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## The external morphology of *Prionus laticollis* Drury (Coleoptera: Cerambycidae).

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The External Morphology of Prionus laticollis Drury  
(Coleoptera: Cerambycidae)

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The External Morphology of Prionus laticollis Drury  
(Coleoptera: Cerambycidae)

Charles H. Daniels

Thesis submitted for the degree of  
Master of Science

Massachusetts State College

Amherst

1938

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## INTRODUCTION

A coleopterist, Tanner, has pointed out that of the twenty thousand species of beetles listed by Leng in his Catalogue of the Coleoptera, probably not more than one-fourth can be identified positively from the original description.

As taxonomy is based upon morphology, it may be assumed that the deplorable condition mentioned above is due in part to an incomplete understanding of the morphological characters available for the differentiation of species. Accordingly, this study was undertaken in an effort to provide a trustworthy guide to the morphology of a beetle.

Prionus was chosen for study because it is a representative of a family which contains more than eleven hundred described species in North America alone. The complete morphology of a Cerambycid has never been worked out before. In addition, the large size of Prionus makes it suitable for classroom study, and it is hoped that this study may prove useful in that respect.

Prionus laticollis Drury

Generic name. In Linnaeus' "Systema Naturae," tenth edition, 1758, Prionus was not known as a genus. Insects belonging to the genus Prionus were probably included in the Linnaean genus Cerambyx.

The generic name Prionus is derived from the Greek prion, meaning "a saw," and is probably meant to be descriptive of the toothed margin of the prothorax.

The name Prionus was first proposed by E. L. Geoffroy in 1764. In 1775 this genus appeared, with a short description, in the Systema Entomologiae of Fabricius. In 1777 Scopoli listed it in a publication. In Sherborn's Index Animalium, covering the period from 1758 (the date determining priority) to 1800, the genus Prionus is noted in the order mentioned above.

Agassiz, in the "Nomenclator Zoologicus," lists Prionus and indicates Geoffroy (1764) as its author. Casey, in his "Memoirs on the Coleoptera," recognizes Geoffroy's claim to the genus.

Leng, in 1920, credits the name Prionus to Fabricius. As far as can be determined, this is erroneous, in view of the law of priority. Westwood's 1837 edition of

Drury's Insects (1770) calls an unnamed, described insect (evidently Prionus) Cerambyx laticollis. This generic name is incorrectly applied, in view of Geoffroy's designation in 1764, and by later designations occurring previous to 1837. On this basis, Geoffroy should be designated the originator of the genus Prionus.

To summarize:

1764 Prionus proposed for this insect by Geoffroy.

1770 Drury described the insect but failed to name it.

1775 The genus Prionus was recognized by Fabricius in his "Systema Entomologiae."

1837 Westwood, in naming the insects described by Drury in 1770, called Prionus laticollis, Cerambyx laticollis.

Specific name. The latin specific name, laticollis, from which comes the common English name of the insect, "broad necked Prionus," is derived from two latin words, namely, latus meaning broad or wide, and collum meaning neck.

The specific name, laticollis, was first employed by D. Drury in the second volume of the first edition of his work in 1773. The first volume of 1770 gives a full description, and pictures the insect, but fails to

provide a name for it. Westwood, who published the above-mentioned edition of this work in 1837, states, in page V of the preface to that edition, that an appendix to the second volume provided specific names for both the first and second volumes, although no specific names appeared in the body of the work. As no other specific name was applied to the insect in the interim between the appearance of the first and second volumes, laticollis Drury is valid under the code.

In 1801, Fabricius created the synonym brevicornis. Leng's catalogue lists four other synonyms which were proposed by Casey in 1912. They are as follows: kempi, oblongus, parvus, and validiceps. Sherborn's Index Animalium recognizes Drury as the originator of the specific name of Prionus laticollis.

General Description. Prionus laticollis, - a broad, stout beetle - is the largest beetle commonly found in New England. According to Casey (1912), its dimensions are as follows: length of male 27. to 30. mm.; female 33. - 39. mm.; width of male 11. - 12. mm.; width of female 15. - 18. mm. The most conspicuous features of the head



are the long 12-segmented serrate antennae, which arise from a latero-dorsal position in front of the large reniform compound eyes, and the huge prognathous mandibles which dominate the anterior portion of the head. Both the head and prothorax are closely punctate. The latter has a thin tridentate lateral margin. The elytra are coarsely rugose with three slight, raised, longitudinal lines. The scutellum is U-shaped and prominent.

#### GENERAL MORPHOLOGY

##### Head

Head Capsule. The dorsal wall of the head capsule is composed of the following areas: two parietals (pa), a postclypeus (pc), an anteclypeus (ac), and a labrum (la). The ventral wall comprises the following areas: gula (gu), submentum (sm), which is considered in connection with the labium, two genae (ga), and two postgenae (pge). With a few exceptions, the limits of the above areas are not definite, but gradate one into the other.

A dorsal view of the head is shaped as shown in Figure 1. The coronal suture (cs) divides the head longitudinally, terminating anteriorly in the center of the

frontal pits (fp), called the anterior tentorial pits by Snodgrass (1935). As these pits are the landmarks representing the anterior limits of the frons, it is obvious that the frons is vestigial or lacking. The frontoclypeal suture (fc) appears to occupy the usual position of the frontal sutures.

Flanking the coronal suture laterally are the areas known as the parietals (pa). These form the greater part of the vertex of the head, extending from the frontoclypeal suture to the occipital foramen. There are no definitely marked temporal areas, and the parietals merge with the genae and postgenae. The genae (ga) comprise the small areas cephalad of the compound eye and ventrolaterad of the parietals, extending ventrally to the lateral margin of the submentum. There is no definite suture between them, but the two areas are abruptly and sharply demarked by surface markings. The surface of the submentum is coarsely punctate and roughened, while the contiguous genal area is smooth, finely and sparsely punctate. A ginglymus-like formation in the ventral margin of the gena receives the mandibular condyle. The postgenae (pge) form the greater part of the posterior region of the head. The occipital region is not demarked from the postgenae.

The reniform compound eyes (e) caudad of the antennae extend from the margin of the submentum ventrally, almost to the coronal suture dorsally. The anterior margin of the eye is incised, the sclerotized emargination giving support to the base of the antennae. The scape is flattened opposite the emargination to allow the antennae to lie flat against the head.

Immediately anterior to the fronto-clypeal suture (fc) is the heavily sclerotized post clypeus (pc). At its lateral margins, very weak sutures demark the paraclypeus (pac), which is smooth, sparsely and finely punctate, unlike the coarsely punctate area of the post-clypeus adjacent to it. The small paraclypeus furnishes a condyle-like process for the dorsal articulation of the mandible. Cephalad of the postclypeus is the semi-membranous anteclypeus (ac), and cephalad of the anteclypeus is the flexible labrum (la). The ventral surface and distal margin of the labrum are covered with setae.

From a ventral aspect (fig. 3) it may be seen that the ventral region of the head capsule consists principally of two well demarked sclerites. Extending from the occipital foramen to the posterior margin of the submentum, is the area known as the gula (gu). It is smooth-surfaced

and while there is but the merest hint of a ridge between it and the submentum, the line of demarkation is very distinct, due to the differences in their surface textures. Laterally, the gula is bounded by the parallel gular sutures (gs). The gular pits, external manifestations of the invaginations forming the posterior arms of the tentorium, extend along these sutures.

The sunken submentum lies in a different plane, slightly entad of the adjacent areas. Its rough surface clearly demarks it from the surrounding areas with which it is united, viz., genae, eyes, postgenae, and gula.

Tentorium. The tentorium is the principal internal structure of the head capsule. According to MacGillivray, it consists of the following parts: the metatentoria, the corpotentorium, the pretentoria, and the supratentoria. In Prionus, the metatentoria are invaginated ridges which extend the length of the gular sutures. The lamellate corpotentorium lies on a subhorizontal plane between the extended arms of the metatentoria. The pretentoria arise as invaginated arms at the frontal pits. They extend posteroventrally and join the anterior margin of the corpotentorium. The supratentoria arise from the pretentoria and extend dorso-laterally to a point at the base of, and slightly posterior to, the antennae.

Antennae. The twelve-segmented, serrate antennae (fig. 8) articulate with the head cephalad of the eyes. The scape (sc) is an elongate, thick segment with a bulbous swelling at its base, distad of which the ventral surface is somewhat flattened and slightly concave, evidently to allow it to lie flat against the head. This basal segment articulates proximally with a sclerotized pivotal point or antennifer (af) located on the ventral margin of the antennal socket. The distal end contains a socket for the reception of the proximal end of the pedicel. The second segment or pedicel (pd) is short. It is movably articulated with the scape, and is but slightly movable in its articulation with the third antennal sclerite. Both the scape and pedicel are coarsely punctate. The third segment is approximately four times as long as the pedicel and is subspherical in cross section. Distally it receives the proximal end of the fourth segment, with which it articulates freely. The remaining segments become progressively more triangular, and are movably articulated.

Finely reticulate raised lines are noticeable on the third segment, becoming progressively more distinct on the remaining distal segments. These lines are more

prominent on the ventral surfaces. The distal segment is suboval and is flattened to a very thin edge distally. In one specimen, a small tooth was noted on the eleventh segment; in another case, the eleventh and twelfth segments were so fused as to render the terminal segments independently immovable.

The antennal segments of the male are broader than those of the female and appear more distinctly serrate. In some specimens, the female antennae are so weakly serrate as to appear sub-filiform.

Mandibles. From a dorsal aspect, it may be seen that the thin incisor edge of the left mandible overlaps the corresponding portion of the right mandible when the two are in apposition. A ginglymus (gi) for the reception of the paraclypeal condyle is located on the dorso-basal margin of each mandible, the pit of the left ginglymus (fig. 9) being much broader than that of the right. Ventro-basally a mandibular condyle (co, figs. 7, 10) articulates with a ginglymus of the gena. Both mandibles are practically devoid of hair.

The mandibles are operated by a large flexor muscle which enters the head capsule on the mid-ventral line. Laterally, a smaller extensor muscle serves to open the mandible.

Because of the enormous development of the mandibles, the rest of the mouthparts are greatly reduced. Goldman (1933), correlating coleopterous mouthparts with diet, says of the Prioninae:

"The members of the subfamily Prioninae do not in my opinion show an obvious correlation with the food material. .... The previous conclusion is drawn only with reference to what is now known of the insects' diet. Considered from an evolutionary point of view, it is possible that the large mandibles are a result of specialization in spite of changing food materials."

Maxillae. The maxillae (fig. 4) contain the following sclerites: cardo (cd), stipes (s), palpifer (pf), maxillary palpus (mp), and mala (m). Regarding the latter Goldman (1933) believes that the lacinia is present with no vestige of the galea. However, in view of the fact that there is nothing to indicate which sclerite has been lost, Boving and Craighead's term "mala" has been used to designate the surviving sclerite. The cardo, which articulates with the proximo-lateral margin of the stipes, is a small boot-shaped sclerite, to the toe of which is attached an extensor muscle. Attached to its inner margin and the basal margin of the stipes, is the basimaxillary membrane (b). The stipes is a broad sclerite which is sclerotized proximally and becomes membranous distally. The flexor muscle has an attachment on its mesal corner.

Distad of the stipes is the mala (m) and palpifer (pf). The mala is sclerotized distally and is covered with setae. Semi-membranous tissue links the basal section of the mala to the sclerotized palpifer. The four-segmented maxillary palpus (mp) arises from the palpifer. In common with the other mouthparts, exclusive of the mandibles, the maxillae have been greatly reduced and the four-segmented palpal segments alone retain their normal size.

Labium. The labium (fig. 16) consists of a basal submentum (sm), the mentum (mn), a mental membrane (mm), two palpigers (plg), a ligula (lg), and two labial palpi (lp) composed of three segments each.

The submentum (sm) is large, heavily sclerotized, firmly incorporated in the antero-ventral floor of the head capsule. It is contiguous posteriorly with the gula (gu), and laterally with the genae (ga).

Meso-cephalad of the submentum and connected to it by the basi-maxillary membrane (b) is the mentum (mn). The term mentum in this paper is restricted to the sclerotized area, and the membranous area with which it merges anteriorly is called the mental membrane (mm).



It is not a distinct sclerite but is probably formed by the membranous anterior portion of the mentum.

Cephalad of the mental membrane are found the partially fused palpigers (plg) which have a suture separating them basally. Distally they are separated by the intervening ligula. The palpigers support the three segments of the labial palpi (lp). The first segment of the labial palp is relatively short; the second twice the length of the first and thickened at the distal end; the third segment is clavate, thick at the distal end, and is somewhat flattened on one axis. A sulcus (su) with a nonsclerotized lining extends the length of the long axis on the extreme distal margin of the last segment. The three palpal segments articulate with each other and with the palpiger. All are stiffly movable.

With the exception of the submentum and the palp, the parts of the labium have been much reduced. The glossae and paraglossae have united in a small triangular ligula (lg) which is uniformly sclerotized and covered with coarse setae. From a dorsal aspect, the ligula appears as a hairy triangle extending behind, and obscuring the palpigers, its caudal apex extending well

down behind the mental membrane. Each of its cephalic apices is extended as a short spur densely covered with setae. These spurs are dorsad of the basal labial segment and are hidden by them from a ventral aspect.

### Thorax

Prothorax (Figs. 6, 13, 18, 19). The pronotum consists of a single sclerite which is approximately twice as broad as long. The lateral margins are thin and dentate. The medio-lateral tooth is always prominent, the antero-lateral tooth generally distinct, and the postero-lateral tooth often insignificant (see fig. 6). Casey (1912) used the size and shape of these teeth as characters in differentiating species.

According to one view (Crampton, 1926), the pronotum (pn, figs. 13, 18) extends ventrally to the precoxales (pr) (at which point a prominent nota-sternal carina occurs) and overlaps and obliterates the propleuron. According to other views (Ferris, 1935), the lateral zones are composed of the fused notum and pleuron, and the basal coxal piece is simply the trochantin.

Caudad of the coxa, the pronotum elongates laterally into a sharp postcoxal projection (pcp, fig. 18) which

partially forms the posterior wall of a socket in which the coxa (cx) rotates slightly in an antero-posteriorly direction. The coxal cavities are transverse and open.

A trochantin (tr), which articulates distally with the coxa, represents the only vestige of the propleuron. From the ventral aspect (fig. 18) the trochantin appears to arise from the pronotum at the posterior end of the nota-sternal carina (cr).

Caudad of the coxal cavities, and connecting the pro- and meso-thorax, is a ventral membrane in whose lateral areas are located the prothoracic spiracles (sp, fig. 13). These are protected by the latero-ventral projection of the pronotum.

The prosternum consists of the basisternum and the furcasternum. The basisternum consists of two parts, the prosternal lobe (psl) and the precoxales (pr). The prosternal lobe projects caudally between the coxae, which articulate with it by means of small condyles (fig. 13) on their meso-lateral margins. The precoxales (pr) extends to the pronotum (or pleuron, according to one view).

In the angle between the prosternal lobe and the precoxales (fig. 18) the prosternum extends posterolaterally a short distance forming the floor of a concave shelf in which part of the coxa lies. This shelf is weakly sclerotized and must represent the furcasternum (fs), for from it arises the internal, dorsal-projecting apophysis, the bifid furca (fu, fig. 19). The furcal pits (fup, fig. 18), ordinarily the external indications of the invaginated furca, are located on the posterolateral margin of the furcasternum, directly dorsad of the coxa, which must be removed in order to expose them. The furca serves as a support for muscle attachments. A small apophysis, a muscle disk (mdk), probably serving the same purpose, projects dorsally toward the notum from the area at the base of the trochantin (fig. 19).

The prothoracic leg (fig. 21) consists of the coxa (cx), trochanter (tch), femur (fe), tibia (ti), tarsus (ta), and pretarsus, the latter bearing two ungues (ung) or claws.

The coxa is but slightly movable. Laterally it extends into a cleft formed by the post coxal projection of the pronotum and the precoxales. The trochantin extends mesally from the pronotum to a point on the coxa

(fig. 18). The slightly swollen mesal end of the coxa is inserted in a cavity in the side of the prosternal lobe, a small condyle (fig. 13) on the mesolateral margin of the coxa articulating with the prosternal socket. On the posterior face of the coxa is an irregularly shaped aperture, whose margin has been modified to form articulatory points for the trochanter. A condylar-like process is found on the antero-ventral margin, and a groove is found opposite it. These two devices (see figs. 17,18,21) act as pivotal points for the trochanter, which is operated by large muscles within the coxa.

The visible portion of the trochanter (tch, fig. 17) is subtriangular in shape. At the apex, which is inserted in the cavity of the coxa, there are several processes (fig. 5) for articulation and muscle attachments. The distal margin of the trochanter is immovably fused with the femur.

The femur (fe) is the stoutest segment of the leg. Distally it articulates with the tibia, a small indentation on its ventral distal extremity allowing free flexing of the tibia.

The tibia is somewhat flattened distally. It bears two movable spurs at its distal end, ventrally; terminal

dorsal teeth between which the basi tarsus may flex; and a socket for the reception of the articulatory bulb of the basitarsus.

The tarsus comprises five segments. The basal segment or basitarsus (bt) bears a bulb-like swelling at its proximal end for articulating with the tibia. Its distal end is broad and receives the base of the second tarsal segment with which it is movably articulate. The ventral surfaces of the first three tarsal segments are densely covered with short setae. The basitarsus has a smooth median groove extending nearly to the distal end on its ventral side. The third tarsal segment is heart-shaped with the cleft distad. In the center of its dorsal surface is an articulatory socket which receives the basal end of the fourth segment.

The fourth segment (fig. 2) is greatly reduced and its distal end does not extend beyond the distal margin of the third segment with which it is movably articulated proximally. Its distal articulation with the distitarsus is but slightly movable.

The distal segment or distitarsus (dt) is slightly bowed. It is as long as the second and third segments combined, and is subspherical in cross section. The

distal end, with which two movable claws are articulated, is much broader than the basal end.

In this beetle, the pretarsus (fig. 22) is represented by the following elements: unguis (ung), parempodium (par), empodium (emp), unguitactor (ugt), and unguifer (ugf).

There are two unguis or claws which articulate with the end of the distitarsus. Between them is located the empodium, a median process which is continuous with the unguitactor. It articulates with the bases of the unguis by means of the flexor membrane (fm).

The parempodium consists of two distally protruding setae which are borne on the distal margin of the empodium.

The unguitactor, a sclerotized ventral plate of the pretarsus, is concealed in the invaginated tip of the distitarsus.

The unguitactor tendon (ut) extends from the proximal margin of the unguitactor to muscles in the tibia. Tension from these muscles is transmitted through the unguitactor plate to flex the unguis.

On the ental surface of the dorsal wall of the distitarsus near its distal end is a bifid sclerotized process called the unguifer, whose function is to articulate the

dorsal surface of the distitarsus with the ungues. According to Holway (1937), this articulation takes place through an intermediate sclerite, the orbicula, which is not distinguishable in Prionus laticollis.

Mesothorax (figs. 11, 12, 14). The prescutum (prs, fig. 14) is represented by a membrane which extends from the anterior margin of the scutum to a phragma of the pronotum, and by the prescutal phragma or prephragma which serves to strengthen the mesothorax, thus aiding in the support of the elytra and the alar muscles of the pterothorax.

The scutum (sct) occupies most of the anterior portion of the mesotergum and is superficially divided into two distinct areas. The first area is coarsely punctate with numerous short setae, and on its antero-mesal margin, a small cleft tends to divide it longitudinally. The scutum projects antero-laterally forming a process which supports the articulation of the elytra. This articulation is accomplished by means of two axillary sclerites embedded in the membrane between the scutum and the dorsal portion of the mesoepisternum. The membrane is partially sclerotized and the axillary sclerites are not distinct. On a lower plane, the scutum projects



laterally forming a cradle for the support of the elytron when at rest. The anterior portions of the scutum are concealed by the overlapping pronotum, and the postero-lateral portions of the scutum are covered by the elytra.

The shield-shaped scutellum (scl), which is the only part of the mesothorax visible dorsally in the undissected beetle, is smooth and very sparsely punctate. It is seen between the antero-mesal margins of the elytra and the pronotum. The meso-cephalic margin of the elytron is held under the lateral margin of the scutellum, between it and the membrane surrounding it.

The mesopleuron (pl) comprises the episternum and epimeron. Separating the episternum and the epimeron is the pleural suture (ps) which extends from the wing process dorsally to the coxal cavity (cxc) ventrally. This suture is the external manifestation of an internal ridge or plate to which muscles are attached.

Upon removing the coxa, one may see the slender trochantin (tr) which lies in close apposition to the anterior margin of the coxal cavity. It originates at the lower end of the pleural suture and extends ventrally to the suture demarking the basisternum.

The episternum is divided, by a carina, into two regions, the anepisternum (aes) and the katepisternum (kes). The anepisternum, bearing numerous short setae, extends dorsally and forms a pivotal point for the elytron which conceals its dorsal portion. The katepisternum is separated from the anepisternum by a carina (cr). Ventrally it extends to the basisternum, being separated from it by a suture which is the external manifestation of an internal ridge which extends ento-mesally through the floor of the coxal cavity to the base of the furca.

Caudad of the episternum is the epimeron, which is divided by a carina near its dorsal margin into an upper region or anepimeron (aem), and a lower region or katepimeron (kem). The anepimeron is a small inflexed area covered by the elytron. The katepimeron is a larger area bounded cephalically by the pleural suture, dorsally by the carina demarking the anepimeron, caudally by the suture which separates it from the metathoracic episternum, and ventrally by the coxal cavity of the mesothoracic leg. The mesothoracic spiracle (sp) is located under this sclerite and may be seen only by a dissection. Air is probably received through the space between the epimeron and the metathorax.

Mesosternum (figs. 11, 12). The mesosternum, which is dwarfed by the larger prosternum and much larger metasternum, is composed of two sclerites, the basisternum (bs) and the furcasternum (fs) or sternellum. The basisternum is bounded antero-laterally by a suture which separates it from the episternum, and postero-laterally by the furcasternum or weakly sclerotized floor of the coxal cavity. Its cephalic margin is overlapped by the prosternal lobe. Caudally it is bounded by the meta-thoracic sternum.

Upon removing the coxae, it will be noted that the floor of the coxal cavity is formed by a weakly sclerotized tissue which protrudes into it from the postero-lateral margin of the basisternum and the anterior margin of the metasternum. In its antero-mesal surface, are the furcal pits which mark the position of the internal anteriorly-directed furca. These apophyses extend through the thorax and unite with the pleural ridge, thus forming a stout bow for the attachment of the coxal muscles.

In view of the fact that the furca arises from the floor of the coxal cavity, it is believed that this area represents, in part, the furcasternum. The remaining

portion is probably metasternal in origin. However, this lining is homogeneous and there are no ridges or sutures to aid in determining the exact extent of the furcasternum.

Mesothoracic leg. The mesothoracic leg differs from the prothoracic leg in but a few respects, and is not figured. The coxa is somewhat shorter transversely and is convex and protruding. Unlike the prothoracic tibiae, the distal end of the mesothoracic tibia bears three distinct spurs, two of which are movable. The third, formed by the elongation of the dorsal wall of the tibia, is immovable.

Metathorax (figs. 11, 12, 14, 15). Metatergum (fig. 14). There are four tergal regions present in the metatergum, namely, the prescutum (prs), scutum (sct), scutellum (scl), and postscutellum or postnotum (psc). The first three regions are demarked areas of a single wing-bearing plate, the alinotum, while the postscutellum or postnotum is a distinct plate lying behind the alinotum.

The prescutum is represented by a sclerotized prephragma, which, due to overlapping by the mesotergum, lies in close proximity to the mesothoracic prephragma.

The scutum (sct), comprising the greater part of the metathoracic tergum, is bounded laterally by the alar membranes, mesally by the notal grooves, behind by the postscutellum, and in front by the alar membrane and the mesoscutellum. It is divided into two areas by the notal grooves. Its antero-lateral margin bears the anterior notal wing process (anp, fig. 15). The postero-lateral margin extends laterally to form the posterior notal wing process (pnp).

The scutellum lies between the postero-mesal margins of the scutum and the postscutellum. It protrudes anteriorly between the notal grooves, terminating at the prescutal membrane. From an internal aspect it may be seen that the scutoscutellar sutures (scts) which demark the postero-lateral margins of the scutellum are the external manifestations of internal ridges.

The postscutellum or postnotum (psc), from an external aspect, appears as a narrow membranous area extending along the first abdominal tergite. It bears the internal irregularly shaped postphragma (pph). Mesally this phragma has become lobe-like, small lobes extending anteriorly under the first abdominal tergite. Laterally, the postphragma

takes the form of a recurved ventrally-projecting apophysis. It ends laterally as an apophysis which extends along the anterior margin of the large first abdominal spiracle and supports the membrane surrounding it. A phragma extends anteriorly along the margin of the posterior notal wing process.

The metapleuron (fig. 11) consists of the episternum (eps) and epimeron (epm). Because the pleural suture which separates these two areas is horizontal, the epimeron appears to lie above, or dorsad, of the episternum. Both areas project antero-dorsally in the formation of the wing process.

While the wing process is apparently not divided externally into an episternum and epimeron, such a division is readily determined internally by tracing the pleural ridge of which the pleural suture is the external manifestation. This distinct ridge extends from the coxal cavity anteriorly to the tip of the wing process. Near the tip of the wing process it apparently forks, the anterior branch extending to the tip and strengthening it, the posterior branch terminating in a spur-like apophysis, which, from an internal aspect, lies behind a large muscle disk (mdk) which originates on the anterior margin of the wing process.

A carina (cr), which has no functional internal ridge associated with it but merely serves as a shelf to help support the elytron, divides the episternum into an anepisternum and a katepisternum. The anepisternum is covered with ventrally-pointing setae which are evidently intended to keep foreign matter from entering the area under the elytron. It extends antero-dorsally to unite with the anepimeron in the formation of the pivotal point of the wing. Internally, there is a large muscle disk on the anterior margin of the anepisternal wing process.

The katepisternum comprises the greater part of the metapleuron. It is bounded ventrally by the basisternum, from which it is separated by a suture; caudally by the eucoxa; and anteriorly by the suture demarking the mesothorax.

The anepimeron (aem) is represented by a narrow area extending along the dorsal margin of the wing process. It is not apparent externally, but is readily determined from an internal aspect, being separated from the episternum by the internal pleural ridge. It has become membranous dorsally.

The metathoracic spiracles lie in the membrane dorsad of the epimeron and are covered by the elytra.

Dorsally, the katepimeron tends to become membranous and merges with the alary membrane. Posteriorly, it projects as a spur which protects the end of the coxa.

The metasternum (fig. 12) is smooth, shiny, and covered with very minute setae. The basisternum (bs) embraces most of its area. A median suture (mds), the external evidence of a thin internal ridge which terminates posteriorly in the base of the furca, divides the sclerite longitudinally.

Caudad of the basisternum is a small furcasternum or antecoxal piece (acp) which supports the internal furca. The furca consists of a base and two dorsally extending arms, each branching once near the notum. The furcasternum is divided medially by the median suture. On the posterior margin of the furcasternum is a small projection which articulates with the coxa as a condyle-like process fitting into a slight cavity on the ventro-mesal end of the eucoxa.

Extending laterally from the base of the furca internally is a ridge which becomes gradually smaller and disappears near the lateral margin of the basisternum. This ridge is denoted externally by laterally-extending



parafurcal sutures (pfs) which demark narrow areas, the antecoxales (an), on the posterior margin of the basisternum laterad of the furcasternum.

A large oblong muscle disk is attached to the ridge-like ental margin of the furcasternum laterad of the furca.

Metathoracic leg (fig. 20). The coxa is broad and flattened, and only slightly movable. It is composed of two parts, an anterior region, the eucoxa (eu), and a posterior region, the meron (mr). The latter is closely attached to the sternum, a slight socket in the cephalo-mesal margin articulating with the prolonged posterior margin of the furcasternum.

From the posterior margin of the eucoxa, a tooth projects caudally into the coxal cavity to serve as a pivotal point for the articulation of the trochanter. Opposite the tooth on the ventral or ental surface of the coxa, a small aperture is left where the eucoxa and meron do not meet in the suture separating these two areas. A projection of the trochanter protrudes through the aperture, thus forming the second articulatory point of the trochanter. Proximally the trochanter articulates freely with the coxa. Distally it is immovably fused to the femur.

The femur (fe) is a stout segment, grooved distally on the flexor surface to allow the tibia, with which it is movably articulated, free flexing.

The tibia (ti) is somewhat compressed and bears two movable spurs (spu) on its distal or flexor margin. The extensor surface of the tibia elongates slightly, forming a weak terminal spine. The mobile spurs often have bifid ends or bear a small tooth on one margin.

The tarsus (ta) is similar to the mesothoracic tarsus.

#### WINGS AND AXILLARIES

Wings and Axillaries (figs. 15, 23). The meta-thoracic wings articulate with the body by means of several sclerites including four axillaries.

The first axillary sclerite (1 ax) lies laterad of the scutum, its mesal margin abutting the anterior notal wing process of the tergite. Its distal margin is cleft. Anteriorly it is associated with the base of the subcosta although not united with it.

The second axillary (2 ax) lies in the cleft of the first axillary and is hinged to its distal margin.

The antero-mesal margin of the third axillary (3 ax) articulates with the second axillary. The postero-mesal margin articulates with the posterior notal wing process (pnp) of the tergum. Distally the sclerite is prolonged into a rectangular process.

The fourth axillary (4 ax) usually located between the third axillary and the posterior notal wing process, is a small sclerite located in the membrane mesad of the third axillary and cephalad of the postnotal wing process.

Located in the alar membrane cephalad of the anterior notal wing process are two small sclerites. One is the humeral plate (hp) of Snodgrass, the other is probably the undeveloped tegula (teg).

In the proximal areas of the wing are several lightly sclerotized areas. Among them is the so-called median plate (mep). This plate is flexible and bends as the wing is extended and retracted.

Metathoracic Wing. Due to the unique and complicated venation of the coleopterous wing, there has been little agreement in the interpretation of its venation. In considering the wing of Prionus, the interpretations of Forbes (1922) have been followed. Because of the general lack of knowledge of the origins and homologies of the anal veins, it would probably be simpler to include them under the term "vannal veins" as proposed by Snodgrass (1935). A comprehensive treatment of the wing venation

would involve the tracing of the wing development through a long series, starting with primitive coleopterous forms and progressing to the Prioninae. As such a treatment is beyond the scope of this paper, other authors have been followed.

Costa (C) is the anteriormost of three closely crowded veins which lie along the costal edge of the wing. Basally it is swollen and bears a hook for articulatory purposes. Distally it appears to fuse with subcosta and radius.

Subcosta (Sc) originates as a swollen sclerotized area articulating with the anterior margin of the first axillary sclerite. It extends distally for about half the length of the wing, at which point it is crowded costally, by the strong radial trachea, and fuses with radius.

Radius, a convex vein, is characterized by a strong trachea. It bends anteriorly and fuses with subcosta distally. Radial sector (Rs) whose basal portion is not distinct, is represented by a small curving vein in the antero-distal portion of the wing. A radial crossvein has evidently fused with it.

Media. Basally media is hardly distinguishable, but as it approaches the distal portion of the wing it becomes distinct, appearing as an anterior spur of cubitus. It is called by Forbes the medial recurrent vein. It splits into two branches representing M 1 and M 4. M 4 fuses with Cu and reaches the wing margin.

Forbes regards cubitus as a simple vein with no branches and suggests that the second branch of cubitus has either fused with the surviving branch or atrophied on the posterior side of it. In Prionus, there is a vein which apparently branches from Cu basally. While it is usually regarded as an independent vein, it might represent either a vestige of the first anal vein or the second branch of cubitus. In this paper, it is regarded as a branch of cubitus, as suggested by the presence of a cubito-anal crossvein (cu-a). The anterior branch of Cu is distinct throughout its course and in the apical portion of the wing it fuses with M 4. The posterior branch extends distally but a short distance and terminates at the cubito-anal crossvein.

The first anal vein (1A) is indistinct basally, appearing to rise from the second anal vein.

The second anal vein arises from a point adjacent to the third axillary sclerite. It branches twice.

The third anal vein arises at the same place as the second anal vein, and branches once, the anterior branch fusing with the second anal vein, and the posterior branch reaching the wing margin as a distinct vein.

The fourth anal vein originates along the mesal margin of the third axillary and extends posteriorly into the basal portion of the wing.

Cross veins. There are two radio-medial crossveins, one whose base has atrophied but which probably extended from the basal portion of media to the radial sector, and another which extends from the distal portion of media to the radial sector, and lies along the margin of the distal fold of the wing.

A cubito-anal crossvein extends from the second branch of cubitus to the second anal vein. Forbes refers to this vein as the "anal arculus."

## ABDOMEN

The abdomen comprises ten apparent segments. From the dorsal aspect (fig. 27) the seventh tergite is visible beyond the elytra. The eighth, ninth, and tenth segments are normally retracted within the body when not in use. For illustrative purposes, the segments have been extended in the plates. Upon removing the elytra and metathoracic wings it will be noted that the tergites as a whole are not heavily sclerotized and that between each one is a membranous area, thus allowing for expansion and contraction of the abdominal cavity. The abdomen is heavily sclerotized ventrally and there is no prominent membranous area between the sternites. The ninth segment bears the genital appendages and the anal opening is through the posterior end of the much-reduced tenth segment.

There are seven abdominal spiracles (sp) situated in the membrane between the sternites and tergites. The first abdominal spiracle is the largest spiracle of the abdomen, being nearly twice the size of the following five subequal spiracles. The seventh spiracle, located laterad of the anterior portion of the pygidium, is slightly smaller than the spiracle preceding it. All the spiracles are concealed and protected by the elytra.

There are eight abdominal tergites (tg). Of these, the first three are similar and but lightly sclerotized. Beginning with the fourth, the tergites become progressively more sclerotized until a complete sclerotization is attained in the seventh tergite. This tergite, called the pygidium (pyg), often extends beyond the distal ends of the elytra, especially in gravid females. The first six tergites are subequal in width, the seventh is narrower and elongated along the long axis of the body. The eighth tergite is nearly twice as long as wide and tapers caudally. It is protrusile and ordinarily is hidden by the pygidium. The tip is often visible in the case of egg-laden females. The ninth tergite is membranous proximally and is given some rigidity by two baculi (vb, fig. 26), sclerotized rods embedded in the membrane. This segment is discussed further in a later paragraph. The tenth tergite serves as a roof and sides for the extremity of the alimentary canal. It is called the proctiger (prc).

There are seven apparent sternites (str, fig. 25). Of these, five are readily apparent upon superficial examination of the venter. The first sternite has completely disappeared and the second may have been reduced



to a narrow sclerotized strip in the membrane between the metathorax and abdomen. Sternites three, four, five, and six are heavily sclerotized and subrectangular in shape, tapering slightly as they progress caudally. The seventh sternite has a broadly ovate distal margin. The eighth sternite, normally retracted into the body and concealed by the seventh segment, is sclerotized but has a mesal membranous area extending along the long axis. The ninth sternite, membranous except for two baculi, bears the sclerotized genital appendages. It is discussed more fully in connection with the genitalia. The sternite of the tenth segment, or proctiger, evidently forms the floor of the anus and is concealed by the coxites (cxt) of the ninth segment.

The ninth segment bears the genital appendages, which consist of the so-called valvifer-baculi (vb), two coxites (cxt), and two styli (sty). The term valvifer-baculi is used by Tanner (1927) in describing the conditions produced when the valvifers have become so altered that they are no longer distinct sclerites. The valvifer-baculi are sclerotized rods in the integument. The coxite is two-segmented, the first segment being lightly sclerotized and strengthened by a baculum. The

second segment of the coxite is heavily sclerotized and bears a lateral stylus near the distal end. Each stylus bears several setae (se). This type of genitalia has been designated by Tanner as the "elongate type," as opposed to the "compact type."

Male Genitalia (figs. 24, 28). The male genitalia consists basically of an eversible tube formed by the invagination of the seventh, eighth, ninth, and tenth segments of the abdomen. Normally, the eighth, ninth, and tenth segments of the male are concealed by the seventh segment under which they have been retracted.

The seventh segment has a distinct shield-shaped sternite and tergite. The sternite is not as wide as the tergite and is slightly emarginated caudally.

In the eighth segment, the tergite is distinct and comparable to the seventh in shape. The sternite is distinct distally but its basal portion appears to have fused onto the floor of the seventh sternite.

To date, the origin of the components of the male genitalia has not been satisfactorily worked out, although it is generally agreed that they represent parts of the ninth abdominal segment.

In view of the varied interpretations of the parts of the genital segment and the resulting lack of uniformity in the applied terminology, it has been considered best to adopt an established set of terms in this paper. Accordingly, the terms proposed by Sharp and Muir (1912) have been employed in the following description.

In general, that part of the genital tube that is reflected and forms the external portion of the organ is termed phallic. The sclerites of the phallic portion of the tube form two groups, those which are farthest from the body wall when the tube is protruded and compose the median lobe; and those situated nearer the body wall and called the tegmen. These two groups of sclerites are connected by membranes. The median lobe plus the tegmen is termed the aedeagus.

The median lobe (fig. 24) is subtubular, the opening at its distal end is called the median orifice (mo), and the opening at the basal end is called the median foramen (mf). In addition to a prominent muscle which is attached directly to the base of the median lobe, two apodemes, called median struts (ms) provide support for muscles.

The tegmen (tgm, fig. 28) consists of two parts, the basal piece and a pair of lateral lobes (ll). The heavily sclerotized basal piece extends caudally. Its caudal

margin is deeply cleft and bears minute setae. A lateral lobe lies on each side of the median lobe.

Close to the aedeagus is a sclerotized Y-shaped rod called the spicule (spc). A distal tip of the Y lies on each side of the tegmen. The base of the Y is connected by a membrane to the distal tips of the lateral lobes. Hopkins (1911) believes that the spicule represents the ninth sternite.

The internal sac is drawn into the median lobe. The ejaculatory duct (ej) which extends caudally and passes through the cleft of the median strut ends in this sac between two sclerotized "hooks" which lie on its floor.

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### Explanation of Figures

- Fig. 1 Dorsal view of the head  
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segment  
" 3 Ventral view of the head  
" 4 Maxilla  
" 5 Trochanter showing internal processes  
" 6 Dorsal view of the lateral margins of the  
pronotum  
" 7 Ventral view of right mandible  
" 8 Antenna  
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" 10 Ventral view of left mandible  
" 11 Basi-lateral view of pterothorax  
" 12 Ventral view of pterothorax  
" 13 Ventral view of prothorax  
" 14 Dorsal view of pterothorax  
" 15 Dorsal view of axillary sclerites  
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showing articulation of coxa and trochanter  
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" 22 Pretarsus  
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5, 6, 7, and 8 are partly diagrammatic

## Abbreviations

- A - anal vein  
a - anus  
ac - anteclypeus  
acp - antecoxal piece  
aem - anepimeron  
aes - anepisternum  
an - antecoxale  
anp - anterior notal wing process  
ap - apophysis  
apd - apodeme  
as - antennal socket  
ax - axillary sclerite
- b - basimaxillary membrane  
bs - basisternum  
bt - basitarsus
- C - costa  
c - clypeus  
cd - cardo  
co - condyle  
cr - carina  
cs - coronal suture  
Cu - cubitus  
cvt - cavity for articulation of the trochanter  
cx - coxa  
cxc - coxal cavity  
cxt - coxite
- dt - distitarsus
- e - compound eye  
ej - ejaculatory duct  
emp - empodium  
epm - epimeron  
eps - episternum  
eu - eucoxa
- fc - frontoclypeal suture  
fe - femur  
fm - flexor membrane  
fp - frontal pits  
frp - furcal pit  
fs - furcasternum  
fu - furca

g - galea  
ga - gena  
gi - ginglymus  
gl - glossa  
gp - gular pits  
gs - gular suture  
gu - gula

hp - humeral plate

kem - katepimeron  
kes - katepisternum

l - lacinia  
la - labrum  
lb - labium  
lg - ligula  
ll - lateral lobes  
lp - labial palpus  
lr - alifer

M - media  
m - mala  
md - mandible  
mdk - muscle disk  
mds - median suture  
mep - median plate  
mf - median foramen  
ml - median lobe  
mm - mental membrane  
mn - mentum  
mnn - mesonotum  
mo - median orifice  
mp - maxillary palpus  
mr - meron  
ms - median strut  
mtn - metanotum  
mx - maxilla

ng - notal groove

pa - parietal  
pac - paraclypeus  
par - parempodium  
pc - postclypeus  
pcp - post coxal projection  
pd - pedicel  
pf - palpifer

pfs - parafurcal suture  
pge - postgena  
pl - pleuron  
plg - palpiger  
pm - parameres  
pn - pronotum  
pnp - posterior notal wing process  
pp - pivotal point  
pph - postphragma  
pr - precoxale  
prc - proctiger  
prs - prescutum  
ps - pleural suture  
psc - postscutellum  
psl - prosternal lobe  
pyg - pygidium  
R - radius  
r-m - radio medial crossveins  
RS - radial sector

s - stipes  
Sc - subcosta  
sc - scape  
scl - scutellum  
sct - scutum  
scts - scutoscutellar suture  
se - seta  
sm - submentum  
sp - spiracle  
spc - spicule  
spn - spine  
spu - spur  
ss - spinasternum  
str - sternite  
sty - stylus  
su - sulcus

t - tergite  
ta - tarsus  
tch - trochanter  
te - temples  
teg - tegula  
tg - tergite  
tgm - tegmen (basal piece plus lateral lobes)  
ti - tibia  
tr - trochantin of coxa

ugf - unguifer  
ugt - unguitractor  
ung - ungues or claws  
ut - unguitractor tendon

vb - valvifer baculi

xx - fulcral points

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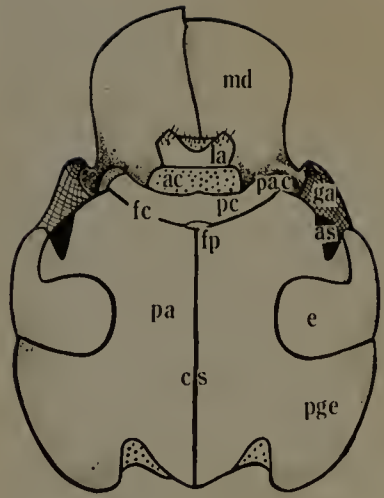


Fig. 1



Fig. 2

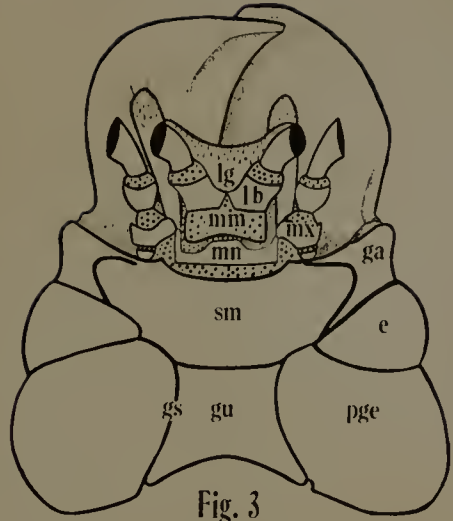


Fig. 3

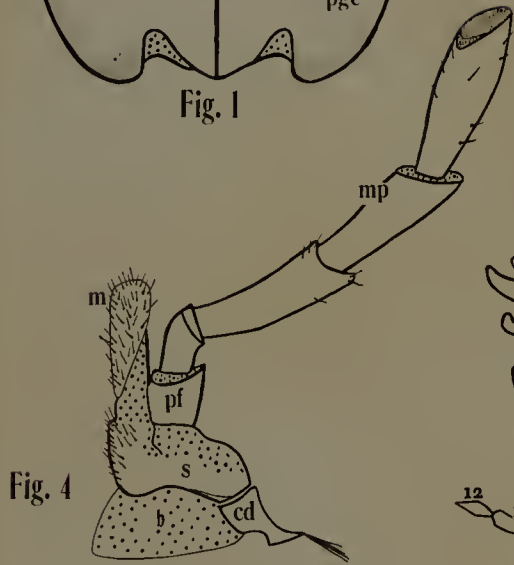


Fig. 4



Fig. 5



Fig. 6

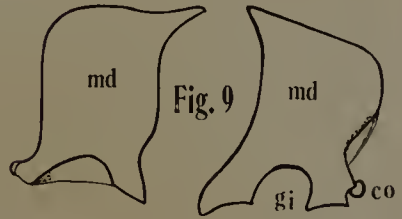


Fig. 9

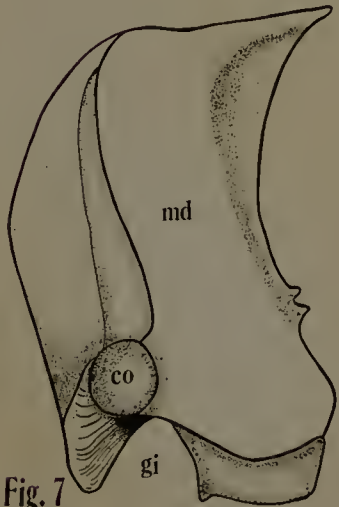


Fig. 7

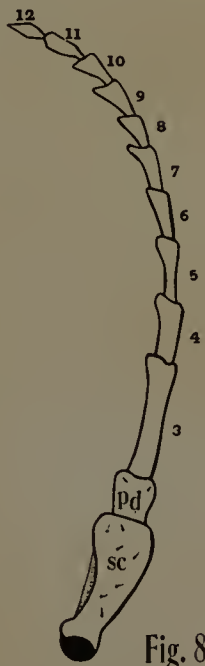


Fig. 8

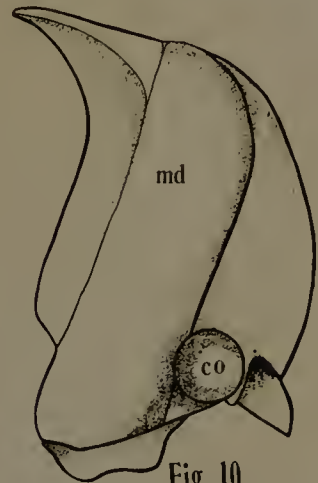


Fig. 10



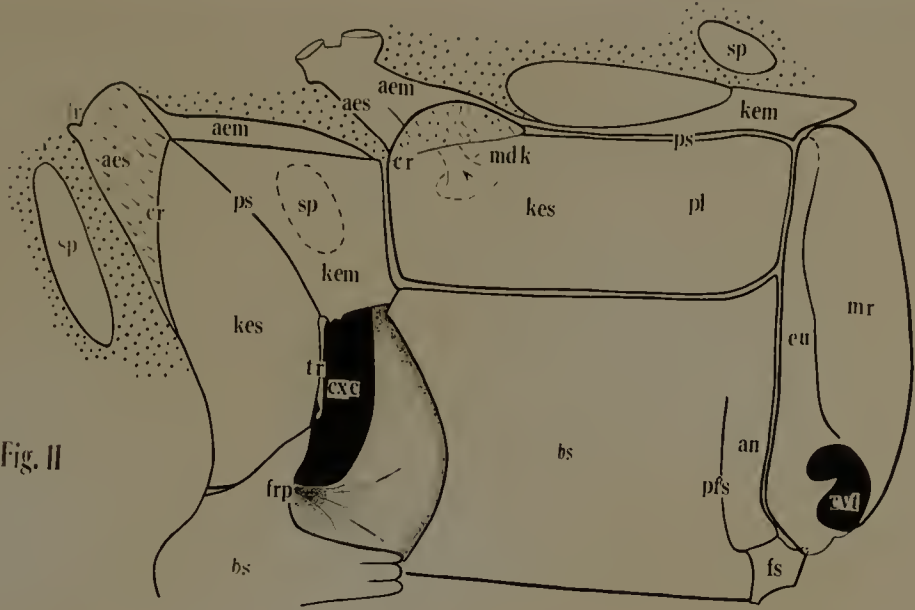


Fig. 11

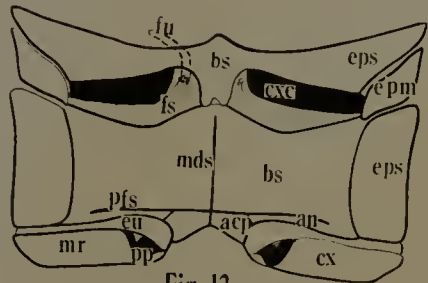


Fig. 12

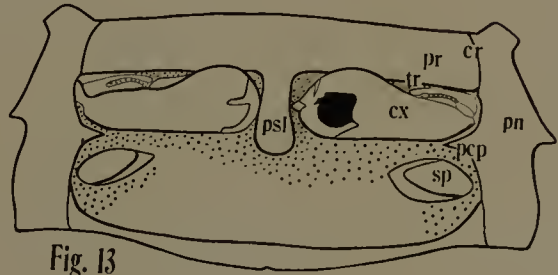


Fig. 13

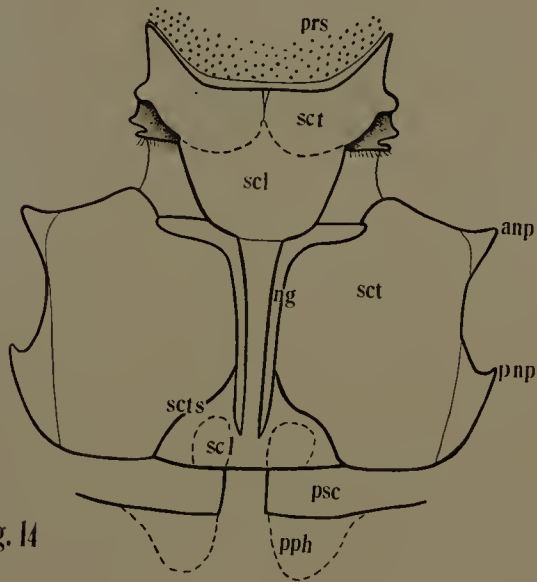


Fig. 14



Fig. 15

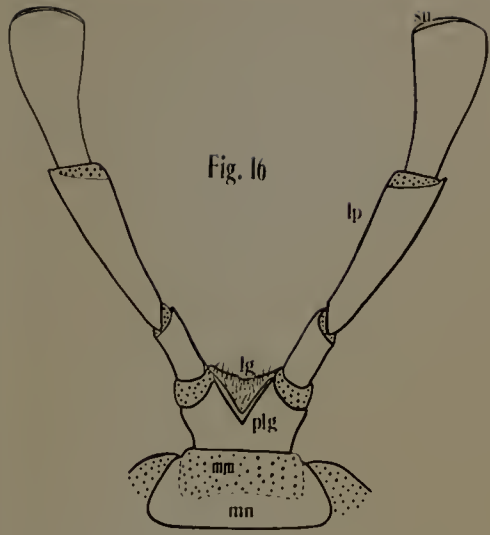


Fig. 16

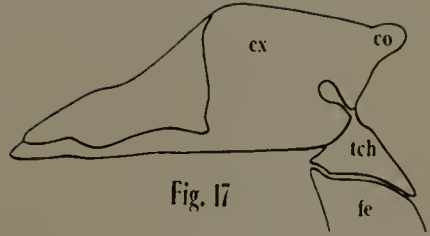


Fig. 17

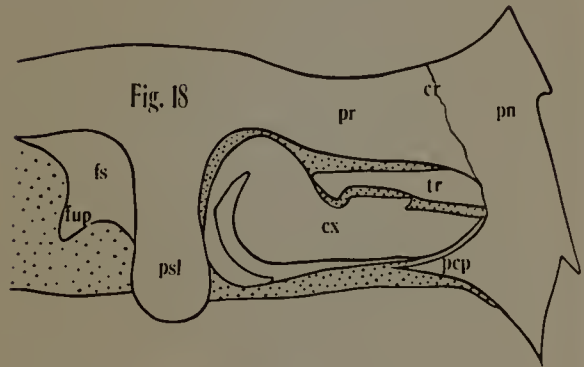


Fig. 18



Fig. 20

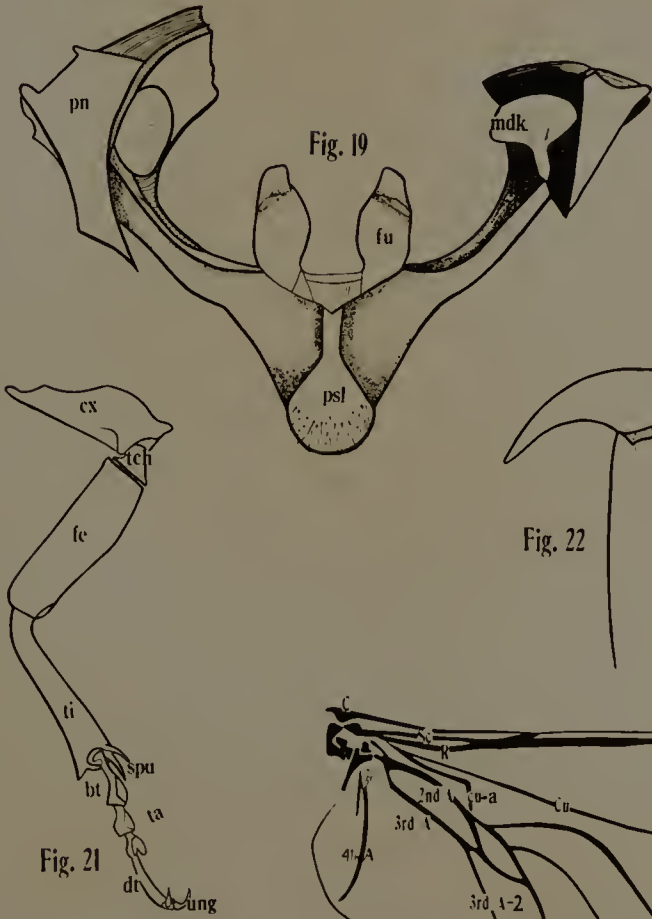


Fig. 21

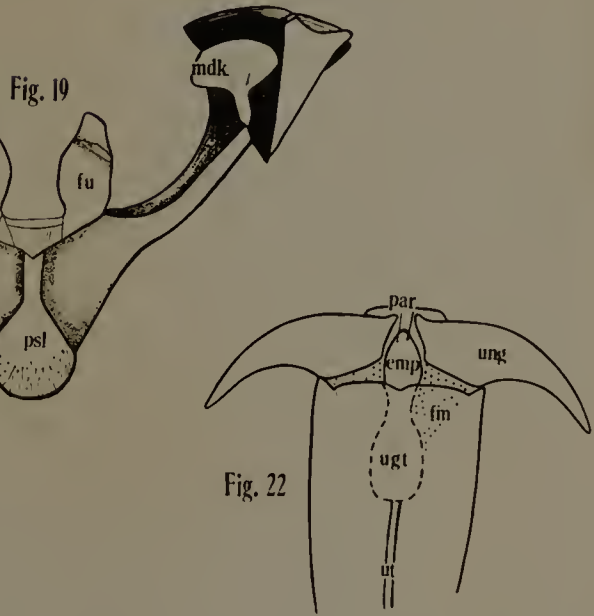


Fig. 19

Fig. 22

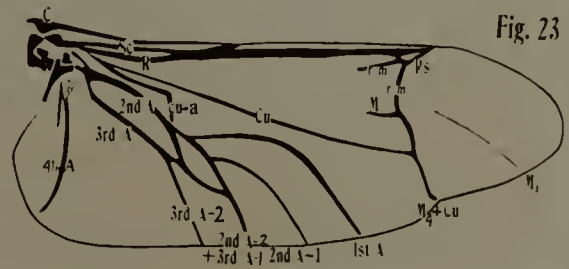


Fig. 23

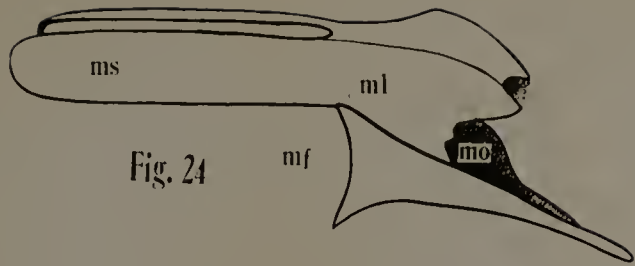


Fig. 24

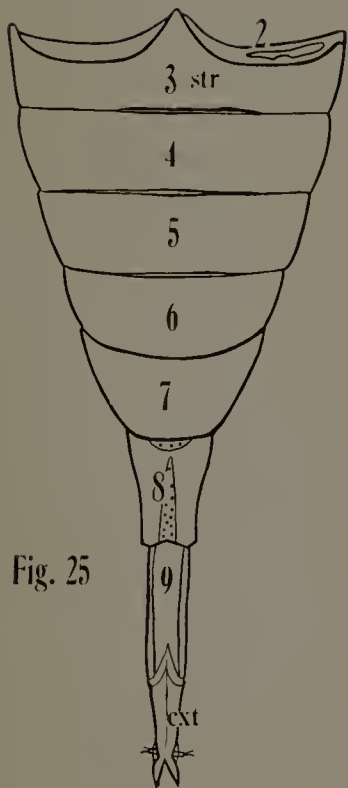


Fig. 25



Fig. 26

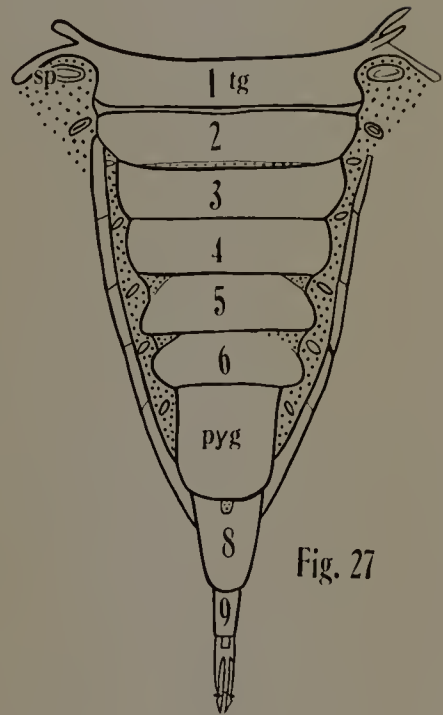


Fig. 27

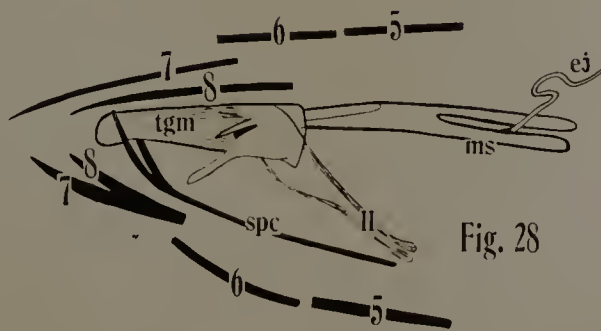


Fig. 28

Approved by

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June 2, 1938

