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The comparative morphology of the insect pretarsus

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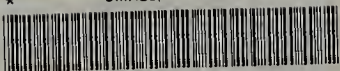
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THE COMPARATIVE MORPHOLOGY
OF THE INSECT PRETARSUS

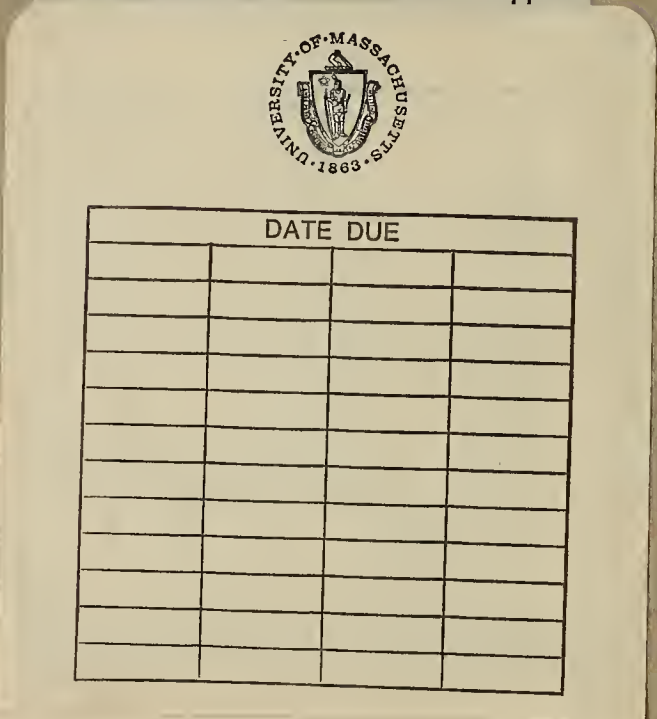


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THE COMPARATIVE MORPHOLOGY OF THE INSECT PRETARSUS

by

Richard T. Holway

Submitted as a Thesis to the Faculty of the Graduate School
in partial Fulfillment of the Requirement for the
Degree of Doctor of Philosophy

Massachusetts State College

June 1937

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INTRODUCTION

The terminal structures of the insect leg represent a development of the dactylopodite of lower (Crustacean) Arthropods, according to most recent authorities on comparative anatomy. This interpretation, first suggested by Milne-Edwards (1872) and amplified and illustrated by DeMeijere (1901), is supported by Snodgrass (1927, 1938), Ewing (1928), and others, and gives to the claw segment a status equal to that of the other main divisions of the leg. That is, the subcoxa or pleuron, coxa, coxal trochanter, femoral trochanter, femur, tibia, tarsus, and pretarsus are homologous with the Crustacean leg segments, respectively, pleuropodite, coxopodite, basipodite, ischiopodite, pereopodite, carpopodite, protopodite, and dactylopodite.

The view that the claw segment is a distinct portion of the insect leg is further strengthened by the complexity and the continuity of the components which make up this structure. The work of Ockler (1890) and De Meijere (1901) have been the first to emphasize the nature of the claw-segment and to describe the various types which occur in the orders of insects. DeMeijere first presented conclusive evidence that the terminal parts should be considered as an independent leg segment and not merely a sixth tarsomere. To this segment he gave the name pretarsus and this term is becoming established, although it has been widely criticised because it is not an appropriate designation.

We find considerable authoritative agreement concerning the origin and morphological significance of the pretarsus as a whole but there remains the utmost confusion concerning the terminology applied to its component structures and the comparative morphology of these parts in the various orders. For German students this confusion does not exist to such an extent, due to the work of Ockler and De Meijere, who have applied a consistent terminology and interpretation throughout the class insects. For the sections of the world where classical languages are used for scientific work these studies are of limited value because of their entirely German terminology. It was found impossible adequately to interpret many of the important results until an original study of the pretarsus in all types of insects had been made and compared with the figures and terms of these students.

The purpose of this work is to attempt: First, standardization of the terminology of the pretarsus for American entomologists by coordination of the results of German students with the definitions receiving most general acceptance by present day authorities on insect morphology; second, extension of the knowledge of the comparative morphology of the pretarsus by study of a larger series within the various orders than has hitherto been examined; and, third, indication of possible phylogenetic or taxonomic implications in the various structural modifications of the parts of the pretarsus.

General Discussion of the Pretarsus

The component structures of the pretarsus may be listed under five headings, to facilitate discussion.

1. The claws or ungues.

The claws are hollow, sclerotized diverticula of the dorsolateral region of the originally membranous pretarsus and in the latter are developed the various parts which comprise this segment in the adult insect. The lumens of the claws are continuous with that of the pretarsus. The theory that the claws are modified setae is believed untenable because, as pointed out by Snodgrass (1927), the claws are multicellular and may themselves bear setae. The claws articulate with the dorsal rim of the distitarsus by means of a small structure called the unguifer.

2. The unguitractor.

The unguitractor is a ventral sclerotization and is ~~is~~ partially or completely invaginated into the distitarsus. The unguitractor tendon extends from the proximal rim of the unguitractor through the tarsomeres to the flexor of the claws which is located in the tibia. Traction of this muscle is transferred by the tendon, unguitractor ~~pale~~ ^{plate} and flexor ~~membrane~~ to the bases of the claws so that they are pulled downward on the articulations with the unguifer at the dorsal margin of the distitarsus. A levator of the claws

does not occur in insects and they are extended "by the elasticity of their basal connections when the flexor muscles relax, or by the weight of the insect on the supporting surface" (Snodgrass, 1927, p.32).

The unguitractor is a structure peculiar to insects and is easily identified by the proximal attachment of the unguitractor tendon, heavy sclerotization, and general appearance which is always the same although size and shape may vary. The ventral surface of the unguitractor often appears to bear small nodules which are sometimes raised or spine-like. These nodules appear to correspond with the polygonal cells of the hypodermis and the cells may be seen through the cutin with high magnification.

3. The arolium.

The arolium is defined as a median hollow lobe continuous with the lumen of the pretarsus. In lower insects the arolium is a simple, pad-like structure and is often provided with a concave ventral surface which probably acts as a suction disk for clinging to smooth surfaces. The arolium may be much more complicated in higher types, especially in Hymenoptera, where it may be bilobed and provided with various sclerotized areas for support. MacGillivray's term, arolanna, is retained for these distal lobes of the arolium.

The arolium is termed Haftlappen throughout the class by Ockler; De Meijere uses Haftlappen in lower insects and some Hymenoptera but employs the term empodium for what seems to be the same structure in other Hymenoptera and Diptera. MacGillivray also applies different names to the median lobe in the various orders where it occurs. However, there does not seem to be sufficient reason for using a different term for homologous structures and it is believed that the series presented in this paper indicates the homology of the arolium throughout.

Extension of the original membrane which forms the distal limits of the undifferentiated pretarsus results in the formation of the membranous pouch or sac known as the arolium. Sclerotization of areas in the dorsal or ventral walls of this pouch produces various structures such as orbicula and surarolia or planta, empodium and camera. In some cases (Diptera, with the exception of Tipulidae) this membranous pouch is reduced (or not developed) dorsally while its ventral surface is extended and supplied with numerous retinaria or becomes heavily sclerotized, setiform and glabrous. The family Spiniidae (Lepidoptera) illustrates this view for there are three distinct types in the genera Hemaris, Pholus, and Sphinx: First, with the arolium well developed; Second, with the arolium greatly reduced and the plantal-empodial area extended; Third, with the arolium reduced to a small membranous area above the well-developed empodium (see Figs. 311 to 316). A similar situation is found in the Andrenidae.

4. The empodium.

Perhaps no other structure of insect anatomy has been the subject of as much confusion and misconception as the empodium. The definition of this term used by the three most recent workers who have touched on the pretarsus (Crampton, 1923; Snodgrass, 1935; Hayes and Kearns, 1934) is taken as a starting point in an attempt to clarify the situation. The empodium is defined as a prolongation of the unguitractor plate; it is usually glabrous and heavily sclerotized and may bear setae or parempodia (Crampton, 1923). Ockler (1890) states "Die Streckborste (i.e., empodium) geht stets direkt aus der Streckplatte (i.e., unguitractor) hervor." The empodium occurs in its most typical form in practically all Odonata and Coleoptera, and in many Hymenoptera, Diptera, and Orthoptera.

In a preliminary note on the pretarsus (Psyche, 1935) the median pulvilliform pad of Diptera was interpreted not as an empodium but as an arolium (following Crampton, 1923, and MacGillivray, 1923). However, further study of Dipterous pretarsi indicates that in this order there is a transition from pulvilliform empodium to setiform empodium. That is, the median structure, whether pulvilliform or setiform, is an empodium and is formed by sclerotization of the floor of the developing pretarsal sac. Evidence for this conclusion is presented and discussed in the section on Diptera and supports the theory of Ockler (1890) that the median "Haftorgan"

(holding organ) of Diptera is a modification of the "streckborste" (empodium).

Another structure, the planta, must be discussed at this time. This is a ventral sclerite located at the base of the arolium. It is variable in degree and extent of sclerotization and represents an area of the membrane distal to the unguitractor; possibly it becomes sclerotized to a greater or less degree depending on the stress to which it is subjected. Because of this variability it is often better to speak of the plantal area rather than a distinct sclerite. When the arolium is absent the planta usually is not present in its typical form but appears as an empodium, that is, it is fused proximally with the unguitractor and is extended distally so that in many cases it cannot be distinguished from a typical empodium. Because of this confluence of planta and empodium there is considerable overlapping in the use of the terms. However, in general, the word planta is used to indicate that there is no distinct fusion with the unguitractor.

Thus it appears that planta and empodium are merely modifications in extent of sclerotization of the membrane which forms the ventral surface of the pretarsus. This conclusion was reached after study of many types but before it was discovered that a similar interpretation had been made by Becker (1930). He states that the "strecksohle" (planta) is a modification of the "streckborste" (empodium). A glance at his figures and labels indicates the interpretation of these

terms. Evidence for the above interpretation of planta and empodium is indicated in the discussion of figures under the various orders.

The following conceptions of the empodium found in the literature are rejected because they do not agree with the usage of present-day workers or with the results of this study, and do not contribute to the development of a standard interpretation of the pretarsus.

The term onychium has been discarded by Crampton, Snodgrass, and Hayes and Kearns, because it has been applied to such a variety of structures that it is impossible to determine its proper usage. As used by MacGillivray it refers to the empodium of Coleoptera and the setiform empodium of Diptera, and his usage of empodium is restricted to the pulvilliform empodium of Diptera. MacGillivray (1923, p. 249) states "There is absolutely no reason for considering the empodium (pulvilliform empodium) and onychium (setiform empodium) as homologous structures." It is hoped that the present study presents sufficient evidence to prove the homology of these two structures.

De Meijere (1901) calls the pulvilliform empodium, Schlenklappchen; the setiform empodium, Schlenborste; and the planta, Strecksohle (process plantaris). The membranous dorsal lobe or sac which he labels empodium can be only what is generally known as the arolium in this country.

5. The pulvilli.

The pulvilli are membranous pads which are located beneath the claws and arise from the membrane at the claw bases. Among the Diptera, in some cases, the pulvilli are very similar in form and structure to the pulvilliform empodium. On the ventral surface they bear numerous microscopic setae or retinaria, exactly like those which occur on the ventral surface of the empodium; dorsally they are membranous and in this membrane sclerotized areas may develop similar to the areas in the membrane dorsal to the empodium.

The pulvilli may be coriaceous and compressed in some Coleoptera; and in many Lepidoptera they are bilobed. Sometimes the pulvilli have migrated to a position more lateral than ventral with respect to the claws. The pulvilli probably arise as lateral diverticula of the definitive membrane as indicated by De Meijere. His term for the pulvilli in Diptera is Seitenlappchen; in Hemiptera, Krallenlappchen.

The basipulvilli are sclerites located at the bases of the pulvilli, or on either side of the planta at the bases of the claws when the pulvilli are absent. Sometimes they extend laterally around the bases of the claws to the unguitractor. In Tipulidae they are fused with the planta to form a narrow sclerite which extends across the ventral surface of the pretarsus distal to the unguitractor.

These five groups of structures comprise the important elements of the pretarsus and may be homologized in all of the insectan orders in which they occur according to the conclusions of this study. Various auxiliary parts are also present and these are interpreted in the discussion of the taxonomic divisions.

Glossary of the Terminology of the Pretarsus

Names which are retained and proposed for a standard terminology based on the conclusions of this study are marked with an asterisk. The name in parentheses indicates the originator of the term.

- Afterkralle - Epodius of Leptogaster (Diptera). Because of its unguiform appearance Ockler considered this structure a third claw rather than a true epodius, but examination of related genera supports De Meijere's conclusion that it is an epodius.
- Apodeme - Unguitractor tendon (Snodgrass).
- Artendon - Unguitractor tendon (MacGillivray).
- *Arolana - Distal membranous lobes on the arolium of Hymenoptera (MacGillivray).
- Arolella - Pulvilli of Hemiptera (MacGillivray).
- *Arolium - A membranous pouch located between the claws and formed by extension of the definitive membrane of the pretarsus. It is subject to various modifications in the various orders in which it occurs.
- Aroloidea - Euplantulae of some Hemiptera (MacGillivray).
- Auxillae - Basipulvilli (in Diptera at bases of pulvilli as well as when pulvilli are absent, (MacGillivray).
- Articularia - Pretarsus (MacGillivray).

- Basipulvilli - sclerotized areas at the bases of the pulvilli or at the bases of the flexor membranes and lateral of the plantal area when pulvilli are absent (Crampton).
- Bogon - Camera (Cockler).
- Bugel - Camera (Arnheart).
- Calcanea - Unguitractor plate (MacGillivray).
- Camera - A heavily sclerotized band on the ventral surface of the arolium in Trichoptera, Lepidoptera, Mecoptera, and Hymenoptera; the Hymenopterous camera is recurved dorsally and sometimes fused with the suraroliae (plates supporting the arolia); sometimes it is also fused with a ventral process of the orbicula (MacGillivray).
- Chitinstreifen - Narrow seta-bearing sclerotizations of the plantal area (Chrysopa, some Fulgorids) (Demeijere).
- Dactylopedite - The terminal segment of the primitive arthropod leg.
- Digitule - An elongated seta or hair with clavate tip; characteristic of Coccidae and Collembola.
- Distitarsus - The last, or distal, tarsomere (Crampton).
- Druckplatte - Stutzplatte; the orbicula (Dahl).
- Empodium - A sclerotization (variable in degree) and extension of the ventral surface of the undifferentiated pretarsal sac; it is usually continuous with the unguitractor.

- aplanulae - Small pad-like structures on the under side of the tarsal subsegments (Crampton).
- aplexor membranes- Areas of the original membrane which pass from the disto-lateral margins of the unguitractor to the bases of the claws.
- Gelenkhaut - Flexor membrane (Ockler).
- Gelenkhocker - Unguifer (DeMeijere).
- Gleitfläche - Plantella (DeMeijere).
- Gleitrinne - Plantella (Ockler).
- Hafthaar - Digitule (DeMeijere).
- Haftapparat - Arolium and associated structures (Arnhart).
- Haftlappchen - Arolium, pulvilliform epodum and pulvilli (Ockler).
- Haftlappen - Arolium (DeMeijere).
- Kalbenhaar - Digitule (DeMeijere).
- Kralle - Claw.
- Krallenanhang - Dorsal enlargement of the claw of Simuliidae (DeMeijere).
- Krallenglied - Pretarsus (Arnhart).
- Krallenhocker - Unguifer (Ockler).
- Krallenlappchen - Pulvilli of Hemiptera (DeMeijere).
- Onychium - This term has been rejected by recent workers because it has been used in such a variety of ways that it is impossible to define correctly. For example, it may be applied to entirely

different structures in Hymenoptera, Lepidoptera, and Coleoptera. Arolium, empodium, distitarsus, and other structures have been designated by this name.

- *orbicula - A median dorsal sclerite which often articulates with the unguifer. It usually bears setae and may vary greatly in form. Sometimes it passes down between the claws and fuses with the unguitractor (or in some Hymenoptera with the camera) (MacGillivray).
- *Original or Limiting Membrane - The limiting membrane between the claws which forms the end of the pretarsus when arolium, empodium, etc. are not developed.
- *Parempodia - Elongate setae borne by the empodium (Crampton).
- Paronychia - Parempodia.
- *Plantella - A process of the ventral surface of the distitarsus which extends out between the claws and conceals the empodium (MacGillivray).
- *Planta - A variably sclerotized area distal to the unguitractor.
- Pseudarolia - Pulvilli. Lobes beneath the claws of Hemiptera.
- Pulvicornia - Pulvilli of Meloid Coleoptera and of Lepidoptera (MacGillivray).
- *Pulvilli - Membranous lobes or pads which are located beneath the claws and arise from the membrane at their base.

- Retinaria** - Microscopic seta-like projections on the ventral surface of pulvilli and pulvilliforma exopodum; they are hollow and secrete an adhesive substance (MacGillivray).
- Schutzplatte** - Broad, plate-like dorsal portion of the orbicula (Ockler).
- Sehne** - Unguitractor tendon (Dahl).
- Seitenlappen** - Pulvilli (DeMeijere).
- seitlicher anhang** - Seta-like projections of the flexor membranes in Campodea and Psocus. May be pulvilli. (DeMeijere).
- Skelettplatte** - Basipulvillus (Diptera and Hemiptera) and ventral projection of the orbicula (Hymenoptera) (Ockler).
- Sohlenborste** - Exopodium (DeMeijere).
- Sohlenfortsatz** - Exopodium of Syrphidae (DeMeijere).
- Sohlenlappchen** - Pulvilliforma exopodium (DeMeijere).
- Solea** - Euplantula (MacGillivray).
- Streckborste** - Exopodium (Ockler).
- Streckplatte** - Unguitractor plate (Dahl).
- Strecksohle** - Planta (Ockler).
- Stützplatte** - Orbicula (DeMeijere).
- Sturrolia** - Sclerites in the dorsal membrane of the lobes of the arolium.
- Tarsalrand** - Distal rim of the distitarsus (Ockler).

- Tarsulus - Pretarsus (Crampton).
- Tasthaar - Parempodium (Ockler).
- Tibialstift - Tibial spur (Ockler).
- Tubercula - Unguifer (MacGillivray).
- Tulillus - Any membranous pad on tarsomeres or pretarsus (MacGillivray).
- *Ungues - Claws.
- Unguiculus - Empodium (Collembola) (Folsom).
- *Unguifer - Thickened and infolded dorsal rim of the distitarsus by which the claws and orbicula articulate (Crampton).
- Unguis or Ungula - The pretarsus (Schiodte).
- *Unguitractor - The heavily sclerotized ventral plate to the proximal edge of which is attached the unguitractor tendon (Crampton).
- *Unguitractor Tendon - The tendon which transmits tension from the muscles in the tibia through the unguitractor plate to the claws (Crampton).
- Ungulis - Basipulvillus of Hemiptera (MacGillivray).

APTERYGOTA

The apterygotan pretarsus is much more difficult to understand than that of other insect groups. Probably this is due to the small size and to the absence of large differentiated groups in which intermediate types might be found. For this reason it is not possible to homologize with any certainty the elements of the apterygotan pretarsus with those of other insect groups or lower Arthropods. This is true at least for the present extent of knowledge of the pretarsus. The most recent studies of the apterygotan pretarsus are those of DeMeijere (1901), Snodgrass (1907, 1935), and Swing (1938); and their results are briefly reviewed at this time.

DeMeijere's contention (now generally accepted by authorities) is that the claw segment of insects, arachnids and Myriopods, is a development of the dactylopodite. He suggests that the claws are evaginations of the base of the dactylopodite and uses dorsal claw-like structures on the dactylopodite of isopods (Fig. 15), such as Jaera, Janira, and Gunn, to support this view. Although there is no direct evidence of this in insects as yet, Snodgrass, as well as DeMeijere, seems to favor such a derivation for the claws. The fact that the lumen of the claw is continuous with that of the pretarsus is significant and fits in with the theory

that all pretarsal structures (arolium and pulvilli, as well as claws) are either developments of the original claw-like dactylopodite or at least of the original membrane which persists on suppression of the median claw. Snodgrass (1927) believes it more likely that empodium, pulvilli, and arolium are all secondary formations rather than transformations of the body of the dactylopodite.

Swing (1928) has figured and discussed several types of claw segment in the Apterygota and presents considerable evidence that the pretarsus was originally three-clawed in insects. The middle claw represents the dactylopodite a.s., and the presence of the unguitractor plate and unguitractor tendon at its base is the most important bit of evidence for the view that the locus of the median claw-like dactylopodite later produces the differentiated pretarsal elements. The unguitractor plate and tendon are always found at the base of the arolium or whatever type of median structure is best developed (see Thermobia sp., Fig. 2 - right claw removed to show dactylopodite).

The Japygidae seem to have more Pterygotan features than most of the Apterygota. The unguitractor is hugely developed in them and a dorsal vestige of the dactylopodite is present in Japyx (Fig. 6), while in Heterojapyx (Figs. 3-5) there are lateral protuberances and a short median process to the unguitractor (This knob-like process of the unguitractor must be

must be interpreted as an empodium). A narrow sclerotized band extends from the empodium, between the claws, to the ungulifer in Heterojapyx and a similar sclerite occurs in the naiad of Plecoptera (Pteronarcys, Fig. 29), in Blattids (Figs. 23, 31), Cicadidae (Fig. 76), and in the larva of Corydalis. That this plate is homologous with the orbicula of Hymenoptera is indicated by its position, i.e., it is located in the dorsal membrane, between the claws and distal to the ungulifer. Whether the arolium is present or absent does not affect the location of the orbicula for if the arolium is not developed the orbicula naturally is allowed to descend so that it nearly touches the planta or empodium. See Spinix (Fig. 316) where a rudimentary arolium occurs between the orbicula and empodium. Possibly the orbicula throughout the Apterygota represents a dorsal remnant of the dactylopedite.

Swing (1926, Fig. 13) shows that Pauropus has a median claw-like dactylopedite (d) and smaller lateral claws which have lobes attached to their bases. They appear to be typical pulvilli but such an interpretation must be rather uncertain because there are no similar structures between this "sub-insect" and Coleoptera, where true pulvilli first occur. Many apterygota are provided with only two claws, or a single median claw; Swing indicates that the one- or two-clawed condition is secondary and he illustrates this conclusion by a series from Pauropus where one lateral claw becomes reduced and finally

disappears altogether. Also in Synhyalella there is a large median claw (dactylopedite) and one small lateral claw. (The median claw in these cases, and in fact in all Arthropods, probably should be considered as the dactylopedite.)

The thysanuran, Campodea sp., bears between the claws a feather-like ventral appendage (according to Fwing, 1928) which arises from the unguitractor tendon or plate and therefore satisfies the definition of empodium. There is no vestige of the claw-like dactylopedite which is present in the Lepismatidae. Demeijere's figure of Campodea staphylinis Westw. (Fig. 7) indicates the presence of a short protuberance at the base of the dactylopedite which may represent the developing empodium since the unguitractor tendon is attached to its proximal margin. Lateral projections from the base of the dactylopedite (Fig. 7) resemble similar structures occurring in the Psocids (Fig. 57) and may represent prototypes of pulvilli, but Demeijere indicates that this is only a suggestion.

The Collembola present a variety of types ranging from the single-clawed (dactylopedite) to the three-clawed type with a ventral appendage. There seems to be considerable disagreement as to the interpretation of these structures. Fwing has figured several of the variations. Only the claw-like dactylopedite appears in Podura, but in Achorutes (Fig. 10) this structure bears a ventral appendage, the unguiculus (Felson, 1916), inferior claw (Guthrie, 1903), or empodial appendage (Carpenter, 1916). Hansen considers this smaller element to

be a true claw and believes that by shifting to a dorsal position, the two-clawed condition of higher insects was developed. The only evidence for this is the fact that the ventral appendage is not always median but may be somewhat to one side of the mid-ventral line as shown by Dethlefsen (Fig. 9). However, Ewing (1923) figures types of Tomocerus in which small paired claw-like appendages arise from the base of a large dactylopedite while the ventral appendage, "empodium" or "unguiculus" is also present. See Lubbock's figure of Psintaurus fucus (Fig. 12) for another example of claw-like lateral outgrowths of the dactylopedite. Psintaurus sp. figured by Dethlefsen (Fig. 11) indicates a relation between the ventral appendage and the unguitractor tendon and this would be evidence that the ventral appendage is homologous with the empodium of Campodea. Ewing concludes that the so-called unguiculus or empodial appendage of collembola is probably not a true claw but is a secondary development, possibly representing only a modified seta.

The condition in the Proturan, Acerentulus (Fig. 1), where the structure labeled anterior claw by Ewing is associated with the unguitractor plate and tendon, indicates that it is an empodium; in this case the "posterior claw" would represent the dactylopedite.

In summarizing the knowledge of the apterygotan pretarsus the following tentative interpretation was developed. The same formula applied to the pterygotan pretarsus may be used, i.e., a median dactylopodite is replaced by dorsal (aroliar) and ventral (sepidial) structures and is accompanied by paired, dorso-lateral outgrowths or claws. Transformation of the typical claw-like dactylopodite into something more suggestive of an aroliar structure is seen in the Collembola (see Figs. 10, 11, 12). The typical empodium is found in Acroterulana (Fig. 1), Heteroajapyx (Fig. 4), and in a rudimentary stage in Gammoda staphylinia West. (Fig. 7). Being figures a species of Gammoda with a very typical empodium; it is ventral, elongate and setiferous, and in appearance very similar to a type of empodium common in Diptera. It is more difficult to homologize the ventral appendage of Collembola with the empodium but the attachment of the unguitractor tendon (Fig. 11) indicates such a homology because the association of empodium and unguitractor is constant throughout the Pterygotan orders.

PTERYGOTA - PALEOPTERYGOTA

ODONATA

Five families were studied and no fundamental variations were found. The odonatan pretergus is distinctly the empodial or Coleopterous type, i.e., the empodium alone is well developed; it is heavily sclerotized and glabrous but lacks the parempodia so characteristic of polyphagous Coleoptera. The distal portion of the empodium is usually broader than the proximal part where it arises from the unguitractor plate. The unguitractor (ut) is typical and from its latero-distal margins the flexor membranes (fa) pass to the bases of the claws.

In Phalligera (Ctenagrionidae, Fig. 16) the empodium is much broader in the median portion than it is at the tip and junction with the unguitractor. There is some evidence of progressive increase in the length of the empodium from Cygoptera to higher Anisoptera (Figs. 16-22).

The plantella (pt), a projection of the ventral surface of the distitarsus, is well developed and may extend outward between the claws for a considerable distance (Fig. 21) so that it may conceal the empodium completely. The development of this structure is also found in many Coleoptera and Hemiptera.

SPINERIDA

Median developments of the definitive membrane have not been found in the Spinerida and the characteristic feature in this order is the nature of the claws. That is, the ventral surfaces of the claws are membranous. In some cases, Spiorus (Figs. 24,25) there is an asymmetrical condition and one of the claws is represented by a broad, flat dorsal sclerite in this membrane. In Siphonurus (Figs. 26,27) the claws are symmetrical but are also membranous ventrally. Other Spinerida have normal claws with the membrane entirely lacking.

These membranes are continuous with the membrane distal to the unguitractor and this suggests a possible relationship with the pulvilli. However, another possibility is worth considering, i.e., that they represent unsclerotized areas of the claws; if the claws are diverticula of the definitive membrane, variation in extent of sclerotization would result in the types of claws found in the Spinerida.

NEOPTERYGOTA

Cursorial Orthoptera

Blattidae (Figs. 28-32).

In the Blattidae there is typically a large arolium which is concave on the ventral surface, probably to aid in clinging to smooth surfaces by suction. At the base of the arolium and distal to the unguitractor there is a quadrate plate, the planta (pl), which may bear one to several setae; small plates (basipulvilli - bp) occur on each side of the planta and are contiguous with it. Flexor membranes (fm) pass from the basipulvilli to the bases of the claws. The relation of these membranes to the basipulvilli (when basipulvilli are present) is the same throughout the orders and furnishes some evidence for the hypothesis that the pulvilli are evolved by evaginations of such membranes.

The condition described above is found in Periplaneta americana L. (Fig. 28) and in Panochlora, Blattella, and other Blattid genera. However, in the adult of Archimandrita (Fig. 29) and the nymph of Blaberus (Figs. 30, 30) the arolium is absent and a cap-like sclerite (or) occurs between the claws. This sclerite is interpreted as the orbicula because of its position with respect to claws and unguitractor (Fig. 31). A similar sclerite is found in Hymenoptera, Lepidoptera, Hemiptera, and Filicoptera. Extension of the original membrane between the orbicula and planta would produce the typical condition in which

the membranous arolium is developed and bears the orbicula on its dorsum and the planta (empodium) on its venter (see Fig. 316).

Blaberus (Fig. 30) shows a partial fusion of the basipulvilli with the planta and in Archimandrita (Fig. 32) the fusion is complete. This tendency for the planta and basipulvilli to fuse appears in several orders, such as the Isoptera, Embioptera, Plecoptera, Neuroptera, etc., and in the Tipulidae. The presence of setae on the planta in the Blattidae should be noted; such a condition is often a characteristic of this sclerite.

Blattidae (Fig. 36).

An arolium has not been found in Blattidae thus far observed and such a structure may not occur in this family. The general plan follows closely that of the roach, although setae are absent from the planta. The flexor membranes are large and especially noteworthy are their lateral expansions, which, if further produced, might easily take on the appearance of pulvilli.

Isoptera (Figs. 33-35).

The basic plan follows closely that of the Blattidae and Mantidae, although the planta is much smaller in the Isoptera and the seta, in such Isoptera as Terapsalis (Fig. 33), does not arise from the planta itself but from the membrane. This

condition may be taken as evidence for the view that the planta is a variably sclerotized area of the membrane between the claws. There is no arolium in Ternstroemia but a small plate, probably the orbicula, occurs between the claws. In Hastotermes (winged form, Fig. 34) a rudimentary arolium occurs which is not found in the soldier caste of this species (Fig. 35). The unguitractor and basipulvilli, like those of the mantids, show no significant variations from the Blattid type.

We find that the cursorial Orthoptera, as a group, are characterized by the close association of basipulvilli and planta, in contrast with the saltatorial Orthoptera in which the basipulvilli are entirely lacking or are indistinguishably fused with the planta. The proximity of these three groups (Blattidae, Mantidae, Isoptera) has been noted many times by students of insect morphology and the presence of a common type of pretarsus is in agreement with this grouping.

ORTHOPTERA

The presence of the arolium is a variable feature throughout the class insects, and even within a family, some genera will have a well developed arolium while others lack such a structure altogether (e.g., Blattellidae, Spalangidae). There may be a slight exception to this statement in the saltatorial Orthoptera because, generally speaking, from the species examined the Acrididae are characterized by presence of the arolium and Tettigoniid and Gryllid types exhibit development of the empodium with absence of the arolium.

Acrididae (Figs. 37-39).

A typical arolium, planta and unguitractor are developed in these insects although the basipulvilli are absent, possibly fused with the planta. Varying degrees in development of the arolium are shown by Dissosteira (Fig. 37), Radnotatum (Fig. 38), and Scopedon (Fig. 39).

Tettigidae (Fig. 40).

Tettigidea lateralis may exhibit a small arolium; otherwise it conforms to the Acridid type.

Tridactylidae (Fig. 50).

There is some indication that the original membrane of Tridactylus is slightly extended, and if this extension represents a developing arolium, the condition would link this family with the Acrididae. However, as already stated, the presence of the

erolium is not reliable as a phylogenetic guide and Tridactylus is placed here on the basis of present-day taxonomic conceptions of the family.

Tettigoniidae (Figs. 41-43); Gryllidae (Figs. 44, 45);
Stenopelmaticidae (Figs. 46, 48).

These three families illustrate the fusion of the planta with the unguitractor, a stage in the direction of the development of a typical empodium which is so completely fused with the unguitractor that it becomes a process of the latter. This does not necessarily mean that the planta is always formed first and is then followed by sclerotization of the intervening membrane, but merely indicates that different areas may become sclerotized in varying degrees. In Oecanthus (Fig. 49) there is no sclerotization of the original membrane and this is a condition often found among small insects.

Figures 41, 42, 43, 44, and 45 show the various forms of the intermediate planta-empodium structure which occur in this group of families. The lateral protuberances of the planta are usually present.

Gryllotalpidae (Fig. 46); Gryllacridae (Fig. 47);
Grylloblattidae (Fig. 51).

The pretarsi of these families are linked by the presence of typical empodia which bear parempodia. Gryllacris is more suggestive of the Tettigoniid type than either Gryllotalpa or Grylloblatta.

Phasmatidae (Fig. 58).

A well developed areolium, small triangular plants and absence of basipulvilli are the significant features of the pretarsus of Anisomorpha and this condition is more like that found in the Acrididae than in any other group of Orthopteroids.

Cylindroacanthidae (Fig. 59).

Only the unguitractor is present.

DIPLOGLOSSATA - Hemimeridae (Fig. 60).

Only the unguitractor is present.

ORTOPTERA (Figs. 61, 62).

Only the unguitractor is present.

There is no trace of either areolar or apical structures in the representatives which were examined of the three groups above. The area distal to the unguitractor is entirely membranous and in many cases even portions of the unguitractor are completely sclerotized.

Summary of the Orthopteroid Pretarsus

The groupings of the Orthopteroid families used in the above discussion should not be construed as having any phylogenetic significance. They are based entirely on the type of pretarsus and are followed merely for convenience. On the basis of the limited number of species examined, a tentative classification of the types of pretarsus found in Orthopteroid insects may be indicated in the following key.

Cursorial Orthoptera

- A. Basipulvilli present. (Blattidae, Mantidae, Isoptera)
- B. Basipulvilli absent. Saltatorial Orthoptera and non-leaping types exclusive of three families above.
 - 1. arolium present (small or well-developed); plants distinct.
Acrididae, Phasmodae, Tettigidae,
(Tridactylidae?)
 - 2. arolium absent
 - a. plants partially fused with unguitractor and bears disto-lateral prongs; setae absent
Tettigeniidae, Gryllidae², Stenopelmatidae
 - b. typical empodium, i.e., it is distinctly a process of the unguitractor; setae or parempodia present
Gryllotalpidae, Gryllacridae, Grylloblattidae
 - c. neither plants nor empodium present; area distal to the unguitractor membranous
Cylindrachetidae, Hemimeridae, Dermaptera
- C. There is no sclerotization of the definitive membrane in Decanthus.

It is interesting to note that this arrangement, as inconclusive as it must necessarily be, does, nevertheless, agree with the phylogenetic grouping of the Orthopteroids proposed by Manalirach. He derives Acridoidea, Phasmoidea, and Tridactylidae from one stem; another main branch divides very early (Triassic) to give the Locustid and Gryllid lines. From the Gryllid stem are thrown off Dermaptera (Cretaceous), Hemimeridae (Cenozoic), and Gryllotalpidae (Cretaceous). Types like Hemimerus and Dermaptera which have no species structures developed from the original membranes, find their counterpart on the Gryllid stem in Oecanthus.

PLECOPTERA

A large arolium is typical of Plecoptera and it is usually supported dorsally by a broad sclerite, the orbicula. Basipulvilli are usually present and are contiguous with the planta when the latter is sufficiently sclerotized to give it a definite margin. Pteronarcidae and Perlidae are linked by the presence of a broad arolium (in Pteronarcys the arolium may have partially demarked lateral lobes) and by the absence of a long seta arising from each basipulvillus. In Pteronarcys the planta is distinct but in other Plecoptera the area may be not at all or only slightly sclerotized, as in Perla (Fig. 53).

The basipulvilli of Nemouridae (Figs. 60, 61) and Capniidae (Fig. 62) are extended in long seta-like processes; the arolium is smaller and narrower than that of Pteronarcys or Perla.

In the naiad of Pteronarcys (Fig. 80) there is no arolium, and a narrow band-like sclerite, the orbicula, extends from the unguitractor down between the claws to the unguitractor. Compare the nymph of Blaberus (Figs. 33-34), adult Archimandrita (Fig. 35), and the Cicada (Fig. 78). A narrow area of the flexor membranes (fm) is lightly sclerotized.

EMBIOPTERA

The arolium is absent. The planta is a narrow transverse sclerite and the basipulvilli are contiguous with it on either side. Oligotoma sp. (Figs. 61-63).

The type of pretarsus found in Plecoptera and Embioptera (i.e., relation of planta and basipulvilli) leads on one hand to the cursorial Orthopteran types, and on the other to those of the Neuroptera, as will be indicated when this group is discussed.

PLECOPTERA

Lyopseocus (Fig. 66) is noteworthy only for the ribbon-like appendages which arise at the bases of the claws. It is difficult to say whether they represent modified digitules or rudimentary pulvilli. Dedeijere's figure of Psephenus sp. (Fig. 67) shows two kinds of appendages, one pair, located on the

claws, are typical digitules, and the other pair which he calls "seitlicher anhang" arises from the membrane at the base of the claws and may be precursors of pulvilli. Note similar structures in Memouridae and Capniidae (Figs. 60-62).

THYSANOPTERA

The bladder foot of thrips is well known and is here interpreted as a true arolium. The claws are minute and appear to be merely sclerotized areas of the aroliar membrane as they are closely associated with this membrane (Trichothrips angusticeps Hood, Fig. 63). On the ventral surface there is a definite sclerotization of the plantar area (an empodium) fused with the unguitractor. Narrow sclerotized strips are present laterad of the empodium and similar structures occur in Cercopidae and some Neuroptera. There is a definite correlation between the pretarsus of Trichothrips and Cercopidae (Figs. 72, 74).

HEMiptera

Cercopidae - Fulgoridae - Cicadellidae - Membracidae - Psyllidae

as in the Thysanoptera the claws of these families are closely associated with the arolium. In the dorsal membrane of the Cercopid arolium there is a Y-shaped sclerite which in Fulgorids and Cicadellids has divided to form two lateral

sclerites (Figs. 71, 73, 69, 86). These are termed surarolia (sa) and differ from the orbicula in that they are located in a more distal portion of the arolium, whereas the orbicula is situated close to the unguifer. The relationship of these two structures may be seen in the Hymenoptera where both are present (see Figs. 365, 370, 379 - or, sa).

Along with the division of the surarolium, the arolium itself begins to separate into two lobes. This is shown in Cicadellidae (Figs. 82, 83, 85) and Membracidae (Figs. 86, 87). Such a condition suggests a different interpretation of the pulvilli of Hemiptera, i.e., that they arise by division of the Homopterous arolium. The pulvilli of Psyllia (Figs. 88, 89) are very similar to those of a large group of Hemipterous families as typified by Anasa tristis Latr. (Figs. 90, 91).

The unguitractor of Psyllia is only partially sclerotized but the empodium is sharply defined and bears a long, parempodium on each of two protuberances. The pulvilli have a striated appearance under high magnification, are separated from the claws, and are supported by basal sclerites. The Cereid unguitractor is heavily sclerotized but the empodium, parempodia, and pulvilli are very similar to those of Psyllia. The tendency for the empodium to be two-pronged is found in other Hemiptera (Figs. 96, 97 - Miridae, and Fig. 98 - Reduviidae).

Thus it would appear that the Psyllia pretarsus is more allied with that of Hemiptera than it is with the type occurring in other Homoptera. Such a condition, if supported by other

structures, would tend to place the origin of Psyllidae (and Coccidae) far back on the Protohomopterous stem, perhaps midway between other Homoptera and Hemiptera.

It is difficult to say whether the pulvilli of Psyllids should be interpreted as the result of a divided areolium or as typical pulvilli which arose from the membrane at the base of the claws. At present the latter view seems to be the more acceptable.

The plantal area of this group of Homoptera which have no areolium is variably sclerotized in the primitive families (Fulgoridae, Fig. 70; Cercopidae, Figs. 72, 74), and in the Cicadellid, Braeculacephala mollipes Say (Fig. 82). Other Cicadellidae (Figs. 83, 85) and Membracidae (Fig. 86) show this area sclerotized as a definite empodium.

Cicadidae - Apsididae - Alcurodidae - Coccidae

The pretarsus in this group of Homoptera is variable. There is no areolium but they have little else in common.

Cicadidae - Tibicid canicularis Harris (Figs. 75, 76).

There are no developments of the original membrane with the exception of an orbicula between the claws.

Apsididae - Brevicoryne brassicae L. (Figs. 77, 78).

There is a triangular unguitractor, a distinct quadrate planta, and a single large seta which arises from the membrane distal to the planta.

Aleurodidae - Dialeurodes citri Ash. (Fig. 79).

An extremely long setiform empodium is the only characteristic feature of this family.

Coccidae - Pseudococcus trifolii Forbes (Fig. 80).

There is great specialization in the Coccidae and one claw is entirely gone. The unguitractor and tendon are located at the base of the single claw. Long setae with enlarged tips (digitules) arise from the claw and distitarsus and are characteristic of the family.

ANOPLURA

Pediculus capitis DeG. (Fig. 81, after Ockler) has a single claw with the unguitractor located at its base.

HEMIPTERA

Coreidae - Cydnidae - Aradidae - Miridae

Coreidae - Anasa tristis DeG. (Figs. 90, 91).

As described in the discussion of the Psyllidae, the pretarsus of Anasa is typical of a large group of Hemipterous families which Handlirsch derives from a single stem.

Families examined in which this type was found - Coreidae, Pentatomidae, Lygaeidae, Cydnidae (Fig. 92), Pyrrhocoridae,

Aradidae (Fig. 93). If the ventral lobes of the claws of Tingitidae were considered to be sclerotized pulvilli, this family would also be placed with the above families, as is done by Handlirsch.

The pulvilli of Aradidae (Fig. 93) do not have the striated appearance which is found in the other families of this group and the dorsal and basal sclerites are also lacking. This condition may represent a transition from the large pulvilli of Coreidae to the extremely small type found in the Miridae.

The pulvilli of Miridae vary in size from the large form of Dicyphus agilis Uhl. (Fig. 94) to the much reduced sub-ungual lobes of Capsus ater L. (Fig. 97). Another transition found in the Miridae is the change from typical setae (pam) (Fig. 94) to flattened, leaf-like expansions (Figs. 96, 97). These structures have usually been termed areolia by students of Miridae but their origin in the empodium and unguitractor indicates their homology with parempodia.

Reduviidae - Phymatidae - Cimicidae

In the Reduviidae (Hemiscerus purcis Drury, Fig. 98) we find a good example of a partially sclerotized empodium. The two parempodia arise from thickened areas of the membrane distal to the unguitractor; in the dorsal membrane there is an orbicula.

The Phymatid, Phymata erosa L. (Fig. 99), has a heavily sclerotized, cup-shaped empodium. The Cimicid, Cimex lectularius L. (Fig. 100), is much the same.

Hepidae - Corixidae - Notonectidae - Gerridae - Gelastocoridae -
Belostomatidae

These families are characterized by the typical development of the empodium; there is no sign of arolium or pulvilli.

Hepidae - Banatra kirkaldyi Bueno (Fig. 102).

The empodium is somewhat elongate and narrows towards the distal portion. There are no parempodia.

Corixidae - Arctocoria sp. (Fig. 103).

There is no sclerotization of the plantal area.

Notonectidae - Notonecta lobata Hung. (Fig. 104).

There is a short rounded empodium with two parempodia.

Gerridae - Gerris sp. (Fig. 105).

The empodium is like that of Notonecta. The sub-apical claws, typical of this family, are shown in figure 106.

Gelastocoridae - Gelastocoris sp. (Figs. 107, 108).

There is a short, rounded empodium with three parempodia. Slight variation of shape is shown between empodium of the prothoracic tarsus (Fig. 107) and that of the meso - or meta-thoraces (Fig. 108).

Belostomatidae - Genacis griseus Say (Figs. 109, 110).

The oespodium is large and much broader in its distal portion which is bordered with a fringe of short hairs or setae. The distal view (Fig. 110) shows a small diverticulum of the membrane which may represent a rudimentary arolium and illustrates how such a lobe may have been formed.

COLEOPTERA

The empodium and parempodia are characteristic features of the Coleopterous pretarsus and the empodium is here more varied and specialized than it is in any other order. The arolium and associated structures apparently do not occur at all in the Coleoptera and pulvilli have been found in only a few families and these are almost all in the superfamily Hordeloidae.

The shape of the unguitractor as a reliable phylogenetic character has been abandoned in all orders and therefore is not discussed in detail. The variations of outline of the unguitractor may be seen by comparison of the figures 111 to 210.

About ninety genera have been studied and the general conclusions are in accord with the statement of Hayes and Kearns (1934) that there is a considerable lack of uniformity in the empodium of Coleoptera. In a few super-families it may be possible to say that the empodium follows some very general type, but variations are so common that there is little evidence which the student of phylogeny may use for tracing relationships. Individual, sexual, and segmental differences so complicate the study from the standpoint of the grouping of the higher categories that the problem becomes essentially one for taxonomists in the various groups concerned.

The degree of association of empodium and unguitractor is variable although as a rule the former is an actual process of the latter. Sometimes there is incomplete fusion, and in a few cases, as pointed out by Hayes and Kearns (1934), there is evidence to indicate that the empodium may be retracted within the unguitractor. It seems more likely that what appears to be a hollow space within the unguitractor is merely an area of lighter sclerotization.

ADEPHAGA

As stated by Hayes and Kearns (1934), this sub-order is the only group in which the pretarsus shows any consistency of structure. Parempodia were not found in the Adephaga and this condition was also reported by Hayes and Kearns, although they indicate that Ockler (1890, Plate 13, Fig. 48) figures a species of Carabus with two parempodia. However, this is due to misinterpretation of the figure numbers in Ockler's paper, for the number 48 in this paper refers to the figure beneath, which is a dorsal view of Carabus and does not show parempodia; the figure above (with parempodia) which they interpreted as 48, is really figure 47 and is a ventral view of Anisoplia horticultura.

It appears that absence of parempodia may be considered to be a characteristic of the Adephaga. A few cases occur in the Polyphaga in which parempodia are lacking, but as a rule, two to many parempodia are present in this sub-order.

CARABOIDEA

Cicindellidae.

The empodium is short and the various types found in four species of Cicindela (formosa generosa Dej., dorsalis Say, purpurea Oliv., saxguttata Fab.) and Tetracha carolina L. (Figs. 112-115 and Fig. 111), are figured. The final decision as to the value of this structure as a taxonomic character for the Cicindellidae is left to the specialist.

Carabidae.

The empodium is longer than it is in the Cicindellidae and three types may be distinguished. First, with an expanded distal portion (Carabus auratus Fab., Fig. 116; piceus purpuratus Bon., Fig. 120; Chlaenius sp., Fig. 121; Harpalus caliginosus Fab., Fig. 122). Second, with a setiform empodium (Scarites subterraneus Fab., Fig. 119). Third, with distal margin of the empodium serrate (Calosoma, Figs. 117, 118). The empodium of C. scutellare Lec. (Fig. 117) appears to be broader at the base than that of C. axyridanta L. (Fig. 118), but this may be merely an individual variation.

Dytiscidae.

The empodium of Dytiscus verticalis Say (Fig. 123) is similar to that of the Carabid, Chlaenius sp. (Fig. 121).

GYRINOIDEA

Gyrinidae.

In Dineutes there is a slight difference between the empodium of the prothoracic tarsus (Fig. 124) and that of the meso- and meta-thoracic tarsi (Fig. 125).

POLYCHAETA

Almost every conceivable variation and specialization of the empodium occurs in this sub-order. Parempodia are usually present but when they are lacking, the empodium is seldom like that of Adophaga; i.e., it may be short and spine-like but never setiform or broad, as it is in the Adophaga.

HYDROPHILOIDEA

Hydrophilidae.

In the male Hydrous triangularis say the empodium is long and bears a variable number of parempodia. There is a difference in the shape of the unguitractor and empodium and in the number of parempodia between the prothoracic tarsus (Fig. 126) and the meso- and meta-thoracic tarsi (Fig. 127). Hayes and Kearns (1934) find that in the female only two parempodia are present on all three pretarsi. Several authors have figured different species of Hydrophilidae and from these reports it appears that the number of parempodia may vary from two to nine. As a rule the protarsus has the greater number,

Tropisternus glaber Hbst. (Fig. 130) has only two parempodia and the empodium is quite different from that of Hydrous triangularis. The partial reduction of one claw of this insect (Fig. 126) possibly indicates the way in which the single clawed condition is brought about.

On this basis of various morphological characters, the Hydrophilidae have sometimes been placed with the Adephaga (Stichney, 1923, on the head capsule; and Tanner, 1927, on the female genitalia). However, the nature of the pretarsus would indicate that they belong in the Polyphaga and this fact, with Forbes' evidence of the wings (1923) and Williams (ms.) evidence of the mouthparts, furnishes added support for the classification of Long (1920).

SILPHOIDEA

Silphidae.

It is possible that the differences in the empodium of Silpha surinamensis Fab. (Fig. 129), Necrophorus americanus Oliv. (Fig. 130), N. sayi Lap. (Fig. 131), and N. tomentosus Web. (Fig. 132), may be of some taxonomic significance.

STAPHYLINOIDEA

Staphylinidae.

The empodium is short and rounded but bears two parempodia in both Creechellus maxillosus villosus Grav. (Fig. 133) and Staphylinus maculosus Gray (Fig. 134).

Histeridae.

There is no sclerotization of the membrane distal to the unguitractor and consequently no typical structures are developed in Hister obtusatus Harris (Fig. 135).

CANTHAROIDEA

Lycidae.

In Coleopteron reticulatus Fab. (Fig. 136) the parempodia appear to arise directly from the unguitractor because the empodial area is unsclerotized. In Fros aurora Hbst. (Fig. 137) there is a small empodium which is barely distinguishable from the unguitractor.

Phengodidae.

The empodium of Phengodes plumosa Oliv. (Fig. 138) is larger than that of the Lycidae and is almost circular. There are two parempodia.

Cantharidae.

In Chauliognathus pennsylvanicus Scd. (Fig. 139) the empodium is very small, as it is in the Lycidae, but in Cantharis consors Lec. (Fig. 140) there is a large empodium with a broad distal portion. This is an example of the unreliable nature of the empodium as a phylogenetic guide in the Coleoptera. A sclerotized lobe or tooth occurs on one claw of each pretarsus in Cantharis and in the two genera of

Lampyrids which were examined (Figs. 140, 141, 142). In each case this projection is on the outside claw when the foot is resting on the ground in a "normal" position. Thus, on preteral of the right side this structure occurs on the right claws, and on the left side, on the left claws.

Lampyridae.

Parempodia are lacking in Luciola atra Fab. (Fig. 141) and the empodium is very small, but in Photuris pennsylvanicus DeG. (Fig. 142) there are two parempodia and the empodium is somewhat larger.

Melyridae.

The empodium of Malechius aeneus L. (Fig. 143) is very small but there are two parempodia. Basipulvilli and large pulvilli occur in this insect and this is one of the few Coleopterous families in which such structures have been found.

Cleridae.

In Trichodes aivorus Germ. (Fig. 144) there is a small, narrow empodium which bears two parempodia.

Corynetidae.

The empodium of Necrobia violacea L. (Fig. 145) is short and broad, and bears two parempodia. The flexor membranes and basal portions of the claws are somewhat enlarged.

There seem to be two types of epodium in both the Cantharidae and the Lampyridae. Chauliognathus (Cantharid) and Lucidota (Lampyrid) have a very small epodium, while Cantharis (Cantharid) and Photuris (Lampyrid) have a broad epodium. The same division occurs again in the Kelyridae (small epodium) and Corynetidae (large epodium). The two genera of Lycidae exhibit the reduced epodium and Phengodes (Phengodidae) has a large epodium. The epodium of the Clerid, Trichodes, is different from these two types, for it is narrow, fringed with short hairs, and bears two parempodia.

COCELOLOIDEA

Cephaloidea.

The epodium of Typitium unguis Loc. is large and the distal three-quarters is considerably broader than the basal portion; there are two small parempodia. The narrow pulvilli, which arise from the basal membrane, are closely applied to the serrate claws. In Cocheloon lepiturides Hewn. (Figs. 147, 148) the pulvilli are broad and are attached to the claws at their bases.

Cedemeridae.

Nacerda melanura L. (Fig. 149) has a broad epodium and short parempodia. Pulvilli are absent but the membranes at the bases of the claws are large and are covered with minute setae or thickened hairs.

Mordellidae.

In Mordellistena sp. (Fig. 150) the empodium is somewhat triangular and parempodia are absent. The pulvilli are narrow and are fringed with short hairs. Anaspis rufa Say (Fig. 151) has a broad, ovate empodium which bears two parempodia. Pulvilli similar to those of Mordellistena are present.

Rhipiphoridae.

The empodium of Rhipiphorus styloides Hewn. (Fig. 152) bears three small parempodia on its broadened distal portion. The claws are serrate and pulvilli are absent.

Meloidae.

Long, narrow, coriaceous pulvilli occur in all Meloids examined. They are as long as the claws and are often so closely applied to the sides of the claws that they are not readily observed. The empodium of Pomphopoea sayi Lec. (Fig. 153) is broader in the mesal portion than at the base or tip and bears two long parempodia. Epicauta lemniscata Fab. (Fig. 154) and Macrobasis albida Say (Fig. 155) are similar, but Macrobasis has three parempodia instead of two. The shape of the empodium and the three small parempodia of Neognatha lutea Lec. (Fig. 156) suggests the condition in Rhipiphorus (Fig. 152); the claws in both of these species are serrate but

there are no pulvilli in Rhipiphorus styloides Newm. In Tricrania sanguinipennis Say (Fig. 157) the distal portion of the epodium is broad and the two paracodia are long.

Pythidae.

The epodium of Pytho niger Kby. (Fig. 158) is similar to that of Anaspis; there are no pulvilli.

Pyrochroidae.

In Dendroides bicolor Newm. (Fig. 159) the epodium is typical. There are no pulvilli.

Pedilidae.

The epodium of Pedilus collaris Say (Fig. 160) exhibits no significant variations. Pulvilli are absent.

The superfamily Mordelloidea has the unstable type of variation noted in other Coleopterous groups, i.e., the pretarsus of Typitum (Cephaloidea) is more like that of Hemognathus (Meloidea) than it is like a member of its own family, Cephaloon (Cephaloidea). Rhipiphorus (Rhipiphoridae) is also similar to Typitum and Hemognathus.

The restriction of the occurrence of pulvilli to such a small section of the Coleoptera is noteworthy. They were found only in the family Melyridae of the Cantharoidea and in the families Cephaloidea, Mordellidae, and Meloidea of the Mordelloidea. More detailed study of the presence of pulvilli in these groups is necessary to determine their taxonomic significance.

ELATEROIDEA

Elateridae.

There is a slight difference of outline between the empodium of Alaus oculatus L. (Fig. 161) and that of Ludius pyrrhus Hbst. (Fig. 162). Both are typical and have two paraspodia.

Euprestidae.

No empodium is present in Hippomelae spherica Lec. (Fig. 163), and in Chalcophora virginiana Drury (Fig. 164) the empodium is represented by a short spine.

The pretarsi of the Euprestidae and Elateridae are quite different on the basis of the empodium.

DRYOPOIDEA

Dryopidae.

In Dryops productus Lec. (Fig. 165) there is a small semi-circular empodium with two paraspodia.

HYPEROIDEA

Dermostidae.

The empodium of Dermostes vulpinus Fab. (Fig. 166) is somewhat elongate and the distal portion is expanded; the side-portion is fringed with short hairs.

Byrrhidae.

In Byrrhus americanus Lec. (Fig. 167) the base of the empodium is very narrow and the distal portion is rounded. There are two parempodia.

CUCUJOIDEA

Ostomidae.

The empodium of Teneochila viridescens Say (Fig. 168) is broader through its median portion than at the base or tip.

Nitidulidae.

A tuft of short hairs is present at the base of the small empodium of Glischrochilus obtusus Say (Fig. 169).

Cucujidae.

The empodium of Cucujus clavipes Fab. (Fig. 170) is similar to that of Glischrochilus but there is a fringe of hairs on the middle portion of the empodium of Cucujus.

Erotylidae.

In Megalodacna fasciata Fab. (Fig. 171) the empodium arises from a narrow unguitractor and its distal portion is broad.

Endomychidae.

The empodium of Lycoperdina sp. (Fig. 172) is very small but bears two parempodia.

Coccinellidae.

Coccinella novemnotata Hbst. (Fig. 173) and Epilachna corrupta Muls. (Fig. 174) have empodia which are practically identical. As in the Endomychidae, the empodium is very small; parempodia are lacking but a group of hairs covers the tip of the empodium.

As in other Coleopterous super-families it is not possible to group these families on the basis of the pretarsus. However, a few similarities between the species of Cucujoidea examined may be indicated. The Nitidulidae, Cucujidae, and Dermestidae have a fringe of hairs on the empodium; the empodium is greatly reduced in both the Endomychidae and Coccinellidae but there are no parempodia in the Coccinellids; the empodium of the Protylin, Megalodacne, is in general more like the Tenebrionid type.

TENEBRIONIDAE

Alleculidae.

The empodium of Isomira quadristriata Couper (Fig. 175) is short and broad, and bears three parempodia.

Tenebrionidae.

In Phloeodes diabolicus Lec. (Fig. 176) the empodium is a short spine. This is radically different from the type found in the other genera of Tenebrionidae which were examined. The empodium of Eleodes argata Lec. (Fig. 177) is of moderate length

and is expanded at the tip and narrow at the base. There are three paraspodia. In Alobates pennsylvanicus DeG. (Fig. 178) the exopodius is pedunculate at the base and broad in the distal portion. There are only two paraspodia. Tarpeia nicensis Fab. (Fig. 179) exhibits an exopodius similar to that of Alobates but there is a broader distal portion and three paraspodia.

Legriidae.

The exopodius of Arthromacra seneca Lat. (Fig. 180) is broadly joined with the unguitractor and there are four paraspodia.

Melanodryidae.

In Penthe obliquata Fab. (Fig. 181) there is a broad exopodius which bears two paraspodia.

In the super-family Tenebrienoidea the exopodius exhibits a variety of forms. The presence of three or four paraspodia instead of the usual two is a condition often found in this group.

BOSTRICHOIDEA

Bostrichidae.

The exopodius of Polyceon stauti Lat. (Fig. 182) is narrow at the base and only slightly wider at the tip. There are two paraspodia.

Ptiniidae.

The empodium of Mezium americanum Lap. (Fig. 132) is narrow and of moderate length; there are six parempodia, and this condition, together with the shape of the unguitractor, is somewhat suggestive of the type found in the Cerambycid, Glycobius (Fig. 124).

SCARABAEOIDEA

Scarabaeidae.

In Copris tullius Oliv. (Fig. 134) the empodium is absent because there is no sclerotization of the membrane distal to the unguitractor.

The empodium of Phyllophaga sp. (Fig. 135) is in the form of a broad oval which is much narrower at the base where it joins the unguitractor. There are two parempodia.

The reverse condition is found in Popillia japonica Newm. (Fig. 136) in which the empodium is broad at the base and somewhat narrower at the tip. There are two small parempodia.

In Osmoderma scabra Beauv. (Fig. 137) the basal portion of the empodium has the form of a long narrow stalk which broadens in the distal region before it narrows to a tip. There are two parempodia.

The empodium of Gynastes sp. (Fig. 138) is very long and is slightly broader near the base. On each margin of the distal portion there are four parempodia. In another species of Gynastes (Fig. 139) the mid-portion of the empodium is much broader and two groups of five parempodia each arise from each

side of the arrow-like tip. Another large parempodium arises from each side of the mid-portion.

These genera represent nearly every type of empodium which has been found in the Coleoptera. The range of variation within the Scarabaeidae (from empodium absent to the highly specialized type of empodium in Dynastes) is further evidence for the conclusion that the pretarsus of the Coleoptera is of little value for studying the phylogeny of the larger groups. However, the specialist may find the pretarsus of considerable use within family or generic limits.

Lucanidae.

The empodium of Pseudolucanus capreolus L. (Fig. 130) is very long and narrow and bends upward between the claws. There are six to seven parempodia.

Passalidae.

The empodium of Passalus cornutus Fab. (Fig. 131) exhibits a narrow basal stem and a longer, wider distal portion. There are two parempodia.

CERAMBYCOIDEA

Cerambycidae.

The expodius of Cerobrachus brunneus Forst. (Fig. 192), Prionus laticollis Drury (Fig. 193), and Glycobius speciosus Say (Fig. 194) are similar, but in Glycobius there are five paraexpodia and in Cerobrachus and Prionus there is only one. There is a reduction of the expodium in Conochamus scutellatus Say (Fig. 195) and the two paraexpodia are small and hair-like. In Monilemma gigas Lec. (Fig. 196) and Tetraopes collaris Horn (Fig. 197) the expodium is further reduced so that it appears as a short spine-like process of the unguitractor, and paraexpodia are lacking.

Chrysomelidae.

The expodium is reduced in the three genera of this family which were examined. In Labidomera clivicollis Kby. (Fig. 198) it is a minute lobe, and in Calligrapha lunata Fab. (Fig. 199) this lobe is somewhat larger and is fringed with hairs. The expodium of Chelymorpha cassidea Fab. (Fig. 200) is spiniform.

Mylabridae.

Mylabris pinorum L. (Fig. 201) has a small spine-like expodium similar to that of Chelymorpha.

The Cerambycoidea as a whole seem to be characterized by a reduction of the expodium, although in four of the six genera of the family Cerambycidae which were examined, a moderately well developed expodium was found.

BRENTOIDAE

Brentiinae.

The empodium of Rupealis minuta Gray (Fig. 202) is spiniform and is practically identical with that of Chelymopsis and Hyalaria.

CURCULIONOIDAE

Platystomidae.

In Puparius marmoreus Oliv. (Fig. 203) the empodium is broad in its distal portion and bears a single empodium.

Belidae.

The empodium of Ithycerus novaboracensis Forst. (Fig. 204) is spine-like and similar to that of the Brentid, Puparius, but bears a single parempodium.

Curculionidae.

In Brachyrhinus sulcatus Fab. (Fig. 205) the empodium is spiniform and bears two parempodia. The distal portion of the empodium in Hylobius pales Boh. (Fig. 207) is somewhat expanded and bears two parempodia. In Lixus concavus Say (Fig. 208) the empodium is short but fairly wide and bears one parempodium.

Aggenophoridae.

There are no structures developed from the membrane in Metamasius sericeus Latr. (Fig. 209).

SCOLYTIDAE

Scolytidae.

The empodium of Pendroctonus valens Lec. (Fig. 310) is triangular in shape and bears two parapodia.

Summary of the Coleoptera

The Coleopterous pretarsus is characterized by the development of the empodium and the nearly complete absence of all other pretarsal structures. The only exception to this statement is the occurrence of pulvilli in the Helyridae and a few families of the Cordilloidea. The size and shape of the empodium is extremely variable throughout the order and the family Scarabaeidae exhibits many of the different types. The most generalized empodium might be considered to be that in which the base is narrow and the distal portion is in the form of a broad oval which bears two parapodia. (Figs. 152, 154, etc.).

NEUROPTERA

There are two main types of pretarsus in the Neuroptera; in one the empodium is the most prominent structure, and in the other the arolium is developed at the expense of the empodium. This tendency for specialization of two distinct types of pretarsus occurs in nearly every order of insects.

NEUROPTERA WITH AN EMPODIAL PRETARSUS

Stelidae.

Corydalis cornuta L. (Fig. 211). The planta is triangular and the basipulvilli are contiguous with its lateral margins. There is no arolium or other development of the original membrane.

Chauliodes sp. (Fig. 212). There is a typical "coleopteroid" empodium with the expanded distal portion and the parempodia.

Raphidiidae.

Raphidia oblita Hagen (Fig. 213). The empodium is similar to that of Chauliodes but is much broader.

Ascalaphidae.

Ululodes sp. (Fig. 214). The empodium is practically identical with that of Chauliodes.

Myrsoleonidae.

Myrsoleon sp. (Fig. 215). There is a broad exopodium which is only partially fused with the unguitractor. Several short parempodia are present.

Homopteridae.

Eroce sp. (Fig. 216). Four parempodia are borne on a broad exopodium.

These families form a homogeneous group (from the standpoint of the character of the pretarsus) which is contrasted sharply with the second group of Neuropterous families in which the arolium is well developed. The only possible transitional forms between these two groups are Corydalis (Fig. 211) and Ithone (Fig. 213). Both have a planta and basipulvilli, but in Ithone the original membrane is extended to form an arolium. These two types may be traced back to similar types in the Blattellidae where the relationship between planta and basipulvilli is the same and the arolium may be present or absent. (Compare Corydalis (Fig. 211) with the roach Blaberus (Fig. 30), and Ithone (Fig. 213) with the roach Periplaneta (Fig. 32).)

NEUROPTERA WITH AN AROLIUM PROTRACTOR

Ithoniidae.

Ithona sp. (Fig. 213). The basipulvilli are contiguous with the plantae and unguitractor and are provided with three small setae. The arolium is a simple lobe or pad and has no sclerotized areas.

Coniopterygidae.

Coniopteryx sp. (Fig. 217). There is a simple arolium with no sclerotized areas distal to the unguitractor.

Mantispidae.

Mantispa brunnea Say (Figs. 219, 220). The arolium is large and bilobed. The unguitractor has a median distal process. Each basipulvillus is much larger than usual and is divided into two portions, a small mesal area which bears three setae as in Ithona, and a larger lateral area which extends laterally around to the unguifer (see dorsal view, Fig. 220). The claws of Mantispa are broad, somewhat scoop-shaped and the distal portions are toothed.

Homerobiidae.

Horionyla longifrons Walk. (Fig. 221). The arolium is broad and there are two sclerites, euraerolia, in the dorsal membrane. The plantal area is only partially sclerotized and is covered with many short setae. The basipulvilli are completely divided so that they form two sclerites on each side of the plantal area.

Hemerobius stigmaterus Fitch (Figs. 222, 223). The pretarsus in this insect is practically the same as it is in Horionyx. The dorsal view (Fig. 223) shows the partially sclerotized surarolia.

Polystoechotidae.

Polystoechotes punctatus Fab. (Fig. 224). A partially sclerotized transverse band occurs in the ventral membrane of the small arolium and this may represent the first occurrence of the camera which is a characteristic structure of Mecoptera, Lepidoptera, and Hymenoptera. The plantal area is like that of Hemerobiidae in that it is setiferous and the basipulvilli are completely divided; long setae occur on the mesal pair of basipulvilli as they do in Hantisona.

Sisyridae.

Climaciella sp. (Fig. 225). The arolium is broad and a single pair of basipulvilli is present. There are no other developments in the membrane of the plantal area.

Chrysopidae.

Chrysopa sp. (Figs. 226, 227, 228). The arolium is like that of Hemerobiidae, Sisyridae, and Polystoechotidae. The mesal basipulvilli bear the three characteristic setae and the plantal area is unsclerotized. The dorsal view (Fig. 227) shows the ungulifer and lateral basipulvilli. The claws (Fig. 228) have a basal sclerotized projection.

The homogeneous nature of this group of Neuroptera, as contrasted with those which have the exopodial type of pretarsus, is apparent. As is the case with other morphological characters, the pretarsus in the Neuroptera as a whole is more generalized than it is in any other order. It would not be difficult to construct a hypothetical prototype from the elements found in these families, from which the pretarsi of all Holometabola could be derived. The only structure not found in the Neuroptera is the pulvillus.

MEGOPTERA

In this order, also, there is the division into exopodial and aroliar types of pretarsus.

Panorpidae.

Bittacus sp. (Fig. 220). One claw is lacking so that there can be no development of the original membrane and we find the usual condition of single-clawed pretarsi in which the unguitractor is located at the base of the claw.

Panorpa rufescens Ramb. (Fig. 220). The arolium is large and is supported by a distinct camera (ca). The planta is a narrow transverse sclerite and basipulvilli are present on either side of this planta. The condition in Panorpa is similar to that in Plecoptera and Embioptera, on the one hand, and to that in Lepidoptera and Hymenoptera on the other.

Borane sp. (Fig. 231). The basipulvilli have a fringe of short hairs and this condition is like that in Tipuloid Diptera and Lepidoptera. There is no arolium but a typical empodium with two long parasepods is present.

DIPTERA

The preterans of Diptera was found to be the most complicated and the most difficult to understand. This has been due primarily to the merging of empodium and arolium which occurs in the Diptera, and to the presence of the pulvilliform empodium. Ockler (1930) indicates that he considers the middle holding pad of Diptera to be a modification of the setiform empodium but does not present much evidence to support this conclusion. Probably it would be more correct to say that the pulvilliform empodium and setiform empodium are homologous, because they represent different types of development of the ventral membrane distal to the unguitractor. The terms setiform empodium and pulvilliform empodium have been used a great deal in the literature, but no definite proof seems to have been given that the structures referred to are homologous.

However, it is possible to show by a series of the Dipterous empodium the variation from the lobe-like to the long narrow setiform type. (See diagrammatic representation of intermediate forms, A-J, Fig. 234) The problem is

complicated by the presence of a dorsal membrane which can only be interpreted as a reduced or undeveloped arolium. The various degrees of development of this membrane are shown in the diagrammatic lateral views, K-P, Fig. 294. Blackened areas represent the location of the claws.

K represents the typical aroliar type. Two sclerites have formed in the primitive protarsal sac: the planta in its ventral membrane and the orbicula (or euraroliar) in the dorsal membrane. This is the normal condition in the Tipulidae. L, M, N, O indicate further sclerotization of the ventral membrane to form the empodium and the stages in the reduction of the aroliar membrane. The Bibionid (Fig. 298) and Coenomyid (Fig. 267) are examples of this type.

P represents the type in which the arolium has entirely disappeared and the empodium alone is developed. The Asilid (Fig. 275) presents an example of this type in the Diptera, but the same condition is found in some members of practically all orders, and in some orders (Coleoptera) it is the only type to be found.

NEOTROPICA

Tanyderidae.

Protoplessa fitchii C.F. (Pl. 272). Basipulvilli are present but there is no extension of the original membrane either as an arolium or empodium. The plantal area is only weakly sclerotized. The claws are fringed with minute hairs.

Ptychopteridae.

Ptychoptera rufocincta C.F. (Fig. 273). This lateral view shows the relationship between the empodium and the aroliar membrane.

Pittacomorpha clavipes Fab. (Fig. 274). The ventral view shows the basipulvilli and planta; lateral arms of the planta extend along the margins of the empodium and this condition is characteristic of many tipuloid insects. The empodium and basipulvilli are covered with short hairs.

Tricoceridae.

Tricocera garretti Alex. (Fig. 275). The pretarsus is similar to that of the Tipulidae. The planta and basipulvilli are fused to form a transverse sclerite which bears a fringe of long hairs. The dorsal membrane or arolium is well developed as it is in the crane-flies.

Tipulidae.

In the Tipulidae an attempt to make a sharp distinction between arolium and empodium breaks down, for here the two

structures merge. At first such a condition may appear to be inconsistent with the conception of the pretarsus developed in this study. However, the basic principles of evolution presuppose that sooner or later intermediate forms must break down our arbitrary classifications, and it is on this basis that the tipuloid pretarsus is interpreted. In most Diptera some degree of sclerotization or other development of the ventral membrane occurs to which the term empodium may be applied. In many Tipulids, however, this ventral surface is entirely membranous and the whole structure is therefore a typical arolium. Because the line must be drawn somewhere, and because dipterologists have long used the term empodium for this structure, it is suggested that the designation empodium be retained throughout the Diptera for the median structure, with the understanding that it refers to the unsclerotized ventral membrane in Tipuloid insects, while the term arolium refers to the dorsal membrane or the structures formed in it.

Cylindrotoma americana D.W. (Fig. 236), Tipula aestivalis Say (Fig. 238), Pedicia conterranea Walk. (Figs. 239, 240), and Glyptoceros helmsi Shuck (Figs. 241, 242) have a long narrow "empodium" and well developed lateral area to the plantae. The ventral surface of Cylindrotoma is thickly setiferous. In the large dorsal membrane of Glyptoceros and Pedicia there is a hood-like sclerite, the surarolium. In Stenophora apicata D.W. (Figs. 241, 242, 243) this structure is divided into two lateral

sclerites. The latero-distal area of the planta curve dorsad and fuse with the margins of the surarella. The empodium of Ctenophora and Tricyphena constans Doane (Fig. 237) is shorter and broader than that of the above species. The pretarsus of Ctenophora is similar to that of Trichocera. In Limenia sciophila J.S. (Fig. 246) there is no development of the membrane distal to the fused planta and basipulvilli, but Tokunaga (1930) figures a species of Limenia, (Limenia (Dicranomyia, monostromia Tok.) in which a typical empodium with characteristic long, hollow setae is present. According to this figure, the condition in monostromia is more like that in the Ptychopteridae or Anisopidae than it is like other Tipulidae.

Anisopidae.

Anisopus fenestralis Scop. (Fig. 245, after DeMeijere). There is a typical pulvilliform empodium and at the base of each claw is located a small tuft of hairs which probably represents the basipulvillus.

Anisopus sp. (Figs. 247, 248, 249). The empodium is provided with a thick "brush" of hairs. The areolar or dorsal membrane is not as large as it is in most Tipulidae and is more like that of the Ptychopteridae. The planta and basipulvilli are fused in the manner typical for all Tipuloid insects which were examined.

Simuliidae.

Simulium sp. (Figs. 250, 251). The ventral view shows the separate plantae and basipulvilli and the setifera empodium which is fringed with short hairs or setae. The area between the base of the empodium and the plantae is incompletely sclerotized. The lateral view shows the arolar membrane and its dorsal sclerite, the surarolium. The strange development of the dorsal portion of the claw in this insect shown in the figures has been noted by DeMeijere (1901). Apparently the function or significance of this structure is not known.

Chironomidae.

Chironomus ferrugineo-vittatus Latr. (Fig. 252). The setiform empodium arises directly from the unguitractor and bears a ventral fringe of hairs. Pulvilli and basipulvilli are large and the pulvilli are provided with numerous, microscopic, hollow setae or retinacra. They are said to exude a sticky substance which permits the insect to cling to smooth surfaces.

Culicidae.

Psorophora ciliata Fab. (Fig. 253, 254). The empodium is setiform and is much like that of Chironomus. There are no basipulvilli or pulvilli, although the membranes at the bases of the claws are large and thickly covered with hairs.

According to Tokunaga's figure of the pretarsus of the Nymphomyiidae fly, Nymphomyia alba Tok. (1935) the empodium is

very similar to that of the Chironomidae and Culicidae. He does not show pulvilli.

Bibionidae.

Aspilota berolinensis Meig. (Fig. 256, after Demeijere). The pulvilli are small and narrow and both the empodium and pulvilli are supplied with retinaria.

Bibio sp. (Fig. 257, 258). The large empodium is pulvilliform and at its base a planta is partially demarked; from the margins of this plantal areolarine several long setae. The pulvilli and basipulvilli are typical. The lateral view (Fig. 258) shows the areolar membrane and orbicula.

Mycetophilidae.

Leptomorphus sp. (Fig. 259). The empodium is pulvilliform but small. Large basipulvilli occur in their typical position at the bases of the claws.

Mycetophila fungorum Des. (Figs. 260, 261). Although the empodium is pulvilliform the areolar membrane is almost completely reduced. The claws are deeply toothed.

Sciara thomae L. (Fig. 262, after Demeijere). This figure shows the pulvilli developing as diverticula of the original membrane.

Cecidomyiidae.

Cecidomyia rosaria Loew (Fig. 263, after DeMeijere). The empodium is pulvilliform but there are no pulvilli. A short tooth is present at the base of each claw.

Summary of the Pretarsus of the Nematocera

The nematocerous pretarsus may be classified under four headings:

1. The Aroliar Type.

The arolium is well developed and there is little, if any, sclerotization or other indication of the formation of a true empodium. Trichoceridae, Tipulidae.

2. Intermediate Type.

A large arolium with a dorsal sclerite is present, as well as a setiform empodium. Simuliidae.

3. Setiform Empodial Type.

The aroliar membrane is entirely reduced and a ventral process of the unguitractor is the characteristic feature. Chironomidae, Culicidae.

4. Pulvilliform Empodial Type.

A pulvilliform empodium, continuous with the unguitractor, is well developed and the aroliar membrane is variable but usually reduced. Tanyderidae, Ptychopteridae, Anisopidae, Cecidomyiidae, Mycetophilidae, Bibionidae.

Pulvilli were found in the Chironomidae, Mycetophilidae, and Bibionidae.

BRACHYCERA

Division ORTHORHINAPHA

Stratiomyidae.

Stratiomyia badia Loew (Fig. 264). The pretarsus of this insect is much like that of Bibio (Fig. 258). These are the only dipterous insects examined in which a partially demarked plantal area was found within the empodium.

Xylophagidae.

Xylophagus reflectens Walk. (Figs. 265, 266). The pretarsus is similar to that of Stratiomyia. The dorsal view (Fig. 266) shows the unguifer, orbicula, and pulvilli.

Coenomyidae.

Coenomyia pallida Say (Figs. 267, 268). The condition in this insect is practically the same as that in Xylophagus.

Acroceratidae.

Oncodes sp. (Figs. 269, 270, 271). The empodium is lacking and the narrow empodium and plantal area are strongly setiferous.

Bombyliidae.

Exoprosopa sp. (Figs. 272, 273). The pulvilli are very narrow and are partially sclerotized. The empodium arises directly from the unguitractor and is somewhat expanded and

setiferous in the distal portion. This empodium probably represents an intermediate stage between that of the Mycetophilid, Leptomorphus (Fig. 239) or Oncodes (Fig. 271), and that of the Asilidae (Fig. 274).

Asilidae.

Diectria baumbaueri Meig. (Figs. 274, 275). The empodium is setiform but is somewhat broadened in the mid-portion. The pulvilli are large and a rudiment of the arolier membrane persists. Other Asilidae have a glabrous, setiform empodium like that of Mydas (Fig. 276) and the majority of Cyclorrhapha.

Mydidae.

Mydas sp. (Fig. 276). In the Orthorrhapha, Mydas and some Asilid species, were the only cases in which the setiform glabrous empodium so characteristic of the Cyclorrhapha was found. Mydas also has large pulvilli.

Epididae.

Rhamphomyia sp. (Fig. 277). The empodium is practically identical with that of the Asilid, Diectria.

Liancalus sp. (Fig. 278). In this insect there appears to be a dorsal expansion of the empodium which may represent a modification of the arolier membrane.

Large pulvilli and basipulvilli occur in the Epididae.

Dolichopodidae.

Dolichopus sp. (Figs. 230, 231). The empodium is short and broad and bears many long setae. The lateral view (Fig. 231) shows the reduced arolier membrane. Typical pulvilli are present.

Summary of the Pretarsus of the Orthorrhapha

In the Stratiomyidae, Xylophagidae, Coenomyidae, Tabanidae, Acroceratidae, and Therevidae the pulvilliform empodium with a reduced dorsal or arolier membrane is present. In the Bombyliidae, Asilidae, and Mydidae the empodium varies from a blade-like to a setiform type. The Empidae and Dolichopodidae exhibit an empodium similar to that of the Asilidae. These five families (Bombyliidae, Asilidae, Mydidae, Empidae, and Dolichopodidae) might be considered as intermediates (on the basis of the pretarsus) between the remaining families of the Orthorrhapha and the Cyclorrhapha.

The Orthorrhapha are characterized by the presence of two main types of empodium, pulvilliform and setiform, and this condition makes them an ideal intermediate between the Hematocera in which the arolier-pulvilliform type of empodium is predominant and the Cyclorrhapha in which the empodium is practically always strongly setiform and glabrous.

Pulvilli were found in all species examined in this group.

CYCLORHAPHA

Lonchopteridae.

Lonchoptera lutea Panz. (Fig. 232, after DeMeijere).

There is a minute empodium and large pulvilli with their retinaria.

Phoridae.

Phora sp. (Fig. 233). The empodium is setiform and glabrous. The pulvilli are small.

In the following seven families there were no significant variations in the species examined. In all of these the empodium is setiform and glabrous and the pulvilli are large.

Syrphidae.

Eristalis tenax L. (Fig. 234).

Tachinidae.

Tachina sp. (Fig. 235).

Sarcophagidae.

Sarcophaga sp. (Fig. 236).

Muscidae.

Euscina pascuorum Meig. (Fig. 237).

Gastrophilidae.

Gastrophilus equi Clark (Fig. 238).

Tetanoceridae.

Tetanocera plebeja Loew (Fig. 239). The empodium is exceptionally long.

Ortaliidae.

Casentonsura sp. (Fig. 290). The pulvilli are ovate.

Hippoboscidae.

Lynchia americana Leach (Figs. 291, 292, 293). The empodium is setiform but is somewhat swollen at the base; the distal portion bears a double row of short setae. The pulvilli and basipulvilli are large and the claws have two elongate teeth.

Summary of the Preterans of the Cyclorrhapha

The Cyclorrhapha are the most homogeneous group of the Diptera from the standpoint of the preterans. They are characterized by an elongate and glabrous setiform empodium and by the presence of pulvilli.

TRICHOPTERA

The trichopterous pretarsus is identical with that of some Lepidoptera and this condition is to be expected because of the close relationship of these two orders. Among lower groups the pretarsus of the Mecopteran, Panorpa, most closely approaches the Trichoptera-Lepidopterous type.

Phryganilidae.

Ptilostomis postica Walk. (Figs. 295, 296). There is a typical arolium supported by a narrow, curved sclerite, the camera (ca) which is located at the base of the arolium. Distal to the unguitractor there is a distinct transverse sclerite, the planta (pl). The pulvilli arise somewhat laterad of the base of the claws and are narrow membranous structures which are fringed with hairs. The dorsal view (Fig. 296) shows the relationship between unguifer, orbicula, and arolium. Compare Ptilostomis with the Tortricid, Fig. 304.

Limnephilidae.

Allegophylax subfasciata Say (Fig. 297). The pretarsus of this insect is like that of Ptilostomis with the exception of the pulvilli which are much broader, are not fringed with hair, and have distinct basipulvilli at their bases.

LEPIDOPTERA

The typical lepidopterous pretarsus has a large arolium supported by a heavily sclerotized camera. The camera is plainly visible from either the dorsal or the ventral surface and has the appearance of a black rod or band. In the dorsal membrane at the base of the claws is located the orbicula (or) which often bears a single seta and distal to the orbicula on the lobes of the arolium occur flat paired sclerites, the surarolia (sa). The plantal area in Lepidoptera is variable; the pulvilli are often bilobed and are usually setiferous.

HETEROCERA

Micropterygidae.

Mnemonica sp. (Fig. 298). The arolium and pulvilli are typical but the camera and planta are not sclerotized.

Hepialidae.

Hepialus sp. (Fig. 299). The arolium and camera are present but the pulvilli are represented only by the setiferous basipulvilli. The plantal area is unsclerotized.

Letostacyl sp. (Fig. 300). There are no setae on the basipulvilli and the planta is partially sclerotized.

Cossidae.

Cossus macnurtrelli Peale (Fig. 301). The basipulvilli are setiferous but the arolium is not developed. There is a definite planta. The distal view (Fig. 302) shows the unguifer and single seta which arises from the locus of the orbicula which is unsclerotized.

Mimallonidae.

Cicinnus melsheimeri Harris (Fig. 303). The arolium is very large and the pulvilli are only about half their usual length. The plantal area is unsclerotized.

Tortricidae.

Archips rosaceana Harris (Fig. 304). This may be considered to be the most generalized Lepidopterous pretarsus, since all structures are present in an unspecialized condition. Compare with the Trichopteran, Ptilostomis (Fig. 295).

Pyralididae.

Galleria sp. (Figs. 305, 306). The arolium and planta are typical but the pulvilli have developed an inner lobe which is about half the length of the outer lobe; both are setiferous. The orbicula is present in the dorsal membrane.

Naturniidae.

Tropaea luna L. (Figs. 307, 308, 309). The orbicula with its seta is present and the surarolia and camera are developed. The extremities of the camera fuse with the surarolia, a condition which is very common in the Hymenoptera with a bilobed arolium. The plantal area is sclerotized just distal to the unguitractor in the form of a lateral band. The pulvilli are broad at their bases where they arise from the basipulvilli but become narrow and setiferous at the distal portion.

Geometridae.

Brevhes infans Kosch. (Fig. 310). The arolium and pulvilli are typical. The plantal area is unsclerotized but is covered with short setae.

Spingidae.

The three genera of this family which were studied illustrate the two fundamental types of insect pretarsus, i.e., the aroliar and espedial types. In practically every large order we find two groups in one of which the arolium is well developed at the expense of the espedium, and in the other the reverse condition is the case.

Hemaris thysbe Fab. (Fig. 311). There is a typical lepidopterous pretarsus except for the bilobed condition of the pulvilli. Note the large arolium.

Pholus satellitia pandorus Hbn. (Figs. 312, 313, 314).

The arolium is reduced to a small lobe but the camera is still discernible. The pulvilli and basipulvilli are narrow but are not bilobed. The transverse planta is almost fused with the newly sclerotized area of the ventral membrane which indicates the development of the empodium. Dorsal (Fig. 313) and lateral (Fig. 314) views show the orbicula and reduced aroliar membrane.

Sphinx chersis Hbn. (Figs. 315, 316). The arolium is completely lost and the pulvilli are reduced to setiferous lobes while the empodium has become elongated.

Aegeriidae.

Melittia satyriniformis Hbn. (Fig. 317). The arolium is typical but the plantal area is unsclerotized. The pulvilli are reduced (or not developed) to broad lobes on which are located several groups of long setae.

Noctuidae.

Probus odora L. (Fig. 318). The arolium and planta are typical but the unguitractor is very short. The pulvilli are bilobed and the inner lobe is the longer. As in most Lepidoptera the pulvilli are curved around the base of the claw and a pulvillus removed and spread out is shown in the figure (pv).

Arctiidae.

Apanteles virgo Linn. (Figs. 319, 320). All structures are present and typical with the exception that the pulvilli are bilobed; the outer lobe is the longer in this case.

RHOPTALOCERA

Hesperidae.

Hesperia tityrus Fab. (Figs. 321, 322). The claws have a large basal tooth, the pulvilli are bilobed and the basipulvilli are larger than usual. All other structures are typical.

Pieridae.

Callidrias eubula Godt. (Figs. 323, 324). All structures are typical with the exception of the pulvilli, which are very broad and not setiferous.

Colias philodice Godt. (Fig. 325). There is no arolium; the planta is a distinct transverse sclerite and the pulvilli are reduced to small triangular lobes.

Papilionidae.

Papilio glaucus L. (Fig. 326). The pretarsus of this insect is practically identical with that of Colias. It is interesting to note that the other genus of Pieridae examined, Callidrias, is not like the Papilionid, but is more like the Hesperiid and Heterocerous type.

Nymphalidae.

Aglais antiopa L. (Fig. 227). The arolium is present but there is apparently no camera. The pulvilli are long and narrow with a rudiment of the inner lobe persisting.

Summary of the Pretarsus of the Lepidoptera

The pretarsus of this order can not be classified into general groups as has been done in some orders, because of the uniformity of fundamental features and the irregular variation of other characteristics. A condition found in the Lepidoptera which was not found in any other group is the bilobed nature of the pulvilli in many species. In general a simple arolium with its camera and setiferous pulvilli are the characteristic features of Trichoptera and Lepidoptera.

HYMENOPTERA

The pretarsus of the Hymenoptera is much like that of the Lepidoptera and differs chiefly in the increased specialization of the arolium and absence of pulvilli. Development of the orbicula is a characteristic of the Hymenoptera and in many cases a ventral process of the orbicula extends down to fuse with the camera.

CHALANTHROGASTRA

Xyelidae.

Macroxyela sp. (Figs. 320, 322). The arolium is well developed and has two types of sclerites in its dorsal membrane, namely, the orbicula (or) and the surarolia. The orbicula extends from the unguitractor to the base of the aroliar lobes and the surarolia are sclerotized portions of these lobes. There is a short process of the unguitractor which might be interpreted as an empodium but because a true planta is usually present distal to the unguitractor in Hymenoptera, and because this process exhibits the striated appearance so characteristic of the unguitractor, it is interpreted as a variation in the shape of the unguitractor rather than as a true empodium. The plantal area is unsclerotized but two long setae are present; small basipulvilli occur at the bases of the flexor membranes.

Pamphiliidae.

Neurotoma sp. (Fig. 330). The lateral lobes of the arolium (aroliella (al)) are apparently beginning to develop. These lobes are much more specialised in higher types of Hymenoptera. Cassera and surarolia are typical. The orbicula is large and the central portion is broad and bears four long setae.

Xiphydriidae.

Xiphydria canadensis Prov. (Fig. 331). With the exception of the broader arolium, better sclerotized plantal area, and narrow orbicula, the pretarsus of Xiphydria is much like that of Macroxyela.

Circiidae.

Tremex columba L. (Figs. 332, 333, 334). The arolium is reduced to a small dorsal membrane and the surarolium is represented by a small sclerite. The orbicula is present but is also small. Ventral and lateral views (Figs. 333, 334) show these structures and the well developed planta with its four setae.

Cimbicidae.

Cimbex americanus Leach (Fig. 335). There is a typical development of all structures. Compare with Xiphydria (Fig. 331).

Diprionidae.

Diprion lecontei Fitch (Figs. 336, 337). The aurarolia are provided with short spines and the orbicula is peculiar in that the distal portion is composed of two long narrow arms; several long setae occur on the median portion. The ventral view (Fig. 337) shows a typical development of all structures.

ICHOSEPTA

Oryziidae.

Oryzus navi Westw. (Figs. 338, 339). Basipulvilli are lacking and there are no setae on the plants. The distal portion of the orbicula is very broad.

CLITTOGASTRA
ICHNEUMONOIDEA

Braconidae.

Macrocentrus uniformis Prov. (Fig. 340). As in Oryssus the basipulvilli are not present. The planta is setiferous.

Ichneumonidae.

Opheltes sp. (Figs. 341, 342). The surcarolia are large and their ventral margins are fused with the camera. A ventral process of the orbicula joins the central portion of the camera. The planta is large and triangular, and bears many long setae.

Aulacidae.

Odontaulacus abdominalis Cress. (Fig. 343). The claws have two ventral teeth and a process of the orbicula joins the camera. Other structures are typical.

STENHOIDEA

Pelecinidae.

Pelecinus polyturator Drury (Fig. 344). All parts are typical but the basipulvilli are lacking. Note the shape and setiferous nature of the orbicula.

Cynipidae.

Ibalia maculipennis Haldr. (Fig. 345). The preterans of Ibalia is very similar to that of Pelecinus, and practically the only difference is found in the shape of the orbicula.

VESPOIDEA

Pachnocharidae.

Ceropalus bimaculata Say (Figs. 346-349). The dorsal view (Fig. 346) shows the long orbicula and its ventral process which is fused with the camera. The aroliella are well developed and are held folded back over the ventral portion of the arolium by the spring-like action of the bowed camera. When the foot is applied to a smooth surface, the lateral lobes are pulled outward and down to form a broader holding pad. This condition is similar to that occurring in other specialized Hymenoptera and is described in detail by Snodgrass in his work on the honey-bee (1923).

The lateral view of the orbicula shows the ventral process. Ventral structures (Fig. 347) are typical. There is a slight difference between the first and second thoracic claws (Fig. 348) and the third thoracic claw (Fig. 349).

Chrysididae.

Chrysis sp. (Fig. 350). The arolium is typical but the aroliar lobes are not developed and the basipulvilli are lacking.

Mutillidae.

Mutilla occidentalis L. (Fig. 351). The arolium is typical but the planta and the process of the unguitractor are setiferous. Four long setae are located on the swollen base of the orbicula.

Scoliidae.

Scolia sp. (Fig. 352). The arolia are prominent and basipulvilli are present. The distal margin of the orbicula is fringed with long setae and the ventral process extends forward and down to the camera.

Camponotus schipplingi Say (Figs. 353-356). The dorsal view (Fig. 353) shows the surarolia, arolia, and broad plate-like orbicula with its setae. Figure 354 is a ventral view of the orbicula to show its ventral process. All ventral structures (Fig. 355) are typical. Compare with scolia (Fig. 352). The lateral view (Fig. 356) shows the relative positions of the orbicula with its ventral process, the camera, planta, and arolia.

Formicidae.

Myrmica scabrinodis schencki Forel (Fig. 357). Dorsal view. The usual pretarsal structures are present.

Dorymyrmex pyramicus niger Pera. (Fig. 358). Ventral view. The arolia is small; otherwise the pretarsus is typical.

Camponotus herculeanus pennsylvanicus DeG. (Fig. 359). The arolia is small but the planta is larger than usual and bears scattered setae.

Basipulvilli were not found in the species of this family which were examined. The variation in the shape of the orbicula in these three genera should be noted.

Vespididae.

Monobia sp. (Fig. 360). All typical pretarsal structures are present.

Polistes sp. (Fig. 361). The arorella are large and well developed. The distal margin of the planta is prolonged into a small spine and two long setae arise from each of the lateral margins. Basipulvilli are present on each side of the unguitractor process. The orbicula is large and its distal portion, where it joins the camera, is expanded.

SPHECOIDEA

Sphecidae.

Tachytes distinctus Smith (Figs. 362,363). All typical structures are present and the arorella are especially large. A long seta arises from each side of the unguitractor process.

Philanthus solivagus Say (Fig. 364). The pretarsus of Philanthus is similar to that of Tachytes.

Bembex spinolae Lep. (Figs. 365,366). All structures are typical but there is a spine at the distal margin of the planta. Compare with Polistes (Fig. 361).

Hylaeidae.

Colletes inaequalis Say (Fig. 367). All structures are typical except for the absence of setae on the planta.

Andrenidae.

Halictus radiatus Say (Fig. 369). The pretarsus of Halictus is like that of Colletes.

Homada sp. (Fig. 369). The orbicula, as well as other pretarsal structures, is like that of Colletes and Halictus.

Hellinodes desponsa Smith (Figs. 370, 371). All structures are typical.

Xylocopa mordax Smith (Figs. 372, 373, 374). The arolium is reduced to a small dorsal membrane and the planta is large and empodiform. Basipulvilli are present. The orbicula is a large, flat plate on which setae are lacking.

Megachilidae.

Megachile sp. (Figs. 375, 376, 377). As in Xylocopa the arolium is reduced to a small membrane and the planta is empodiform.

Bombidae.

Bombus sp. (Figs. 378, 379, 380). The arolium of Bombus is small and represents a stage between the condition in Xylocopa or Megachile in which the arolium is entirely lacking, and that occurring in most Hymenoptera (for example, Hellinodes, Figs. 370, 371) in which the arolium is well developed.

Although the arolium of Bombus is very small, it retains the typical sclerites of a fully developed arolium. The orbicula is much larger than normal and bears many setae.

Summary of the Pretarsus of the Hymenoptera

The pretarsus of the Hymenoptera, like that of the Lepidoptera, is subject to a type of variation which makes it of little value for determining the relationships of families or higher groups. Possibly the specialist would find the orbicula a useful character in the classification of species or genera. As a whole, the Hymenoptera are characterized by complete absence of pulvilli, specialization of the arolium, and extensive variation of the orbicula. A few cases were found in which the arolium is reduced and the planta (empodium) is developed.

General Summary

The pretarsus constitutes a definite segment of the insect leg and represents a modification of the dactylopedite of Crustacea. The various structures which comprise the pretarsus are developed from the original membranous sac (or unsclerotized dactylopedite) by evaginations, extensions, and sclerotizations. A generalized, hypothetical pretarsus would contain the following structures: dorsally - unguifer (distal rim of the distitarsus), claws, orbicula, arolium, arolella, surarolia; ventrally - unguitractor tendon, unguitractor plate, planta or empodium, paracarpodia, camera, basipulvilli, pulvilli.

The condition in the Apterygota indicates that the original insect pretarsus was three-clawed (a middle claw-like dactylopedite and two lateral claws which may have arisen as evaginations of the base of the dactylopedite) and the middle claw was probably the precursor of the specialized structures of the Neopterygota. Throughout the insect orders there appears to be a tendency for either ventral (empodial) or dorsal (arolar) structures to develop, but there is seldom an equal specialization of both of these types.

In the Ephemeroidea there are no structures developed in the membrane distal to the unguitractor and the ventral surfaces of the claws are membranous. The Odonata are characterized by

the presence of a typical empodium. In the Orthoptera there are both empodial and aroliar types. The cursorial Orthoptera, Plecoptera, and Embloptera have a planta and basipulvilli, but no pulvilli. The arolium may be present or absent within a single family. An arolium was found in all Acridid types examined but in none of the Tettigoniid and Gryllid types in which the empodium is developed. In other Orthopteroids (Cylindrachetidae, Dermaptera, Diploglossata) only the original membrane is present distal to the unguitractor.

Both empodial and aroliar pretarsi occur in the Hemiptera. The Hemiptera are characterized by the presence of the empodium and pulvilli, and the absence of the arolium. The pulvilli probably arise as in other insect orders, as diverticula of the original membrane at the bases of the claws, but there is some indication that they result from a divided arolium.

The Coleoptera are characterized by development of the empodium and complete absence of the arolium. Pulvilli have been found in the Maloidae and Melyridae only.

In one group of neuropterous insects, the arolium is well developed, and in another group, the coleopteroid or empodial type is present. Both types are also found in the Mecoptera. In these two orders, types of pretarsi occur from which excellent pretarsal prototypes for the Holometabola could be constructed, although pulvilli have not been observed in any neuropteroid insects.

The Diptera are characterized by a typical arolium (Tipulidae) and two types of empodium (pulvilliform and setiform). When the pulvilliform empodium is present, a dorsal membrane or remnant of the arolium is usually retained. Pulvilli are better developed in the Diptera than in any other order.

In the Trichoptera and Lepidoptera, there is a well developed arolium with its supporting sclerite or camera and setiferous pulvilli which are often bilobed. The pretarsus of the Lepidoptera may be derived from a type similar to that of the Mecopteran, Panorpa.

The Hymenoptera are characterized by the presence of a specialized arolium and by the absence of pulvilli throughout the order.

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EXPLANATION OF FIGURES

abbreviations

al	-	areololla
ar	-	areolus
bp	-	basipulvillus
ca	-	camera
d	-	dactylopedite
dg	-	digitule
dt	-	distitarsus
em	-	empodium
fm	-	flexor membrane
or	-	orbicula
pes	-	parempodia
pl	-	planta
pt	-	plantella
pv	-	pulvillus
sa	-	surareolus
uf	-	unguifer
un	-	ungues (claws)
ut	-	unguitractor
utt	-	unguitractor tendon

Except where otherwise noted, the figures are original and were drawn from the right meta-thoracic pretarsus. In many cases in which the claws and associated membranes are of no significance, only the unguitractor with its empodium is figured.

- Fig. 1. Acerentomidae. Acerentulus barberi.
Tarsus I "optical section." (After Hwing)
- Fig. 2. Lepismatidae. Thermobia sp. One claw removed -
lateral.
- Fig. 3. Japygidae. Heterojapyx sp. Dorsal.
- Fig. 4. Japygidae. Heterojapyx sp. Ventral.
- Fig. 5. Japygidae. Heterojapyx sp. Lateral.
- Fig. 6. Japygidae. Japyx sp. Ventral. (After Snodgrass)
- Fig. 7. Campodeidae. Campodea staphylinis Westw. Lateral.
(After DeMeijere)
- Fig. 8. Entomobryidae. Isotoma sp. From the inside.
(After DeMeijere)
- Fig. 9. Entomobryidae. Isotoma sp. Ventral. (After DeMeijere)
- Fig. 10. Poduridae. Achorutes sp. Lateral. (After Hwing)
- Fig. 11. Sminthuridae. Sminthurus sp. Lateral.
(After DeMeijere)
- Fig. 12. Sminthuridae. Sminthurus fucus. Lateral.
(After Lubbock)
- Fig. 13. Pauropoda. Paurotus sp. Dorsal. (After Hwing)
- Fig. 14. Isopoda. Oniscus sp. Lateral.
- Fig. 15. Isopoda. Oniscidae. Lateral. (After Hwing)
- Fig. 16. Coenagrionidae. Enallagma sp. Ventral.
- Fig. 17. Agrionidae. Agrion aequabile Say. Unguitractor and
empodium.
- Fig. 18. Aeshnidae. Aeshna sp. Unguitractor and empodium.
- Fig. 19. Aeshnidae. Anax junius Drury. Ventral.
- Fig. 20. Cordulegasteridae. Cordulegaster maculatus Selys.
Ventral.
- Fig. 21. Cordulegasteridae. Cordulegaster maculatus Selys.
Distitarsus and plantella.

- Fig. 22. Libellulidae. Libellula semifasciata Burm. Ventral.
- Fig. 23. Heptageniidae. Epeorus sp. Lateral.
- Fig. 24. Heptageniidae. Epeorus sp. Dorsal.
- Fig. 25. Heptageniidae. Epeorus sp. Ventral.
- Fig. 26. Siphuridae. Siphurus sp. Lateral.
- Fig. 27. Siphuridae. Siphurus sp. Ventral.
- Fig. 28. Blattidae. Archimandrita marmorata Rehn. Ventral.
- Fig. 29. Blattidae. Blaberus craniifer Burm. Nymph. Dorsal.
- Fig. 30. Blattidae. Blaberus craniifer Burm. Nymph. Ventral.
- Fig. 31. Blattidae. Blaberus craniifer Burm. Nymph. Lateral.
- Fig. 32. Blattidae. Periplaneta americana L. Ventral.
- Fig. 33. Isoptera. Termopsis angusticollis Walk.
Winged form. Ventral.
- Fig. 34. Isoptera. Nastotermes darwiniensis Frog.
Winged form. Ventral.
- Fig. 35. Isoptera. Nastotermes darwiniensis Frog. Soldier.
Ventral.
- Fig. 36. Mantidae. Paratenodera sinensis Sauss. Ventral.
- Fig. 37. Acrididae. Dissosteira sp. Ventral.
- Fig. 38. Acrididae. Boopodon maculatus Caud. Ventral.
- Fig. 39. Acrididae. Radnotatus sp. Ventral.
- Fig. 40. Tettigidae. Tettigidea lateralis Say. Ventral.
- Fig. 41. Tettigoniidae. Neoconocephalus sp. Unguitractor
and empodium.
- Fig. 42. Tettigoniidae. Microcentrum rhombifolium Sauss.
Unguitractor and empodium.
- Fig. 43. Tettigoniidae. Amblycorypha rotundifolia Scud.
Unguitractor and empodium.

- Fig. 44. Stenopelmastidae. Geuthophilus maculatus Say. Unguitractor and empodium.
- Fig. 45. Stenopelmastidae. Stenopelmatus sp. Unguitractor and empodium.
- Fig. 46. Gryllotalpidae. Gryllotalpa borealis Burm. Unguitractor and empodium.
- Fig. 47. Gryllacridae. Gryllacris signifera Stoll. Ventral.
- Fig. 48. Gryllidae. Oecanthus sp. Ventral.
- Fig. 49. Gryllidae. Gryllus assimilis Fab. Ventral.
- Fig. 50. Tridactylidae. Tridactylus sp. Ventral.
- Fig. 51. Grylloblattidae. Grylloblatta sp. Unguitractor and empodium.
- Fig. 52. Cyliandrachetidae. Cyliandracheta sp. Ventral.
- Fig. 53. Hemimeridae. Hemimerus sp. Ventral.
- Fig. 54. Dermaptera. Paalis sp. Ventral.
- Fig. 55. Dermaptera. Anisolabis sp. Ventral.
- Fig. 56. Phasmodidae. Anisomorpha buprestoides Stoll. Ventral.
- Fig. 57. Perlidae. Perla isomarginata Say. Dorsal.
- Fig. 58. Perlidae. Perla isomarginata Say. Ventral.
- Fig. 59. Pteronarcidae. Pteronarcys dorsata Say. Nymph. Ventral.
- Fig. 60. Nemouridae. Taeniopteryx nivalis Fitch. Dorsal.
- Fig. 61. Nemouridae. Taeniopteryx nivalis Fitch. Ventral.
- Fig. 62. Capniidae. Allocaenella pygmaea Burm. Ventral.
- Fig. 63. Embioptera. Oligotoma sp. Ventral.
- Fig. 64. Embioptera. Oligotoma sp. Dorsal.
- Fig. 65. Embioptera. Oligotoma sp. Lateral.
- Fig. 66. Psocoptera. Myopsocus lugens Say. Ventral.
- Fig. 67. Psocoptera. Psocus sp. Lateral. (After DeMeijera)

- Fig. 68. Thysanoptera. Trichotarips angusticeps Hood. Lateral.
- Fig. 69. Fulgoridae. Cixius basalis V.D. Dorsal.
- Fig. 70. Fulgoridae. Cixius basalis V.D. Ventral.
- Fig. 71. Cercopidae. Aphrophora saratogensis Fitch. Dorsal.
- Fig. 72. Cercopidae. Aphrophora saratogensis Fitch. Ventral.
- Fig. 73. Cercopidae. Monocophora bicincta Say. Dorsal.
- Fig. 74. Cercopidae. Monocophora bicincta Say. Ventral.
- Fig. 75. Cicadidae. Tibicen canicularis Harr. Ventral.
- Fig. 76. Cicadidae. Tibicen canicularis Harr. Distal.
- Fig. 77. Aphididae. Brevicoryne brassicae L. Ventral.
- Fig. 78. Aphididae. Brevicoryne brassicae L. Lateral.
- Fig. 79. Aleoerodidae. Lialeurodes citri Ash. Lateral.
- Fig. 80. Coccidae. Pseudococcus trifolii Forbes. Lateral.
- Fig. 81. Anoplura. Pediculus capitis DeG. Lateral. (After Ockler)
- Fig. 82. Cicadellidae. Brachycephala mollipes Say. Ventral.
- Fig. 83. Cicadellidae. Graphocephala coccinea Forst. Ventral.
- Fig. 84. Cicadellidae. Agallia constricta V.D. Lateral.
- Fig. 85. Cicadellidae. Agallia constricta V.D. Ventral.
- Fig. 86. Membracidae. Tetanebronia amelopsideis Harr. Dorsal.
- Fig. 87. Membracidae. Tetanebronia amelopsideis Harr. Ventral.
- Fig. 88. Psyllidae. Psylla pyricola Foerst. Lateral.
- Fig. 89. Psyllidae. Psylla pyricola Foerst. Ventral.
- Fig. 90. Coreidae. Anasa tristis DeG. Lateral.
- Fig. 91. Coreidae. Anasa tristis DeG. Ventral.
- Fig. 92. Cydnidae. Galgula nitiduloides Wolff. Lateral.
- Fig. 93. Aradidae. Antrus inconstans Uhl. Lateral.

- Fig. 94. Miridae. Dicyphus agilis Uhl. Lateral.
- Fig. 95. Miridae. Miris dolabratus L. Lateral.
- Fig. 96. Miridae. Miris dolabratus L. Unguitractor and empodium.
- Fig. 97. Miridae. Capsus ater L. Ventral.
- Fig. 98. Reduviidae. Hannacerus purcis Drury. Ventral.
- Fig. 99. Phymatidae. Phymata erosa L. Ventral.
- Fig. 100. Cimicidae. Cimex lectularius L. Ventral.
- Fig. 101. Tingitidae. Corythocera sp. Lateral.
- Fig. 102. Nepidae. Ranatra kirkaldyi Bueno. Ventral.
- Fig. 103. Corixidae. Arctocoria sp. Ventral fore-leg.
- Fig. 104. Notonectidae. Notonecta lobata Hung. Ventral fore-leg.
- Fig. 105. Gerridae. Gerris sp. Unguitractor and empodium.
- Fig. 106. Gerridae. Gerris sp. Distitarsus, lateral.
- Fig. 107. Gelastocoridae. Gelastocoria sp. Prothoracic tarsus.
- Fig. 108. Gelastocoridae. Gelastocoria sp. Meso- and meta-thoracic tarsus.
- Fig. 109. Belostomatidae. Belostomatidae Belostomatidae Belostomatidae Say. Ventral.
- Fig. 110. Belostomatidae. Belostomatidae Belostomatidae Belostomatidae Say. Distal.
- Fig. 111. Cicindellidae. Tetracha carolina L. Unguitractor.
- Fig. 112. Cicindellidae. Cicindela formosa generosa Dej. Unguitractor.
- Fig. 113. Cicindellidae. Cicindela dorsalis Say. Unguitractor.
- Fig. 114. Cicindellidae. Cicindela purpurea Oliv. Unguitractor.
- Fig. 115. Cicindellidae. Cicindela sexguttata Fab. Unguitractor.

- Fig. 116. Carabidae. Carabus auratus Fab. Unguitractor.
- Fig. 117. Carabidae. Calosoma semilaeve Lec. Unguitractor.
- Fig. 118. Carabidae. Calosoma arcophanta L. Ventral.
- Fig. 119. Carabidae. Scarites subterraneus Fab. Unguitractor.
- Fig. 120. Carabidae. Picaelus purpuratus Mon. Unguitractor.
- Fig. 121. Carabidae. Chlaenius sp. Ventral.
- Fig. 122. Carabidae. Harpalus caliginosus Fab. Unguitractor.
- Fig. 123. Pyticidae. Pyticus verticalis Say. Unguitractor.
- Fig. 124. Gyrinidae. Dicentes sp. Unguitractor, prothoracic
tarsus.
- Fig. 125. Gyrinidae. Dicentes sp. Unguitractor, meso- and meta-
thoracic tarsus.
- Fig. 126. Hydrophilidae. Hydrous triangularis Say. ♂ Ventral.
Prothoracic tarsus.
- Fig. 127. Hydrophilidae. Hydrous triangularis Say. ♂
Ventral. Meso- and meta-thoracic tarsus.
- Fig. 128. Hydrophilidae. Tropisternus glaber Hbst. Unguitractor.
- Fig. 129. Silphidae. Silpha surinamensis Fab. Ventral.
- Fig. 130. Silphidae. Necrophorus americanus Oliv. Unguitractor.
- Fig. 131. Silphidae. Necrophorus sayi Lap. Unguitractor.
- Fig. 132. Silphidae. Necrophorus tomentosus Web. Unguitractor.
- Fig. 133. Staphylinidae. Creophilus maxillosus villosus Grav.
Unguitractor.
- Fig. 134. Staphylinidae. Staphylinus maculosus Grav.
Unguitractor.
- Fig. 135. Histeridae. Hister obtusatus Harris. Unguitractor.
- Fig. 136. Lycidae. Calopteron reticulatus Fab. Unguitractor.
- Fig. 137. Lycidae. Eros zureira Hbst. Unguitractor.

- Fig. 138. Phengodidae. Phengodes plumosa Oliv. Unguitractor.
- Fig. 139. Cantharidae. Chauliognathus pennsylvanicus DeG. Unguitractor.
- Fig. 140. Cantharidae. Cantharis consors Lec. Ventral.
- Fig. 141. Lampyridae. Lucidota atra Fab. Ventral.
- Fig. 142. Lampyridae. Photuris pennsylvanica DeG. Ventral.
- Fig. 143. Melyridae. Malochius aeneus L. Ventral.
- Fig. 144. Cleridae. Trichodes apivorus Germ. Unguitractor.
- Fig. 145. Corynetidae. Necrobia violacea L. Ventral.
- Fig. 146. Cephaloidae. Typitium unguare Lec. Ventral.
- Fig. 147. Cephaloidae. Cephaloon lepturides Newm. Ventral.
- Fig. 148. Cephaloidae. Cephaloon lepturides Newm. Lateral.
- Fig. 149. Cedemeridae. Nacerda melanura L. Ventral.
- Fig. 150. Mordellidae. Mordellistena sp. Ventral.
- Fig. 151. Mordellidae. Anaspis rufa Say. Unguitractor.
- Fig. 152. Rhipiphoridae. Rhipiphorus stylopides Newm. Ventral.
- Fig. 153. Meloidae. Pomphopoea sayi Lec. Ventral.
- Fig. 154. Meloidae. Epicauta lemniscata Fab. Unguitractor.
- Fig. 155. Meloidae. Macrobasis albida Say. Unguitractor.
- Fig. 156. Meloidae. Hemognatha lutea Lec. Ventral.
- Fig. 157. Meloidae. Tricrania sanguinipennis Say. Unguitractor.
- Fig. 158. Pythidae. Pytho niger Kby. Unguitractor.
- Fig. 159. Pyrochroidae. Dendroides bicolor Newm. Unguitractor.
- Fig. 160. Pedilidae. Pedilus collaris Say. Unguitractor.
- Fig. 161. Elateridae. Alaus oculatus L. Unguitractor.
- Fig. 162. Elateridae. Ludius pyrrhus Hbst. Unguitractor.

- Fig. 162. Buprestidae. Hippodamia spherica Lec. Ventral.
- Fig. 164. Buprestidae. Chalcophora virginianensis Brery. Ventral.
- Fig. 165. Dryopidae. Dryops productus Lec. Unguitractor.
- Fig. 166. Dermestidae. Dermestes vulpinus Fab. Unguitractor.
- Fig. 167. Byrrhidae. Byrrhus americanus Lec. Unguitractor.
- Fig. 168. Ostomidae. Temnochila virescens Say. Unguitractor.
- Fig. 169. Nitidulidae. Glischrochilus obtusus Say. Unguitractor.
- Fig. 170. Cucujidae. Cucujus clavipes Fab. Ventral.
- Fig. 171. Protylidae. Megalodacne fasciata Fab. Ventral.
- Fig. 172. Endomychidae. Lycoperdina sp. Unguitractor.
- Fig. 173. Coccinellidae. Coccinella novemnotata Hbst.
Unguitractor.
- Fig. 174. Coccinellidae. Epilachna corrupta Guls. Ventral.
- Fig. 175. Alleculidae. Isosira quadristriata Couper.
Unguitractor.
- Fig. 176. Tenebrionidae. Philosodes diabolicus Lec.
Unguitractor.
- Fig. 177. Tenebrionidae. Rheodes armata Lec. Unguitractor.
- Fig. 178. Tenebrionidae. Alobates pennsylvanica Deg.
Unguitractor.
- Fig. 179. Tenebrionidae. Tarpeia micans Fab. Unguitractor.
- Fig. 180. Lagriidae. Arthronacra senae Ant. Unguitractor.
- Fig. 181. Melandryidae. Penthe obliquata Fab. Unguitractor.
- Fig. 182. Ptinidae. Mazius americanus Lap. Unguitractor.
- Fig. 183. Bostrichidae. Polycnon stenti Lec. Unguitractor.
- Fig. 184. Scarabaeidae. Copris tullius Oliv. Ventral.
- Fig. 185. Scarabaeidae. Phyllophaga sp. Ventral.
- Fig. 186. Scarabaeidae. Popillia japonica Newm. Unguitractor.

- Fig. 187. Scarabaeidae. Oanozema scabra Beauv. Ventral.
Fig. 188. Scarabaeidae. Dynastes sp. Unguitractor.
Fig. 189. Scarabaeidae. Dynastes sp. Unguitractor.
Fig. 190. Lucanidae. Pseudolucanus capreolus L. Ventral.
Fig. 191. Passalidae. Passalus cornutus Fab. Unguitractor.
Fig. 192. Cerambycidae. Derobrachus brunneus Forst. Unguitractor.
Fig. 193. Cerambycidae. Prionus laticollis Drury. Unguitractor.
Fig. 194. Cerambycidae. Glycobius speciosus Say. Ventral.
Fig. 195. Cerambycidae. Monochamus scutellatus Say. Unguitractor.
Fig. 196. Cerambycidae. Monilemma gigas Lec. Unguitractor.
Fig. 197. Cerambycidae. Tetraopes collaris Horn. Unguitractor.
Fig. 198. Chrysomelidae. Labidomera olivicollis Mby.
Unguitractor.
Fig. 199. Chrysomelidae. Calligrapha lunata Fab. Unguitractor.
Fig. 200. Chrysomelidae. Chelymorpha cassidea Fab. Ventral.
Fig. 201. Mylabridae. Mylabris isorus L. Ventral.
Fig. 202. Brentidae. Eupsalis minuta Drury. Unguitractor.
Fig. 203. Platystosidae. Euparius marmoratus Oliv. Unguitractor.
Fig. 204. Belidae. Ithycerus novaboracensis Forst. Unguitractor.
Fig. 205. Curculionidae. Brachyrhinus sulcatus Fab. Unguitractor.
Fig. 206. Curculionidae. Brachyrhinus sulcatus Fab. Lateral.
Fig. 207. Curculionidae. Hyllobius pales Bon. Unguitractor.
Fig. 208. Curculionidae. Lixus concavus Say. Ventral.
Fig. 209. Sychophoridae. Metamsius sericeus Latr. Ventral.
Fig. 210. Scolytidae. Dendroctonus valens Lec. Ventral.
Fig. 211. Gialidae. Corydalis cornuta L. Ventral.

- Fig. 212. Sialidae. Chauliodes sp. Ventral.
- Fig. 213. Raphidiidae. Raphidia oblita Hagen. Ventral.
- Fig. 214. Ascalaphidae. Ululodes sp. Unguitractor.
- Fig. 215. Myrmeleonidae. Myrmeleon sp. Ventral.
- Fig. 216. Nemepteridae. Croce sp. Ventral.
- Fig. 217. Coniopterygidae. Coniopteryx sp. Ventral.
- Fig. 218. Ithonidae. Ithone sp. Ventral.
- Fig. 219. Mantispidae. Mantissa brunnea Say. Ventral.
- Fig. 220. Mantispidae. Mantissa brunnea Say. Dorsal.
- Fig. 221. Hemerobiidae. Boriomyia longifrons Walk. Ventral.
- Fig. 222. Hemerobiidae. Hemerobius stigmaterus Fitch. Ventral.
- Fig. 223. Hemerobiidae. Hemerobius stigmaterus Fitch. Dorsal.
- Fig. 224. Polystoechotidae. Polystoechotes punctatus Fab.
Ventral.
- Fig. 225. Gysyridae. Climaciella sp. Ventral.
- Fig. 226. Chrysopidae. Chrysopa sp. Ventral.
- Fig. 227. Chrysopidae. Chrysopa sp. Dorsal.
- Fig. 228. Chrysopidae. Chrysopa sp. Claw, lateral.
- Fig. 229. Panorpidae. Bittacus sp. Ventral.
- Fig. 230. Panorpidae. Panorpa rufescens Ramb. Ventral.
- Fig. 231. Panorpidae. Boreus sp. Ventral.
- Fig. 232. Tanyderidae. Protoplasa fitchii O.S. Ventral.
- Fig. 233. Ptychopteridae. Ptychoptera rufocincta O.S. Lateral.
- Fig. 234. Ptychopteridae. Bittacomorpha clavipes Fab. Ventral.
- Fig. 235. Trichoceridae. Trichocera garretti Alex. Ventral.
- Fig. 236. Tipulidae. Cylindrotoma americana O.S. Ventral.
- Fig. 237. Tipulidae. Tricyphona constans Doane. Ventral.

- Fig. 238. Tipulidae. Tipula abdominalis Say. Ventral.
- Fig. 239. Tipulidae. Pedicia contermina Walk. Dorsal.
- Fig. 240. Tipulidae. Pedicia contermina Walk. Ventral.
- Fig. 241. Tipulidae. Gtenophora apicata O.S. Dorsal.
- Fig. 242. Tipulidae. Gtenophora apicata O.S. Ventral.
- Fig. 243. Tipulidae. Gtenophora apicata O.S. Lateral.
- Fig. 244. Tipulidae. Clytocosmus helmsi Skuse. Ventral.
- Fig. 245. Tipulidae. Clytocosmus helmsi Skuse. Lateral.
- Fig. 246. Tipulidae. Limonia sciophila O.S. Ventral.
- Fig. 247. Anisopidae. Anisopus sp. Dorsal.
- Fig. 248. Anisopidae. Anisopus sp. Ventral.
- Fig. 249. Anisopidae. Anisopus sp. Lateral.
- Fig. 250. Simuliidae. Simulium sp. Ventral.
- Fig. 251. Simuliidae. Simulium sp. Lateral.
- Fig. 252. Chironomidae. Chironomus ferrugineo-vittatus Zett.
Ventral.
- Fig. 253. Culicidae. Psorophora ciliata Fab. Ventral.
- Fig. 254. Culicidae. Psorophora ciliata Fab. Lateral.
- Fig. 255. Anisopidae. Anisopus fenestralis Loep. Ventral.
(After DeMeijere)
- Fig. 256. Bibionidae. Aspistes berolinensis Meig. Ventral.
(After DeMeijere)
- Fig. 257. Bibionidae. Bibio sp. Ventral.
- Fig. 258. Bibionidae. Bibio sp. Lateral.
- Fig. 259. Mycetophilidae. Leptomorphus sp. Ventral.
- Fig. 260. Mycetophilidae. Mycetophila fungorum DeG. Lateral.

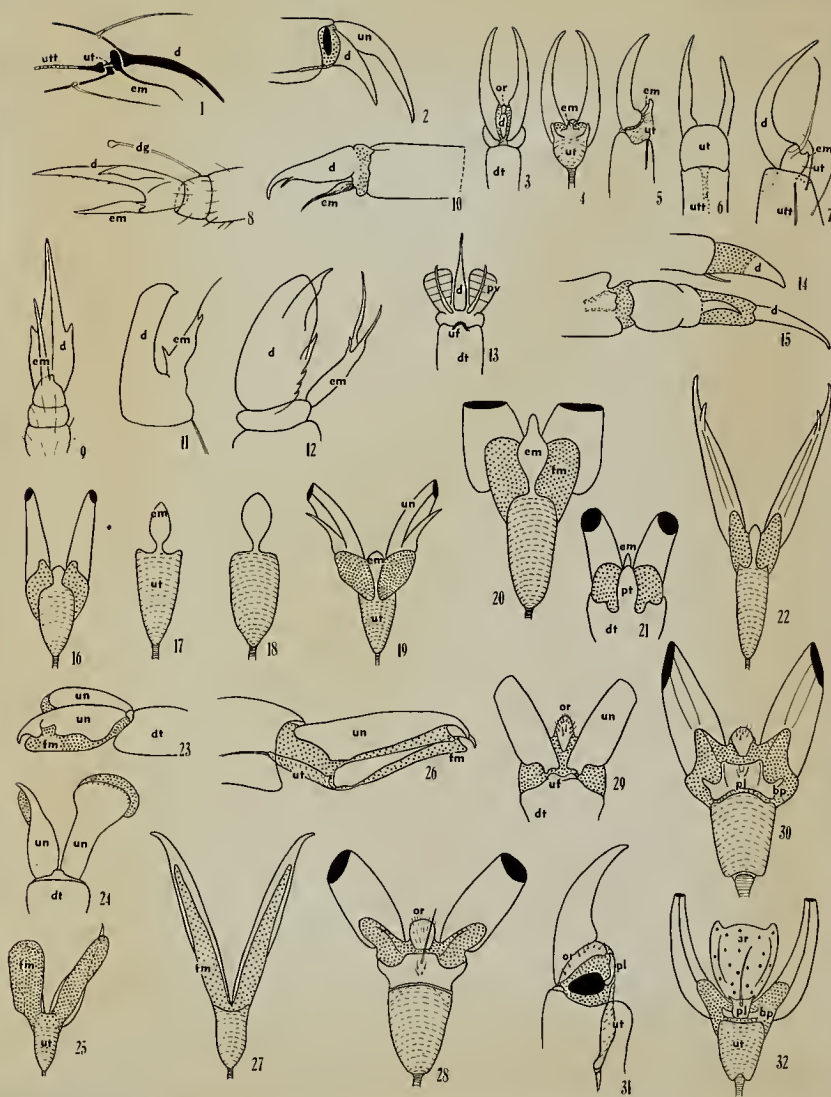
- Fig. 261. Mycetophilidae. Mycetophila fungorum Des. Ventral.
Fig. 262. Mycetophilidae. Sciara thomae L. Ventral.
(After DeMeijere)
Fig. 263. Cecidomyiidae. Cecidomyia rosaria Low. Ventral.
(After DeMeijere)
Fig. 264. Stratiomyidae. Stratiomyia badia Loew. Lateral.
Fig. 265. Xylophagidae. Xylophagus reflectens Walk. Lateral.
Fig. 266. Xylophagidae. Xylophagus reflectens Walk. Dorsal.
Fig. 267. Coenomyiidae. Coenomyia pallida Say. Lateral.
Fig. 268. Coenomyiidae. Coenomyia pallida Say. Ventral.
Fig. 269. Acroceratidae. Oncodes sp. Dorsal.
Fig. 270. Acroceratidae. Oncodes sp. Lateral.
Fig. 271. Acroceratidae. Oncodes sp. Ventral.
Fig. 272. Bombyliidae. Exoprosopa sp. Lateral.
Fig. 273. Bombyliidae. Exoprosopa sp. Ventral.
Fig. 274. Asilidae. Plectria baumhaueri Meig. Ventral.
Fig. 275. Asilidae. Plectria baumhaueri Meig. Lateral.
Fig. 276. Hydalidae. Hydas sp. Unguitractor.
Fig. 277. Empidae. Rhamphomyia sp. Unguitractor.
Fig. 278. Dolichopodidae. Liancalus sp. Ventral.
Fig. 279. Empidae. Cyrtoma saurium Fall. Ventral. (After
DeMeijere)
Fig. 280. Dolichopodidae. Dolichopus sp. Ventral.
Fig. 281. Dolichopodidae. Dolichopus sp. Lateral.
Fig. 282. Lonchopteridae. Lonchoptera lutea Panz. Ventral.
(after DeMeijere)
Fig. 283. Phoridae. Phora sp. Ventral.

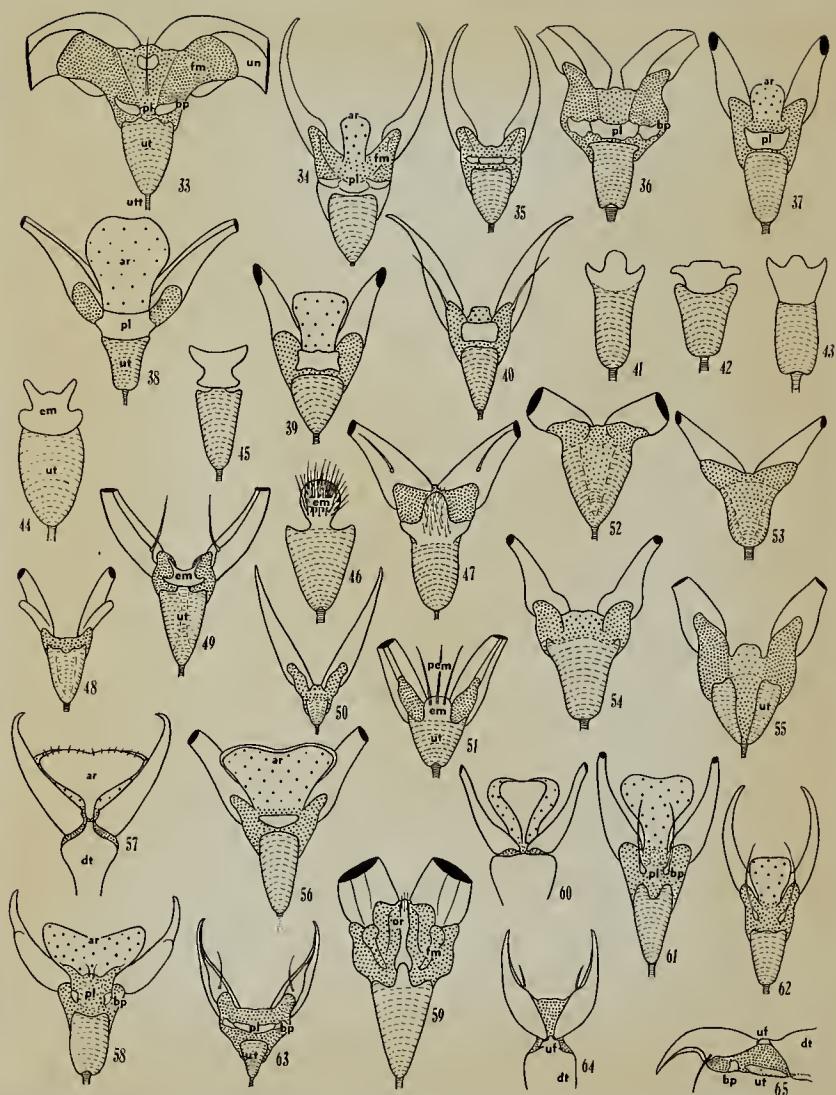
- Fig. 284. Syrphidae. Eristalis tenax L. Unguitractor.
- Fig. 285. Tachinidae. Tachina sp. Unguitractor.
- Fig. 286. Sarcophagidae. Sarcophaga sp. Ventral.
- Fig. 287. Muscidae. Muscina pascuorum Meig. Unguitractor.
- Fig. 288. Gastrophilidae. Gastrophilus equi Clark. Unguitractor.
- Fig. 289. Tetanoceridae. Tetanocera plebeja Loew. Unguitractor.
- Fig. 290. Ortalidae. Camptoneura sp. Ventral.
- Fig. 291. Hippoboscidae. Lynchia americana Leach. Lateral.
- Fig. 292. Hippoboscidae. Lynchia americana Leach. Dorsal.
- Fig. 293. Hippoboscidae. Lynchia americana Leach. Ventral.
- Fig. 294. Diagrammatic representation of various types of dipterous empodium. A-J ventral. K-P lateral.
- Fig. 295. Phryganidae. Ptilostomis postica Walk. Ventral.
- Fig. 296. Phryganidae. Ptilostomis postica Walk. Dorsal.
- Fig. 297. Lianophilidae. Allegophylax subfasciata Say. Ventral.
- Fig. 298. Micropterygidae. Mnenonica sp. Ventral.
- Fig. 299. Hapialidae. Hapialus sp. Ventral.
- Fig. 300. Hapialidae. Leto stacyi Sc. Ventral.
- Fig. 301. Cossidae. Cossus macurtreii Peale. Dorsal.
- Fig. 302. Cossidae. Cossus macurtreii Peale. Ventral.
- Fig. 303. Mimallonidae. Cicinnus holshuiseri Harris. Ventral.
- Fig. 304. Tortricidae. Archips rosaceana Harris. Ventral.
- Fig. 305. Pyralididae. Galleria sp. Dorsal.
- Fig. 306. Pyralididae. Galleria sp. Ventral.
- Fig. 307. Saturniidae. Tropaea luna L. Dorsal.
- Fig. 308. Saturniidae. Tropaea luna L. Lateral.
- Fig. 309. Saturniidae. Tropaea luna L. Ventral.

- Fig. 310. Geometridae. Brephos infans Mosch. Ventral.
- Fig. 311. Sphingidae. Hemaris thysbe Fab. Ventral.
- Fig. 312. Sphingidae. Pholus satellitia pandorus Hbn. Ventral.
- Fig. 313. Sphingidae. Pholus satellitia pandorus Hbn. Dorsal.
- Fig. 314. Sphingidae. Pholus satellitia pandorus Hbn. Lateral.
- Fig. 315. Sphingidae. Sphinx chersis Hbn. Ventral.
- Fig. 316. Sphingidae. Sphinx chersis Hbn. Lateral.
- Fig. 317. Aegeriidae. Melittia satyriniformis Hbn. Ventral.
- Fig. 318. Noctuidae. Trebus odora L. Ventral and pulvillus.
- Fig. 319. Arctiidae. Apantesis virgo Linn. Ventral.
- Fig. 320. Arctiidae. Apantesis virgo Linn. Dorsal.
- Fig. 321. Hesperiidae. Spargyreus tityrus Fab. Ventral.
- Fig. 322. Hesperiidae. Spargyreus tityrus Fab. Dorsal, with
claw and pulvillus.
- Fig. 323. Pieridae. Callidryas eubula Boisd. Dorsal.
- Fig. 324. Pieridae. Callidryas eubula Boisd. Ventral.
- Fig. 325. Pieridae. Colias philodice Lat. Ventral.
- Fig. 326. Papilionidae. Papilio glaucus L. Ventral.
- Fig. 327. Nymphalidae. Aglais antiopa L. Ventral.
- Fig. 328. Xyelidae. Macroxyla sp. Dorsal.
- Fig. 329. Xyelidae. Macroxyla sp. Ventral.
- Fig. 330. Pamphiliidae. Neurotoma sp. Dorsal.
- Fig. 331. Xiphyriidae. Xiphyria canadensis Prov. Ventral.
- Fig. 332. Siricidae. Tremex columba L. Dorsal.
- Fig. 333. Siricidae. Tremex columba L. Ventral.
- Fig. 334. Siricidae. Tremex columba L. Lateral.

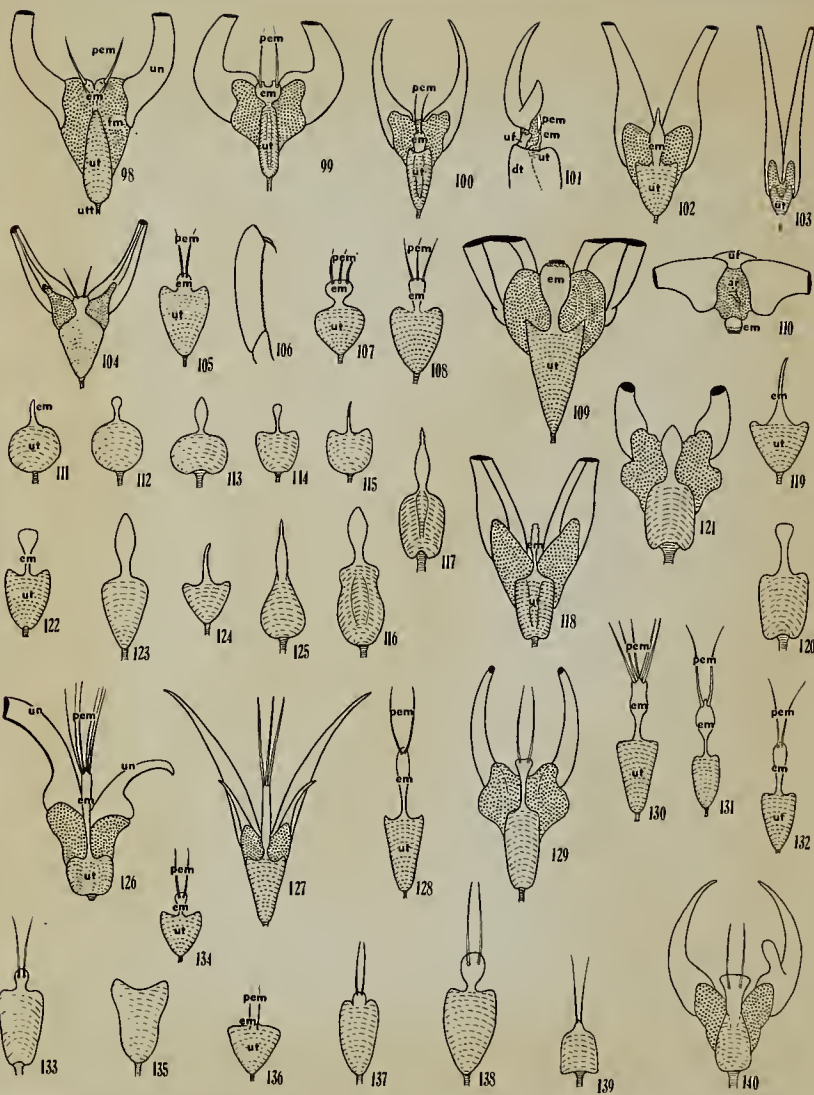
- Fig. 335. Crabronidae. Crabro americana Lach. Ventral.
- Fig. 336. Diprionidae. Diprion lacontel Fitch. Dorsal.
- Fig. 337. Diprionidae. Diprion lacontel Fitch. Ventral.
- Fig. 338. Cryssidae. Cryssus sayi West. Ventral.
- Fig. 339. Cryssidae. Cryssus sayi West. Dorsal.
- Fig. 340. Braconidae. Microcentrus uniformis Prov. Ventral.
- Fig. 341. Ichneumonidae. Opheltes sp. Dorsal.
- Fig. 342. Ichneumonidae. Opheltes sp. Ventral.
- Fig. 343. Aulacidae. Plantariacus abdominalis Cress. Dorsal.
- Fig. 344. Peleciidae. Pelecinus polyturator Emery. Ventral.
- Fig. 345. Cynipidae. Ibalia maculipennis Halic. Ventral.
- Fig. 346. Psammocharidae. Ceropales bipunctata Say. Dorsal.
- Fig. 347. Psammocharidae. Ceropales bipunctata Say. Ventral.
- Fig. 348. Psammocharidae. Ceropales bipunctata Say. Claw 1 and 2.
- Fig. 349. Psammocharidae. Ceropales bipunctata Say. Claw 3.
- Fig. 350. Chrysididae. Chrysis sp. Ventral.
- Fig. 351. Mutillidae. Dasymutilla occidentalis L. Ventral.
- Fig. 352. Scolidae. Scolia sp. Ventral.
- Fig. 353. Scolidae. Campomeris ephippium Say. Dorsal.
- Fig. 354. Scolidae. Campomeris ephippium Say. Orbicula, ventral view.
- Fig. 355. Scolidae. Campomeris ephippium Say. Ventral.
- Fig. 356. Scolidae. Campomeris ephippium Say. Lateral.
- Fig. 357. Formicidae. Myrmica scabrinodis senencki Forel. Dorsal.
- Fig. 358. Formicidae. Formyrmex parvicornis niger Pers. Ventral.
- Fig. 359. Formicidae. Camponotus larculeus pennsylvanicus Halic. Ventral.

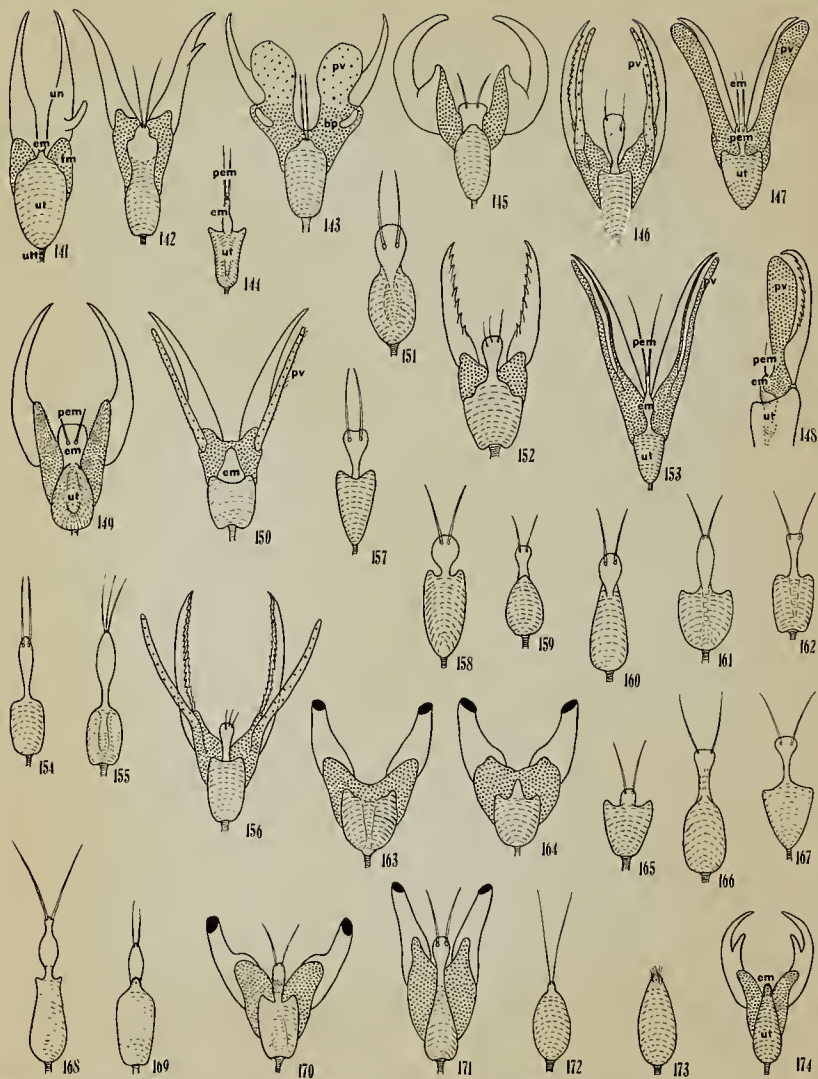
- Fig. 360. Vespidae. Monobia sp. Ventral.
- Fig. 361. Vespidae. Polistes sp. Ventral.
- Fig. 362. Sphecidae. Tachytes distinctus Smith. Dorsal.
- Fig. 363. Sphecidae. Tachytes distinctus Smith. Ventral.
- Fig. 364. Sphecidae. Philanthus solivagus Say. Ventral.
- Fig. 365. Sphecidae. Bembex spinolae Lep. Dorsal.
- Fig. 366. Sphecidae. Bembex spinolae Lep. Ventral.
- Fig. 367. Hylaeidae. Colletes inaequalis Say. Ventral.
- Fig. 368. Andrenidae. Halictus radiatus Say. Ventral and orbicula.
- Fig. 369. Andrenidae. Nomada sp. Orbicula.
- Fig. 370. Andrenidae. Hellisodas desponsa Smith. Dorsal.
- Fig. 371. Andrenidae. Hellisodas desponsa Smith. Ventral.
- Fig. 372. Andrenidae. Xylocopa mordax Smith. Ventral.
- Fig. 373. Andrenidae. Xylocopa mordax Smith. Dorsal.
- Fig. 374. Andrenidae. Xylocopa mordax Smith. Lateral.
- Fig. 375. Megachilidae. Megachile sp. Dorsal.
- Fig. 376. Megachilidae. Megachile sp. Lateral.
- Fig. 377. Megachilidae. Megachile sp. Ventral.
- Fig. 378. Bombidae. Bombus sp. Dorsal.
- Fig. 379. Bombidae. Bombus sp. Lateral.
- Fig. 380. Bombidae. Bombus sp. Ventral.



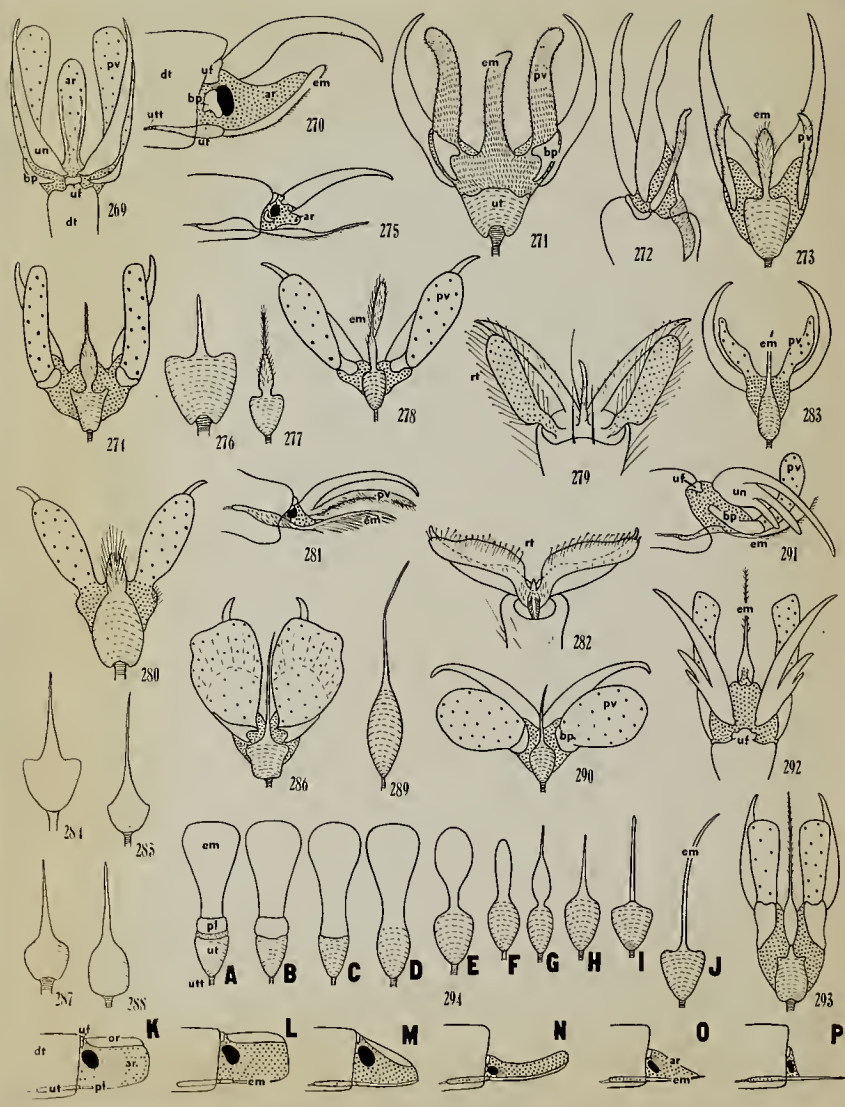


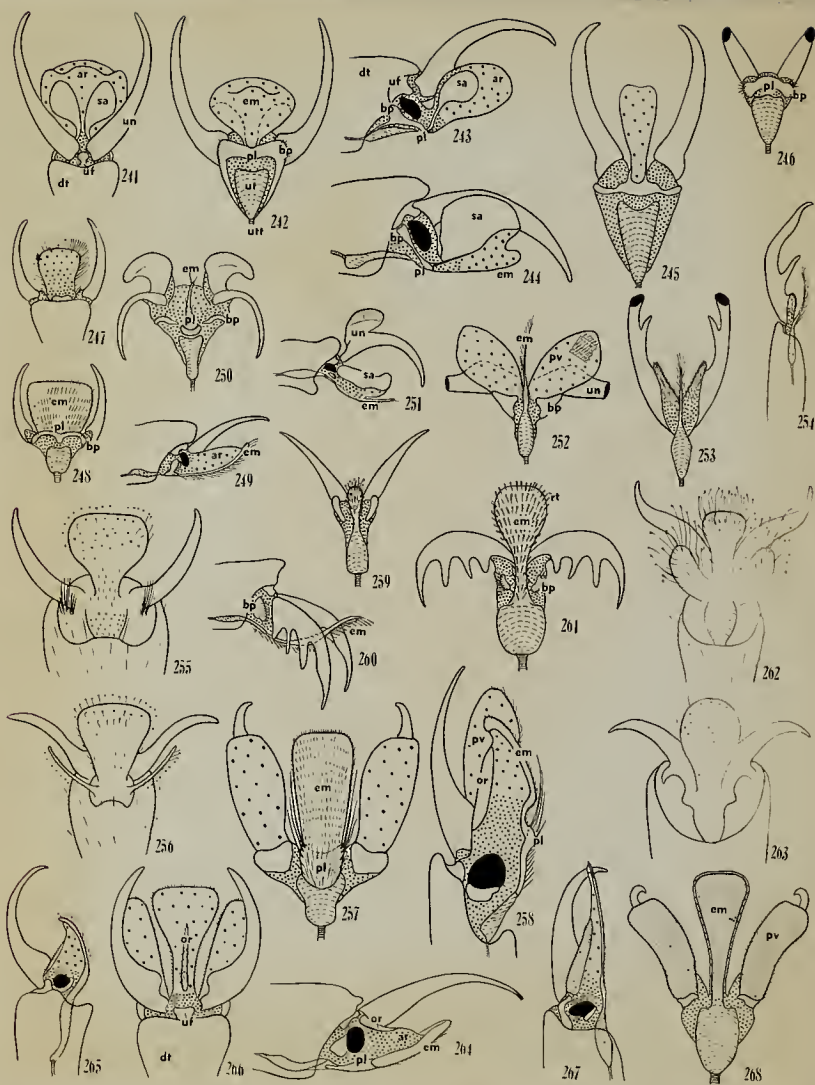




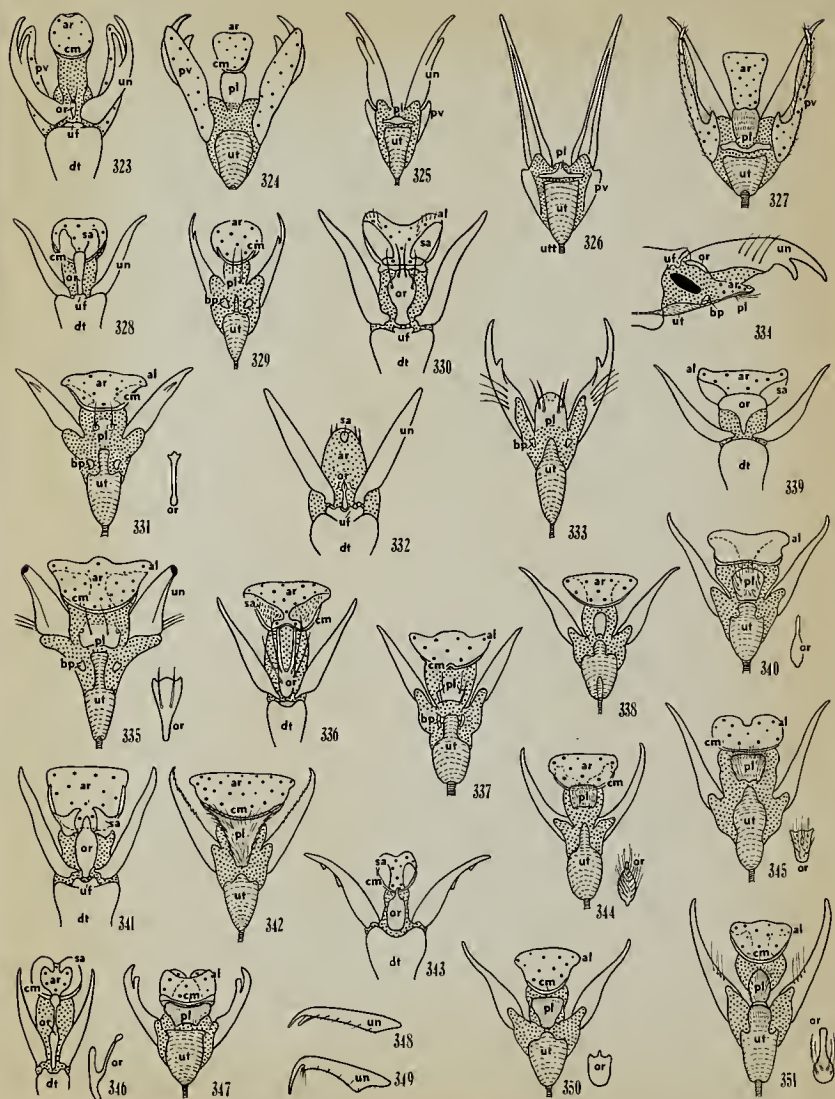


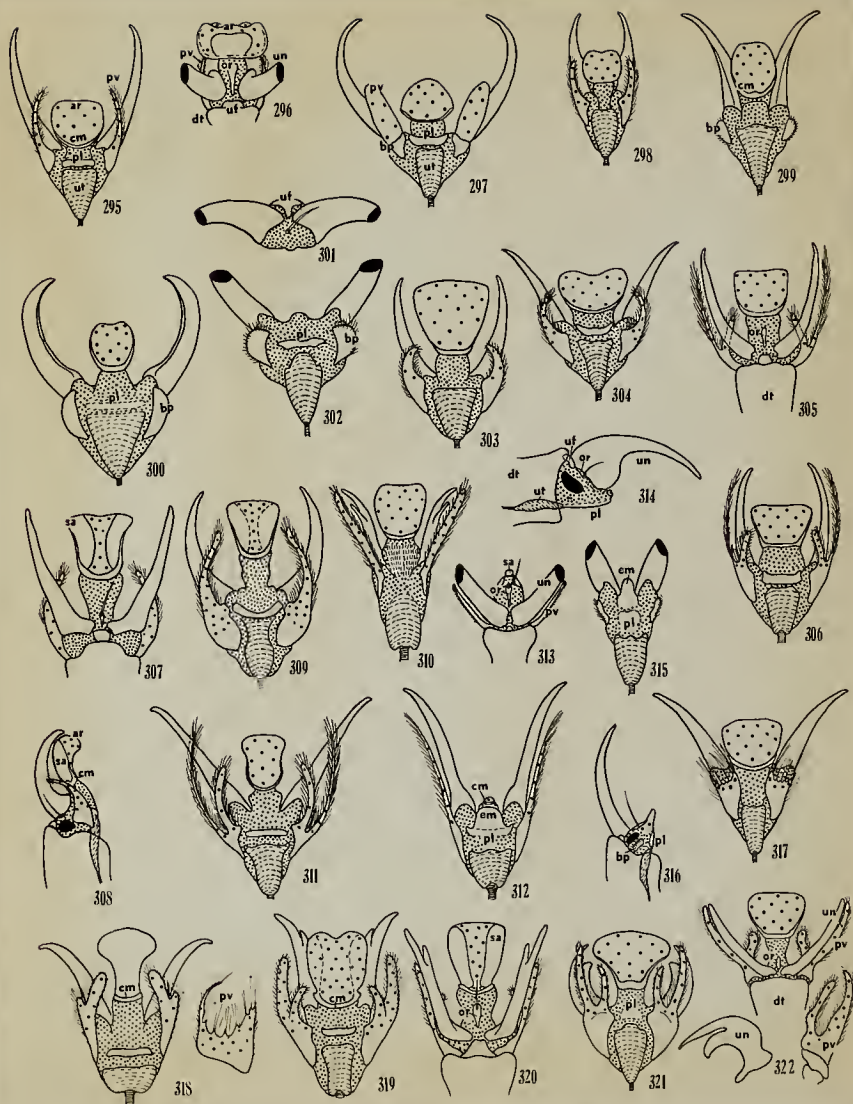


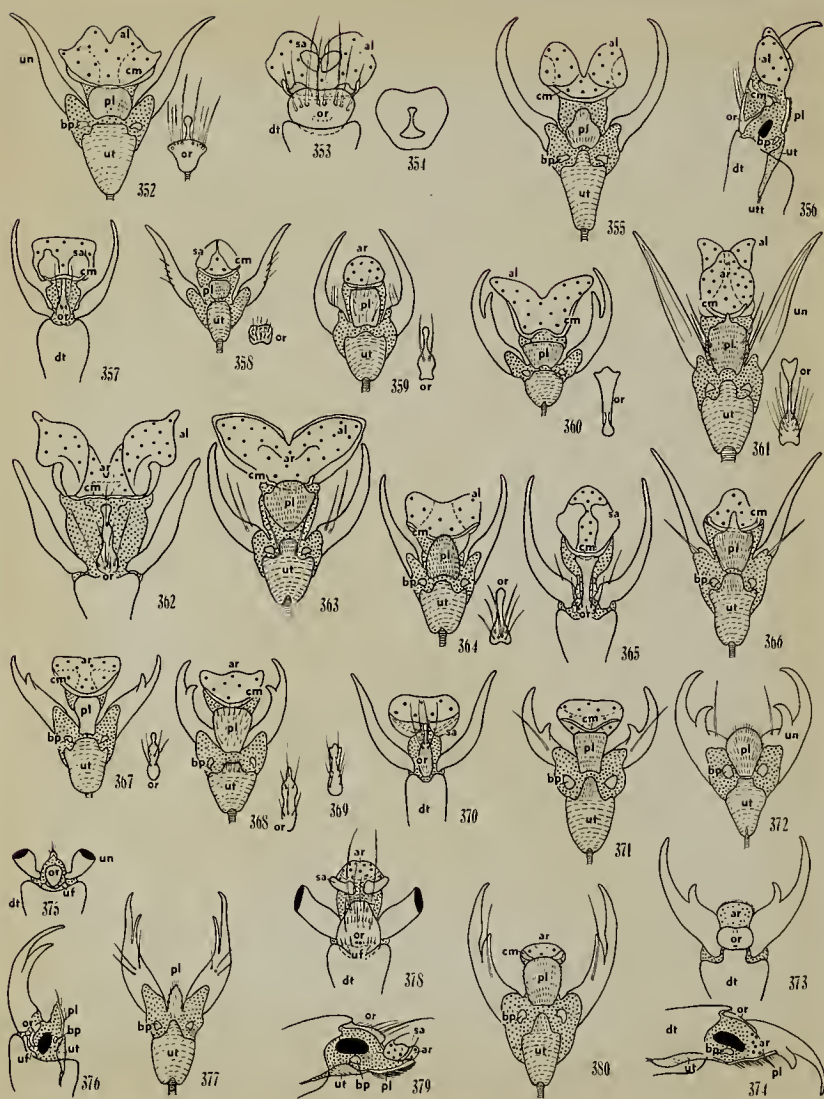












Approved

William Doran

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Date June 4, 1937

