.

(*c*) *Sternal muscles of the prothorax.* $Ibm_1$, Prosternal-anterocoxal, anterior rotator of the first leg (fig. 6). Positional name original; functional name from Snodgrass. Homologues in other insects: M. pedalis prothoracis, I, Voss, page 429; muscle K, Snodgrass, anterior rotator (pp. 201, 202, '35). Present in all orders but Psoc., Ephem., Coleoptera, Maki, page 314.

A segmental, sternocoxal, flat, ribbon-like, leg muscle, originating by fleshy fibers from the prosternum just beneath and anterior to the profurca; the muscle extends laterad and slightly cephalad, to insert into the latero-anterior coxal rim. Function: See name; there may also be some slight adduction.

$Ibm_2$, Profurcotrochanteral, adductor of the first leg, sternal depressor of the telepodite (figs. 6, 7). Positional name original; functional name from Snodgrass. Homologues: M. pedalis IV prothoracis, extensor, elevator trochanteris, Voss, page 430. Muscle N, adductor of the coxa, muscle 133d, sternal body branch of the depressors of the telepodite, Snodgrass (pp. 201, 202, 205, 206, '35). Present in all but Trich., Lepid., Col., Isop., Embi., Psoc., Ephem., Maki, page 314.

A segmental, profurcotrochanteral, flat, ribbon-like, leg muscle, originating by fleshy fibers from the lateral edge of the profurca; the muscle extends ventrad between $Ibm_1$ and $Ibm_3$ to insert on a common trochanteral apodeme with $Ipm_2$. Function: see functional name.

$Ibm_3$, Profurco-posterocoxal, posterior rotator of the first leg (figs. 6, 7). Positional name original; functional name from Snodgrass. Homologues: M. pedalis VII, Voss, page 430, muscle L, posterior rotator, Snodgrass, pages 201, 202. Present in all but Derm., Thysan., Maki, page 314.

A segmental, flat, sternocoxal, ribbon-like leg muscle. The origin is by fleshy fibers from the lateral profurcal basis and side; the muscle extends laterad, inserting by a broad flat tendon along the posterocoxal rim, directly anterior to the articulating plates of the prothorax, under the coxal corium. Function: see name; there may also be some adduction.

$Izm_1$, Prosternopleural, profurcopleural (figs. 6, 7). Positional names original, adapted from Snodgrass. Homologues: M. furcae lateralis prothoracis, Gabelseiten-muskel, Voss, page 431; muscle G, Snodgrass, pleurosternal muscle (p. 189, '35). Found by Maki in Orth., Plec., Psoc., Odon., Thysan., Hemip., Hymenoptera, page 314.

A segmental, pleurosternal, small, flat, ribbon-like muscle. The origin is by a long, flat, transparent, tendon drawn out



from the profurca; the muscle extends laterad, to insert by a flat short tendon, into the pleural ridge, near the pronotum. Smaller species of the Odonata have very transparent muscles, quite hard to see. The function is problematical, "l'elevateur du corselet, Strauss Dürckheim, elevator prothoracis, Burmeister u. Luks," (Bauer, in Korschelt, p. 594).

## GENERAL REMARKS ON THE MUSCLES AND THEIR MECHANISM

The thoracic musculature of the adult anisopterous dragonfly is highly specialized, powerful, efficient, and is greatly simplified, when compared with the larval musculature (the study of which is still in progress) or the more primitive musculature of an orthopteroid insect such as Gryllus domesticus, as reported by F. Voss ('05). Comparison of my results with those of Voss are shown in table 3, below.

TABLE 3

*A comparison of the thoracic musculature between Odonata as reported by the writer, and Orthoptera (Gryllus domesticus), as reported by F. Voss ('05). Stigma muscles are excluded*

| MUSCLES | ODONATA | | | | G. DOMESTICUS | | | |
|---|---|---|---|---|---|---|---|---|
| Segment | Meta | Meso | Pro | Total | Meta | Meso | Pro | Total |
| Intersegmental ventral | 2 | 0 | 5 | 7 | 3 | 3 | 12 | 18 |
| Dorsal | 0–1 | 1 | 3–2 | 3–5 | 4 | 4 | 5 | 13 |
| Dorsoventral | 1 | 0 | 3 | 4 | 1 | 1 | 6 | 8 |
| Segmental dorsoventral | 7 | 7 | 4 | 18 | 6 | 7 | 7 | 20 |
| Pleural | 8 | 8 | 2 | 18 | 12 | 13 | 9 | 34 |
| Sternal | 2 | 2 | 4 | 8 | 6 | 9 | 8 | 23 |
| Total | 20–21 | 18 | 20–21 | 58–60 | 32 | 37 | 47 | 116 |

From the standpoint of evolution of actual flight muscles, it appears to the writer that the dragonfly adult has progressed far beyond the cricket, and, in contrast to the opinion of Snodgrass, conforms closely to the general plan of arrangement of wing musculature in all pterygote insects, excepting that the flexing mechanism is lost. A comparison with the account of Snodgrass for a generalized insect is brought out in the following discussion, to show how close the actual conformation occurs.

The wing of most insects is capable of four cardinal movements (see Snodgrass, '27, p. 64), elevation, depression, flexion, extension, and in addition, the wing is capable of a slight rotation on its long axis. In Odonata, there are but two cardinal movements, elevation and depression; in addition, the wing rotates, or pronates, on its long axis. The action may be compared with a sculling action, as in rowing a boat. The wing is a lever, swinging on a fulcrum formed by the wing process. The muscles which elevate the wing are mesad to the fulcrum, forming on the upstroke a lever of the first order, with the fulcrum between the power and the weight; the muscles which depress the wing attach to the wing base laterad to the fulcrum, forming on the downstroke a lever of the third order, with the power between the fulcrum and the weight. The mechanism of the wing action has been analyzed by Tillyard, Snodgrass, '35, and Sargent. Lengthier accounts are contained in these papers.

Elevation, or the upstroke of the wings, is effected in Odonata, as in other insects, by direct and indirect wing muscles. All wing elevators in the dragonfly are mesad to the fulcral or wing process. The direct wing elevators on both alate segments are exact homologues, the coxoalar muscles, $dvm_{6-7}$. These muscles are the only ones which differ from the 1935 account of Snodgrass for wing muscles in the generalized insect. Their origin is on the meron of the coxa, as is the subalar muscle 3E″ of Snodgrass, but instead of attaching to what might be the subalar region, they attach to a semi-detached notal sclerite which articulates with the wing base humeral process, and to a more posterior semi-detached notal plate. The Odonate coxoalars elevate the wing, while the coxoalars of Snodgrass (subalars), depress the wing. Maki finds them peculiar to Odonata (table XIX, p. 314). Note, however, remarks under $dvm_7$, where Berlese finds a homologue.



The indirect wing elevators in Odonata are the exact homologues in each alate segment, the tergosternals $dvm_{1-2}$, and the notocoxal, $dvm_5$. The very large first tergosternal $dvm_1$ is the principal elevator; $dvm_2$ is very small, acting with $dvm_1$. The indirect principal elevators $dvm_{1-2}$ buckle down the notum, thus elevating the wing, are assisted in this action but slightly by the notocoxal, $dvm_5$. The tergosternals homologize with muscle C, tergosternal, of Snodgrass ('35); the notocoxal homologizes with muscle I, tergal promotor of the leg, Snodgrass, '35.

Depression, or the downstroke of the wings, is also effected, as in other insects, by direct and indirect wing muscles. The direct wing depressors are the pleuro-tergal, lateral muscles, consisting of the anterior group, the first and second basalars, $dvm_{3-4}$, and the posterior group (subalars), the pleuroalars $pm_{1-3}$ (pleuroradial, pleuroaxillary, pleurocubital, designated by the wing veins they most nearly attach to at the wing base). I agree with Maki in naming the basalars as such. The epipleural sclerites of the basalar group may be invaginated, in Odonata, becoming the cap-tendons of the basalars, instead of an external basalar plate. There is a close homology with muscle 1 E′ of Snodgrass, basalars, in function, origin, and attachments.

The basalars $dvm_{3-4}$ are intimately connected with the humeral angle of the wing (compare Snodgrass, fig. 103B, p. 187, '35, p. 231, '35). They may be classed also as pleural muscles, but their larval origin is not completely worked out, and they may be the larval coxoalar promotors. The pleuroalar muscles $pm_{1-3}$ might be called subalars, since the cap-tendons are possibly invaginated subalar sclerites. Indeed, Maki calls them pleuro-subalars. I have followed Berlese in the nomenclature in part, since his nomenclature clearly separates the three and designates attachment more clearly. Moreover, the coxosubalar group is displaced in Odonata, as noted above, under the wing elevators. The epimeral-subalar, 1 E″, of Snodgrass ('35), homologizes exactly with the pleuroalars $pm_{1-3}$ in Odonata.

The dragonfly basalar and pleuroalar (subalar) groups are the most powerful of the wing muscles. The basalars depress the anterior part of the wing; the pleuroalars depress the posterior part of the wing. Alternate action of one group, then the other group, will rotate the wing on its long axis, and simultaneous action by both groups will depress the entire wing, antagonizing the elevator action.

The indirect wing depressors in Odonata are the dorsal longitudinals, $dlm_1$, meso- and metanotal muscles, and the powerful $IIIism_1$, metathoracic intersegmental dorsoventral muscle. The meso- and metanotal muscles homologize with muscle A, median dorsal longitudinal muscle, of Snodgrass ('35). They indirectly depress the wings by restoring the notum to its original shape. The metanotal muscle $IIIdlm_1$ is reduced but present in the lower genera, and entirely absent in the higher genera, and when present probably has but little effect. The reduction is explained by the presence of the powerful $IIIism_1$, indirect wing depressor, which tends to reduce the action or necessity for a metanotal muscle. The necessity for an ism muscle in the mesothorax has been eliminated by the fusion of the meso- and metathorax. There is one present in the larva, however. Muscle $IIIism_1$ homologizes exactly with muscle F, lateral intersegmental, of Snodgrass (p. 189, '35).

The remaining wing muscles are the very small pleurotergal (fulcroalar) muscles, $pm_{4a-b}$, and the pleurotergal (fulcronotal) muscle $pm_5$, exactly homologized in each alate segment. These small muscles must play an important part in the more refined mechanism of flight, for each is attached to the fulcral or wing process, which is the axis upon which the wing acts. The Odonate fulcroalars, $pm_{4a-b}$, depress the hind margin of the wing, and correspond to the oblique lateral dorsal, 1A, of Snodgrass ('35) which is also a wing depressor, acting with the longitudinal tergals in the generalized insect. In Odonata, they also increase the curvature of the wing. Wing curvature is also increased by the pleuroalar (subalar) group, and is important in reverse movement (Snodgrass, '35). Another possible homologue is with the muscle D, axillary muscle, wing flexor, of Snodgrass ('35). Snodgrass finds that the axillary muscles, tergopleural in origin, are highly variable (p. 188, '35).



The Odonate fulcronotal muscle $pm_5$ seems to act in the opposite direction from the fulcroalars, and pronates the wing, rotating it along its long axis. It may be homologized with the variable muscle B of Snodgrass (p. 188, '35). Pronation is effected also by action of the basalars, and according to Snodgrass ('35, p. 235), is effected by action on the second axillary sclerite, which corresponds to the wing or fulcral process in Odonata, Snodgrass ('09, p. 554).

The fusion of the meso- and metathorax has obviated the necessity for mesothoracic longitudinal ventral muscles. They are present, however, in the larvae. The ventral longitudinal muscles of the metathorax provide for the protraction of the abdominal sternites, affording a ventral abdominal curvature necessary in egg-laying, copulation and the vestigial sting-reaction observed when a dragonfly is handled. Dragonflies do not require an abdomen for normal or nearly normal flight (personal observation).

The action of the prothoracic muscles may be shortly analyzed: the ventral muscles of the prothorax provide for the retraction of the prothoracic sternum, $Ivlm_{1-2}$, for retraction of the prothoracic sternum, $Ivlm_3$, and protraction of the first abdominal sternum, $Ivlm_3$; for depression of the head, $Ovlm_2$; for abduction (?) of the head, $Ovlm_1$. The extreme mobility of the head and prothorax requires more intersegmental muscles than do the other segments. The dorsal muscles of the prothorax provide for retraction and abduction of the head, $Odlm_1$; for tergal retraction and a slight possible prothoracic rotation, $Idlm_{1-2}$; for elevation of the head (with $Oism_2$), muscle $Odlm_1$. The dorsoventral intersegmental muscles of the prothorax are all connected with the head, and provide for abduction and retraction of the head, $Oism_3$; for elevation, abduction, and rotation of the head, $Oism_2$; for rotation of the head, $Oism_{1-2-3}$ and others. All of the intersegmental muscles between the prothorax and the head are complex in function; it is difficult to analyze just how many functions has each muscle, because of the possibility of single action on one side, of one muscle or a group, and the possibility of multiple action of the muscles of both sides of the body, individually or in groups.

There is but one adult pleurosternal muscle in the dragonfly, $Izm_1$, the prosternal-pleural muscle. Similar muscles are present in all three segments of the thorax in the larva, but the plastron fusion in the synthorax has eliminated the adult zm muscles here. The function of the zm muscles is problematical; they may assist in retracting the pleuron during the moulting periods in the larva.

The remaining muscles to be discussed are the thoracico-coxal and the thoracico-trochanteral muscles. The coxa is suspended freely from the pleuron in the adult Odonata, and the leg may swing forward or backward on a transverse or vertical coxal axis, or it may turn on the plane of its base on an axis through the middle of the coxa, and it may swing inward and outward on a longitudinal axis. Table 4, given below, compares the action of the thoracico-leg muscles of Odonata with the action as described in a typical generalized insect by Snodgrass ('35, p. 201, '35, pp. 189, 190).

Table 4 shows the extreme mobility of the first leg of the dragonfly, adapted for cleaning movements, and the handling of prey, and the lesser mobility of the second and third dragonfly legs, adapted for the basket formation for prey, and for clinging to objects.

While the first leg possesses a full functional complement of muscles, easily analyzed, the muscle actions in the alate segments are less clear and harder to analyze. It should be noted (see table 4), that the second leg is less mobile than the first, and that the third leg is less mobile than the second. In the second leg, there is no apparent morphological anterior rotator; in the third leg, there is little or no anterior rotation, promotion, or remotion. In addition, the second and third legs possess the leg-wing muscles, $dvm_{5-6-7}$. The leg muscles



of the second and third legs are exact homologues. The difference in function of the homologues is due to the orientation of the transverse axis of the third leg through an angle of almost 90 degrees, changing promotors of the second leg ($dvm_5$, $pm_6$), to abductors in the third leg ($dvm_5$, $pm_6$). The remotors of the second leg ($dvm_{6-7}$, $bm_1$), become adductors in the third leg ($dvm_{6-7}$, $bm_1$).

With regard to the muscle $bm_1$ of the adult, in the larva it may be three muscles, the anterior rotator, the adductor, and

TABLE 4

*A comparison of the thoracico-leg muscles, between Odonata and the generalized account of Snodgrass ('35)*

| FUNCTION | GENERALIZED INSECT Muscle | ODONATA Pro | Meso | Meta |
|---|---|---|---|---|
| Promotion | I<br>M | $Idvm_{2-3}$ | $IIdvm_5$<br>$IIpm_6$ | ? |
| Remotion | J | $Idvm_4$ | $IIdvm_{6-7}$<br>$IIbm_1$ | ? |
| Abduction | M | $Ipm_2$ | $IIpm_{6-7}$ | $IIIpm_{6-7}$<br>$IIIdvm_5$<br>$IIIbm_{1-2}$ |
| Adduction | N | $Ibm_2$ | $IIbm_{1-2}$ | $IIIdvm_{6-7}$ |
| Rotation, anterior | K | $Ibm_1$ | ? | ? |
| Rotation, posterior | L | $Ibm_3$ | $IIbm_1$ | $IIIbm_1$ |

posterior rotator. In the adult, however, it has been considered by Maloeuf as one muscle, by myself as one muscle which may be two or three fused as one, by Maki as two mesothoracic, one metathoracic, muscles (34, 37, 57), and by Berlese as three muscles, "dagli sterniti alle zampe," in Diplax, figure 475, page 429, muscles 61, 62, 64. It should be noted that the muscles attaching to the trochanter in all three legs are also depressors of the telepodite in addition to the functions assigned to them, above.

Work on the larval muscles should clear up the status of the adult muscles $dvm_{3-4}$, which may be the tergosternals, or may be the notocoxal second and third leg promotors; such work as has been done has shown the duality of $Ivlm_{1-2}$.

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SUMMARY

1. The adult thoracic musculature of the anisopterous dragonfly has been reported upon by at least eleven investigators, from Chabrier (1820) to Maki ('38). No description has been found to be complete; this paper attempts to correct, complete, and compare the various accounts.

2. The nomenclature and abbreviations have been revised to a modified Voss-Berlese-Snodgrass system; the nomenclature is purely topographical throughout; function is denoted by an additional name, where possible.

3. About 100 specimens, comprising twelve genera, were examined, and it was found that comparison revealed an explanation of the discrepancies between the various reports.

4. The findings of Chabrier, Poletaiew, Lendenfeld, Luks, Amans, Calvert, Berlese, Cremer, Maloeuf, and Maki are compared with those of the writer, on two tables.

5. In the prothorax, the writer has found one muscle not previously described, and independently confirms Maki on five muscles not reported by other investigators. Not seen were the ventral transverse and the anterior tergopleural muscles found by Maki in Crocothemis servilia. The writer found that his muscle $Oism_1$, reported first by Maloeuf, is variable in origin and insertion.



6. In the pterothorax, the writer found that the dorsal longitudinal metathoracic muscle, reported by Poletaiew (1879), and Amans (1884, 1885), but not since then, was present in some genera, but not in others. The writer independently confirms Maki on a muscle not reported since 1879 by Poletaiew, as a constant, obscure, accessory to the principal elevator. The writer confirms Maloeuf as to the duality of the fulcroalar muscle, not recognized by Maki ('38). Not seen were the ventral mesothoracic transverse muscles of Maki, although they are present in the larvae, and Maki's first anterior tergosternal of the mesothorax; the fourth intersegmental muscle of Berlese and Tillyard has not been confirmed. The writer differs from Maki in the duality of the sternocoxal leg muscle.

7. The mechanism of the muscles is discussed, with references to the generalized insect of Snodgrass ('35). It was found that every muscle could be homologized with those in other insects, excepting the anterior coxoalar, which may be a displaced subalar muscle. The writer believes that the highly efficient, simplified thoracic musculature of the dragonfly is not at all unusual, but conforms closely with the general arrangement of pterygote insect musculature, as described by Snodgrass ('35).

8. Anax junius is quite typical of all anisopterous Odonata, containing all muscles present in some, and absent in other, species. An annotated list, accompanied by seven camera lucida figures, illustrates many muscles for the first time.

9. Work on the larval musculature may solve the origin of some of the adult muscles. The identities of certain adult skeletal structures were solved in this way, and are given in this paper.

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## APPENDIX

Author's names corresponding to the symbols III, II, (?), IAb, in table 1. The authors are considered in chronological order. Symbols are from the last column.

CHABRIER. IIIvlm$_1$-Abaisseur de l'abdomen; IIIvlm$_2$-no mention; dlm$_1$-Abaisseur, Dilatateur, mesothorax only; IIIism$_1$-Releveur de l'abdomen; dvm$_1$-sternali-dorsaux, releveurs de l'aile; dvm$_2$, no mention; dvm$_3$-Premier pectoral, muscles pectoraux anterieures, abaisseurs de l'aile; dvm$_4$-petit muscle abaisseur anterieur, auxiliare des abaisseurs; dvm$_5$-3°muscle du jambe; dvm$_6$-anterieur auxiliare au sternali-dorsaux, 1°muscle du jambe; dvm$_7$-2°muscle du jambe, posterieur auxiliare au sternali-dorsaux; pm$_1$-Second pectoral; pm$_2$-auxiliare du pectoraux; pm$_3$-auxiliare au pectoral; pm$_{4a-b}$, fulcro-basilaire; pm$_5$-petits muscles ou ligamens tranversaux; total, 25 for meso-metathorax.

POLETAIEW. IIIvlm$_1$-Un sternal muscle; IIIvlm$_2$-no mention; dlm$_1$-Auxiliare sternaux, anterieures, posterieurs; IIIism$_1$-Auxiliare sternali-dorsal; dvm$_1$-Elevateur, troisieme chef, le plus gros; dvm$_2$-elevateur, petit chef, tres court; dvm$_3$-Abaisseur anterieur; dvm$_4$-additionel de l'abaisseur anterieur; dvm$_5$-elevateur, l'autre petit chef, plus long; dvm$_6$-additionel anterieur de l'elevateur; dvm$_7$-additionel posterieur de l'elevateur; pm$_1$-abaisseur posterieur; pm$_2$-additionel anterieur de l'abaisseur posterieur; pm$_3$-additionel posterieur de l'abaisseur posterieur; total, 24, for meso-metathorax.

LENDENFELD. Dvm$_1$-Tensor alae, pars major; dvm$_3$, Abductor alae; dvm$_4$-pronator radii primi; dvm$_5$ (?) Tensor alae; dvm$_6$, Pronator alae; dvm$_7$-supinator alae; pm$_1$, flexor alae; pm$_2$, flexor radii quinti; pm$_{4a-b}$-adductor radii quinti.; total, 18, for meso-metathorax.

LUKS. IIIvlm$_1$-protractor abdominis; dvm$_1$-extensor alae; dvm$_{3-4}$-flexor alae; dvm-$_5$ (?) refers to muscle, but which is not known, since account and figures do not agree; dvm$_{6-7}$-(?) rotator alae, but account and figures do not agree; pm$_{1-2}$-rotator alae; pm$_3$-(?) rotator alae, account and figures do not agree. Totals for meso-metathorax, 17 or 19.

AMANS (1883–1884, 1885). He changed some names in 1885 paper, listed below after 1883–1884 names. IIIvlm$_1$-Constricteur du flanc; dlm$_1$-dorsal abaisseur muscle; IIIism$_1$-constricteur du flanc; dvm$_1$-sternali-dorsal; dvm$_3$-premier pectoral, grand preaxilliare anterieure; dvm$_4$-petit abaisseur, petit preaxillaire anterieure; dvm$_5$-petit elevateur, adjuvant des sternali-dorsaux; dvm$_6$-abaisseur moyen, anterieur pedio-dorsaux, elevateur; dvm$_7$-abaisseur moyen, posterieur pedio-dorsaux, elevateur; $pm_1$-second pectoral, grand postaxilliare; $pm_2$-abaisseur posterieur, petit postaxillaire; $pm_3$-abaisseur posterieur, petit postaxillaire; $pm_{4a-b}$-fulcrobasiliare, muscle du tampon; $pm_5$-elevateur transverse, pleuro-dorsal. Totals: 26, meso-metathorax.

CALVERT. $IIIvlm_1$-lateral thoracico-abdominal; $IIIvlm_2$-submedian ventral thoracico-abdominal; $IIIism_1$-auxiliary sternodorsal; $dvm_1$-principal elevator; $dvm_3$-anterior depressor; $dvm_4$-accessory of anterior depressor; $dvm_5$-part of principal elevator; $dvm_6$-anterior accessory elevator; $dvm_7$-posterior accessory elevator; $pm_1$-posterior depressor; $pm_2$-second accessory of posterior depressor; $pm_3$-first accessory of posterior depressor; $pm_4$-adductor radii quinti; $pm_5$, a small muscle, from tendon of insertion of principal elevator to fulcral process. Totals, 14, meta, 11, meso-thorax, total 25.

BERLESE. $IIIvlm_1$-M. ventrale (intersegmentale) del 1° urite; $IIIvlm_2$-M. pleuro sternale quinto; $dlm_1$-M. del mesonoto (reports only mesothoracic muscle); $IIIism_1$-M. intersegmentale primo del metatorace; $dvm_1$-M. tergosternal primo; $dvm_3$-M. tergosternale terzo; $dvm_4$-M. tergosternale quarto; $dvm_5$-M. notocoxal primo; metathoracic only; $dvm_6$-M. dorsoventrale undecimo; $dvm_7$-M. laterale endopterocoxale; $pm_1$-M. pleuroradiale; $pm_2$-M. pleurometapterale; $pm_3$-M. laterale settimo; $pm_4$-M. fulcroalare; $pm_6$-M. sternopedale primo (in error, this is not a sternopedale muscle); $bm_1$-M. pedale terzo; $bm_2$-fig. 475, p. 429, 61-62-64, as possibly 3 muscles, not noted in report. The leg muscle accounts are not accurate, and are therefore marked (?). Totals, 26 muscles, plus 3 doubtful leg muscles, for the synthorax.

TILLYARD. See Calvert and Berlese, from whose accounts Tillyard has adapted the double nomenclature in his tables. Changes from Calvert's nomenclature are: $IIIism_1$-first auxiliary sternodorsal; $dvm_5$, notocoxal (see Berlese), for metathorax only; $pm_{2-3}$ are reversed in names; $pm_4$- fulcroalar, adductor of the secondary anal vein. Since Berlese erred in the leg muscles, so did Tillyard; his table has typographical errors which are therefore marked (?). Total, 26 muscles, plus four doubtful leg muscles, in the synthorax.

CREMER. His names are adapted from Lendenfeld's, changes are as follows: $dvm_1$, Tensor alae, without "pars major, minor," of Lendenfeld. $Dvm_5$-elevator coxae; $dvm_6$-Tensor radii primi; $pm_3$-not reported by Lendenfeld, abductor radii quinti; $pm_5$-not reported by Lendenfeld, adductor meso-meta-pleurontis. Totals, 22, for synthorax.

MALOEUF. Muscles not named are numbered. $IIIvlm_1$- (68); $IIIvlm_2$ (66); $dlm_1$ (25); $IIIism_1$- (67); $dvm_1$-primary elevator; $dvm_3$-primary pronator depressor; $dvm_4$-secondary depressor pronator; $dvm_6$-secondary elevator; $dvm_7$-tertiary elevator; $pm_1$-depressor; $pm_2$-primary depressor reductor; $pm_3$-secondary depressor reductor; $pm_{4a-b}$-primary, secondary depressors of the hind margin of the wing; $pm_5$-pronator; $pm_6$-coxal promotor; $pm_7$-pleural depressor of the telepodite; $bm_1$-sternal coxal remotor; $bm_2$-sternal depressor, telepodite. Totals, 34, for synthorax.



MAKI. $IIIvlm_1$-posterior ventrals; $IIIvlm_2$-ventral muscle, first abdominal segment; $dlm_1$-lateral dorsals; $IIIism_1$-posterior tergosternals; $dvm_1$-first anterior tergosternals; $dvm_2$-second anterior tergosternals; $dvm_3$-sternobasalar; $dvm_4$-sternobasalar; $dvm_5$-tergal promotor of the leg; $dvm_{6-7}$-coxoaxillaries; $pm_{1-2-3}$-pleurosubalars; $pm_4$-pleuroaxillaries; $pm_5$-ordinary tergopleural; $pm_6$-pleural abductor; $pm_7$-pleural depressor of the trochanter; $bm_1$-(meta) ordinary coxal sternal remotor of the leg; (meso) sternal promotor, coxal remotor of the leg, 2 muscles; $bm_2$-sternal depressor of the trochanter. Totals, 38, for the synthorax, excluding notations on table 1.

The numbers on table 2 are those used in the several reports, and should suffice for cross references.