MORPHOLOGY OF THE COLEOPTEROUS FAMILY STAPHYLINIDAE

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CONTENTS

INTRODUCTION

One of the chief justifications for the study of the morphology of any group of organisms is the importance of this branch of the science in the classification of those organisms. Morphology is one of the important foundations of classification because it supplies the easiest and most usable key to the relationships between individuals. The discovery and evaluation of these relationships is an important part of our attempts at classification.

The purpose of such a morphological study as this may be stated as follows: In the first place, it is an attempt to increase the knowledge of the external morphology of the Staphylinidae as a basis for a better understanding of their classification. It is furthermore an attempt to add something to the knowledge of the morphology of beetles in general. This very large and important field has been so poorly explored up to the present time that any attempts to make additions are not only justified but very much to be desired.

In any very large group of animals the number of species whose morphology can be investigated in detail is necessarily limited by considerations of time and expense of publication. Any conclusions drawn from the comparatively few representatives examined must necessarily be only tentative and suggestive, and they must await the less detailed examination of the numerous other species for confirmation.

The large order Coleoptera is one of the best known of all the groups of insects. One of the largest included families is the Staphylinidae, containing approximately one-tenth of all the known species of beetles. The study of this family, however, has been relatively neglected and the list of known species probably does not include one-fifth of those actually in existence, and even from North America it is doubtful if over one-half the species have been recorded. This condition is due to the difficulties which attend the study of this family when it is carried on by the methods formerly employed by many entomologists—methods which fail to provide an adequate knowledge of the comparative morphology of the group. These difficulties vanish in large part when the study is approached in the right manner.

To a student of the Coleoptera desiring to undertake a comparative morphological study of some group as a basis for its classification, the family Staphylinidae has much to commend it. It is sufficiently large to show a wide range of structure; the total number of species is large enough to provide ample material for the full development of one's ideas of the principles of classification; a great number of its members are common enough to be very easily obtained; the ma-

jority of specimens are small enough to be suited to examination with the compound microscope; and, not the least, very little has been known of its fundamental structure and relationships.

The present study deals with a family which contains nearly 20,000 known species. The fact that it would be impossible to study all of these in detail is a very potent additional reason for studying a few representatives as well as possible with the goal of establishing a foundation and working outline of the external morphology which can later be used to support a classification or which may be tested and enlarged by further investigations on additional material.

It gives me pleasure gratefully to acknowledge the help and encouragement of Prof. G. F. Ferris, under whom this study has been carried out. I am also much indebted to R. E. Snodgrass, who has read the manuscript and given many very helpful suggestions.

The Literature on the Staphylinidae

In a brief review of the literature relating to the family Staphylinidae it is not necessary to go back beyond the works of Erichson in 1839 and 1840. Previous to his time most of the work done was a bare description of new genera and species. In the " Käfer der Mark Brandenburg " in 1839 Erichson began the studies that resulted the following year in his masterly volume " Genera et Species Staphylinorum ". This work contains a fairly complete classification of the family, with keys to genera, and descriptions of all species known at that time. It is undoubtedly one of the masterpieces of early systematic entomology.

From the time of Erichson there has been a continual stream of descriptions of new genera and species, published in many languages and in hundreds of different periodicals. Many of the most important studies of the staphylinids have been made in connection with large faunal monographs. But by far the largest part of the information published concerning this family has never been assembled in any way, with the one exception of the bibliographic catalogue in the publication of Junk and Schenkling, the " Coleopterorum Catalogus ". The student finds it necessary continually to go to the original publications, and he finds many of the keys for identification unsatisfactory or incomplete.

Any knowledge of the morphology of this family is exceedingly difficult to obtain from the literature. Most of the discussions are restricted to a certain species or to a certain group of structures on that species. Practically no real comparative study has been made of even

one set of characters, the only possible exception to this being the work of Eichelbaum and of Sharp and Muir on the genitalia.

MATERIAL

The material available for this study includes chiefly specimens from North America supplemented by additional ones from Central America and Europe. Wherever possible one of the common species was selected.

Eichelbaum (1909) listed 15 subfamilies of the Staphylinidae. In these he recognized 43 tribal groups. The present study includes representatives of 10 subfamilies and 25 tribes. The subfamilies of which representatives were not available are: Megalopinae, Lepto-typhlinae, Euaesthetinae, Trichophyinae, and Cephaloplectinae. Besides these, the tribes not represented include: Neophonini, Apateticini, Platyprosopini, Pygostenini, Trichopseniini, Deinopsini, Gymnusini, Myllaenini, Pronomaeini, Diglottini, Hygronomini, and Digrammini.

The species selected in each tribe are not considered as actual representatives or types but merely as members of that group and examples of it. In several cases more than one species has been used within a tribe because of the great variation in certain characters, but lack of time and space has prevented the further extension of the list.

It is very much to be regretted that members of the subfamily Aleocharinae are so difficult of identification while so abundant everywhere. Only the larger tribes are represented in this material, and this means that the aberrant and unusual forms have not been studied or included in the comparisons.

All the American species were identified by the writer. Most of the European species were obtained from Emmerich Reitter of Vienna.

PREPARATION OF MATERIAL

The preparation of material so that it can be adequately studied is one of the most important steps in the solution of any systematic problem. In the treatment of the specimens first consideration should be given to the making available of all characters which might be of value in the study. How far this ideal is from the condition actually attained in much systematic work has been discussed at length by Ferris (1928), and a similar inadequacy is often shown in morphological studies.

Three general means of mounting and preservation have been em-
ployed by entomologists. These are: On pins, in fluid such as alcohol,
and on microscope slides. According to Chamberlin (1931):

It may be said that the important thing in the preparation of material for
study is not the following of any particular set method, but rather the treatment
of material in such a way that the structures which it is necessary to employ
in systematic work (that is, those structures, regardless of size or obscurity,
which the study of comparative morphology shows to be significant for such
purposes) shall be rendered clearly visible.

In no group of insects will either of the first two methods alone
suffice to this end, and in all of the groups of minute insects the slide
preparations, supplemented in certain cases by the other methods,
have unquestionably proved to give not merely better results but the
only reasonably complete and satisfactory ones.

The Staphylinidae may properly be regarded as a group of minute
insects, as only a comparatively small percentage of them exceed 8 mm
in length, and the average length is probably below 5 mm. The actual
size ranges from slightly over 5 cm down to less than 1 mm.

The usual methods of mounting small beetles on pins and paper
points permit an examination of only the larger and more obvious
characters, and is utterly useless in any detailed study of the mor-
phology. It is essential in this type of work that the separate elements
of the body wall be carefully dissected and perhaps examined with
transmitted light, and this requires a considerable preparation of the
material.

The method of preparation worked out for the present study is
outlined below. It is a modification of the practice generally employed
in the study of minute insects such as scale insects and lice.

Because of the methods used in the past in the examination and
description of species and the establishment of classifications, it is
impossible to correlate with the literature identifications in the Staphy-
linidae made from slide preparations. For this reason specimens
should first be mounted on fine paper points on pins in the usual
manner and identified as accurately as possible using all available aids.

The special technique is as follows: The specimen is dropped into
a 10 percent solution of KOH and heated to near the boiling point
for about half a minute. This is to soften the body sufficiently to
prevent breakage when the elytra and wings are dissected off, which
is done by removing the specimen to water in a watch glass and work-
ing under the binocular microscope with fine dissecting needles. The
abdomen is now dissected away behind the metasternum, the head
separated from the prothorax, and the prothorax from the remainder

of the thorax. These four parts of the body are replaced in the KOH and allowed to boil gently for about one minute. The elytra and wings are transferred from the water to 95 percent alcohol for several minutes and then mounted as described below. After boiling the body, it is removed again to water, where the disintegrated viscera may be pressed out and the antennae, mouthparts, legs, and genitalia dissected off. If any of these parts (notably the head and thorax) are too heavily pigmented to permit easy study with transmitted light they should now be placed in a 3 percent solution of hydrogen peroxide to which has been added a small amount of ammonia (about one drop per cm³ of peroxide). It is essential that fresh ammonia be used and that the mixture be not allowed to stand before using. It quickly loses its efficacy after being mixed. Two to six hours in this solution will suffice to bleach the darkest sclerites, and this treatment has the great advantage of leaving the edges and sutures darker than the rest. These parts are now placed again in the boiling KOH for a few seconds to remove the peroxide and are then returned to the water to remove the KOH. Now all parts are transferred to alcohol for several minutes and then mounted. The most satisfactory mounting medium known to me is euparal. (This can be obtained at a considerably reduced price under the name of Diaphane.) Specimens are arranged in a drop of the medium on the slide and a cover glass gently pressed down until all surplus medium is squeezed out. If necessary the cover glass may be supported by means of paper rings, which prevent the flattening and consequent distortion of the objects. The slides are then labeled and dried for two or three days.

Material prepared in this way has a few disadvantages. The parts can be studied only in the position in which they are mounted. The color and general shape or habitus of the insect is lost in large measure. But these are much more than offset by the ease of examination under the compound microscope and the fact that one can approach the ideal of being able to see and use all of the characters that are actually present on the body of the beetle.

Illustrations

The illustrations, which form an important part of this study, are intended to serve primarily two purposes. First, they illustrate the detailed anatomy of a typical staphylinid, together with that of other special structures found only on other species; and second, they illustrate briefly the variations within the family of each of the structures treated. They have been prepared with these two aims in mind,

and the figures showing variation have for the most part not been burdened with interpretations of structure. It is believed that this latter will be obvious upon comparison with the morphological figures. As far as possible, all unusual or extreme structures are described in the text.

The figures have all been drawn directly from slide mounts by means of a camera lucida. No attempt has been made to indicate or calculate the magnification attained, as this is believed to be purely incidental and of no importance to a knowledge of the morphology. Figures have been drawn to uniform sizes to show comparable details in the different species regardless of the original size.

The abbreviations used are the same on all the figures and are listed and explained at the end of the paper. They are for the most part the same as those adopted by Snodgrass in his recent papers.

It should be borne in mind that each figure is more or less of a composite, having been checked with as many specimens as possible and frequently drawn from parts of several.

MORPHOLOGY OF THE STAPHYLINIDAE

General Considerations

Because of the fact that there does not exist any single work which deals in any considerable degree of completeness with the comparative morphology of the Coleoptera as a whole, it has not been possible to adopt any one system of study or any single terminology. In the case of those structures that have been separately studied in a comprehensive way, an attempt has been made to follow that work in general. A very large part of the structure of beetles, however, has never been monographed comparatively, with the result that the present study has necessarily been built upon the basic works of Snodgrass and others, in which the Coleoptera are treated only as a whole along with the other orders of insects.

In the case of the structure of the head capsule, the interpretation adopted here is that worked out by Snodgrass and Böving. Its applications to the order Coleoptera have not previously been presented.

The orientation of the legs is a matter of common inconvenience. The fundamental position of the leg is assumed to be as follows: The leg is extended at right angles to the body, with each part extended distally and the empodium of the pretarsus facing downward, the coxa suspended from the body by the condyles at its proximal end. Following this orientation, it is possible to see four chief aspects of the leg, the anterior and the posterior, and the dorsal and the

ventral. The bicondylar joints all have one condyle anterior and one posterior with the exception of the trochantero-femoral joint which has one dorsal and one ventral. The claws are thus placed one anterior and one posterior.

An isolated leg can usually be readily oriented. The shape of the coxa will immediately determine the thoracic segment from which it came. Whether the leg came from the right or left side of the animal can frequently be told by the vestiture. On the coxae the vestiture is generally lacking on the posterior aspect except as the tip. The orientation of the posterior coxae can often be recognized at a glance by the expansion over the base of the trochanter, which occurs only on the anterior aspect.

The wing venation has been interpreted according to the scheme proposed by Forbes (1922). There was some hesitation, however, in accepting this course, as it is believed by some writers that the darker bands in the distal part of the wing do not represent veins that are in any way homologous with any veins in other insect wings. Certain parts can, however, be definitely correlated with other beetle wings, so that the classification of the veins of this family is probably as correct as that for the order as a whole. The spiracles of the thorax are four in number. One pair is situated in the conjunctivum between the prothorax and mesothorax on the ventral aspect, and the other pair is in the membrane just anterior to the base of the hind wing on the dorsal aspect. They are totally different in structure externally, the former resembling the abdominal spiracles very closely in appearance. They belong to the mesothorax and metathorax respectively.

The abdomen is 10-segmented in all staphylinids, and probably in all beetles in a morphological sense. The last two or three segments form the genitalia, whereas the first two are frequently much reduced or united to the metathorax. In all staphylinids the first segment is present only on the dorsum and is more closely united to the metathorax than to the second abdominal segment. It is practically always dissected off with the thorax.

As far as the family Staphylinidae is concerned only the genitalia have been treated in anything approaching a complete comparative study, and even in that case there has been no comprehensive summary except that given for the males by Sharp and Muir (1912). Their terminology has been followed chiefly, though it is rather artificial and obscures the true relationships. In the case of the genitalia of the female, it has been found necessary to modify somewhat the

interpretation of Tanner (1927). He has considered only one staphylinid, *Creophilus villosus*.

The spiracles are the chief landmarks of the abdomen. They occur on each segment from one to eight. They are in all insects morphologically a part of the tergum and in these forms are generally actually in the tergites. A curious error is made regarding these by Leconte and Horn (1883), as follows: " The breathing pores, or *spiracles*, are situated in the connecting membranes, or in the upper inflexed portions of the ventral segments." In the present family, at least, they are always very definitely placed in the tergal elements.

STRUCTURE OF A REPRESENTATIVE SPECIES

The species *Creophilus villosus* (Grav.) has been selected to be the subject of detailed investigation for the following reasons: It is one of the commonest, most widespread, and most readily attainable of American staphylinids; it very closely resembles related species that are common throughout most of the world; it is a typical staphylinid, being very similar to the type genus of the family; and it has been used, more than any other staphylinid species, as the basis for previous studies of the morphology of this family.

THE HEAD

The walls of the head are continuously heavily sclerotized on the dorsal, lateral, and ventral aspects. These walls thus form a solid capsule (fig. 1 F) with an opening at the posterior end, the foramen magnum. The walls of this capsule are formed of certain sclerites which have become united, with a corresponding obliteration of the sutures between them.

The dorsal aspect of the head (fig. 1 A) is occupied by a single large sclerite extending anteriorly from the rim of the foramen magnum (*for*) to the membranous anteclypeus (*aclp*) and occupying the entire width of the head. This area is the epicranium (*epi*) and is formed by the obliteration of sutures which would divide it into frons, vertex, genae, postgenae, and occiput. The occiput (*oc*) is represented by a narrow band around the dorsal and lateral rims of the foramen magnum, but it is undifferentiated from the vertex (*vx*). This is due to the obliteration of the occipital suture. The ventral continuations of the occiput on the sides of the head are the postgenae (fig. 1 A, E, *pge*). Since the occipital sutures, if present, would extend to the base of the labium and maxillae, it follows that the areas included by them, the postgenae, occupy in this species the two regions

on the sides of the gula (*gu*) and extending from the maxillary
articulation to the foramen magnum and the lateral extensions of
the occiput, from which they are not separated. The vertex itself
occupies nearly the entire dorsal aspect of the head and most of the
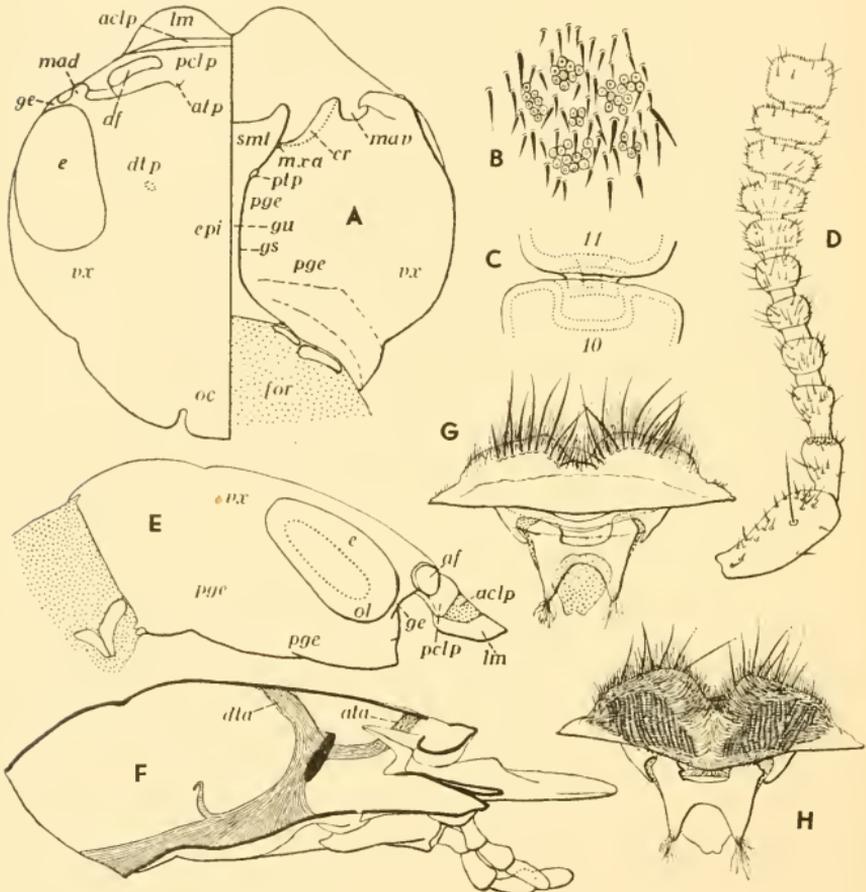

FIG. 1.—Morphology of the head of *Creophilus villosus* (Grav.).

A, dorsal and ventral aspects of head with appendages removed. B, minute
setae and pores from terminal segment of antenna. C, detail of joint between the
tenth and eleventh segments of antenna. D, antenna. E, lateral aspect of head
with appendages removed. F, sagittal section of head to show tentorium. G, dorsal
aspect of labrum. H, ventral aspect of labrum.

lateral aspects as well. The area between the eyes, from the anterior
tentorial pits to the occiput and the areas immediately behind and be-
neath the eyes as far as the postgenae are all a part of this sclerite
(fundamentally a pair of sclerites, one on each side of the midline

or epicranial suture). The term gena is used to designate the area (fig. 1 E, *ge*) on the lateral aspect of the head between the eye and the dorsal articulation of the mandible. It is not set off as a separate sclerite. The frons is present as an area in all insects to be defined by the frontal sutures and the epistomal suture, if present, but bearing the origin of the labral retractor muscles. In the present species neither the frontal nor the epistomal sutures are present, and the frons is therefore represented only in a triangular area behind the line of the anterior tentorial pits.

The clypeus is divided into two distinct sclerites, the postclypeus (fig. 1 A, E, *pclp*) and the anteclypeus (*aclp*). The postclypeus is fused with the frons at the line of the anterior tentorial pits and extends around the antennal fossae. The anteclypeus is a membranous strip between the anterior margin of the postclypeus and the labrum (*lm*).

The labrum (fig. 1 G, H) is a broad bilobed sclerite attached to the cephalic end of the clypeus. It is continuous with the rest of the dorsal surface of the head. Its anterior dorsal margin is clothed with both stout and fine setae, whereas the remainder of its dorsal surface is smooth and less heavily sclerotized. The ventral surface is covered with very fine recumbent hairs, with two large areas of cross-hatched ridges. The ventroposterior projections of the labrum are the tormae (*tor*) and carry the insertion of the retractor muscles of the labrum.

Lying between and posterior to the tormae and caudad of the ventral surface of the labrum is an **H**-shaped sclerite (fig. 1 G, H) which appears to articulate with the inner faces of the tormae. Its posterior arms taper regularly to a stubby point, from which arise a cluster of very fine fibers or hairs. This sclerite is apparently united by membrane to the tormae.

The epipharynx is apparently not present as even a definite area unless possibly it is represented by the two ribbed areas on the ventral surface of the labrum (fig. 1 H).

The ventral aspect of the head (fig. 1 A) is occupied by three sclerites or regions. These are a median and two lateral areas. The first is the gula (*gu*), a narrow longitudinal sclerite with an expansion at the posterior end. The lateral areas are the ventral prolongations of the caudolateral parts of the epicranium. These represent the postgenae and the subocular parts of the vertex as described above.

The gula (fig. 1 A, *gu*) is believed to be a sclerotization of the neck membrane posterior to the submentum and the tentorial pits and between the ventral extensions of the postocciput. The cephalic migration of the tentorial pits from the foramen magnum has extended the

postoccipital sutures anteriorly along the ventral aspect as the gular sutures (*gs*). The result is a gular sclerite which is narrow between the postgenae, expands posteriorly along the ventral edge of the foramen magnum, and is continuous with the submentum anteriorly at the line of the tentorial pits. Posteriorly the gula closes the base of the foramen magnum and is in close contact with the cervical sclerites.

The anterior portion of the ventral aspect of the cranium bears on its inner surface a thickening or ridge known as the crassa (fig. 1 A, *cr*) (MacGillivray, 1923). This ridge extends from the region of the maxillary articulation to the mesal side of the ventral articulation of the mandible, and it is presumed to function as a support of this latter structure. Stickney (1923) interprets this as the occipital suture, and if this interpretation is correct, the ridge would be properly called the hypostomal ridge.

A number of other sclerites are present on the head of many beetles, but they are small and relatively unimportant. The oculata (fig. 1 E, *ol*) is a wide ringlike shelf on the inside periphery of the eye. There is apparently in this species no sclerite that can be identified with the antennal sclerite, which is normally situated within the antennal fossa.

Certain parts of the head capsule are modified to form rather definite condyles for the movable parts. These are of considerable importance because they are usually very definite and permanent in position and are thus very useful landmarks for identifying the other parts. The antenna generally articulates with the head by means of an obscure sclerite, the antennal sclerite, mentioned above. This has not been observed, but the condyle is probably present in some form as an articulating surface. The mandible articulates with the head by means of two condyles, forming the dorsal (fig. 2 J, *mad*) and the ventral (fig. 2 F, *mav*) articulations. The dorsal articulation is formed by a rounded protuberance, situated in front of the eye at the antero-lateral corner of the head, which fits into an hemispherical acetabulum on the mandible. The ventral condyle is situated on the mandible and articulates with an acetabulum at the anterior end of the crassa (*cr*). The articulation of the maxilla is a small condyle on the mesal end of the cardo, which articulates in a small concavity on the inner face of the postgena at the mesal end of the crassa (*cr*). In the present species this condyle is undeveloped and is not actually in contact with the postgena.

The median anterior part of the lateral aspect of the head is occupied by the compound eye (fig. 1 E, *e*). This organ is ovate in

outline, somewhat convex, and the facets are moderate in relative size. The oculata is large, occupying nearly three-quarters of the area of the eye, as already described. No ocular suture or independent ocular sclerite has been observed, but there is a narrow unpigmented band separating the faceted part from the vertex. Ocelli are not present.

The vestiture of the head consists of a moderately dense clothing of setae along the posterior margin dorsally, with a few very large and long setae placed as follows: A pair at the anterior edge of the vertex at the corners of the postclypeus; one above the base of each antenna; one near the middle of the inner edge of the eye; and one to three in the area between the eye and the posterior constriction. The posterior areas are continued around onto the lateral and somewhat onto the ventral surface.

THE APPENDAGES OF THE HEAD

The appendages of the head consist of a pair of antennae, a pair of mandibles, a pair of maxillae, a hypopharynx, and a labium. With the exception of the antennae, which are sensory in function, these are all concerned with ingestion of food and are known collectively as the mouthparts or trophi.

The antennae (fig. 1 D) are situated at the anterior edge of the epicranium. They are inserted ·into an opening or antennal fossa (fig. 1 A, *af*). They are 11-segmented and feebly clavate, with the first segment elongated, as long as the second and third together. The segments diminish in length from the first to the fifth, and increase in width from the sixth to the tenth. The seventh to eleventh segments are covered completely with minute setae, and the eleventh alone has these setae interspersed with groups of minute pores (fig. 1 B). The outer joints (fig. 1 C) allow only a limited amount of movement, whereas the basal ones permit a much wider latitude. All the segments have a sparse vestiture of longer setae which are situated rather at random.

The mandibles (fig. 2 F, J) are prominent, falciform jaws, heavily sclerotized, and each articulated with the anterior margin of one side of the head. The expanded proximal part is produced into a slender, curved distal part which tapers to a blunt point. The lateral margin of the latter is regularly continuous with the curved outer margin of the basal part. The anteromesal corner of the basal part is produced to form two small, bluntly acute teeth (*mat*). The notch separating the two teeth of the left mandible (fig. 2 J) is nearly three times as deep as the corresponding notch on the right mandible (fig. 2 F).

The more distal tooth of the right mandible is actually double, there being another smaller tooth immediately beneath it, arising from the ventral surface of the mandible rather than from the inner edge as do the others (fig. 2 F). There is no definite molar surface on the inner face of the mandible, but the edge is divided longitudinally so that a groove is formed, extending from the dorsal condyle (*mad*) to the base of the tooth (*mat*). In the floor of this groove and about midway on the inner face is an oblong foramen (*prf*) from which extends a membranous lobe or prostheca (*prth*). This lobe is nearly one-third as long as the entire mandible and half as wide, and its inner edge is regularly divided into a series of equal lobes, about 15 to 20 in number. The entire structure is densely clothed with minute hairs.

Near the lateral edge of the dorsal aspect of the mandible is a shallow fold (fig. 2 J, *maf*) extending from the condylar region at the base to the end of the expanded proximal part of the mandible. Under this fold are the openings of a series of pores (*spc*) which apparently communicate with the interior cavity of the mandible. They lie nearly parallel to the dorsal surface of the mandible and project mesad from the fold. They may be branched (fig. 2 E) or unbranched, but the tip of each branch forms a capsule, the walls of which are traversed by numerous small canaliculi (*can*), which are little larger than the canaliculi normally found in most sclerotized integuments.

Just distad of the anterior end of the fold (fig. 2 J, *maf*) and at the lateral edge of the mandible there appears to be another pore (*mp*). This is not connected with the serial pores of the fold, but under high magnification is seen to be merely a thinning of the sclerotic wall in the form of a narrow sac or tube on the inside and a slight indentation of the outer surface (fig. 2 I). The reason for the existence of this structure as well as of the serial pore organ is entirely unknown to me.

The mandible is articulated with the head by means of one dorsal and one ventral condyle. The dorsal one is situated on the gena (fig. 2 J, *mad*) and the ventral one on the mandible (fig. 2 F, *mav*). The dorsal articulation is an hemispherical acetabulum on the mandible which fits over a spherical projection of the head capsule immediately in front of the eye. The posterior articulation is a spherical projection on the base of the ventral or outer face of the mandible. It fits into a crescent-shaped acetabulum at the anterior extremity of the crassa.

The maxillae (fig. 2 G) are situated immediately ventrad of the mandibles at each side of the labium. Each is composed of four parts,
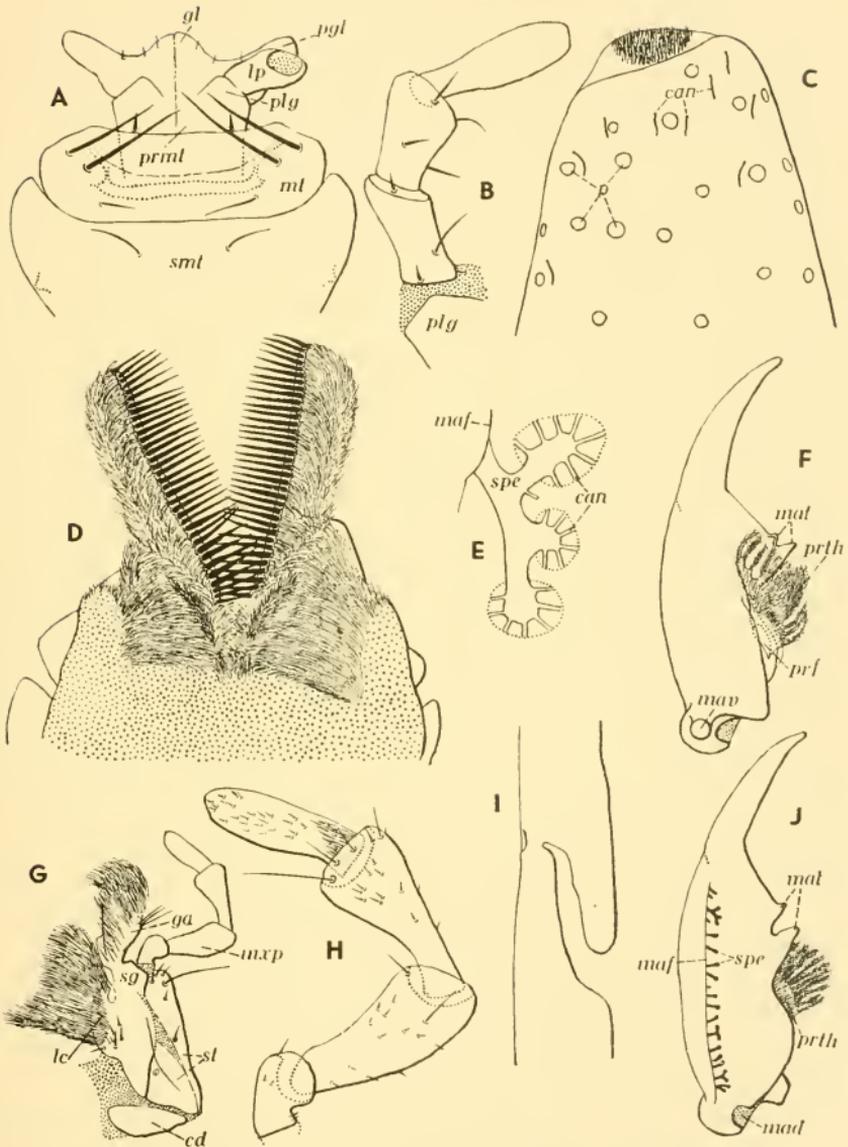
FIG. 2.—Morphology of the trophi of *Creophilus villosus* (Grav.).

A, ventral aspect of labium, without palpi. B, labial palpus. C, detail of tip of terminal segment of labial palpus. D, dorsal aspect of hypopharynx. E, detail of one of the serial pores from dorsal side of mandible. F, ventral aspect of right mandible, showing prostheca. G, ventral aspect of left maxilla. H, maxillary palpus. I, detail of median pore organ from outer edge of mandible. J, dorsal aspect of left mandible.

the body of the maxilla, separated into several sclerites, two distal lobes, the galea (*ga*) and the lacinia (*lc*), and the maxillary palpus (*mxp*). The body of the maxilla is composed fundamentally of three parts, the cardo, the stipes, and the palpifer. The cardo (*cd*) is the basal sclerite, which articulates at its mesal edge with the subgenae. The stipes (*st*) is secondarily divided into two sclerites, apparently the proximal or mesal one bearing the large lacinia (*lc*) and the galea (*ga*), while the distal or lateral one bears the palpus on its extremity. The lacinia is a large, densely hairy lobe, which is movable on the stipes but is apparently united to a considerable extent to the base of the galea (*sg*). The galea is covered with hairs similarly to the lacinia, but is placed distad of that organ and curved around the tip of it. The lateral corner of the galea bears a few long setae. The stipes bears the maxillary palpus on its extremity without the differentiation of a definite palpifer, the first segment of the palpus being joined to it by a membrane. The palpus (fig. 2 H) is four-segmented and nearly filiform. The basal segment is very small and is strongly geniculate. This arrangement allows the second segment to extend laterally at right angles to the axis of the maxilla. The second segment is rather swollen and larger than any of the others, and it is somewhat arcuate. The third segment is narrow at the base but expands at the apex to approximately the same size as the second. It extends cephalad from the tip of the second and is also slightly arcuate. The last segment is nearly straight, cylindrical, and both shorter and narrower than the two preceding. It is, however, slightly wider than the third at the base, and is obtusely rounded at the apex. All the segments are very sparsely beset with small setae, and the first three bear longer setae near their apices. The terminal segment also bears at the base of its dorsal surface an area of small close-set setae. The distal end of this segment bears a small area of what appear to be sensory papillae, extremely minute and gathered in a slight emargination in the tip. The distal two-thirds of the segment have a few scattered pores similar to those found on the labial palpi (fig. 2 C, *p*) but somewhat larger. There are also a few fine canaliculi as described from that organ (*can*).

The labium (fig. 2 A) is composed of three parts, the submentum, mentum, and prementum, the last bearing a pair of segmented palpi and three membranous lobes. The basal piece is the submentum, which attaches the labium to the head. It is separated from the postgenae by the submental sutures and is continuous with the gula between the tentorial pits.

The submentum is expanded anteriorly to clasp the base of the mentum. The mentum is a transverse sclerite, heavily sclerotized, and

bearing a pair of large setae on each side. The prementum arises from the inner or dorsal surface of the mentum. It is much narrower than the latter and roughly square in outline. Its distal end is expanded into two pairs of lobes, an inner pair of glossae and an outer pair of paraglossae. The glossae (*gl*) lie on either side of the median line, fused throughout their length except at the tip, which is slightly notched. They are ordinarily visible between the labial palpi (*lp*) on the ventral aspect. The paraglossae (*pgl*) are expansions of the anterolateral corners of the prementum. They are more distinctly produced than the glossae, but are almost always hidden behind the first segment of the labial palpi (*lp*). Both the glossae and the paraglossae are membranous, unpigmented, and translucent. They have no vestiture with the exception of a few scattered hairs on the anterior margin between the glossae and the paraglossae. The prementum bears on each side at its median lateral margin a large imperfectly differentiated lobe, the palpiger (*plg*) which bears the labial palpus (*lp* and fig. 2 B) on its distal end. There is a single stout seta at approximately the base of each palpiger. The labial palpus is three-segmented with the first two segments nearly equal in size and the terminal one somewhat elongated. This palpus differs from the maxillary palpus in being devoid of setae, except for a very few long hairs. The extreme tip of the third segment is slightly emarginated and bears a small median area of what appear to be sensory papillae (fig. 2 C, *senp*). The surface of the tip is also set with relatively very large pores (*p*), with a few of what appear to be minute canaliculi (*can*) ending at the surface in a small, dark dot.

On the inner or dorsal surface of the labium is a large appendage, the hypopharynx (fig. 2 D). This arises from the region between the mentum and submentum and the mouth opening, and bears two slender lobes distally. These lobes extend in a narrow V-shape behind the paraglossae of the labium and are armed along the inner edge with a comb of long stout setae. This entire organ is very membranous and translucent, and the distal portion is covered with a very dense vestiture of short fine hairs. It is so exactly beneath the labium (that is, dorsal to it) that the tips of the comb-bearing lobes appear to be the paraglossae of the labium, even in dissections. It is firmly attached to the ental surface of the labium.

THE TENTORIUM

Each half of the tentorium or internal skeleton of the head is composed of a posterior arm (fig. 1 F, *pta*), an anterior arm (*ata*), and

a dorsal arm (*dta*). The posterior arm extends along the ventral wall of the head to the foramen magnum, with the edge of which it is completely united. It is marked on the exterior of the head by a small pit or invagination at the cephalic end of the gular sutures. This is the posterior tentorial pit (*ptp*). The anterior arm of the tentorium extends to the anterior dorsal region of the head near the base of the antennae. The point at which it reaches the head wall is marked on the exterior by a shallow anterior tentorial pit (*atp*). This is situated just mesad of the antennal fossa (*af*). The dorsal arm of the tentorium extends dorsad and somewhat caudad to the dorsal wall of the head. This point is marked on the exterior by a slight unevenness of the surface, and the body wall itself is much thinner, or at least less heavily pigmented, at that place. This point (*dtp*) represents the dorsal tentorial pit. The two halves of the tentorium meet and fuse at the midline of the head just caudad of the line of the base of the mandibles. This union is the cephalic bridge or body of the tentorium (*cp*). There has apparently been no study of the muscles which are attached to the tentoria of Coleoptera, but the normal insect type is given by Snodgrass (1928), who shows that many of the muscles of the mouthparts and antennae are attached to specific parts of the tentorium.

THE CERVIX

The neck region or cervix is largely membranous but contains certain sclerites which have been interpreted by some writers as parts of a primitive cervical segment. Three pairs of sclerites are present in this species. Two of these pairs lie in the membrane at the lateral posterior corners of the gula. The third pair is more closely united to the prothorax, and in dissections is most frequently retained on the lateral cephalic edges of the prosternum.

In the dorsal parts of the membrane near its union with the thorax are two areas bearing a few short setae. They are not sharply defined and are apparently unsclerotized.

THE THORAX

The thorax is very obviously divided into two regions, owing to the distinct separation of the prothorax from the rest (fig. 3 A) and the close union of the mesothorax and metathorax to the abdomen.

The pronotum (fig. 3 A, *pron*) occupies the entire dorsal aspect of the prothorax. Its posterior and lateral margins are inflexed upon the ventral surface and are separated from the sternum by the sterno-

notal sutures (*sns*). The lateral and caudal margins are occupied by a fine ridge or thickening (*mrn*), which, near the anterior lateral angles, passes onto the ventral aspect and disappears. The area set off by the marginal ridge is known as the hypomera (*hypo*) or the inflexed part of the pronotum. The dorsal surface of the pronotum is moderately convex, nearly quadrate with the angles broadly rounded, and very slightly wider than long. The broad median area is smooth and even on the surface, but it is traversed by numerous fine canaliculi, which appear to be larger and more definite in arrangement than the usual irregular canals in sclerotized integuments. Each canal ends at the surface in a minute puncture which appears to bear an extremely fine and short point or setula. The sides of the dorsal surface are beset with moderate setae which are set in large punctures. This area is continued at the anterior corners onto the lateral and ventral aspects by the continuation of the marginal ridge.

The hypomera is itself slightly deflexed along the margin of the coxal cavity, and this deflexed part is set off by a rather definite line which extends posteriorly for some distance. Just caudad of the coxal cavity and nearly over the mesothoracic spiracle, this deflexed part is expanded medially into a membranous lobe (fig. 3 A, *prnl*, C) which partially closes the cavities behind. Its anterior edge is densely covered with very fine membranous processes (figs. 3 C, D) of two types. Single slender and finely pointed processes occupy the greater part of the area, and shorter fimbriate groups of five to seven points occur in a band around the margin. These groups and the single points are connected in series by fine folds of the surface and appear to be merely expansions of these folds. The posterior parts of the hypomera bear no setae but have many of the fine canaliculi on the lateral portions.

The ventral aspect of the prothorax is occupied by the sternum, the hypomera, the coxal cavities, and the anterior and posterior foramina, which receive parts of the head and mesothorax respectively. A considerable caudal area is membranous, and one sclerite (fig. 3 A, *peri*) lying in this area belongs to the mesothorax. This is the sclerite that bears the so-called prothoracic spiracle (*sp*), which is undoubtedly morphologically a part of the mesothorax.

The prosternum is composed of two sclerites, the basisternum (fig. 3 A, *bs*) and the furcasternum (*fs*), separated by a suture (*stcs*), the sternacostal suture. The basisternum is a transverse sclerite along the ventral or posterior border of the anterior foramen (*afor*), extending laterally to the notosternal suture (*sns*) and forming the

anterior border of the coxal cavities. It is heavily sclerotized and pigmented, and bears a few setae on its mesal part and a group of five or six minute punctures near the middle of each lateral side.
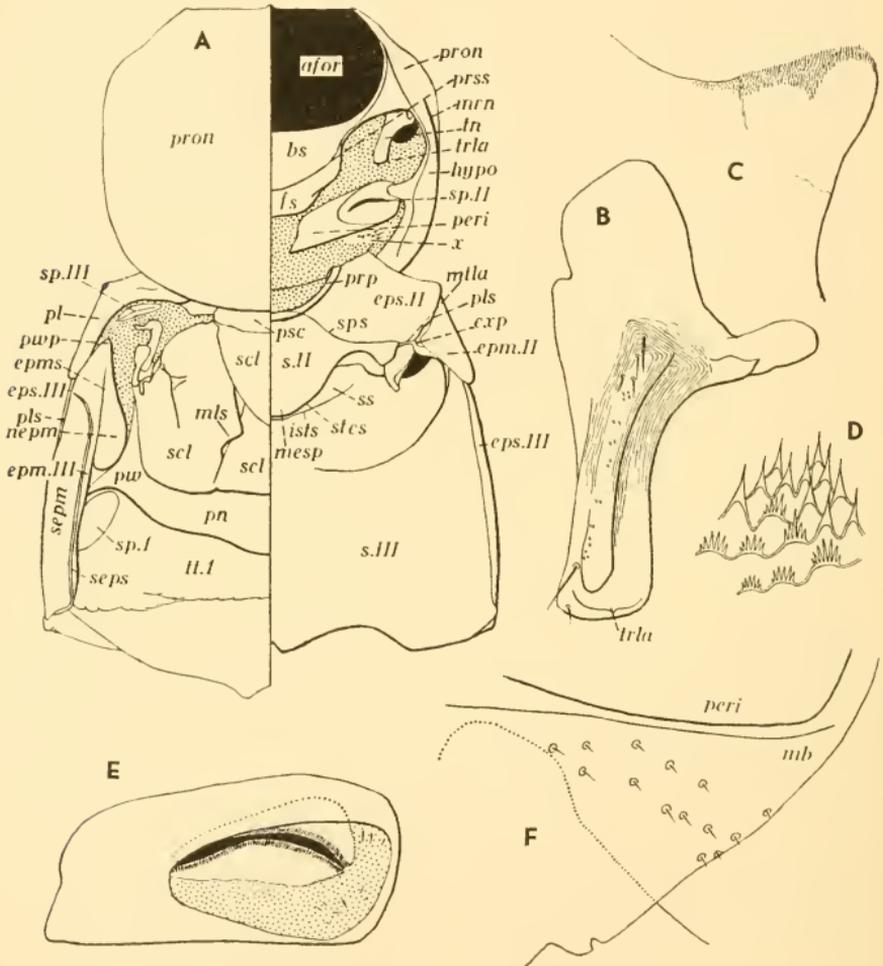

Fig. 3.—Morphology of the thorax of *Creophilus villosus* (Grav.).

A, dorsal and ventral aspects of thorax, showing general relationship of parts. B, prothoracic trochantin. C, notal lobe of prothorax. D, detail of processes of pronotal lobe. E, mesothoracic peritreme and spiracle. F, group of setae from membrane between prothorax and mesothorax.

The furcasternum is much shorter than the basisternum, less heavily sclerotized, and without vestiture or sculpture, except for the minute pores or pits found on most of the prothoracic integuments.

The remainder of the venter is occupied by the membranes lining the coxal cavities (fig. 3 A, *cxc*) and that connecting the prothorax and the mesothorax (*mb*). In the lateral parts of this latter membrane and just caudad of the coxal cavities lies the pair of sclerites, the peritremes, bearing the spiracles of the mesothorax.

The pleural elements appear to have been so far reduced by the approximation of the notum and sternum as to have disappeared entirely as separate sclerites. This area normally forms the major articulation of the coxa (the anterior or dorsal articulation). In the present species the trochantin, whose apical end forms the posterior or ventral articulation, is prolonged around the base and provides also the dorsal articulation. This may be interpreted as an indication that the pleural elements have united with the trochantin and are represented only in that sclerite.

The trochantin of the prothorax (fig. 3 A, *tn*, B) is a long narrow sclerite with a lobate projection on the lateral side. This lobe bears the dorsal articulation of the coxa as described above. The cephalic part projects under the anterior margin of the coxal cavity. The caudal part, projecting into the coxal cavity, is more heavily sclerotized and thicker than the rest. It is elevated into a longitudinal ridge which bears a few setae and a series of the minute punctures with setulae. The surface, especially that bordering the ridge, is strigulose. The posteromedian end articulates with the inner edge of the coxa.

The mesothorax is much shorter than the prothorax or the metathorax and is closely united to the latter (fig. 3 A). It is united to the prothorax by a membrane (*mb*) which is of considerable extent on the ventral aspect, extending to the coxal cavities of the prothorax.

In this membrane lies the peritreme (fig. 3 A, *peri*, E) bearing the mesothoracic spiracle (*sp*). The peritreme is an oblong sclerite, placed transversely, and nearly two and one-half times as wide as long. It is thought to be a secondary sclerotization of the intersegmental membrane. The spiracle is located in the lateral three-fourths of the sclerite and is similar in appearance to the first abdominal spiracle (fig. 9 D). There are a very few scattered setae on the membranous declivity surrounding the sieve processes. At the sides just ventrad and caudad of the spiracles is an area bearing a few minute setae in relatively very large punctures (fig. 3 A, *x*, F). This area is not differentiated from the remainder of the membrane and is unsclerotized.

The dorsal aspect of the mesothorax is nearly covered by the projecting caudal edge of the pronotum (fig. 3 A). Its most conspicuous sclerite is the central shield-shaped area (fig. 4 C, A) which is gen-

erally known as the scutellum. It is formed by the union of the three normal sclerites of the mesonotum, the prescutum, scutum, and scutellum.

The posterior triangular portion is the scutellum (figs. 4 C, 3 A, 4 A, *scl*), which overlaps the metatergum posteriorly and is separated in front from the prescutum by an obvious transverse suture. Its surface is rather densely setigerous, with a narrow impunctate anterior margin. A rectangular area (*sclp*) on the ental surface of the posterior part of the scutellum is the part that is in close contact with the anterior edge of the metanotum. The anterior margins of the area are continued forward as the axillary cords of the wings (*axc*) which appear to proceed from the sides of the prescutum.

The part of the shield anterior to the scutellum is the prescutum (figs. 4 C, 3 A, 4 A, *psc*). It overlaps the scutellum somewhat posteriorly, especially at the sides. The prescutum is short and transverse, bearing the anterior notal wing process (*anp*), the lateral emargination (*em*), and a second process posterior to this. An irregular transverse line extends between the anterior wing processes dividing the prescutum into two areas. The posterior of these bears numerous setae, somewhat smaller than those of the scutellum, on its caudal half, and also a very few exceedingly fine setae at the anterior angles near the wing processes. The anterior area bears a small group of six to eight setae on each side of the center on the caudal margin, and also a median pair of very large setae (fig. 4 C).

The scutum (fig. 4 A, *sct*) of the mesothorax is completely separated by the union of the scutellum and the prescutum along the line of the suture *pss* into two parts. It projects laterad from beneath the shield and forms the posterior notal wing processes. Its exact outline is obscure as it is more or less united to the other sclerites entad. The axillary cord (*axc*) appears to arise from the scutum but probably merely traverses it from the margin of the scutellum of which it is the continuation. The ectal surface on each side is apparently transversely traversed by a fine suture (*scts*) which marks an ental apodeme.

The sternum of the mesothorax is represented chiefly by a single large sclerite (*s. II*) on the median part of the ventral aspect. It is separated from the anterior margin by a narrow strip, the prepectus (*prp*), which extends from the anterior portion of one episternum along the margin in front of the sternum and onto the other episternum. The prepectus may not be a distinct sclerite, but it is separated from both the sternum and the episternum by a distinct line or ridge and is somewhat inflexed. It appears to be divided into three

parts by the end of the sternopleural suture, and fuses with the episterna at its extreme anterior ends. It has no vestiture or sculpture.

The mesosternum is prolonged laterally in a narrow piece which forms part of the anterior margin of the coxal cavity and posteriorly in a broad median lobe, the mesosternal process (fig. 3 A, *mesp*). There are a few scattered very slender setae on the central part, particularly on its caudal margin, and almost the entire surface is densely covered with very fine punctures which appear to bear very minute setulae. On the lateral extensions these punctures are rather sparse, but the setulae are larger and more definite.

Posteriorly the mesosternum is separated from the metasternum by a narrow sclerite, the spinisternum (fig. 3 A, *ss*). This is a secondary sclerite formed from the intersegmental membrane and united to the mesothorax. It is very narrow medially, expanding somewhat on the floor of the coxal cavities. It is separated from the mesosternum by the spinisternal suture (*sss*) and from the metasternum by the suture *ists*. It bears no sculpture or vestiture.

The pleuron of the mesothorax is larger than either the mesonotum or the mesosternum. It occupies the lateral part of both the dorsal and ventral aspects and forms the processes that project into the prothorax for articulation. It is composed of the episternum, the epimeron, and the articulations of the coxa, and bears on its anterodorsal part the base of the elytra.

The episternum (fig. 3 A, *eps. II*) is the largest sclerite of the mesothorax. It is separated from the sternum by the sternopleural suture (*sps*). Its posterior corner extends to the rim of the coxal cavity and forms an articulation for the trochantin. Its ental projection fuses with part of the epimeron to form the pleural coxal process (*cxp*). On the ventral surface the episternum is completely separated from the epimeron by the pleural suture (*pls*), but this suture extends only to the lateral edge and is not continued on the dorsal aspect. Thus the episternum and epimeron are united on the dorsal surface, and this sclerite, the pleuron (*pl*), forms the anterior projections of the mesothorax.

The episternum is rather sparsely set with setae, which are short at the prepectal margin and become larger and longer toward the pleural suture. The lateral and dorsal parts, particularly anteriorly, are finely strigulose, the lines being considerably more apparent than the normal very fine markings of sclerotic surfaces. The ventral part is also sparsely set with the minute lageniform punctures similarly to the pronotum.

The epimeron (fig. 3 A, *epm. II*) appears as a distinct sclerite on the ventral surface of the mesothorax but is united to the episternum on the dorsal aspect to form an undifferentiated pleuron. Posteriorly it overlaps the end of the metathoracic sternum and episternum, and forms the lateral wall of the mesothoracic coxal cavity. Its surface bears a few long sparse setae, similar to the adjacent area of the episternum, and has also the minute punctures. The dorsal aspect of the pleuron bears no setae but is strigulose as described above.

From the dorsal side of the anterior projections of the mesothorax arise the elytra. Discussion of the articulation of these will be left for the section dealing with the wings.

The trochantin of the mesothorax (figs. 3 A, *th*, 4 B) is smaller than that of the prothorax but is similar in arrangement and structure. It is an arcuate sclerite, nearly three times as long as wide, and tapering distally to form a blunt condyle for the coxa (*trla*). Its proximal portion forms a condyle that articulates with the projecting corner of the episternum (*mtla*). Its ventral or ectal surface is thickened into a broad ridge, and the proximal ental part is submembranous. A single long seta is set in a large puncture at the middle of the longitudinal elevation, and the surface is longitudinally strigulose.

The metathorax is the caudal one of the three thoracic segments and is larger than either of the others. It is very closely united to the mesothorax in front and to the abdomen behind. The tergum is in rather close contact with the tergite of the first abdominal segment, whereas the sternum is rather loosely joined by membrane to the sternite of the third abdominal segment.

The tergum of the metathorax (figs. 3 A, 4 F) is divided into five parts: The prescutum (*psc*), the two separated scutal areas (*sct* and *sctt*), the scutellum (*scl* and *sclt*), and the postnotum (*pn*). The prescutum, scutum, and scutellum are fundamental parts of the tergum, but the postnotum or postscutellum is a secondary sclerite formed from the intersegmental membrane caudad of the metatergum and subsequently joined to it (see Snodgrass, 1909).

The central triangular part of the metatergum is the scutellum. It is separated from the two scutal areas by two internal ridges, the V-ridges (figs. 5 A, 4 F, *vr*), and two curved sutures. It is separated anteriorly from the prescutum by a membranous area, and posteriorly from the postnotum by a suture (*acs*) extending between the bases of the wings. Since the posterior margin of the scutellum is morphologically continuous with the hind margins of the wings, this area is considered as extending laterad along the suture to the wings, and it is therefore fused with the posterior part of the scutum on each

side. The anterior half of the scutellum is very densely invested with short fine setae, and the posterior half has two large lateral, finely strigulose areas bearing numerous circular and occasionally anastomosing pores of unknown function.

The scutum of the metathorax is divided into two parts by the approximation of the prescutum and the scutellum. Medially these are separated from the scutellum by the suture of the V-ridge, but posteriorly they are continuous with the lateral extensions of the scutellum to the wing bases. From the prescutum and the axillary and subalar sclerites it is separated by the prescutoscutal suture (figs. 3 A, 4 F, *pss*). At the sides the combined scutum and scutellum form the posterior notal wing process (*pnp*), and just anterior to this process are two small invaginations and a process that articulates with the base of the first axillary sclerite (*ax. 1*). The entire surface of the scutum is densely, finely muricate, the posterior median part being likewise strigulose with the minute but rigid points born on the summits of the strigulae. Two small groups of fine setae are present on each area of the scutum. One is on the median lobe (*mls*) that overlaps the suture of the V-ridge; the other is on the lateral margin just mesad of the articulation of the first axillary sclerite (*axp*).

The prescutum is normally almost entirely covered by the mesonotum, but is readily recognizable in dissections as an irregular band along the anterior border of the scutal areas (fig. 4 F). It is rather irregularly and less heavily sclerotized and is broken up into a number of areas or sclerites. The transverse median part bears on its ectal surface a broad lobe (*pscl*) reflected so as to overlie somewhat the central membranous area between the prescutum and the scutellum. This lobe is exceedingly smooth and flat, without sculpture or vestiture of any kind. Near the anterior angles of the scutum, the prescutum is broken up into two small sclerites on each side. The inner one is very small and triangular and overlaps the median portion ectad. The outer one is also subtriangular, but it is larger and forms the very blunt anterior notal wing process (*anp*) which lies under the distal end of the first axillary sclerite (*ax. 1*). These two sclerites, as well as most of the median part, are very minutely muricate, and the membranous central area has a group of minute setae which is continuous with that of the scutellum as described above.

The postnotum (figs. 3 A, 4 F, *pn*) is the short transverse sclerite extending across the dorsum from one pleuron to the other and separated from the scutum and the scutellum by the postnotal suture (*pns*). It is connected by a very short membrane to the first abdominal tergite, and at the sides is reflected around the first abdominal
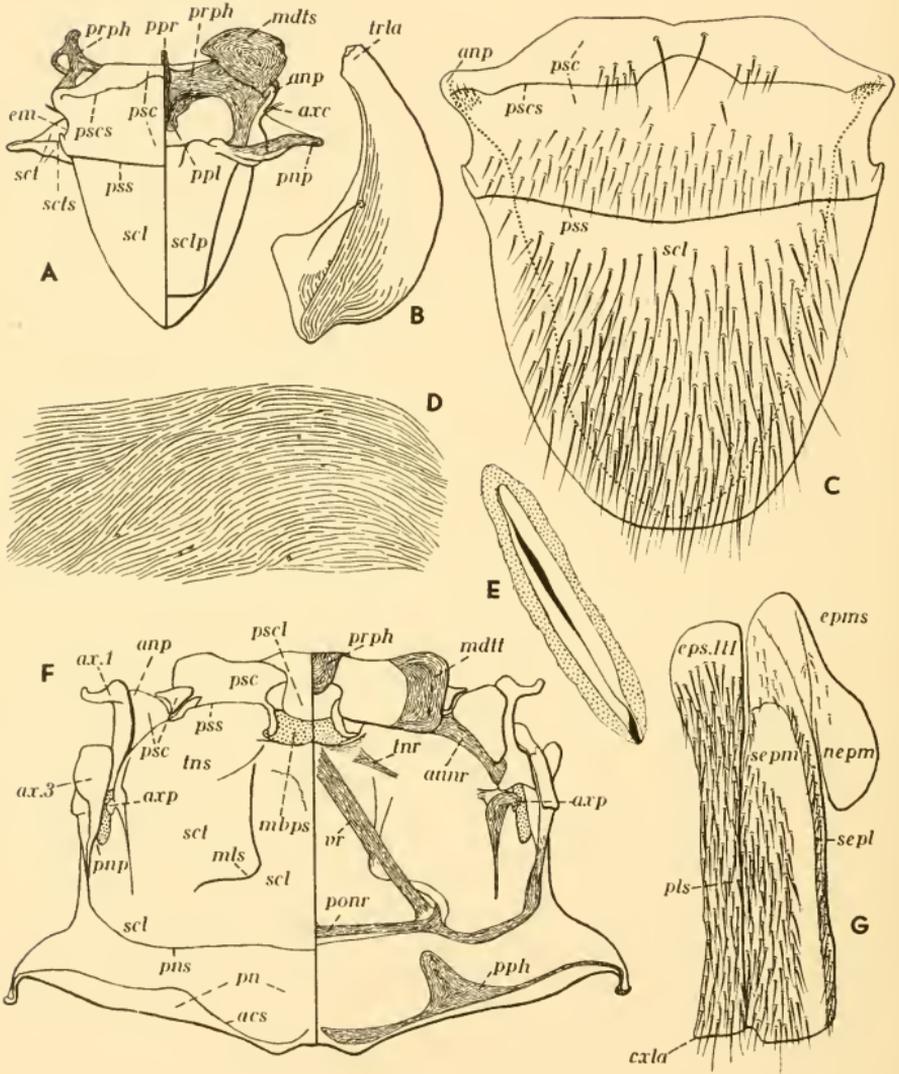
FIG. 4.—Morphology of the thorax of *Creophilus villosus* (Grav.).

A, ectal and ental aspects of tergum of mesothorax. B, trochantin of meso-thorax. C, "scutellum" of mesothorax. D, detail of surface of notepimeron of metathorax. E, metathoracic spiracle. F, ectal and ental aspects of tergum of metathorax. G, pleurites of metathorax.

spiracle (*sp. 1*) to form an articulation with the epimeron (*pna*). The lateral anterior angles are extended along the antecostal suture to the axillary region. Along the posterior part of the sclerite extends a suture from the postnotal articulation to the midline, marking the location of an interior ridge. This is the antecostal suture (*acs*). There is no vestiture on the postnotum, but the narrow area caudad of the antecostal suture is finely muricate. The central area is densely covered with extremely minute rounded papilliform processes or excrescences.

The axillary sclerites will be described in the section dealing with the wings.

The ventral aspect of the metathorax is occupied by a single very large sclerite, the metasternum (fig. 3 A, *s. III*). It extends from the coxal cavities of the mesothorax to those of the metathorax, and bears no sutures with the exception of a line from the anterolateral angles around the coxal declivity. This line disappears medially and is more of the nature of a fold, as it bears no internal expansions or processes. The metasternum is separated from the mesosternum (*s. II*) by a suture (*ists*) which disappears for a short distance on the floor of the coxal cavity. Posteriorly the metasternum bears a small triangular median emargination bounded by two rounded lobes, the sternal articulations of the coxae (*stca*). Laterad of each articulation is a broad shallow coxal emargination, and a slight expansion of the sternum overlaps the coxal articulation with the pleuron. The entire surface behind the line of the postcoxal folds is densely clothed with long hairlike setae. The floor of the coxal cavity is finely strigulose and nearly reticulate, and the area between the coxal depressions and the poststernum is finely muricate. A narrow border of small setae lines the posterior edge of the coxal depression on the anterior or inner side of the coxal fold.

The pleuron of the metathorax is divided longitudinally into the usual two sclerites, the episternum, and the epimeron. The episternum (figs. 3 A, 4 G, *cps. III*) or the dorsal sclerite is very slender and rather rectangular, and its posterior dorsal angle forms an articulation for the lateral extremity of the metathoracic coxa. This articulation is the pleural coxal articulation (*cxla*). With the exception of a narrow band along the cephalic edge, the surface of the episternum is densely clothed with long setae. Also the entire surface is strigulose, the strigulae forming tiny folds over the base of each of the setae.

The epimeron of the metathorax is larger than the episternum and is secondarily marked with several longitudinal lines or sutures (fig. 4 G). One of these sutures (*cpms*), marked by an internal ridge,

separates the epimeron into two parts, the notepimeron (*nepm*) and the sternepimeron (*sepm*). The sternepimeron lies along the episternum, separated from it by the pleural suture (*pls*), and is slightly longer and considerably wider than it. Its posterior part overlaps the lateral end of the first abdominal tergite and the spiracle of that segment, as well as the tip of the postnotum of the metathorax and, anteriorly, the caudal end of the epimeron of the mesothorax. Its cephalic end is the pleural wing process (*pwp*) but apparently is not specially modified. Its surface is rather convex and marked with a distinct impressed line (*sepl*) which sets off the anterior quarter and a narrow band along the dorsal edge. The surface is clothed with setae similarly to the episternum except for a space dorsad and caudad of the sternepimeral line. The anterior part bears only a few small scattered setae. The notepimeron (*nepm*) is united to the sternepimeron at its cephalic end, at which point the former is a narrow band. It expands posteriorly into a flat oval plate, bearing a few small setae anteriorly and a few minute sensory pores on the sides of the disk, and its surface is rather strongly strigulose (fig. 4 D).

The metathoracic spiracle (figs. 3 A, *sp. III,* 4 E) lies in the membrane anterior to the epimeron and along the dorsal side of the mesothoracic pleuron. It is very pale and membranous, without sculpture or vestiture, and is not surrounded by a definite sclerite. It is entirely unlike the spiracles of the mesothorax and abdomen as it has no sieve apparatus, being composed of two sclerotic lips which fold together to close the opening. It is longer and much more slender than the other spiracles and is difficult to differentiate from the surrounding membrane.

THE ENDOTHORAX

The endoskeleton of the thorax is known collectively as the endothorax. It is composed of invaginations of the tergal, pleural, and sternal regions of each segment, and these apodemes are termed the endotergites, the endopleurites, and the endosternites respectively. The sclerotized tendons and some small invaginations are part of the endoskeleton but are not considered here.

The endotergites (fig. 5 A) are found typically only in the mesothorax and metathorax. In the prothorax the endotergites are represented only by a rather indefinite group of processes on the hypomera in the region of the coxal cavity and the trochantin. These bear a large muscle disk (fig. 5 A). In the mesothorax the anterior margin of the prescutum is deflexed to form a transverse ridge—the antecostal ridge or prephragma (*prph*), which bears a pair of large muscle

disks (*mdts*) at its ends. There is apparently just behind this small ridge and corresponding with a line or suture on the ectal surface, the prescutal suture (fig. 4 A, *pscs*), a large transverse phragma ex-
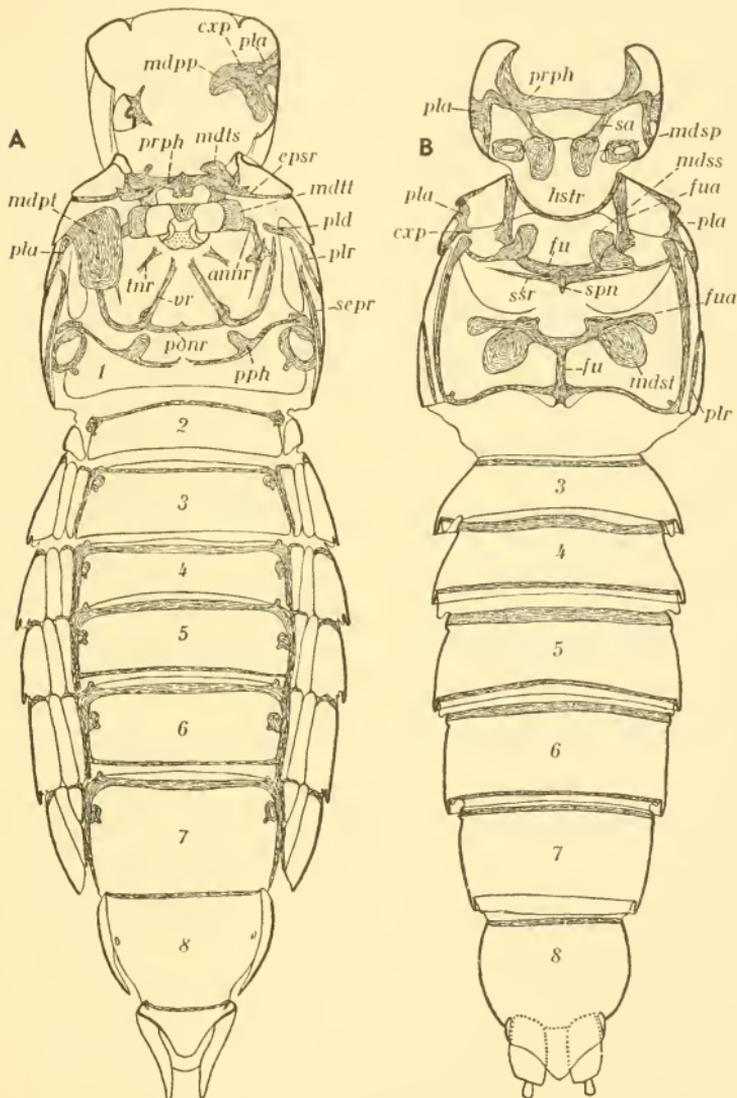

Fig. 5.—Endoskeleton of trunk of *Creophilus villosus* (Grav.).
A, endoskeleton of the dorsum. B, endoskeleton of the venter.

tending between the anterior notal wing processes (fig. 4 A, *anp*), and posteriorly at the sides to the prescutoscutellar suture (*pss*), and more or less united to the prephragma. On the midline this phragma

bears a longitudinal ridge (*ppr*), and a rounded posterior lobe next to it on each side (*ppl*). The ental side of the posterior notal wing processes (*pnp*) of the scutum bears a small transverse phragma of unknown homology.

The endotergites of the metathorax are much more extensive than those of the mesothorax. The most conspicuous are the two **V**-ridges (figs. 4 F, 5 A, *vr*) converging anteriorly near the center of the segment. These mark the lateral boundaries of the scutellum but are not marked on the ectal surface by definite sutures. Posteriorly each **V**-ridge seems to coalesce with a transverse apodeme, the posterior notal ridge (*ponr*), which is formed from the posterior edge of the scutum and scutellum and extends from the base of one wing to the base of the other. Just laterad of the anterior end of the **V**-ridge is a short transverse apodeme called the transverse notal ridge (*tnr*). The central part of the anterior edge of the prescutum bears a lobate phragma, the prephragma (*prph*), which is more or less connected laterally to the large muscle disk (*mdtt*). The prescutoscutal suture (*psss*) marks the invagination of the anterior notal ridge (*annr*), which extends around to the base of the wings, where it approaches a small apodeme supporting the axillary process (*axp*). The posterior part of the postnotum (*pn*) bears a transverse suture (*acs*) marking a long apodeme, the postphragma (*pph*), which supports the postnotal articulations (*pna*) and is expanded into a pair of lobes which project over the posterior ends of the **V**-ridges and appear to be more or less connected with the posterior notal ridge (*ponr*).

The endopleurites are present in all three of the thoracic segments. Since the pleuron of the prothorax is greatly reduced and united with the trochantin, it is this combined sclerite that bears the pleural apophysis. This is a large crescentic process which projects under the inflexed hypomera. There is an oval sclerotization on the ental surface of the peritreme, but this is a structure of the endopleuron of the mesothorax.

The endopleurites of the mesothorax are very small. The pleural apophysis (fig. 5 B, *pla*) is formed between the episternum and the epimeron and projects into the coxal cavity to form the pleural coxal process (*cxp*). An apodeme also extends from the pleural apophysis along the posterior edge of the episternum or pleuron to the region of the muscle disk of the endotergites and to the base of the elytra.

The endopleurites of the metathorax are relatively much more developed than those of the mesothorax. The pleural apophysis (fig. 5 A, *pla*) is composed of a pleural ridge (*plr*) formed between the episternum and the epimeron along the pleural suture, and an ental ex-

tension, the pleuradema (*pld*). The dorsal edge of the sternepimeron bears the sternepimeral suture (fig. 3 A, *seps*), which marks the invagination of the sternepimeral ridge (fig. 5 A, *sepr*). Apparently arising from the cephalic end of the episternum is the very large pleural disk (*mdpt*) which extends posteriorly, overlapping the base of the wing.

The endosternites of the prothorax consist of a broad prephragma (fig. 5 B, *prph*) and the sternal apophysis (*sa*). The prephragma arises from the anterior edge of the basisternum (fig. 3 A, *bs*) and forms the ventral border of the anterior foramen (*afor*). It extends the width of the basisternum and unites with the sternal apophysis entad of the sternonotal suture (*sns*). From each lateral corner of the furcasternum (*fs*) arises a sternal apophysis which extends along the lateral edge of the sclerite to unite with the prephragma and the pleural apophysis. Near the base of each sternal apophysis is the large muscle disk (*mdsp*).

In the mesothorax the sternum bears a transverse ridge on its posterior margin. This ridge is the furca (fig. 5 B, *fu*) and has two anterior projections, the furcal arms (*fua*). The two muscle disks (*mdss*) apparently arise from the furcae also. The spinisternum (fig. 3 A, *ss*) also bears a small transverse ridge (fig. 5 B, *ssr*) with a median cariniform projection, the spina (*spn*).

The metathoracic endosternites (fig. 5 B) are more properly termed the furca than those of the mesothorax. The prominent part is the median bar (*fu*) arising from the posterior border of the sternum and projecting anteriorly in the interior of the thorax. In approximately the middle of the metathorax it divides into two lateral branches, the furcal arms (*fua*), each of which bears a large muscle disk (*mdst*). A narrow ridge is formed on the ental surface of the caudal and lateral margins of the sternum, extending anteriorly to the region of the pleural coxal process of the mesothorax.

THE APPENDAGES OF THE THORAX

THE WINGS

The elytra are highly modified wings of the mesothorax. They have a horny texture and considerable rigidity but are not used in flight. They are held apart at an angle with the body to allow freedom of motion of the wings, but when at rest are laid along the dorsum of the mesothorax and metathorax, meeting along the midline. They serve as covers for the wings, but are so small in this species that the wings must be folded transversely under them several times.

The elytron is irregularly oval in outline (fig. 6 F), with a straight mesal edge that fits against a similar edge of the opposite elytron, and an oblique anteromesal edge that fits against the side of the " scutellum " of the mesothorax. The two outer angles are broadly rounded. The greater part of the surface is flat and even, but the sides become
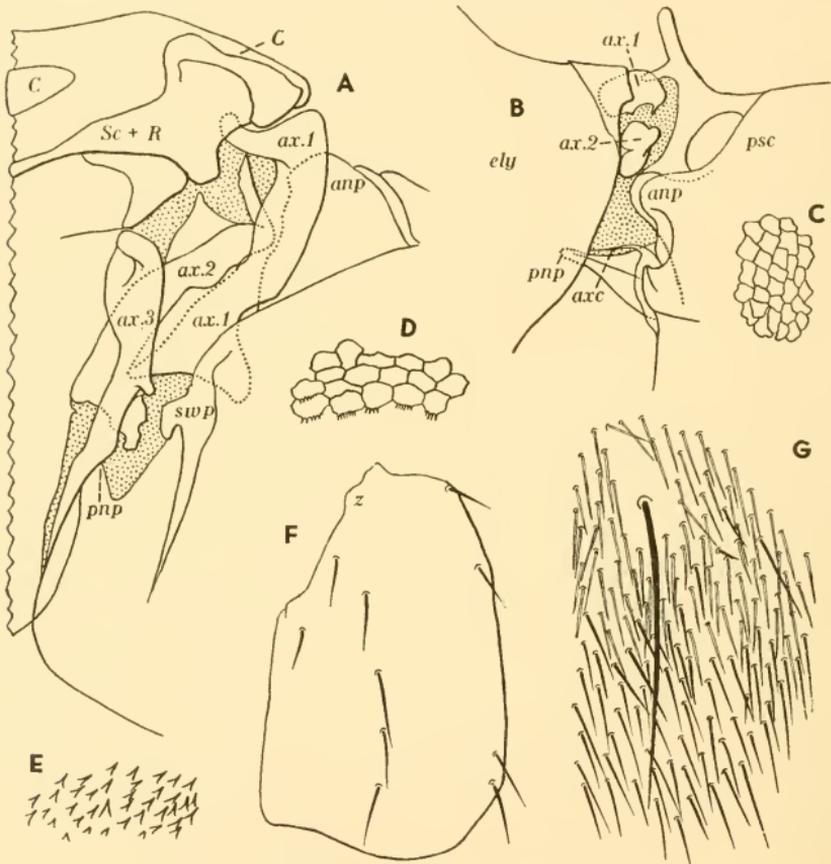

FIG. 6.—Morphology of the wing bases and elytra of
Creophilus villosus (Grav.).

A, base of hind wing, showing axillary sclerites. B, base of elytron. C, D, E, details of elytral sculpture. F, right elytron (smaller setae omitted). G, detail of three types of setae of elytron.

very convex, being deflexed somewhat onto the lateral aspect of the body.

The entire surface is densely covered with setae (fig. 6 G) of rather uniform size, and bears also a few much longer setae (figs. 6 F, G) placed in a regular pattern. There are three series of these setae: One along the lateral margin of the deflexed area, of four or five setae;

another along the axis of the disk, of three to six setae; and the third of one to three setae along the scutellar margin. Each seta is set in a puncture at the center of a small smooth area, so that it is somewhat isolated from the surrounding smaller setae. The dense smaller setae are of two colors, pale and black. They are arranged in fairly definite groups, thus giving rise to the black and white markings of the elytra. Rather frequently interspersed among the setae are several types of pores or punctures which appear to be glandular.

Certain parts of the surface are sculptured in various ways (fig. 6 C, D, E). The point indicated at z in figure 6 F probably forms part of the articulation of the elytra with the mesonotum and appears to be very finely scaly (fig. 6 C). This area extends for a short distance on both the dorsal and ventral surfaces of the elytron, and the scales grade off anteriorly into minute points (fig. 6 D, E).

The elytron articulates with the mesonotum by means of the two wing processes (fig. 6 B, anp, pnp). The connecting membrane bears two irregular, very lightly sclerotized areas, which have been interpreted as the first and second axillary sclerites ($ax. 1$, $ax. 2$). The axillary cord (axc) proceeds from the margin of the scutellum. As the actual movement of the elytron is rather slight, the whole articulating mechanism is much less developed than that of the hind wings.

The hind wings (fig. 7 A) are well developed, being nearly as long as the entire body. The wing is approximately one-third as wide as long, with a distinct and heavily sclerotized hinge just proximad of the stigma, and a large separate anal lobe. The venation is greatly reduced and not easily homologized. The following scheme is tentatively adopted here.

The most conspicuous vein is the one arising from the articulation with the first axillary sclerite (fig. 6 A, $ax. 1$) and extending to the hinge, enclosing a narrow costal area. This vein is the subcosta united with the radius (fig. 7 A, Sc, R). It is apparently double, as shown, the anterior and the basal parts representing the subcosta, the distal part being chiefly radius. The costa is anterior to the subcosta but is rather indefinite. It is represented by an oval area (fig. 7 A, C, and 7 D) near the base of the wing and by the anterior basal edge of the wing. The base of the subcosta articulates with the first axillary sclerite (fig. 6 A), but the costa is the only part of the wing that could come in contact with the anterior notal wing process (anp). The subbasal area (fig. 7 D) appears to be a raised sclerotic plate bearing numerous setae. It is surrounded by membranous areas and does not touch the margin of the wing. This is the only part of the wing bearing true setae.
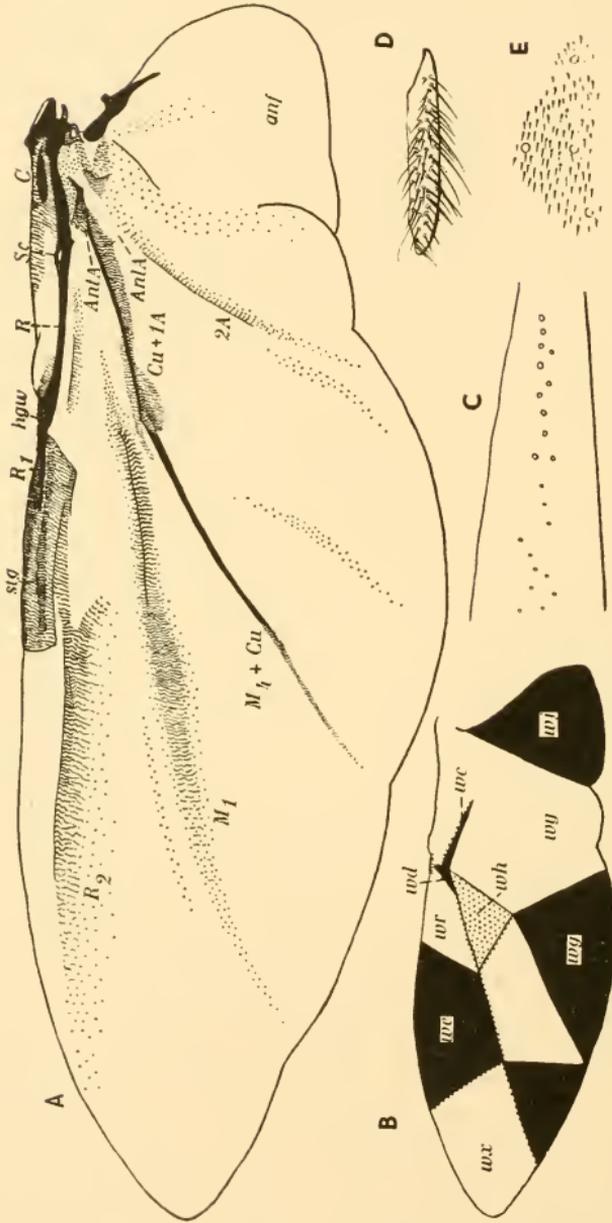
Fig. 7.—The wing of *Creophilus villosus* (Grav.).

A, left wing. B, diagram of folding pattern. C, detail of base of radius vein. D, sclerotized plate of costa vein. E, detail of microtrichia of wing surface near the base.

The base of the subcosta overlies the basal part of the radius as shown in figure 6 A, and a short distance from the base it divides into two parts. The anterior of these is the subcosta. It is continued distally nearly to the hinge but is covered by the radius except near the base where they overlap somewhat. Near the point at which the subcosta passes under the radius, the posterior edge of the radius has a small projection which approaches a projection from the cubitus and is interpreted as the anterior arculus ($AntA$). Apparently in nearly all beetles the radius is characterized by the presence of tiny pores on the dorsal surface near the arculus. These pores (fig. 7 C) appear immediately distad of the separation of the radius from the subcosta. They serve as a ready means of identifying this vein. The radius typically arises from the second axillary sclerite, but here the base is united with the subcosta and its union with the second axillary is not apparent, though they do approximate each other. The radius is extended distally to form the large rectangular stigma (stg) near the middle of the anterior margin. A disconnected branch of radius (R_2) extends from near the stigma toward the tip of the wing, but it is rather indefinite and not strongly sclerotized.

Posterior to R_2 is another indefinitely sclerotized area which represents the first branch of the media (fig. 7 A, M_1). Its basal part is entirely lost, and the only other branch that remains of the media is considered to be united with the distal part of the cubitus (M_4+Cu).

The cubitus is a definite vein extending from the anterior arculus (fig. 7 A, $AntA$) diagonally across the wing. Its distal part is united with M_4, and its proximal part with the first anal vein. There is a distinct angle between these proximal and distal parts, and this point approaches rather close to the base of M_1. The anterior arculus is on the dorsal edge of the base of the vein, and just distad of this on the ventral edge is the anal arculus ($AnlA$). The cubitus is supposed to arise from the third axillary sclerite, but this connection is not apparent in this form.

The anal veins are all very indefinite. The first anal is apparently united with the proximal part of the cubitus (fig. 7 A, $Cu+1A$). This is the vein that forms the anal arculus, which extends toward the second anal vein. The second, third, and fourth anals are merely darker streaks in the wing membrane. It is apparently the third (or the second branch of the second) that marks the anal fan (anf).

The surface of the wing is marked by streaks of darker color, whereas the hinge (fig. 7 A, hgw) and the stigma (stg) are very dark and opaque. The entire surface of the wing, both dorsally and ventrally, is covered with minute points or setulae which grade off on the

posterior and anal areas into tiny rounded or truncated conical pro-
jections. In the costal area also they are replaced by minute rounded
tubercles. Along the posterior margin of the wing these setulae are
frequently twice as long as on the surface, but they are still minute
and are merely processes, not setae.

The wing is articulated to the metanotum by means of the two notal
wing processes (figs. 4 F, 6 A, *anp, pnp*) and the three axillary scle-
rites (*ax. 1, ax. 2, ax. 3*). Figure 6 A shows the relations of these
parts to the wing. The united subcosta and radius ($Sc+R$) is the only
vein that is prominent at the wing base, and it forms a definite articula-
tion with the first axillary sclerite (*ax. 1*). Near the base of the first
and second axillaries is a process of the scutum which evidently forms
a condyle for the base of the second and middle portion of the third
axillaries. This is tentatively designated the scutal wing process
(*swp*) as it has apparently been unnoticed heretofore.

THE LEGS

The legs are composed of five main divisions, the coxae, trochanters,
femora, tibiae, and tarsi. The first four divisions consist of a single
segment each, the tarsus consisting of five subsegments or tarsomeres,
the last of which bears the pretarsus and its ungues.

The anterior legs (fig. 8 F) are short and stout and very densely
covered with setae. The coxa (*cx*) is rather cylindrical and fusiform.
Its proximal end articulates with a proximal process of the trochantin
by means of a condyle (fig. 8 H, *cxa*) and with the distal end of the
trochantin by a somewhat indefinite projection (*tra*). The distal end
of the coxa bears the articulation of the trochanter (fig. 8 F, *tr*)
upon its ventral side. This articulation (fig. 8 G) is a large mem-
branous area with several rather indefinite projections which serve as
condyles. The dorsal and anterior surfaces of the coxa are densely
set with slender setae, even more densely than shown in figure 8 F,
but the ventral and posterior surfaces are glabrous and impunctate,
with the following exception. Along the posterior edge of the ventral
face, from the middle to the distal end, is a row of long and slender
setae. The punctures are small and placed in a regular series at first,
but distally are crowded and somewhat irregular. Some of the setae
attain a length equal to half the width of the coxa. The dorsal vesti-
ture is also denser near the distal end of the coxa.

The trochanter of the prothoracic leg (fig. 8 F, G, *tr*) is rather
elongate and somewhat triangular. It is immovably attached to the
base of the femur, thus forming the articulation of the latter with
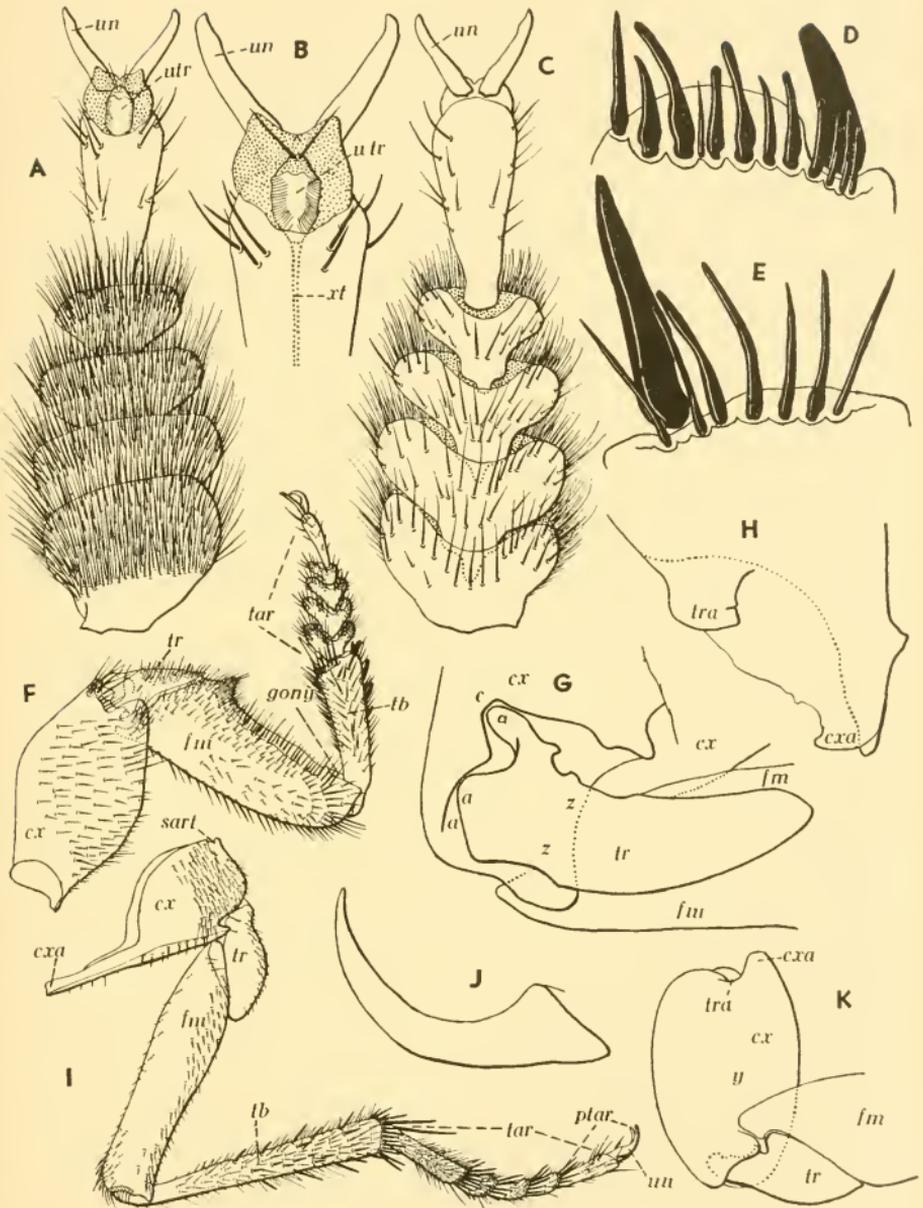
FIG. 8.—Morphology of the legs of *Creophilus villosus* (Grav.).

A, ventral aspect of tarsus of prothorax. B, ventral aspect of pretarsus of prothorax. C, dorsal aspect of tarsus of prothorax. D, comb of setae and calcar from anterior side of tibia of prothorax. E, comb of setae and calcar from posterior side of tibia of prothorax. F, prothoracic leg. G, trochanter of prothoracic leg. H, articulations of base of coxa of prothoracic leg. I, metathoracic leg. J, claw of metathoracic leg. K, coxa and trochanter of mesothoracic leg.

the coxa. The trochanter articulates with the coxa by means of two rather indefinite condyles (*a, c,* and *a, a*) which permit a dorsoventral movement only. The distal two-thirds of the exposed surface bears numerous moderately long setae, and the area at *z* (fig. 8 G) has a very few large pores which are quite distinct from the setigerous punctures.

The femur (fig. 8 F) is the largest segment of the leg. It tapers somewhat distad and bears a large tubercle on its ventral proximal margin. The proximal end is obliquely truncated and is immovably united to the trochanter by a flat surface. The distal end bears a dorso-ventral groove in which the tibia articulates. This groove is known as the gonytheca (*gony*). The proximal dorsal tip forms an acutely rounded projection which appears to articulate to some extent with a socket on the outer edge of the coxa. The posterior surface of the femur is moderately densely set with setae, more sparsely proximad and dorsad. The setae of the anterior surface are similarly arranged, being very dense along the tubercle, very sparse on the basal dorsal part, and entirely lacking from a narrow strip along the ventral face, which is outlined on both the anterior and posterior faces by an ir-regular longitudinal series of more closely placed setae. Another series, of more widely spaced setae, extends along the dorsal face into two smooth areas. The setae are somewhat longer and more dense near the dorsal apical margin and show some tendency to serial arrange-ment across the tip. With transmitted light one may observe the minute pores which occur in clusters of two to five about the base of each seta. The surface is extremely finely and irregularly, but linearly and longitudinally, striate in great part.

The tibia is the fourth segment of the leg. In the prothoracic leg (fig. 8 F, *tb*) it is shorter than the femur and about one-half as thick, expanding slightly toward the apex. It articulates with the femur by means of a rounded head on its proximal end, which fits into the groove or gonytheca of the femur (*gony*) and is held there by a pair of condyles on each side. This head is somewhat curved toward the femur, allowing the tibia to lie along the ventral edge of the femur at rest. The distal end of the tibia is rather rounded and membranous. It bears the tarsus and the two tibial spurs as well as numerous very stout heavy setae around the tip. The spurs are known as the calcaria (*cal*). They are inserted within the membranous area of the tip, but are apparently merely slightly modified setae. The larger one is in-serted on the posterior side of the tarsus and the smaller one on the anterior side, both of them slightly ventrad of the middle. The tip is nearly circled by two series of very large and heavy setae, one on

the anterior and one on the posterior face. Those of the posterior series
(fig. 8 E) are longer and more slender than those of the anterior series
(fig. 8 D), but the latter series contains more setae (about 12) and
extends farther across the tip. The main part of the tibia bears two
types of setae. The most conspicuous is the large thick and blunt
setae similar to those of the terminal series but shorter and some-
what more regular in outline. They occur scattered sparsely on the
posterior aspect, there being perhaps 15 in all, but there are none on
the anterior face. The other type is the smaller tapering setae which
form the normal vestiture. They are sparse on the posterior aspect,
none occurring close to the proximal end, and they approximate the
length of the larger terminal series on the distal portion, being gradu-
ally smaller toward the base. The anterior aspect and the dorsal
portion are clothed with these finer setae similarly to the posterior
face, but the ventral aspect of the tibia is very much more densely
clothed. The base of nearly all of these setae is surrounded by a group
of two to four pores as on the femur, and the anterior face is sup-
plied with additional scattered pores. The surface of the tibia is very
minutely transversely strigulose in contrast to the femur, which is
longitudinally striate.

The tarsus of the prothoracic leg (fig. 8 F, *tar*) is rather loosely
united to the tibia. The latter bears a rather large terminal membranous
area into which the basal segment of the tarsus, the so-called metatarsus,
is inserted. There are two rather indefinite condyles on the tarsus,
one anterior and one posterior, but no definite corresponding condyles
have been observed on the tibia. The tarsus consists of five tarsomeres
or tarsites, of which the first four are greatly expanded into trans-
verse plates (fig. 8 A, C). The first and second are approximately the
same size, the next two decreasing successively in width and length.
On the dorsal aspect each of these four tarsomeres is broadly emargi-
nate anteriorly, whereas the anterior margin of the ventral side is
expanded in a broad curve forming a large flat plate. The space be-
tween the dorsal emargination and the ventral plate is membranous
and receives the base of the next segment (fig. 8 C). The fifth tarso-
mere is elongate, nearly three times as long as wide, and is inserted
upon the dorsal side of the preceding tarsomere similarly to the others.
It is expanded rather strongly and regularly toward the apex and
is rather cylindrical in form. On its distal end the fifth tarsomere bears
a pair of claws (fig. 8 B, *un*) and an expanded membranous lobe carry-
ing a small ventral plate, the unguitractor plate (*utr*). The claws (fig.
8 J) are slightly compressed dorsoventrally, rather strongly curved
and tapering, and they articulate with the rounded end of the dorsal

surface of the last tarsomere. From the proximal end of the ungui-
tractor plate arises the tendon of the retractor muscle of the claws
(xt). The unguitractor plate is rather quadrate, tapering proximally
into the tendon, and is partly inserted into the end of the last tarsomere.
Its distal end is somewhat indefinitely produced into an unsclerotized
area bearing two large setae. This is the empodium.

The dorsal aspect of each tarsomere (fig. 8 C) bears a few scattered
moderately long but fine setae, and the ventral side of the fifth seg-
ment is similarly clothed. The ventral aspect of each of the first four
tarsomeres (fig. 8 A) is very densely set with long fine hairs, which are
absent from the basal portion of each tarsomere. These four tarso-
meres are thus united into a single hairy pad. The two setae on the
empodium have been called parempodia (Hayes and Kearns, 1934)
and are stated to arise from conspicuous trichophores on the empo-
dium. They are, however, perfectly normal setae, and it is doubtful
whether they have any such significance as is implied to them. Their
insertion is very inconspicuous as is usual on such lightly sclerotized
areas.

The mesothoracic legs are longer than the prothoracic legs but not
quite as long as the metathoracic ones. As they are similar to the
others in structure and general arrangement, they are treated briefly
and not figured completely.

The coxa of the mesothoracic leg (fig. 8 K) is shorter and ovate.
It is strongly convex and somewhat excavated on the ventral aspect to
receive the base of the femur at rest. The proximal end is slightly
produced on the outer side to form the coxal condyle (cxa), which
articulates with the pleural coxal process. The trochantinal articulation
is situated near the center of the proximal end and is retracted to form
a concavity that receives the end of the trochantin. The distal end of
the coxa is deeply grooved to receive the trochanter. The anterior lip
of the groove forms a rounded condyle that articulates in a small
socket on the trochanter. The ventral side of the latter is prolonged
proximad into the coxa, forming a large muscle attachment. The an-
terior aspect of the coxa is somewhat more densely clothed than the
prothoracic coxa, but the vestiture is practically restricted to the inner
or mesal half, only a very few scattered setae occurring on the con-
cavity laterad of the line y. The distal end of the posterior aspect also
bears a few setae similar to the anterior side. At the tip of the inner
face the setae form a long dense brush, and the punctures are so
close as to merge with one another.

The trochanter is moderately densely set with long setae on the
ventral and anterior sides. Each of the punctures has one or more

relatively large pores close to it. The posterior face is more sparsely punctured than the anterior.

The femur of the mesothoracic leg is slightly longer and considerably thicker than that of the prothorax. The anterior aspect bears numerous moderately long setae which are much sparser at the base and much shorter along the dorsal edge. The posterior face is glabrous but is extremely minutely longitudinally striate. The ventral part of the gonytheca bears a few scattered short setae.

The tibia of the mesothoracic leg is very similar in form to that of the prothoracic leg. It is nearly one-half again as long and exceedingly roughly sculptured. The terminal combs of setae are very similar, and the other vestiture differs chiefly in being longer and more dense. The large blunt setae are longer and more irregular in shape and much more abundant. The calcaria are similar to those of the metathoracic leg (fig. 8 I).

The tarsus is almost exactly similar to that of the metathorax (fig. 8 I). It is very slightly shorter and bears more of the large terminal dorsal setae on each tarsomere.

The metathoracic legs (fig. 8 I) are longer and slightly stouter than the other legs, but the sculpture and vestiture are not as evident as on either of the others. The coxa (*cx*) is short and very transverse, being rather globular medially with a narrow lateral extension that bears the pleural articulation (*cxa*), which is rather indefinitely associated with the tip of the episternum. The median proximal part forms the articulation with the metasternum. The median distal part articulates with the trochanter (*tr*) by two sets of condyles, one anterior and one posterior. The anterior aspect is sparsely clothed with moderately fine setae which become denser and larger toward the apex. There is a slight concavity extending diagonally across the coxa from the median anterior angle and this irregular band is impunctate. The posterior aspect is glabrous except for the median and apical areas which are clothed similarly to and continuously with the anterior parts. The caudal or ventral edge of the transverse lateral part is slightly concave and bears an irregular row of small setae.

The trochanter (fig. 8 I, *tr*) is rather oval in form with its proximal ventral part extended into the interior of the coxa for muscle attachment. It is immovably attached to the posterior side of the proximal end of the femur as in the other legs. Its anterior surface is moderately closely set with small setae, among which are a few of the tiny pores. The posterior aspect is glabrous except for a few setae which are continued around from the anterior side. The femur of the metathoracic leg (*fm*) is tapered to a blunt point proximally and truncated

distally. The gonytheca is rather broad and extends half way down the ventral side as a distinct groove. This groove bears an irregular row of short setae. The anterior surface is clothed with moderately long setae, rather more sparse at the base and longer around the apex. These are also more densely placed ventrad along the edge of the ventral groove. The posterior surface (fig. 8 I) bears a few small setae along the border of the ventral groove, and near the apex a few which are continued around from the anterior side. There is also a series of longer close-set setae along the distal truncated margin, which is continued onto the dorsal margin also. This posterior surface is also very minutely longitudinally striate.

The tibia (fig. 8 I, *tb*) is rather slender, cylindrical, and somewhat regularly expanded distad. Its apex bears a complete circle of large setae very similar to those on the prothoracic tibia (figs. 8 D, E) but the calcaria are much larger and more conspicuous. The anterior vesti-ture is rather dense and the setae long. It is much denser toward the apex and the dorsum. The large thick setae are scattered irregu-larly over the surface, there being perhaps 10 or 12 present. The posterior surface (fig. 8 I) is more sparsely clothed and lacks entirely the larger setae except in the apical series. There is a dorsal series of four or five of the larger setae. The calcaria are unequal in length, the posterior being much the longer, and nearly as long as the first tarsomere. Their surface has an irregular scaly appearance.

The tarsus of the metathoracic leg (fig. 8 I, *tar*) is nearly as long as the tibia, five-segmented like the others, and very nearly cylindrical. The first tarsomere is elongate, nearly as long as the next three to-gether, the latter decreasing in length slightly among themselves distally. The fifth tarsomere is somewhat shorter than the first and bears two claws and the empodium, which are very similar to those of the prothoracic leg (fig. 8 B). Each of the first four tarsomeres is a little more extended ventrad than dorsad and therefore is in-serted apparently a trifle more on the dorsal aspect. They are rather densely clothed with small setae except for the base of the distal four, and the surface of the first is roughly sculptured. The apex of each tarsomere, particularly ventrally, bears a number of very long setae which often reach to the apex of the succeeding tarsomere. The last one is more sparsely clothed with the longer setae and bears the two long setae on the empodial end of the unguitractor plate.

THE ABDOMEN

The abdomen (fig. 9 A) or third region of the body is composed of a series of 10 segments, of which the last two form the genitalia.

Each of the first eight segments bears a pair of spiracles in the tergum, and each one except the eighth has one or two paratergites on each side between the tergite and the sternite.

The first segment is more closely united to the thorax than to the abdomen (fig. 3 A, *tt. 1*). The sternite of this segment is not present, the tergite (fig. 9 A, *tt. 1*), one paratergite on each side (*ptt. 1*), and the large spiracles (*sp. 1*) composing the tergum. The tergite is wider than any of the other tergites and is expanded laterally to nearly twice the length at the middle. Anteriorly it is closely united to the postnotum of the metathorax and posteriorly is rather widely separated from the tergite of the second segment. The surface is not marked by any sutures and is rather lightly sclerotized. A narrow strip along the lateral margin (*y, y*) is somewhat elevated and rather densely clothed with setae. This area is wider posteriorly, and the setae are long in front but becoming much longer posteriorly. The punctures are separated by two to four times their own width and are interspersed with tiny circular nonsetigerous punctures. The remainder of the surface except near the midline is sparsely set with very small setae in small punctures, with scattered nonsetigerous punctures also. The surface is finely strigulate except at the middle, where the posterior area is very densely and finely, but strongly, muricate. This murication is continued onto the membrane behind the tergite and expands somewhat laterally. On the ental surface of the tergite the strigulae are serrate on the posterior edge over nearly the entire surface.

The paratergites (fig. 9 A, *ptt. 1*) of the first abdominal segment consist of a single broad plate on each side of the tergite. They are about one-half as long as the lateral margin of the tergite and are nearly quadrate. Anteriorly each is deeply emarginate to receive the end of the spiracle (*sp. 1*). The paratergites are clothed similarly to the lateral parts of the tergite except that the setae are a little shorter and are densest in front. The posterior margin is unclothed but bears the scattered small punctures similarly to the rest.

The spiracle of the first abdominal segment (fig. 9 A, *sp. 1,* D) is the largest spiracle on the body. It is about twice as long as wide and occupies the anterior half of the lateral margin of the first tergite. It is formed of an oval plate with a large irregularly oval aperture, which is almost completely closed by two series of narrow branching lobes along the sides, which project in one plane over the aperture and, by means of their very dense covering of minute hairlike projections, form a sieve plate over the whole aperture. These microscopic points
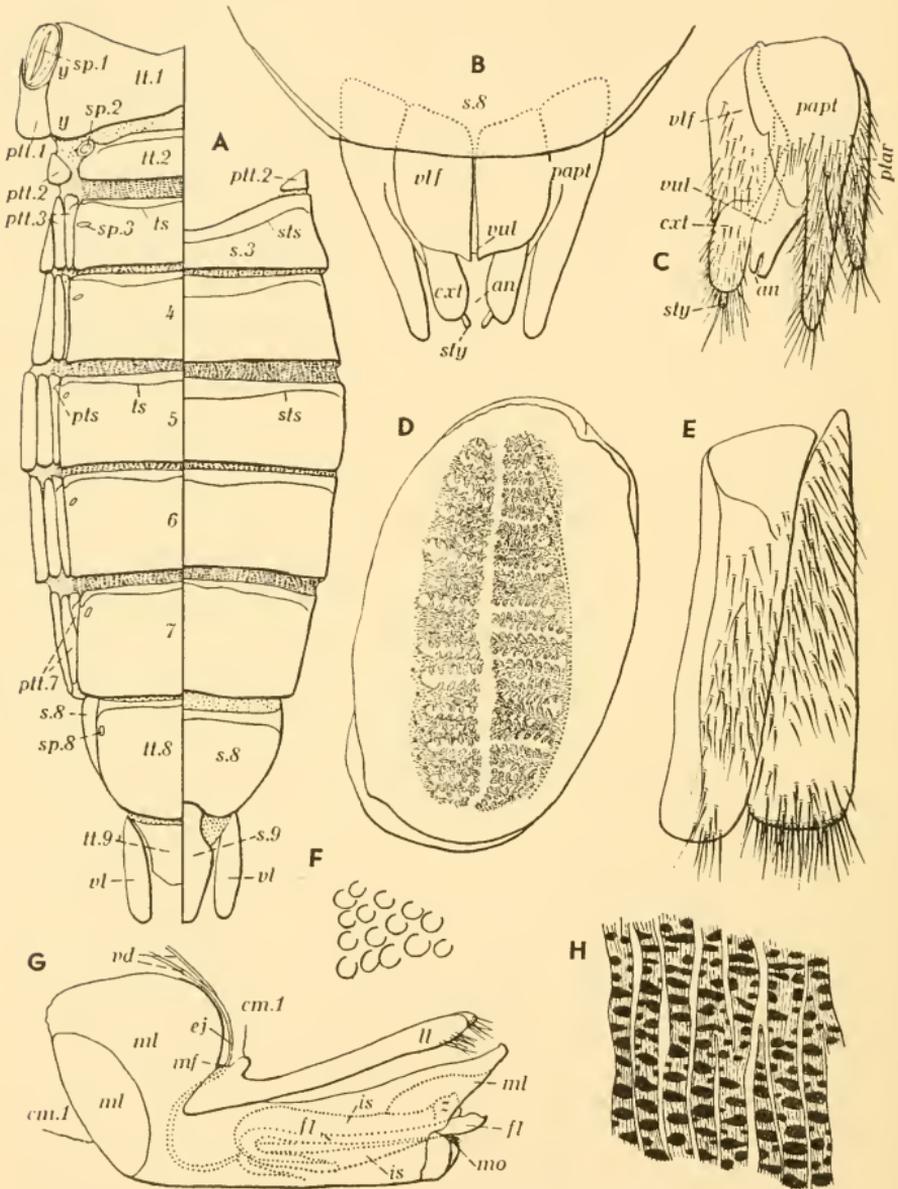
FIG. 9.—Morphology of the abdomen and genitalia of
Creophilus villosus (Grav.).

A, dorsal and ventral aspects of abdomen of male. B, dorsal aspect of female
genitalia. C, lateral aspect of female genitalia. D, spiracle of first abdominal seg-
ment. E, paratergites from left side of third abdominal segment. F, sculpture of
inner side of median orifice of male genitalia. G, lateral aspect of male genitalia.
H, mosaic pattern of intersegmental membranes.

are placed in tiny circular groups, and these are continued out onto the surface of the plate giving it a striated and spotted appearance.

The second abdominal segment is composed of a small tergite and one small paratergite on each side extending around onto the ventral aspect. The spiracles are more or less united to the tergite.

The tergite of the second segment (fig. 9 A, *tt. 2*) is about equal in width to the succeeding segments but is shorter than any. The segments from two to eight, in fact, increase regularly in length. The shape is somewhat fusiform, and the anterolateral angle is produced to enclose the spiracle. The surface is longitudinally marked by a strong suture parallel to the anterior margin, and the vestiture consists of a small group of long setae at the posterolateral angles and a very few scattered setae along the posterior margin. The surface is very finely transversely strigulose throughout and is rather densely beset with relatively large lageniform pores.

The second segment has one paratergite (fig. 9 A, *ptt. 2*) on each side of the tergite. They are rather wider than long, tapering toward each end and are curved around onto the dorsal aspect. No vestiture or sutures have been observed, but the surface is sculptured similarly to the tergite.

The sternum of the second segment is entirely membranous and unrecognizable.

The anterolateral corners of the second tergite are slightly produced to embrace a small circular sclerite bearing the spiracle of the second segment. This sclerite is the second abdominal peritreme (fig. 3 A, *peri*). The spiracle is approximately one-fourth as large linearly as the first abdominal spiracle but is slightly larger than the following ones. The spiracle is very similar in structure to the first abdominal one, having the processes covered with minute hairs that form the sieve plates.

The membrane separating the tergites of the second and the third abdominal segments bears a minute but very definite pattern of more heavily sclerotized or pigmented areas which are arranged on longitudinal irregularly anastomosing strips separated by clear membranes (fig. 9 H). This type of membrane is found between the tergites of the second to seventh segments and between the sternites of the third to seventh segments. It fades off laterally to normal membrane in the region of the paratergites.

The tergites of the segments three to seven (fig. 9 A), are all nearly rectangular and are marked by a sinuous transverse fold or suture (*ts*) along the anterior margin. Each bears a spiracle near each anterolateral angle and is bordered on each side by a pair of paratergites.

The narrow strip between the fold and the anterior margin bears a very few long, well-separated setae on the caudal margin, except on the seventh segment, where these setae are about twice as numerous. The main part of the tergite has a rather conspicuous vestiture of long setae. These are set in punctures not noticeably larger than the base of the setae, and separated from each other on the median area by from three to five times their own width, but near the sides by slightly less. At the sides of the seventh segment this vestiture is even slightly denser. Anteriorly on each segment the setae become more sparse and leave a narrow irregular impunctate strip just posterior to the fold or suture. Along the posterior margin the setae are arranged in a single series close to the edge. They are close-set, with the punctures anastomosing, and thus form a kind of marginal fringe. These setae are nearly twice as long as the discal ones. This occurs only on the third to sixth segments. The surface of all these tergites is minutely transversely strigulose, and the setae are interspersed with numerous tiny lageniform pores.

The eighth tergite is the last exposed tergite and is broadly tapered and rounded behind. The sculpture and vestiture are similar to the preceding segments, except that the discal setae are less conspicuous, separated by three to five times the width of their punctures, and not arranged in a definite posterior marginal series.

The sternites of the third to seventh abdominal segments (fig. 9 A) are very similar in structure, vestiture, and sculpture, but differ slightly among themselves in form. They decrease in width slightly from the fifth posteriorly, while increasing in length from the third to the seventh. They extend around the lateral aspect onto the dorsum and are marked with an anterior marginal fold or suture (*sts*) similarly to the tergites. This suture is somewhat arcuate and disappears near the side of the ventral aspect. The third sternite (*s. 3*) is narrowed in the middle so that it is about one-half as long at that point as at the sides. The eighth sternite (*s. 8*) is narrowed and rounded posteriorly similarly to the tergite in the female, but in the male is broadly and shallowly emarginate at the middle. Each of these six sternites is clothed very similarly to the tergites. The setae are long and slender, the punctures small and placed at three to five times their own width apart, a little more numerous at the sides of the venter, and arranged in a single closely spaced series along the posterior margin. This series is present on all the sternites from the third to the eighth. The strip anterior to the suture is sparsely clothed, and a narrow line posterior to it is smooth. The longitudinal strigulations are much finer than on the tergites, being very indistinct except on the

strip anterior to the sternal suture. The lageniform pores are very abundant, especially on the posterolateral portions of the ventral aspect of each sternite.

The paratergites (fig. 9 A, *ptt*, E) are narrow longitudinal sclerites on the dorsal aspect between the tergites and the up-turned edges of the sternites. There is one on each side of the first abdominal tergite, one on each side of the second tergite, and two on each side of the segments from the third to the seventh. The eighth segment alone has no paratergites. The first two segments have already been described. The paratergites of the third to the seventh segments are very similar in form and arrangement throughout. The median one is slightly expanded and truncated anteriorly and more or less tapering caudally. The outer one is rather larger posteriorly but rounded, and tapers somewhat anteriorly. On the seventh segment the inner paratergite is much shorter, being only half the usual length and more sharply tapering. All the others are equal in length to the rest of the segment. The inner paratergite of each segment bears a raised line or fold (*pts*) near the anterior end in such a position as to appear to be a continuation of the tergal suture (*ts*).

The endoskeleton of the abdomen consists chiefly of narrow apophyses along the margins of the segments. These are sometimes known as plicae, and MacGillivray has proposed a system of naming them.

Each of the dorsal segments from the second to the ninth has a narrow phragma near the anterior margin which extends along the sides to the posterior angles except on the second, eighth, and ninth segments (fig. 5 A). These phragmata are marked externally by sutures (fig. 9 A) except on the second, eighth, and ninth segments, in which the phragmata are at the anterior edge of the segment. Each spiracle, except those on the eighth segment, has a small roughly circular apophysis on its ental surface. On the fifth and sixth segments there is a very small transverse apophysis just in front of the margin. These are apparently not marked on the exterior.

The tergal or dorsal member of each pair of paratergites has a narrow apophysis along the anterior end and the median edge. This is found only on the third to seventh segments.

The ventral segments from the third to the eighth each have an anterior apophysis similar to the dorsum. A transverse posterior apophysis is present on the third to sixth sternites.

THE GENITALIA

The abdominal segments posterior to the eighth form the genitalia. Owing to special modifications, these are very different in the two

4

sexes. The genitalia of the female (fig. 9 B, C) are comparatively slight modifications of the ninth and tenth segments. The tergite of the ninth segment $(tt. 9)$ is the sclerite termed the proctiger by Tanner (1927). The anus (an) is borne not at the end of this sclerite but on another lobe beneath this, the dorsal surface of which represents the tenth tergite. The homology of the pair of elongate lobes, called paraprocts by Tanner, which lie along the sides of the true " proctiger " or tenth segment, are not known. They most likely are parts of the ninth tergum which have become separated from the tergite. The sternum of the ninth segment is represented in the two rectangular sclerites (vlf) meeting along the midline and called the valvifers by Tanner. These bear a pair of two-segmented appendages composed of a basal coxite (cxt) and a stylus (sty). This interpretation differs somewhat from that of Tanner, as he considered the valvifers to be the basal segment of the appendages of the ninth segment. The opening of the vulva (vul) is behind (entad) and between the apices of the sternal plates. The distal portions of the ninth tergite and the lateral lobes, the valvifers, the coxites, and the styli are clothed with rather long but pale setae. The surface of the membrane about the vulva is finely muricate with rather blunt pustules.

The genitalia of the male (fig. 9 G) are much more highly specialized or modified than those of the female in this species. The several sclerites caudad of the eighth segment of the abdomen but not actually forming part of the aedeagus have not heretofore been considered as part of the male genitalia. Since they correspond rather closely to the parts of the ninth segment in the female, they are here included with the genitalia of the male.

The ninth segment appears to be present as four distinct parts. The median dorsal surface (fig. 9 A, $tt. 9$) is almost entirely unsclerotized but bears numerous setae. This area is assumed to represent the ninth tergite. On each side is an elongate lobe (vl), heavily sclerotized and densely clothed with setae, which is interpreted as the appendage of the ninth segment, the valvula. The sternum is occupied by a sagittate sclerite $(s. 9)$ which is undoubtedly the ninth sternite. It is densely clothed with setae similarly to the valvulae and the eighth sternite.

The male genital tube consists of a strong median lobe and a pair of united lateral lobes. The median lobe (fig. 9 G, ml) has a large bulbous base and bears the median orifice (mo) at its distal end. On the ventral side at the junction of the bulbous part and the distal tube is the small median foramen (mf) through which passes the ejaculatory duct (ej). This duct opens to the exterior through the tip of the flagellum (fl), which is somewhat coiled and apparently double

and projects somewhat from the median orifice (*mo*). The internal sac (*is*) is rather large and nearly encloses the flagellum. Its ventral surface is rather coarsely muricate, whereas the dorsal surface is densely set with tiny spines or pointed processes. The internal surface just below the flagellum at the point *z* is sculptured into minute scalelike protuberances (fig. 9 F), while just dorsal to the flagellum is a small lobe projecting from the median orifice and very densely clothed with long but fine hairs or setae. The two lateral lobes are united on the ventral aspect except at the tip. They are very nearly as long as the median lobe and very slender, with a small group of long setae on the dorsal side at the tip.

The outer surface of the aedeagus bears no sculpture or vestiture, except for the frequent very minute pores which traverse the integument.

COMPARATIVE MORPHOLOGY OF THE FAMILY

The following section is intended to give a brief review of the variation within the family of certain of the more important characters as they are found in the series of species studied. There are very probably many further modifications to be found in other species, but the present study will serve to show the chief types and the general trend of variation.

THE HEAD

The head capsule shows a great many modifications in structure as well as a wide variety of form and sculpture. The proportions of length to breadth are found in all stages from 2:1 to 1:2 (figs. 10, 11). The shape may vary considerably within a single genus or even a single species, or it may be fairly constant in a larger group.

The dorsal surface of the head, or epicranium, is generally not divided by sutures as in more generalized insects. Of the species studied, only *Tachyporus* (fig. 10 C), *Tachinus,* and *Erchomus* (all in the tribe Tachyporini) show any trace of the anterior part of the coronal suture. A few species have a very short part of the suture visible at the posterior margin of the epicranium. These include *Pseudopsis, Paederus, Lathrotropis, Lithocharis, Trachysectus, Pinophilus, Xantholinus, Staphylinus, Philonthus, Cafius, Glenus, Acylophorus* (fig. 11 G), *Quedius, Bolitobius* (fig. 11 F), and *Xenodusa.*

The frontal sutures are complete between the anterior tentorial pits in all the Tachyporinae studied except *Hypocyptus* (fig. 10 D) as well as the Habrocerinae and Oxyporinae. They were also found in this condition in certain Oxytelini and Piestini. The following are noted

in this group: *Trigonurus* (fig. 10 A), *Bledius, Aploderus, Oxyporus* (fig. 11 D), *Habrocerus, Tachyporus* (fig. 10 C), *Tachinus, Erchomus,* and *Bolitobius* (fig. 11 F). However, in none of these species
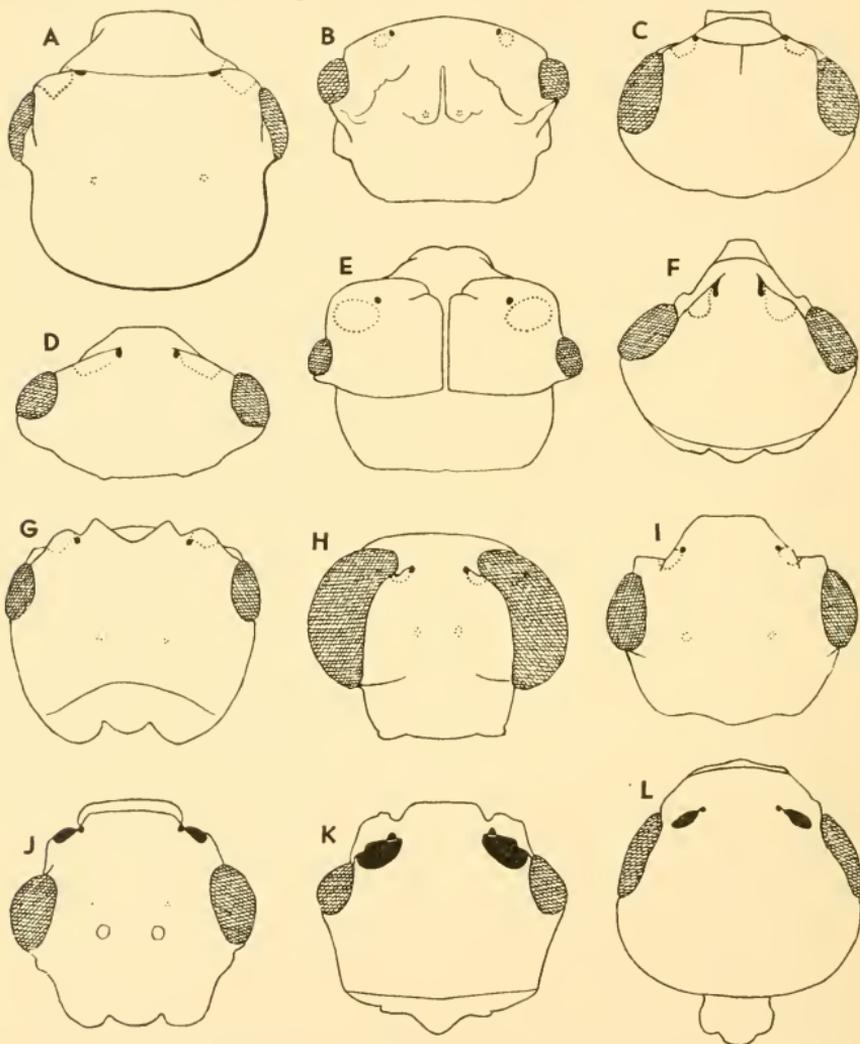

FIG. 10.—Intrafamily variation in the form and structure of the dorsal aspect of the head (continued on fig. 11).

A, *Trigonurus crotchi* Lec. B, *Micropeplus punctatus* Lec. C, *Tachyporus jocosus* Say. D, *Hypocyptus longicornis* (Payk.). E, *Leptochirus mexicanus* Er. F, *Alcochara lata* Grav. G, *Platystethus americanus* Er. H, *Stenus sculptilis* Csy. I, *Proteinus limbatus* Mäkl. J, *Pelecomalium testaceum* (Mann.). K, *Xenodusa sharpi* Wasm. L, *Lorinota cingulata* (Lec.).

is there any evidence of the presence, as a sclerite, of the frons. This sclerite is normally bounded laterally and posteriorly by the frontal sutures and anteriorly by the frontoclypeal or epistomal su-

ture, or, if this suture is absent, approximately by a line drawn be-
tween the anterior tentorial pits. Since in these forms the frontal
sutures unite to form a nearly straight line, it is obvious that the true
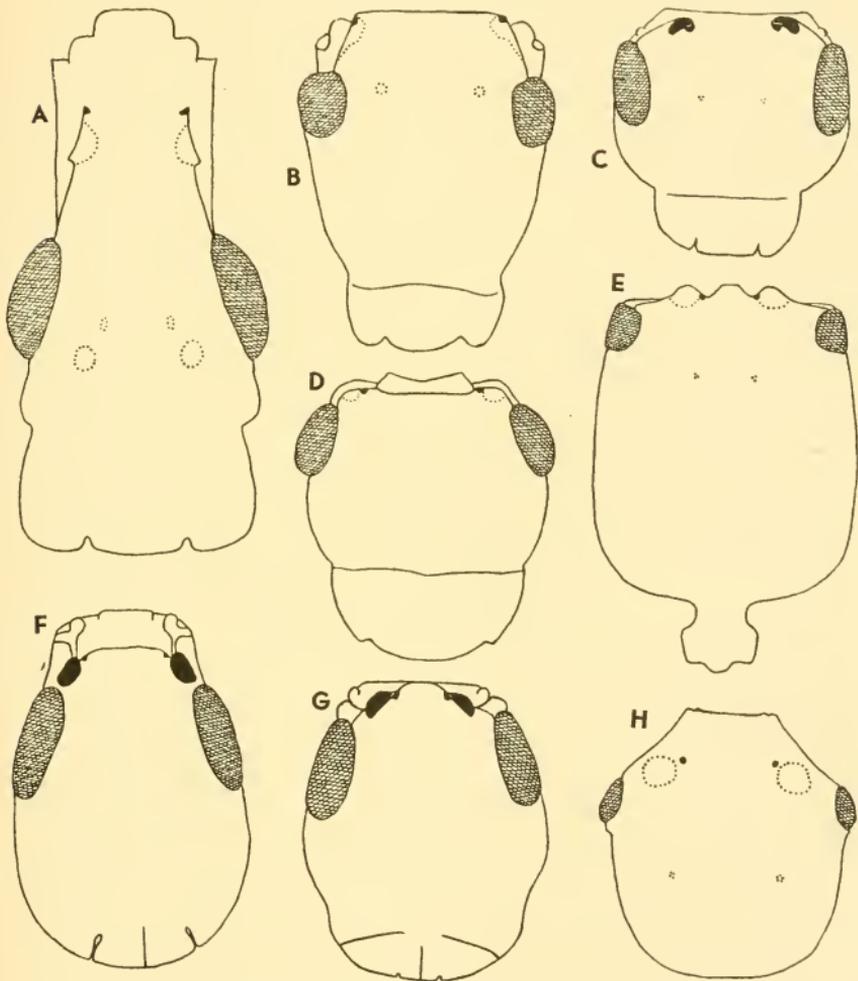
FIG. 11.—Intrafamily variation in the form and structure of the
dorsal aspect of the head (continued from fig. 10).

A, *Tanyrhinus singularis* Mann. B, *Hesperobium pallipes* (Grav.). C,
Philonthus aeneus (Rossi). D, *Oxyporus lateralis* Grav. E, *Metoponcus varians*
Shp. F, *Bolitobius cinctus* (Grav.). G, *Acylophorus flavicollis* Sachse. H,
Osorius mundus Shp.

frons is undifferentiated from the other parts. The area anterior to
the tentorial pits is therefore the postclypeus. A portion of the hy-
postomal suture or epicranial arm is sometimes present, extending

from the tentorial pit toward the eye, as is *Tanyrhinus* (fig. 11 A) and *Philonthus* (fig. 11 C). A definite postclypeal area is present in *Tanyrhinus* (fig. 11 A), *Leptochirus* (fig. 10 E), *Osorius* (fig. 11 H), *Hypocyptus* (fig. 10 D), *Lorinota* (fig. 10 L), etc.

The posterior part of the epicranium is frequently marked by a transverse suture which is believed to be the occipital suture. It is generally rather short and disappears on the lateral aspect, but it may extend onto the ventral surface, as in *Oxyporus* (fig. 12 D) and *Philonthus* (fig. 12 J). In *Aploderus* (fig. 12 E) it even unites with the gular sutures below. The following show this suture in some form: *Platystethus* (fig. 10 G), *Aploderus* (fig. 12 E), *Gastrolobium, Hesperobium* (fig. 11 B), *Paederillus, Paederus, Lathrotropis, Stilicus, Trachysectus, Orus, Astenus, Xantholinus, Staphylinus, Ocypus, Philonthus* (fig. 11 C), *Cafius, Glenus, Acylophorus* (fig. 11 G), *Quedius, Oxyporus* (fig. 11 D), *Bolitobius, Liparocephalus, Xenodusa* (fig. 10 K), *Aleochara* (fig. 10 F), and *Baryodma*. It should be noted that *Paederillus littorarius* is the species having the suture, whereas *P. pugetensis* apparently does not. Of the major subfamilies, only Omaliinae and Steninae are not represented in this list.

The head is frequently suddenly constricted behind at the point to which it may be inserted into the prothorax. This point is frequently but not always at about the region of the occipital suture. Extreme examples of constriction are *Metoponcus* (fig. 11 E) and *Lorinota* (fig. 10 L).

The position of the antennal fossa varies considerably and has been used extensively in classification schemes. Since the anterior arm of the tentorium is invariably closely associated with the antennal fossa, and the tentorial pits mark the posterior boundary of the frons or frontal region, it follows that the antennae are never inserted " under the margin of the front " or " at front of front " or " upon the front," but can only be situated at some point along the anterior margin of the vertex. In the cases in which the postclypeus is completely lacking, the antennae will be inserted along the anterior margin of the head. In those cases in which the postclypeus is present but does not reach the eyes, the antennae will be inserted at the lateral corners of the vertex, usually near the eyes. In those cases in which the postclypeus is large and attains the eyes, the antennae will be inserted into the upper surface of the epicranium, between the eyes. In the first group are to be found all the Paederinae and Staphylininae, including *Hesperobium* (fig. 11 B), *Metoponcus* (fig. 11 E), *Philonthus* (fig. 11 C), and *Acylophorus* (fig. 11 G). In the second group are all the Micropeplinae, Omaliinae, Oxytelinae, Habrocerinae, and Tachyporinae, in-
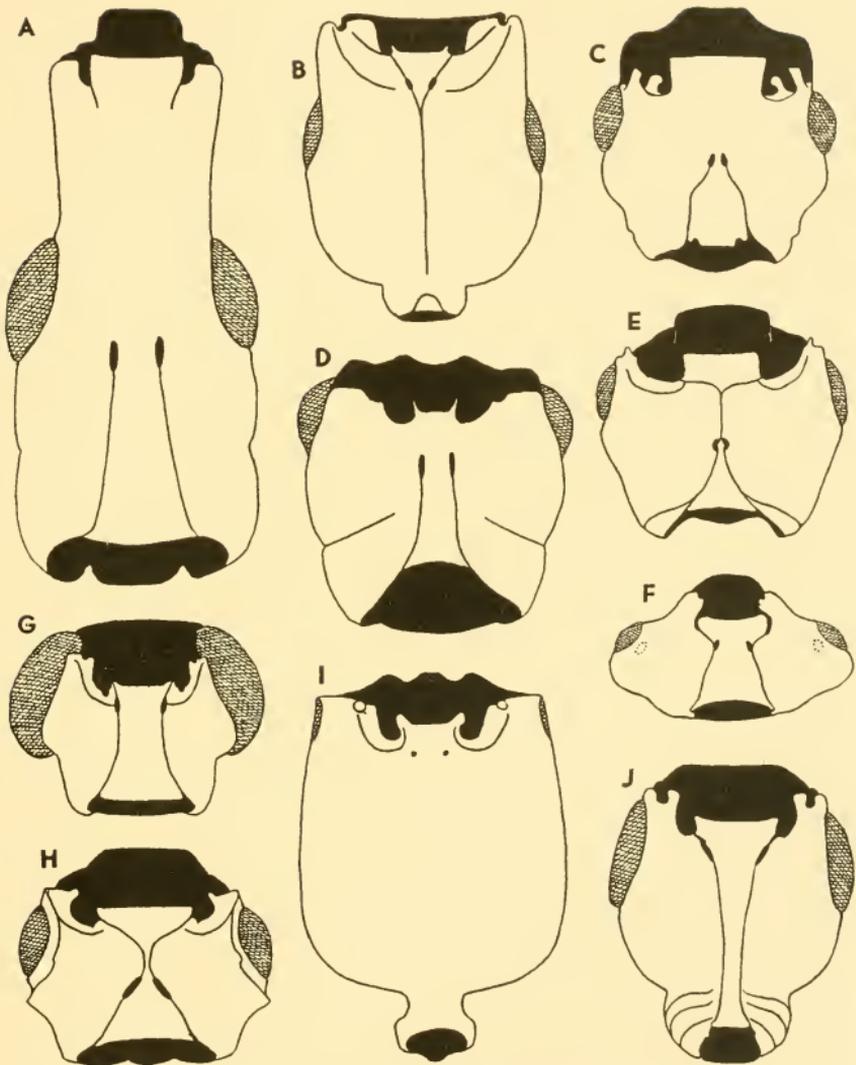
FIG. 12.—Intrafamily variation in the form and structure of
the ventral aspect of the head.

A, *Tanyrhinus singularis* Mann. B, *Astenus discopunctatus* (Say). C, *Eumalus nigrella* (Lec.). D, *Oxyporus lateralis* Grav. E, *Aploderus linearis* Lec. F, *Hypocyptus longicornis* (Payk.). G, *Stenus sculptilis* Csy. H, *Lathrimaeum pictum* Fvl. I, *Metoponcus varians* Shp. J, *Philonthus alumnus* Er.

cluding *Micropeplus* (fig. 10 B), *Peleconalium* (fig. 10 J), *Tanyrhinus* (fig. 11 A), *Proteinus* (fig. 10 I), *Leptochirus* (fig. 10 E), *Platy-stethus* (fig. 10 G), *Osorius* (fig. 11 H), *Oxyporus* (fig. 11 D), *Hypocyptus* (fig. 10 D), *Tachyporus* (fig. 10 C), and *Bolitobius* (fig. 11 F). In the third group are all the Steninae and Aleocharinae, including *Stenus* (fig. 10 H), *Xenodusa* (fig. 10 K), *Lorinota* (fig. 10 L), and *Aleochara* (fig. 10 F). It should be noted that *Acylophorus* shows a tendency toward the second group, whereas *Hypocyptus* seems to approach the third group.

The compound eyes are normally situated at the sides of the head but frequently slightly more on the dorsal aspect than on the ventral. They vary greatly in size, as in *Stenus* (fig. 10 H) and *Leptochirus* (fig. 10 E). They are so far as observed always complete and undivided and never more than slightly emarginate at any point. The facets vary considerably in relative size and in convexity, and may be interspersed with fine hairs, as in *Liparocephalus*.

The opening from the eye into the interior of the head is the ocular foramen. It is generally much smaller than the eye itself because of the development of the oculata. The ocular foramina are indicated in figure 12 F by two small dotted circles near the eyes. Ocelli are present in one subfamily—the Omaliinae. They appear to be entirely characteristic of this group, being found only here and in all the members except one genus which is doubtfully retained. This genus, *Vellica*, has not been available for study. The ocelli are situated on the vertex, one on each side, between or behind the posterior parts of the compound eyes. In dried specimens they usually appear as pale convex protuberances, but in slide preparations are visible only as lighter spots in the wall of the vertex where the sclerotization is less thick or the pigment less evident. The ocelli are indicated in the drawings by solid lines and must not be confused with the ends of the dorsal arms of the tentorium, indicated by dotted lines. *Tanyrhinus* (fig. 11 A) and *Peleconalium* (fig. 10 J) illustrate these organs.

The anterior tentorial pits as already stated mark the position of the epicranial arms or frontal sutures. Since the frons is apparently always missing in this family, a line between the anterior tentorial pits may be taken as the line of fusion of the postclypeus and vertex. The tentorial pits are always situated near the antennal fossae, usually at their mesal or anterior corners. They may be situated at some point on the surface of the epicranium before or between the eyes. They are shown in the figures as black spots but are seldom, if ever, visible from the exterior in dry specimens. Their actual location is to be

determined only by following the anterior tentorial arms to their anterior extremity.

The ends of the dorsal arms of the tentorium are likewise invisible from the exterior in unprepared specimens. By following the dorsal arms the point of insertion is determined. This point is indicated in the figures by a tiny circle of dots, and it is found on the vertex generally between the eyes, one on each side of the center. In many species the dorsal arms apparently do not reach the vertex. These include *Acylophorus* (fig. 11 G), *Oxyporus* (fig. 11 D), *Hypocyptus* (fig. 10 D), *Tachyporus* (fig. 10 C), *Bolitobius* (fig. 11 F), *Xenodusa* (fig. 10 K), *Lorinota* (fig. 10 L), etc.

The ventral aspect of the head, similarly to the dorsal, is considerably modified by the obliteration of sutures and the consequent fusion of primitive elements. The vertex extends around behind the eyes and is continuous with the genae, if present, and sometimes with the median gular area and the postgenal area.

In the forms already listed as possessing an occipital suture, the vertex is separated by it from the occiput and to a greater or less extent from the postgenae, which are continuous with the occiput. Where no occipital suture is present the vertex, occiput, and postgenae are all united to form the epicranium. The postoccipital sutures are said to be the most constant of all the head sutures. However, this suture is not evident on any of these species (except possibly *Philonthus,* fig. 12 J) until it reaches the ventral side of the head and becomes the gular sutures.

The gular sutures are formed by the relative anterior migration of the posterior tentorial pits and normally extend from the foramen magnum to the base of the labium, separating the ventral aspect into three parts. Enclosed between these sutures is a sclerite known as the gula. Stickney states that it is always complete in the Staphylinidae, but even under the present interpretation the additional material proves the contrary to be the case. The gula may be considered to be complete when it extends from the foramen magnum to the tentorial pits, where it unites with the submentum.

The gula has been found to be incomplete in 13 of the species used in this study. Three types of conditions are found among these 13. In some the gula is separated from the pits by the meeting of the gular sutures on the midline, as in *Leptochirus, Bledius, Osorius, Gastrolobium, Stilicus, Astenus* (fig. 12 B), *Xantholinus, Staphylinus,* and *Cafius.* Some have the gular sutures incomplete posteriorly, such as *Paederillus, Lathrotropis,* and *Trachysectus.* One species, *Metoponcus* (fig. 12 I), shows no sign of the gular sutures at all; the posterior

tentorial pits, however, are located in this species near the base of the labium and indicate a possible relationship with the supposedly closely related *Xantholinus,* in which the sutures are confluent on the midline.

THE APPENDAGES OF THE HEAD

The intrafamily variation in the antennae is considerable, but these variations are mostly rather superficial and are not very constant within the subfamilies. Omitting the aberrant *Micropeplus* (fig. 13 M), in which the antenna is only nine-segmented with a much enlarged terminal segment, the forms are either 10- or 11-segmented. In the former group are the Hypocyptini (fig. 13 N) and two genera of the Aleocharinae (*Oligota* and *Decusa*). All other members of the family examined have the antennae clearly 11-segmented.

Figure 13 shows some of the variations in form of the antennae. The method of insertion of the second segment into the first determines the amount of movement possible as well as the amount of geniculation. Strongly geniculate antennae are found in *Acylophorus* (fig. 13 L), *Osorius* (fig. 13 K), and some of the Paederini (subtribe Cryptobia). Great variation is found in the shape of the basal segment, as well as in its size and method of insertion in the antennal fossa.

The vestiture of the antennal segments ranges from the large sparse tactile setae of figure 13 I to the dense minute pile indicated on the distal segments of figure 13 H. No segment anywhere has been observed that is entirely without vestiture, though on some (as fig. 13 L) it may be exceedingly minute and indistinct. The exceedingly minute vestiture is generally accompanied by numerous pores, which give a glandular appearance to the surface (fig. 1 B). The extent of this type of vestiture is rather definite in each species and varies considerably throughout the family. In some it is distinctly confined to certain segments, but in others diminishes gradually from the apex and becomes indistinct on the basal segments. In *Micropeplus* only the terminal (ninth) segment is so clothed. *Creophilus* has this type of vestiture on the last five segments; *Hadrotes* on the last six. Those with it on the last seven include *Tanyrhinus, Leptochirus, Glenus, Bolitobius,* and *Aleochara.* Those with it on the terminal eight segments include *Oxytelus, Xantholinus, Philonthus,* and *Quedius.* The following have it on all but the two basal: *Gastrolobium, Lathrotropis, Hesperobium,* and *Pinophilus.* From this it can be seen that the vestiture of the antennae is not stable within certain tribal limits, and in some cases even in smaller groups there is considerable variation.
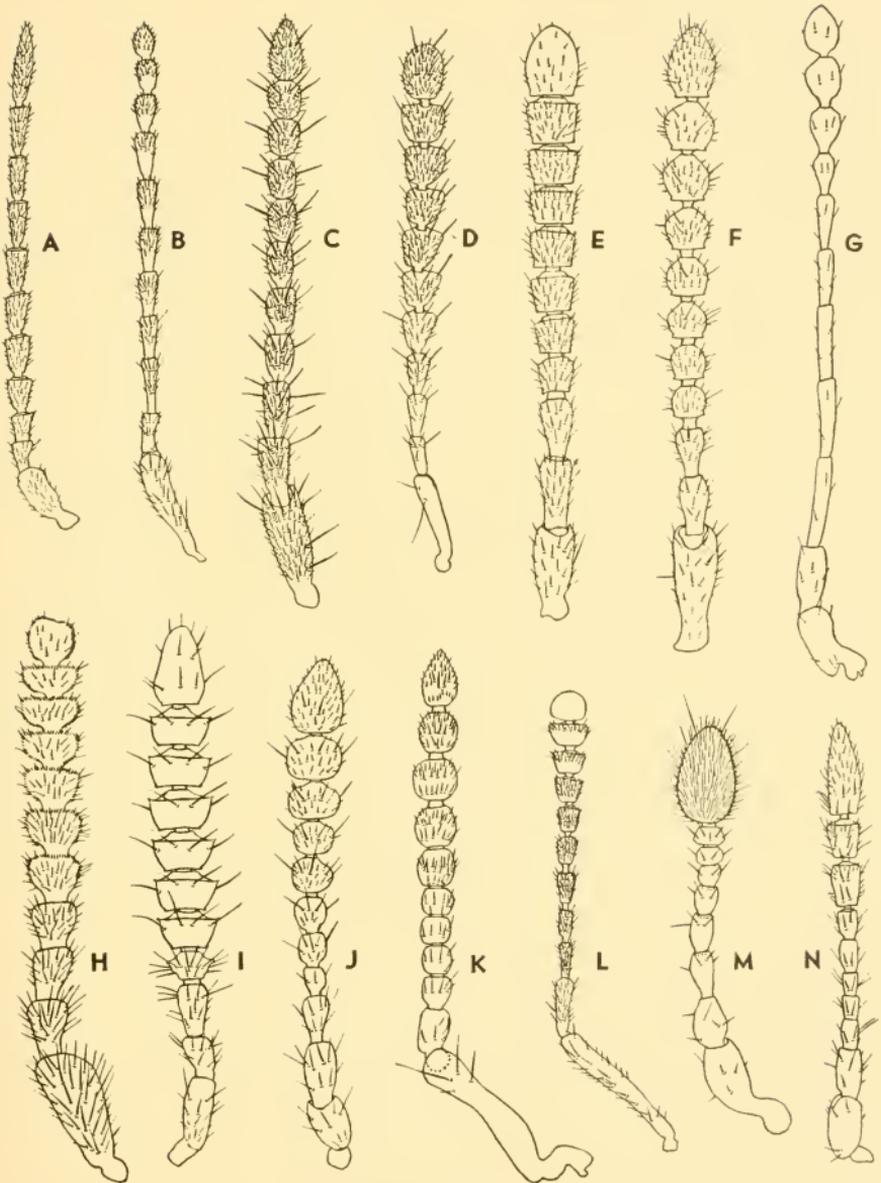
FIG. 13.—Intrafamily variation of the antenna.

A, *Xenodusa sharpi* Wasm. B, *Gastrolobium bicolor* (Grav.). C, *Lithocharis ochracea* (Grav.). D, *Bolitobius cinctus* (Grav.). E, *Lorinota cingulata* (Lec.). F, *Aploderus linearis* Lec. G, *Stenus sculptilis* Csy. H, *Glenus flohri* Shp. I, *Aleochara lata* Grav. J, *Phloeocharis subtilissima* Mann. K, *Osorius mundus* Shp. L, *Acylophorus flavicollis* Sachse. M, *Micropeplus punctatus* Lec. N, *Hypocyptus longicornis* (Payk.).

The considerable variation in the form and relative size of the labrum is very hard to classify because of the large number of slight variations which grade from one to the other. Figure 14 shows a few of the types. The presence of the membranous processes, such as on
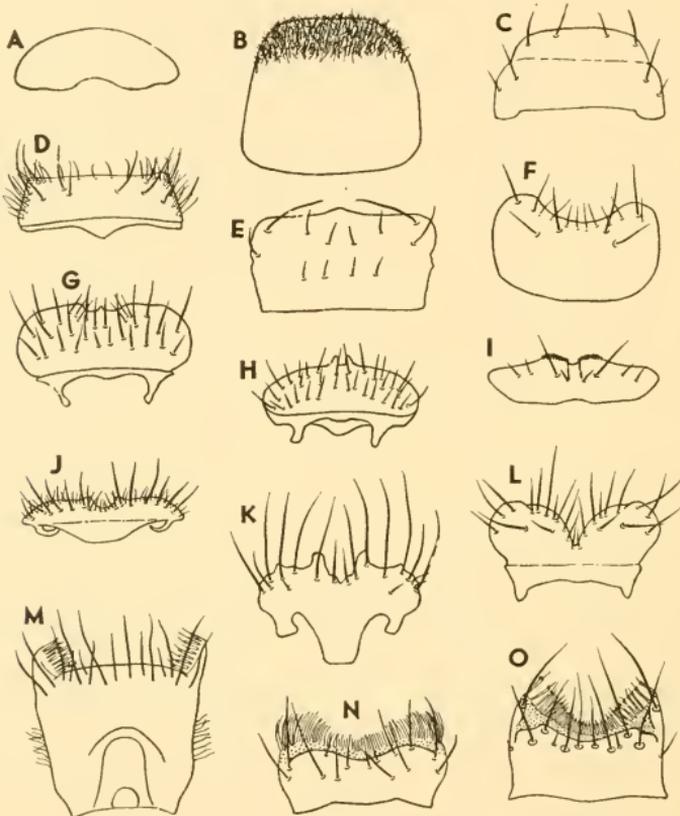

FIG. 14.—Intrafamily variation in the labrum.

A, *Stenus sculptilis* Csy. B, *Xenodusa sharpi* Wasm. C, *Micropeplus punctatus* Lec. D, *Liparocephalus brevipennis* Mäkl. E, *Pseudopsis obliterata* Lec. F, *Tanyrhinus singularis* Mann. G, *Lithocharis ochracea* (Grav.). H, *Stilicus angularis* Er. I, *Astenus discopunctatus* (Say). J, *Pinophilus parvipennis* Csy. K, *Trachysectus confluentus* (Say). L, *Lathrotropis jacobina* (Lec.). M, *Osorius mundus* Shp. N, *Tachinus limbatus* Mels. O, *Platystethus americanus* Er.

Osorius (fig. 14 M) and *Platystethus* (fig. 14 O), is definite and usable, as well as the entirely glabrous character of *Stenus* (fig. 14 A).

The variation in the form and structure of the mandibles is extremely great. Every gradation is found between massive blunt types with a large molar area, such as *Micropeplus* (fig. 15 C), and the very slender acute type without mola, such as *Astenus* (fig. 15 L). In some the terminal tooth is the only one present, as in some species of *Geo-*

dromicus, Pelecomalium (fig. 16 A), *Tanyrhinus, Lathrimaeum, Proteinus* (fig. 15 A), *Trigonurus, Osorius, Tachyporus, Bolitobius* (fig. 15 H), *Xenodusa* (fig. 15 D), and *Lorinota*. In others from two
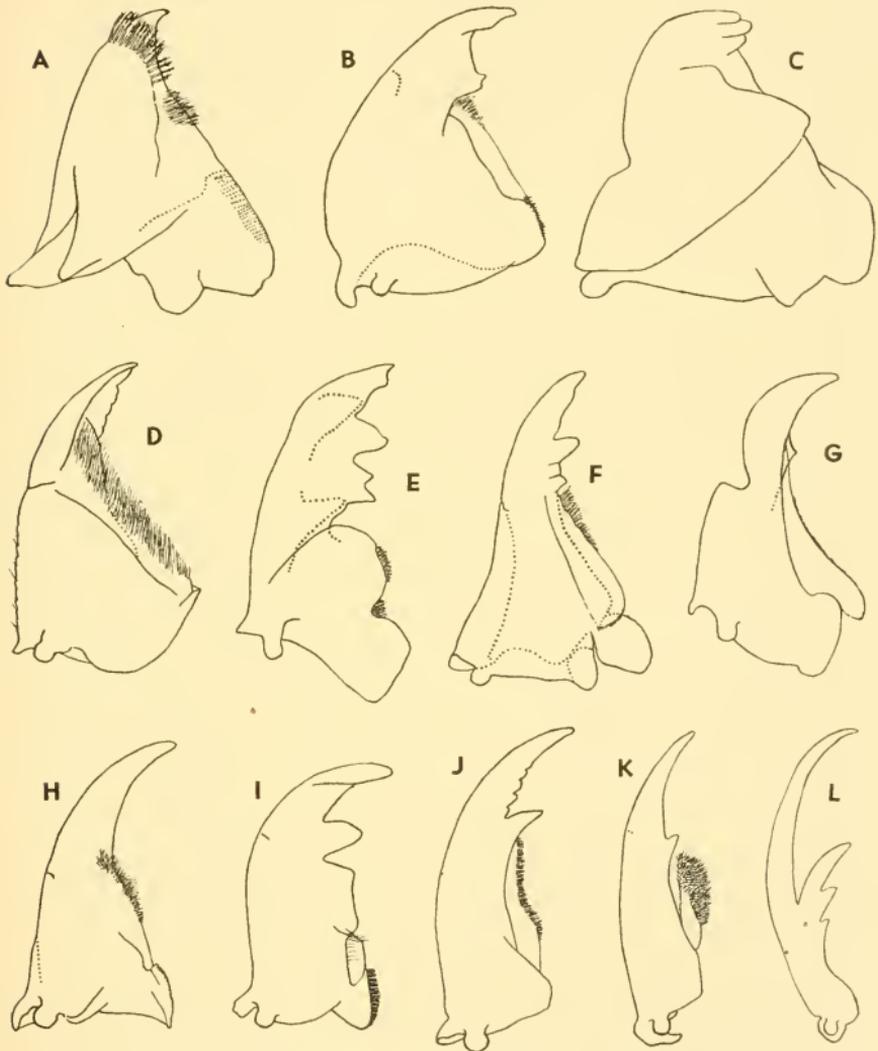

Fig. 15.—Intrafamily variations of the mandibles (continued on fig. 16).

A, *Proteinus limbatus* Mäkl. B, *Phlococharis subtilissima* Mann. C, *Micropeplus punctatus* Lec. D, *Xenodusa sharpi* Wasm. E, *Leptochirus mexicanus* Er. F, *Aploderus linearis* Lec. G, *Oligota esmeraldae* Csy. H, *Bolitobius cinctus* (Grav.). I, *Pseudopsis obliterata* Lec. J, *Liparocephalus brevipennis* Mäkl. K, *Glenus flohri* Shp. L, *Astenus discopunctatus* (Say).

to many teeth may be produced, placed either near the tip or at any point along the inner face. One species, *Oxyporus* (fig. 16 H), has a very small isolated tooth near the outer margin of the mandible

at the middle. The condyles are fairly constant in position. The ventral one is a rounded protuberance and is located on the proximal end of the ventral side near the outer angle. In *Oxyporus* (fig. 16 H) this condyle is situated much nearer the inner edge. The dorsal articulation is sometimes a definite rounded acetabulum but frequently is only a hollow curve along the face of an irregular projection. The prostheca offers considerable variety in form, size, and position. It is
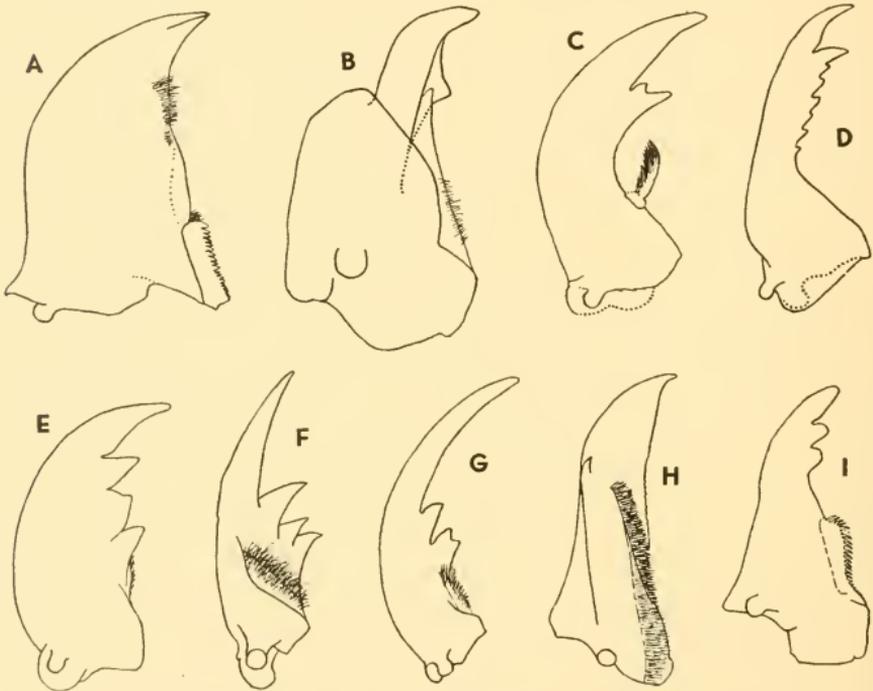

Fig. 16.—Intrafamily variation of the mandibles (continued from fig. 15).

A, *Pelecomalium testaceum* (Mann.). B, *Hypocyptus longicornis* (Payk.). C, *Paederillus pugetensis* Csy. D, *Stenus sculptilis* Csy. E, *Lithocharis ochracea* (Grav.). F, *Acylophorus flavicollis* Sachse. G, *Hesperobium pallipes* (Grav.). H, *Oxyporus lateralis* Grav. I, *Bledius monstratus* Csy.

apparently lacking in *Micropeplus* (fig. 15 C), *Astenus* (fig. 15 L), and *Stenus* (fig. 16 D). In *Glenus* (fig. 15 K), *Paederillus* (fig. 16 C), and *Creophilus* (fig. 2 F) the prostheca is a definite projecting lobe with numerous minute hairlike processes, while in many other species it is apparently represented by a more or less definite row or area of processes proceeding from the surface of the mandible or a groove thereon, such as in *Pelecomalium* (fig. 16 A), *Proteinus* (fig. 15 A), *Acylophorus* (fig. 16 F), *Oxyporus* (fig. 16 H), *Bolitobius* (fig. 15 H), and *Xenodusa* (fig. 15 D).

The maxillae present a rather large amount of variation in form and of modification from the typical arrangement of parts. The typical form has been described for *Creophilus* (fig. 2 G).
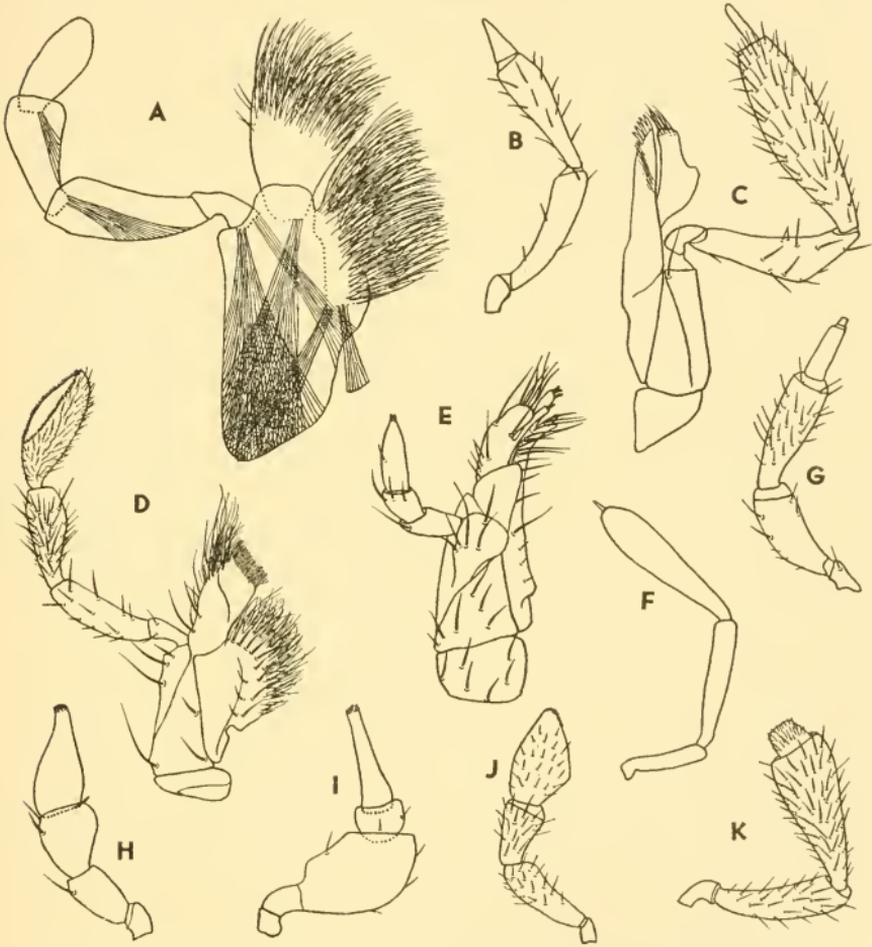
FIG. 17.—Intrafamily variation in the maxillae and the maxillary palpi.

A, musculature of maxilla of *Thinopinus pictus* Lec. B, palpus of *Gastrolobium bicolor* (Grav.). C, maxilla of *Hypocyptus longicornis* (Payk.). D, maxilla of *Pinophilus parvipennis* Csy. E, maxilla of *Osorius mundus* Shp. F, palpus of *Stenus sculptilis* Csy. G, palpus of *Baryodma bimaculata* Grav. H, palpus of *Acylophorus flavicollis* Sachse. I, palpus of *Micropeplus punctatus* Lec. J, palpus of *Pelecomalium testaceum* (Mann.). K, palpus of *Paederus lactus* Er.

The relative sizes of the cardo, stipes, galea, and lacinia are subject to much variation. The subfamily Staphylininae is very homogeneous, there being little variation in any parts from *Creophilus* and *Thinopinus* (fig. 17 A). In some species the lacinia is more elongate and

extends distad almost or quite as far as the galea. These forms gen-
erally have both these structures less hairy and frequently armed
with spines. Of the species examined *Geodromicus, Pelecomalium,
Leptochirus, Eumalus, Trigonurus,* all the Oxytelini, Steninae, Paede-
rinae (fig. 17 D), Staphylininae (fig. 2 G), Oxyporinae, Tachyporini,
and Bolitobiini have the lacinia much shorter than the galea, whereas
it is elongate in *Micropeplus, Tanyrhinus, Lathrimaeum, Phloeocharis,
Pseudopsis, Osorius* (fig. 17 E), *Habrocerus, Hypocyptus* (fig. 17 C),
and all the Aleocharinae.

The maxillary palpi are four-segmented in all the species except
Aleochara and *Baryodma* (fig. 17 G), in which there is a small ad-
ditional fifth segment. With the exception of *Stenus* (fig. 17 F), the
first segment is always small and geniculate. It is apparently im-
movably united to the second segment, at least in *Thinopinus* (fig.
17 A). Any of the succeeding segments may be much expanded, as
the second in *Micropeplus* (fig. 17 I), the third in *Hypocyptus* (fig.
17 C) and *Paederus* (fig. 17 K), or the fourth in *Pinophilus* (fig.
17 D). Occasionally the fourth is longer than any of the others, as
in *Acylophorus* (fig. 17 H) and *Osorius* (fig. 17 E), but more fre-
quently it is greatly reduced, as in *Gastrolobium* (fig. 17 B), *Hypo-
cyptus* (fig. 17 C), and *Stenus* (fig. 17 F). In *Paederus* (fig. 17 K)
the terminal one is short, truncated, and strongly compressed.

In nearly every labium studied the mentum and submentum are
the only heavily sclerotized parts. The submentum is continuous with
the gula between the tentorial pits and is generally separated at the
sides from the postgenae by the submental sutures. These sutures
may be complete from the base of the mentum to the tentorial pits,
they may be incomplete either anteriorly or posteriorly, they may be
united on the midline for a distance in front of the pits, or they may
be entirely lacking. They are complete in *Lathrimaeum* (fig. 12 H),
Stenus (fig. 12 G), *Astenus* (fig. 12 B), *Hypocyptus* (fig. 12 F), and
all others not listed in the three following categories. The anterior
ends of the sutures have disappeared to a varying extent in *Pseudop-
sis, Trachysectus, Orus, Philonthus* (fig. 12 J), *Cafius, Creophilus,
Ocypus, Thinopinus, Hadrotes, Glenus, Acylophorus, Quedius, Tachi-
nus, Tachyporus,* and *Erchomus.* They are visible only at the anterior
end in *Tanyrhinus* (fig. 12 A). In *Trigonurus, Bledius, Platystethus,
Oxytelus, Aploderus* (fig. 12 E), and *Osorius* they have become united
in front of the tentorial pits so that the submentum is a wholly dis-
tinct sclerite. The sutures are apparently entirely lacking in *Micro-
peplus, Eumalus* (fig. 12 C), *Metoponcus* (fig. 12 I), and *Oxyporus*
(fig. 12 D).

The mentum is frequently united to the submentum between the projecting anterior corners of the latter. It is usually trapezoidal in form but may be variously lobed in front, as in *Leptochirus* (fig. 18 G), *Oxyporus* (fig. 18 A), and *Liparocephalus* (fig. 18 E). It frequently bears a few large setae and is nearly always sparsely set with large pores.
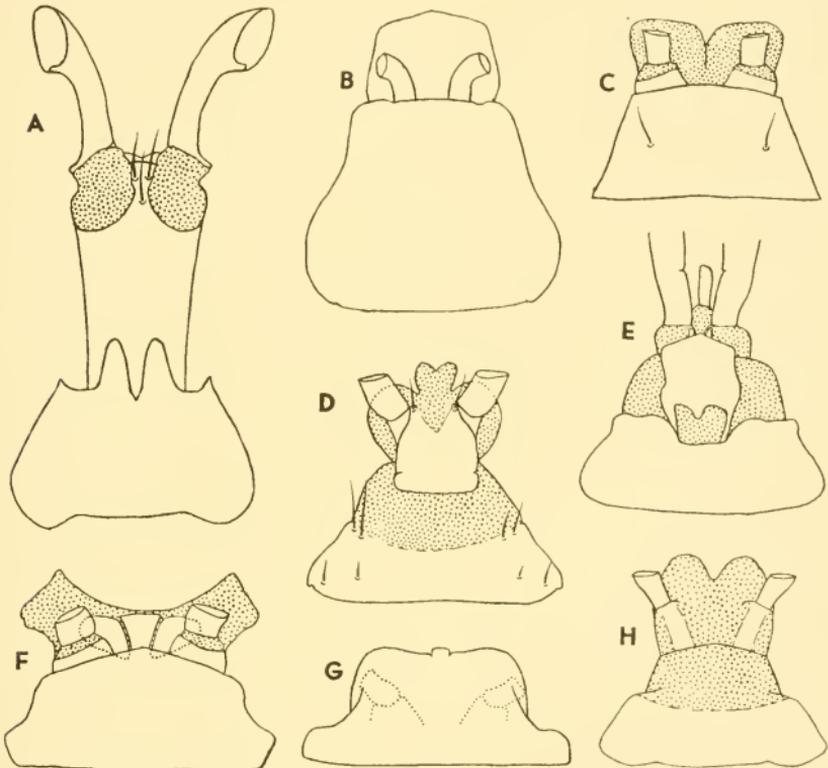

Fig. 18.—Intrafamily variation in the form and structure of the labium. (Only the basal segment of the palpi shown.)

A, *Oxyporus lateralis* Grav. B, *Osorius mundus* Shp. C, *Lathrimaeum pictum* Fvl. D, *Baryodma bimaculata* Grav. E, *Liparocephalus brevipennis* Mäkl. F, *Trigonurus crotchi* Lec. G, *Leptochirus mexicanus* Er. H, *Gastrolobium bicolor* (Grav.).

The prementum is frequently only partly sclerotized. In *Trigonurus* (fig. 18 F) there are three small triangular sclerites lying in the membrane between the paraglossal lobes; in *Osorius* (fig. 18 B) there is a single large quadrate plate anterior to the base of the palpi; in *Oxyporus* (fig. 18 A) the entire basal part of the prementum is sclerotized as a long plate; and in other forms there is more or less sclerotization of the area between the mentum and the base of the palpi. The

5

palpigers may not be differentiated from the rest of the prementum, and are frequently entirely membranous. Frequently there are no glossal or paraglossal lobes visible, as in *Osorius* (fig. 18 B) and *Leptochirus* (fig. 18 G), but in some forms they appear to have united into a pair of lobes or even a single lobe, as in *Lathrimaeum* (fig. 18 C) and *Gastrolobium* (fig. 18 H), whereas in others there are both glossae and paraglossae distinct, as in *Baryodma* (fig. 18 D). In *Liparocephalus* (fig. 18 E) there is a united glossa or ligula which is prolonged into a cylindrical sclerotized piece projecting cephalad for nearly half the length of the first segment of the palpi.

Any of these parts may occasionally bear large setae or minute setulae. It must always be borne in mind in examining the labium that the hypopharynx almost invariably is furnished with a pair of lobes bearing combs of setae which project up behind the paraglossae and are likely to be mistaken for them. They are always membranous like the paraglossae, and the distinction between them is sometimes difficult to make.

The number of segments in the labial palpi is said to vary from one to four. None have been recorded with less than three except from the subfamily Aleocharinae, and the only examples with four are there also. In almost no cases are there definite articulations between the segments of the palpi, each one being united to the next by a relatively wide area of membrane. Frequently also the segments are rather indefinitely sclerotized but usually sufficiently so to prevent any difficulty in counting them.

No specimens have been studied which have only one segment in the labial palpi. One species has been observed with two-segmented palpi. This is *Liparocephalus* (fig. 19 B), in which the basal segment is partially divided into two. It is evidently an intermediate step in the formation of either the three-segmented from the two-segmented condition or the reverse. The closely related genus *Diaulota* frequently shows both the extremes and all the intermediate steps in a single lot of the one species.

The three-segmented condition of the labial palpi is almost universal throughout the family, but a great deal of variation in form is apparent. As a rule the labial palpus cannot be said to be filiform, though certain segments may be slender in certain species. The basal segment may be longer than either of the others, as in *Habrocerus* (fig. 19 E) and *Stenus* (fig. 19 C), or shorter, as in *Hypocyptus* (fig. 19 F) and *Osorius* (fig. 19 J). It may be rather strongly geniculate as in *Stenus* (fig. 19 C) and *Osorius* (fig. 19 J), or may be large and

cylindrical as in *Aleochara* (fig. 19 A) and *Habrocerus* (fig. 19 E). The middle segment may be greatly expanded as in *Stenus* (fig. 19 C) or very short as in *Trigonurus* (fig. 19 H). The terminal segment is generally small and narrow as in *Stenus* (fig. 19 C), *Hypocyptus* (fig. 19 F), and *Paederus* (fig. 19 I), but is greatly expanded in *Oxyporus* (fig. 19 D) into a very large, compressed, obconical body.
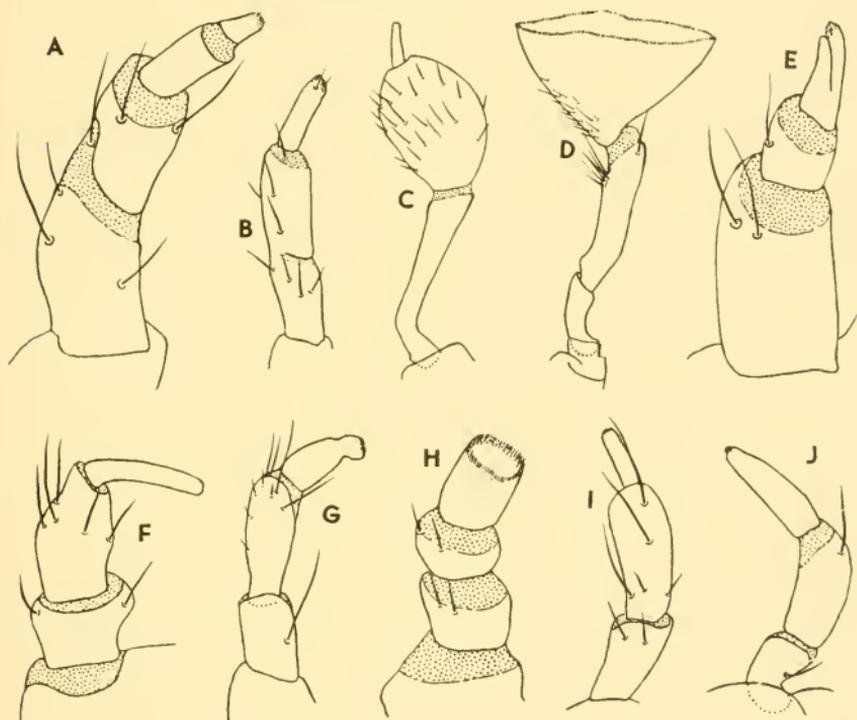

FIG. 19.—Intrafamily variation in the labial palpi.

A, *Aleochara lata* Grav. B, *Liparocephalus brevipennis* Mäkl. C, *Stenus sculptilis* Csy. D, *Oxyporus lateralis* Grav. E, *Habrocerus schwarzi* Horn. F, *Hypocyptus longicornis* (Payk.). G, *Pinophilus parvipennis* Csy. H, *Trigonurus crotchi* Lec. I, *Paederus laetus* Er. J, *Osorius mundus* Shp.

A four-segmented labial palpus was found only in *Aleochara* (fig. 19 A). The palpi of other Aleocharinae are said to be similar.

THE THORAX

A great deal of variation is exhibited in the shape of the pronotum (figs. 20, 21). It is hard to classify the types, as nearly all gradations are to be found and nearly every genus or even species is somewhat different from its near, as well as from its more distant, relatives. Figures 20 and 21 show some of the forms that occur. Almost any
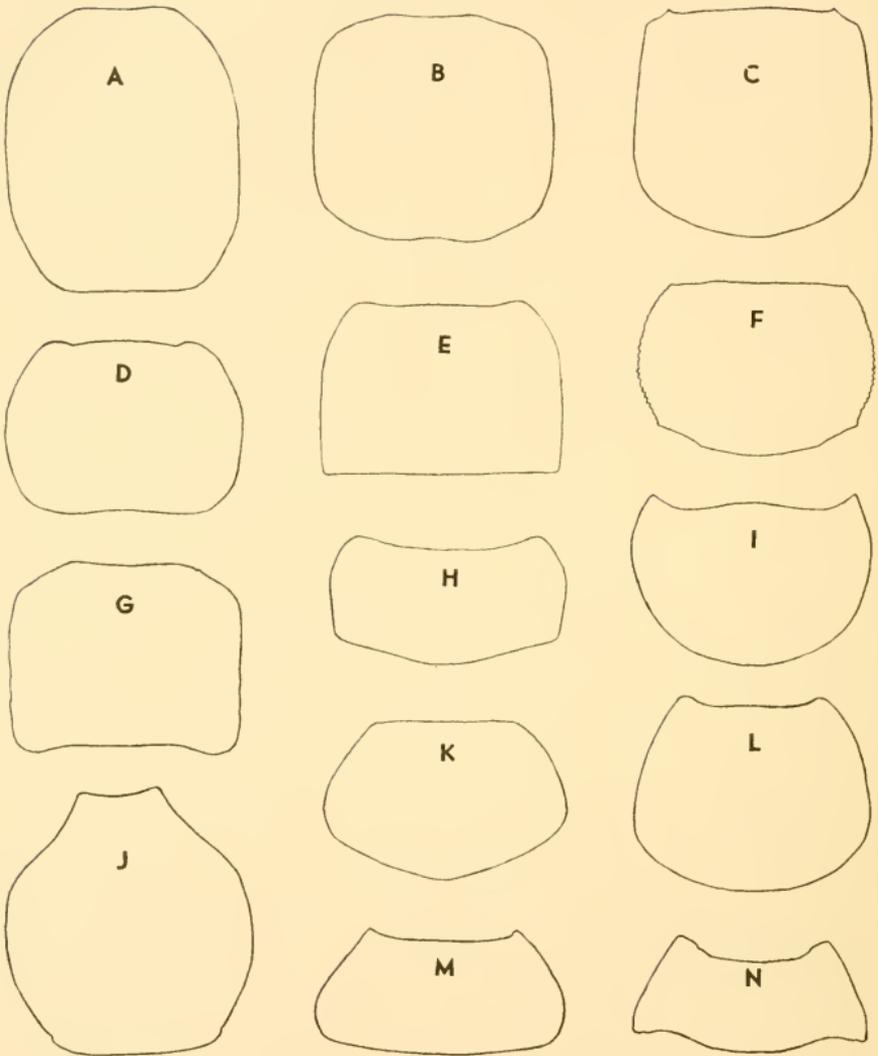
Fig. 20.—Intrafamily variation of the pronotum (continued on fig. 21).

A, *Lathrotropis jacobina* (Lec.). B, *Lithocharis ochracea* (Grav.). C, *Ocypus ater* (Grav.). D, *Pelecomalium testaceum* (Mann.). E, *Trigonurus crotchi* Lec. F, *Pseudopsis obliterata* Lec. G, *Leptochirus mexicanus* Er. H, *Proteinus limbatus* Mäkl. I, *Platystethus americanus* Er. J, *Stilicus angularis* Er. K, *Aleochara lata* Grav. L, *Acylophorus flavicollis* Sachse. M, *Tachyporus jocosus* Say. N, *Micropeplus punctatus* Lec.

of these may be found in any of the larger subfamilies. It is obvious that the shape of the pronotum cannot be used in the higher classification. In certain groups it is useful in generic and specific segregation.

The inflexed portion of the pronotum is generally closely united with certain elements of the ventral surface and will be discussed in the section dealing with the prosternal area.

The ventral aspect of the prothorax affords a considerable amount of variation in structure. The fundamental condition is frequently
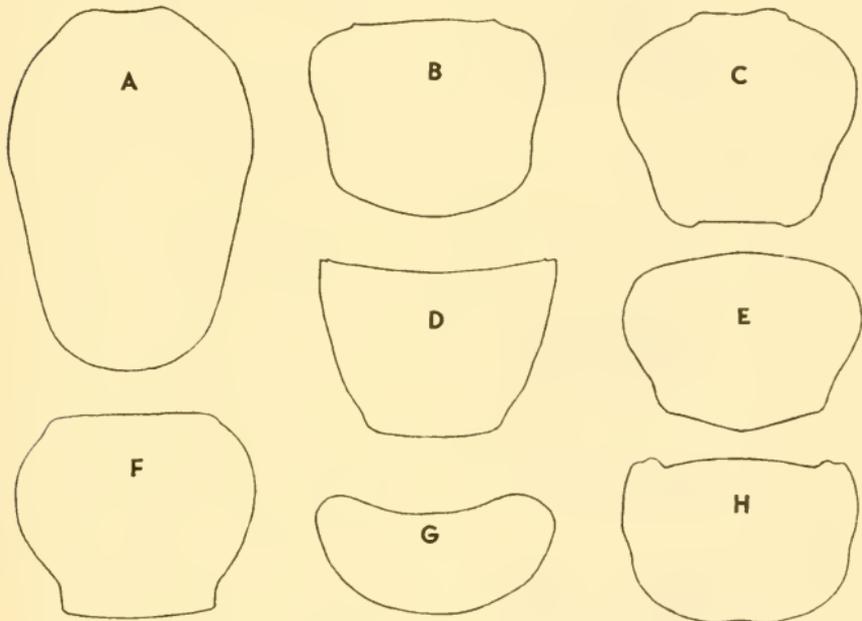


Fig. 21.—Intrafamily variation of the pronotum (continued from fig. 20).

A, *Metoponcus varians* Shp. B, *Cafius lithocharinus* Lec. C, *Lorinota cingulata* (Lec.) ; D, *Osorius mundus* Shp. E, *Liparocephalus brevipennis* Makl. F, *Geodromicus brunneus* (Say). G, *Hypocyptus longicornis* (Payk.). H, *Aploderus linearis* Lec.

obscured by the reduction of sclerites and the obliteration of sutures, but several important characters are available.

The amount of inflection of the pronotum varies somewhat, but the size of the postcoxal lobe is more important and usable. These lobes tend to close the coxal cavities behind, being almost successful in *Leptochirus* (fig. 22 F). In *Lithocharis* (fig. 22 B) and *Xantholinus* (fig. 23 D) they are lacking entirely.

The sternum varies greatly in length. The longest exposed area occurs in *Leptochirus* (fig. 22 F), but the large posterior lobe of

Astenus (fig. 23 A) surpasses it somewhat though covered by the coxae. *Aleochara* (fig. 22 A) has the shortest and most reduced sternum. This structure is often produced posteriorly between or under the coxae. *Trigonurus* (fig. 22 D) has a very small projection,
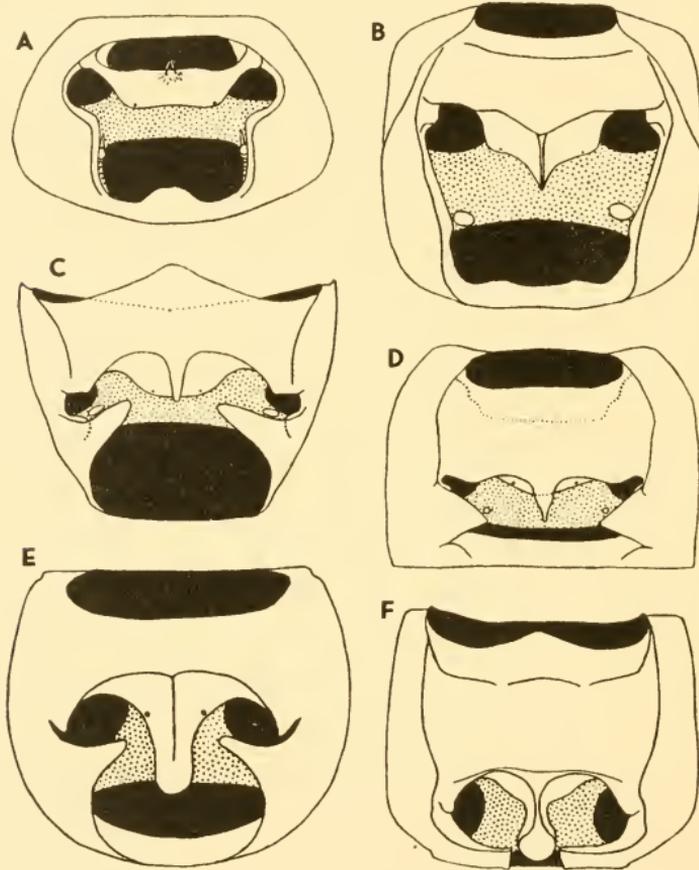
FIG. 22.—Intrafamily variation in the form and structure of the prosternal area (continued on fig. 23).

A, *Aleochara lata* Grav. B, *Lithocharis ochracea* (Grav.). C, *Osorius mundus* Shp. D, *Trigonurus crotchi* Lec. E, *Bledius monstratus* Csy. F, *Leptochirus mexicanus* Er.

while the extreme development is reached in *Astenus* (fig. 23 A) and *Pinophilus* (fig. 23 B). In these last two the prosternal lobe reaches the lobes of the inflexed pronotum, thereby closing the coxal cavities behind. In *Pinophilus* this closure is completed by the actual fusion of the sternal lobe to the underside of the lateral lobes.

In *Xantholinus* (fig. 23 D) and *Metoponcus* there is a pair of large triangular sclerites anterior to the sternum and lying free in the edge of the anterior foramen. They occur in no other group and are said to be present in only a few genera of the Xantholinini.

The spiracles of the mesothorax normally lie in the intersegmental membrane in the vicinity of the pronotal lobes. They usually lie in the
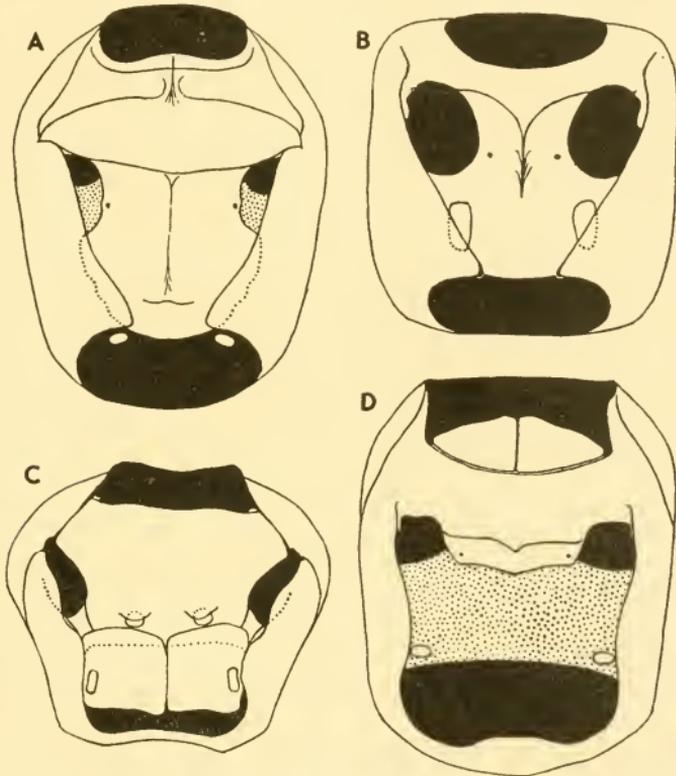
FIG. 23.—Intrafamily variation in the form and structure of the prosternal area (continued from fig. 22).

A, *Astenus discopunctatus* (Say). B, *Pinophilus parvipennis* Csy. C, *Lorinota cingulata* (Lec.). D, *Xantholinus picipennis* Lec.

unsclerotized membrane as in *Lithocharis* (fig. 22 B) and *Trigonurus* (fig. 22 D), but are incorporated into the posterior lobe of the pro-sternum in *Pinophilus* (fig. 23 B). In *Aleochara* (fig. 22 A) they are surrounded by the small peritremes, while in *Lorinota* (fig. 23 C) these sclerites are so large as completely to close the coxal cavities behind.

The shape of the elytron is almost as individual as that of the pronotum (fig. 24). It is impossible to classify these organs by form,
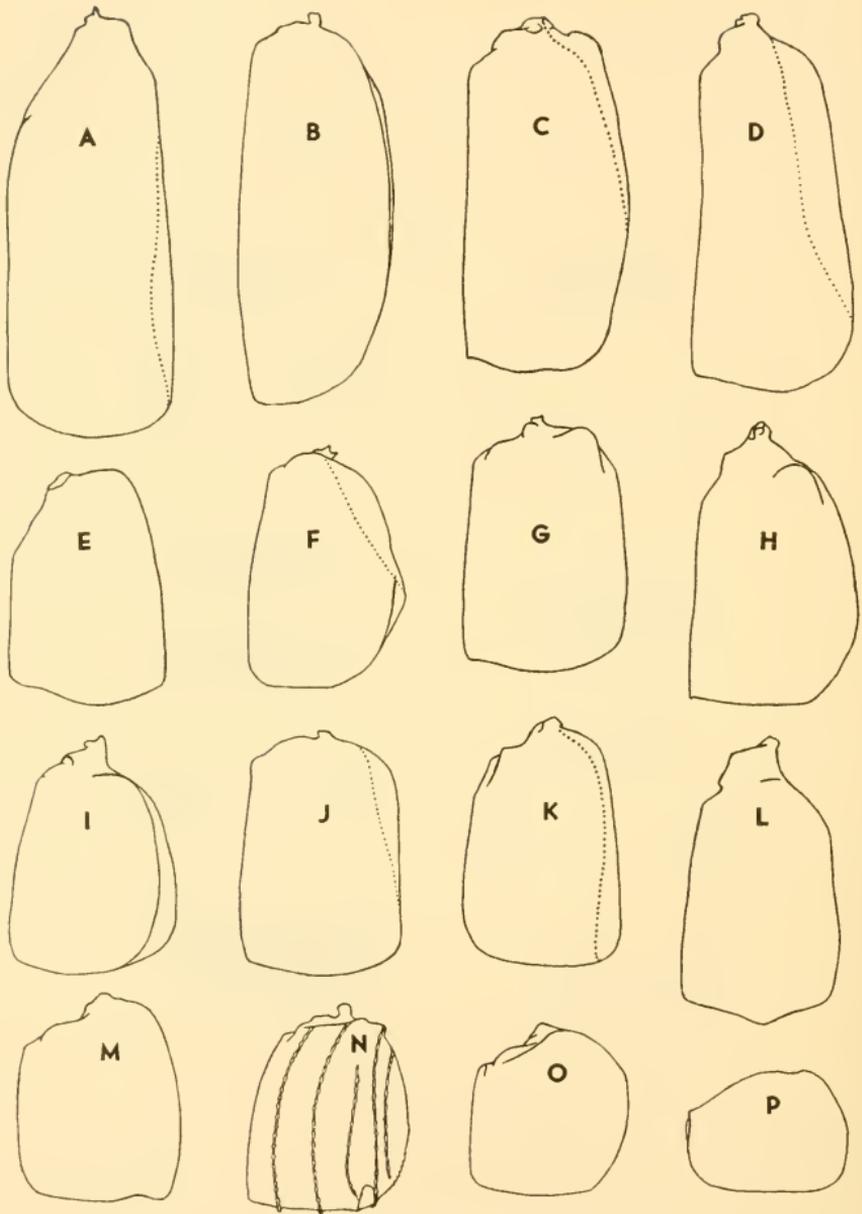
Fig. 24.—Intrafamily variation of the elytra.

A, *Metoponcus varians* Shp. B, *Tanyrhinus singularis* Mann. C, *Trigonurus crotchi* Lec. D, *Geodromicus brunneus* (Say). E, *Acylophorus flavicollis* Sachse. F, *Proteinus limbatus* Mäkl. G, *Oxyporus lateralis* Grav. H, *Osorius mundus* Shp. I, *Bledius monstratus* Csy. J, *Tachyporus jocosus* Say. K, *Platy-stethus americanus* Er. L, *Paederillus pugetensis* Csy. M, *Xenodusa sharpi* Wasm. N, *Micropeplus punctatus* Lec. O, *Aleochara lata* Grav. P, *Liparo-cephalus brevipennis* Mäkl.

but the series shows the range from the long slender types of *Meto-poncus* and *Tanyrhinus* to the short transverse one of *Liparocephalus*.

The extent of deflection of the sides of the elytra depends in great part on the convexity of the thorax. In many species this area is rather abruptly deflexed and of considerable size (figs. 24 D, F, K). This area has frequently been called the epipleurae, but if this term be used, it should be borne in mind that it is a convenient name for a region rather than for a definite morphological unit. The epipleuron is occasionally separated from the discal portion of the elytron by a raised line as in *Bledius* (fig. 24 I) and *Tanyrhinus* (fig. 24 B). The epipleuron may bear a distinct line parallel to the outer margin. This is called the pleural fold by Casey but is more properly termed the epipleural fold, although its exact significance is not known.

In most of the Xantholinini, such as *Metoponcus* and *Xantholinus*, the so-called elytral suture or median edge of the elytron is somewhat abnormal. The thickness of the elytron along this edge is gradually diminished so that the whole edge appears to be beveled. This beveled surface is smooth and unclothed and usually less heavily pigmented than the rest of the elytron. These two edges overlap one another when the elytra are at rest. No special morphological significance is attributed to this feature as it is only a slight modification of the normal suture.

The structure of the sterna of the mesothorax and metathorax is influenced to a large extent by the size, shape, and position of the coxal cavities of the mesothorax. The actual points of insertion of the coxae may be widely separated (fig. 25 C) or close together (fig. 25 B) without changing the relation of the parts. In these two examples the more widely separated ones are still confluent on the midline, whereas the approximate ones are separated by the two sternal processes.

It should be understood that in speaking of the coxal cavities, one is referring to the entire depression occupied by the coxae. This depression is bounded anteriorly by the mesosternum and generally is set off posteriorly by a line on the metasternum. The floor of this depression is made up of the deflexed portions of the mesosterna and metasterna, and it is generally more or less elevated in the middle to form a ridge between the two coxal cavities. However, unless the actual surface of the two sterna meet on the midline or are closely approximated, the cavities are considered to be confluent. The posterior border of the two cavities is usually marked by a line which is common to both and delimits anteriorly the process of the metasternum.
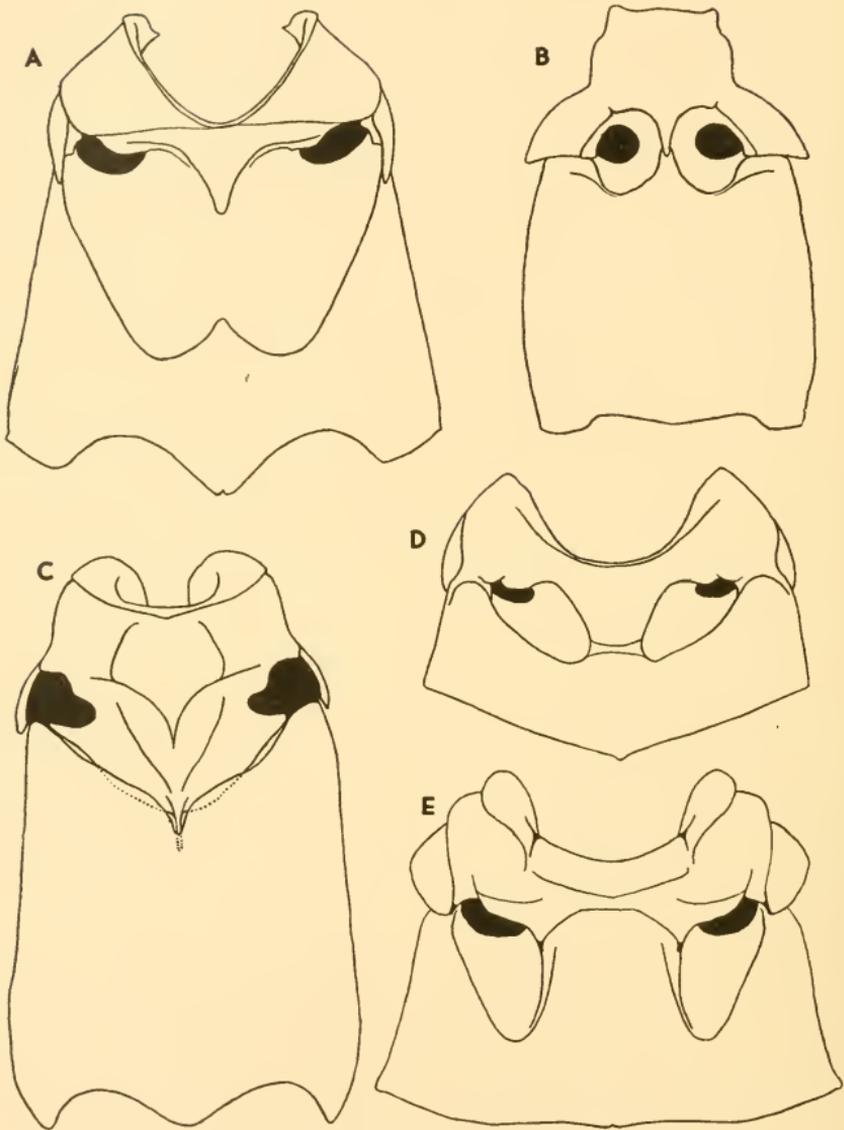
FIG. 25.—Intrafamily variation in the structure of the
mesothoracic and metathoracic sterna.

A, *Ocypus ater* (Grav.). B, *Leptochirus mexicanus* Er. C, *Metoponcus varians* Shp. D, *Hypocyptus longicornis* (Payk.). E, *Oxyporus lateralis* Grav.

The most common situation in this family is for the two cavities to be confluent on the midline. That is, the processes from the mesothorax and metathorax do not meet. In nearly all cases, however, the mesothoracic process projects more or less between the coxae. This group includes *Geodromicus, Pelecomalium, Lathrimaeum, Proteinus, Eumalus, Pseudopsis, Bledius, Oxytelus, Aploderus, Osorius,* all the Paederinae, *Metoponcus* (fig. 25 C), all the Staphylinini (fig. 25 A), Xanthopygini, and Quediini, *Habrocerus,* and *Liparocephalus.*

In *Stenus, Hypocyptus* (fig. 25 D), and *Aleochara* the mesothoracic process attains the metasternum, thereby separating the coxal cavities without the aid of a metathoracic process.

This situation is just reversed in *Platystethus* and *Oxyporus* (fig. 25 E), in which the metathoracic process attains the mesosternum and separates the cavities.

Frequently, however, the two processes meet midway and take equal part in the separation. In this group are the following species: *Micropeplus, Leptochirus* (fig. 25 B), *Trigonurus, Phloeocharis, Tachyporus, Tachinus, Erchomus, Bolitobius, Oligota, Xenodusa, Lorinota,* and *Baryodma.*

The mesosternum is usually very short and not separated from the pleural areas. Considerable reduction has taken place in some of the pleural sclerites, but in some species they are distinct and separate.

The metasternum may be very short and transverse as in *Hypocyptus* (fig. 25 D) or rather elongate as in *Metoponcus* (fig. 25 C). In general it is deflexed anteriorly to form most of the floor of the coxal cavities, but in *Metoponcus* this part is formed by the inflexed portion of the mesosternum, and the metasternum has a narrow emargination at the middle which receives a slender process of the mesosternum.

The metasternum is always completely separated from the metapleurites. It is variously emarginate posteriorly to fit the coxae of the metathoracic legs, and generally shows the articulations of the coxae at the middle.

THE LEGS

The greater part of the large amount of variation in the legs is due to the relative sizes of the parts rather than to any fundamental differences in structure. The presence or absence of calcaria or other setae and the variation in number of tarsal subsegments or tarsomeres constitute the principal structural differences.

The musculature of the leg of *Thinopinus* (fig. 26 A) is very similar to that of a typical insect leg as given by Snodgrass (1927). It is not known whether there is any large amount of variation in other members of the family.

The number of tarsomeres varies from three to five. In some cases the number differs on the same individual—the so-called heteromerous condition. The great majority of species in this family have five tarsomeres in each tarsus. This condition is found throughout the subfamilies Omaliinae, Oxytelinae (except Oxytelini), Steninae, Paederinae, Staphylininae, Oxyporinae, Habrocerinae, and Tachyporinae (except Hypocyptini).

The exceptions include *Micropeplus* and the Oxytelini with three tarsomeres in each tarsus, *Hypocyptus* and *Oligota* with four, *Liparocephalus* with four in the front and middle tarsi and five in the posterior tarsi, and *Lorinota* and *Xenodusa* with four in the front tarsi and five in the middle and posterior ones. *Aleochara* and other aleocharinids have all the tarsi with five tarsomeres. Thus it can be seen that the heteromerous condition is restricted to certain aleocharinids, and that five is the normal number. It might be noted that in certain aleocharinids individuals may be found on which the two tarsi of one pair differ. They show the actual fusion or division of the tarsomeres taking place at the present time.

The claws are simple in all the species studied. They vary somewhat in proportions and curvature, but are all similar to the ones shown (fig. 8 J, etc.).

Several species have been found to have a few very curiously modified setae (fig. 26 L) along the ventral edge of certain of the segments. In *Pelecomalium* they occur on the fore legs in a long line on the tibia and in a small group at the middle of the ventral edge of the femur, and on the middle legs similarly on the tibia and three or four on the trochanter. In *Lathrimaeum* they are situated on both the fore and middle legs in a double row on the tibiae and a few on the trochanters. In *Proteinus* they occur only on the middle legs, a very few near the tip of the tibia and on the trochanter. These setae are very distinct and easily recognizable. On the dorsal extremity of the anterior tibia of *Phloeocharis* is situated a single seta of unusual shape. It is short and stout, resembling considerably those of figure 26 L. The fore tibiae of *Bledius* are much expanded and bear a large number of very heavy short setae (fig. 26 E).

The union of the femur to the trochanter is subject to considerable variation. In some the trochanter is attached to the side of the femur, and in some to the truncated end (figs. 8 F, 26 B, C, D, H, K). The
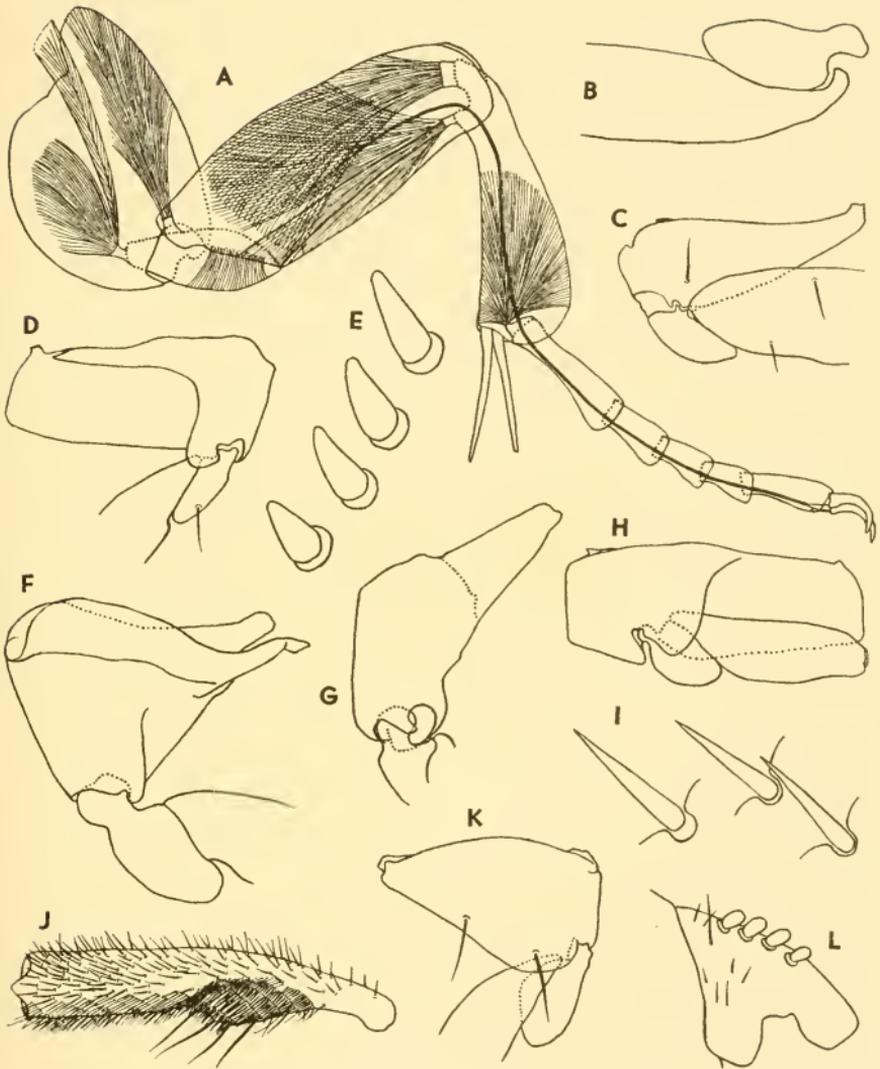
FIG. 26.—Details of the structure of the legs.

A, musculature of the middle leg of *Thinopinus pictus* Lec. B, trochantero-femoral joint of posterior leg of *Bolitobius cinctus* (Grav.). C, posterior coxa of *Oxytelus sculptus* Grav. D, posterior coxa of *Erchomus ventriculus* (Say). E, group of setae from anterior tibia of *Bledius monstratus* Csy. F, posterior coxa of *Paederus laetus* Er. G, posterior coxa of *Stenus sculptilis* Csy. H, posterior coxa of *Hypocyptus longicornis* (Payk.). I, group of setae from middle coxa of *Tachinus limbatus* Mels. J, anterior tibia of *Lathrotropis jacobina* (Lec.). K, posterior coxa of *Habrocerus schwarzi* Horn. L, group of setae on middle trochanter of *Proteinus limbatus* Mäkl.

situation is frequently very different on different legs of the same specimen, but the one from the same thoracic segment of different species can be compared.

The present subfamily classification of the Staphylinidae is based largely on the shape of the posterior coxae. These segments are classified as globose, conical, triangular, or transverse, and a distinction is often attempted between coxae that attain the pleural pieces of the metasternum and those that do not.

In all the species studied, and indeed almost necessarily so from a functional viewpoint, the posterior coxae have articulations in two places. Morphologically the more important of these is the pleural articulation which is situated at the lateral extremity of the coxa and at the posterior end of the metathoracic pleurites. This is the most fundamental point in the coxal area and the articulation is probably never lost. The coxa has also a second articulation with the sternum, usually near the midline. Frequently the lateral parts of the coxa are covered by the sternum and are more or less invisible from the exterior. It is, then, the exposed portion which has given rise to the above classification, but obviously this is not a fundamental separation.

The differences between coxae that are " small and globose " (fig. 26 G), those that are conical (fig. 26 F), those that are triangular (fig. 26 K), and those that are transverse (fig. 26 C, D, H) are matters of degree and form a continuous series. It should be possible to find a more consistent and fundamental character to express the apparent differences.

There seem to be three distinct types of coxal structure. In many species the coxa is conical or triangular without expansions beyond the lines connecting the three articulations. In others the side of the coxa is expanded laterally and caudally into a plate which lies underneath the femur and below (dorsad) the level of the sternum. In the third group there is an upper lamella of the coxa which is expanded laterally and posteriorly into a plate which is nearly at the level of the sternum and completely covers the lower portion of the coxa. These three are the only morphological types recognized.

The following species belong to the first group, having the coxa not expanded laterally and caudally: *Osorius, Stenus* (fig. 26 G), the Paederinae (fig. 26 F), the Staphylininae, and possibly *Liparocephalus*. These are the ones generally said to have the coxae conical or triangular.

The second group, those having the coxae expanded laterally and caudally into a plate that is partly covered by the femur in repose, frequently also have a slight expansion over the base of the tro-

chanter but not extended laterally. It includes *Micropeplus,* the Omaliinae, all the Oxytelinae except *Osorius, Hypocyptus* (fig. 26 H), *Tachyporus, Tachinus, Erchomus* (fig. 26 D), *Bolitobius,* and all the Aleocharinae except possibly *Liparocephalus.* These are chiefly the forms said to have the coxae transverse.

The third group contains only *Habrocerus* (fig. 26 K). The coxa is rather triangular, but the upper surface is broadly expanded into a lamella which covers part of the femur in repose and extends laterally clear to the pleural articulation.

Micropeplus appears to be distinct from all the others in the presence of a narrow separate strip extending from the trochanteral articulation to the pleural one. It may be a secondary separation from the coxa but is entirely unique.

THE ABDOMEN

The abdomen of Staphylinidae is composed of 10 segments in all the species studied. In all cases the first segment is represented only by the tergite and rarely a paratergite on each side behind the spiracle (fig. 9 A, *ptt. 1*).

The second segment may be entirely membranous, as is apparently the case with *Micropeplus.* It may be represented by a tergite alone, as in *Trigonurus, Phloeocharis, Osorius, Stenus, Gastrolobium, Hesperobium, Paederillus, Paederus, Lathrotropis, Hypocyptus, Liparocephalus, Xenodusa, Lorinota, Aleochara,* and *Baryodma.* A pair of small paratergites is present at the sides in *Geodromicus, Tanyrhinus, Lathrimaeum, Pseudopsis, Creophilus* (fig. 9 A) and all the Staphylinini, *Glenus, Acylophorus, Quedius, Oxyporus, Habrocerus, Tachyporus, Tachinus, Erchomus, Bolitobius,* and possibly *Oligota.* Besides these sclerites the following also have some sclerotization of the sternite: *Pelecomalium, Proteinus, Eumalus, Xantholinus,* and possibly *Metoponcus.* The greatest development of this segment, however, is in the tribe Oxytelini. The species of this tribe have all the sclerites completely developed so as to appear identical with the succeeding segments in structure.

The third, fourth, fifth, sixth, and seventh segments are very similar in structure. They each have a normal tergite and sternite and usually one or two paratergites on each side. Only *Leptochirus, Eumalus,* and *Osorius* are entirely without paratergites, and the following have only one on each side: *Micropeplus,* all the Omaliinae (fig. 27 D), *Proteinus, Trigonurus, Phloeocharis, Pseudopsis, Stenus,* and *Habrocerus.* All the other species examined have two paratergites

on each side of the segments from three to seven. Figure 9 A shows the normal form of these sclerites. Modifications are chiefly in size, distinctness of the sutures, and vestiture. *Xenodusa* has the paratergites modified to form the hairy lobes or trichomes (fig. 27 B) which project over the succeeding segment.
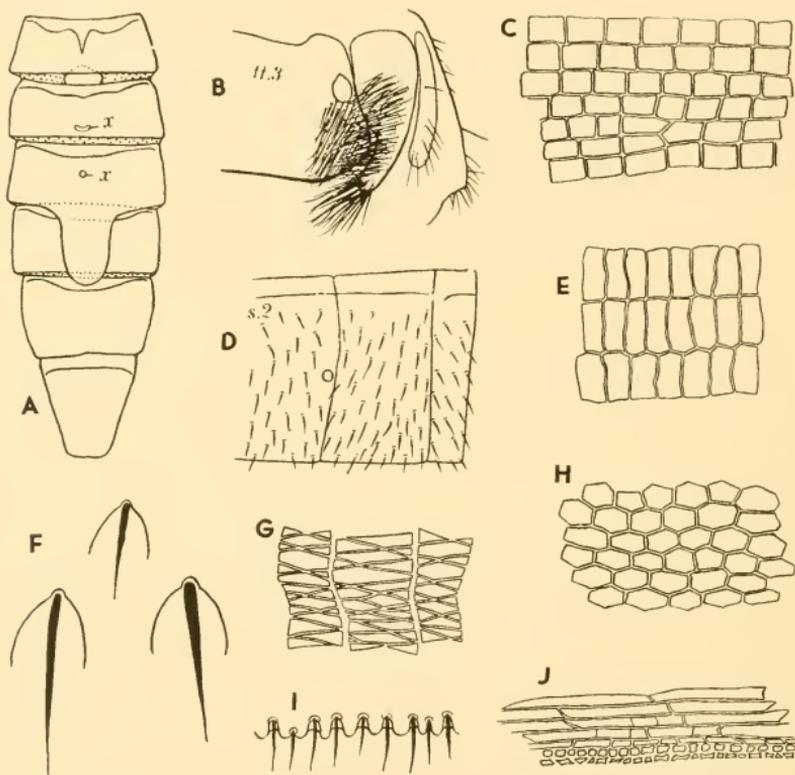
FIG. 27.—Details of the structure of the abdomen, and the intrafamily variation in the pattern of the intersegmental membranes.

A, ventral aspect of abdomen of *Gastrolobium bicolor* (Grav.). B, paratergites and trichome of *Xenodusa sharpi* Wasm. C, pattern of intersegmental membrane of *Lathrotropis jacobina* (Lec.). D, paratergite of *Geodromicus brunneus* (Say). E, pattern of *Paederus laetus* Er. F, group of setae from sternite of *Bolitobius cinctus* (Grav.) ; G, pattern of *Xantholinus picipennis* Lec. H, pattern of *Stenus sculptilis* Csy. I, posterior margin of sixth tergite of *Acylophorus flavicollis* Sachse. J, pattern of *Osorius mundus* Shp.

The membranes between these intermediate segments are usually marked in a definite pattern with minute spots of regular shape and deeper color. They appear to be actual sclerotizations in the membrane. These patterns are fairly constant in the various groups. The most frequent pattern is one of small rectangular areas arranged either in transverse or in longitudinal rows or both, often changing from

one to the other in a single membrane (fig. 27 C, E). This pattern is found on *Micropeplus,* all the Omaliinae, all the Paederinae, *Oxyporus,* and *Bolitobius.*

Two species have a definitely hexagonal pattern (fig. 27 H). They are *Leptochirus* and *Stenus.* In *Eumalus, Pseudopsis,* and *Osorius* (fig. 27 J) the areas are very small and angular in shape and grade into elongate transverse pieces near the edges of the membrane.

The subfamily Staphylininae is characterized by a pattern of ir-regular-sized areas arranged in longitudinal bands separated by clear membrane (fig. 9 F). *Xantholinus* and *Metoponcus* differ somewhat in having the areas strongly angular and frequently triangular or lozenge-shaped. *Acylophorus* is more or less intermediate between these and the typical form for the subfamily, and *Quedius* is marked only with longitudinal rows of very small spots.

Oxytelus and *Bledius* have a pattern very similar to that shown in figure 9 H except that the bands run transversely. In *Aploderus* and *Platystethus* there is no actual pattern, as the minute dots appear like an even stipple.

In some the membranes appear perfectly clear even under a fairly high magnification. These include *Proteinus, Trigonurus, Habrocerus, Hypocyptus, Tachyporus, Tachinus, Erchomus,* and all the Aleochari-nae studied.

Various modifications of form and vestiture are found on the ab-domen, but these are not very constant and are frequently modifica-tions of only one sex. The large posterior lobes on the fifth seg-ment of certain males of *Gastrolobium* (fig. 27 A) and the circular or crescentic groups of setae and pores on the same species are ex-amples of sexual modifications. These groups of setae (fig. 27 A, *x*) are called foveae in the literature and consist of a circle or band of setae set in moderate sockets and completely surrounded by a large number of pores which give a very rough appearance to the surface.

The discal setae of *Bolitobius* (fig. 27 F) do not have a definite socket but are set into the apex of a U-shaped area marked only by a fine line on the surface. The posterior margins of the intermediate segments of *Acylophorus* (fig. 27 I) are crenulate with the depressions much deeper on the ectal surface than on the ental. A rather large seta is set at the anterior end of each depression.

The eighth segment is composed of only a tergite and a sternite. The tergite bears a spiracle similarly to the preceding segments and generally is narrower and rather strongly tapering. The eighth seg-ment is usually considered to be part of the genitalia. In the case of the female it is therefore treated in that connection, but in the males

it is more convenient to restrict the discussion of the " genitalia " to the consideration of the genital tube or aedeagus alone. For this reason the eighth and ninth segments of the males will be discussed briefly here.

The posterior border of the eighth segment is frequently modified in the male. This modification may take the form of lobation, emargination or incisure, abnormal vestiture or sculpture, etc. It is generally the last visible segment of the abdomen, though it may be so far retracted within the preceding segments as to be invisible.

The ninth segment is represented by a tergite, a sternite, and two small lateral plates bearing the valvulae or gonapophyses. The gonapophyses are present only in the subfamily Staphylininae excepting the Xantholinini. In the other species studied the lateral plates (morphologically the bases of the segmental appendages) are present, generally large, and frequently appear much like gonapophyses but without any sign of basal articulation. In some species these two plates are joined by a narrow or wide bridge on either the dorsal or the ventral aspect. The species in which these lateral plates are thus united include *Geodromicus, Pelecomalium, Tanyrhinus, Lathrimaeum, Stenus, Gastrolobium, Hesperobium, Lathrotropis, Stilicus, Trachysectus, Hypocyptus, Tachyporus* (fig. 28 D), and *Bolitobius*. The species examined in which these sclerites are not united include *Trigonurus, Phloeocharis, Bledius, Oxytelus, Metoponcus, Xantholinus, Xenodusa, Lorinota, Aleochara,* and *Baryodma*. The greatest amount of union was found in *Bolitobius* in which the long sclerite formed is obviously dorsal. On the other hand in *Tachyporus* the union is said by Muir (1920) to be ventral, and the present observations confirm this.

A very much more remarkable modification than any other is found in the eighth and ninth segments of *Habrocerus* (fig. 28 E). The spiracles of the eighth segment are the most important landmarks and are situated on the dorsal aspect (sp. 8). According to the interpretation of Muir (1920), which differs somewhat from that of Weber (1911):

. . . . the eighth segment is highly modified and consists of four pieces. A large pair of pleural plates, on which the eighth spiracles are situated, embrace the lateral area, and from the apex of each a large, spine-like style arises; the dorsal aspect consists of a very short tergite, and the sternite consists of a large plate more heavily chitinized round the edges. . . . . The lateral portion of the eighth tergite articulates with the lateral edges of the sternite and also articulates in a depression at the base of the pleural plates. . . . The ninth segment is highly modified and shaped like an oat. The distal and visible portion consists of a pair of pointed and slightly curved lobes connected in a V-shaped piece on the dorsal aspect; the basal and internal portions consist of a mem-

branous plate chitinized along the edges. On the ventral aspect at the meeting of the lobes there is a small trident body attached to a rod which lies free within the segment. . . . . The anus opens on a membrane between the lobes; the rectum can be protruded.

Since Muir's figures of *H. capillaricornis* agree essentially with the structure of *H. schwarzi*, a discussion of his interpretation in the light of the present material seems to be justified. The large pleural plates are in the present species membranous except for a framework of sclerotic rods or struts. The spiracles lie on the dorsal aspect of these and identify them as paratergites. The transverse piece behind these and articulating with them probably does represent the tergite, but it is completely fused with the ventral plate by means of the sclerotized bars. The trident body appears in this species to be distinct from the ninth segment, and the lateral parts seem to articulate with the middle one and with the end of the supporting rod. The membranes forming the aedeagus are practically invisible in this specimen.

THE GENITALIA

The male genital tube in this family is characterized by the high state of specialization, by the modification of the median lobe for the evagination of the internal sac by blood pressure, and by the absence of a basal piece. Some of the most extreme modifications occur in the lateral lobes, which are always present and usually separate.

The most frequent type of genitalia is that represented in figures 9 G and 28 J, K. It consists of a strong sclerotic tube with a bulbous base, and a median foramen small and situated ventrally at the junction of the tube and bulb and between the base of the lateral lobes. The lateral lobes may be united into a plate basally but form two narrow lobes which usually lie along the median lobe. This type has been found in the following species: *Geodromicus, Pelecomalium, Lathrimaeum, Eumalus, Trigonurus, Phlococharis* (fig. 28 J), *Creophilus* (fig. 9 G), *Staphylinus, Ocypus, Philonthus* (fig. 28 K), *Cafius, Hadrotes, Acylophorus,* and *Quedius.* It seems to characterize the subfamily Staphylininae except for the tribe Xantholinini.

The Xantholinini are said by Sharp and Muir (1912) to be " one of the most highly specialized forms of Coleoptera." The two species studied do not show the complicated structure of the tip of the aedeagus of Sharp and Muir's species but are rather simpler than many others. In *Xantholinus* (fig. 28 F), according to Sharp and Muir (1912):

. . . . the bulbous median lobe is of an extreme form, being egg-shape, with a small membranous distal portion to which the greatly reduced lateral lobes are attached. The median lobe is formed of dorsal and ventral sclerites, round, and
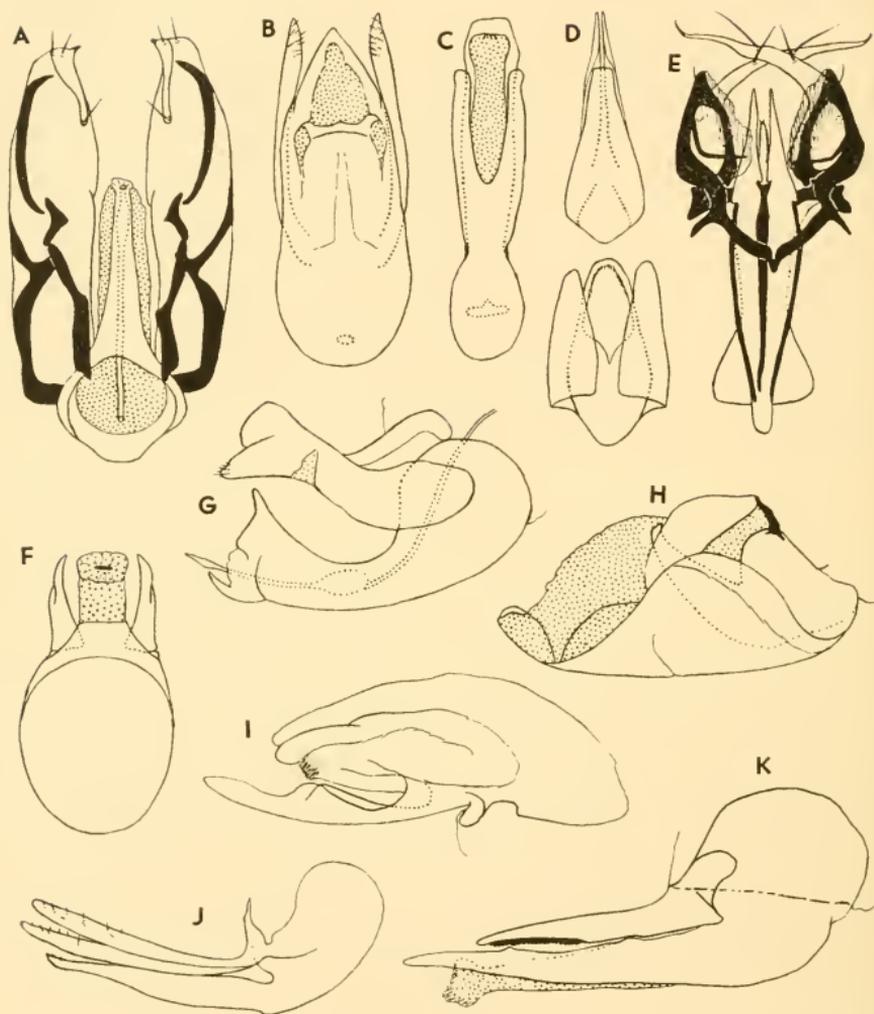
Fig. 28.—Intrafamily variation in the genitalia of the male.

A, *Hypocyptus longicornis* (Payk.). B, *Stenus sculptilis* Csy. C, *Micropeplus punctatus* Lec., ventral aspect. D, ninth segment and genital tube of *Tachyporus jocosus* Say, dorsal aspect. E, eighth and ninth segments and genital tube of *Habrocerus schwarzi* Horn, dorsal aspect. F, *Xantholinus picipennis* Lec., dorsal aspect. G, *Liparocephalus brevipennis* Mäkl., lateral aspect. H, *Xenodusa sharpi* Wasm., lateral aspect. I, *Lathrotropis jacobina* (Lec.), lateral aspect. J, *Phlococharis subtilissima* Mann., lateral aspect. K, *Philonthus aeneus* (Rossi), lateral aspect.

connected by a semi-membranous band; the median orifice is at the distal end, and the median foramen slightly in front (or basal) on the ventral face. These two openings are separated only by a chitinous plate formed by the basal part of the lateral lobes which are extremely reduced.

This description of *Xantholinus glabratus* (p. 499) is equally applicable to our species, *X. picipennis*. In *Metoponcus* the basal part of the median lobe is much more elongate and the lateral lobes are more slender than in *Xantholinus*.

In some forms there are more heavily sclerotized bars or struts in the median and lateral lobes. They are apparently strengthening or supporting structures and frequently articulate with each other. In *Hypocyptus* (fig. 28 A) the lateral lobes each bear three of these structures, articulating with each other and with a fourth pair connected to the median lobe. This latter pair is thought to be the pair of median struts mentioned by Sharp and Muir (1912). The lateral lobes are present on all forms examined. In *Xantholinus* (fig. 28 F) and *Metoponcus* they are very small and not specially modified. In *Cafius* they are also rather short but are otherwise similar to the other Staphylinini. *Hypocyptus* (fig. 28 A) represents the greatest development of these organs in point of size.

In *Micropeplus* (fig. 28 C) the lateral lobes arise from the sides of the median lobe and unite for a short distance on the dorsal surface. They are flat and unmodified and do not extend as far as the tip of the median lobe.

The genitalia of the female consist of the eighth, ninth, and tenth segments of the abdomen and their appendages. The eighth segment is present as a distinct tergite and sternite; the ninth segment is membranous except for a pair of three-segmented appendages and occasionally a sternal sclerite; and the tenth segment is represented only by the tergite. This is substantially the characterization given by Tanner (1927) for beetles in general.

The members of the Staphylinidae for the most part appear to be different from any forms studied by Tanner in the amount of reduction and loss of parts. Only a very few of the species included in the present study have any coxites or styli, the valvifers are absent in at least one species, and the paraprocts are frequently lacking. The one Staphylinid studied by Tanner, *Creophilus villosus*, is one of the very few which possess all the typical structures.

The eighth tergite and sternite are generally not specially modified in the female. They are broadly rounded as in *Oxyporus* (fig. 29 A) or truncated as in *Aleochara* (fig. 30 E). The only outstanding exceptions are in the subfamily Tachyporinae, where there are very
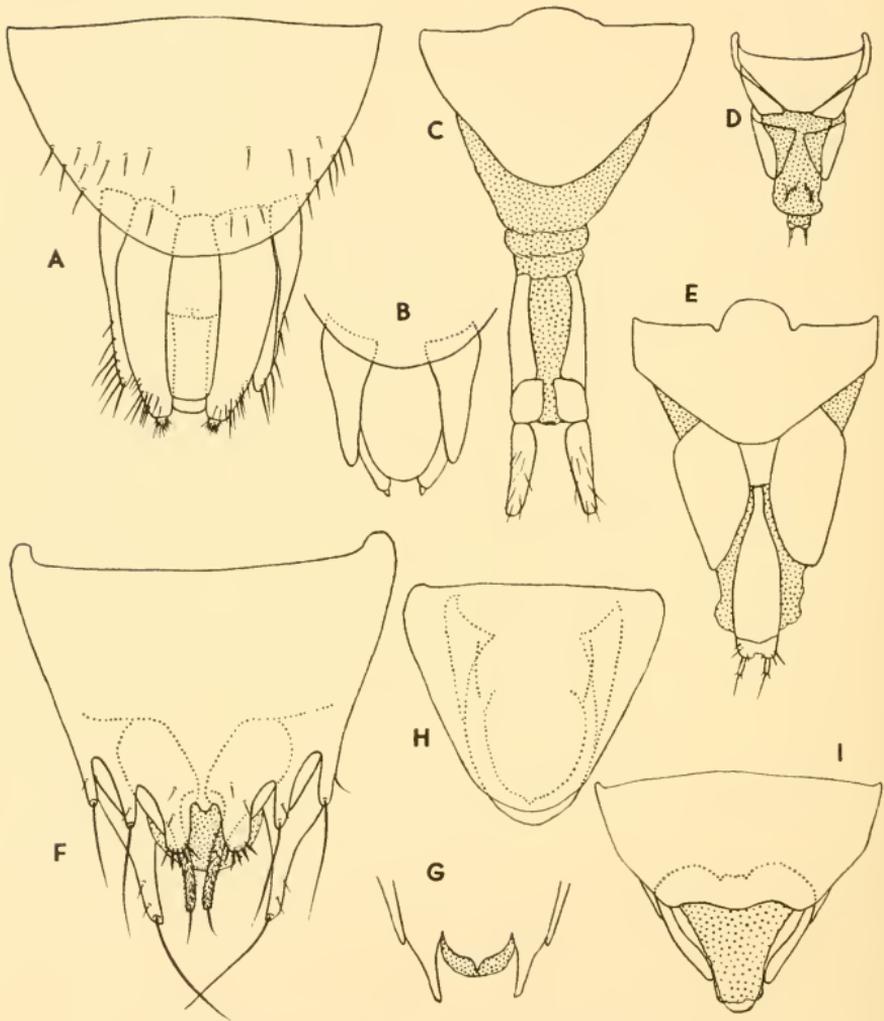
Fig. 29.—Intrafamily variation in the genitalia of the female
(continued on fig. 30).

A, *Oxyporus lateralis* Grav., ventral aspect. B, same, dorsal aspect. C, *Geodromicus brunneus* (Say), ventral aspect. D, *Lathrimaeum pictum* Fvl., dorsal aspect. E, same, ventral aspect. F, *Tachinus limbatus* Mels., ventral aspect. G, same, dorsal aspect. H, *Trigonurus crotchi* Lec., ventral aspect. I, *Oxytelus sculptus* Grav., ventral aspect.

great modifications of the posterior border of both these sclerites. In *Tachinus* the tergite (fig. 29 G) is divided into three lobes. The two outer ones are slender, and each bears a very long seta at its apex. The median process is semicircular but produced into a sharp point at the middle. In other species this median process may be much longer than the lateral ones, or it may itself be bifid or even trifid. The
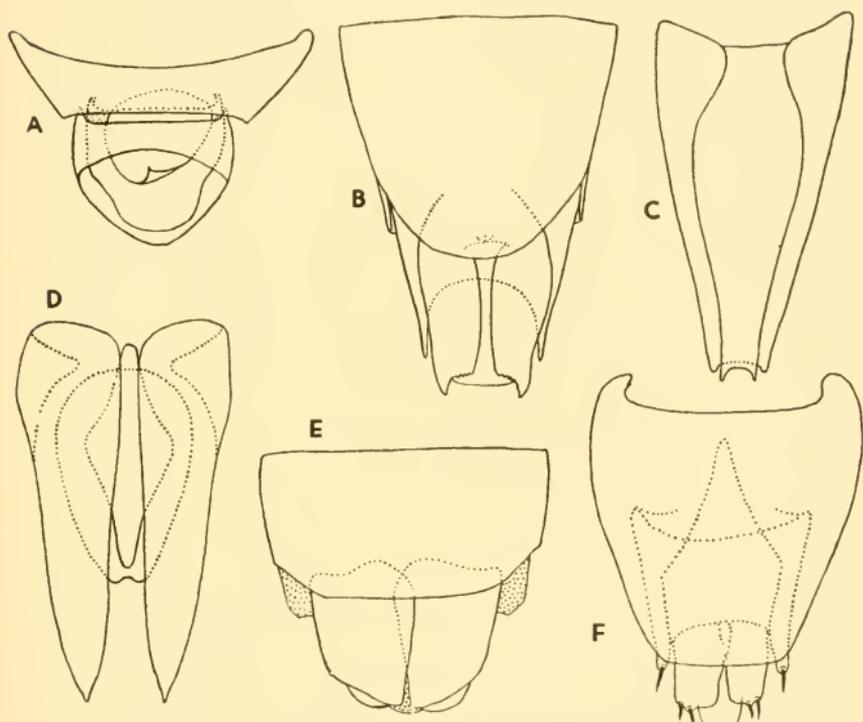
Fig. 30.—Intrafamily variation in the genitalia of the female (continued from fig. 29).

A, *Micropeplus punctatus* Lec.; B, *Stenus sculptilis* Csy.; C, *Pinophilus parvi-pennis* Csy.; D, *Paederus lactus* Er.; E, *Aleochara lata* Grav.; F, *Pseudopsis obliterata* Lec. All ventral aspects.

sternite is even more highly modified in *Tachinus* (fig. 29 F). The border is divided into six lobes of about equal length, but considerably shorter than the lateral lobes of the tergite. The outer pair on each side are rather slender, and each bears a long seta at the apex. The two median lobes are wider, and each bears a brush of six very straight short setae.

The ninth tergite and sternite are said to be nearly always membranous (Tanner, 1927). The only exceptions recorded by him are

two species with a sclerotized tergite and one with a sternite. In the present family there are apparently several more exceptions in the sternites. *Paederus* (fig. 30 D) has a distinct sagittate sternite of the ninth segment which lies between and under the large valvifers. *Pinophilus* (fig. 30 C) appears to have a large sternite also.

In practically every species examined there is a pair of large sclerites on the ventral surface which are interpreted as the valvifers. In most cases, therefore, it is found that the coxites are entirely lacking. Complete coxites with styli are found in all the Staphylinini, Xanthopygini, Quediini, and Oxyporinae studied, and also in all the Omaliini. This latter tribe is very different from the others, however, in that the genitalia are much elongated and have large membranous areas between the sclerites. The first group includes *Creophilus* (fig. 9 B, C) and *Oxyporus* (fig. 29 A, B). The Omaliini examined in this regard were *Geodromicus* (fig. 29 C), *Tanyrhinus,* and *Lathrimaeum* (fig. 29 D, E). In *Oxyporus* there are apparently no styli on the coxites. In *Geodromicus* the coxites are two-segmented but lack styli. In *Lathrimaeum* the valvifers appear to be fused to form an elongate median ventral sclerite, bearing apically the two small coxites and their styli.

The sternite of the tenth segment is entirely membranous in all members of the family, but the tergite is represented by a large broad sclerite, the proctiger (figs. 9 C, 29 B). Apparently only a few species possess the appendages of the ninth segment called the paraprocts by Tanner. They are present in *Creophilus* (fig. 9 B, C) and other Staphylininae, in *Oxyporus* (fig. 29 A), in *Lathrimaeum* (fig. 29 D, E), and probably others.

In *Oxytelus* (fig. 29 I) the entire ventral aspect of the ninth and tenth segments is membranous. The dorsal side is composed of a wide proctiger and a pair of narrow lobes at the sides. *Micropeplus* (fig. 30 A) is still more reduced. At first sight the eighth tergite and sternite appear to be part of the genitalia, but the tergite bears a pair of tiny but distinct spiracles. The genitalia form a more or less circular structure without any definite sclerites.

DISCUSSION

VARIATION AND RANGE OF STRUCTURE

Though it has often been said that the beetles, and even the entire class of insects, are characterized by a remarkable degree of uniformity of structure, a beetle almost always being immediately recognizable as a beetle, yet it is equally true in both the order and the

entire class that there is an amazing variety of divergence in the less fundamental characters. The family Staphylinidae, being one of the largest natural families of animals, is remarkably homogeneous in general habitus and form, but presents considerable range of variation in many of its structures.

In a group of this size it is to be expected that certain characters which are constant in one series of species will be more variable in others. This is found frequently to be the case. A certain subfamily shows a regular development of a given character which thus characterizes it, but the same character may occur scattered here and there in other groups, being too variable for use in classification.

Before any character can be safely used in classification, it is necessary to know the extent of variation of that character throughout the group being classified. If it is reasonably constant and varies only in definite ways and within definite limits, then it can be safely used. If, on the other hand, it be found to be very variable within small groups, or to vary through a large number of slightly separated forms, it can be used only with extreme care or only in certain cases.

The range of variation in each structure or set of structures is discussed in detail in the section on the comparative morphology of the family. It may be seen therein that the amount of variation in the numerous characters differs very greatly.

Characters Available for Classification

The existing classification of the Staphylinidae, as has been pointed out, is based almost entirely upon such characters as can be seen in pinned specimens and with an absolute minimum of dissection, amounting to no more than the removal of a leg to permit its examination under a microscope. The study here made reveals a long series of structures that may be added to the list of available characters.

Obviously, out of the many structures to be seen on the body of an insect, not all will be of aid in attempting a classification of the higher groups. Some are apparently usable only for the identification of species; some appear only in small groups such as genera. Some are evidently variable, and others, considered in the light of the totality of structures, seem to have no phylogenetic significance. We are compelled, then, to exercise a certain degree of judgment, based upon an examination of as many species as possible, in selecting those characters which will probably be significant as affording bases for defining the various categories. Out of the survey here presented the following list of characters has been selected as offering probably the

most significant indications of relationship. That is, they present
tangible differences between the various groups, while at the same
time they are of sufficient constancy throughout any one or more
groups to present an appearance of reliability. It is evident, however,
that only an examination of a very large proportion of the species of
the family can permit a dependable evaluation. The following are the
structural characters suggested:

1. Condition of the coronal suture.
2. Condition of the epicranial arm or frontal sutures.
3. Condition of the clypeal area.
4. Condition of the occipital suture.
5. Position of the antennal fossae.
6. Presence of ocelli.
7. Absence of dorsal tentorial pits.
8. Condition of the gular area.
9. Segmentation of the antennae.
10. Presence of processes on the labrum.
11. Dentition of the mandibles.
12. Condition of the prostheca.
13. Presence of serial pores on the mandibles.
14. Relative size and shape of the lacinia and galea of maxillae.
15. Segmentation of the maxillary palpi.
16. Size and shape of the terminal segments of the maxillary palpi.
17. Shape of the submentum.
18. Shape of the glossae and paraglossae.
19. Segmentation of the labial palpi.
20. Shape of the terminal segment of the labial palpi.
21. Condition of postcoxal lobe of pronotum.
22. Condition of the prosternal area.
23. Enclosure of the front coxal cavities by various means.
24. Condition of mesothoracic peritremes.
25. Presence of corneous plates in the anterior foramen of prothorax.
26. Separation of middle coxal cavities.
27. Condition of elytral suture.
28. Segmentation of the tarsi.
29. Specially modified setae of the legs.
30. Trochantero-femoral joint.
31. Structure and position of the posterior coxae.
32. Condition of second abdominal segment.
33. Paratergites of abdomen.
34. Mosaic patterns of intersegmental membranes of abdomen.
35. Presence of gonapophyses in male genitalia.
36. Condition of lateral plates in female genitalia.
37. Modifications of the aedeagus in the male.
38. Condition of valvifers, coxites, paraprocts, and proctiger in the female
     genitalia.
39. Modifications of the eighth segment in the female.
40. Condition of the ninth and tenth segments in the female.

The Value of Existing Classifications and Some Suggestions
Concerning Them

As far as the present study is concerned, no major changes are
indicated in the existing classification of the higher categories of the
family. However, there will be numerous changes in position or in
the relative degree of isolation of certain groups.

It has been very frequently noted that the conventional statement
of a character used in a classification may have no precise morpho-
logical meaning except as indicating that some peculiarity exists. Some
of these characters are discussed below.

The present subfamily classification, as well as that of all the smaller
categories, is to a large extent based on " key " characters. That is,
there has generally been in this family no distinction between classi-
fication and identification. This has led necessarily to a system based
on obvious and readily observable characters, rather than on the ones
particularly suited to show the fundamental relationships. Each of
these characters has been discussed by itself in the comparative section.

The differences between existing classifications are chiefly those
of the differences of opinion regarding the isolation of each group,
and the components of it, and are to a large extent due to the use
of an insufficient number of categories. Although the family un-
doubtedly contains several large and homogeneous groups, there are
also a number of very isolated and extreme forms which have no very
close relatives and are yet obviously members of the family. Some
authors tend to unite these with their nearest neighbors, whereas others
attempt to show the great divergence by separating them as distinct
tribes or subfamilies. The purpose of classification is to show not
only the relationships between animals but also the degree of the
difference between them.

In European catalogues the genus *Micropeplus* has sometimes been
united with the subfamily Omaliinae. More frequently, however,
it is given subfamily rank. It seldom shows the typical structure of
the family but has several modifications not found elsewhere. It ap-
pears to be more isolated from all the other Staphylinids than the ex-
tremes of that family are from each other. It is therefore thought
probable that it will have to be removed as a separate family. This
has already been done by some writers.

In the Leng Catalogue (1920) *Proteinus, Leptochirus, Eumalus,
Trigonurus, Phlococharis,* and *Pseudopsis* are united in the subfamily
Piestinae, and thereby are separated from the Oxytelinae. In the
catalogue of Eichelbaum (1909) these are all included in the Oxyteli-

nae. They have sufficient characters in common which differ from the Oxytelini to justify a separation between the two groups. Leng's arrangement is perhaps better for this reason.

Osorius is quite distinct in many respects from the Oxytelini. Its relationship is perhaps best expressed by an assignment as a tribe in the subfamily Oxytelinae equal to the rest of the subfamily or the tribe Oxytelini.

The members of the Xantholinini studied are very distinct from the rest of the Staphylininae. They differ from the tribe Staphylinini more than do the members of the tribes Xanthopygini and Quediini, and perhaps should be more isolated in the system. It may be that they should rank as a separate subfamily, but this would obscure the facts of their relationship to the other Staphylininae.

Habrocerus and *Hypocyptus* both differ considerably from the other Tachyporinae. *Habrocerus* differs perhaps more widely and is probably correctly placed as a separate subfamily, although its nearest relatives are the Tachyporini. *Hypocyptus* is more distinct from the Tachyporini and Bolitobiini than they are from each other, but perhaps insufficiently so to be isolated in a separate subfamily.

The linear arrangement of subfamilies is unsatisfactory as it precludes the possibility of showing relationships except in special cases. No better system has been suggested, and it is merely necessary to bear in mind the fact that the arrangement is more or less arbitrary.

The classifications in use have been gradually improved to the point where they seem to reflect the general facts in a true picture. Minor refinements will probably be necessary for a long time to come, and the judgment of individual workers will probably indicate many changes.

LIST OF SPECIES STUDIED

Subfamily MICROPEPLINAE
> *Micropeplus punctatus* Lec.

Subfamily OMALIINAE
> Tribe OMALIINI
>> *Geodromicus brunneus* (Say)
>> *Pelecomalium testaceum* (Mann.)
>> *Tanyrhinus singularis* Mann.
>> *Lathrimaeum pictum* Fvl.

Subfamily OXYTELINAE
> Tribe PROTEININI
>> *Proteinus limbatus* Mäkl.
> Tribe LEPTOCHIRINI
>> *Leptochirus mexicanus* Er.

Tribe ELEUSININI
>>>> *Eumalus nigrella* (Lec.)

Tribe PIESTINI
>>>> *Trigonurus crotchi* Lec.

Tribe PHLOEOCHARINI
>>>> *Phloeocharis subtilissima* Mann.

Tribe OXYTELINI
>>>> *Bledius monstratus* Csy.
>>>> *Platystethus americanus* Er.
>>>> *Oxytelus sculptus* Grav.
>>>> *Aploderus linearis* Lec.

Tribe OSORIINI
>>>> *Osorius mundus* Shp.

Subfamily STENINAE
>>>> *Stenus sculptilis* Csy.

Subfamily PAEDERINAE
Tribe PAEDERINI
>>>> *Gastrolobium bicolor* (Grav.)
>>>> *Hesperobium pallipes* (Grav.)
>>>> *Paederillus littorarius* (Grav.)
>>>> *Paederillus pugetensis* Csy.
>>>> *Paederus laetus* Er.
>>>> *Lathrotropis jacobina* (Lec.)
>>>> *Lithocharis ochracea* (Grav.)
>>>> *Stilicus angularis* Er.
>>>> *Trachysectus confluentus* (Say)
>>>> *Orus punctatus* Csy.
>>>> *Astenus discopunctatus* (Say)

Tribe PINOPHILINI
>>>> *Pinophilus parvipennis* Csy.

Subfamily STAPHYLININAE
Tribe XANTHOLININI
>>>> *Metoponcus varians* Shp.
>>>> *Xantholinus picipennis* Lec.

Tribe STAPHYLININI
>>>> *Creophilus villosus* (Grav.)
>>>> *Staphylinus cinnamopterus* Grav.
>>>> *Ocypus ater* (Grav.)
>>>> *Thinopinus pictus* Lec.
>>>> *Philonthus politus* (Linn.)
>>>> *Philonthus alumnus* Er.
>>>> *Cafius canescens* Mäkl.
>>>> *Cafius seminitens* Horn
>>>> *Cafius lithocharinus* Lec.
>>>> *Hadrotes crassus* (Mann.)

Tribe XANTHOPYGINI
>>>> *Glenus flohri* Shp.

Tribe QUEDIINI
>>>> *Acylophorus flavicollis* Sachse
>>>> *Quedius limbifer* Horn

Subfamily OXYPORINAE
>>> *Oxyporus lateralis* Grav.

Subfamily HABROCERINAE
>>> *Habrocerus schwarzi* Horn

Subfamily TACHYPORINAE
>> Tribe HYPOCYPTINI
>>> *Hypocyptus longicornis* (Payk.)

>> Tribe TACHYPORINI
>>> *Tachyporus maculicollis* Lec.
>>> *Tachinus limbatus* Mels.
>>> *Erchomus ventriculus* (Say)

>> Tribe BOLITOBIINI
>>> *Bolitobius cinctus* (Grav.)

Subfamily ALEOCHARINAE
>> Tribe OLIGOTINI
>>> *Oligota esmeraldae* Csy.

>> Tribe BOLITOCHARINI
>>> *Liparocephalus brevipennis* Mäkl.

>> Tribe MYRMEDONIINI
>>> *Xenodusa sharpi* Wasm.
>>> *Lorinota cingulata* (Lec.)

>> Tribe ALEOCHARINI
>>> *Aleochara lata* Grav.
>>> *Baryodma binaculata* (Grav.) ·

ABBREVIATIONS USED ON FIGURES

1A, first anal vein.
2A, second anal vein.
AnlA, anal arculus.
AntA, anterior arculus.
a, condyle.
ab, abdomen.
acs, antecostal suture.
aclp, anteclypeus.
af, antennal fossa.
afor, anterior foramen of prothorax.
an, anus.
anf, anal fan of wing.
annr, anterior notal ridge.
anp, anterior notal wing process.
ata, anterior arm of tentorium.
atp, anterior tentorial pit.
ax. 1, first axillary sclerite.
ax. 2, second axillary sclerite.
ax. 3, third axillary sclerite.
axc, axillary cord.
axp, axillary process.

bp, basal piece of male genitalia.
bs, basisternum.

C, costa vein.
c, condyle.
cal, calcar of tibia.
can, canaliculi.
cd, cardo.
cm. 1, first connecting membrane of male genitalia.
cp, body of the tentorium.
cr, crassa.
ct, coxo-trochanteral joint.
Cu, cubitus vein.
cx, coxa.
cxa, coxal condyle.
cxc, coxal cavity.
cxla, coxal articulation.
cxp, pleural coxal process.
cxt, coxite.

dta, dorsal arm of tentorium.
dtp, dorsal tentorial pit.

e, compound eye.
ej, ejaculatory duct.
ely, elytron.

em, emargination.
emp, empodium.
epi, epicranium.
epm, epimeron.
epm, II, mesothoracic epimeron.
epm, III, metathoracic epimeron.
epms, epimeral suture.
eps, episternum.
eps. II, mesothoracic episternum.
eps. III, metathoracic episternum.
epsr, episternal ridge.

fl, flagellum of male genitalia.
fm, femur.
for, foramen magnum (occipital fora-
    men).
fr, frons.
fs, furcasternum.
fu, furca, sternal apophyses united on
    median base.
fua, lateral arms of furca.

ga, galea.
ge, gena.
gl, glossa.
gony, gonytheca.
gs, gular sutures.
gu, gula.

hgw, hinge of wing.
hphy, hypopharynx.
hypo, hypomera, inflexed margin of
    pronotum.

I-III, thoracic segments.
1-10, abdominal segments.
is, internal sac of male genitalia.
ists, intersternal suture.

lb, labium.
lc, lacinia.
ll, lateral lobes.
lm, labrum.
lp, labial palpus.

M_1, first branch of media vein.
M_4, fourth branch of media vein.
mad, dorsal articulation of mandible.
maf, mandibular fold.
mat, mandibular tooth.

mav, ventral articulation of mandible.
mb, intersegmental membrane or con-
    junctivum.
mbps, membranous area of prescutum.
md, mandible.
mdpp, prothoracic pleural muscle disk.
mdpt, metathoracic pleural muscle
    disk.
mdsp, prothoracic sternal muscle disk.
mdss, mesothoracic sternal muscle disk.
mdst, metathoracic sternal muscle disk.
mdts, mesothoracic tergal muscle disk.
mdtt, metathoracic tergal muscle disk.
mesp, mesosternal process.
mf, median foramen of male genitalia.
ml, median lobe of male genitalia.
mls, median lobe of scutum.
mo, median orifice of male genitalia.
mp, mandibular pore.
mrn, marginal ridge of pronotum.
mt, mentum.
mtla, episternal articulation of tro-
    chantin.
murc, retractor muscle of claws.
musd, muscle disk.
mx, maxilla.
mxa, maxillary articulation.
mxp, maxillary palpus.

nepm, notepimeron.

o, ocellus.
oc, occiput.
ocs, occipital suture.
ol, oculata.

p, pore.
papt, paraproct.
pclp, postclypeus.
peri, peritreme.
pge, postgena.
pgl, paraglossa.
pl, pleuron.
pla, pleural apophysis.
pld, pleuradema.
plf, palpifer.
plg, palpiger.
plns, pleuro-notal suture.
plr, pleural ridge or apophysis.
pls, pleural suture.

pn, postnotum.
pna, postnotal articulation.
pnp, posterior notal wing process.
ponr, posterior notal ridge.
pos, postoccipital suture.
pph, postphragma.
ppl, prephragmal lobe.
ppr, prephragmal ridge.
prf, prosthecal foramen.
prmt, prementum.
prnl, pronotal lobe.
pron, pronotum.
prp, prepectus.
prph, prephragma.
prss, prosternal suture.
prth, prostheca.
psc, prescutum.
pscl, prescutal lobe.
pscs, prescutal suture.
pss, prescutoscutellar suture.
psss, prescutoscutal suture.
pta, posterior arm of tentorium.
ptar, pretarsus.
ptgr, proctiger.
ptp, posterior tentorial pit (gular pit).
pts, paratergal suture.
ptt. 1, first abdominal paratergite.
ptt. 2, second abdominal paratergite.
ptt. 3, third abdominal paratergite.
ptt. 7, seventh abdominal paratergite.
pwp, pleural wing process.

R, radius vein.
R₁, first branch of radius vein.
R₂, second branch of radius vein.

s. I, prothoracic sternite.
s. II, mesothoracic basisternum.
s. III, metathoracic basisternum.
s. 2, second abdominal sternite.
s. 3, third abdominal sternite.
s. 8, eighth abdominal sternite.
s. 9, ninth abdominal sternite.
sa, sternal apophysis.
sart, sternal articulation.
Sc, subcosta vein.
scl, scutellum.
sclp, scutellar process.
sclt, scutellum.
sct, scutum.

scts, scutal suture.
sctt, scutum.
senp, sensory papillae.
sepl, sternepimeral line.
sepm, sternepimeron.
sepr, sternepimeral ridge.
seps, sternepimeral suture.
sg, subgalea.
smt, submentum.
sns, sternonotal suture.
sp, spiracle.
sp. II, mesothoracic spiracle.
sp. III, metathoracic spiracle.
sp. 1, first abdominal spiracle.
sp. 2, second abdominal spiracle.
sp. 3, third abdominal spiracle.
sp. 8, eighth abdominal spiracle.
spe, serial pores.
spn, spina.
sps, sternopleural suture.
ss, spinisternum.
ssr, spinisternal ridge.
sss, spinisternal suture.
stc, sternacosta.
stca, sternal coxal articulation.
stcs, sternacostal suture.
stg, stigma of wing.
st, stipes.
sts, sternal suture of abdomen.
sty, stylus.
swp, scutal wing process.

tar, tarsus.
tb, tibia.
th, thorax.
tn, trochantin.
tnr, transverse notal ridge.
tns, transverse notal suture.
tor, tormae.
tr, trochanter.
tra, distal trochantinal coxal articulation.
trla, coxal condyle of trochantin.
ts, tergal suture of abdomen.
tt. 1, first abdominal tergite.
tt. 2, second abdominal tergite.
tt. 3, third abdominal tergite.
tt. 8, eighth abdominal tergite.
tt. 9, ninth abdominal tergite.

un, claw or ungues.

utr, unguitractor plate.

vd, vas deferens.

vl, valvula.

vlf, valvifer.

vp, ventral piece of male genitalia.

vr, ridge between scutum and scutellum (V-ridge).

vul, vulva.

vx, vertex.

wc, antemedian area.

wd, pivot (distal pivot) area.

we, first costo-apical area.

wg, first anal area.

wh, principal area.

wj, jugal or axillary area.

wr, stigmatal area.

wx, first dorso-apical area.

wy, anal area.

x, point reference.

xt, tendon of retractor muscle of claws.

y, reference to vestiture.

z, reference to sculpture.

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