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THE EXTERNAL MORPHOLOGY OF THE PRIMITIVE TANYDERID DIPTERON PROTOPLASA FITCHII O. S., WITH NOTE ON THE OTHER TANYDERIDAE

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The External Morphology of the Primitive Tanyderid Dipteron *Protoplasa fitchii* O. S., with Notes on the other Tanyderidae

by

Inez W. Williams

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INTRODUCTION

The purpose of this thesis is to furnish a complete description of the external anatomy of one of the most primitive representatives of the order Diptera, Protoplasa fitchii O.S., and to summarize the literature dealing with the family Tanyderidae; in addition, to present a revised key to the genera of this family.

The material for morphological study consisted of alcoholic and dried specimens kindly furnished by Dr. G. C. Crampton and dried specimens from the collection of Dr. C. P. Alexander. With the exception of two of the Tanyderid wings which have been figured, all of the wash drawings were made from wing mounts contained in Dr. C. P. Alexander's unrivaled crane-fly collection.

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EXTERNAL MORPHOLOGY

GENERAL APPEARANCE.

The adult of Protoplasa fitchii O. S. is predominantly grayish-brown in color, is relatively slender and measures about eight millimeters in length. The head is gray tinged with black and the sixteen-segmented antennae are smoky gray-brown with a blackish tinge. The large, black, compound eyes are of particular interest because they have many short setae arising between the ommatidia causing a "hairy-eyed" condition which is characteristic of the Tanyderids. The most conspicuous structures of the head are the long, brown maxillary palpi which lie at the sides of the proboscis. Except for three faint brown stripes on the prescutum and the pale scutellum, the thorax is gray tinged with black. The wings are about eight millimeters in length and are striking in appearance due to the pattern which is composed of three bands of ring-like brown spots with paler brown centers. A supernumerary crossvein present in cell M_3 of the wing is the character which distinguishes Protoplasa fitchii from all other members of the family. The halteres are rather inconspicuous, pale, with brown

clubs. The legs are long and slender and are yellowish-brown except the distitarsus and the distal portions of the femur and tibia which are dark brown. They have short, rather sparse setae and conspicuous tibial spurs. The abdomen is brown with the posterior margins of the segments pale. The dististyles of the male hypopygium are bifid and have several strong setae at the tip of the inner margin of the longer process.

HEAD.

There are no distinguishing sexual differences in the head and mouthparts of *Protoplasa fitchii*, so that the head of the male here figured will serve to illustrate the parts for both sexes.

In general the head is irregular in outline but the region of the head capsule behind the fronto-clypeus is subglobose. The occiput *ocp* is the part of the head capsule immediately behind the compound eyes *e* and dorsad of the occipital foramen *of* (Figs. 1,2,and 4). On each side of the occiput there is a small structure called the occipital condyle *occ* which provides a point of articulation of the head with the laterocervicale *lc* possibly facilitating a nodding movement.

The occipital foramen of shown in Fig. 4 is the posterior opening of the head capsule through which the alimentary tract and nerves pass caudad into the thorax. Dorsally and laterally the occipital foramen is bounded by "chitinized thickenings" th which Peterson (1916) believes "arise from the ental surface of the paraocciput, a narrow piece about the dorsal and lateral margin of the occipital foramen." Figs. 3 and 4 indicate that these thickenings extend into the region of the gular pits gp.

Cephalad of the occiput in the dorsal region of the head is the vertex v (Fig. 1) which extends forward between the compound eyes to the posterior limits of the antennal fossae. In its anterior portion the vertex is curved convexly. On the area behind the antennal fossae are two protuberances (Figs. 1 and 2) which are more pronounced in some individuals of the species than in others.

The lateral margin of the antennal fossa bears a small projecting portion, the antennifer anf (Figs. 1 and 2) which is roughly triangular in shape and serves as a pivot for the antenna. The anterior margin is bordered by the narrow gena ge.

The fronto-clypeus fc, an irregularly shaped sclerite cephalad of the genae and the antennal fossae, is formed by the fusion of the frons and clypeus. This portion of the head capsule is strongly curved and apparently serves as a shield for the bases of the mouthparts which are situated directly ventrad of it. Anteriorly the fronto-clypeus is bordered by the labrum l. The sclerotization of the labrum is reduced to a rather slender and indefinite medial portion while the remaining area is membranous. The labrum extends between the maxillary galeae and is closely associated with the epipharynx.

The ventral regions behind the large compound eyes e are the postgenae pge. Between the postgenae is the membranous gular region on each side of which is a gular pit gp.

Fig. 3 shows the head capsule with the dorsal portion removed to expose the internal structures. The tentorium tnt is reduced to two slender rods which probably represent the fused anterior and posterior arms. These rods extend from the gular pits or the mouths of the invaginations forming the posterior arms, into the region of the fronto-clypeus.

APPENDAGES OF THE HEAD.

Antennae. Osten-Sacken (1859) in his original description of *Protoplasa fitchii* recorded the antennae as having fifteen segments. Alexander (1927b) states that they are sixteen-segmented. Figure 7 clearly shows the scape, pedicel, postpedicel, and thirteen flagellar segments, totaling sixteen. The scape sca is a relatively short and wide segment with a projection which serves as a pivot for the second segment, the subglobose pedicel pd. The postpedicel ppd is subovoid. With the exception of the terminal segment of the flagellum, the remaining segments are subcylindrical and vary in width, thereby appearing to taper somewhat. The terminal segment, however, is more slender than the preceding ones.

Mouthparts. The mouthparts include the labium, maxillae, hypopharynx, and epipharynx; the mandibles are lacking.

As is shown in Fig. 9 there is no trace of a sclerotized gula and submentum. The mentum mn is reduced to a small and weakly sclerotized area which merges with the surrounding membrane. The sclerite labelled "pgr" is formed by the uniting palpigers.

However, the fusion of the palpigers is not complete because the sclerites are still separated by a suture.

As in Mecoptera, the labial palpi are two-segmented. Together, the two segments form the labellum lbl. The basal segments are separated by membrane and are termed the basilabellum bl. The distal segments which form the distilabellum dl are weakly sclerotized with their inner margins membranous.

In comparison with the slender labium of Tanyderus (figured by Crampton 1925b) that of Protoplasa is relatively short and stout and lacks the ligula or united glossae and paraglossae. The mentum of Tanyderus is definite, elongate and well sclerotized. The underlip of Macrochile is also elongate and has a definite and well sclerotized mentum.

The maxillae lie at the sides of the labium with the well developed maxillary palpi mxp extending some distance beyond the distilabellum (Figs. 6 and 9). These palpi are composed of five segments, the first of which is subglobular in shape; the succeeding two segments are subequal in length, while the fourth is shorter. The terminal or fifth segment is the

longest and is rounded at the tip. Between the maxillary palpus and the basilabellum is the maxillary galea ga which is blade-like and extends forward a distance equaling the length of the distilabellum. A small sclerite labelled "pfr" which lies between the first segment of the palpus and the stipes probably represents the palpifer. The stipes sti is extremely long and slender extending caudad nearly to the region of the gular pits.

Ventrad of the labrum-epipharynx and closely associated with it is the hypopharynx hp (Fig. 8). As is shown in Figure 8, the hypopharynx is lance-shaped and is divided into a distal, unpaired, median piece and a proximal paired area (Peterson 1916). According to Peterson (1916), the salivary duct sd enters the proximal end of the hypopharynx just dorsad of its attachment to the labium and extends through it to its distal end.

The epipharynx ep (Fig. 5) is attached laterally to the membranous area of the labrum and is composed of a sclerotized median piece and lateral sclerotized pieces. Peterson terms these lateral structures "tormae" to. The bases of the tormae have a hinge-like connection with the basipharynx.

The basipharynx bp (Fig. 8) or the fulcrum is a sclerotized tube-like structure. It is closely associated with the basal portions of the epi- and hypopharynx and Peterson (1916) believes that it is formed by the fusion of the basal regions of these two structures. The posterior part of the basipharynx is extended to form two projections called the "cornua" cu. In the membranous region between these projections the oesophagus opens anteriorly.

THORAX.

The thorax of *Protoplasa fitchii* has been figured by Crampton (1925a and 1926b). In his 1926 publication he also includes figures of the thoraces of the Tanyderid genera *Macrochile*, *Tanyderus*, and *Péringueyomyina*, and in general the thoraces of these genera bear a striking resemblance to one another. The prothorax and metathorax are greatly reduced while the mesothorax or wing-bearing segment is large to accommodate the muscles of flight. The metathorax bears the halteres.

NECK REGION.

The walls of the membranous neck region which is cephalad of the prothorax are strengthened by two large plates, the laterocervicalia lc (Fig. 10).

In *Protoplasa* these plates are relatively short and broad. In *Tanyderus*, however, they are long and slender thereby forming an extremely long neck region. *Macrochile* and *Péringueyomyina* have small laterocervicalia which are more or less closely associated with the prothorax. The neck of *Protoplasa* is intermediate between the long-necked condition of *Tanyderus* and the shorter one of *Macrochile* and *Péringueyomyina*. On its anterior border the laterocervicale has a ventral finger-like projection, the cephaliger *ce* (Fig. 2), which articulates with the occipital condyle of the head. Its posterior border reaches the prothorax. A ventral view (Fig. 6) shows that each laterocervicale has a small and nearly elliptical, membranous area which has been called the "laterofenestra" *lcf* (Crampton 1925c).

PROTHORAX.

The pronotum *pn* or dorsal area of the prothorax is divided into the antepronotum *apn* or anterior portion and the postpronotum *ppn* or posterior portion. The postpronotum is the restricted area between the prescutum of the mesothorax and the membrane surrounding the mesothoracic spiracle. The prothoracic pleuron is composed of an episternum *es* or anterior sclerite and an epimeron *em* or posterior sclerite.

Dorsally the episternum es is fused with the antepronotum although its dorsal limit is the region of the notch into which the dorsal part of the laterocervicale fits. The epimeron em is demarked from the episternum by an indistinct suture and extends dorsad from the region of the coxa to fuse with the postpronotum. The sternum of the prothorax is demarked into a presternum, basisternum, and furcasternum. The presternum is the most anterior and is a small, ovate sclerite lying between the caudal limits of the laterocervicalia. Between the prothoracic coxae and caudad of the presternum is the basisternum which is rather small and nearly square. The furcasternum is shield-shaped with its anterior portion lying in the area between the coxae and its posterior portion extending caudad between the ventral limits of the mesothoracic sternopleura. The coxa cx_1 is subcylindrical and about equals the size of the eucoxa of the mesothorax or the coxa of the metathorax.

MESOTHORAX.

The mesothoracic spiracle sp lies in the membrane between the postpronotum and the anterior division of the mesothoracic anepisternum. In the mesonotum the

prescutum, scutum and scutellum are demarked by sutures. The prescutum $\underline{psc_2}$ and the scutum $\underline{sc_2}$ together form a dome-like region. The prescutum occupies the anterior and dorsal extent of this dome-like region and the scutum occupies the remainder. The scutum is divided into an anterior and posterior portion by a transverse scutal suture ss. The scutellum $\underline{sl_2}$ is lobe-like and is separated from the postscutellum by a membranous area. Sutures divide the postscutellum into a median sclerite or mediotergum $\underline{mt_2}$ and two lateral sclerites or pleuroterga $\underline{pt_2}$. The pleural suture c which extends from the region of the eucoxa $\underline{ec_2}$ dorsad to some indefinite point near the base of the wing, divides the mesothoracic pleuron into an episternal and an epimeral region. Cephalad of this suture is the episternum which is divided by the anepisternal suture a into a dorsal region, the aepisternum $\underline{aes_2}$ and a ventral region, the sternopleurum $\underline{spl_2}$. A membranous cleft which extends downward as far as the anepisternal suture a splits the anepisternum into an anterior part, which is fused with the sternopleurum, and a posterior part. In Tanyderus the membranous cleft is short and broad while in Macrochile it is represented

only by a suture. The anepisternal suture in both of these genera extends cephalad only as far as this cleft as is the case in Protoplasa. The ventral portion of the episternum is fused with the sternum and is termed the sternopleurum spl_2.

The small irregular subalifer saf lies between the anepisternum and the anepimeron with its posterior limit demarked by the pleural suture c. Close relatives of the Tanyderids (the Psychodids and Ptychopterids) as well as the other Tanyderids figured by Crampton (1925a and 1926a) have the subalifer clearly demarked and of the same contour as that of Protoplasa. The epimeron is the posterior region of the pleuron and is demarked by the transverse anepimeral suture b into a dorsal area or anepimeron aem_2 and a ventral area or meropleurum mpl_2. The meropleurum is formed by the fusion of the meron and the katepimeron. This fusion of the meron with the epimeron to form the meropleurum is characteristic in the Nematocerous families Tanyderidae, Ptychopteridae, and Psychodidae. No other Nematocera with the exception of the Blepharoceridae exhibit this condition. Although the sternum of the mesothorax lacks a presternal region, there is a small basisternum lying between the sternopleura and a relatively

large furcasternum which separates the eucoxae. The eucoxa $\underline{ec_2}$ alone forms the basal segment of the mesothoracic leg, the meron having fused with the epimeron as mentioned above.

METATHORAX.

Like the prothorax, the metathorax is greatly reduced. The metanotum $\underline{mtn_3}$ is a narrow region extending along the posterior border of the post-scutellum of the mesothorax. Dorsad of the episternum of the metathoracic pleural region is the metathoracic spiracle sp. The episternum $\underline{es_3}$ is reduced to a wedge-shaped sclerite and is demarked from the narrow and elongate epimeron $\underline{em_3}$ by a pleural suture. The metasternum is represented in lateral view by a small triangular sclerite labelled $\underline{st_3}$. In ventral aspect, however, it is composed of a small basisternum which is faintly demarked and fused with the poorly defined furca-sternum caudad of it. The coxae $\underline{cx_3}$ lie at the sides of the furcasternum.

APPENDAGES OF THE THORAX.

The legs of Protoplasa are essentially the same, therefore that of the prothorax has been figured as representative. It is very slender and longer than the body. Figure 13 shows that the coxa cx is of

moderate size and that the trochanter *tr* is small. The coxa of the mesothorax differs from the coxae of the other segments in that it is composed of the eucoxa alone. The femur *fe* and the tibia *ti* of the prothoracic leg are subequal in length. At the distal end of the tibia there are two well developed and movable spines. The basitarsus *bta* is equal to about three-fourths of the length of the tibia, and like the tibia bears two spines distally. The second tarsal segment is about one-half the length of the basitarsus and bears two spines; the third segment is about one-half the length of the second or preceding one and also bears two spines, while the fourth segment is smaller than the third and has no spines. The distitarsus *dta* or terminal segment bears several spines and two ungues or claws *un*.

The wing of *Protoplasa fitchii* has been figured many times and its venation is recognized as being very primitive. Figure 12 shows the various distinguishing features interpreted according to Tillyard. With the exception of the supernumerary crossvein of cell M_3 most of the characters are present in Tanyderids in general.

The subcosta is two-branched $Sc_{1,2}$; the radius is five-branched $R_{1,2,3,4,5}$; the media four-branched

$M_{1,2,3,4}$; and the cubitus *Cu* has one branch. There are two anals *1st A* and *2nd A*. Cell R_2 is shorter than its petiole and has its base lying beyond the midlength of the distal section of R_1. Cell *1st* M_2 is long, broadened distally and is closed. The two cells beyond are comparatively short. Cell M_3 has a supernumerary crossvein peculiar to *Protoplasa*. Between the cubitus *Cu* and the first anal *1st A* there is an indefinite vein or fold which runs close to *Cu* for about three-fourths of its length and is labelled *pa* in Figure 12. According to Tillyard this would be Cu_2 but according to Comstock it is *1st A*. Crampton (1926a) calls it the "preanal." The second anal *2nd A* forms the so-called "T" vein characteristic of the Tanyderids as a whole. The radio-medial crossvein *r-m* has what appears to be the stub of a vein at its anterior end. Crampton (1926a) suggests its possible phylogenetic significance. The medial crossvein *m* is always present in Tanyderids. The humeral *h* and the medio-cubital *m-cu* crossveins are of no particular importance.

The haltere *ha* (Fig. 11) is stalked and knob-like at the end. Basally it is mostly membranous and the stalk is only weakly sclerotized. The distal

end is subglobose with a transverse suture or fold which divides it into two distinct hemispherical parts, the dorsal one of which is the larger and overlaps the other. The smaller portion bears three setae.

ABDOMEN.

The abdomen of *Protoplasa fitchii* has nine distinct segments; the tenth and eleventh are fused and indefinite. Crampton (1926a) has indicated the same condition in *Macrochile*, and in his 1931 publication (Crampton 1931a) the figures show that the primitive Mecopteran, *Notiothauma*, which is closely allied to the Diptera, is strikingly similar. There is a marked "telescoping" of all the segments and this condition tends to make them appear more variable in length than they are actually. Figure 20 shows that the first, second, and eighth segments are relatively short; the third, fourth, and fifth are intermediate; while the sixth and seventh are the longest. The ninth and fused tenth and eleventh are indefinite because of their modification. Figures 16, 19, and 20 show clearly that the first eight segments are composed of a dorsal sclerotized region or tergite *1t* to *8t* separated from the ventral sclerotized area or sternite *1s* to *8s* by a lateral

membranous area. In this membrane between the tergite and sternite, the spiracle sp of the segment is borne. The first abdominal spiracle, however, is situated more dorsally in the membrane between the metathoracic epimeron and the first abdominal tergite.

In the male there is a strong twisting or torsion of the terminal segments to facilitate mating. Figure 20 shows this twisted condition as a result of which the tergites of the seventh, eighth, and ninth segments occupy a lateral position instead of being dorsal as they are normally. The male differs from the female in that the ninth segment is the first to show modification. The ninth tergite 9t which Crampton (1926a) termed the "epandrium" in *Macrochile*, is bilobed (Figs. 18, 19, and 20). In *Macrochile* the lobes are not so pronounced as they are in *Protoplasa*. The cerci bc of the male are reduced to one segment. These basicerci, as they are called, lie in the membrane behind the ninth tergite and at the sides of the area which corresponds to the anus-bearing proctiger of *Macrochile*. The basicerci represent the basal portions of the cerci. In *Macrochile* the cerci are

likewise one-segmented but the proctiger or anus-bearing structure is more clearly demarked. The gonopods or copulatory limbs are composed of two segments. The basal segment bst (Figs. 14, 18, 19, and 20) of the gonopod is variously termed by different authors as basistyle or coxite. As yet it is unsettled as to whether the basal segments are coxites or merely segments of the style. In *Protoplasa* these so-called coxites or basistyles bst are either united basally or fused with adjacent structures such as the ninth sternite, etc., as Crampton suggests in the case of *Macrochile*. The distal portion dst of the gonopod variously termed style, gonostyle, diststyle, or clasper is rather deeply forked in *Protoplasa*, forming a comparatively short basal process sap and a longer distal process ap which bears a peculiar tuft of spines at the tip of its inner margin. Like *Protoplasa*, *Macrochile* has a forked style or diststyle with an elongate distal process and a rather short basal process. In *Tanyderus* and *Péringueyomyina* the style or dististyle is not forked. It is short in *Tanyderus*, but in *Péringueyomyina* it is very long and slender and has a series of spines along its inner margin.

Each coxite or basistyle has on its dorsal surface a weakly sclerotized, lobe-like structure int which perhaps corresponds to the interbase (Figs. 14, 17, and 18). The so-called gonapophyses gap are probably represented by a pair of elongate projections flanking the aedeagus and having their bases imbedded in the basal region of the coxites or basistyles (Figs. 14, 17, 18, and 19). A sclerotized process aed with three prongs shown in Figures 14, 17, and 18, together with a supporting collar-like portion may represent the aedeagus. This structure lies in the membranous area between the coxites or basistyles and the basicerci. The aedeagus in Macrochile is an elongate and bifid structure.

Differentiation of the terminal segments of the female of Protoplasa begins in the eighth abdominal sclerite which is not so much reduced as in the male. The eighth sternite 8s bears a pair of lobe-like projections vv but these apparently are not homologous with the structures called the ventral valves in Macrochile. There is a small sclerite ls between the ninth tergite and the eighth sternite which may possibly be the reduced ninth sternite. In Protoplasa there is no structure homologous to the

mediogynium or projection between the ventral valves of *Macrochile*. Unlike that of the male, the cercus of the female has two segments, the basicercus bc and the disticercus dc. Both of these segments are relatively large and rounded. In *Macrochile* the disticercus is reduced to a pointed process and the basicercus is bilobed.

GENERAL ACCOUNT OF THE FAMILY TANYDERIDAE

The Family Tanyderidae represents a group of the most primitive of all living Diptera. Osten-Sacken (1859, 1869, 1880, 1886) and Philippi (1865) considered that its members belonged to the family Tipulidae. Handlirsch (1909), however, grouped them with the Ptychopteridae as the subfamilies Tanyderina and Macrochilina. Enderlein (1912), Alexander (1913), and Riedel (1921) likewise classified them as a subfamily under the Ptychopteridae. In 1919, Alexander in a key to the crane-flies of Northeastern North America included these flies as a distinct family, the Tanyderidae, characterized by possessing five branches of the radius which reach the wing margin and by the presence of a

single anal vein. Crampton (1926b) showed that because of their close affinities to the Psychodidae, these primitive flies should be placed in the superfamily Psychodcidea rather than in the Tipuloidea as was formerly the case. Studies of the recently discovered immature stages of Protoplasa fitchii, which is considered representative of the family, proved the group to be isolated from either the Psychodidae or Ptychopteridae (Alexander 1930a; Crampton 1930a, 1930b). The Bruchomyiinae which are now placed as a subfamily of the Psychodidae (Alexander 1928a; Crampton 1925a, 1926a; Tonnoir 1922) were previously considered as representing a subfamily of the Tanyderidae (Alexander 1920c, 1927b).

Knowledge of the immature stages of the Tanyderids was lacking until June 1929 when Alexander (1930a) and Crampton (1930a, 1930b) discovered the larva and pupa of Protoplasa fitchii on the Gaspe Peninsula, Quebec. Prior to this time, a unique Dipterous larva from the vicinity of Washington, D. C. described by Alexander (1920c) as the "supposed larva" of Protoplasa fitchii was the only immature form considered as possibly representing the family.

Because of the recent discovery of the larva and pupa of Protoplasa fitchii, students of Diptera are at a loss as to the exact affinities of this "supposed larva."

Phylogeny: The oldest known Tanyderid is the Baltic Amber Macrochile spectrum Loew. Crampton (1926a) places this insect at the base of one of the lines of descent of Diptera which leads to the Psychodoids. Handlirsch (1909) derives Macrochile from the Archiptychoptera in the latter part of the Cretaceous period and, according to him, from Macrochile arise Protanyderus, Protoplasa, Tanyderus, Radinoderus, and Mischoderus in the Tertiaries. According to Alexander (1932), the Lower Tertiary Etoptychoptera (Handlirsch, 1910) shows certain points of resemblance to Macrochile in the nature of the radial and medial fields of the wing but has two anal veins. The Mesozoic Eoptychopteridae also differ from the Tanyderidae. Tillyard's Permotipula described from the Permian deposits of New South Wales (Tillyard 1929) shows a highly modified radial field of the wing and indicates that Diptera arose in the Palaeozoic era.

Genera: The genera composing the Tanyderidae number ten living and one fossil. Macrochile Loew (1851), the fossil genus, was the first to be described. It is known only from the Lower Oligocene Baltic Amber. For some time Osten-Sacken and Meunier thought this genus to be synonomous with the recent genus Protoplasa. In 1859 Protoplasa was described by Osten-Sacken. Philippi (1865) defined the genus Tanyderus in which most of the known species were placed until Handlirsch (1909) proposed Protanyderus, Mischoderus, and Radinoderus as new generic groups. Alexander (1927b) regarded these groups proposed by Handlirsch as valid subgenera and added Neoderus for the Neotropical Tanyderus patagonicus Alexander (1913) and Nothoderus for the Australasian Tanyderus australiensis (Alexander 1922). In 1928, however, Alexander (1928b) recognized these subgenera as having full generic rank. Péringueyomyina was described by Alexander in 1921 as a new and very striking genus. Eutanyderus was described by him in 1928 (Alexander 1928b) and Araucoderus in 1929 (1929b).

The following key to the genera of the Tanyderidae is a revision of that given by Alexander (1928b).

KEY TO THE GENERA OF THE TANYDERIDAE

1. Front prolonged into a slender rostrum that is longer than the combined head and thorax, the reduced mouthparts being borne at the extreme apex; wings immaculate; male hypopygium with the styli very elongate.
   (Ethiopian: Cape Colony)
   PERINGUEYOMYINA Alexander (Fig. 22)

   Front not greatly prolonged, the rostrum relatively short, any elongation that exceeds the head in length being due to the palpi and other mouthparts; wings pictured in all recent species; male hypopygium with the styli short. 2

2. Wings immaculate.
   (Fossil: Lower Oligocene, Baltic Amber)
   MACROCHILE Loew (Fig. 21)

   Wings pictured, the pattern usually cross-banded brown and subhyaline. 3

3. Wings with the free tip of Sc preserved.
   (Australasian: Tasmania)
   NOTHODERUS Alexander (Fig. 23)

   Wings with the free tip of Sc atrophied. 4

4. Cervical sclerites shorter than the pronotum, the neck-region short; male hypopygium with the dististyle more or less bifid. 5

   Cervical sclerites elongate, equal to or exceeding the pronotum, the two together form a conspicuous neck-region; male hypopygium with the dististyle simple, terete. 6

5. A supernumerary crossvein in cell M_3 of the wing.
(Eastern Nearctic) PROTOPLASA Osten-Sacken
(Fig. 33)

No supernumerary crossveins in any cells of the wing.
(Western Nearctic; Palaearctic)
PROTANYDERUS Handlirsch
(Figs. 30, 31, 32)

6. No supernumerary crossveins in any cells of the wing. 7

Supernumerary crossveins in two of the radial cells of the wing. 9

7. Wings with a short fusion of veins R_{2+3+4}, basal section of R_5 subequal to this element.
(Australasian: Papua, Australia)
RADINODERUS Handlirsch
(Figs. 35, 36, 37)

Wings with R_s before the level of r-m, the elements R_{2+3} and R_{4+5} being entirely separate. 8

8. Antennae 15-segmented; cell R_2 of the wings shorter than its petiole.
(Australasian: Victoria)
EUTANYDERUS Alexander
(Fig. 26)

Antennae 18-segmented; cell R_2 of the wings longer than its petiole.
(Neotropical: Chile) ARAUCODERUS Alexander
(Fig. 29)

9. Wings without a supernumerary crossvein in cell R_4, these being in cells R_3 and R_5.
(Neotropical: Patagonia) NEODERUS Alexander
(Fig. 27)

Wings with supernumerary crossvein in cell R_4. 10

10. Wings with supernumerary crossveins in cells R_4 and R_5; a short element R_{2+3+4}.
(Neotropical: Chile) TANYDERUS Philippi
(Fig. 34)

Wings with supernumerary crossveins in cells R_3 and R_4; R_s forking far before the level of r-m, veins R_{2+3} and R_{4+5} distinct.
(Australasian: New Zealand)
MISCHODERUS Handlirsch
(Figs. 23, 24, 25)

Species of the Tanyderidae:

The genus *Araucoderus* contains a single species *A. gloriosus* Alexander (1929b) which is Neotropical from Central Chile (Fig. 29).

Eutanyderus has but one species *E. wilsoni* Alexander (1928b) which is Australasian being found only in the mountains of Victoria, Australia (Fig. 26).

Macrochile is likewise a monotypic genus. *Macrochile spectrum* Loew (1851) was described from the Lower Oligocene Baltic Amber. Figure 21 is copied from Crampton (1926a).

Mischoderus has five species all of which are Australasian being confined to New Zealand. *M. annuliferus* was described by Hutton (1900)(Fig. 24); *M. forcipatus* by Osten-Sacken (1880) (Fig. 23); *M. marginatus* Edwards (1923) and *M. neptunus* Edwards (1923) which may not represent distinct species but merely variations of *M. forcipatus*; and *M. varipes* Edwards (1923) Fig. 25).

Neoderus has but one species, *N. patagonicus* Alexander (1913) which is Neotropical, occurring only in Patagonia. Figure 27 is after that of Alexander (1913).

Nothoderus is likewise represented by a single species, N. australiensis Alexander (1922) which is Australasian, occurring only in the mountains of southern Tasmania (Fig. 28).

Péringueyomyina has one species P. barnardi Alexander (1921) from Cape Colony in the Ethiopian region (Fig. 22).

Protanyderus has four species, all of which are Holarctic. P. beckeri Riedel (1920) was taken in Turkestan (Fig. 31); P. vanduzeei Alexander (1918) (Fig. 30) and P. vipio Osten-Sacken (1877)(Fig. 32) were taken in western North America; and the recently described P. esakii Alexander (1932) is from Japan (text figure).

Protoplasa has a single species, P. fitchii Osten-Sacken (1859), occurring in eastern Nearctic region (Fig. 33).

Radinoderus includes seven species, all from the Australasian region. R. dorrigensis Alexander (1930b) is from northern New South Wales (Fig. 35); R. mirabilis De Meijere (1915) is from New Guinea (Fig. 37); R. occidentalis Alexander (1925) is from western Australia; R. oculatus Riedel (1921) is from New Guinea; R. ornatissimus Doleschall (1858) is from Amboina, Obi; R. solomonis Alexander (1924) is from the Solomon Islands (Fig. 36); and R. terraē-reginaē Alexander (1924) is from Queensland (Fig. 38).

Tanyderus as now restricted is represented by a single species, T. pictus Philippi (1865), which is Neotropical, being found only in Central Chile.

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ABBREVIATIONS

a - anepisternal suture
aed - aedeagus
aem - anepimeron
aes - anepisternum
anf - antennifer
ap - apical or outer process
apn - antepronotum

b - anepimeral suture
bc - basicercus
bl - basilabellum
bp - basipharynx
bst - basistyle
bta - basitarsus

c - pleural suture
ce - head bearing process (cephaliger) of lateral cervical plate
cu - cornua
cx - coxa

dc - disticercus
dl - distilabellum
dst - dististyle (claspers)
dta - distitarsus

e - compound eye
ec - eucoxa
em - epimeron
ep - epipharynx
es - episternum

fc - frontoclypeus
fe - femur
fl - flagellum

ga - galea
gap - gonapophysis (paramere)
ge - gena
gp - gular pit

ha - haltere
hp - hypopharynx

int - interbase

l - labrum
lbl - labellum
lc - lateral cervical plate (laterocervicale)
lcf - laterocervical fenestrae
ls - ? 9th sternite

mn - mentum
mpl - meropleurum
mt - mediotergum
mtn - metanotum
mxp - maxillary palp

occ - occipital condyle
ocp - occiput
oes - oesophagus
of - occipital foramen

pd - pedicel
pfr - palpifer
pge - postgena
pgr - palpiger
pn - pronotum
ppd - postpedicel
ppn - postpronotum
psc - prescutum
pt - postalare or pleurotergum

s - sternite
saf - subalifer
sal - subalare
sap - basal process of dististyle
sc - scutum
sca - scape
sd - salivary duct
sl - scutellum
sp - spiracle
spl - sternopleurum or katepisternum
ss - scutal suture
st - sternum
sti - stipes

t - tergite
ti - tibia
th - thickening
tnt - tentorium
to - tormae
tr - trochanter

un - ungues or claws

v - vertex
vv - lobes of 8th sternite of female

1st A - first anal
2nd A - second anal
C - costa
Cu - cubitus
h - humeral crossvein
m - medial crossvein
M_1 - 1st branch of media
M_2 - 2nd branch of media
M_3 - 3rd branch of media
M_4 - 4th branch of media
m-cu - medio-cubital crossvein
pa - "preanal vein"
R_1 - 1st branch of radius
R_2 - 2nd branch of radius
R_3 - 3rd branch of radius
R_4 - 4th branch of radius
R_5 - 5th branch of radius
R_s - radial sector
r-m - radio-medial crossvein
Sc_1 - 1st branch of subcosta
Sc_2 - 2nd branch of subcosta

EXPLANATION OF PLATES

PLATE I

Fig. 1 - Dorsal view of the head
Fig. 2 - Lateral view of the head
Fig. 3 - Head with dorsal portion removed to show tentorium
Fig. 4 - Caudal view of the head
Fig. 5 - Epipharynx
Fig. 6 - Ventral view of the head
Fig. 7 - Antenna
Fig. 8 - Hypopharynx
Fig. 9 - Labium and maxillae

PLATE II

Fig. 10 - Lateral view of the thorax
Fig. 11 - Haltere
Fig. 12 - Wing
Fig. 13 - Prothoracic leg of male

PLATE III

Fig. 14 - Ventral view of the terminal abdominal structures of the male
Fig. 15 - Ventral view of the terminal abdominal structures of the female
Fig. 16 - Lateral view of the terminal abdominal structures of the female
Fig. 17 - Dorso-caudal view of the terminal abdominal structures of the male
Fig. 18 - Dorsal view of the terminal abdominal structures of the male
Fig. 19 - Lateral view of the terminal abdominal structures of the male
Fig. 20 - Lateral view of the abdomen of the male

PLATE IV

Fig. 21 - Wing of *Macrochile spectrum* Loew (Copied from Crampton's figure)
Fig. 22 - Wing of *Péringueyomyina barnardi* Alex.
Fig. 23 - Wing of *Mischoderus forcipatus* O.S.
Fig. 24 - Wing of *Mischoderus annuliferus* Hutt.
Fig. 25 - Wing of *Mischoderus varipes* Edw.

PLATE V

Fig. 26 - Wing of <u>Eutanyderus</u> <u>wilsoni</u> Alex.
Fig. 27 - Wing of <u>Neoderus</u> <u>patagonicus</u> Alex. (After Alexander)
Fig. 28 - Wing of <u>Nothoderus</u> <u>australiensis</u> Alex.
Fig. 29 - Wing of <u>Araucoderus</u> <u>gloriosus</u> Alex.

PLATE VI

Fig. 30 - Wing of <u>Protanyderus</u> <u>vanduzeei</u> Alex.
Fig. 31 - Wing of <u>Protanyderus</u> <u>bockeri</u> Riedel
Fig. 32 - Wing of <u>Protanyderus</u> <u>vipio</u> O. S.
Fig. 33 - Wing of <u>Protoplasa</u> <u>fitchii</u> O. S.

PLATE VII

Fig. 34 - Wing of <u>Tanyderus</u> <u>pictus</u> Phil.
Fig. 35 - Wing of <u>Radinoderus</u> <u>dorrigensis</u> Alex.
Fig. 36 - Wing of <u>Radinoderus</u> <u>solomonis</u> Alex.
Fig. 37 - Wing of <u>Radinoderus</u> <u>mirabilis</u> DeMeij.
Fig. 38 - Wing of <u>Radinoderus</u> <u>terrãe-reginãe</u> Alex.

TEXT FIGURE - Wing of <u>Protanyderus</u> <u>esakii</u> Alex.

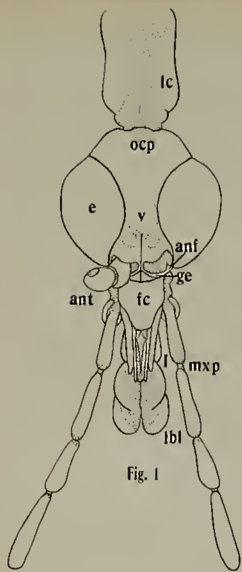


Fig. 1

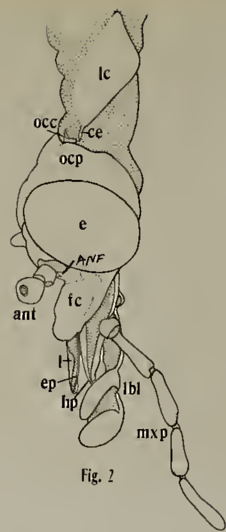


Fig. 2

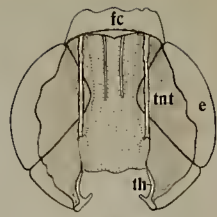


Fig. 3

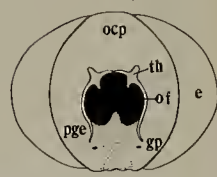


Fig. 4

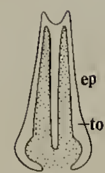


Fig. 5

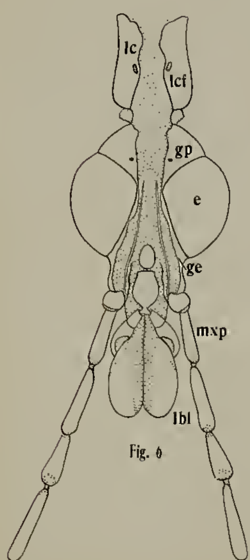


Fig. 6

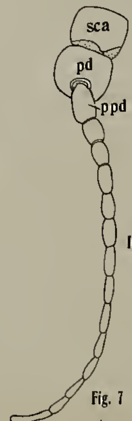


Fig. 7

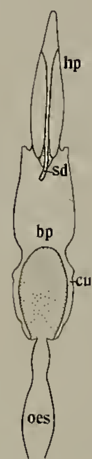


Fig. 8

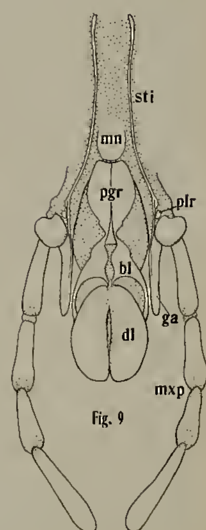


Fig. 9

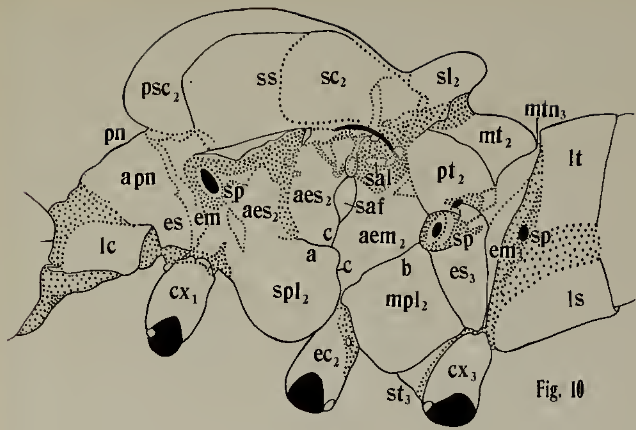


Fig. 10

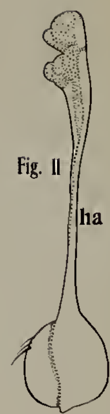


Fig. 11

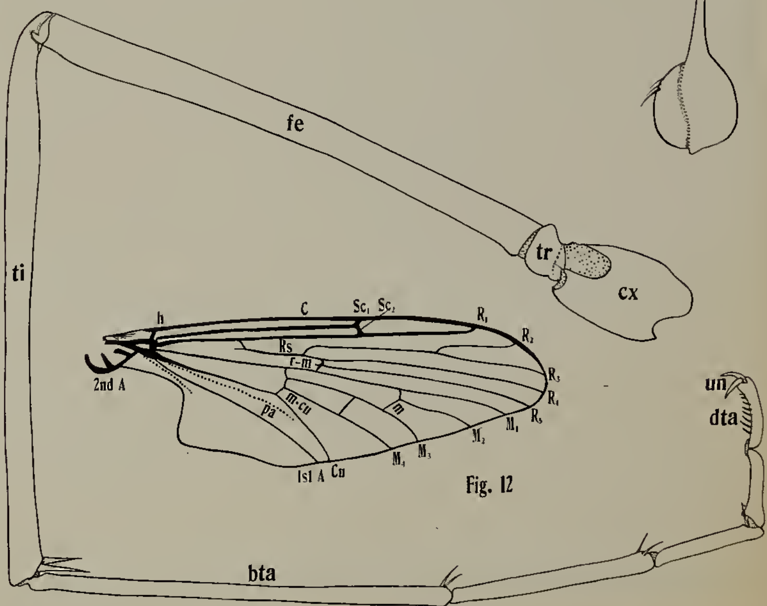
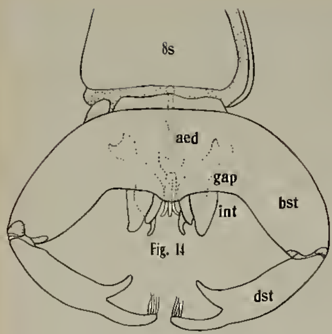


Fig. 12

Fig. 13



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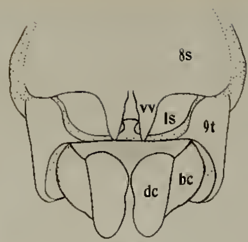


Fig. 15

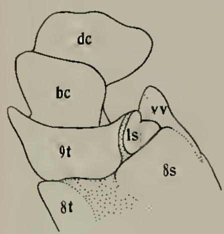


Fig. 16

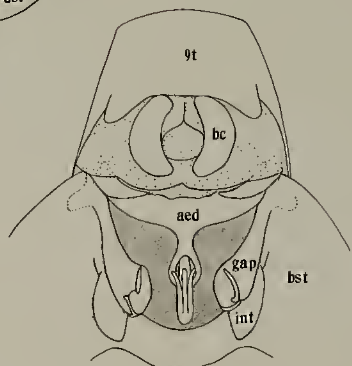


Fig. 17

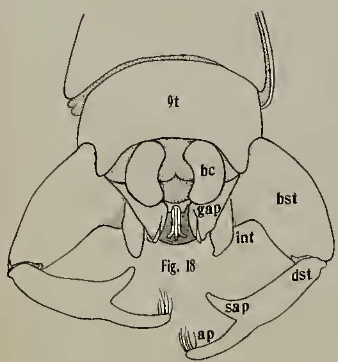


Fig. 18

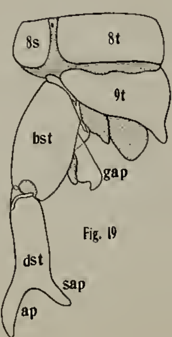


Fig. 19

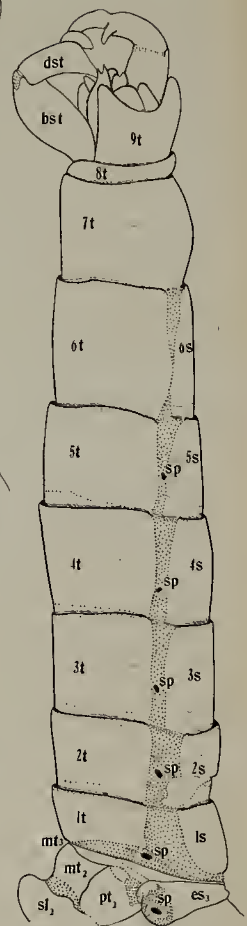
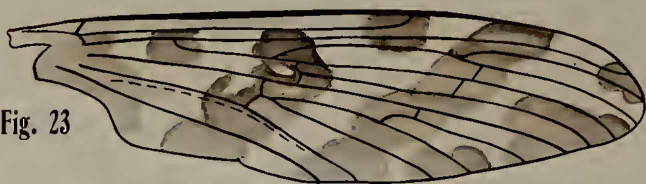


Fig. 20


Fig. 21


Fig. 22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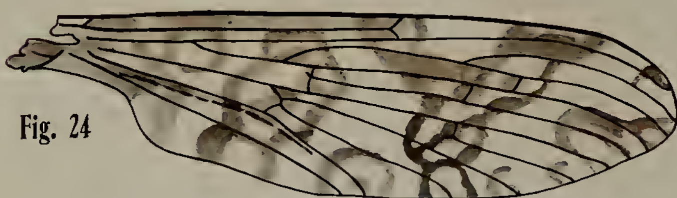


Fig. 24


Fig. 25

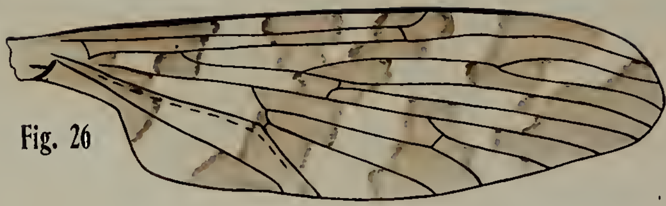


Fig. 26

Fig. 27

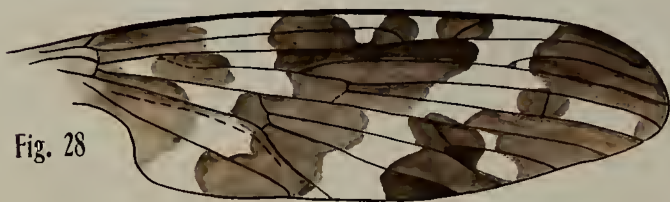


Fig. 28

Fig. 29

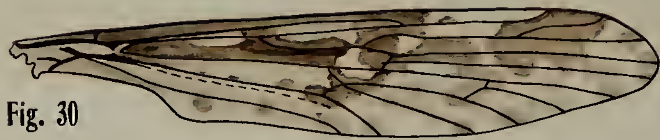
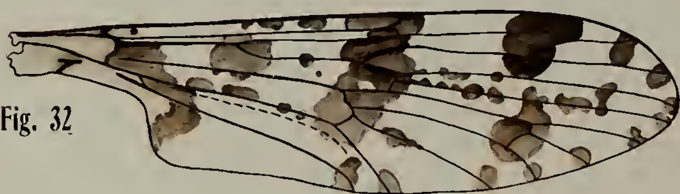


Fig. 30

Fig. 31



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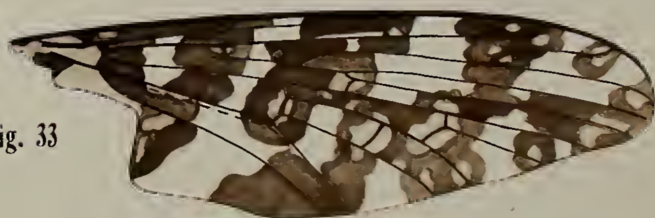
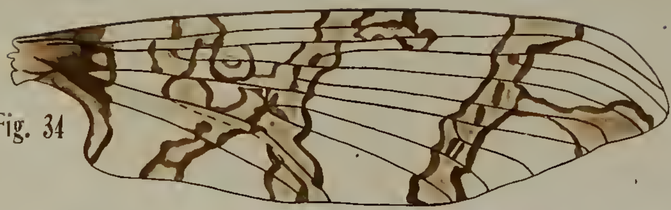


Fig. 33



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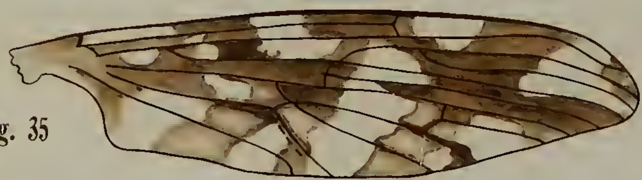

Fig. 35

Fig. 36

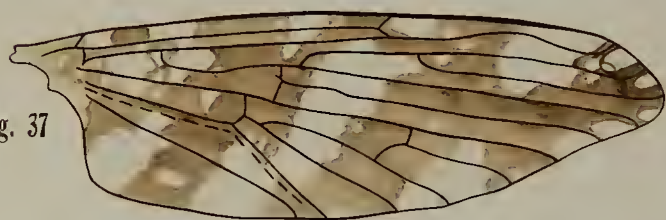

Fig. 37

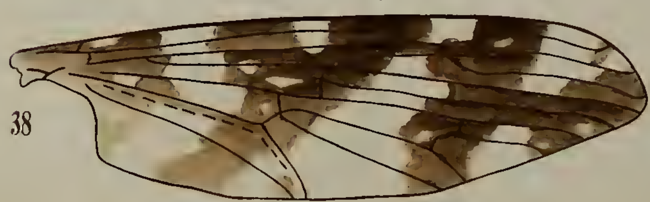

Fig. 38

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