

COMPARATIVE EXTERNAL MORPHOLOGY,
PHYLOGENY, AND A CLASSIFICATION
OF THE BEES (HYMENOPTERA)

CHARLES DUNCAN MICHENER

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INTRODUCTION

THIS PAPER IS THE RESULT of a study of the external morphology of bees. Its primary objectives are to add to the knowledge of the morphology of the Insecta and to the understanding of the interrelationships of the genera of bees. In the taxonomic papers on bees the same term is often applied to different structures by different authors, and many terms which must be incomprehensible to most entomologists (e.g., dog-ear plate) are in common use. A third objective of this paper, therefore, is to suggest a morphological terminology for the use of bee students and of hymenopterists generally, which, if adopted, should encourage future uniformity in the use of descriptive terms.

The method applied in attempting to fulfill these objectives has been to study in detail the morphology of a single species, establishing its structure and the terminology of its parts by frequent comparisons with other Hymenoptera; then to compare numerous other bees with this species; and finally, with these comparisons as a basis, to work out the interrelationships of the various genera and a classification for them. The bee selected for intensive study was *Anthophora edwardsii* Cresson. It was selected because of its availability and because, while *Anthophora* is near the top of the apoid phylogenetic tree, it retains at least vestiges of most of the structures found in primitive bees. It is thus in a sense intermediate between the primitive and the most modified bees, and homologies may easily be drawn between structures of *Anthophora* and those of any other bee.

Part 1, the section on the integumental morphology of *Anthophora*, includes a summary of the terminology of structures, which is applicable to all bees and to many other groups of Hymenoptera. Part 2, on the comparative external morphology of bees, is primarily a record of differences among numerous genera with certain suggestions as to

how some of these differences may have come about. It may be assumed that nearly all the characters described in part 1, but not mentioned in part 2, are characters which all bees possess in common. In part 3 the characters described in previous sections are analyzed, and the phylogenetic history of the bees, as it appears to the writer, is discussed. Finally in part 4 the classification, a by-product of this concept of phylogeny, is presented.

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The author, having left the American Museum for service in the Army of the United States, has been unable to give close attention to the final preparation of this paper for the editor and printer. Grateful acknowledgement for work in this connection is made to Miss Annette L. Bacon of the American Museum of Natural History, who has checked many of the bibliographical citations in part 4.

PART 1. EXTERNAL MORPHOLOGY OF *ANTHOPHORA EDWARDSII* CRESSON

THIS ROBUST SPECIES is about 12 mm. long, 5 mm. broad across the thorax, and with forewings about 9 mm. in length. The integument, except where thin and flexible to permit movement, is thick and heavily sclerotic. This is particularly true of the head and thorax, a fact no doubt correlated with the need for firm bases for the articulation of the mouthparts and locomotor organs. This heavily sclerotized integument is black, except for most of the labrum and clypeus and parts of the paraocular areas which are yellow in the male. The surface sculpturing of the integument consists of coarse punctures on the clypeus, especially in the female, fine punctures

on the higher part of the face and on the thorax, and rather fine piliferous punctures on the abdomen. In addition to the punctation, most of the head and thorax is dull because of minute roughening resembling tessellation. The vestiture of the exposed parts of the body, except as elsewhere described, consists of long, dense, more or less erect hairs furnished with numerous very short branches throughout their lengths (fig. 4). The hairs of the abdominal sterna and of the third and following terga are shorter than those on the head and thorax. The eyes are bare, as is also most of the posterior face of the propodeum.

HEAD

HEAD CAPSULE

Like other Hymenoptera, this is a hypognathous insect in which that part of the head above the foramen magnum is expanded upward, so that the main axis of the head becomes vertical and the face nearly so. The cranium or head capsule is rigid, the only movable nonappendicular sclerotic structure of the head being the labrum. Antero-posteriorly the head is compressed; seen from front or rear the dorso-ventral length of the head is considerably less than the width, especially in the male.

The most conspicuous surface structures of the head are the large, strongly convex, elongate-oval *compound eyes*, which occupy almost the entire lateral areas of the head. The area between the anterior margins of the eyes is the *face*. Above, this area is somewhat concave due to the swollen eyes; below, it is convex because of the strongly protuberant and convex clypeus.

The *clypeus* (fig. 1) is a large, irregularly trapezoidal area on the lower part of the face. It is strongly convex, so that the lower lateral areas are parallel to the long axis of the insect, as shown in figures 3 and 6. This condition is perhaps correlated with the elongation of the mouthparts, which is accomplished in part by the lengthening of the prementum and

stipites, the anterior ends of which, in repose, fit close behind the lower margin of the clypeus. Above and laterally the clypeus is delimited by the arched *epistomal suture* (fig. 1). The median portion of this suture, between the *dorso-lateral angles of the clypeus*, is straight; the lower halves of the lateral portions, between the dorso-lateral and the *lateral angles of the clypeus*, are strongly bowed outward toward the eye margins, which are closely approached in the male. The extremities of the suture are just mesad from the anterior mandibular articulations. Since in most insects these articulations are on the clypeus itself, it may well be assumed that at least the extreme lateral portions of the epistomal suture are not parts of the definitive epistomal suture but are secondary features, the primary ends of the suture having disappeared. In certain *Chalastogastra*, e.g., *Abia americana* (Cresson), the ends of the epistomal suture are distinctly lateral to the anterior condyles of the mandibles, so that these mandibular articulations are with the clypeus.

Although the anterior ends of the tentorium are large and complex and broadly attached to the integument of the face, the small pits on the epistomal suture a short distance below the dorso-lateral angles of the

clypeus may well be called the *anterior tentorial pits* (fig. 1). Clearly they have migrated far upward along the epistomal suture from their position in most primitive insects near the anterior articulations of the mandibles. This is a characteristic of all Hymenoptera except those in which the clypeus is secondarily much shortened, and the resulting elevated position of the tentorium is of primary importance in allowing for the deep invagination of the hypostomal area and the maxillary articulations of most Hymenoptera, resulting in the deep proboscoidal fossa. This position of the tentorium was, then, a prerequisite to the evolution of the type of mouthparts found in the bees. Throughout its entire length, except for the area on which the tentorium arises, the epistomal suture is represented internally by a distinct ridge, which is strongest between the dorso-lateral angles of the clypeus.

The lower margin of the clypeus is defined medially by the *labro-clypeal suture*, which is but little overhung by the produced clypeal margin. Laterally the lower margin is somewhat expanded (fig. 1) and is free, the integument which continues backward from this free margin being part of the soft conjunctival membrane which supports the labio-maxillary complex. The lower margin of the clypeus, as in many bees, is somewhat depressed and impunctate and may be known as the *marginal area of the clypeus*. This is broader in the female than in the male, and the line between this area and the remainder of the clypeus is represented within by a ridge which forms part of the surface of articulation for the labrum.

The *labrum* (fig. 10) is a short, rectangular sclerite, strongly convex anteriorly and concave posteriorly, thus fitting the convexity of the lower margin of the clypeus upon which the labrum is articulated. The base of the labrum at each side is furnished with a low, rounded bulla, represented within by a concavity. Toward the apex the labrum is marked by several transverse impressions (fig. 3). The area basad from these may represent the elevated *basal area of the labrum*, commonly known as the "process" of the labrum in *Andrena* and certain other genera. Attached to the base of the labrum, one at each side, are the two slender tendon-like

labral apodemes, which extend upward and are attached to short muscles inserted in the vicinity of the supraclypeal area.

The epipharynx and hypopharynx, while not of appendicular origin, are considered in connection with the labio-maxillary complex because of their close association with that mechanism.

That portion of the face above the clypeus presents a number of problems in morphology and terminology. In Hymenoptera the only landmarks present in the area are the antennal sockets and the three ocelli. The λ -shaped epicranial suture of lower insects is absent in Hymenoptera, or so modified as to be recognizable only with difficulty. According to Snodgrass (1935), the frontal sutures primitively diverge from the coronal suture above the anterior ocellus, pass mesad from the antennal sockets, and end on the epistomal suture. The area enclosed between these frontal sutures above the epistomal suture is the frons. If frontal sutures exist at all in the Hymenoptera, which seems doubtful since they are clearly evident in none of the Chalcidogastra which I have examined, they have fused to a point far below the anterior ocellus, diverge not far above the antennal sockets, and are represented below by the subantennal sutures. Thus the frons would be separated by the formation of a parietal bridge into two parts, a small one around the anterior ocellus and a larger one or antefrons (Crampton, 1921a) above the clypeus. Duncan (1939), Salman (1929), and Snodgrass (1928, 1935) show indistinct sutures diverging from above the antennal bases in *Vespula*, *Pepsis*, and *Apis*, respectively, which lend weight to this theory. Yet Duncan calls the large area above the antennae the frons, as has been done by most taxonomists and by Snodgrass in 1925, although it clearly is not the frons if this theory is correct. The median line below the anterior ocellus, called the frontal suture by Duncan (1939) and Linsley and Michener (1937) and the coronal suture by Linsley and Michener (1939), supposedly formed by fusion of frontal sutures, is conspicuous in most Hymenoptera.

Since the evidence for a divided frons, as suggested above, is found only in the higher Hymenoptera and since there is little indication of frontal sutures of any sort in lower

Hymenoptera, it seems best to assume, awaiting more conclusive evidence, that there are not true frontal sutures in bees and wasps. The nomenclature here proposed, therefore, is noncommittal as to homologies. A number of terms for various areas are suggested, not because of the need for them in ordinary morphological work but because the areas designated are commonly referred to in systematic literature.

Arising at each dorso-lateral angle of the clypeus and extending toward the antennal socket is the *outer subantennal suture* (fig. 1). It is represented internally by the attachment of the upper portion of the anterior end of the tentorium and in some forms extends directly toward the *subantennal pit* (fig. 1), which represents the point of origin of a thickening of the tentorium. Because of the curvature, as seen in cross section, of the upper anterior part of the tentorium in *Anthophora*, each subantennal suture extends toward the inner margin of the antennal socket. That portion of the suture between the subantennal pit, which lies near the outer margin of the antennal socket, and the apparent upper end of the subantennal suture is merged with the antennal suture. The subantennal sutures, as indicated above, may represent the lower ends of the frontal sutures, or may be secondary sutures which arose with the great expansion of the tentorium, an explanation which seems more likely in view of their fundamental direction toward the subantennal pits, not toward the inner margins of the antennal sockets. The *inner subantennal sutures* (fig. 1) extend from points near the inner margins of each antennal socket to the epistomal suture mesad from the dorso-lateral angles of the clypeus. These sutures, absent in many bees, are scarcely discernible in *Anthophora* but are represented internally by feeble ridges which arise on the tentorium. The small area below each antennal socket, delimited laterally by the inner and outer subantennal sutures and below by the epistomal suture, may be known as *subantennal areas* (fig. 1). In American literature they have usually been known as dog-ear plates, because of the resemblance of the marks which they bear in the form described as *Perdita canina* Cockerell to the ears of a hound (Cockerell, 1896).

The area above the epistomal suture, between the inner subantennal sutures if present or between the outer subantennal sutures if the inner ones are absent, and below an imaginary line drawn between the antennal sockets is the *supraclypeal area* (fig. 1) or antefrons. It is convex, especially above. In some forms it is elevated, and a wedge-shaped elevation extends into the supra-antennal region above the antennal bases. In such cases the entire elevated area may well be called the supraclypeal area.

The bases of the antennae are about midway between the upper and lower extremities of the face, are rather widely separated, and lie in broad depressions of the face so that the area between them is convex. The rounded base of each scape fits into a nearly circular *antennal socket* (fig. 1) which is furnished with a conical peg-like projection, the *antennifer* (figs. 7, 8, 9) arising on the margin of the socket near the subantennal pit. A narrow elevated area, the *antennal sclerite* (fig. 1), surrounds each antennal socket and is separated from the rest of the face by a rather inconspicuous suture, the *antennal suture* (fig. 1) which is represented within by a ridge.

The *supra-antennal area* lies above a transverse imaginary line drawn between the antennal sockets, below a similar line drawn just beneath the anterior ocellus, and between approximately vertical lines drawn roughly tangent to the outer sides of the antennal sclerites. It is convex and furnished medially with a longitudinal elevated line (an impressed line in many groups) which may be called the *frontal line* (fig. 1). This name seems appropriate since the line is either on the frons proper or represents the united frontal sutures. As already stated, the supra-antennal area has been called frons by most students of the Hymenoptera.

The *vertex* is the summit of the cranium and is limited posteriorly by the preoccipital ridge or upper margin of the declivity of the posterior surface of the head, anteriorly by an imaginary horizontal line drawn beneath the anterior ocellus, and laterally by the compound eyes. It bears the three *ocelli*, which are arranged in a broad triangle (fig. 1). A narrow area more or less completely surrounding each ocellus is slightly elevated, but the mar-

gin of this elevation is indicated within by a mere line, not by a strong ridge as in the case of the externally somewhat similar antennal sclerites.

The remaining areas of the face lie immediately mesad from the inner margins of the compound eyes and are limited below by the positions of the anterior mandibular condyles, above by an imaginary horizontal line immediately below the anterior ocellus, and mesally by the epistomal, outer subantennal, and antennal sutures and by vertical lines tangent to the outer margins of the antennal sclerites. These areas have usually been known as the sides of the face, but the term *paraocular areas* (fig. 1) seems more satisfactory. The lower portions of these areas have been termed parafrontals in the Ichneumonidae (Pratt, 1940), but in view of our meager knowledge of the frons and the need in bee taxonomy for a term for the larger areas here defined, the name paraocular area seems justified. In certain bees the upper part of each paraocular area is furnished with a depressed *facial fovea*. Adjacent to the inner margin of the compound eye, each paraocular area is furnished with a *paraocular carina*, which in some forms diverges from the eye at its lower extremity and extends toward the anterior mandibular articulation. The paraocular carinae are not associated with the sharp internal *circumocular ridges* (ocular diaphragms of Ferris, 1940) which surround the retina and are closer to it than are the paraocular carinae.

The posterior surface of the head is perforated in the middle by the foramen magnum and is strongly indented beneath by the deep *proboscoidal fossa* or trophicava, in which the proboscis is folded in repose. The large median area of the posterior side of the head is concave. The broadly rounded angle which separates this concavity from the genal areas at the sides and the vertex above is the *preoccipital ridge* (fig. 2). Since no occipital suture is present, it is impossible to determine the exact extent of the occiput, but in *Cephus* and in *Pepsis* (Salman, 1929) and *Vespula* (Duncan, 1939) the occipital suture, except at its lower extremities, follows the preoccipital ridge. It therefore seems reasonable to term the large, impunctate but tessellate, concave area between the preoccipital

ridge and the postoccipital suture the *occiput*. The sides of the head between the eyes and the preoccipital ridges are the *genal areas* (fig. 2). The *postoccipital suture* completely surrounds the foramen magnum, although its upper portion is lobate and broken, and its course in that region is therefore difficult to determine. A pair of arcuate linear impressions, the *occipital sulci* (fig. 2), the lateral sulci of postgena of Duncan (1939), extend far out into the occiput from the upper portion of the postoccipital suture. These are the external indications of the lines of attachment of large tentorial sheets. The *posterior tentorial pits* (fig. 2) are a pair of large pits on the lower parts of the postoccipital suture. That part of the postocciput below the position of these pits is the homologue of the postoccipital element of the gula of prognathous insects and may be known as the *postoccipital bridge*. A small part of the postoccipital bridge is invaginated with the proboscoidal fossa and forms a part of its posterior dorsal wall. The hypostomal suture and the postoccipital suture unite for a short distance along the lower margin of the postoccipital bridge, so that the postgenae (lower portions of occiput) do not fuse below the postoccipital bridge as they do in most bees. Such a fusion product below the postoccipital bridge is the *postgenal bridge*. The formation in the Clistogastra of the postoccipital, postgenal, and hypostomal bridges separates the membranous cervix from the membranes of the labio-maxillary complex, with which they are continuous in many Chalastogastra. This condition results in greater rigidity of the neck region, the chief head movement being up and down, lateral movements being very slight. The development of the cervical sclerites in certain bees is a further advance in the same direction, since these sclerites have nothing to do with the articulation of the head on the thorax but merely serve to stiffen the membrane below the points of articulation. Perhaps these evolutionary developments were advantageous because of the need for a firm basis for the head in view of the many and complex functions of the powerful mandibles of the Clistogastra.

The *postocciput* is smooth and shining, except for the finely punctate postoccipital bridge, and is elevated toward its inner lobate

margin, which surrounds the *foramen magnum*. The primary lobes of this margin are an upper and a lower pair. Immediately below the upper pair, at the widest point of the foramen, the cervical membrane is evaginated upward and attaches to the head outside of the foramen magnum along the line marked "a" in figure 2. Each of the lower lobes is furnished with a small projection (fig. 2), immediately above which the occipital processes of the propleura, upon which the head rocks, meet the margin of the foramen. Each of the lobes is larger than is evident from an examination of figure 2 because they project strongly posteriorly. On the midventral margin of the foramen, the cervix is attached to the postgenal bridge along line "b" outside the apparent margin of the foramen magnum. *Cervical sclerites* are absent or fused with the propleura as in most Hymenoptera, although a pair of minute ones is present in some bees as secondary sclerotizations of the cervical membrane immediately below the occipital processes of the propleura.

The small areas between the lower ends of the eyes and the bases of the mandibles are *malar areas*. According to the interpretation of Snodgrass (1928, 1935), these must be compound areas consisting of the pleurostomata and parts of the parietes. Although Duncan describes weak pleurostomal sutures in *Vespula*, I have seen no such sutures well developed in Hymenoptera. The subocular sutures found in certain Hymenoptera (Pratt, 1940) are absent in *Anthophora*.

Sutures which have commonly been regarded as *hypostomal sutures* (Duncan, 1939) are conspicuous in most Hymenoptera. These structures may well be secondary developments, consequent upon the formation of the deep proboscidal fossa, but the term hypostomal suture or groove seems justifiable. The hypostomal sutures arise near the posterior mandibular articulations and extend mesad nearly to the margins of the proboscidal fossa, which margins they follow posteriorly for a short distance and then dorsally until they meet above the fossa.

The large area between the posteriorly connected hypostomal sutures, including the proboscidal fossa, is the *hypostoma*.¹ Through-

¹ The term is here used in the singular, since the two

out their length, except for the short distance where the hypostoma is in contact with the postoccipital bridge, the hypostomal sutures are closely paralleled anteriorly and mesally (figs. 2, 6) by the *hypostomal carinae* (Sandhouse, 1939), which for most of their lengths form the margins of the proboscidal fossa. Antero-laterally the hypostoma is developed into broad *paramandibular processes* (fig. 6) which close the mandibular sockets within and reach, but do not fuse with, the clypeus. These processes are strengthened by the *paramandibular carinae* which arise just within the proboscidal fossa close to the *anterior angles of the hypostomal carinae* (fig. 6). In *Andrena* these carinae are very strong and curved and furnished in the females with a series of stiff setae which has been called the subgenal coronet by Timberlake (1941). Setae of paramandibular carina seems a more appropriate term. Deeper within the fossa another anterior projection of the hypostoma on each side provides the structure on which the base of the maxillary cardo rocks and may be known as the *maxillary process of the hypostoma*. The rigidity of these processes is insured not only by the strong anterior margin of the hypostoma below and between them, but by their strong connections (which will be described later) with the tentorium above them.

The remainder of the hypostoma consists of rather thin integument forming the side walls and roof of the great proboscidal fossa. The region of the roof is intimately connected with the tentorium. The curved line (fig. 6) connecting the maxillary processes of the hypostoma represents the line of fusion between the anterior margin of the hypostoma and the secondary tentorial bridge. It is also the line upon which the posterior conjunctiva of the labio-maxillary complex is attached to the head. That portion of the proboscidal fossa in front of this line is the *Rüsselloch*, that part behind it the *Rüsselgrube*, according to the terminology of Ulrich (1924). Posterior to this line, the side walls and sides of the roof of the proboscidal fossa are composed of

primitive hypostomata are always united by a hypostomal bridge in bees. This usage is comparable to the commonly accepted term glossa for the fused glossae of Hymenoptera.

thin sheets of hypostoma (figs. 6, 7, 9), but the median portion of the roof of the fossa, the *hypostomal bridge*, is strongly concave and differentiated by distinct lines from the rest of the walls of the fossa. These lines represent the lines of fusion between the hypostomal bridge and broad sheets which extend mesad from the main longitudinal bars of the tentorium (see cross-sectional view, fig. 9). It is to be noted that in most bees the hypostomal bridge area is not set off from the rest of the hypostoma, but is nevertheless the median portion of the fused hypostomata.

The development of the hypostomata, ordinarily small and simple regions of the insect head, into one of the largest and most complicated portions of the cranium is a remarkable feature of bee morphology and probably took place simultaneously with the development of the proboscis. The deep proboscideal fossa made necessary a great expansion of the hypostoma. The bases of the maxillae are carried far forward and upward into the head, a condition which makes room for the folding of the proboscis. By their fusion, the tentorium and hypostoma are both strengthened, and great strength is given to the otherwise weak maxillary articulations.

The *tentorium*, like the hypostoma, is an unusually complex structure. Practically the entire internal skeleton of the head is developed from the anterior arms of the definitive tentorium. Both anterior and posterior roots are greatly expanded and attached in a complicated manner to the cranial wall. The *primary tentorial bridge* is very slender and nearly straight, immediately in front of the foramen magnum (figs. 2, 8), but a broad *secondary tentorial bridge* fused along its posterior margin with the hypostoma lies in front of, and beneath, the primary bridge (fig. 8).

The anterior roots of the tentorium consist of a vertically expanded fan-shaped sheet on each side. Both upper and lower margins of each sheet are strengthened by heavy thickenings which terminate in the subantennal pits and anterior tentorial pits, respectively. Each of these sheets is attached to the cranium along the curved line formed by part of the epistomal suture, the outer subantennal suture, and the lower part of the an-

tennial suture. The major curves in these sheets obviously lie at the summits of the subantennal sutures and are accentuated by a dorso-mesal carina on each sheet, which anteriorly leaves the tentorium and extends onto the inner surface of the integument of the face, forming the ridge which is represented externally by the inner subantennal suture, and which posteriorly extends onto the secondary tentorial bridge. The sheets between the upper and lower thickenings of the tentorium are diminished posteriorly until the latter fuse. The thickenings do not lose their identity upon fusion, however, but twist slightly in relation to one another, the ventral ones becoming at first lateral, then dorsal, and finally expanding into broad, thin, funnel-shaped sheets which enclose, except for a ventral opening, a pair of cavities on either side of the foramen magnum. These cavities are just within the posterior wall of the cranium. The outer portions of the sheets forming them meet the occiput along the occipital sulci; the inner portions are attached along the postoccipital suture between the posterior tentorial pits and the inner ends of the occipital sulci. The slender primary tentorial bridge arises from these sheets just above the posterior tentorial pits (fig. 8). The thickenings which are dorsal at the anterior ends of the anterior tentorial arms, as they twist, come to lie between the anteriorly ventral thickenings and continue to the posterior tentorial pits. In their middle and posterior portions, each of these thickenings gives off toward the middle a thin sheet which anteriorly fuses with its fellow to form the secondary tentorial bridge, mesally fuses with the hypostoma, as elsewhere described (fig. 8), and posteriorly fuses with that part of the postoccipital suture between the posterior tentorial pit and the outer margin of the hypostomal bridge plate. The anteriorly ventral thickenings of the tentorium are fused with the hypostoma far forward (fig. 7) and appear to give rise ventrally on each side to a hypostomal thickening which fuses with and strengthens each maxillary process of the hypostoma. The complexity of the tentorium and the extensive buttressing of its roots are quite clearly specializations for strengthening the walls of the cranium against collapse.

Since they are features seen in those Hymenoptera in which the mandibles are powerful tools, the buttresses probably serve to prevent distortion of the cranium by the contraction of the mandibular adductor muscles.

APPENDAGES OF THE HEAD

The *antennae* are rather short structures of the general form shown in figure 17. The *scape* is elongate, constricted near the base, the region basad of the constriction being a large ball or bulb (Crampton, 1932) which fits into the antennal socket. The *pedicel* is slightly broader than long. The *flagellum* consists of 11 segments in the male, 10 in the female, the first of which in both sexes is long and slender except for the expanded apex.

As in other Hymenoptera, the mandibles are widely separated from the other mouthparts in function. The mandibles are very heavily sclerotized and serve for digging burrows in hard soil, etc. The maxillae and especially the labium are but feebly sclerotized in comparison. They are used for gathering nectar and in nest building, for gathering water and for surfacing the nest cells within. Hence the mandibles are firmly articulated on the antero-ventral angles of the cranium, while the maxillae and labium are united with one another by conjunctival membranes and articulate with the head only through the maxillary cardines, whose places of attachment have already been discussed.

The *mandibles* are curved appendages of considerable strength which lie one over the other in repose. Each bears on its inner margin, nearer the apex in the male than in the female, a small rounded tooth (fig. 11). As in other Pterygota, the mandibles can move only in a single plane because of the double articulation, which consists of an anterior *mandibular acetabulum* fitting over a condyle near the lateral angle of the clypeus and a large posterior *mandibular condyle* (fig. 12) which fits in an acetabulum in the cranium below the eye. On the outer margin of the base of each mandible is a distinct *abductor swelling* (figs. 1, 11, 12) to which the *apodeme of the abductor muscle of the mandible* is attached. This apodeme is bifid, having a slender anterior branch about as long as the mandible and a broad, sheet-like, posterior branch about half as long as the mandible.

Except for the extreme base, where it is distinctly sclerotized, this apodeme is thin and transparent throughout. To the *adductor angle of the mandible* is hinged the *apodeme of the adductor muscle of the mandible*. At its base this structure is heavily sclerotized, but otherwise it consists of a broad, transparent sheet about as long as the mandible, bearing on its posterior margin near the base a long, slender, tendon-like branch which expands into a small sheet apically. The *labio-maxillary complex* (Duncan, 1939) or *proboscis* is the very large and complicated organ whose evolution has probably more profoundly affected the specialization of the head capsule than any other factor. The labium has lost its sclerotic connection with the head capsule but is closely connected with the maxillae, whose cardines support the distal parts of the proboscis. The proboscis, from its base to the bases of the prementum and galeae, consists of a single large conjunctival *labio-maxillary tube*, whose cavity is continuous with the cavity of the cranium and in the walls of which lie various sclerites which govern the manner in which the tube folds and provide the muscle attachments and skeletal elements necessary to produce its movements. The membrane of the tube is known among German authors as *Mundfeldsack*, *Kehlhaut*, *Mundfeldwulst*, etc. It is attached to the under surface of the head at the base of the labrum, whence the line of attachment extends laterally above and behind the anterior margin of the clypeus to the paramandibular processes of the hypostoma, thence to the maxillary processes of the hypostoma and to the anterior end of hypostomal bridge along the curved line (fig. 6) between the maxillary processes.

The *mouth opening* is a transverse slit lying on the anterior surface near the base of the membranous tube described above. Immediately above the mouth opening is a projecting membranous triangular area with an apical point and a ventral longitudinal ridge. This is the *epipharynx*. It is not so well developed or so freely movable as in *Apis* and *Bombus*, being adherent at its margins except apically to the rest of the tube. The *hypopharynx* is not well developed but, as pointed out by Hilzheimer (1904), is represented by the large membranous area between the

mouth opening and the opening of the salivarium. Immediately below the mouth opening there is a small, membranous, bilobed lip which represents a part of the hypopharynx. As shown by Ulrich (1924), who calls it the *Innenlippe* or mesolabium, this lip forms the roof of a small suboral cavity in some specoid wasps. Apically, toward the opening of the salivarium, the hypopharyngeal membrane bears some hairs and has been regarded as the hypopharynx in *Andrena* by Snodgrass (1925). This area is in reality only a part of the hypopharynx and is called the *Speichel-lippe* by Ulrich (1924).

A short distance within the mouth the *pharynx*¹ is strengthened and held open by a transverse *pharyngeal plate* (fig. 19), which is a sclerotization of the posterior surface of the pharynx. This plate is provided with a pair of short arms extending toward the mouth and a pair of long *pharyngeal rods* extending away from the mouth in the wall of the pharynx. In the anterior wall of the pharynx, just below the pharyngeal plate, a small, longitudinally elongate sclerite may be seen (fig. 19).

The labio-maxillary tube is strengthened on its anterior surface by a pair of narrow, flexible, longitudinal, *anterior conjunctival thickenings*, *interlorae*, or *Segelhalter*. Their lower ends lie very near the articulation of the mentum with the prementum (fig. 15). Thence each extends upward, close to the stipes of the maxilla (fig. 14), leaving the maxillary region near the base of the lacinia and passing lateral to the mouth and epipharynx to a point in the conjunctiva very near the line where the latter meets the clypeus. Here it turns posteriorly and follows around the side of the labio-maxillary tube very near its base to the apex of the paramandibular process of the hypostoma. Some bees have additional pairs of these thickenings both on the anterior and posterior faces of the labio-maxillary tube. They are evidently secondary developments to provide great strength and yet retain flexibility in the membrane. The anterior conjunctival thickenings are termed *suspensorial rods* of the hypopharynx by Snodgrass (1942).

¹ As pointed out by Snodgrass (1935), this region, which is the sucking pump of the bee, consists of the pharynx, buccal cavity, and perhaps even the cibarium.

The labio-maxillary tube is primarily strengthened at its base by the *cardo* of each *maxilla*. These rod-like structures lie in the conjunctiva at each side of the tube. Their expanded bases rock on the maxillary processes of the hypostoma, while each stipes rocks on the apex of a *cardo*, forming a joint which bends in a longitudinal, vertical plane. A lateral process of the submentum extends beneath the apex of each *cardo* and lies in a groove on the outer surface of the latter, forming a very firm but flexible articulation.

The *stipites* (fig. 13) are flattened sclerites, one on each side of the distal part of the labio-maxillary tube. Each, as shown in figure 14, bears a thin posterior lamella which hangs free from the tube, only its anterior portion forming part of the wall of the tube. The apices of the stipites project beyond the distal end of the labio-maxillary tube. Each bears a slender internal process (fig. 14) which separates the conjunctiva of the tube from that between the stipes and galea and supports the base of the lacinia; each also is produced distally at the posterior apical angle into a process which reaches the galea. A row of coarse bristles found on the posterior distal margin of each stipes (fig. 13) forms the *comb of the stipes*. The *maxillary palpi* arise in small membranous areas or *Tasterausschnitt* in front of the posterior apical processes of the stipites (fig. 13). They are slender, six-segmented structures. As pointed out by Crampton (1923), this is an interesting condition since the primitive number of maxillary palpal segments in insects is apparently five, and since the modifications of this number are usually by reduction. It is possible, although improbable, that the first segment represents the palpifer secondarily dissociated from the galea. The *galeae* are long, slender, blade-like structures, the base of each of which is flexibly attached to the stipes at two points, namely, in front of the base of the palpus and at the apex of the process of the stipes behind the palpus. The base of each galea is flexible at the point at which it appears narrow in figures 13 and 14, thus allowing it to bend back on the stipes in repose. Each galea is a thin sheet, convex on the outer side, concave within, and provided on the inner surface from base to apex with a small, projecting lamella (fig. 14). This lamella, or its counter-

part, is provided with a row of coarse setae, the *comb of the galea*, in some bees. The *laciniae* are reduced to small, scale-like sclerites which are contiguous with the anterior basal angles of the galeae and with the anterior internal processes of the stipites already described.

A second set of sclerites, which lie in the wall of the labio-maxillary tube, is the modified basal portion of the *labium*. As has been already pointed out, the labium has lost its primitive basal connections with the head capsule, and being incorporated basally in the labio-maxillary tube, its movements are necessarily coordinated with those of the maxillae. The sclerites of the base of the labium are situated in the posterior wall of the tube. The *submentum* (lorum of most bee students) is a V-shaped sclerite (fig. 15) with its narrow apex directed, at least in repose, toward the base of the labio-maxillary tube, and its divergent arms articulated, as already described, with the apices of the cardines. Snodgrass (1935) intimates that he doubts the homology of the lorum of bees with the submentum of tenthredinids and other insects. In tenthredinids the submentum is a flat plate lying between the cardines and often more or less contiguous with them laterally. In bees such as *Colletes*, we have a condition intermediate between that found in tenthredinids and in higher bees, the submentum being a flat plate, but like the lorum bent forward on either side of the mentum. Therefore it seems certain that the lorum is the homologue of the submentum.

The *mentum* is a long, slender, flattened sclerite, broadest distally, and curled anteriorly at the base to the point of its firm articulation with the anterior, basal, median portion of the submentum (figs. 15, 16). Snodgrass (1925), Liu (1925), and many others have regarded this sclerite as the submentum, and the prementum as the mentum, but Snodgrass (1935) has pointed out that the submentum of earlier workers lies basad from the insertions of the posterior cranial muscles of the labium and is, therefore, the mentum.

The *prementum* is a large, elongate sclerite (figs. 15, 16), only the extreme base of which is actually included in the labio-maxillary tube, although a conjunctiva continuous with that of the anterior face of the tube extends

along the anterior side of the prementum to the opening of the salivarium (fig. 16). The sclerotization of the prementum is strongly convex posteriorly, concave anteriorly, the concavity thus formed being closed by the hypopharyngeal membrane. This cavity, of course, is continuous with that of the labio-maxillary tube and contains the muscles of the glossa and paraglossae.

The prementum bears near the apex of its anterior surface, at the base of the glossa, the opening of the *salivarium* (fig. 16). At its apex, seen from behind, the prementum is trilobed, the broad, antero-posteriorly expanded, lateral lobes supporting the labial palpi, the slender median lobe being produced as a heavily sclerotic ribbon (the subligular plate or *Trägerspange*) which extends around the distal end of the prementum and supports the glossa and paraglossae at their bases.

The *labial palpi* (fig. 15) are elongate, four-segmented structures. The base of the first segment of each is considerably distad from the lateral apical lobes of the prementum just described, but the intervening space is stiffened by a feeble sclerotization, the *palpiger*, on the outer surface of each membranous palpal base. This condition allows the palpi to bend back on the prementum in repose, the point of greatest flexibility being in the distal part of the palpiger. If this palpiger is not a secondary sclerotization but is indeed the homologue of that of lower insects, it clarifies the error of MacGillivray (1924), who regarded the first palpal segment as the palpiger, and the possible error of Crampton (1925, 1928), who, not finding a palpiger, suggested that it might be fused with the sclerite now known as the prementum. The first two segments of the palpi are elongate, connate with one another, and greatly flattened. A longitudinal median line in each is thick and heavily sclerotic, while the lateral margins are produced as thin, transparent but stiff lamellae on either side of the median line. Thus these palpal segments are sheath-like, their outer surfaces being convex, the inner concave. The last two segments are short, and since the third arises subapically on the second, are directed posteriorly (or outward or inward, depending on the degree of twisting of the first two segments).

The glossa and paraglossae arise in close

proximity near the apex of the anterior surface of the prementum and, being partly retractile into the prementum, can be moved in and out of flowers in feeding. The *paraglossae* are thin, membranous, compressed structures. The *glossa* is presumably the fusion product of the two primitive glossae. Its base is curled into a deep pocket in the distal part of the prementum; the evolution of this curling is shown in a series of diagrams by Demoll (1908). The *glossa* is nearly round in cross section, with a deep posterior groove and with numerous transverse striations and transverse rows of strong setae (fig. 15). At its apex it is furnished with a minute thin plate, the *flabellum*, narrowed basally and with the apical margin digitate.

We may here consider briefly the movements of the various parts of the proboscis with relation to one another. As already stated, action of the labium is coordinated with that of the maxillae because these structures are basally all parts of the labio-maxillary tube. At rest, the cardines are directed posteriorly from the maxillary processes of the hypostoma along the roof of the proboscival fossa, their distal ends lying at about the posterior end of the fossa. Between them and even higher in the fossa lies the mentum, its basal end supported by the sub-

mentum, its distal end projecting slightly beyond the posterior end of the fossa. The cardines, mentum, and submentum are included in the first section of the proboscis, which is directed posteriorly in repose. The second section, directed anteriorly, consists of the prementum and the stipites, which lie on either side of it in repose, as well as the palpigers and bases of the galeae. The distal end of the second section fits into the proboscival fossa immediately behind the labrum and clypeus. The third section, which is again directed posteriorly, consists of the galeae, labial palpi, paraglossae, and glossa. The apices of these parts, except the paraglossae, reach the anterior coxae in repose.

When the proboscis is extended, the third section bends anteriorly until it is nearly in line with the second, and at the same time the first section rocks forward until it attains an approximately vertical position below the maxillary processes of the hypostoma, thus lowering the second and third sections with respect to the head. Snodgrass (1925) gives a good account of the action of the proboscis of *Apis* in feeding, while Ulrich (1924) does likewise for sphecoid wasps, whose feeding mechanism is probably similar to that of bees such as *Colletes*.

MESOSOMA

In all Clistogastra the first abdominal segment or propodeum is immovably united with the thorax so that the median tagma of the body consists of four rather than the usual three segments. It is, therefore, preferable for morphological purposes to use the term *mesosoma* instead of thorax when referring to all four segments together. The metasoma, then, consists of the second and following abdominal segments, and is separated from the mesosoma by a strong constriction. For purposes of purely taxonomic work, it is probably permissible to follow the usual practice, regarding the propodeum as part of the thorax and numbering the segments of the metasoma from one upward, calling them abdominal segments. For purposes of the present work, however, the first metasomal segment will be called the second abdominal segment.

One may reasonably state that the most important function of the pterygote thorax is to provide support and musculature for the structures of locomotion. The form of the mesosoma of *Anthophora* is admirably suited to subserve this function. With the exception of the pleural and sternal portions of the prothorax, all the major mesosomal sclerites are immovably joined together to form a heavily sclerotic and nearly spherical shell. This shape is the best possible to withstand the contraction of the great muscle masses which nearly fill the mesosoma. Additional strength is obtained by the inflection of the margins of many sclerites to produce heavily sclerotized internal ridges, and the whole mass is braced by the branches of the fused sternal furcae.

It seems worth suggesting here that the transfer of the first abdominal segment from

the posterior to the median tagma may be associated with the development of more powerful flight. In the relatively weak flying *Chalastrogastra*, the thorax is subcylindrical. Correlated with the need for strong pterothoracic walls in connection with strong flight, an oval or eventually spherical thoracic region arose. This shape was achieved by constriction at both ends. The cervical region became narrowed. Posteriorly, the metanotum being short even in the tenthredinids and hence unable to occupy a large, vertical, posterior mesosomal face, the constriction took place behind the first abdominal segment. The broad connection between the thorax and the first abdominal segment permitted the posterior expansion of the second phragma far into the cavity of the latter, providing space for the long, indirect, longitudinal flight muscles. Zander (1910) has shown that even in ontogeny the metanotum of *Apis* becomes short before the constriction is very strong.

THORAX

PROTHORAX

The *prothorax* is a small segment. The *pronotum* (fig. 22) is immovably fused with the mesothorax and forms a complete ring around the anterior end of the latter, being produced at the sides as *postcoxal processes* which meet and fuse on the midventral line (fig. 21). Mid-dorsally the pronotum is relatively narrow, but dorsolaterally it is broad, being produced posteriorly over the first thoracic spiracles as broad *posterior lobes of the pronotum* (fig. 22), known as "tubercles" in much taxonomic literature. An impressed line separates each tubercle anteriorly from the rest of the sclerite. Anterior to the dorsal margins of the posterior lobes are the areas which are elevated in many bees and known as the *lateral angles of the pronotum*. The anterior margin of the pronotum is but little inflexed. The impressed line in front of each posterior lobe of the pronotum is represented within by a distinct ridge, which is continuous not only with the rather strong dorsal inflexion of the posterior margin of the pronotum between its posterior lobes but also with the less strongly inflexed posterior margins of the postcoxal processes.

The large opening surrounded by the pro-

notum is nearly circular, a little higher than broad. From it projects the *propectus*, or pleura and sternum of the prothorax, which are the only major parts of the thorax not immovably fixed to adjacent sclerites. The propectus is the movable suspensorium of the head and anterior legs. As a result of the lateral expansion of the pronotum, the propleura have taken a ventral position and are partly overlapped by notum.

Each *propleuron* is an irregularly five-sided plate, sharply flexed at nearly right angles along a line between two of the five angles so that it is divided into a vertical *lateral portion of the propleuron* concealed beneath the pronotum and a subhorizontal, exposed *ventral portion of the propleuron*. These ventral portions meet but do not fuse on the midventral line and thus hide the anterior margin of the prosternum. The conjunctiva arising on the mesal propleural margins is infolded and is attached to the lateral margins of the prosternum. The lateral portion of each propleuron has two margins other than that on which it meets the ventral portion and is provided with a large *marginal apodeme*, projecting as a continuation of the posterior of these two margins and arising from the angle between them. The possible homologies of this apodeme are discussed by Duncan (1939). The posterior margin of the lateral portion of the propleuron is broadly inflexed and lobate in its lower half, this inflexion being continued submarginally in the upper half to the strong inflexion of the long upper margin known as the *transverse propleural brace* (fig. 28). The inflexion of the posterior margin is marked externally by a suture (fig. 24) which Snodgrass (1910) has regarded as the pleural suture. Since the necessity of recognizing the existence of true pleural sutures in nonpterothoracic segments seems doubtful, and the evidence concerning the nature of this suture in Hymenoptera is not conclusive, I have refrained from using the terms *propimeron* and *proepisternum*, but refer to the whole structure as propleuron. The anterior coxae are articulated immediately above the lower ends of the posterior margins of the lateral, vertical parts of the propleura. There are no true condyles but only swellings of the margins on which the coxae rock. As usual in

insects, except in Psocoptera and Mallophaga, there are no ventral articulations of the anterior coxae. The exposed or ventral portions of the propleura are quadrate, broader on their outer than inner margins (fig. 21), all the margins inflexed (fig. 28), the anterior margins each with a submarginal depressed sulcus (fig. 21). The anterior angles are produced to the inwardly directed *occipital processes* or cephaligers of the propleura (figs. 21, 28), which support the cervical membrane in which they lie and whose articulations with the postocciput have already been discussed. These processes are continuous with the inflexions of the adjacent margins of the propleura. Each occipital process is produced as a posterior apodeme for muscle attachment, the *posterior ramus of the occipital process*. Crampton (1909, 1926) has regarded the sclerites here called propleura as fusion products of pleural and cervical origin, a logical theory since cervical sclerites carry the occipital processes in lower insects. Snodgrass (1910) and Weber (1925) regard the entire structures as pleural in origin. Having found no additional information which would help to settle this question, I have arbitrarily followed the latter authors.

Beneath the propleura and extending posteriorly to a point beneath the midventral portion of the pronotum lies the *prosternum* (fig. 21). Its anterior margin, including the median *anterior process of the prosternum* (figs. 25, 26), is hidden by the propleura. The remainder is a rectangular plate with the anterior lateral angles somewhat produced as *lateral processes of the prosternum* and with the broadly rounded posterior margin hidden by the pronotum. The rest of the sclerite is hidden by the anterior coxae, except for a depressed anterior median portion bounded by two sharp ridges, which converge posteriorly and fit the basal portions of the mesal margins of the anterior coxae when in repose. The posterior portion of this depressed area is strongly concave and is the *prosternal apophyseal pit*. Behind this pit, a weak longitudinal median line is the *median prosternal groove*, the external indication of the line of attachment of the vertical plate of the prosternal apophysis. This line may be a discrimin, in which case all the posterior portion of the

so-called prosternum is of subcoxal origin. This seems doubtful because the posterior vertical plate of the apophysis arises far laterad from the median line.

The largest part of the prosternum, however, is internal, consisting of the greatly expanded *prosternal apophysis* (figs. 25, 26, 27). This apodemal portion of the sternum arises from the posterior half of the exposed part of the sclerite, over which a slightly elevated platform, the *horizontal plate of the prosternal apophysis*, is formed. This is supported by a longitudinal median lamella, the *vertical plate of the prosternal apophysis*, which is expanded anteriorly to form a continuous sheet between a pair of strongly diverging arms arising from the apophyseal pit. Posteriorly this plate becomes lower and is continuous with the posterior and lateral inflection of the margin of the sternum, the *posterior vertical plate of the prosternal apophysis*, which also serves to support the horizontal plate. Beneath the horizontal plate, then, are two cavities, open only anteriorly and separated from one another by the vertical plate. Above the horizontal plate, the apophysis is produced latero-dorsally and broadened antero-posteriorly to form the large *prosternal apophyseal arms*, whose summits or *outer crests of the apophyseal arms* converge to the *posterior angles of the apophyseal arms*, and diverge to the produced *antero-dorsal angles of the apophyseal arms* (outer process of first furcal arm, Duncan, 1939). Below the latter angles, on the anterior margins of the arms, lie the *antero-median angles of the apophyseal arms*. In this species there is considerable variation in the relative lengths of these two anterior angles, the dorsal one being much produced in some, about the same length as the median in others. Posteriorly each apophyseal arm is provided with an *inner crest* (fig. 27), which is somewhat lower than the outer, to which it is united at the posterior angle of the apophyseal arm and from which it is separated by a deep trough. Anteriorly each inner crest is produced as a thin, free, spatulate *anterior process of the inner crest of the apophyseal arm* (inner process of the first furcal arm, Duncan, 1939). In some bees the inner crests become fused, closing the neural foramen (Snodgrass, 1942), so that a hori-

zontal *apophyseal bridge* is formed. In such cases the fused summits of the inner crests often remain as an erect, longitudinal lamella, the *median crest of the prosternal apophysis*, arising from the apophyseal bridge.

An examination of fresh specimens shows a possible reason for the great apophyseal development of the prosternum, for the muscles which move the head, the forelegs, and the prosternum itself are attached to the apophysis. The backward production of the posterior angles of the apophyseal arms serves to provide for the great length of the muscles attached to the walls of the trough between the inner and outer crests.

MESOTHORAX

The *mesothorax* is the largest of the mesosomal segments and contains practically all the flight musculature, since it bears the large and powerful forewings, which probably to a large degree carry the hind wings through their vertical motions by means of the hamuli.

As will be seen from figure 22, almost the whole of the more or less horizontal portion of the dorsum of the thorax is the *mesonotum*. The largest of the sclerites into which the mesonotum is subdivided is the *mesoscutum*, the roughly square sclerite of the anterior part of the mesonotum (fig. 20). Its anterior margin bears medially the short, broad, gently rounded *first phragma* (fig. 29), to which the lowermost fibers of the indirect longitudinal muscles of flight are attached. This phragma is directed strongly forward into the prothoracic cavity, only its lower margin being vertical. The acrotergite is exceedingly narrow, if present at all. Laterally the anterior margin of the mesoscutum is strongly inflexed, the resulting transverse vertical plate of each side bearing against the posterior pronotal inflexion. This *antero-lateral mesoscutal inflexion* is not apodemal in nature, since conjunctival membrane arises at its lower extremity and extends upward to attach to the pronotum. Between the *antero-lateral angles of the mesoscutum* and the anterior ends of the tegulae the mesoscutum is more produced laterally than at any other point, forming the obliquely truncated *antero-lateral processes of the mesoscutum*. Their distal margins are slightly inflexed and abut

upon the upper margins of the posterior lobes of the pronotum. Arising at the posterior distal angle of each antero-lateral process, a strong *supra-alar carina* extends posteriorly in a broad curve, then more mesally to the transscutal suture. Especially posteriorly this carina is margined mesally by a narrow groove. The regions laterad from the supra-alar carinae are vertical, impunctate, and glabrous, and may be known as *preaxillae*, since they, like the axillae, are secondary subdivisions of the mesoscutum. Each preaxilla is furnished with several ridges (fig. 29), which, like the supra-alar carinae, are marked within only by greater or lesser changes in contour. These ridges, the strong supra-alar carinae, and the vertical position of the preaxillae themselves all add to the strength of these structures, which bear at the posterior ends of their free lower margins, next to the terminations of the transscutal suture, a pair of lobes, one in front of the other, which articulate with the first axillary sclerite. Together they constitute the *anterior mesonotal wing processes* (fig. 29). The differentiation and strengthening of the preaxillae, characteristic of the Clistogastra, are no doubt associated with the need for strong supports for these processes in insects with powerful flight. The outer surface of the anterior portion of each preaxilla is furnished above its lower margin with a horizontal shelf, the *tegular ridge* (fig. 29), narrowest medially, broad and transparent anteriorly, and produced outward as a small process posteriorly. On the tegular ridges the mesal margins of the large *tegulae* (fig. 20) lie. The single point of articulation of each tegula with the notum is a slight elevation of each tegular ridge a little behind its middle. The posterior margin of the mesoscutum is marked medially by the *scuto-scutellar suture*. Because the axillae, while morphologically part of the mesoscutum, are functionally part of the scutellum, the lateral parts of the scuto-scutellar suture are less flexible as well as less conspicuous than the median part and are here called axillar sutures. The counterpart of the flexibility of the median portion of the scuto-scutellar suture is provided at the sides by the *transscutal sutures*, which separate the axillae from the remainder of the scutum. The posterior margins of the mesoscutum

proper and of the preaxillae are slightly and rather delicately inflexed.

On the dorsal surface of the mesoscutum there are several significant marks. Its anterior portion is provided with an impressed *median mesoscutal line* (fig. 20), feebly visible on the inner surface. Laterally, mesad from the bases of the tegulae, a short impressed line on each side is the *parapsidal line*. On the inner surface these lines are similar in appearance to, but less conspicuous than, the median mesoscutal line. The term line is used rather than furrow because these lines are often elevated or merely impunctate rather than impressed in bees. These lines have often been called notauli or notaulices by systematists. On the anterior margin of the mesoscutum two slight broad depressions are seen, each of which represents a true *notaulus* (fig. 20). (For details concerning the derivation and use of this term, see Forbes, 1940.) The course of the more posterior portions of these lines is indicated within by the divisions between the areas of attachment of longitudinal and of vertical indirect flight muscles. If the view taken by Crampton (1919), Tulloch (1929), and others is correct, the notauli delimit at least the lateral extent of the prescutum.

As has already been indicated, the functional unit known as the scutellum actually consists of the scutellum proper plus the axillae, which are of scutal origin as shown by an examination of a series of Hymenoptera (Snodgrass, 1910). The *axillae* or parascutella (figs. 29, 30) have narrow, anterior, apodemal margins at the sides which are overlapped by the posterior margins of the preaxillae. Laterally each axilla forms a small process, very near the anterior side of which the lower or basal process of the first axillary sclerite lies. The fourth axillary does not closely approach this process but lies in the excavation immediately in front of the lateral extremity of the scutellum. The *scutellum* is broadly rounded posteriorly, of moderate length medially where it is marked by a longitudinal, raised, *median mesoscutellar line* (fig. 20). The scutellum is greatly narrowed laterally because, laterad from the inner ends of the transcutal sutures, the scuto-scutellar suture, there known as the *axillar suture*, is directed posteriorly to the mesal ends of the deep *axillar*

fossae (fig. 29), which it follows to its terminations. The space between the axillar fossae and the metanotum is small and is occupied at each side by a high ridge, the *scutellar crest*, which extends forward beneath each axilla, as seen from the side (fig. 29), and receives the inner end of the axillary cord of the forewing at its apex.

From within, the anterior margin of each axilla is seen, as already stated, to be an anteriorly directed apodemal margin beneath the preaxilla. Both anterior and posterior margins of the scutellum proper are provided with very strong inflexions, the *anterior* and *posterior scutellar inflexions*, whose ventral margins are directed toward each other and thus nearly enclose the large space between them and beneath the scutellum (fig. 30). These apodemes make the scutellar region a very rigid part of the thorax. The lateral portions of the anterior inflexion, which follow the axillar sutures, have been called endodorsal ridges. Another posterior inflexion of the scutellum exists at each side, the *posterior lateral scutellar inflexion* (fig. 29), which arises behind the posterior scutellar inflexion, being formed along the posterior edge of each scutellar crest. It is concave posteriorly and receives the anterior lateral metanotal inflexion; it is not an apodeme, since a conjunctival membrane arises at its lower margin and extends upward to the metanotum.

The major remaining portion of the mesonotum is the invaginated *second phragma* (fig. 29). Except laterally, where the slender *rami of the second phragma* are articulated with the posterior lateral scutellar inflexions, it has lost entirely its primitive notal connections by evolutionary developments described by Snodgrass (1910). Between the rami the phragma extends backward as a great arch through the metathoracic cavity nearly to the posterior wall of the propodeum and ventrally nearly to the bases of the posterior legs. From its anterior concave surface the longitudinal indirect muscles of flight extend forward and attach to the median part of the mesoscutum from immediately in front of the scuto-scutellar suture to the anterior margin of the first phragma. The arch of the second phragma bears a deep midventral notch through which the heart passes (fig. 23). On

its posterior surface the arch of the second phragma bears a pair of large impressions (fig. 29) surrounded by ridges which laterally, especially ventro-laterally, are produced into strong lamellae. These impressions serve as areas of attachment for short muscles which extend thence to the propodeum immediately above the metasomal articulation.

The connections of the phragmal rami with the rest of the thorax have puzzled students of morphology of Hymenoptera generally. Each ramus is somewhat expanded anteriorly, as shown in figure 29a, and provided with a deep groove bounded by lamellae, the inner one of which is far higher than the outer. Into this groove, between the lamellae, the posterior lateral scutellar inflection of each side fits, so that there is a strong phragmal lamella anterior to this scutellar inflection. With this articulation as a hinge, the phragma is capable of a certain amount of up and down movement, with perhaps antero-posterior sliding along the scutellar inflection as well. While the anterior ends of the rami may be in part mesopostnotal in origin, a small sclerite on each side, movably articulated with the extreme anterior end of each phragmal ramus, is undoubtedly of postnotal origin. These sclerites may be known as *mesopostnotal sclerites*, and the long, slender, tapering apodeme of each, projecting postero-mesally and lying close to the anterior scutellar inflection, is the *mesopostnotal apodeme* (fig. 29). In the *Chalastogastra*, *Vespula*, etc., the mesopostnotal sclerite remains immovably fixed to the second phragma, so that the apodeme has been called the anterior process of that phragma. That the apodeme is actually postnotal and not phragmal in origin is shown by the location of that part of the integument to which it is attached, separated from the phragma as the mesopostnotal sclerite in bees, in the external conjunctiva immediately behind the lateral extremity of the scutellum and behind the base of the axillary cord. The mesopostnotal sclerite is thus obviously a sclerite of the external body wall, not an entirely internal apodemal structure. Immediately in front of the mesopostnotal sclerite the axillary cord of each forewing traverses the conjunctiva to attach to the lateral scutellar process, and immediately anterior to this cord lies the fourth axillary sclerite. Thus the

mesopostnotal sclerite and the fourth axillary are closely associated, and the former, since it can easily be dissociated from adjacent sclerites and pulled out with the axillary sclerites, has been regarded as an accessory sclerite of the wing base and labeled "y" by Snodgrass (1910, 1925). The same author in 1942 called this sclerite the axillary lever and indicated its homology, which he had independently determined.

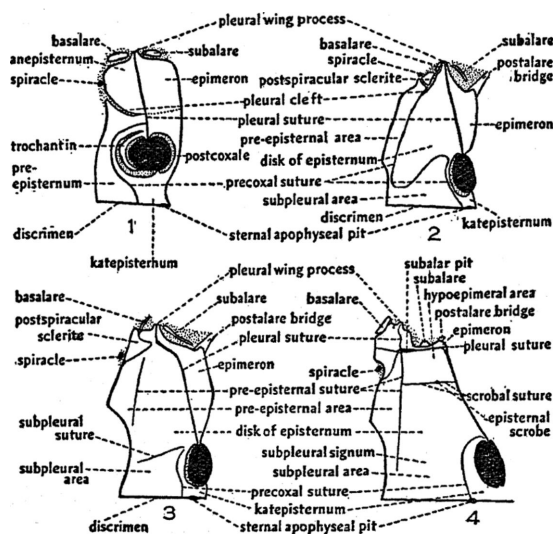
Another small sclerite on each side was labeled "x" by Snodgrass (1925), while in 1942 it was called, without indication of its origin, the supporting sclerite of the subalare. It was regarded as a detached tip of the ramus of the second phragma by Duncan (1939). It is attached in a slightly but not freely movable manner to the anterior edge of the mesopostnotal sclerite. Somewhat flattened and slightly curved, it extends forward to a depression, in which its anterior end fits, in the inner margin of the broadly inflected dorsal part of the mesepimeron. It lies for most of its length along the margin of this inflection, laterad from the tendon-like apodeme of the subalare and thus appears to be a truly internal structure. This is not the case, however, for the broad dorsal surface of the inflection is fundamentally external, the conjunctiva attached to its inner margin extending upward to the sclerites of the wing bases. The small sclerite in question lies in this membrane. We are thus dealing with an invaginated sclerite lying between the mesopostnotum and the mesepimeron; clearly this is a remnant of the conspicuous postalare bridge of lower Hymenoptera and may be known as the *postalare bridge sclerite* (fig. 29).

The pterothoracic sterna have been subject to considerable recent discussion. Snodgrass, Weber, and others have amply elaborated the now classical idea that each thoracic segment contains a notum, a sternum, and pleural regions of subcoxal derivation. Ferris (1940a), on the contrary, holds that pterothoracic sterna are rare except as secondary sclerotizations and that the ventral sclerites of the pterothorax, like the lateral ones, are of subcoxal origin. There is much in insect structure to commend this theory, while little support can be found for the classical theory because it fails to explain the presence of a longitudinal median suture on the ventral

side of most insects as well as the absence in so many insects of sternopleural sutures in the positions close below the coxae, which they should occupy according to the latter concept.

Because an explanation of the theory recently presented by Ferris is not found in any general work on insect morphology, it is briefly explained with slight modifications here. The subcoxa of each side is regarded as having spread out onto the body surface, not merely upward but in all directions from the proximal end of the coxa. In so far as I have been able to deduce from the recent works of Ferris and his students (Ferris, 1940, 1940a; Ferris and Pennebaker, 1939; Ferris and Rees, 1939; Rees and Ferris, 1939; Campau, 1940; and Cope, 1940), the accompanying diagram (diagram 1) is indicative of their conception of the subcoxal elements of a pterothoracic segment of the primitive insect. Except for the coxal socket, the most constant landmarks of the subcoxal region are the midventral discrimen, resulting from the meeting of opposite subcoxae whose contiguous margins have been infolded posteriorly to form the sternal apophyses, and the pleural suture extending from the dorsal articulation of the coxa to the pleural wing process. The postcoxae, which in some forms connects these two structures behind the coxa, is usually absent. The episternum itself is considerably subdivided. The trochantin is a small sclerite in front of the coxa which often provides an antero-ventral coxal articulation and which never reaches the discrimen. Its dorsal portion often becomes separated from the lower end of the pleural suture, perhaps through fusion with the katepisternum. The katepisternum extends around the anterior side of the coxa from the pleural suture to the discrimen in the vicinity of the sternal apophyseal pit. It is separated from the pre-episternum, which also reaches the discrimen, by a suture, indicated within by a muscle-bearing ridge, called by Ferris the pleural costa. Since it seems inadvisable to call the external impressed line or suture a costa, it seems best to designate it as the precoxal suture. The pre-episternum is separated from the anepisternum by the pleural cleft.

Applying this concept of the subcoxal elements to the Hymenoptera, we find the discrimen and apophyseal pits conspicuous and the pleural sutures easily traceable in the lower families. The trochantins are absent. An examination of a cephid such as *Cephus cinctus* Norton (diagram 2) shows a suture on each side of the mesothorax extending laterally from the discrimen immediately in



DIAGRAMS 1-4. 1, Pterothoracic subcoxal elements of a hypothetical primitive insect; 2, mesothoracic subcoxal elements of *Cephus cinctus* Norton; 3, mesothoracic subcoxal elements based on a tenthredinid; 4, mesothoracic subcoxal elements based on *Vespa*.

front of the mesosternal apophyseal pit close to the anterior margin of each middle coxal socket. Clearly this is the precoxal suture. Near the summit of the coxa, instead of continuing toward the pleural suture as in more primitive insects, it is bent strongly forward and extends toward the anterior end of the discrimen, which it reaches in certain other cephids. Near the anterior end of its middle segment the precoxal suture becomes very faint, but, as shown in diagram 2, it turns dorsally and extends more or less parallel to the anterior margin of the mesepisternum to the lower end of the small pleural cleft. The pleural cleft, with the mesothoracic spiracle, has moved far up on the pleuron and has come to be directed anteriorly rather than posteriorly toward the pleural suture. It is thus clear that the katepisternum and anepi-

sternum of each mesosubcoxa fused as a result of a shift in the courses of the precoxal suture and the pleural cleft. I am much indebted to Dr. G. F. Ferris for suggesting this explanation of the sutures of the mesosubcoxa.

An examination of other Hymenoptera shows that one or more of the three sections of the precoxal suture is frequently lost and, furthermore, that the three sections usually become separated from one another, as shown in diagram 3. It has, therefore, seemed best, for the sake of the taxonomist, to apply different names to the three portions of the suture. The term precoxal suture is retained for the portion extending from the discrimen toward the upper mesocoxal articulations. The median, often more or less horizontal, portion of the suture has often been regarded as the sternopleural suture in spite of its position above the coxa posteriorly and is represented by a broad groove, the sternaulus, in certain groups (especially the cryptine ichneumonids). Because it usually lies at the lower margin of the lateral, as opposed to ventral, part of the mesepisternum, this median part of the precoxal suture is here called the subpleural suture. The vertical portion between the pleural cleft (which disappears in higher forms) and the anterior end of the subpleural suture is the pre-episternal suture.

The areas below the subpleural sutures and in front of the precoxal sutures are known as subpleural areas of the pseudosternum; the subpleural sutures themselves when reduced to a mere elevated or depressed spot on each side, as in the higher Hymenoptera, are known as subpleural signa. The area in front of each pre-episternal suture is the prepectus of Ichneumonoidea, Sphecoidea, and Apoidea, although very different in origin from that of Chalcidoidea.¹ The area behind this suture and above the subpleural suture is the disk of the episternum.

In the Cephidae and Tenthredinidae a small separate sclerite is found a short distance in front of each mesopleural wing process. Since it lies immediately behind the first thoracic spiracle, it is here termed the postspiracular sclerite. It is apparently a

fragmentum of the mesepisternum. Snodgrass (1910) has called it a perapterum, although, being nonmusculated, it is clearly not associated with wing movement. The large, internal, muscle bearing disk which lies immediately mesad from each postspiracular sclerite is not attached to it, as appears on first dissection, but unites through a slender tendon-like apodeme to the lower margin of the true basalar. Parenthetically we may add here that, although these disk bearing basalare apodemes seem to be a specialized development in the lower Hymenoptera (found also in many Coleoptera), it is possible that the slender, tendon-like basalare apodemes of the higher forms arose from such disks, as suggested by diagrams of Weber (1924a).

Even in some tenthredinids (as in diagram 3), the movement of the postspiracular sclerite becomes limited, and their rear angles extend posteriorly toward slight bends in the pleural sutures. In the higher Hymenoptera each mesopleural suture develops two very strong bends (diagram 4), eliminating most at the epimeron. At the anteriormost bend a deep subalar pit is formed. The postspiracular sclerite, now solidly fused with the episternum, reaches this pit but is distinguishable from the episternum proper by the feeble sutures. This is the condition in *Vespa*. In the higher Hymenoptera, also, a pit or episternal scrobe often occurs on the disk of each mesepisternum above the middle, and a scrobal suture sometimes passes through this pit from the pre-episternal suture to the posterior margin of the mesepisternum, separating the small hypoepimeral from the large subscrobal or discal area of the mesepisternum (diagram 4).

If we now examine the *mesosubcoxal elements* of *Anthophora*, we see each to be very large and strongly convex externally, but taken together slightly and broadly concave midventrally where they meet to form a longitudinal median elevated line, the *discrimen*. There is no postcoxale, so that the middle coxae lie between the mesepisterna and the metepisterna. The *mesopleural sutures* from the coxae nearly to the summits of the pleura are the same as the intersegmental lines, so that the mesepimera are eliminated except dorsally (fig. 22). From

¹ In many Chalcidoidea a sclerite on each side, which appears to be the greatly enlarged postspiracular sclerite, has been called the prepectus.

each of these *pleurointersegmental sutures* arise two large, thin, internal lamellae closely appressed to each other. The anterior ones, firmly attached to the posterior margins of the mesepisterna and closely associated with the mesofurcal arms (fig. 31), are the *pleural ridges* or pleural folds. The posterior ones, slightly larger than the anterior, firmly attached to the anterior margins of the metepisterna and free from the furcal arms, possibly represent posterior components of the same folds, possibly intersegmental inflections (fig. 31). Nearly at the summits of the pleura the mesopleural sutures bend strongly anteriorly, become increasingly profound impressions, and end in the *subalar pits*, above which they are obliterated. Above the *horizontal abscissae of the pleural sutures* lie the narrow remnants of the *mesepimera*, fused anteriorly with the dorsal extremities of the mesepisterna. The mesepimera are called subalar mesopleural ridges by Duncan (1939). Posteriorly each mesepimeron is produced upward, as in many other Hymenoptera, to form a small lobe (fig. 22). Internally the horizontal portions of the pleural sutures are represented by very heavy, nodulose ridges (figs. 33, 34) whose upper surfaces are fundamentally external, as previously explained. These surfaces bear the pressure of the lateral processes of the axillae and scutellum when the dorso-ventral indirect flight muscles are contracted. The course of the pleural sutures here described is regarded as doubtful by Duncan (1939), but seems highly probable in view of their comparable course in the metathorax.

That part of each mesopleuron (combined mesepimeron and mesepisternum) above the subalar pit may be known as the *subalar area* (subtegular plate of Linsley and Michener, 1939). It is very thick, rises far above the notal wing process (fig. 22), and bears on its inner margin the small *mesopleural wing process*. The upper, outer margin of the subalar area is biemarginate. In front of each subalar pit a feeble ridge extends to the anterior margin of the mesepisternum above the posterior lobe of the pronotum. This is the remnant of the upper margin of the post-spiracular sclerite, described above in connection with *Chalastogastra*, and marks the ventral limit of the anterior part of the subalar area.

Each *mesepisternum* is divided into a number of areas. The *pre-episternal sutures*, or upper portions of the precoxal sutures, extend downward from the subalar pits, in many bees far down toward the anterior coxae, in which case they have been known as the pleural grooves or prepectal sutures. In front of each pre-episternal suture lies the *pre-episternal area*. In *Anthophora* the pre-episternal sutures end at the points where they meet the *scrobal sutures*. The latter are horizontal impressed lines, each of which extends anteriorly from a point on the posterior margin of the mesepisternum through a pit, the *episternal scrobe*, to the pre-episternal suture (fig. 22). The pre-episternal and scrobal sutures are not indicated internally in *Anthophora*, although they are represented by internal ridges in some bees. The episternal scrobes, likewise, are not evident internally in *Anthophora*. The area above the scrobal suture and behind the pre-episternal suture of each side is the *hypoepimeral area*; the large area below the scrobal suture, behind the pre-episternal suture and above the subpleural signum is the *disk of the mesepisternum*. This term may be used, in the absence of the pre-episternal suture, for the combined pre-episternal and true discal areas. It usually happens that approximately the anterior two-thirds of each pre-episternal area faces forward at a distinct angle from the rest of the pleural portion of the episternum, which faces laterally. In this case the portion directed anteriorly may be known as the *anterior face of the mesepisternum*; the other pleural portion, including all its subdivisions, is the *lateral face of the mesepisternum*.

The anterior margin of the combined mesepisterna is thickened and overlain throughout by the pronotum. Ventrally this margin is broadly emarginate (figs. 21, 33) and but narrowly covered. Laterally the margin of each is more broadly overlapped by the pronotum and produced to form the *anterior lobe of the mesepisternum*, which lies immediately below the emargination corresponding to the lateral lobe of the pronotum. This episternal lobe is not an apodeme but is fundamentally external even though hidden, as shown by the conjunctiva which arises at its anterior margin and extends outward to the pronotum, that from the upper

margin of the lobe being attached to a ridge on the inner surface of the posterior lobe of the pronotum. As shown in figures 33 and 34, a strong although rather low internal ridge extends downward from each thickened subalar area, close to the anterior margin of the mesepisternum, and gradually disappears below.

As has already been intimated, each mesepisternum may be divided into a lateral *pleural portion of the mesepisternum* and a *ventral portion of the mesepisternum* or *pseudosternum*. The separation between these portions is indicated by a small, elevated, impunctate spot, indicated internally by a small depression. This is the *subpleural signum* or mesopleural tubercle of Salman (1929), the remnant of the subpleural suture or median segment of the precoxal suture. The *precoxal sutures* in the restricted sense arise on the pleural sutures immediately above their lower extremities (fig. 22) and extend downward close to the coxae and, bending posteriorly, meet on the discrimen just behind the *mesosternal apophyseal pit*. Although in *Anthophora* the apophyseal pit has not retained its primitive position between the katepisterna but lies in front of the precoxal sutures, these sutures in certain bees are bent strongly forward near the discrimen so that the pit lies behind the sutures. The narrow zone behind each precoxal suture is the *katepisternum*. Because of the absence of an intersegmental suture ventrally, the posterior limits of the mesokatepisterna cannot be determined. Those portions of the mesepisterna in front of the precoxal sutures and below the subpleural signa are the *subpleural areas*. Anteriorly the mesothoracic discrimen is deepened into an *anterior discrimen pit*, which, as pointed out by Duncan (1939) who used the name mesosternal pit for it in connection with *Vespula*, is not a true apophyseal pit. The *condyle of the dorsal articulation* of each middle coxa is a round tubercle on the pleuro-intersegmental suture, hidden from view by the slight downward production of the dorsal margin of the *middle coxal cavity* but easily seen from internal view (fig. 31). The *condyle of the ventral coxal articulation* is a peg-like

¹ It seems reasonable to use the term sternal with reference to this pit, since any existing undivided median sternum must lie in it.

process of the katepisternum lying on the antero-ventral portion of the margin of the coxal socket.

The furcal structures and wings including the axillary sclerites and the epipleurites will be considered later.

METATHORAX

The *metathorax* is much reduced, consisting only of a narrow band surrounding the mesosoma in front of the propodeum (fig. 22). It is bent strongly forward in the region of the posterior wing bases, which are thus brought close to the bases of the anterior wings.

The *metanotum* consists of a narrow transverse band, bent distinctly anteriorly at the sides. Medially it is simple and parallel-sided. At each side a suture crosses the metanotum diagonally, slanting posteriorly and laterally. This is the *transmetanotal suture*, whose anterior or mesal end is deepened and broadened to form the *metanotal pit* (fig. 22). Laterally this suture does not reach the posterior margin of the metanotum but is directed transversely, parallel to the posterior margin of the metanotum. The narrow zone behind it is continuous with the metepimeron, thus constituting a *metapostalar*, perhaps combined with a remnant of the metapostnotum. This condition is by no means uniform in the bees, the posterior extension of the metepimeron often connecting with the dorsum of the propodeum. The extreme lateral portions of the metanotum which bear the wing processes are depressed, separated from the regions mesad from them by the *transmetanotal ridges* (fig. 22) and known as the *lateral metanotal segments*. The zones at each side between the transmetanotal ridges and the transmetanotal sutures are the *dorso-lateral metanotal areas*.

In view of the structure of *Anthophora* one immediately suspects that the median portion of the metanotum is postnotal, only the dorso-lateral areas and lateral segments being truly metanotal. In the absence of a third phragma, this theory can only be disproved by a study of other Hymenoptera, as follows:

1. Metanotum and metapostnotum both distinct complete transverse bands (*Chalastogastra*, many ichneumonids, some psammocharids, etc.).

2. Metapostnotum greatly narrowed medially, presented laterally by crests similar to those of *Vespula* (male *Photopsis* in the Mutillidae).

3. Metapostnotum wanting medially, present only as small lateral crests, fused with the metepimera (*Vespula*). It would seem best to call these structures postalare sclerites, since they are doubtless derived from the postalare bridges of more primitive forms rather than from the postnotum proper.

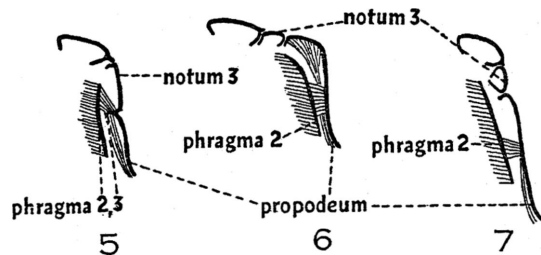
4. Postalare sclerites each narrowed to a mere ribbon or bar, the inner end of which sometimes becomes fused with the metanotum proper, sometimes with the upper margin of the propodeum. Secondary transmetanotal sutures cut off lateral, wing bearing sclerites (Sphecoidea, Apoidea).

These facts show that the postnotum has been entirely eliminated from the metathorax except perhaps for minute lateral areas attached to the epimera. It is not fused with the propodeum, as was believed by Snodgrass (1910).

Snodgrass may have based his belief partly on the fact that muscles extend from the second phragma directly to the propodeum in bees without attachment to the metathorax. This condition might be interpreted as evidence that the original position of the now vanished third phragma was on the propodeum. The migration of these muscles as well as those primitively extending from the third phragma to the first metasomal antecosta is indicated by the accompanying diagrammatic longisections of the posterior mesosomal regions of certain Hymenoptera (diagrams 5, 6, and 7). From the preceding paragraph it is clear that the phragma persists in *Vespula* even though there is no postnotum behind it except laterally.

Internally the metanotum bears the *anterior metanotal inflection* and the *posterior metanotal inflection*, similar in many ways to the inflections of the mesoscutellum. The inflections of the metanotum, between the metanotal pits, meet at their inner margins, forming a closed transverse tube. Laterad from the metanotal pits, the inflection of the anterior margin is broadly expanded (fig. 31), while the posterior one remains rather narrow. The lateral expanded portions of the anterior inflections are not apodemes, con-

junctiva being attached to their lower margins. They fit the concavities of the posterior surfaces of the posterior lateral scutellar inflections.



DIAGRAMS 5-7. Longisections through mesoscutellum, second phragma, metanotum, and propodeum of (5) *Vespula*, (6) *Halictus*, and (7) *Anthophora*.

The depressed lateral segments of the metanotum are very short and broadly triangular; each ends in a small squarish apodeme, the *lateral apodeme of the metanotum*, which is furnished with a distal anterior process (fig. 40). The *anterior metanotal wing processes* are long and conspicuous, attached to the ends of the anterior inflection of the metanotum, and constricted basally so that they are very flexible, perhaps allowing considerable up and down movement of the wing base itself. The wing process of each side is bifurcate (figs. 39, 40), having a large anterior process and a shorter posterior one, to the rear margin of which the first axillary sclerite is articulated. The lower end of this sclerite is articulated with a small point above the base of the lateral apodeme of the metanotum. There are no posterior metanotal wing processes for articulation of the third axillaries.

The *metathoracic subcoxal areas*, like the metanotum, are narrow bands (figs. 21, 22). For convenience each *metepisternum* may be divided into a narrow *intercoxal region* between the middle and posterior coxae and broader *pleural* and *pseudosternal regions*. As with the mesothorax, the *metepimera* are reduced to narrow dorsal margins of the metapleural regions, and the *metapleural sutures* end dorsally in *subalar pits*, not extending thence dorsally to the *metapleural wing processes*. Immediately in front of each metapleural wing process is the small, slit-like opening of the metathoracic spiracle, in front of which is a small sclerite perhaps best regarded as a *peritreme*. The posterior margin

of each metapleuron is marked in its lower portion with a pair of pits, the *upper* and *lower metapleural pits*. At the lower metapleural pit each pleuro-intersegmental suture turns posteriorly and extends to a point on the dorsal margin of the posterior coxal socket. That portion of this suture close to the socket is very feeble, the suture seeming at first sight to be continuous with the submarginal groove of the propodeum (fig. 22) rather than to follow its expected course downward to the coxa.

The internal inflections of the anterior margins of the metapleura have already been described in connection with the mesothorax. The posterior margins are each marked internally by a *metapleural ridge*, which is particularly strong above the point where it is met by the furcal arm (fig. 34). At its summit it divides, the lesser anterior branch or pleural ridge following the pleural suture toward the subalar pit, the larger posterior branch immediately becoming the heavy, internal marginal inflection of the propodeum.

The intercoxal portions of the metasubcoxae are very narrow externally, but each is furnished with a large, internal *intercoxal lamella*, which will be described later. As in the case of the mesothorax, postcoxae are absent.

The pseudosternal portions of the metasubcoxae meet to form a medial line or *discrimen*, marked posteriorly by the *metasternal apophyseal pit* (fig. 21). The mesokatepisternum is fused indistinguishably with the metapseudosternal area.

The *posterior coxal cavities* are smaller than the median ones (fig. 21), and each is provided with two condyles, the *condyle of the dorsal* or *outer coxal articulation* near the lower extremity of each pleural suture and the *condyle of the ventral* or *inner coxal articulation* near the anterior median angle of each cavity.

STERNAL FURCAE

Internally the pterothorax is braced by an extensive system of apophyses, the fused mesothoracic and metathoracic *furcae*, which arise from the discrimen and the sternal apophyseal pits already described. The discrimen, for its entire length from the anterior end of the mesothorax to the posterior end of the metathorax, is represented internally by the *vertical plate of the sternal apophyses*.

Except as otherwise indicated, this plate is thin and rather delicate. It is low anteriorly and posteriorly and reaches its maximum height a little behind its middle (fig. 32). Between the bases of the metafurcal arms and the anterior end of the vertical plate of the sternal apophyses, the latter is expanded to form the thin *horizontal plate of the sternal apophyses* (fig. 33). This plate is somewhat concave dorsally, expanded anteriorly onto the anterior margin of the subpleura, and provided middorsally in front of the bases of the mesofurcal arms with a short, erect lamella, the *vertical lamella of the mesosternal apophysis*. The anterior discriminal pit represents the point where the contiguous margins of the vertical plate, the horizontal plate, and the vertical lamella reach the external surface.

Posteriorly the large mesosternal portion of the vertical plate of the sternal apophyses is limited by a thickening of this plate, which slants obliquely forward from the mesosternal apophyseal pit to near the bases of the mesofurcal arms (fig. 32). The inner ends of the *intercoxal lamellae* are attached to this thickening. Their lower margins, as already described, arise on the intercoxal portions of the metasubcoxae; their outer ends are attached to the bases of the lower ends of the metapleural ridges (fig. 34) so that, while the inner margins of the pleural ridges are free, both they and the ends of the intercoxal lamellae are indicated externally by the same suture. The dorsal margin of each intercoxal lamella is expanded except mesally for the attachment of a basalar muscle. The intercoxal lamellae taken together are the homologue of the transverse vertical plate of the metasternal apophysis of Duncan (1939).

The posterior margin of the metasternal portion of the vertical plate of the sternal apophysis is formed by a thickening extending from the metasternal apophyseal pit to the bases of the metafurcal arms (fig. 32). This thickening is furnished with a small posterior tubercle.

The *free basal portions of the mesofurcal arms* are slender and slant anteriorly and laterally from their origins on the sides of the horizontal plate of the sternal apophyses to a point where they are connected by the flattened *mesofurcal bridge* (figs. 31, 33). From the ends of the bridge they slant backward

and outward for a short distance, fusing with the upper ends of the *free basal portions of the metafurcal arms*. These are flattened (in some individuals of this species expanded, as shown in fig. 31), arise close together at the posterior end of the horizontal plate of the sternal apophyses, and slant anteriorly and outward to the point where they meet the mesofurcal arms. Beyond the points of fusion of the mesofurcal and metafurcal arms, the *coalesced furcal arms* slant outward for a short distance, then separate into *free distal portions of mesofurcal and metafurcal arms*, which become thin and very delicate as they expand greatly in vertical planes. Those of the metathorax fuse with their pleural ridges (figs. 31, 33), while those of the mesothorax terminate as broad, exceedingly thin sheets overlapping, but apparently not actually attached to, the mesopleural ridges. The *dorsal process of the free distal portion of the metafurcal arm* of each side is a thin erect structure, as shown in figures 31 and 33.

WINGS AND WING BASES

We are now in a position to discuss the wings and their articulations, which lie between the nota and pleura. Although a few notes on the mechanism of flight are made below, the work of Stellwaag (1910) and Snodgrass (1942) on *Apis*, in which the structure of the wing base is very similar to that of *Anthophora*, makes extensive consideration of this subject unnecessary. The *epipleurites* are small sclerites, the largest being the *basalares* of the mesothorax (figs. 36, 37). The latter lie immediately basad of the costal sclerites and are hinged in the anterior emarginations of the summits of the subalar areas of the mesopleura in such a manner that they rock inward when the muscles attached to them contract. Each bears a dorsal posterior process (fig. 37) so that the inward motion has a greater effect in drawing the costal margin of the wing down. A tendon-like apodeme arises low on the inner surface of each basalar and extends downward near the inner surface of the pleuron. In addition to two minute basal branches, each apodeme gives off a strong anterior branch, itself bifurcate, just below which the main axis of the apodeme is sclerotized for a short distance

(fig. 36). The apices of these apodemes become broad thin sheets for muscle attachment.

The metathoracic basalares are not hinged after the manner of those of the mesothorax but are attached quite freely by their anterior angles to the metepisterna in front of the pleural wing processes. Each bears a process directed outward and lying under the margin of the costal sclerite (fig. 38). Two tendon-like apodemes arise at a single point on each metabasalar; the anterior apodeme is longer and more expanded distally than the other and is sclerotized along its anterior margin distally.

Each mesothoracic *subalare* (fig. 37) is a small triangular sclerite whose lower margin is hinged to the epimeron behind the subalar area of the mesopleuron. The summit of the subalare is produced upward, and a tendon-like apodeme is attached to this dorsal process so that when the muscle to which this tendon is attached contracts, the subalare rocks inward, drawing the membrane near the third and fourth axillary sclerites, and no doubt the sclerites themselves, downward.

The metathoracic subalares each consist of a minute linear sclerite, to the lower end of which is attached a rather broad membranous apodeme (fig. 38).

The relatively free metathoracic epipleurites are perhaps correlated with the up and down movement of the hind wing bases made possible by the flexibility of the metanotal wing processes.

Because of the position of the pleural wing processes high above the notal wing processes, the axillary sclerites are difficult to study. They never have the exact relations to one another illustrated in figures 36 and 38, since all are not in the same plane. Furthermore, their relations to the upper and lower membranes of the wing bases are not shown in these two figures. As stated by Snodgrass (1927), the first axillary sclerite is a structure of the dorsal membrane, the second is exposed on both surfaces, while the upper surfaces of the third and median axillaries are more exposed than the lower. These conditions are shown in figure 37. The *first axillary sclerites* of both pairs of wings occupy a vertical position. As has already been explained in part, that of each forewing lies in the notch

between the two posterior lobes of the pre-axilla, which together constitute the anterior notal wing process. The pointed lower extremity of each first axillary of the forewing is nearly contiguous with the lateral ventral process of the axilla, and its dorsal hook fits behind the produced posterior end of the tegular ridge of the preaxilla. In this position it can rotate somewhat on its vertical axis. The notal articulations of the first axillary sclerites of the posterior wings have been described in connection with the metanotum. The distal or dorsal ends of the first axillaries of both wings are in close proximity to the base of the costal sclerites. It is through the first axillaries of the forewings that the power of the downward movement of the notum is transmitted to the wing bases to produce the upward stroke of the wings.

The position of the *fourth axillary sclerites* of the forewings has been described in connection with the axillae. In the hind wings they are fused with the *third axillary sclerites*, which have in both pairs of wings a nearly vertical position. The lower or basal end of each mesothoracic third axillary lies in the membrane close to the fourth axillary; that of each metathoracic third axillary is in the membrane behind the conspicuous metanotal wing process of each side. Each third axillary sclerite of the forewing is furnished at its lower end with a short, tendon-like apodeme which flares out abruptly to form a muscle attachment (fig. 36). In the hind wing, because of the fusion of the third and fourth axillaries, this apodeme arises from about the middle of the resultant sclerite and is furnished at its apex with a small sclerotic area to which a muscle is attached.

The *second axillary sclerite* in all the wing bases slants downward and posteriorly, its lower end or a process thereof articulating with, or lying very close to, the third axillary, its upper end being supported by the pleural wing process and lying beneath the posterior end of the radial sclerite. In the hind wing each second axillary sclerite bears an anterior process which fits into a pocket in the outer (morphologically ventral) surface of the first axillary.

The remaining sclerites of the wing bases lie in a horizontal plane when the wings are in horizontal extended positions. The *costal*

sclerite [*Präcostal-platte* of Stellwaag (1910), parategula of Crampton (1928a) and Salman (1929)] is a basal and posterior expansion of the costal vein of each wing; the *radial sclerite* is a similar expansion of the radial vein and lies immediately behind and beneath the costal sclerite. Distad to these sclerites the costal and radial veins fuse for a short distance, then separate again (figs. 36, 38). Immediately behind and in the forewings slightly above the radial sclerite lie the *median axillary sclerites* or *Costalplatte* (Zander, 1910a). In the forewing each is a broad plate bearing a ventral process which supports the anterior part of the vannal sclerite. In the hind wing they are slender rods bent medially nearly at right angles, the posterior portions close to the anterior processes of the reduced vannal sclerites. The *vannal sclerite*, or enlarged base of the vannal vein of each wing, rides on the median axillary sclerite and on the upper or distal end of the third axillary sclerite.

The base of each vein $M+Cu$ approaches but does not fuse with the median axillary sclerite.

The nomenclature of the *wing veins* of Hymenoptera has been a subject of much discussion. Rohwer and Gahan (1916) have summarized the topic up to 1916 and proposed a terminology for the use of taxonomists which has much to commend it but which in no way suggests the homologies of the veins. Since the time of their paper, however, several authors have proposed far simpler systems than those suggested prior to 1916 for homologizing the veins with those of other orders. Since these have been reviewed by Ross (1936) and Duncan (1939), it seems unnecessary to discuss them here. Suffice it to say that the most logical as well as simplest system is that of Ross, and it is here adopted with a few changes made desirable by the nomenclature used for insect wing veins by Snodgrass (1935). Figure 35 shows the manner in which this terminology is applied to *Anthophora*. It seems practically as simple for the use of the taxonomist as that proposed by Rohwer and Gahan. However, it is very frequently desirable to refer to the cells first R_1 , first R_2 , and second R_2 collectively. They may be known as the first, second, and third *submarginal cells*, respectively. Rohwer and

Gahan's term, cubital cells, is rejected because in the terminology of Ross we call certain entirely different cells by that name. The veins between these cells, first abscissa of R_1 , first r-m and second r-m may be known as the first, second, and third *intercubiti*. Cell second R_1 may well retain, for taxonomic purposes, the name *marginal cell*, and the first abscissa of vein R_1 , the name *prestigma*. Since the shape of the wings and their venation are so easily and adequately portrayed in illustrations, no attempt will be made to describe them in detail. A few other characteristics of the wings will, however, be considered. The wing veins are dark and heavily sclerotic. The membrane is hard, tough, transparent, and practically devoid of hairs. That part distad from the area strengthened by veins is furnished with numerous small tubercles, the *alar papillae*, which appear as small dark spots on the membrane (fig. 35). These papillae are absent along two brownish streaks in each forewing, one representing the continuation of vein M nearly to the margin of the wing, the other the continuation of vein Cu to the margin of the wing.

The anterior margin of each front wing between the *pterostigma* and the wing base is ordinarily turned downward so that the costal cell is not visible from above unless the wing is pressed flat. The dotted lines on the wings in figure 35 represent concave lines in the wing membrane. Wherever these lines cross the veins, the latter are pale for a short distance. These short pale sections are the *alar fenestrae*. Ross (1936) has suggested that certain of these lines represent atrophied veins. The anterior margin of each posterior wing beyond the apex of the costal cell is furnished with a row of *frenal hooks* or *hamuli*, which in flight engage the downcurled and heavily sclerotic *frenal fold* of the posterior margin of the forewing.

Each wing exhibits a *vannal fold* and a *jugal fold*. The latter crosses no veins, but the former, like the lines mentioned above, crosses veins at fenestrae. The *vannal area*, *vannal lobe*, or *vannus* of each wing is the area between these two folds and is separated from the *remigium* at the margin of the wing by the *vannal incision*; the *jugal lobe* or *jugum*, behind the jugal fold, which in the hind wing easily folds under the base of the

wing, is separated at the wing margin from the vannus by the *jugal incision*.

LEGS

The *legs* exhibit a number of interesting modifications and considerable sexual dimorphism. The coxal articulations with the body have been partly described in connection with the thorax; only those features not yet considered will be mentioned here. The *anterior coxae* (figs. 21, 22, 24, 45) lie close on the prosternum and anterior portion of the mesepisternum, and their movement is primarily an anterior-posterior rocking. Each bears a large *outer lobe* on its external surface near the base, from which lobe it tapers to the apex. Above this lobe lies a concavity, margined exteriorly by the *procoxal carina*. Because of the outward directed distal end of the coxa, the trochanters can be folded back into this cavity, directing the telopodite of the leg laterally and anteriorly. The motion of the middle and posterior coxae is on the axes of the condyles already described. These axes slant mesally and slightly anteriorly toward their lower ends. The movements of these coxae account for much of the antero-posterior leg movement. The posterior coxae are more freely movable than the middle ones, since their cavities lack posterior sclerotic walls and are provided anteriorly with large, exposed *coxal coria*. Furthermore, motion of the middle coxae is particularly limited by the intercoxal lamellae, which with the surface walls of the thorax form strong, more or less cylindrical capsules in which these coxae rotate. Each middle coxa is greatly elongated basally on a dorso-ventral axis at right angles to the principal long axis of the segment. Its trochanteral articulation is in its lower, outer portion and is but little produced from the side of the body. Each middle coxa is furnished with a strong carina extending from its upper articulation with the pleuron to its anterior articulation with the trochanter. This is the *mesocoxal carina*, immediately in front of which lies the *mesocoxal groove* (fig. 22). The posterior coxae, on the other hand, while laterally compressed, are primarily elongated on their principal axes.

The *trochanters* are small, slightly compressed segments, tapering toward their

bases and obliquely truncate at their apices. The posterior trochanters of the male are more slender than those of the female, a fact no doubt correlated with the slender male femora. Because of the posteriorly directed front coxae, the anterior coxae move antero-posteriorly in a more or less horizontal plane. The other trochanters, however, move in a vertical plane.

The *femora* are elongate and slightly variable in shape, those of the fore and middle legs a little longer than the corresponding tibiae, those of the hind legs a little shorter than the hind tibiae. In the female the femora are broadest very near their bases instead of nearer their midpoints (figs. 41, 46), as in the male. The femora are clothed with hairs primarily on their lower surfaces.

The *tibiae* are narrowest at their incurved bases. Like the femora, those of the male are more slender than those of the female. The anterior and middle pairs are provided in the male with an upcurved spine or tooth on the anterior margin at the apex. Similar teeth are found on all the tibiae of both sexes in many bees and may be known as the *tibial spines*. The outer surfaces of the tibiae in many bees are provided with numerous small tubercles or *tibial spiculi*, each usually bearing a spine-like seta. Arising on the under surfaces near the apices of all the tibiae are one or two *tibial spurs*. The anterior tibiae each have a single spur which forms part of the *strigilis* or antenna-cleaner. The *malus* or thickened, spine-like portion of the *strigilis* is sharply pointed apically and bears on its inner margin a broad, transparent lamella, the *strigilar scraper* or *velum* (fig. 44). The middle tibiae each bear a single very long spur (fig. 42) which is slightly curved apically in the male, strongly so in the female. Its upper surface (that is, the surface close to the basitarsus) is concave, and the two sharp margins which are thus formed, one on either side of the concavity, are finely serrate. Each posterior tibia bears two spurs, which are but slightly curved in both sexes, otherwise very similar to the middle tibial spur. They may be distinguished from each other as the *inner hind tibial spur* and the *outer hind tibial spur*. At the base of each posterior tibia on the outer surface is a small, flat, glabrous, elevated plate, the

basitibial plate (figs. 41, 46), much larger and better differentiated in the female than in the male. Rayment (1935) has correlated this structure, often called the knee plate, with the burrowing habit, stating that it is used to support the bees in their holes. The tibiae in the male are bare or with very short hairs on their inner posterior surfaces, otherwise rather sparsely covered with longer hairs of the same type as those found on the body, that is, with numerous very short branches. The female tibial pubescence is similar except that the outer surfaces of the middle tibiae are very densely covered with rather short hair which is a little more fully plumose than the body hair, while the outer surfaces of the posterior tibiae are covered with long, coarse, simple hairs which constitute the *scopa* in which pollen is collected.

The *tarsi* are five-segmented and considerably longer than the tibiae. The first segment or *basitarsus* of each tarsus is large and nearly as long as the next four segments taken together. Segments two to four are small and constitute the *mediotarsus*, while the fifth segment is rather elongate and is the *distitarsus*. The anterior basitarsi (fig. 44) have a deep semicircular incision, the *concavity of the strigilis*, on their inner margins. The surface of this incision is smooth and polished in *Anthophora*, but in some forms it is furnished with a *strigilar comb* of fine setae. The middle basitarsi are flattened, broader in the female than in the male. The posterior basitarsi are large and flat, those of the male with a large tooth on the anterior margin of each, those of the female each with a broad process beyond the base of the second tarsal segment. This is the *distal process of the posterior basitarsus* (fig. 46). The under surfaces of all the basitarsi are densely covered with rather appressed hair which appears reddish in certain lights and is longest on the posterior legs of the female. Except for the posterior basitarsi of the female, whose outer surfaces are clothed with long, simple, scopal hairs like those of the tibial scopa, the outer surfaces of the basitarsi are sparsely covered with rather short hairs provided with many very short branches, thus resembling the body hairs. The upper surface of the distal process of the posterior basitarsus of the female is furnished with a dense *posterior basi-*

tarsal brush of fine hairs; the lower surface is armed with several coarse setae. Similar coarse setae are found on the apices of the lower surfaces of all the basitarsal and mediotarsal segments and make up the *tarsal combs*.

Each mediotarsus consists of three small segments which are widest at their apices and narrow basally. In the front tarsi of both sexes the mediotarsal segments are short, the first two of equal length, the third shorter. As with those of the other legs, all are somewhat chordate, being flattened, with the dorsal apical margin of each emarginate for the reception of the succeeding segment. In the cases of the other legs the second tarsal segment is longer than the third, which in turn is longer than the fourth. The mediotarsal segments of the middle legs, especially in the male, are quite elongate, even the most distal one being considerably longer than broad. Those of the hind legs of the male are short; in the female, however, the second tarsal segment is longer than the next two together.

The distitarsi are narrowest basally, gradually expanded toward the widest points, which are subapical (figs. 41, 46). They are larger in the male than in the female. The apex of each distitarsus is furnished with a broad, ventral, truncated emargination and a dorsal rounded emargination in which lies the *unguifer*, a separate crescentic sclerite whose ends articulate with the bases of the claws (fig. 47).

The *pretarsi*, consisting of the claws and associated structures, are illustrated in figures 47 and 48. A tapering dorsal sclerite, the *orbicula*, arises in the apical emargination of each unguifer, whose margin it overlaps slightly. It is furnished with several setae, two of which are much larger than the rest. While it is here included among the pretarsal elements, it may well be derived from the apex of the distitarsus. Ventrally the most proximal pretarsal element is the *unguitractor plate* which is covered with short setae, has a rounded base with a median notch and a median, produced, subtruncated process on the otherwise broadly truncated apex. The basal portion of the unguitractor plate in each leg is invaginated by the infolding of the conjunctiva surrounding it into the apex of the distitarsus. To the base of the unguitrac-

tor plate in each leg is attached the long, tendon-like *unguitractor apodeme* which extends through the tarsal segments to the depressor muscle of the pretarsus in the tibia. In the conjunctival membrane on either side of the distal process of the unguitractor plate lies a small triangular sclerite, the *auxilium* or basipulvillus, which probably serves to transmit the movements of the unguitractor to the adjacent lower basal angle of the claw. The *claws* or *ungues* are basally placed in the membrane just distad to the auxilia, their upper basal angles being notched and articulated with the ends of the unguifer. Each claw bears two long, simple, curved setae on its ventro-external surface. In the males the claws are bifid (fig. 49); in the females the inner tooth is reduced (fig. 50). On the ventral surface of the pretarsus between the bases of the claws is a rather weakly sclerotized plate, the *planta*, furnished with numerous short setae. It is truncate apically, tapering to the broadly rounded base. Distad of the planta lies the broad membranous *arolium*, strengthened by a sclerotic band, the *camera*, which extends around the arolium near the base. The cameral ring is broken dorsally, the upper ends of the sclerotic band being slightly expanded.

PROPODEUM

The remaining mesosomal element is the first abdominal tergum or *propodeum*. As shown in figure 23, it is one of the largest sclerites of the mesosoma, forming almost the entire posterior face of that tagma. Because of the anterior arching of the metathorax at each side, carrying the metathoracic wing bases far forward, the propodeum extends anteriorly on the sides of the mesosoma, as shown in figure 22. The dorsal margin of the propodeum, which is contiguous with the metanotum, is furnished with a rather shallow but thick inflection (fig. 34) continuous at its ends with the metapleural ridge, as already explained. This is the *anterior propodeal inflection*. Laterally the propodeum is firmly fused with the metapleurae, the pleuro-intersegmental sutures themselves becoming very faint near their lower ends. The posterior or lower margin of the propodeum forms the articulation with the metasoma. It is strengthened by the *internal submarginal*

ridge (fig. 34) of the propodeum, which is continuous at its ends with the lower extremities of the metapleural ridges, and is represented externally by the *submarginal groove of the propodeum* (figs. 22, 23), which, like the submarginal ridge, meets the metapleural sutures below the lower metapleural pits. Medially the submarginal ridge is produced to form a pair of *internal propodeal teeth*, similar in size and shape to the propodeal teeth described below and lying immediately anterior to them. As shown in figure 23, the submarginal groove of the propodeum is variable in depth and appears as a series of pits of varying sizes and shapes. A single median pit lying above the submarginal groove is absent in *Anihophora* but present in most bees. This is the *propodeal pit*; the internal swelling which it represents is the point of attachment of the muscles from the second phragma.

That portion of the propodeum behind the submarginal groove is the *posterior marginal area of the propodeum*. It is directed posteriorly rather than downward as is most of the rest of the propodeum. Since the conjunctiva which extends backward from the propodeum arises not far behind the internal submarginal ridge, the posterior marginal area is largely duplicated, that is, with its posterior portion inflected and appressed to the dorsal uninflected portion, as in the case

of the other abdominal segments. The posterior marginal area is broadest laterally and dorsally. The lateral expansions are thin and form the *apical scales of the propodeum*. The median expansion is thick and produced into two hard *propodeal teeth* which nearly surround a circular opening (fig. 23). On each side the propodeum is provided with a large, slightly curved, vertical, slit-like *propodeal spiracle* surrounded by an impressed line. The *spiracular suture*, represented internally by a low ridge (figs. 22, 34), extends upward from each propodeal spiracle toward the upper margin of the propodeum. Below the spiracle similar but weaker internal ridges not indicated externally may be seen (fig. 34). On the posterior face of the propodeum, extending from the lateral parts of its upper margin to the submarginal groove near its middle, a pair of weak lines not represented internally delimit the *triangular area of the propodeum*. In many bees, such as *Halictus*, the upper portion of the triangular area is horizontal rather than vertical, is coarsely sculptured, and is limited posteriorly by a carina or an angle. This is the *basal area of the propodeum*, commonly known as the enclosure.

The *sternum* of the first abdominal or propodeal segment is very short and entirely membranous except for a small, rather weakly sclerotic, Y-shaped area at each side (fig. 21).

METASOMA

The *metasoma*, usually called the abdomen, consisting of the second and following abdominal segments, is separated from the mesosoma by a strong constriction. As explained in the introductory remarks on the mesosoma, the metasomal segments will be numbered as second, third, etc., abdominal segments. The metasoma is short, robust, somewhat compressed dorso-ventrally, with both upper and lower surfaces convex. Seen from above, it is broadest in the region of the third abdominal segment.

PREGENITAL STRUCTURES

In the male there are seven exposed metasomal segments (fig. 51), while in the female there are but six (fig. 52). All these exposed

terga and sterna have free apical margins resulting from folding back of their apices, which become closely appressed against the under surfaces of the noninflected portions. Thus the conjunctiva extending posteriorly from any segment arises on the internal surface of that segment in front of its posterior margin and extends to the anterior margin of the following segment. The posterior margin of each segment is, therefore, duplicated, and the internal lamina of each of these margins may be called the *duplication*. The anterior margin of the duplication is, of course, morphologically the posterior margin. There is no indication on the outer surface of the position of the anterior margin of a duplication. The condition here described appears to be a

characteristic of the Hymenoptera; it provides for a sclerotic internal surface on each segment upon which the following segment can slide.

Pleurites are absent in the abdomen. The exposed abdominal *terga* greatly overlap the *sterna* and are, therefore, bent strongly downward and mesally at the sides, so that each has in addition to the large *dorsal surface* a lateral or *ventro-lateral surface*. The *sterna*, on the other hand, are smaller and curved upward but little at the sides.

The anterior margin of the second abdominal segment, in addition to being constricted, is greatly strengthened to form the articulation with the propodeum and is hardly invaginated within the propodeum, even the acrotergal and acrosternal portions being exposed. Crampton (1931) has shown the evolution of the acrotergite into a specialized articular structure. The *antecostal suture* traverses the second tergum at the posterior end of the constricted portion or *petiole* (fig. 51). The antecostal suture is represented at the sides by an internal *antecosta*, which merges into a large convexity medially. The narrow and horizontal *acrotergite* or *petiole* in front of the antecosta is thickened and bears a transverse external ridge, which forms the front wall of a groove across the acrotergite into which the propodeal teeth fit. This groove is interrupted medially by the *vertical plate of the petiole*, which stands upward between the propodeal teeth (fig. 53). The remainder of the second tergum consists of a large, vertical, broadly concave *anterior surface* provided with a longitudinal groove, which is marked internally by a ridge, a rather short dorsal surface, shorter in the male than in the female, and large latero-ventral areas separated from the anterior face by angles and extending farther downward than those of any other tergum (fig. 51). The second tergal spiracles are elongate, each surrounded by a narrow elevation, and lie at the lateral margins of the anterior face of the tergum about midway between upper and lower edges of this face. They are the only exposed metasomal spiracles. The anterior margin of the duplication of the second tergum is broadly emarginate laterally.

Terga three to six in the female and three to seven in the male are each furnished with

a distinct transverse line on their outer surfaces near the bases. This is the *gradulus* (fig. 54). The areas basad from the graduli, or *pregradular areas*, although somewhat inclined forward, are elevated at their posterior margins above the *postgradular areas*. Laterally the graduli bend posteriorly, the spiracles being anterior to them. Internally the graduli are invisible or represented by only a slight change in the contour of the tergum. The *posterior marginal areas of the terga* are impunctate and in many bees depressed. Very close to the anterior margin of each of these terga is a strong internal transverse ridge, the *antecosta*. In front of this ridge a very narrow *acrotergite* is visible on certain terga, although commonly it is reduced to a mere line. A narrow apodemal anterior margin traverses each tergum in front of the antecosta. This is produced anteriorly at each side of each of the terga under discussion, except the third, to form a small, roughly triangular *tergal apodeme* (fig. 58). Because of the curvature of the terga, their apodemes lie in nearly vertical planes. As in the case of the second tergum, the anterior margin of each duplication is broadly and gently emarginate at each side.

The exposed portions of these terga, except for the glabrous apical marginal areas, are covered with rather long hairs with very short branches like those of the head and thorax. These hairs are longer on the second and third than the following terga, short and inconspicuous on the dorso-lateral areas. The posterior part, except for the marginal area, of the sixth tergum of the female is densely covered with loosely plumose hairs with rather long branches. These constitute the *prepygidial fimbria*. Hairs of a similar type are found on the seventh tergite of males of some species of *Anthophora* [e.g., *A. pacifica* (Cresson)].

Having discussed the fundamental features of these terga, we shall now mention some of the minor differences among them. The spiracles on the fourth and following terga are shorter and more rounded than on the preceding. The fifth tergum of the male is similar to the fourth, which is illustrated in figure 58, except that the spiracle is a little farther from the gradulus. In the female the fourth and fifth terga are similar to those of

the male, but the gradulus is slightly nearer to the anterior margin of the sclerite. The sixth tergum in the male (fig. 61) is similar to the fifth but with broader tergal apodemes and sharper lateral bends in the gradulus. In lateral view the sixth tergum of the female is similar to that of the male. As seen from above (fig. 64), it is narrowed posteriorly with a gentle median emargination, in front of which a narrow area is slightly depressed. Although it can hardly be so called, this area is probably the homologue of the *pseudopygidial area* found on the sixth tergite of female and the seventh tergite of male bees of some groups. The seventh tergum of the male is similar to the sixth, having similar apodemes, but it is narrowed posteriorly and more strongly convex. Although the posterior margin of the sixth tergum is simple in this species, it is provided with a weakly developed pseudopygidial area in some species of *Anthophora*.

The seventh tergum of the female (figs. 68, 69) is considerably modified as compared to preceding terga. Except for the posterior median *pygidial process*, it is much shortened. Its anterior margin, strengthened by the antecosta as in other terga, is broadly concave, so that the tergal apodemes form the apices of anterior lateral lobes of the tergum. The gradulus is absent. The *pygidial plate* is a flat glabrous area on the dorsum of the tergum, covering the entire upper surface of the pygidial process and margined laterally by vertical walls. Arising on either side, simple hairs form the *pygidial fimbria*. The duplication of the seventh tergum is particularly broad medially, covering the entire under surface of the pygidial process.

The eighth and ninth terga of the female will be considered in connection with the sting.

The eighth tergum of the male (figs. 74, 75) is similar in many respects to the seventh of the female, its anterior margin being broadly concave so that the tergal apodemes terminate anterior lateral tergal processes. The gradulus is present, strongly curved laterally, and produced posteriorly to the postero-lateral margins of the tergum. The pygidial process is broad, truncate, flattened but not glabrous dorsally, and not margined by vertical walls extending from its sides ante-

riorly onto the disk of the tergum as in the female. There is no distinct pygidial fimbria. From beneath, the pygidial process is seen to be closed, that is, the duplication, which is not appressed to the roof of the process, extends forward to a point beneath the base of the process where it turns sharply upward to the roof of the tergum, there terminating and giving way to conjunctiva (see fig. 75).

The ninth and last distinguishable tergum of the male is a small, feebly sclerotic plate lying in the roof of the genito-anal chamber. It consists of two rather heavily sclerotic longitudinal bars (fig. 78), each furnished behind the middle with an external process for muscle attachment. These bars are connected by a feebly sclerotic area, except posteriorly where the integument between them is membranous. There are no spiracular openings in the ninth abdominal segment.

The second sternum (figs. 51, 53), like the second tergum, is constricted and strengthened at its base. Unlike that tergum, however, it is rather small and gently convex, not furnished with large anterior and lateral faces. Close to its emarginate anterior edge, where it is most strongly convex, the second sternum bears a transverse internal antecosta marked externally by a groove, the antecostal suture. The *acrostermite* or sternal portion of the petiole in front of the antecosta is thickened, especially laterally, where it is broader than medially. The posterior margin of the second sternum is broadly convex with a deep median incision or notch. The duplication, as in the case of the terga, is rather broad both posteriorly and laterally but only slightly emarginate postero-laterally; its inner and anterior margin is thickened to form a ridge whose position is indicated externally by a sharp ridge parallel to each lateral margin of the sternum. There is, however, little or no external suggestion of the position of the transverse median portion of the anterior margin of the duplication.

Sterna three to six of the female and three to seven of the male, as in the cases of the corresponding terga, are similar to one another in ground plan. Each is broadly convex, but little upturned laterally, with a broadly concave anterior margin strengthened by the strong and rather deep antecosta, in front of which the external portion of the acrosternite

is absent or exceedingly narrow. At each side in front of the antecosta each sternum is produced anteriorly to form a conspicuous *sternal apodeme*. Transverse graduli, directed posteriorly at their ends as are those of the terga, traverse most of the sterna near their bases. Unlike the terga and the second sternum, the duplications of the sterna here under consideration do not extend around the lateral margins of the sclerites but are confined to the posterior margins. As is the case with the terga, the *posterior marginal areas* of most of these sterna are impunctate. The sternal pubescence of the male consists only of sparse, rather short, and inconspicuous hairs. That of the female consists largely of similar hairs, but immediately basad from the posterior marginal areas there are many long hairs, and on the third to fifth sterna they are furnished with numerous short branches like those of the rest of the body. On the fifth and sixth sterna the longer hairs cover a large portion of the sclerites and are more fully plumose, having branches of greater length, than those of the ordinary long hairs of the body.

These abdominal sterna differ from one another markedly. The third sternum lacks long dorsal processes of the sternal apodemes. In the male it is more deeply emarginate anteriorly with smaller apodemes than in the female, in which sex the gradulus is present only medially. The posterior marginal area is undifferentiated medially in the male. The antecosta is larger and more strongly directed anteriorly in the female than in the male. It is largely visible from below in the former, visible from below only medially in the latter.

The fourth and fifth sterna differ from the third in having on the outer or upper margin of each apodeme a slender *dorsal process of the sternal apodemes* (fig. 59). The apical marginal areas are undifferentiated in the male but distinct in the female; the basal emarginations are shallower in both sexes than those of the third sternum, but slightly deeper in the female than in the male. The gradulus is reduced to a short median line in the fourth sternum of the female, absent in the fifth, but well developed and sinuate on both sterna in the male (fig. 60).

The sixth sternum of the male resembles the fifth except for the slightly emarginate

posterior margin, the feeble external lines representing the anterior extremity of the duplication (fig. 63), the anterior bowing of the gradulus so that its median portion nearly reaches the anterior margin of the sclerite, and the somewhat stouter and more posteriorly directed dorsal process of each sternal apodeme. In the case of the sixth sternum of the female (figs. 65, 66), the gradulus and external indication of the posterior edge of the duplication are absent. The posterior margin of the tergum is gently and broadly emarginate medially, and, as a result of the narrowing of the abdomen, the sides of the sternum, especially posteriorly, are flexed upward. The sternal apodemes are directed mesally, and their strongly posteriorly curved dorsal processes have migrated rearward until they constitute nearly separate apodemes of the sternum.

In the seventh sternum of the male (figs. 70, 71) the posterior margin is rather strongly emarginate. The gradulus, while rather short, is very strong medially and represented internally by a distinct change in contour. It is supplemented as a strengthening structure in the sternum by two grooves extending postero-laterally from near the middle of the gradulus. The apodemes of this sternum are rather long, their dorsal processes short and directed strongly posteriorly. Since the eighth and ninth sterna of the male are small and invaginated, the seventh sternum is the one which folds upward against the eighth tergum and closes the genito-anal cavity.

In the female the seventh sternum has large, expanded apodemes (fig. 72), separated by a broad emargination whose margin is medially produced to a broad truncation which seems to be of acrosternal origin. The antecosta is absent medially, and the gradulus is wanting. The dorsal processes of the apodemes are very short. Posteriorly the sternum tapers to the narrow, slightly emarginate apex, while laterally its margins are strongly upturned and are apodemal in nature backward to a point beyond the middle. These marginal apodemes are posterior continuations of the primary sternal apodemes and are broadened near their posterior extremities for muscle attachment (fig. 73). They terminate posteriorly where the margins of the sternum are elevated to form a

small process on each side. This process is closely associated with a projection of each eighth hemitergite and helps to support a conjunctival fold extending upward laterad of each of these hemitergites.

The eighth and following sterna of the female are absent as sclerotic plates, being represented only by a large membranous area beneath the eighth and ninth hemitergites and the sting.

In the male, on the other hand, the eighth and ninth sterna while small and invaginated are heavily sclerotic. The ninth sternum lies directly above the eighth, with its apex not extending so far posteriorly as that of the eighth. The genital capsule lies immediately above the ninth sternum.

The eighth sternum of the male (figs. 76, 77) bears two long anterior arms which carry the sternal apodemes at their apices. The antecostal ridge slopes forward, so that, especially in the depths of the emargination between the anterior arms of the sternum, it is clearly visible from below. The disk of the sternum is broader than long, with the margins rather irregularly lobate and the surface undulate, the lateral margins thick, heavily sclerotic, and upturned. Although this is regarded as an invaginated and hidden structure, its apex may often be seen from the outside through the distal emargination of the preceding sternum.

The small ninth sternum (figs. 79, 80) is very different from any of the others, possessing a slender, compressed, median basal apodeme or *spiculum*, to which muscles providing for movement of the genital capsule are attached. This is a characteristic feature of the ninth sternum of most Hymenoptera. The basal lateral apodemes are reduced, but the antecosta is distinct.

It seems reasonable at this point to discuss briefly the significance from a functional and evolutionary standpoint of certain of the modifications of the metasomal integument. The constriction at the base of the metasoma with the resulting enlarged tergum and thickened acrosternite and acrotergite of the second abdominal segment is necessarily correlated with the propodeal developments, possible reasons for which have been already considered. The antecostae, as in other insects, serve for the attachment of the tergal

and sternal retractor muscles. The development of tergal and sternal apodemes, however, appears to be correlated with the respiratory movements associated with the powerful flight of the higher Hymenoptera. These apodemes proper serve for the attachment of the anterior ends of the intertergal and intersternal extensor muscles, while the dorsal processes of the sternal apodemes serve for attachment of the upper ends of the tergo-sternal extensor muscles. Thus the apodemes are connected with movements of expansion of the abdomen, which are necessary to fill the large abdominal air sacs. Alternate expansion and contraction of the abdomen, easily observed in many bees, would serve, with appropriate opening and closing of spiracles, to draw or force air through the tracheae and air sacs of the thorax close to the muscles of flight. The development of long lobes carrying the apodemes, seen in the posterior terga and sterna of both sexes, is probably associated with the development of longer intertergal and intersternal extensor muscles to provide for rearward movements of these sclerites in such activities as egg laying, stinging, and copulation.

GENITALIA AND ASSOCIATED STRUCTURES

In studying the male genital capsule, considerable difficulty has been encountered in determining the best terminology for the parts because of differences of opinion regarding homologies of the structures concerned. Therefore, a comparative study of the appendages of the ninth abdominal segment of the Insecta was made. It was found necessary to consider first the structures of the ovipositor of female insects. Here the homologies appear to be relatively easily understood, and with the exception of one or two points most authors agree in their interpretation of them.

The ovipositor consists of the appendages of the eighth and ninth abdominal segments. In the Apterygota such appendages apparently occur only in the Machilidae and Lepismidae. Each of these appendages in *Machilis* consists of a broad, flattened coxopodite bearing at the base of its inner margin an endite produced as a process or gonapophysis and at its apex a muscled stylus. The styli

probably represent the telopodites of these appendages. (The similarly shaped but non-musculated "styli" borne on the coxae of the rear thoracic legs in *Machilis* are apparently not homologous to the abdominal styli.) The broad basal plates may be known as coxites, since each is only a part of the coxopodite, the other part being the gonapophysis.

In *Thermobia* the situation is similar, except that a small basal portion of each coxite of the ninth abdominal segment becomes separated from the rest while retaining its attachment to the gonapophysis.

From such a structure it is a simple step to the ovipositor of a pterygotan insect, e.g., Odonata, Hemiptera, Homoptera, Hymenoptera. The coxites of the eighth and ninth segments become the first and second valvifers, respectively, while the gonapophyses become the first and second valvulae. The third valvulae are the styli of the ninth segment, those of the eighth having disappeared. In the orthopteroid groups these styli disappear in the adults. It is for this reason that Snodgrass (1935) believed styli to be absent from the ovipositors of most Pterygota. His third valvulae of Orthoptera are merely subdivisions of the second valvifers. It, therefore, seems reasonable to term the third valvulae of orders other than the orthopteroid groups the gonostyli. The Hymenoptera differ from other orders in exhibiting an articulation between the first valvifer and the tenth tergum.

The copulatory organs of male insects are highly variable. In some the cerci or processes of the eighth, ninth, or tenth abdominal segments are evidently secondarily modified for copulatory purposes. However, the copulatory organs of the majority of male insects, including *Anthophora*, consist of the penis and certain musculated claspers, attached at least in the adult to the ventral or lateral portions of the ninth abdominal segment. It is the homologies of these *primary copulatory organs* with which we are here concerned.

These homologies have been subject to much difference of opinion, some authors having suggested that these organs are all phallic structures which have arisen *de novo* in insects, others that at least some of them are true appendicular structures. Appendages of the eighth, ninth, and tenth abdominal segments have been regarded by various authors

as contributing parts to the male primary copulatory apparatus. Some have believed that the claspers consist largely of styloid processes comparable to the coxal processes of certain Thysanura. Others suggest that the endopodite and exopodite of primitive biramus appendages form the inner and outer claspers, respectively. Many workers who believe in the appendicular origin of the claspers regard telopodite derivatives as contributing to them, while a few believe that, except for the lower orders of insects, only coxopodite derivatives are present.

Some authors (e.g., Crampton, 1919, 1920a; Newell, 1918) have attempted to homologize the parts of the genitalia through many orders of insects, while others (e.g., Snodgrass, 1935) have believed that the claspers in some groups were entirely different in origin from those in others. Thus the outer claspers of Hymenoptera were regarded as phallic structures, while the at least functionally similar claspers of Diptera and Lepidoptera were regarded as periphallallic organs, modifications of walking appendages.

In view of the differences of opinion, it seems necessary first to establish with certainty the segment with which the primary copulatory structures are associated. Apparently the most important evidence is the fact that, as already stated, in the adults they are always articulated on the ninth abdominal segment or lie immediately behind that segment. Since the embryonic appendages of the tenth abdominal segment are retained as larval "legs" or postpedes in many holometabolous insects (Johannsen and Butt, 1941), and since the rudiments of the copulatory structures arise in the larva while these legs are still present, we may be quite certain, as pointed out by Snodgrass (1941), that tenth segment appendages do not enter into the formation of the genitalia in these forms, although, as shown by Else (1934) and Qadri (1940), they appear to do so in Orthoptera. Holometabolous insect larvae, however, do not have "legs" on the ninth abdominal segment, which is the segment upon which the claspers are situated, or if appendages are present, as in the larvae of Trichoptera, they give rise to claspers (Crampton, 1920, 1920a). It seems certain, then, that at least the outer claspers, and the inner ones as well except

possibly in the Orthoptera, are, like the gonopore, associated with the ninth abdominal segment.

The most important evidence concerning the nature of the male copulatory structures is obtained from a comparative study through the orders of insects. It seems desirable, however, to present first certain other facts which support the homologies indicated by the comparisons. The idea that the copulatory organs are new structures (probably of phallic origin) seems far less probable than that they are derived from pre-existing structures. In this connection I quote from the excellent statement of principles suggested by Ferris (*in* Ferris and Rees, 1939) as a guide for morphological work: "The introduction of completely new elements as contrasted with the other means of modification which have been indicated, will be comparatively, or even absolutely, rare. Consequently recourse to the assumption that a completely new structure has appeared should be had only as a last resort in attempting to elucidate an obscure situation." Evidence for the phallic origin of the primary copulatory structures appears to be based primarily on developmental history, the lobes of immature forms which become the genital apparatus of adults not appearing to belong to the same dynamic series as the true appendages, but often arising late in ontogeny and near the position of the developing gonopore. However, the undoubted appendages which appear, at least in the Thysanura, Orthoptera, etc. (Johannsen and Butt, 1941), early in the embryonic history as lobes of the genital segments, disappear in most cases before hatching, so that lobes formed later in ontogeny, even though seemingly in slightly different positions, may nevertheless be redeveloping appendages.

A different line of evidence concerning homologies of the claspers involves the subdivisions of the lobes of the immature forms which develop into the copulatory structure. In the Hymenoptera each of these lobes divides incompletely into processes which later form the inner and outer claspers. In the Trichoptera (Zander, 1901) and Lepidoptera (Zander, 1903) and presumably in the Diptera and Mecoptera, on the other hand, each lobe divides completely, and the lateral mem-

bers migrate outward and come to be the muscled appendages of the ninth somite. Therefore, it appears to me that the claspers are homologous throughout at least the higher orders of insects, the division between the outer and inner pairs being merely less complete in the Hymenoptera than in certain other orders. This evidence is inconclusive, however, since Mehta (1933) claims that the outer claspers of Lepidoptera arise independently from the inner ones, and Singh-Pruthi (1924) makes a similar statement with regard to the Homoptera.

In attempting to establish with greater certainty the homologies of the male terminalia, a study of several sex anomalies has been undertaken. Popov (1937) has recorded and figured a stylopized gynandromorphic specimen of *Halictus eurygnathus* Blüthgen in which the genitalia are divided longitudinally, one-half being male, the other female. A similarly abnormal individual of *Chalcidoma muraria* (Retzius) is described by Bischoff and Ulrich (1929). In these specimens the outer clasper on the male side corresponds to the combined second valvifer and third valvula or gonostylus of the female, while the inner clasper or penis valve of the male probably corresponds to the second valvula, although Popov interprets it as corresponding to the combined first and second valvulae. An intersex of *Ashmeadiella rhodognatha* (Cockerell) is somewhat more female than male (Michener, 1943). The first valvula and valvifer are reduced to a single narrow ribbon. The third valvula has become immovably fixed to the second valvifer, and the two second valvulae are incompletely fused, modifications which would be expected in such a specimen if the homologies are those indicated by the gynandromorphic bees mentioned above. Gynandromorphic specimens of Tettigoniidae described and figured by Cappe de Baillon (1924, 1932) suggest the same homologies, the first valvulae being absent on the male side, the second valvulae apparently corresponding to the penis valves, and the combined second valvifers and third valvulae corresponding to part of the subgenital plate of the male, which is a coxosternum consisting of the fused ninth sternum and at least parts of the corresponding coxopodites. An appar-

ently similar gynandromorph in Gryllidae is briefly described by Ohmachi (1926).

It would be unreasonable not to cite in this connection certain records of gynandromorphs whose structure does not support the homologies between male and female parts suggested above. Thus Popov (1935) describes an *Andrena* and Peacock (1924, 1925) two tenthrinids in which male claspers are present in whole or in part in addition to a full complement of female gonopods. Clearly the evidence derived from gynandromorphs is not conclusive, since even within the bees in which the male claspers are undoubtedly homologous from group to group, certain gynandromorphs suggest homologies between female gonopods and male claspers, while others suggest that the claspers are structures of separate origin from the female ovipositor. The intersex referred to, which is probably more reliable for our purposes than gynandromorphic individuals, and gynandromorphs in widely separated groups lend weight to the idea of homologies between the male and female copulatory parts.

HOMOLOGIES AND TERMINOLOGY

If the homologies suggested by the sexually anomalous *Halictus*, *Chalicidoma*, *Ashmeadiella*, etc., are correct, we can homologize in detail the parts of the male and female appendages of the ninth abdominal segment. The third valvulae or gonostyli of the female become the distal segments of the outer claspers of the male; the second valvifers are sometimes subdivided, their basal portions, or the structure in its entirety if no basal piece exists, representing the basal segments of the outer claspers; the second valvulae probably become the inner claspers or penis valves, commonly more or less completely separated from the outer claspers.

Approximately these same homologies have been suggested by Singh-Pruthi (1924, 1929), who stated that the outer claspers (his subgenital plate) correspond to the second valvulae (lateral ovipositor valves), the penis and its valves (his aedeagus and parameres) correspond to the third valvulae or gonostyli (dorsal ovipositor valves), while the homologues of the ovipositor valves arising on the

eighth segment are absent in most male insects, although present in *Machilis*, and, according to Singh-Pruthi (1924), in a species of *Tipula*.

Before presenting the strong comparative morphological evidence for these homologies, it is necessary to define the various terms used in referring to the parts of the male copulatory apparatus. The terminology here used represents an attempt to use for each structure a name at least not misleading as to homology and neither used for so many different structures as to be meaningless (as is paramere), nor indicative of a shape not at all constant for the structure involved (as is squama).

Gonopods: In the male the pair of segmental appendages of the ninth abdominal segment.

Gonocoxopodites: The coxopodites (including gonobase, penis valves, and volsellae) of the gonopods.

Gonocoxites: The gonocoxopodites except for penis valves, volsellae, and gonobase when present. The gonocoxites are the basal segments of the outer claspers.

Gonobase: The fused basal portions of the gonocoxites when the latter are articulated with the gonobase.

Penis Valves: Mesal basal processes of the gonocoxopodites which usually serve to support the penis. These are the inner claspers of some insects and frequently become detached from the gonocoxites.

Volsellae: Processes of the gonocoxopodites articulated to the inner faces of the latter distad from the bases of the penis valves. These structures usually project freely and are separate from the penis.

Gonostyli: The styli articulated with the apices of the gonocoxites. These are the distal segments of the outer claspers.

Gonoforceps: The fused gonocoxites and gonostyli, or a generalized collective term for both of these structures when present.

Penis: The intromittent organ proper or phallus. This structure, which is not of appendicular origin, terminates in the gonopore.

Aedeagus: The penis and penis valves. The penis valves are sometimes completely fused with the outer wall of the penis.

Genital Foramen: The opening surrounded by the bases of the gonocoxites when the latter are fused both above and below the base of the aedeagus.

Making use of this terminology, the homologies between male and female parts indicated above are shown in the following table and in diagrams 8 and 9.

Coxites of eighth abdominal segment
Gonapophyses of eighth abdominal segment
Coxites of ninth abdominal segment
Gonapophyses of ninth abdominal segment
Styli of ninth abdominal segment

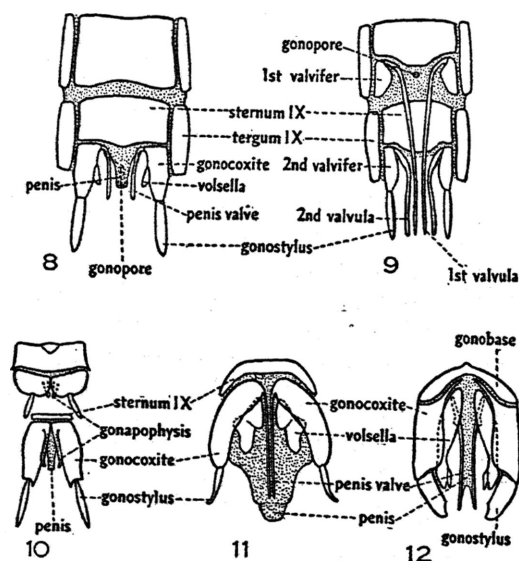
FEMALE
First valvifers
First valvulae
Second valvifers
Second valvulae
Third valvulae or gonostyli

MALE
Absent in Pterygota
Absent in Pterygota
Gonocoxites
Penis valves (?)
Gonostyli

The appendages of the eighth and ninth abdominal segments of the male *Machilis* (diagram 10) are very similar, except for a shortening of the parts, to the comparable appendages of the female. There can be no doubt that the styli, coxites, and gonapophyses of the male are homologous to those of the female. The only external genital structure of

the male without an obvious counterpart in the female is the penis.

Turning to the Pterygota, we find ordinarily no appendages on the eighth abdominal segment of adult males. The appendages of the ninth segment are similar to those of *Machilis* in certain Neuroptera (e.g., *Agulla* in the Raphidiidae). In these structures the



DIAGRAMS 8-12. 8, Ventral view of eighth and ninth abdominal segments of hypothetical primitive male pterygotan insect; 9, ventral view of eighth and ninth abdominal segments of hypothetical primitive female pterygotan insect; 10, ventral view of eighth and ninth abdominal segments of male *Machilis*; 11, ventral view of genitalia and ninth sternum of male *Agulla*; 12, ventral view of genitalia of male *Xiphidria*.

supposedly primitive orthopteroid orders are far more modified than some of the Neuroptera and certain other orders with a complete metamorphosis. In *Agulla* (diagram 11) the gonocoxites, gonostyli, and penis are clearly homologous with those of *Machilis*. The base of each gonocoxite is produced as a thickening in the ventral wall of the penis. While these thickenings may be homologous to the gonapophyses of *Machilis*, their entirely different relation to the penis leaves the homology in doubt. The thickenings are the penis valves. Laterad from the penis valves lies a pair of projecting processes which were called fragmenta of the coxopodites by Ferris and Pennebaker (1939). These processes are apparently homologous with the claspettes of Diptera and the volsellae of Hymenoptera.

The male genitalia of Hymenoptera are sufficiently similar to one another that within the order their parts may usually be definitely homologized (see Snodgrass, 1941). A comparison of the genitalia of *Xiphidria* (diagram 12) with those of *Agulla* shows the relationships of the parts between the two orders. The chief differences between the gonocoxopodites of *Agulla* and of *Xiphidria* are the formation of a gonobase in the latter, the formation of an apodeme at the base of each penis valve and the separation of these valves from the gonocoxites in the hymenopteron, and the position of the entire genital armature of *Xiphidria* in the membrane above (morphologically behind) rather than immediately behind and articulated with the ninth sternum. That the gonobase is actually merely a secondary division of the gonocox-

ites is shown by the observations of Zander (1900), who found that in *Vespa* it is separated from the gonocoxites late in ontogenetic development. This conclusion is supported by Crampton (1938), who notes particularly the notching of the gonobase in *Xyela*. Certain special modifications within the order include fusion of the gonocoxites in the Chrysididae, separation of the penis valves from the penis in most bees, and nearly complete suppression of all parts of the primary copulatory organs except for the large and complex penis in *Apis*.

Snodgrass (1941), although using a terminology very different from that here applied, has admirably established the homologies of the male genital parts within the order. Boulangé (1924), Beck (1933), and Peck (1937) have also contributed much to a comparative study of the genitalia of Hymenoptera, although each uses a different terminology.

Since Snodgrass (1941), in discussing each of his terms, has listed the names used in several of the previous important papers on Hymenoptera for each of the genital structures, it seems necessary here only to correlate the present terminology with that of Snodgrass. The following table will serve this purpose:

SNODGRASS (1941)	PRESENT TERMINOLOGY
Caulis	Gonobase + gonocoxites
Basal ring or lamina annularis	Gonobase
Laminae paramerales or basiparameres	Gonocoxites
Parameres	Gonostyli
Aedeagus	Aedeagus (penis valves + penis)
Laminae aedeagales or penis valves	Penis valves
Aedeagal apodemes	Apodemes of penis valves
Volsellae	Volsellae

The differences between these two terminologies result from differences in understanding of the homologies of the parts involved. The major points indicating the validity of the homologies here accepted have been discussed in the preceding pages. A fuller discussion of these matters will be published elsewhere.

MALE GENITALIA

The male genitalia of *Anthophora* lie in the

genito-anal chamber between the sternum and tergum of the ninth abdominal segment and are ordinarily completely hidden from external view. The gonobase is perforated by the large genital foramen, and its exposed portion is greatly narrowed laterally and ventrally. On each side of this narrow portion, however, a broad apodeme is inflected and partly closes the genital foramen (fig. 82). The gonocoxites are very large structures (figs. 81, 82, 83, 84) firmly attached around their curved basal margins to the correspondingly curved posterior margin of the gonobase. Dorsally as well as ventrally the margins of the two gonocoxites are close together; the anterior dorsal margins, where they come in contact with, or are close to, the broad part of the gonobase are inflected as apodemes (fig. 84). Mid-dorsally at their closest point each gonocoxite is furnished with a depressed process which closely approaches its fellow and forms a sort of hinge which allows for in and out, forceps-like action of the gonocoxites. The dorsal margin of each gonocoxite is inflected, and before the middle of the length of the structure is reached it becomes inflected so far that it meets the ventral margin, forming a closed tube thence posteriorly. The broad mesal basal openings into the gonocoxal cavities thus formed are traversed by the basal apodemes of the penis valves. At their bases the ventral margins of the gonocoxites are each furnished with an immovable ventral basal lobe of the gonocoxite, which is probably not the volsella, which occupies a similar position in some bees but is free and has an outer margin extending laterally above the gonocoxal margin. Distally the gonocoxites are each provided with a large, external, subapical process, a large ventral apical process, and a small ventral mesal angle. Immediately above the base of each ventral apical process the small, slender gonostylus, partly fused to the gonocoxite, arises. The gonoforceps or combined gonostyli and gonocoxites are thus composed primarily of the gonocoxites.

Between the gonoforceps lie the penis valves, which are very heavily sclerotic structures, turned downward and pointed posteriorly (fig. 85), each bearing ventrally and basally a long apodeme of a penis valve which extends into the cavity of the gonobase. The penis valves are united to one another dor-

sally and basally by the *bridge of the penis valves*, which is produced anteriorly in the middle to strengthen the membrane between the gonocoxites. In many bees the bridge is produced posteriorly as a dorsal sclerotization of the *penis*. In *Anthophora*, however, the penis is entirely membranous. Such a dorsal sclerotization is a *spatha*.

STING AND ASSOCIATED STRUCTURES

In the female the genito-anal chamber or sting chamber is occupied by the sting and associated structures (fig. 87). In repose the sting lies on the floor of the cavity directed posteriorly with the valvular rami curved upward anteriorly and the sting bulb and the valves of the first valvulae drawn forward under the eighth and ninth hemitergites. Figure 87 shows these parts spread for illustration in a position never assumed by them in life.

The eighth and ninth terga are both divided longitudinally into lateral plates or *hemitergites* which are feebly sclerotic and invaginated into the sting chamber. The hemitergites of the eighth segment carry near their upper ends the last pair of spiracles. These sclerites are rather irregular in shape and thickened marginally except at the ends near the spiracles. Each bears a short process on the margin, which is ventral in repose. This process lies in the conjunctiva very close to a small marginal process on each side of the seventh sternum and supports the lower end of a conjunctival fold extending backward from the anterior margin of the hemitergite to cover most of the latter, as shown in the figure. The ninth hemitergites or quadrate plates, in so far as their external portions are concerned, are small slender sclerites, but each is furnished along its anterior margin with a large flattened *apodeme of the ninth hemitergite*, considerably larger in area than the exposed part. From their appearance in adult bees alone, it would be difficult to prove the tergal origin of these plates of the ninth segment, but in *Chalastogastra* they are represented, like those of the eighth segment, by complete, exposed terga. In the Aculeata the eighth and ninth terga become invaginated, and in the bees each loses its sclerotization medially. Since the anus is nearly directly above the spiracles of the

eighth segment, it is clear that the membranous dorsal portions of the eighth and ninth terga must be shortened and arched forward in order to pass in front of the anus.

Cercus-like structures borne on the ninth tergum in many Hymenoptera, called cerci by Crampton (1929) and Pratt (1930) but doubtfully referred to as socii by Snodgrass (1935), are absent in bees.

Although the first valvifers and valvulae together are the appendages of the eighth abdominal segment, the *first valvifers* in *Anthophora*, as in other Hymenoptera, each articulate basally with the posterior angle of the ninth hemitergite and with a point on the anterior margin of the second valvifer. They are the small plates, often called triangular plates, whose ventral ends are bent anteriorly and give off posteriorly the first valvulae. The *first valvulae*, which with the fused second valvulae constitute the *sting*, are separated into slender, flexible basal *rami of the first valvulae* and more robust *lancets*, which are dovetailed into the stylet. The base of each lancet bears on its dorsal surface a large *valve of the lancet*. These valves fit into the bulb of the sting and serve to pump poison thence outward through the sting, as has been well described by Snodgrass (1925).

The appendages of the ninth abdominal segment consist of the second valvifers with their basal gonapophyses or second valvulae and their distal processes or third valvulae. The *second valvifers* or oblong plates lie in the conjunctiva beneath and behind the ninth tergal plates and the first valvifers. While their posterior margins are thin and fade gradually into the conjunctiva between them, their anterior margins are thickened, and each bears an *apical process of the second valvifer* and anteriorly (or ventrally) a curved process directed forward, from the apex of which the *second valvula* arises. The *rami of the second valvulae* are similar to those of the first but shorter. Distad from these rami the valvulae are fused dorsally to form a median *stylet* with a ventral trough closed by the lancets. The basal half of the stylet is enlarged to form the *bulb of the sting*, in which the valves of the lancets lie. The base of the bulb gives off above on each side a slender *apodeme of the stylet*, which converges toward and fuses with its fellow. Beneath the base of the

apical process of each second valvifer, a *third valvula*, *gonostylus*, or sting palpus is articulated. It is convex and hairy dorsally, con-

cave ventrally, and in repose lies immediately above the sting.

SUMMARY OF *ANTHOPHORA* MORPHOLOGY

In comparing the structure of *Anthophora* with that of less specialized Hymenoptera one is struck by the remarkable fixity of certain structures throughout the order and indeed throughout the insects. At the same time many features, while remaining fundamentally the same, have been modified in such a way as to appear superficially very different or to perform different functions. Perhaps the most surprising observation to be made in this connection, however, is that most of the outstanding changes in morphology which have occurred during the history of the Hymenoptera have involved specializations subserving a very few functions. Most of the striking modifications of the bees (e.g., *Anthophora*), as compared to *Chalastogastra*, are concerned with two functions, namely, the powerful flight and the collection of food.

Some of the modifications involving flight are: (1) simplification of wing venation; (2) sclerotization of many membranous areas of the thorax; (3) constriction of the neck region; (4) constriction between the first two abdominal segments; (5) development of spherical shape in the mesosoma; (6) reduction of the metathorax and its flight muscles and phragma; (7) development of great flexibility in the metanotal wing processes; (8) anterior migration of the hind wing bases, correlated with reduction of the mesepimera and mesopostalaes so that the wing bases of each side are close together, the wings of each side thus acting more effectively as a single unit; (9) great development and posterior arching of the second phragma; (10) development of the transscutal sutures; (11) strengthening of the mesonotum by the scutellar inflexions and differentiation of the preaxillae; (12) development of great air sacs in the abdomen; and (13) development of tergal and sternal apodemes and dorsal processes of the sternal apodemes. The contributions of each of these modifications to the perfection of the flight mechanism have been discussed in the preceding pages.

Some of the modifications involving collection of food are: (1) extraordinary development of the labio-maxillary complex, all its parts being considerably specialized; (2) development of the proboscis fossa; (3) fusion of the hypostoma and tentorium and development of the maxillary processes of the former high up in the head; (4) arching of the clypeus to make room for the folded proboscis; (5) enlargement of the basitarsi and tibiae and development of specialized hairs of the scopa for collecting pollen.

Certain other specializations observed involve the nesting habits of *Anthophora*. The powerful mandibles with their large apodemes and muscles are used in excavating nesting burrows. In order to strengthen the head capsule against the contractive force of these muscles, the roots of the tentorium have become greatly expanded and complicated, and the tentorium is partly fused with the hypostomal bridge and has developed a secondary bridge of its own. The pygidial plate and the basitibial plates, absent in lower Hymenoptera, are probably of use to bees nesting in the soil.

In the absence of need for an ovipositor, the latter organ has become modified into a sting, as is well known.¹ No doubt this fact is correlated with the invagination and reduction of the apical abdominal segments of the female, which phenomenon is perhaps in turn responsible for similar trends in male Hymenoptera.

Of the modifications discussed above, few are characteristic of the bees or of *Anthophora* alone. Most of them have come, one by one, through the evolutionary history of the order and are represented in greater or lesser degrees of perfection in at least certain of the more primitive groups.

¹ There can be no doubt that originally in the evolutionary history the sting served to paralyze the prey, and that only when the pollen and nectar feeding habits arose did the sting either become an organ of protection alone or, as in some bees, become degenerate.

The following is a list of the various structures, sclerites, areas, etc., discussed in the preceding pages, together with references to the pages on which they are described or defined. It is hoped that future students of the group will find these terms useful in the development of a uniform system of termi-

nology. It will be noted that a few structures (e.g., facial foveae) not found in *Anthophora* are mentioned in the preceding pages and included in the following list. This is done in order to make the list as complete as possible for all the bees.

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PART 2. COMPARATIVE EXTERNAL MORPHOLOGY OF THE BEES DISTINGUISHING FEATURES OF THE GENERA AND HIGHER CATEGORIES

THE PRESENT PORTION of this paper is intended to serve, first, as a study of variations in adult morphology and, second, as a basis for a phylogenetic study and a reclassification of the bees. Morphological features in which the genera resemble and differ from one another are described. Structures common to all bees have been treated in connection with *Anthophora* and are not considered here. The numerous and interesting problems of the evolution and functional significance of certain structures will be discussed in the last section of part 2 and in connection with the phylogenetic considerations in part 3.

For characters not believed to be of great phylogenetic significance, only the extremes of variation are noted in the succeeding pages. However, structures which seem to be of importance in the recognition of the major groups of bees or in the understanding of their interrelationships are described for many genera.

With a few exceptions, the sequence of structures described in this portion of the paper is the same as that in part 1, a large number of characters being considered for numerous genera selected to represent all the major groups of bees. Although several species of many of the genera have been examined in the preparation of part 2 and of parts 3 and 4, it has, of course, been impossible to study all the species in most of the genera. Hence it has seemed wise to give a definite basis for all the statements made in this section by indicating for each genus the name of that species most fully studied.

References to genera in this portion of part 2 refer in all cases, except as otherwise stated, to the particular species listed below; the statements there made do not necessarily embrace all the species of each genus, although in most cases they are believed to do so.

Allodape sp.
Andrena mimetica Cockerell
Anthidiellum robertsoni Cockerell
Anthidium atripes Cresson
Anthophora edwardsii Cresson

Apis mellifera Linnaeus
Bombus vosnesenskii Radoszkowski
Caupolicana yarrowii (Cresson)
Ceratina nanula rigdenae Michener
Chelostoma phaceliae Michener
Coelioxys deani Cockerell
Colletes fulgidus Swenk
Diadasia bituberculata (Cresson)
Dioxys producta (Cresson)
Dufourea mulleri (Cockerell)
Emphor bombiformis (Cresson)
Ericrocis arizonensis Baker
Euglossa sp.
Euprosopis elegans (Smith)
Euryglossa rubricata Smith
Exomalopsis coquillettii (Ashmead)
Fidelia braunsiana Friese
Gnathopasites cressoni (Crawford)
Halictus farinosus Smith
Hemisia rhodopus (Cockerell)
Hesperapis regularis (Cresson)
Hesperonomada melanantha Linsley
Heteranthidium timberlakei Schwarz
Hylaeoides concinna (Fabricius)
Hylaeus cressoni (Cockerell)
Lithurge apicalis Cresson
Macropsis morsei Robertson
Megachile perhirta Cockerell
Melecta californica Cresson
Melipona fasciata guerreroensis Schwarz
Melissodes agilis Cresson
Melitoma grisella (Cockerell and Porter)
Neopasites illinoiensis (Robertson)
Nomada edwardsii Cresson
Nomadopsis anthidius (Fowler)
Nomia nevadensis Cresson
Oreopasites vanduzeei melanantha Linsley
Osmia lignaria Say
Panurginus maritimus Michener
Paracolletes plumosus (Smith)
Perdita ruficauda Cockerell
Protandrena bancrofti Dunning
Protepeolus singularis Linsley and Michener
Protoxaea gloriosa (Fox)
Pseudopanurgus innuptus (Cockerell)
Scrapter semirufa Cockerell
Sphecodes sp.
Stelis rubi (Cockerell)
Stenosmia flavicornis (Morawitz)
Tetralonia sp.
Triepeolus concavus (Cresson)
Trigona sp.

Xenoglossa angelica Cockerell
Xylocopa orpifex Smith
Zacoscma maculata (Cresson)

HEAD

While the compound eyes of bees are always large, convex structures, they vary considerably in shape. In forms such as *Colletes*, *Halictus*, *Hesperapis*, *Hylaeus*, *Nomada*, *Nomia*, *Sphecodes*, *Triepeolus*, and *Trigona* they converge below; whereas in others, such as *Andrena*, *Anthidium*, *Anthophora*, workers of *Apis*, *Bombus*, *Ceratina*, *Megachile*, and *Osmia*, their inner margins are subparallel. In most of these forms the inner ocular margins are somewhat concave so that they converge a little toward both their upper and lower ends. In males of *Apis* and *Protocera* the inner margins of the eyes converge strongly toward the upper end of the face, and in *Apis* they meet on the vertex. Although in most bees the upper ends of the eyes reach the top of the head so that the vertex between them is only gently convex or in some cases concave, in *Ceratina* and *Hesperapis* the upper extremities are well below the upper ends of the sides of the head. The shape of the eyes varies markedly. In *Megachile* and *Osmia* they are broadest near the middle and slightly narrowed toward each end, but in most genera they are broadest near the lower ends. They are nearly half as broad as long in *Ceratina*, *Triepeolus*, and other groups and range from this condition to forms in which they are about one-third as broad as long. The surfaces of the eyes are ordinarily bare, but in *Triepeolus* and certain other genera a few short hairs may be observed on them, and in *Apis*, most species of *Coelioxys*, and certain species of *Neopasites* they are covered with abundant, rather long, erect hair.

The clypeus of bees exhibits much variability. Its general shape, positions along its margins of the anterior tentorial pits, and the degree of protuberance are features of considerable importance in indicating the relationships of the larger groups, while its marginal teeth or indentations and its basal tubercles or processes are, when present, frequently important specific and generic characters.

In *Megachile davidsoni* Cockerell the clypeus is about four times as broad as long. In

Anthophora, *Halictus*, most *Megachile*, *Osmia*, and many other genera it is about twice as broad as long; in *Anthidium* and *Colletes* it is about as broad as long, while in *Hylaeus* it is about one and one-half times as long as broad.

The broadest part of the clypeus is, with few exceptions, at the level of the anterior mandibular articulations, that is, at the ends of the epistomal suture or at the lateral angles of the clypeus. Ordinarily these angles are far below a horizontal line drawn through the middle of the clypeus, the lower margin of which is but little produced downward (figs. 89, 92). In some forms, however, the lower margin of the clypeus is produced forward as in *Colletes* (fig. 88), or more strongly so as in *Andrena* (fig. 91) and *Halictus* (fig. 90), in which genera the lateral angles lie approximately on a horizontal line through the middle of the clypeus. Although in these forms the clypeus is large, the same condition with regard to the comparative positions of the lateral angles and the horizontal median line is found in *Hesperapis* and *Dufourea* in which the short, broad clypeus is only moderately produced downward but in which the upper portion is shortened.

The lower lateral portions of the clypeus are strongly bent to the rear, forming, as seen from below, an emargination for the labrum in *Anthophora* (fig. 6.), *Diadasia*, *Dufourea*, *Emphor*, *Ericrocis*, *Euglossa*, *Hesperonomada*, *Melecta*, *Melissodes*, *Melitoma*, *Neopasites*, *Nomada*, *Nomadopsis*, *Oreopasites*, *Panurginus*, *Perdita*, *Protandrena*, *Protocera*, *Pseudopanurgus*, *Tetralonia*, *Triepeolus*, *Xenoglossa*, and *Zacoscma*. These parts of the clypeus are but slightly curved back in *Allodape*, *Bombus*, *Exomalopsis*, and *Macropis*. On the other hand, the lower lateral parts do not deviate much, except perhaps at the extreme sides, from the general curvature of the lower portion of the clypeus in *Andrena*, *Anthidium*, *Apis*, *Caupolicana*, *Ceratina*, *Chelostoma*, *Coelioxys*, *Colletes*, *Dioxys*, *Euryglossa*, *Fidelia*, *Halictus*, *Hemisia*, *Hesperapis*, *Hylaeus*, *Lithurge*, *Megachile*, *Melipona*, *Nomia*, *Osmia*, *Sphecodes*, *Stelis*, *Trigona*, and *Xylocopa*. Those forms in the first list in this paragraph, for the most part, have the clypeus protuberant, especially below (fig. 3), as contrasted to those of the second long list in which it is but little so (fig. 101).

The epistomal suture presents many important characters. In certain groups it consists of three straight sections, one between the dorso-lateral angles of the clypeus, the others between these and the lateral angles. The lateral sections are often feebly bent at the anterior tentorial pits or near their lower extremities, while the median dorsal section may be feebly arcuate. Genera having such an epistomal suture are *Anthidium* (fig. 89), *Bombus* (fig. 93), *Coelioxys*, *Colletes* (fig. 88), *Dioxys*, *Dufourea*, *Halictus* (suture bent outward at lower extremities, fig. 90), *Hesperapis*, *Hylaeus*, *Megachile*, *Osmia*, and *Stelis*. *Lithurge* falls here, except that the median dorsal section of the epistomal suture is absent, although represented by a broad groove in the male. Among these forms the anterior tentorial pits lie midway between the extremities of the suture and dorso-lateral angles of the clypeus in *Hylaeus*, well above the mid-points of the lateral sections of the epistomal suture in *Anthidium*, *Colletes*, *Dufourea*, *Halictus*, *Hesperapis*, and *Stelis*, and at the summits of these sections in *Bombus*, *Coelioxys*, *Dioxys*, *Lithurge*, *Megachile*, and *Osmia*. In *Ceratina*, *Nomada*, and *Sphecodes* the tentorial pits are at the apices of concave angles in the lateral sections of the epistomal suture, while in *Nomia* they are at the apices of convex angles. There is a large group of bees in which the lateral margins of the clypeus below the tentorial pits are more or less gently concave; the true dorso-lateral angles of the clypeus are at the anterior tentorial pits, as shown by the fact that the lower ends of the outer subantennal sutures are at the upper ends of the pits; and the median section of the epistomal suture is biangularly arched, the angles being at the lower ends of the inner subantennal sutures. Such bees are *Andrena* (fig. 91), *Nomadopsis*, *Panurginus*, *Perdita*, *Protoxaea*, and *Pseudopanurgus*. *Protandrena* is similar, but the lower ends of the outer subantennal sutures are a little above the upper ends of the tentorial pits. In all these bees and especially in *Protandrena* the apparent dorso-lateral angles of the clypeus are at the lower ends of the inner subantennal sutures. In a considerable group of bees the dorso-lateral angles of the clypeus are slightly or considerably above the tentorial pits; the

margins of the clypeus below the pits are a little concave except immediately above the lateral angles where they are strongly convex. Genera so characterized are *Anthophora* (fig. 1), *Caupolicana*, *Diadasia*, *Hemisia*, *Melecta*, *Triepeolus*, *Xenoglossa*, *Xylocopa*, and *Zacosmia*. *Fidelia* is similar, except that the median section of the epistomal suture is arcuate upward. In *Euglossa* the anterior tentorial pits are below the dorso-lateral angles of the clypeus, and the epistomal suture extends downward from each pit, then turns outward at nearly right angles toward the lateral angles of the clypeus. *Allodape* is remarkable for the very long clypeus, narrowest at the anterior tentorial pits which are slightly below its middle; the sections of the epistomal suture between the dorso-lateral angles and the pits are gently arcuate outward but otherwise parallel, while those portions below the pits diverge downward. In *Apis*, *Melipona*, and *Trigona*, as in *Andrena* and the panurgines, the morphological dorso-lateral clypeal angles are at the summits of the tentorial pits. The suture between these points is arched in *Apis* and *Euglossa*, but continues directly upward to false dorso-lateral angles between which it is straight in *Melipona* and *Trigona*. In these latter genera a feeble line suggestive of an inner subantennal suture, but of doubtful nature because of its extreme shortness, arises at each dorso-lateral angle of the clypeus as in *Andrena* and the Panurginae.

As noted in the introductory remarks on the clypeus, there are many remarkable variations in the shape of its lower margin and of its surface. These are found primarily in the Megachilidae, and a few examples will be described here to indicate the extent of this variation. In the female of *Ashmeadiella xenomastax* Michener the lower margin of the clypeus is straight and not in the least produced over the base of the labrum as in nearly all other bees, while the upper margin of the clypeus is elevated. In *Osmia lignaria* Say the lower margin of the clypeus of the female is somewhat produced but has a great median, truncated excision, sometimes so broad as to leave only an arm at each side of it. In *Megachile davidsoni* Cockerell the disk of the clypeus is produced into two broad lobes so thick that their bases occupy almost

the entire height of the clypeus. On the other hand, in *Megachile angelarum* Cockerell the apical margin of the clypeus is nodulose with a small, truncated, median excision. In *Anthidium* (fig. 89), *Heteranthidium*, etc., the anterior margin of the clypeus is usually multidenticulate.

The shape of the labrum is rather variable. In the group of bees in which the lower part of the clypeus is flexed backward at the sides, the lateral portions of the labrum are likewise bent to the rear in order to fit the clypeus. In *Anthidium* (fig. 124), *Chelostoma*, *Coelioxys*, *Dioxys*, *Megachile*, *Neopasites*, *Oreopasites*, and *Osmia*, the labrum is markedly longer than broad, truncate or broadly rounded at the apex, and somewhat broadened at the base, except in *Neopasites* and *Oreopasites* in which the actual line of articulation with the clypeus is rather short. In *Fidelia*, *Lithurge*, and *Melecta* the labrum is but little longer than broad, in *Fidelia* quite large with the outer surface convex. In *Lithurge* the base of the labrum is broadened as in other Megachilidae. The labrum is subrectangular, not very much broader than long, with rounded angles, and with the labral fimbria, if present, inconspicuous and apical in *Anthophora* (fig. 10), *Ceratina*, *Emphor*, *Ericrocis*, *Euglossa*, *Nomada*, *Nomadopsis*, *Protoxaea*, *Triepeolus*, and *Xenoglossa*. The line upon which the labrum is joined to the clypeus is rather short. In *Perdita* the labrum is similar but about twice as broad as long. It is even broader (up to four times as broad as long) in *Apis*, *Bombus* (fig. 93), male *Halictus* (fig. 125), *Hesperapis*, *Melipona*, male *Nomia*, and *Trigona*. Thus far none of the forms in which the labrum is triangular have been considered. This shape is approached in *Hemisia*, although here the two free margins are convex rather than straight. The labrum in this form is less than twice as broad as long. In *Andrena*, *Colletes*, *Hylaeus*, and *Xylocopa* the labrum is triangular and much more than twice as broad as long; in *Xylocopa* the base of the labrum is furnished with three large, elevated tubercles (fig. 92), while in *Andrena* the entire basal area is flat and elevated. In the females of *Halictus* (fig. 126), *Nomia*, and *Sphecodes* the apex of the labrum is provided with a pointed distal

process, broadest in *Sphecodes*, on either side of which the strong labral fimbria arises. Because of this process, the labrum of these forms is often longer than broad.

The face above the clypeus presents a number of characters of importance in the classification. The antennal sockets are conspicuously below the middle of the eyes in *Apis*, *Euglossa*, *Melipona*, *Neopasites*, *Protoxaea*, and *Trigona*, in which genera, also, the epistomal suture is separated from the antennal sockets by less, sometimes much less, than the diameter of the latter. In *Ceratina* and *Hylaeus* the antennal sockets are far above the middle of the eyes. Among the other genera examined, the antennal sockets are at, or but slightly above or below, the middle of the eyes. As in those forms with low antennal insertions, the epistomal suture reaches points close beneath the antennal sockets in *Allodape*, *Diadasia*, *Fidelia*, *Hemisia*, *Melecta*, and certain other genera. This is especially true of *Allodape* and *Fidelia*. In contrast, the sockets in most forms are separated from the epistomal suture by a little more than the diameter of one of the former, while in *Halictus*, *Hylaeus*, *Lithurge*, *Nomia*, *Protandrena*, and *Pseudopanurgus*, they are separated from this suture by two or more diameters of an antennal socket.

Obviously the length of the subantennal sutures and likewise of the subantennal areas varies with the distance from the epistomal suture to the antennal sockets. Those forms with both inner and outer subantennal sutures clearly present (*Andrena*, *Nomadopsis*, *Panurginus*, *Perdita*, *Protandrena*, *Protoxaea*, and *Pseudopanurgus*) have been indicated in connection with the discussion of the shape of the clypeus. Except for a feeble suggestion of an inner pair in *Anthophora*, *Melipona*, and *Trigona*, all the other genera included in the list of species studied exhibit but one such suture on each side, presumably the outer, as shown in part 3. The subantennal sutures are parallel, diverge, or converge depending on the relative positions of their upper and lower ends. The positions of their lower ends have already been discussed. Their upper ends are at, or a little mesad from, the middle of the lower sides of the antennal sockets in *Ceratina*, on the inner margins of the sockets

or directed toward the inner margins in *Allodape*, *Anthophora* (fig. 1), *Caupolicana*, *Colletes* (fig. 88), *Emphor*, *Euglossa*, *Halictus* (fig. 90), *Hemisia*, *Hylaeus*, *Melecta*, *Neopasites*, *Nomada*, *Nomia*, *Oreopasites*, *Triepeolus*, and *Xenoglossa*, while in *Anthidium* (fig. 89), *Apis*, *Bombus* (fig. 93), *Chelostoma*, *Coelioxys*, *Dioxys*, *Fidelia*, *Lithurge*, *Megachile*, *Osmia*, and *Stelis* they are directed toward the outer margins of the sockets. In *Macropis* they are primarily directed toward the inner margins, but near their summits they bend laterally to the outer margins of the sockets.

The supraclypeal area is subject to certain variations in the proportion of length to breadth, depending chiefly upon factors already considered, such as the position of the antennal sockets and of the upper margin of the clypeus. Ordinarily the supraclypeal area is merely convex, continuous with the supra-antennal area, the convexity often accentuated by the elevated lower portion of the frontal line. In *Apis*, *Hylaeus*, *Melipona*, and *Trigona* the supraclypeal area is produced as a wedge-shaped elevation upward into the supra-antennal area. One of the most markedly modified types of supraclypeal areas observed is that of *Lithurge*, which is more than twice as broad as a paraocular area, not elevated medially, slightly elevated at each side in the male, and strongly elevated and projecting upward and outward as a broad, thick process at each side in the female.

The ocelli, while normally in a triangle, form a nearly straight line at the summit of the vertex in *Bombus* (fig. 93), *Ericrocis*, *Melecta*, *Melipona*, and *Trigona*, and in a similarly straight line in front of the summit of the vertex in *Hesperapis*. In other forms examined the ocelli are conspicuously in a rather broad triangle, which is narrowest, only about twice as broad as long, in *Apis*, *Caupolicana*, *Euglossa*, *Protoxaea*, and *Xyllocopa* (fig. 92). Ordinarily the ocelli are at the summit of the vertex as in *Anthophora* (fig. 1), worker *Apis*, *Colletes*, *Euglossa*, *Hylaeus*, *Nomada*, *Nomia*, and *Triepeolus*, or a little in front of the summit as in *Andrena* (fig. 91), *Anthidium* (fig. 89), *Ceratina*, *Megachile*, *Nomadopsis*, and *Osmia*. However, in male *Apis* and in *Caupolicana* and *Xyllocopa* they are far in front of the summit of the vertex,

a condition which reaches its extreme in *Protoxaea*, in which the triangle formed by the median ocellus and the antennal sockets is about the same size and shape as that of the three ocelli.

While in most bees the paraocular areas are simple, in certain genera facial foveae, usually confined to these areas, are present. In *Euryglossa*, *Hylaeoides*, *Hylaeus*, and *Scrapier* a narrow groove parallels the inner upper margin of each eye, and in *Euprosopis* a similar groove diverges from each eye margin toward the ocelli. In *Colletes*, especially females, somewhat broader depressions whose inner margins are hardly defined occur high on the paraocular areas. Facial foveae are found, also, in *Andrena* (fig. 91), *Nomadopsis*, *Panurginus*, *Perdita*, *Protandrena*, and *Pseudopanurgus*. These genera exhibit great variability in the size of the foveae, those of *Andrena* being large, very shallow, and inconspicuous in the male, but deeper and covered with very short hairs giving them a characteristic sheen in the female. Among the other genera the foveae are bare and small, especially so in the males; they are minute and punctiform in males of certain species of *Perdita*, although somewhat elongate in *P. ruficauda* Cockerell.

In addition to a facial fovea, each paraocular area is often provided with a paraocular carina. Such structures are present in *Anthidium* (fig. 89), *Coelioxys*, *Dioxys* (very strong), *Osmia*, and *Stelis*, and in these genera they do not diverge from the lower margins of the eyes toward the anterior mandibular articulations. In *Andrena* (fig. 91), *Anthophora* (fig. 1), *Emphor*, *Nomada*, *Oreopasites*, *Triepeolus*, and *Xenoglossa* similar carinae, sometimes weak or very close to the eyes above, are present. Their lower ends, however, diverge from the ocular margins toward the anterior mandibular condyles. Other groups, including *Exomalopsis*, *Fidelia*, *Hemisia*, *Melecta*, and the panurgines, lack paraocular carinae. In *Macropis* the outer margins of the paraocular areas are abruptly elevated above the inner margins of the eyes, but there are no true carinae.

The genal areas of bees are highly variable in extent, being practically absent in the male of *Apis*, in which the posterior wall of the head extends directly mesad from the

posterior eye margins, but very large, about three times as broad as the width of the eyes in the female of *Osmia armaticeps* Cresson. Usually these areas are a little narrower than the width of the eyes. In *Coelioxys* and *Dioxys* the genal areas are each margined posteriorly by a carina which unites with its fellow behind the vertex.

That portion of the head capsule immediately below the foramen magnum is of considerable interest. In most genera the postoccipital bridge, at least medially, slopes downward and forward to the bottom of a deep transverse groove or depression. The postgenal bridge slants thence downward and backward to the hypostomal carina, which is sometimes broken medially by a depression extending upward from the proboscival fossa for the reception of the mentum and submentum in repose. Such is the condition found in *Andrena* (fig. 98), *Anthidium* (fig. 94), *Caupolicana*, *Colletes* (fig. 95), *Diadasia*, *Emphor*, *Euryglossa*, *Exomalopsis*, *Halictus* (fig. 97), *Hylaeus*, *Lithurge*, *Megachile*, *Melecta*, *Neopasites*, *Nomada*, *Nomia*, *Osmia*, *Protoxaea*, *Sphecodes*, and *Xylocopa* (fig. 96). This general condition is modified in a number of ways. For example, in *Hesperapis* the depression between the postoccipital and postgenal bridges has become a large and exceedingly deep, rounded pit. In *Ceratina* a short median portion of the postgenal bridge is depressed and much narrowed by a narrow upward extension of the proboscival fossa, while in *Apis*, *Euglossa*, and *Trigona* the postgenal bridge is broadly narrowed and slopes to the rear but little, if at all. *Bombus*, *Ericrocis*, *Hemisia*, and *Nomadopsis* have a distinct postgenal bridge but it scarcely slants posteriorly, while in *Triepolus* the same condition is found, except that the postgenal bridge is indistinguishably fused with the postoccipital and hypostomal bridges. The extreme modification of this area is found in *Anthophora* (figs. 2, 6) and *Xenoglossa*, in which the postgenal bridge is completely broken and the postoccipital bridge is flexed forward to form a small part of the roof of the proboscival fossa. In the latter genus the two separated parts of the postgenal bridge are somewhat elevated and not far apart, so that a deep channel lies between them.

Although the hypostomal bridge in *Antho-*

phora is separated as a distinct, very strongly concave structure in the roof of the proboscival fossa (fig. 6), it is ordinarily undifferentiated and is merely the sclerotized part of the roof of the fossa. It varies greatly in length measured along the midline, even among closely related forms. In *Xylocopa* (fig. 110) it is very short, so that the fossa has no sclerotic roof. In *Nomia*, *Osmia*, and *Anthidium* (fig. 107) it is one-third as long as the distance from the rear to the front of the fossa, but in *Megachile* only one-seventh that length. In *Halictus* it is more than half as long as the unusually narrow fossa (fig. 108). It is short in *Andrena* (fig. 109), *Apis*, *Bombus* (fig. 111), and *Hesperapis*, and is exceptionally long in *Nomada* in which it is three-fourths as long as the fossa.

The foramen magnum varies slightly in shape, being sometimes more or less parallel-sided, sometimes broader above than elsewhere. The primary tentorial bridge may be seen at, or somewhat above or below, the middle of the foramen magnum.

Cervical sclerites, each a minute sclerotic area below the occipital process of the propleuron, have apparently developed independently in various groups of bees. Such sclerites exist in *Andrena*, *Apis*, *Halictus*, *Megachile*, *Triepolus*, and *Xylocopa* but are absent in *Anthidium*, *Anthophora*, *Osmia*, etc.

The malar areas vary from linear or absent, when the bases of the mandibles reach the eyes, to much longer than broad. They are long in *Apis*, *Bombus*, and some species of *Colletes* and *Trigona*; short in most other groups, including *Euglossa*.

The form of the hypostoma and its connection with the tentorium are well correlated with the characteristics of the mouthparts. Thus in *Dufourea*, *Halictus*, *Nomia*, and *Sphecodes*, in which the cardines are exceedingly long and their basal articulations high in the head, the hypostoma is fused to the tentorium throughout its length, and the maxillary processes of the hypostoma are very small and practically at the anterior end of the tentorium. *Oreopasites*, although without especially long cardines, exhibits but little less complete fusion of the hypostoma and tentorium. In *Protoxaea* the apex of each maxillary process of the hypostoma almost abuts against the inner surface of the face,

as in *Halictus*, but is a little below the tentorium, and the hypostoma and tentorium are united only in their posterior halves, being connected by heavy bars supporting the maxillary processes as in *Anthophora*. The hypostoma and tentorium are fused, except for the anterior third or fourth of their lengths, and the maxillary processes of the hypostoma are short and each connected to the tentorium by a thickened bar in *Andrena* (fig. 112), *Anthophora* (fig. 7), *Diadasia*, *Emphor*, *Ericrocis*, *Euglossa*, *Hesperapis*, *Melecta*, *Neopasites*, *Nomada*, *Triepeolus*, and *Xenoglossa*. The structure is fundamentally similar in *Exomalopsis*, except that only the posterior half of the tentorium is fused with the hypostoma, and in *Hemisia*, in which only the rear third is fused with the hypostoma. *Protoxaea* is similar to *Exomalopsis* in this regard, except that, as already described, the maxillary processes of the hypostoma are much longer. In *Bombus*, too, the posterior half of the tentorium is fused with the hypostoma (fig. 116). In this genus, however, the maxillary processes of the hypostoma are rather long and bent downward anteriorly and are not connected to the tentorium by a thickening as in the groups just considered. In *Nomadopsis*, *Perdita*, and *Pseudopanurgus* the hypostoma is fused with the tentorium only in the posterior fourth, and the short maxillary processes of the former are far forward and nearly reach the inner surface of the clypeus. The remaining genera of bees examined (*Anthidium*, *Apis*, *Caupolicana*, *Ceratina*, *Colletes*, *Euryglossa*, *Hylaeus*, *Lithurge*, *Megachile*, *Osmia*, and *Xylocopa*) have the hypostoma and tentorium free from each other or united only at the extreme posterior ends.

The paramandibular processes of the hypostoma are variable in length, reaching and abutting against the clypeus in *Andrena* (fig. 109), *Anthophora* (fig. 6), *Bombus* (fig. 111), *Halictus* (fig. 108), *Sphecodes*, and *Triepeolus*, nearly attaining the clypeus in *Megachile*, *Nomada*, *Nomia*, and *Osmia*, and ending conspicuously short of the clypeus in *Anthidium* (fig. 107), *Apis*, *Ceratina*, *Colletes* (fig. 106), *Hesperapis*, *Hylaeus*, and *Xylocopa* (fig. 110). In certain forms, such as *Andrena*, *Anthidium*, *Anthophora*, *Halictus*, *Megachile*, and *Osmia*, each of these processes is strengthened

by a paramandibular carina, which in the females of *Andrena* is armed with a row of setae. In *Apis*, *Hesperapis*, etc., the paramandibular carinae are absent.

In a few genera, such as *Anthophora* (fig. 7), the tentorium is nearly horizontal, but it usually slants at least slightly downward toward the front. The expansion of the anterior ends of the tentorial bars is somewhat variable in extent but always on the same plan as that described for *Anthophora* in part 1. In *Euglossa* each anterior tentorial root has an extra buttress on its outer side, which ends as an inconspicuous suture or line extending across the paraocular area, laterally and slightly downward from the antennal socket to the margin of the compound eye. The posterior end of the tentorium is but little expanded in *Anthidium*, *Apis*, *Ceratina*, *Colletes*, *Ericrocis*, *Halictus*, *Hylaeus*, *Lithurge*, *Megachile*, *Melecta*, *Neopasites*, *Nomada*, *Nomadopsis* (enclosed space suggested), *Nomia*, *Oreopasites*, *Osmia*, *Pseudopanurgus*, *Sphecodes*, *Triepeolus*, and *Xylocopa*. On the other hand, it is furnished on each side with a broad, arched sheet attached to the occiput along an occipital sulcus and enclosing beneath it a space which is open only ventrally in *Anthophora*, *Bombus*, and *Hemisia*. In *Andrena*, *Emphor*, *Hesperapis*, *Protoxaea*, and *Xenoglossa* the enclosed space is rather small. It should be noted that, from an external point of view, the presence or absence of occipital sulci cannot be considered as a certain indication of the presence or absence of these curved tentorial sheets. Thus in certain forms, such as *Colletes*, sulci are present, yet the internal tentorial sheets are absent, while in some forms with small sheets the sulci are absent. In *Euryglossa* the sulci are very strong but are indicated internally only by strong carinae which expand at their upper mesal ends onto the tentorium. The primary tentorial bridge may be either straight or somewhat arched. The opening in front of the secondary tentorial bridge is usually narrowed behind, more or less triangular, but in *Anthophora* and *Nomada* it is approximately round.

The antennae of bees are ordinarily twelve-segmented in the females, thirteen-segmented in the males. There are, however, a few exceptions to this rule; thus the males of

Gnathopasites and *Neopasites* have twelve-segmented antennae like the females, while the females of *Androgynella*, like the males, have thirteen-segmented antennae. (It is possible that *Androgynella* is based on gynandromorphic or intersexual specimens of *Megachile*.) Frequently the antennae are variously modified or merely greatly lengthened in male bees. The scape varies from two to seven or more times as long as broad and may be greatly broadened and flattened, as in *Hylaeus basalis* Smith. The pedicel is never much longer than broad, frequently broader than long, and in some species of *Nomada* is invaginated within the apex of the scape in such a way as to be invisible or nearly so from the exterior. The basal segment of the flagellum is elongate, often as long as the scape, and slender basally in *Caupolicana*, *Hemisia*, and *Oxaea*, and is somewhat elongate, although much shorter than the scape, in *Anthophora*, *Diadasia*, *Melitoma*, *Xenoglossa*, and *Xylocopa*. By contrast the basal segment is but little different from the following ones in *Andrena*, *Apis*, *Anthidium*, *Bombus*, *Ceratina*, *Colletes*, *Euglossa*, *Halictus*, *Hylaeus*, *Megachile*, *Nomada*, *Nomadopsis*, *Nomia*, *Osmia*, *Perdita*, *Protandrena*, and *Stelis*.

The mandibles of bees are typically rather slender, except for the broad bases, and bear subapically on the inner margin of each an angle or tooth. Such is the condition found in *Andrena* (fig. 91), *Anthophora* (fig. 11), male *Caupolicana*, *Colletes* (fig. 130), female *Halictus* (figs. 132, 133), *Hesperapis*, *Sphecodes*, etc. There is little modification of this condition in *Fidelia* (female), except that the mandibles are broader subapically than basally. In *Bombus* (male), *Hylaeus*, and *Xylocopa* the apices of the mandibles are bidentate, the inner tooth but little shorter than the outer. In worker *Apis* the mandibles are spoon-shaped, broadened and edentate at the apices, and in the females of *Bombus* they are somewhat similar but with two notches near the apex. In *Ceratina*, male *Apis*, etc., the mandibles are narrow apically and tridentate. In *Anthidium*, *Megachile*, and *Osmia* the mandibles are broadened, especially in the females, and usually three- to seven-toothed, although bidentate in some males.

The position of the base of the mandible is subject to considerable variation and was used as an important character by Robertson in separating the families of bees. Unfortunately, among the bees which he included in the Anthophoridae and Nomadidae, the posterior mandibular articulations are sometimes far in front of the posterior margins of the eyes, sometimes immediately below these margins. Thus in *Dioxys*, *Ericrocis*, *Melecta*, *Neopasites*, *Nomada*, *Oreopasites*, *Triepeolus*, and *Zacosmia*, all parasitic genera, the posterior mandibular condyles are far in front of the posterior ocular margins; while in *Anthophora*, *Coelioxys*, *Diadasia*, *Emphor*, *Hemisia*, *Melitoma*, *Stelis*, and the other groups of bees, these condyles are close below the posterior margins of the eyes. In *Exomalopsis* and *Xenoglossa* a more or less intermediate condition with respect to this character exists. The anterior position of the mandibles is evidently associated with the parasitic habit and is accentuated by the great breadth of the lower parts of the eyes in the bees exhibiting this character.

Although the epipharynx is a relatively simple, membranous structure, it exhibits variations which seem to offer possible generic or group characters. Thus in *Euglossa* it is several times as long as broad, the distal part laterally compressed and curved anteriorly; in *Hesperapis* it is short with a slender, blunt apical process; in *Ceratina* it is triangular and over twice as long as broad; in *Triepeolus* it is similar but a little shorter; and in *Anthophora*, *Apis*, and *Bombus* it is a rather short triangular lip.

Although the lower ends of the anterior conjunctival thickenings of the labio-maxillary tube are at the extreme base of the prementum in *Anthophora* (fig. 15) and *Ceratina* and in the middle of the lateral margins of that sclerite in *Hylaeus*, they ordinarily lie between one-fifth and one-third of the length of the prementum from its base. Typically they are narrow, but in *Anthidium* (fig. 141), *Megachile*, and *Osmia*, they are broadened in the regions of the laciniae, while in *Apis* they are similarly broadened in spite of the fact that they reach neither the prementum nor the base of the labio-maxillary tube. In *Colletes* the lower part of each thickening is detached as a large, curved

sclerite (fig. 145) whose point of strongest flexure near its middle lies close to the lacinia. In *Halictus*, *Nomia*, and *Sphecodes* a similar but much smaller and straight sclerite is detached from the remainder of each thickening, and a short secondary thickening (fig. 143) in addition to the primary one extends upward from the upper end of each detached sclerite. *Andrena* exhibits remnants of the usual thickenings as small sclerites, similar to the detached sclerites of *Halictus*, close to the margins of the prementum (fig. 146); in addition a pair of thickenings extends part way down the anterior face of the labio-maxillary tube from the pharyngeal plate.

The proboscides of many different types of bees have been described and figured by Saunders (1891), Langhoffer (1898), Demoll (1908), and others. These papers will be useful supplements to the material here presented because drawings of many forms not illustrated in this paper are found in these earlier works.

The maxillae are complicated structures and have been modified in many ways. The cardines are always slender, as long as or a little shorter than the stipites. The stipites are ordinarily rather slender structures, several times as long as broad. In *Xylocopa* (fig. 139), however, the stipites are less than twice as long as broad, and in *Anthophora* (fig. 13) they are less than three times as long as broad. In other genera mentioned below they are more slender. In *Anthophora* and *Xylocopa* the posterior margins of the stipites are broadly emarginate subapically, and the emargination is lined with a row or comb of stout bristles (outer comb, Cockerell, 1924). Every gradation is found between this condition and that in which this comb is represented merely by a few, fine, short setae. Thus in *Anthidium* (fig. 141), *Bombus* (fig. 140), *Ceratina*, *Diadasia*, *Emphor*, *Euglossa*, *Hemisia*, and *Xenoglossa* a comb of moderately robust but sometimes short setae is found in the gentle apical concavity of the posterior margin of each stipes. In *Apis*, *Hesperapis*, *Nomada*, *Triepeolus*, and *Trigona*, there is a slight concavity in each stipes, as described for the above group, but the setae arising in it are few, short, and fine or at least hardly differentiated from some of the other setae of the stipites. Even the con-

cavity is absent and the apical parts of the stipites are glabrous or furnished with short, fine setae in *Andrena* (fig. 137), *Caupolicana*, *Colletes* (fig. 138), *Dufourea*, *Ericrocis*, *Fidelia*, *Halictus*, *Hylaeus*, *Megachile*, *Melecta*, *Nomadopsis*, *Nomia*, *Osmia*, *Protoxaea*, and *Sphecodes*.

Since they vary from six- to two- or three-segmented within a number of groups of clearly related genera, the maxillary palpi have obviously been reduced independently more than once among the bees. In *Oxaea* they are apparently absent. In *Diadasia* the third and fourth segments are furnished with a fringe of long hairs on one side.

The laciniae in most genera are small, oval, sclerotic structures, usually with a number of setae. They are largest in *Anthidium* (fig. 141), *Ceratina*, *Fidelia*, *Hylaeus*, *Megachile*, *Osmia*, and *Stelis*; smaller in *Andrena* (fig. 137), *Anthophora* (fig. 13), *Bombus* (fig. 140), *Caupolicana*, *Hesperapis*, *Nomadopsis*, and *Xylocopa* (fig. 139). In *Dufourea* and *Nomia* they are very small, hairy, and elevated far above their usual positions at the bases of the galeae. In *Euglossa*, *Melecta*, *Nomada*, and *Triepeolus* they are sclerotic but glabrous; in *Hemisia*, submembranous with a few short hairs; in *Apis* and *Trigona*, membranous and glabrous; and in *Colletes* (fig. 138), *Halictus* (fig. 136), and *Sphecodes*, absent.

The galeae are extremely variable in the bees. In *Andrena* (fig. 137), *Caupolicana*, *Colletes* (fig. 138), *Hylaeus*, *Nomadopsis*, and *Nomia* the prepupal portions of the galeae are about as long as the postpalpal portions, and the inner surface of each is provided with a ridge or lamella furnished at least basally with a row of stout bristles (inner comb, Cockerell, 1924) resembling the combs of the stipites of some bees. In *Halictus* (fig. 136) and *Sphecodes* the prepupal portions of the galeae taper to basal points and are twice as long as the postpalpal portions. In these bees there are no internal ridges or combs on the galeae, and a small distal part of each is separated from the more basal portion by a constriction at a point of flexibility. In *Protoxaea* the galeae are similar to those of these forms, like them lacking combs, but their bases do not taper so evenly, and their prepupal portions are hardly longer than the postpalpal ones. In the forms listed below

the galeae lack combs, are long with their postpalpal portions at least as long as the stipites (with variations as noted) and the prepalpal portions relatively short. *Ceratina*, *Hesperapis*, *Melecta*, *Nomada*, *Triepeolus*, and *Trigona* have the postpalpal portions of the galeae about as long as the stipites. In *Eriocrocis* and *Xenoglossa* these portions are somewhat longer than the stipites, but not so long as in *Anthophora*, *Apis*, *Bombus*, *Diadasia*, *Emphor*, *Fidelia*, *Hemisia*, *Megachile*, and *Osmia*, in which the postpalpal portions of the galeae are nearly as long as the stipites and cardines together. In *Lithurge* the postpalpal parts of the galeae are about four times as long as the stipites, and in *Euglossa* these parts of the galeae are even longer.

The submentum in *Caupolicana* is a broad, rather weakly sclerotic structure occupying almost the entire space between the cardines, only its posterior margin, which is elevated and flexed distally at either side of the base of the mentum, being heavily sclerotic. In *Colletes* (fig. 145) the submentum, while fundamentally similar, is much smaller. Each of its lateral margins fits into a groove well before the apex of the maxillary cardo. In *Hylaeus* the submentum is a rectangular plate, longer than broad, which meets the cardines at its distal angles. The submentum in *Andrena* (fig. 146) is broadest at its gently emarginate base and closely approaches the cardines only at its basal lateral angles. The mentum is absent in *Hylaeus*; short, curved medially, and roughly parallel-sided in *Andrena*; short, straight, and a little enlarged toward the apex in *Colletes*; and similar but longer in *Caupolicana*.

In *Halictus* and *Sphecodes* the mentum and submentum are absent, but the membrane of the labio-maxillary tube is strengthened by a pair of conjunctival thickenings which arise at the base of the prementum and extend for a short distance upward between the cardines through the posterior membrane of the tube. In *Nomia* and *Protoxaea* the condition is similar except that the entire membrane between the cardines, with the exception of a zone adjacent to the line of attachment to the hypostoma, is slightly sclerotic, that portion close to the base of the prementum more heavily so and suggesting a remnant of the mentum.

The remaining groups of bees (exemplified by the genera *Anthidium*, **Anthophora*, *Apis*, *Bombus*, *Ceratina*, †*Emphor*, †*Euglossa*, *Fidelia*, †*Hemisia*, **Hesperapis*, *Megachile*, *Melecta*, †*Nomada*, *Nomadopsis*, *Osmia*, *Pseudopanurgus*, *Protandrena*, **Triepeolus*, *Trigona*, †*Xenoglossa*, and *Xylocopa*) have the submentum greatly shortened (longest in *Trigona*), and V-shaped, the ends of the "V" being articulated to the apices of the cardines. The "V" is deep and narrow in most, rather broad in *Anthophora*, *Apis*, *Bombus*, and *Trigona*. The mentum is broadest near its distal end and tapers basally. Except in *Apis*, *Bombus*, and *Trigona*, in which it is less than twice as long as broad, the mentum is from three to ten times as long as broad, and in those genera marked by an asterisk (*) is curled basally, somewhat as shown in figure 16. Such curling is feeble in those genera marked by a dagger (†) and is absent in those that are unmarked.

The prementum in bees is relatively uniform in shape and structure. At the apex of its posterior surface it is incised by a pair of emarginations, which, while usually broad and rounded, are deep and V-shaped in *Andrena* (fig. 146) and *Ceratina*, broadly so in *Hesperapis*, and very deeply V-shaped and close together in *Xylocopa* and *Melecta*. In *Apis* they are absent.

The labial palpi are highly variable structures. In *Andrena* (fig. 146), *Caupolicana*, *Colletes* (fig. 145), *Dufourea*, *Halictus* (fig. 143), *Hylaeus*, *Nomia*, *Panurginus*, *Scapter*, and *Sphecodes* the four segments are similar in form and not greatly different in length, although the first segment is the longest, especially in *Panurginus*. In *Hesperapis*, although the first two segments of the palpi are longer than the others, all are more or less cylindrical. The first segment of each palpus in *Protoxaea* is longer than the remainder taken together and unlike them is broadly flattened, especially basally, with its margins furnished with a fringe of setae. In *Nomadopsis*, *Perdita*, *Pseudopanurgus*, etc., the first segment of each labial palpus is much elongated and flattened, usually longer than the three remaining subcylindrical segments together. In the remaining groups of bees the first two segments of the labial palpi are broadened and flattened and rigidly attached

to one another (except in *Trigona* in which they are hinged). Although in *Chelostoma* the third segment is likewise broad and connate with the second so that there is only a single, small, subcylindrical, "free" segment, the other genera listed exhibit two "free" segments, the third as well as the fourth being subcylindrical. In *Anthidium*, *Chelostoma*, *Coelioxys*, *Fidelia*, *Lithurge*, *Megachile*, and *Osmia* the first segment of each labial palpus is shorter than the second, while in *Anthophora*, *Apis*, *Bombus*, *Ceratina*, *Emphor*, *Ericrocis*, *Euglossa*, *Hemisia*, *Melecta*, *Melipona*, *Nomada*, *Oreopasites*, *Triepeolus*, *Trigona*, *Xenoglossa*, and *Xylocopa* the first segment is longer than the second. In *Dioxys* and certain species of *Osmia* the two segments are of equal length.

Certain peculiar features of vestiture of these palpi are worthy of note. Ordinarily they are provided with a few short hairs, but in *Trigona* (in which segments three and four are extraordinarily long, each nearly as long as the second) the second segment of each palpus as well as the galeae of the maxillae is furnished with a few very long hairs, as long as the second labial palpal segment. In *Anthocopa xerophila* (Cockerell) a very few species of *Osmia*, and in *Proterialdes* the first two segments of the labial palpi and the maxillary galeae are covered with numerous hooked hairs, and in a few species of the latter genus these hairs are not merely hooked, but their apical portions are wavy and bent at an angle to the basal portions.

The paraglossae are for the most part very short or moderately short simple structures, but in *Nomada* and *Triepeolus* they are nearly as long as the first segment of the labial palpi. In the former genus they are robust basally but provided with a slender, filamentous apex. In the latter genus they taper gradually to the sharp apex. The genera *Melecta* and *Zacasmia* have similar but longer paraglossae, tapering to pointed apices which in the former genus reach to the apex of the second segment of the labial palpi and in the latter exceed the first segment. In this connection it is interesting that the genera *Anthophora*, *Diadasia*, *Emphor*, *Ericrocis*, *Hemisia*, and *Oreopasites* have short paraglossae, as do also unrelated genera of parasitic bees such as *Dioxys*, *Melissodes*, *Tetralonia*, *Xenoglossa*,

etc., have long hairy paraglossae whose blunt apices reach at least well beyond the apex of the first segment of the labial palpi.

The glossa is short and broadly truncate or bilobed in *Caupolicana*, *Colletes* (fig. 145), *Hylaeus*, and *Scapter*. It is short and acutely pointed in *Andrena* (fig. 146), *Halictus* (fig. 143), and *Sphecodes*, and short but more slender (several times as long as broad) and acutely pointed in *Hesperapis*, *Nomia*, *Panurginus*, and *Protoxaea*. The flabellum is absent in the genera whose glossal structure is described above, as it is also in *Triepeolus*. In most other groups of bees the glossa is linear and provided with a flabellum at its apex.

It is interesting to observe that in certain unrelated genera, such as *Euglossa*, *Glossoperdita*, *Lithurge*, *Melitoma*, etc., the glossa, labial palpi, and galeae have been greatly lengthened, so that in the case of the first-named genus the proboscis is longer than the body.

The form of the flabellum varies greatly. In *Ceratina* it is entire, twice as long as broad, and formed by the expansion of the margins of the groove of the glossa, a condition not observed elsewhere in the bees. In *Xylocopa* (fig. 147) it is entire, bulbous, finely reticulate, with a few short hairs. In *Apis* and *Bombus* it is flattened with setae along the margin. In *Anthidium*, *Megachile*, and *Osmia* it is a flat disk, attached to the end of the glossa proper by one of its surfaces (fig. 144). In *Anthophora* the margin of the flat flabellum is irregularly digitate (fig. 15).

MESOSOMA

The shape of the pronotum is subject to considerable variation in bees, but for the most part it does not seem very significant from the standpoint of the separation of the larger groups. Thus the otherwise similar genera of the Megachilidae have quite differently shaped pronota. The dorso-lateral angles of the pronotum are sometimes produced to form spines, as in *Colletes fulgidus* Swenk. The profile of the dorsum of the pronotum varies greatly in the degree of concavity and in length, as an examination of figures 22 and 148 to 153 will show.

In most bees (e.g., *Andrena*, *Anthidium*, *Anthophora*, *Apis*, *Bombus*, *Ceratina*, *Halictus*,

tus, *Hesperapis*, *Hylaeus*, *Megachile*, *Nomada*, *Nomadopsis*, *Osmia*, *Sphecodes*, *Triepeolus*, and *Trigona*) the lateral portions of the propleura are large, and each is provided with a long marginal apodeme. In *Colletes*, however, the lateral portion of each propleuron is small, and the marginal apodeme is absent, while in *Nomia* and *Xylocopa* the marginal apodeme is very short, although the lateral portion of each propleuron is large.

The proportions of the external parts of the prosternum vary somewhat among the genera. The anterior process is particularly long and slender in *Anthophora*, while the lateral processes are particularly long in *Bombus*. The apophyseal arms are united to form a bridge in *Andrena*, *Anthidium*, *Apis*, *Colletes*, *Halictus*, *Hylaeus*, *Megachile*, *Nomada*, *Nomadopsis*, *Nomia*, *Osmia*, *Sphecodes*, *Triepeolus*, and *Xylocopa*; but in *Anthophora* and *Bombus* the apophyseal arms are separated. In *Ceratina* the inner crests of the prosternal apophyseal arms are very close together and meet at their posterior angles, so that a very short bridge may be present.

The notauli are ordinarily rather short and linear and indeed in *Osmia* are punctiform. At the other extreme, the notauli of *Halictus* and *Sphecodes* are elongate and reach or nearly reach the posterior margin of the mesoscutum. The axillar sutures are present at least toward their median extremities in all bees examined except *Caupolicana* and *Colletes* (fig. 152) in which they are present only laterally. The scutellar crests are ordinarily rather strongly elevated at the sides and reduced mesally. In *Anthidium*, *Halictus*, and *Sphecodes* they are abruptly reduced mesally, and in *Ericrocis* they are absent. It is interesting that in such genera as *Megachile*, *Melecta*, *Nomia*, and *Osmia*, each apparently related to one of the above-listed genera, the scutellar crests are normal. In the genera *Coelioxys*, *Dioxys*, and *Triepeolus* each axilla is produced posteriorly to form a distinct tooth.

As seen in profile, the mesoscutellum varies considerably in shape. It is gently rounded or nearly flat in *Andrena* (fig. 149), *Anthophora* (fig. 22), *Caupolicana*, *Ceratina*, *Colletes* (fig. 152), *Dioxys*, *Dufourea*, *Fidelia*, *Halictus* (fig. 150), *Hesperapis*, *Hylaeus*, *Megachile*, *Nomadopsis*, *Nomia*, *Osmia*, *Protandrena*,

Protoxaea, *Sphecodes*, and *Xylocopa* (fig. 148). In these genera practically its entire surface, except laterally, is horizontal. On the other hand, in *Anthidium* (fig. 153), *Coelioxys*, *Ericrocis*, *Melecta*, and *Stelis* the posterior part of the mesoscutellum is vertical in contrast to the broad horizontal anterior region. In *Ericrocis* and *Melecta* the longitudinal median line of the scutellum is depressed, so that a bilobed condition is produced. In *Anthidiellum* and *Euglossa* the angle between the horizontal and posterior parts of the scutellum is sharp, so that the posterior surface is directed downward and the scutellum is produced as a broad margin over the metanotum and propodeum. In *Apis*, *Bombus*, and some species of *Trigona* the metanotum is likewise overhung, but in this case by the strongly convex, bulging scutellum.

The mesopleura vary considerably in shape, as is shown in the illustrations, but this variation is closely correlated with more easily described variations in the shape of the thorax as a whole, which result in the variations in the size and position of the metanotum described below. The mesopleura, however, do exhibit some other characteristics which contribute much to our knowledge of phylogeny. In the genera *Caupolicana*, *Colletes* (fig. 152), *Euprosopis*, *Euryglossa*, *Halictus* (fig. 150), *Hylaeoides*, *Hylaeus*, *Paracolletes*, *Protandrena*, *Scaptier*, and *Sphecodes* the pre-episternal suture of each side is represented for its entire length by a conspicuous groove, often traversed by small ridges so that it may appear as a series of pits. It extends far below the scrobal suture, often onto the pseudosternal area. *Dufourea*, *Panurginus*, and *Pseudopanurgus* exhibit the same groove feebly. In *Anthophora* (fig. 22), *Ceratina*, *Diadasia*, *Ericrocis*, *Fidelia*, *Neopasites*, *Nomada*, *Nomia*, *Perdita*, *Protoxaea*, *Triepeolus*, and *Xenoglossa* each pre-episternal suture does not extend below the scrobal suture, but its lower end curves backward to meet the latter, while in the genera *Andrena*, *Apis*, *Bombus*, *Euglossa*, *Melecta*, *Trigona*, and *Xylocopa* the two sutures are even more intimately united, a curved or even nearly straight groove extending from the subalar pit to the pleural scrobe. On the other hand, in *Anthidium*, *Chelostoma*, *Coelioxys*, *Hesperapis*, *Lithurge*,

Macropis, *Megachile*, *Nomadopsis*, *Osmia*, and *Stelis* the pre-episternal sutures and at least those portions of the scrobal sutures in front of the episternal scrobes are absent.

The subpleural signum is usually a slightly elevated tubercle or an impressed line, which frequently comes to be turned at right angles to the primitive direction of the subpleural suture in lower Hymenoptera. It is, however, a rather long impressed line in *Hylaeus*, parallel to the long axis of the body.

The anterior face of the mesepisternum is separated from the lateral face by a carina in *Anthidiellum*, *Ashmeadiella*, *Coelioxys*, *Dioxys*, and *Stenosmia*.

In the following genera the metanotum is horizontal or nearly so and from one-third to one-half as long, measured on the longitudinal midline, as the scutellum: *Andrena* (fig. 149), *Caupolicana*, *Ceratina*, *Chelostoma*, *Colletes* (fig. 152), *Dufourea*, *Exomalopsis*, *Fidelia*, *Halictus* (fig. 150), *Hesperapis*, *Hylaeus*, *Macropis*, *Nomadopsis*, *Nomia*, *Panurginus*, *Perdita*, *Protandrena*, *Pseudopanurgus*, and *Sphecodes*. In these genera also, the anterior portion of the propodeum is horizontal. In genera such as *Anthophora* (fig. 22), *Coelioxys*, *Dioxys*, *Ericrocis*, *Megachile*, *Mellecta*, *Osmia*, *Stelis*, and *Xylocopa*, the metanotum slants backward at an angle of about 45 degrees and is about half as long as the scutellum. The propodeum in these genera is nearly vertical in profile, although its basal portion may be a little more nearly horizontal than the rest, as in the case of *Anthophora*. In the parasitic genera *Coelioxys* and *Dioxys* a narrow, subhorizontal basal zone is set off from the remainder of the propodeum by a carina. *Dioxys* is peculiar in possessing a strong, median, metanotal tooth. In *Anthidium*, *Apis*, *Bombus*, *Euglossa*, and *Trigona* the metanotum and propodeum are vertical, the former very much shorter than the scutellum.

The pleural areas of the metepisterna, being correlated with the middle coxae in development, will be discussed in connection with those coxae.

The area between the mesothoracic and metathoracic sternal apophyseal pits and between the middle and rear coxae varies greatly in shape, being sometimes, as in *Apis*, several times as long as broad, with the

middle coxae nearly as close together as the posterior ones, but usually as broad as, or broader than, long, with the middle coxae much farther apart than the posterior ones. The posterior margin of the metapseudosternum between the posterior coxal condyles may be straight, rounded, or sharply angulate (figs. 160 to 164).

The intercoxal lamellae in some forms, such as *Andrena*, *Anthophora*, *Apis*, *Colletes*, *Hylaeus*, *Nomada*, *Nomia*, *Triepeolus*, and *Xylocopa*, are slightly broadened above, while in *Bombus*, *Halictus*, etc., they are very little broadened above. In *Ceratina* these lamellae are small, while in *Halictus* they are large.

The dorsal process of each free distal portion of the metafurcal arm is long and directed outward in *Andrena* and *Anthophora* (fig. 31); as long as in *Anthophora* but twice as broad in *Megachile*, *Osmia*, and *Xylocopa*; practically absent in *Anthidium* and *Ceratina*; and very small in *Apis*. In *Halictus* it is shorter than in *Anthophora*, more lateral in position, and remarkable for its heavy sclerotization and black pigment. In *Nomia*, in which it occupies a similar position, the process has the usual pale coloration.

The anterior coxae are each furnished with a large apical process or "spine" mesad of the articulation of the trochanter in *Xylocopa* and in males of some species of *Colletes*, *Megachile*, and *Nomada*. In the genera *Epeolus* and *Triepeolus* the anterior coxae, instead of having the usual tapering form, are quadrate, with the trochanters arising from their outer distal angles. In *Protoxaea* each anterior coxa is greatly produced laterally so that the coxae are about two and one-half times as broad as long, while in *Ceratina* and *Xylocopa*, excepting the coxal spine of the latter, they are about twice as broad as long.

The middle coxae vary markedly in size. In *Andrena* they are short, less than half as long as the distance from their summits to the posterior wing bases (fig. 149). The pleural areas of the metepisterna are gradually narrowed toward their lower ends to points just above the summits of the middle coxae, and they each have two pits, the upper one of which is well above the middle of the area. In *Caupolicana*, *Colletes*, *Halictus*, *Hylaeus*, *Nomia*, *Protandrena*, *Protoxaea*, and *Sphecodes* the coxae, while actually rather

elongate, appear similarly short, since their upper portions are covered by the pleura, each upper mesocoxal articulation being hidden far up within the thorax (fig. 158). A condition intermediate between that of *Andrena* and that of the other above-mentioned genera is found in *Hesperapis*, *Panurginus*, *Perdita*, and *Pseudopanurgus*, in which the exposed parts of the coxae are short and only a small portion of each coxa is hidden. As in other genera, the position of the upper mesocoxal articulations may be determined from the outside; they are immediately beneath the lower metapleural pits. Therefore, one may determine without dissection the length of the middle coxae. In all the above-mentioned genera the upper metapleural pits are well above the midpoints of the pleural areas of the metepisterna. Except for *Colletes*, in which these areas are nearly parallel-sided, they are narrowest at the level of the lower metapleural pits. In bees such as †*Anthidium* (fig. 153), **Anthophora* (fig. 22), **Apis*, **Bombus* (fig. 151), **Ceratina*, **Euglossa*, †*Fidelia*, **Hemisia*, **Megachile*, **Melecta*, †*Nomada*, †*Osmia*, †*Stelis*, **Triepeolus*, **Trigona*, and †*Xylocopa* (fig. 148) the middle coxae are as long as, or nearly as long as, the distances from their summits to the hind wing bases, and their summits are but slightly concealed. *Nomadopsis*† is similar with respect to the length of the coxae, but they are more concealed so that they appear intermediate between the *Hesperapis*-*Panurginus* type and the *Anthidium*-*Anthophora* type. The genera marked with an asterisk (*) have the upper metapleural pits well below the middle of the pleural areas of the metepisterna, while those marked with a dagger (†) have the pits at or near the middle. In the parasitic genera *Coelioxys*, *Dioxys*, and *Neopasites* the middle coxae are shorter than in the *Anthidium*-*Anthophora* group, and their upper parts are not covered by the pleura.

The middle and hind tibial spurs are variable in length and curvature but are almost always biserrate or bipectinate, as already described for *Anthophora*. The middle tibial spurs are absent in certain groups of the genus *Megachile*, while the rear tibial spurs are absent in *Apis*, *Melipona*, and *Trigona*. In the females of *Halictus* the inner margin of each inner hind tibial spur has larger teeth than

the outer margin or either margin of the outer spur. These large teeth are in some species very elongate and may be reduced to two or three in number. The middle tibial spurs are bifurcate at their apices in *Ericrocis*.

A basitibial plate is present on each posterior tibia of the following bees: *Andrena*, *Anthophora*, *Diadasia*, *Dufourea*, *Halictus*, *Hemisia*, *Hesperapis*, *Macropis*, *Nomadopsis*, *Nomia*, *Paracolletes*, *Perdita*, *Protandrena*, *Protoxaea*, and *Pseudopanurgus*. In males of many of these genera it is absent or smaller and more feebly defined than in the females. In the female of *Protoxaea* the apices of the rear femora are flattened to form plates supplementary to the basitibial plates. The basitibial plate is absent in both sexes of *Anthidium*, *Apis*, *Bombus*, *Caupolicana*, *Ceratina*, *Coelioxys*, *Colletes*, *Dioxys*, *Ericrocis*, *Euglossa*, *Fidelia*, *Hylaeus*, *Megachile*, *Melecta*, *Nomada*, *Osmia*, *Sphecodes*, *Stelis*, *Triepeolus*, *Trigona*, and *Xylocopa*. In *Ceratina* and *Xylocopa* the outer surface of each posterior tibia is furnished with an apically directed, scale-like projection, especially large in the females.

Small tubercles or tibial spiculi on the outer surfaces of at least the posterior, usually the middle, and sometimes the fore tibiae are found in the parasitic genera *Melecta*, *Neopasites*, *Nomada*, *Oreopasites*, *Triepeolus*, and *Zacasmia*. Each of these spiculi usually bears a short heavy seta. In most females of *Nomada*, also, each rear tibia bears a row of a few stiff setae on its outer surface at the apex. In *Ceratina*, especially the females, small tibial spiculi occur on the rear legs and serve as bases for the hairs of the scopa. In *Lithurge* the females are provided with very large, nonsetiferous spiculi which on the fore and middle tibiae are chiefly arranged in two longitudinal rows and are on these legs directed strongly backward. The males lack such spiculi.

The basitarsi of bees are subject to much variation. In *Xylocopa* they are all longer than the corresponding tibiae, but in the great majority of bees all, or at least the posterior, basitarsi are shorter than the tibiae. In the females of *Apis*, *Bombus*, and *Euglossa* the basitarsi are broad basally, and since they are attached at their anterior basal angles to the anterior distal angles of the

broadened tibiae, the posterior portions of their bases are apposable against the apices of the tibiae. In females of *Anthophora* (fig. 46), *Hemisia*, *Diadasia*, and *Xenoglossa* each posterior basitarsus is produced beyond the base of the second tarsal segment to form a distinct distal process. The second tarsal segment of each rear leg in the females of *Andrena*, *Nomadopsis*, *Nomia*, *Panurginus*, and *Protandrena*, arises slightly before the apex of the basitarsus so that there is a small distal process of the basitarsus.

Since it is usually on the posterior legs, the pollen collecting scopa of nonparasitic female bees is discussed at this point. In *Andrena*, *Caupolicana*, *Colletes*, *Dufourea*, *Halictus*, *Nomia*, *Protoxaea*, and *Scaptier*, pollen collecting hairs are found on the trochanters, femora, tibiae, and basitarsi. In many species of *Nomia* and *Halictus* the long hairs of the abdominal sterna also serve to entangle many pollen grains, and in *Protoxaea* a large tuft of hairs on the third abdominal sternum serves this purpose. In *Anthophora*, *Ceratina*, *Diadasia*, *Hemisia*, *Hesperapis*, *Macropis*, *Xenoglossa*, and *Xylocopa* the scopa is on the outer surfaces of the posterior tibiae and basitarsi. In *Nomadopsis*, *Panurginus*, *Perdita*, *Protandrena*, and *Pseudopanurgus* it is primarily confined to the posterior tibiae.

In *Fidelia* a scopa is found on the outer surfaces of the posterior tibiae and basitarsi and, in addition, on the abdominal sterna. The long straight hairs of the sterna resemble the sternal scopal hairs of *Megachile*, except that they are finer and bear a very few short branches or oblique teeth on their basal parts and are finely wavy apically.

In *Apis*, *Bombus*, *Euglossa*, *Melipona*, and *Trigona* the pollen is collected in corbiculae which consist of large, smooth, glabrous areas on the outer surfaces of the posterior tibiae. Each of these areas is surrounded by a row of very long hairs which are curved inward over the margins of the smooth areas and serve to hold the mass of pollen carried by each posterior leg. In these bees, also (except in *Trigona* subgenus *Lestrimelitta*), the females are provided with a comb of short, stiff setae along the inner distal margin of each posterior tibia.

The arolia are present and well developed in *Andrena* (fig. 173), *Anthophora* (fig. 47), *Apis*, *Bombus*, *Caupolicana*, *Ceratina*, *Col-*

letes, *Dufourea*, *Exomalopsis*, *Fidelia*, *Halictus* (fig. 174), *Hesperapis*, *Hylaeus*, *Macropis*, *Neopasites*, *Nomia*, *Nomada*, *Nomadopsis*, *Osmia*, *Perdita*, *Protandrena*, and *Sphecodes*. In *Melecta*, *Triepeolus*, and *Xenoglossa* they are of the usual length but slender, and in *Protepeolus* they are unusually long and slender except for the enlarged apices. On the other hand, in *Anthidium*, *Coelioxys*, *Euglossa*, *Hemisia*, *Megachile*, *Protoxaea*, *Stelis*, and *Zacosmia*, the arolia are reduced or absent. The same is true of the female of *Lithurge*, although the male exhibits small arolia.

The tarsal claws are usually cleft, or at least with an inner tooth somewhat shorter than the outer, but in females of *Chelostoma*, *Megachile*, *Melipona*, *Osmia*, and *Trigona* they are simple, and in *Ericrocis*, *Melecta*, and *Zacosmia* the inner tooth is flat, lobe-like, and basal. Males of a few species of *Megachile* (e.g., *M. fidelis* Cresson) have a small basal tooth on each claw in addition to the usual cleft apex.

The wings of bees exhibit many interesting characters of phylogenetic importance. Lutz (1924) has given an interesting discussion of the comparative anatomy of the wing venation of bees, while Cockerell and Robbins (1910) have figured the wings of a number of genera of bees. The pterostigmata are large, with the posterior (as contrasted with costal) margin of each conspicuously convex and the width ordinarily much greater than that of the prestigma in *Andrena* (fig. 169), *Ceratina*, *Dufourea*, *Exomalopsis*, *Halictus*, *Hylaeus*, *Macropis*, *Nomada*, *Panurginus*, *Perdita*, *Protandrena*, *Pseudopanurgus*, *Scaptier*, *Sphecodes*, *Stenosmia*, and *Trigona*. In contrast to this condition the genera *Anthidium* (fig. 167), *Anthophora*, *Apis*, *Bombus*, *Coelioxys*, *Diadasia*, *Dioxys*, *Ericrocis*, *Euglossa*, *Fidelia*, *Megachile*, *Melecta*, *Melitoma*, *Neopasites*, *Osmia*, *Triepeolus*, *Xenoglossa*, and *Xylocopa* (fig. 166) have the pterostigmata small, the posterior margins each angulate at the base of vein r but otherwise not, or not much, convex. Genera falling between these two conditions are *Colletes* (fig. 168), *Hesperapis*, *Melipona*, *Nomadopsis*, *Nomia*, and *Oreopasites*. In *Caupolicana* the stigma is linear, quite long, its margin not convex, and in *Hemisia* and *Protoxaea* the stigma is nearly absent.

The marginal cell of each forewing is ordinarily considerably longer than the distance from its apex to the tip of the wing, and the distal end of the marginal cell is usually rounded or pointed and slightly bent away from the wing margin. In *Andrena*, *Hesperapis*, and *Nomada* the marginal cell is not bent away from the wing margin. In *Exomalopsis*, *Neopasites*, *Nomadopsis*, **Panurginus*, **Protandrena*, **Pseudopanurgus*, and *Triepeolus*, the marginal cell is about as long as the distance from its apex to the wing tip, and the apex of the cell is rounded or, in those genera marked by an asterisk (*), truncated. In *Anthophora* (fig. 35), *Fidelia*, *Hemisia*, *Melecta*, *Oreopasites*, *Perdita*, and *Zacoscma* the marginal cell is short, its apex broad, often rounded. The marginal cell in *Neolarra* is exceedingly short, smaller than the pterostigma. In *Melipona* and *Trigona* the marginal cell is open distally. The number of submarginal cells varies from two to three, or rarely, as in *Neolarra* subgenus *Phileremulus*, to one. When there is but one cell, vein second m-cu is absent.

Ordinarily the hairs of the wings are longer and farther apart basally than distally, and when the parts of the wings are glabrous, they are often the basal parts. The wings are hairy throughout or nearly so in *Andrena*, **Anthidium*, *Apis*, **Bombus*, **Caupolicana*, *Ceratina*, *Coelioxys*, **Diadasia*, *Dioxys*, *Dufourea*, **Emphor*, **Euglossa*, *Exomalopsis*, *Halictus*, *Hesperapis*, *Hylaeus*, **Megachile*, *Neopasites*, *Nomada*, *Nomadopsis*, *Nomia*, *Oreopasites*, **Osmia*, *Panurginus*, *Perdita ruficauda* Cockerell (but not certain other species of the genus), *Protandrena*, *Pseudopanurgus*, *Sphecodes*, *Stelis*, **Triepeolus*, *Trigona*, and **Xenoglossa*. On the other hand, **Anthophora*, **Ericrocis*, **Fidelia*, **Hemisia*, **Melecta*, and **Zacoscma* have the wings nearly bare, and **Protoxaea* has only a few large patches of hairs in the basal parts of the wings. **Xylocopa* has the basal two-thirds of the wings hairy. The genera marked with an asterisk (*) have large alar papillae, whereas those which are unmarked lack, or have only small, papillae.

In the posterior wings, vein cu-v is ordinarily transverse and far shorter than the second abscissa of vein M+Cu, which is about as long as vein M (not counting the

usually evanescent apical spur of the latter vein). In view of the relationships as ordinarily understood, it is interesting that *Andrena* (fig. 169), *Exomalopsis*, *Fidelia*, *Nomada*, *Nomadopsis*, *Oreopasites*, *Protandrena*, and *Triepeolus*, have the usual venation with respect to this character or only a slight modification of the usual condition. Although in *Xenoglossa* vein cu-v slants somewhat and is, therefore, rather elongate, this genus falls best in the group listed above, the second abscissa of M+Cu being about as long as M. Conversely in the genera **Anthophora* (fig. 35), **Diadasia*, *Emphor*, *†Ericrocis*, **Hemisia*, *†Melecta*, *Melipona*, and *†Zacoscma* the second abscissa of M+Cu is considerably shorter than M. In those genera whose names are unmarked, the second abscissa of M+Cu is longer than cu-v, in those marked by an asterisk (*) the second abscissa of M+Cu equals cu-v, while in those marked by a dagger (†) the second abscissa of M+Cu is exceedingly short, markedly shorter than cu-v.

The jugal lobe of each posterior wing is short, the jugal incision being nearer to the base of the wing than to the vannal incision in **Anthidium* (fig. 167), *Anthophora* (fig. 35), **Ceratina*, **Chelostoma*, *Hesperapis*, **Megachile*, *Melecta*, *Neopasites*, *Nomada*, *Oreopasites*, **Osmia*, **Stelis*, *Triepeolus*, and *Xylocopa* (fig. 166). In those genera whose names are marked by an asterisk (*) the lobe is rather slender and narrowly rounded apically. In contrast to the preceding list of genera, the following forms have large jugal lobes, the jugal incision of each wing being much nearer to the vannal incision than to the base of the wing: *Andrena* (fig. 169), *Apis* (jugal incision minute), *Caupolicana*, *Colletes* (fig. 168), *Dufourea*, *Halictus* (fig. 170), *Hylaeus*, *Lithurge*, *Nomia*, *Perdita*, *Protandrena*, *Protoxaea*, *Pseudopanurgus*, *Scapter*, *Sphecodes*. The genera *Diadasia*, *Emphor*, *Exomalopsis*, *Fidelia*, *Hemisia*, *Macropis*, *Melipona*, *Melitoma*, *Nomadopsis*, and *Xenoglossa* exhibit a condition intermediate between those described for the above two groups. In *Bombus* (fig. 165) and *Euglossa* the jugal lobe is absent, probably having been reduced by the process, seen far advanced in *Apis*, of narrowing of the posterior wing bases.

METASOMA

The second abdominal tergum varies considerably in the shape of its profile, being gently convex in *Ceratina* and *Nomada*, but usually with anterior and dorsal faces separated by broadly rounded angles. In those genera in which the metanotum is vertical the anterior face is usually considerably longer than the dorsal face (fig. 51), while in those genera in which the metanotum is horizontal, the anterior face is usually not longer than the dorsal face (fig. 177).

The tergal graduli (or at least the gradulus of the third tergum) are commonly directed at their ends toward the spiracles or, especially on the posterior terga, toward points behind the spiracles. Such is the case in *Andrena* (fig. 180), *Anthidium* (fig. 179), *Apis* (tergal graduli largely absent), *Bombus* (fig. 178), *Ceratina*, *Colletes* (fig. 182), *Halictus* (fig. 181), *Hemisia*, *Hesperapis*, *Hylaeus*, *Megachile*, *Melecta*, *Nomada*, *Nomia*, *Osmia*, *Sphecodes*, *Triepeolus*, and *Xylocopa* (fig. 183). In *Anthophora* (fig. 54), *Diadasia*, *Protoxaea*, and *Xenoglossa* the graduli are bent strongly to the rear and pass above and behind the spiracles.

The apodemes of the third tergum are frequently small or absent, and in such cases there is often an angular basal lobe on each side below the point of attachment of the muscles which are usually inserted on the apodeme. The terga behind the third, in such cases, have progressively more obtuse and less conspicuous angles below the apodemes. Genera provided with such angles are †*Anthidium* (fig. 179), †*Colletes* (fig. 182), †*Halictus* (fig. 181), †*Hesperapis*, †*Hylaeus*, †*Megachile*, †*Nomada*, *Nomia*, *Osmia*, *Sphecodes*, †*Triepeolus*, and **Xylocopa* (fig. 183). Genera lacking such angles are †*Andrena*, **Anthophora* (fig. 54), **Apis*, **Bombus* (fig. 178), and *Trigona*. In these lists those genera whose names are marked by an asterisk (*) have a long slender dorsal process of each sternal apodeme on at least certain segments, while those marked by a dagger (†) lack such processes. The genera *Ceratina*, *Megachile*, and *Nomia* have small dorsal processes on certain segments.

The following genera have evident pygidial plates: *Andrena*, *Anthophora*, *Caupolicana* (female only), *Diadasia*, *Dufourea*, *Euryglos-*

sa, **Halictus*, *Hesperapis*, *Melecta*, *Neopasites*, **Nomada*, *Nomia* (female only), *Nomadopsis*, *Panurginus*, *Perdita*, *Paracolletes*, *Protandrena*, *Protoxaea*, *Pseudopanurgus*, *Sphecodes*, **Triepeolus*, *Xenoglossa*, and *Zacasmia*. The genera *Anthidium*, *Apis*, *Bombus*, *Colletes*, *Ericrocis*, *Euglossa*, *Hylaeus*, *Megachile*, *Osmia*, *Stelis*, and *Trigona*, on the other hand, lack pygidial plates. A flat-topped apical process, perhaps representing a pygidial plate, is found on the seventh tergum of females of *Lithurge* and *Xylocopa*, and in the male of *Lithurge* the comparable process of the eighth tergum is expanded into a broad pygidial plate. Females of *Ceratina* have an acutely pointed process on the apex of the seventh tergum. Most other apygidialate bees have the morphological posterior margin of the seventh (female) or eighth (male) tergum rounded. Pseudopygidial areas are found in the females of the genera marked by an asterisk (*) above. Females of all nonparasitic genera having pygidial plates have also prepygidial fimbriae.

The stings of parasitic bees such as *Coelioxys*, *Ericrocis*, *Melecta*, and *Triepeolus* are very long and heavy. In *Dioxys*, however, the sting is greatly reduced. In the long-stinging parasitic groups the seventh sternum of the female is either prolonged to form a guide for the sting or is invaginated, except for a pair of apical processes provided with hooked setae. The seventh tergum is invaginated and hidden in females of *Halictus*, *Neopasites*, *Triepeolus*, etc.

The exceedingly variable eighth and ninth sterna of male bees, except for *Apis* in which the latter (or a subdivision of the former) lies immediately behind the former, are telescoped so that the ninth is situated above the eighth. In *Trigona* the ninth sternum is reduced to a very inconspicuous band, while the eighth has the form and presumably the function of the ninth of other bees. Snodgrass (1941) failed to note this and labeled the eighth as the ninth. In males of *Chelostomoides* all the sterna beyond the fourth are invaginated and more or less modified. A fewer number of sterna are similarly invaginated in *Megachile*, *Osmia*, etc.

The male genitalia are subject to great variation, and, as in the case of the eighth and ninth sterna of the male, it is difficult to

make generalizations concerning them. Hagens (1874), Saunders (1882, 1884, and 1884a), Strohl (1908), and Beck (1933) have described and figured the genitalia of many different genera of bees. Fusion of the gonostyli with the gonocoxites is very frequent. In *Megachile*, *Neopasites*, and *Osmia* the penis valves are united throughout their lengths, or nearly so, by the membranous penis, while in *Andrena* they are fused well beyond the bases and hence are not movable with respect

to one another. Volsellae are distinct in *Andrena*, *Colletes*, *Dufourea*, *Ericrocis*, *Halicetus*, *Hemisia*, *Hesperapis*, *Hylaeus*, *Macropis*, *Melecta*, *Nomada*, *Nomia*, *Perdita*, and *Sphecodes*, but are absent as separate sclerites in *Anthidium*, *Anthophora*, *Apis*, *Bombus*, *Ceratina*, *Megachile*, *Osmia*, *Triepeolus*, *Trigona*, and *Xylocopa*. In *Apis*, but in no other groups examined, the claspers are much reduced and their grasping function apparently is taken over by the complicated eversible penis.

ORIGIN AND FUNCTIONAL SIGNIFICANCE OF CERTAIN CHARACTERS

It would be hopeless to attempt to consider all the differences among genera and to suggest possible reasons for their existence. However, an examination of some of the variable morphological features whose functional significance we best understand may reveal how some of the differences arose. Because we can be more certain of the functional significance of various structures where parallel or convergent evolution has taken place, a large part of the following discussion will deal with cases where different bees have become adapted to similar environmental conditions by similar or different morphological changes. Additional examples of such evolution have been pointed out by Popov (1939), and others are indicated in the section on phylogeny.

PARALLEL DEVELOPMENT AND FUNCTION OF CERTAIN CHARACTERS

We have already observed that the great majority of the specializations of *Anthophora*, as compared to primitive Hymenoptera, involve modifications of the apparatus for food collection and of the mechanism of flight. Among the bees the various later steps in these lines of modification are preserved, so that, for example, while certain bees have mouthparts closely resembling those of sphecoid wasps, others have greatly elongated proboscides. In the various groups of bees, as will be shown in greater detail later, the elongation has taken place in different degrees and in different ways.

One can imagine that flowers with deep tubular corollas arose at the same time as certain bees or other insects with long mouthparts for sucking nectar from such flowers.

Once a flora of deep-flowered plants existed, various groups of anthophilous insects with short mouthparts might, from time to time, evolve species or genera with long proboscides, perhaps especially if competition on the shallow flowers were intense.

By some such process long mouthparts have arisen in many groups of bees by entirely different modifications. Thus in the subgenus *Iomelissa* of the genus *Andrena*, whose other species are provided with short proboscides, the glossa and labial palpi are elongated. Males of the Australian colletid genera *Meroglossa* and *Palaeorhiza* have the glossa acute rather than short and bilobed as in other members of the Colletidae. In the halictids elongation of the proboscis is achieved by the lengthened cardines and prementum, the glossa ordinarily remaining short. In the halictid genera *Sphecodosoma*, *Nesohalictus*, and *Oxyhalictus*, and in certain species of *Patellapis* (according to Cockerell, 1937) and of *Dufourea*, the glossa is itself greatly elongated. This additional lengthening of the proboscis, beyond that usual to the Halictidae, has occurred independently in the above-mentioned genera. The majority of bees with long mouthparts, unlike the halictids, retain the short cardines and prementum of *Andrena* and the colletids, but have the glossa, galeae, and the first two segments of the labial palpi elongate. Many intermediate stages between the short mouthparts of *Andrena* and the long ones of the typical long-tongued bees are found in the panurgines, in which group only the first segment of each labial palpus is commonly elongate. In this group, also, we find many cases of independent elongation of the glossa and labial

palpi in unrelated genera. Thus *Glossoperdita*, a subgenus of *Perdita*, and *Claremontiella*, a subgenus of *Nomadopsis*, have somewhat similarly elongate probosces. The proboscis reaches its greatest length among such bees as *Euglossa* and *Melitoma*, which are not closely related to each other according to the classification presented in part 3.

An interesting case of convergent evolution is found in bees which are regular visitors of the flowers of *Cryptantha*. In this genus of plants the short stamens are concealed within the small, tubular corolla. In three different genera of Megachilidae (e.g., *Proteriadodes*) the proboscis is, as already described, reduced in length and provided with many hooked bristles, which probably serve to pull the pollen out of the corolla tube. In *Andrena osmioides* Cockerell and an undescribed species of the same genus, both of which are oligolectic on *Cryptantha*, numerous erect hooked setae on the outer surfaces of the galeae and on the distal third of the posterior surface of the prementum no doubt serve the same purpose. The subgenus *Verbenapis* of the genus *Calliopsis* (Panurginae) achieves the same end, pulling the pollen from the slender tubular flowers of *Verbena*, by means of curved bristles on the anterior tarsi.

The maxillary palpi presumably take little part in the feeding process of bees and have been reduced both in length and in number of segments repeatedly and independently among most of the larger families of bees; indeed they are entirely absent in *Oxaea*.

The pollen collecting structures of those bees which, on the basis of other characters, are most primitive (Colletinae, Andreninae, etc.) are the elongated and commonly plumose hairs of the posterior trochanters, femora, tibiae, and basitarsi. Many halictids and oxaeines have, in addition, pollen collecting hairs on the basal abdominal sterna. In the more highly specialized groups of bees certain areas are more profoundly modified for the purpose of carrying pollen, while the remaining parts cease to possess specialized scopal hairs. Thus in the anthophorids, among others, the scopa is restricted to the posterior tibiae and basitarsi, and in the megachilids it is confined to the abdominal sterna. The greatest specialization for pollen carrying found in the bees is seen in the

Panurginae, which, with the exception of the genus *Panurgus*, carry pollen in damp, compact masses, one attached to the outer surface of each posterior tibia by a few long scopal hairs, and in the Apinae, which carry pollen in similar masses in the corbiculae.

As with the mouthparts, the scopa has undergone considerable parallel development. Thus in the halictid genus *Sphecodogastra*, in the anthophorine genus *Anthedonia*, and in certain species of the subgenus *Diandrena* of the genus *Andrena*, the scopa consists of simple stiff bristles which are used in collecting the pollen of certain Onagraceae. The pollen grains of these plants are held together by fine, cobweb-like strands, making them difficult for most bees to collect. We have, thus, a case where different types of bees are similarly adapted to oligolecty on a certain group of plants. There are, however, many cases where structural peculiarities of a genus of bees seem to have limited the types of plants from which it sucks nectar or collects pollen. For example, the genus *Diadasia* in the Anthophorinae is remarkable for the coarseness of the plumosity of its scopal hairs; the branches of the hairs are long and far apart. This condition is correlated with the collection of coarse pollens. Most of the species are oligolectic upon species of Cactaceae or Malvaceae, unrelated families of plants having unusually coarse pollen.

The flight mechanism, as we have already seen, is one of the systems of structures most greatly modified in *Anthophora* as compared with the *Chalastogastra*. Unlike the organs of pollen collecting or of ingestion in which very extensive evolution has occurred within the bees, the greater part of the modification of the flight mechanism must have taken place before the bees arose. However, it is possible to note some modifications among bees. Thus in the colletids, andrenids, and in certain megachilids (e.g., *Chelostoma*), anthophorines (e.g., *Exomalopsis*), and xylocopines (e.g., *Ceratina*) the mesosoma is elongate, whereas in most Apidae and Megachilidae it is more nearly spherical, the metanotum being shortened and declivous and the propodeum entirely declivous. It is evident that the formation of an efficient, spherical mesosoma, whose optimum characteristics have been discussed in the section on *Anthophora* mor-

phology, has occurred independently in the Megachilidae and the Apidae, possibly more than once within the latter family.

Reduction of wing venation may be seen in minute bees of several unrelated genera. Thus in *Trigona* (Apinae), *Perdita* (Panurginae), *Neolarra* and *Parammobatodes* (Anthophorinae), and in certain Euryglossinae the distal veins, particularly of the forewings, are absent. There can be no doubt that this condition has arisen independently in the genera mentioned. It seems likely that throughout the Hymenoptera there has been a series of mutations resulting in the reduction of wing venation. Beyond a certain point in moderate-sized and large forms such reduction may be a disadvantage, perhaps leaving the wings too fragile; but when in minute bees the size of the wing as a whole is greatly reduced, such mutations might become established.

The reduction of the vannal lobe of the posterior wings has occurred independently in various groups of bees, for example, the Megachilidae (as shown by the large lobe in *Lithurge*), the parasitic Anthophorinae (as shown by the larger lobes in the pollen collecting groups), the Apinae, and the Xylocopinae.

Another series of characters which shows reduction in several different groups of bees is probably associated with nest building. Bees that nest in unlined burrows in the soil are ordinarily provided, at least in the female, with basitibial plates, a pygidial plate, and a prepygidial fimbria. Parasitic bees belonging to these same groups usually lack the fimbria and the basitibial plates but retain the pygidial plate. However, the Colletinae, which live in burrows lined with a smooth secretion, the Hylaeinae, Megachilinae, and Xylocopinae, which live in holes in wood, and the social bees (Apinae) have independently lost this series of three structures.

STRUCTURAL PECULIARITIES OF PARASITIC BEES

A study of the various so-called parasitic bees, whose larvae feed on the honey and pollen stored by other species, provides much data of entomological interest. If the classification presented below is correct, parasitic forms have arisen independently many times

in the evolution of the bees. As examples we may cite *Psithyrus*, a parasitic genus closely allied to *Bombus*; *Sphecodes* and *Echthralictus*, relatives of *Halictus*; *Exaerete*, allied to *Euglossa*; *Coelioxys* in the Megachilini; *Stelis* in the Anthidiini; and the numerous groups of parasitic genera in the Anthophorinae. Even among the Anthophorinae, several distinct lines of evolution, each beginning with nonparasitic forms, are evident. Certain other parasitic genera (e.g., *Psithyrus* and *Sphecodes*) are probably comparatively recent segregates from their nonparasitic relatives, which they resemble closely in structure and upon which they are, in general, parasitic. Other parasitic groups such as *Nomada* differ widely from any pollen collecting bees; indeed it is probable that the nonparasitic forms from which they arose are no longer in existence. The Nomadini, then, as compared with *Psithyrus* and *Sphecodes*, is an ancient group, profoundly adapted structurally to parasitic life and not confined to any particular genus or family of host bees.

Among the parasitic genera of bees there has been considerable convergent evolution. For example, the pollen collecting scopa is absent in all of them. It is interesting to consider why there are so few bees which retain at least a reduced scopa, yet have adopted parasitic habits and collect no pollen. Through the animal kingdom there are many examples of structures which, although apparently rendered useless by the changed habits of the organism, are nevertheless retained, at least in a reduced form. Other structures, however, such as the scopa and basitibial plates of bees, are apparently lost as soon as their function is eliminated by modification of the habits of the organism. Or perhaps the elimination of these structures resulted in the changed bionomics. The basitibial plates are said by Rayment (1935) to be used in supporting bees in their burrows in the soil; they are found in the females and in many males of all the nonparasitic pygidialate bees. Among the parasitic genera, however, the plate is completely absent in both sexes. It probably serves no more useful function in the males of the nonparasitic forms than in the parasitic genera, yet it is commonly present in the former. The combs of the stipites appear to be always absent in

parasitic bees. Perhaps they are used in handling pollen by the nest building forms. Females of nonparasitic bees having a pygidial area exhibit, with very few exceptions, a prepygidial fimbria. Parasitic bees have no such fimbria, or it is reduced, as in *Melecta*, to a few hairs but little longer than those of the posterior margins of the preceding abdominal terga. The pygidial plate itself has a tendency to disappear in parasitic genera (e.g., *Ericrocis* and *Oreopasites*), but is much more persistent than the prepygidial fimbria.

It is noteworthy that all the parasitic Anthophorinae, regardless of the degree of specialization of other structures, have the jugal lobe of the posterior wing greatly reduced. This is probably a specialization that has taken place independently in the various groups involved. Furthermore, there are several examples among parasitic bees of genera in which the middle coxae have become shortened. Thus *Dioxys* (Megachilidae) and *Neopasites* (Apidae), although belonging to groups whose middle coxae are ordinarily long, have these segments shortened. It may be that the elongate coxae are in some way related to the habits of the pollen collecting and nest building bees.

Not all the parallel developments of the parasitic bees, however, involve reduction or loss of parts. Thus in the females of several parasitic groups (e.g., *Coelioxys* in the Megachilinae, *Exaerete* in the Apinae, and many of the parasitic Anthophorinae) the distal abdominal terga and especially sterna are elongated and provided with very large apodemes forming a slender and probably rather mobile apex to the abdomen. The seventh tergum is sometimes drawn out to form an open tube which serves as a guide for the sting, sometimes concealed except for a pair of apical processes, which are commonly furnished with strong bristles. This latter condition reaches its extreme in *Triepeolus* in which the apical processes are far longer than the greatest breadth of the seventh sternum, whose disk is reduced to a mere transverse bar. The sting in parasitic bees is usually long and powerful, although that of *Dioxys* is much reduced. These adaptations are undoubtedly associated with the parasitic habit; they may have to do with the place-

ment of the eggs, warding off of attacks of the host, or with both.

The parasitic bees belonging to genera which apparently diverged from their pollen collecting ancestors long ago are in many cases characterized by the thick and strong integument provided with large, deep punctures. A sharp carina often marks the angle between the anterior and lateral faces of each mesepisternum, and transverse grooves are often impressed in the abdominal segments as in *Coelioxys* and *Neopasites*. Spines or processes are often present on the posterior part of the thorax (on the axillae in *Coelioxys*, *Epeolus*, etc., on the metanotum in *Dioxys*, and on the scutellum in *Melecta*). All these characteristics may serve to render the insects more or less safe from the attacks of their hosts. It is worthy of note that a few nonparasitic genera (e.g., *Heriades* and *Anthidiellum*) exhibit certain features such as coarse punctation and an abundance of carinae and grooves characteristic of many parasitic genera.

The majority of the parasitic bees, except for those such as *Psithyrus* and *Exaerete* which are closely related to their hosts and resemble them in appearance, are remarkable for their resemblance to wasps. They are usually more elongate than pollen collecting bees, an aspect heightened by the absence of a scopa, and they are usually black with the abdomen red or black with yellow or white abdominal bands. This wasp-like aspect is a result of the elongation of the abdomen already referred to, combined with the coloration, which is often not greatly different from that of at least certain species in the pollen collecting groups from which the parasitic forms arose.

APPARENTLY NON-SELECTIVE CHARACTERS

We have discussed structures whose functions are well known, or evident from their appearance, or at least subject to conjecture. We turn now to a series of characteristics that seem to have no functional significance. Certain characters appear in nearly identical form in several unrelated species, yet because of their frequent absence in species closely related to forms possessing them, they probably have little functional significance. As an

example, the anterior coxae in certain species, but not in others, of four unrelated genera, namely, *Colletes*, *Megachile*, *Nomada*, and *Xylocopa*, are similar in that each bears a large distal spine directed posteriorly and arising mesad from the base of the trochanter. Since it usually has been supposed that natural selection would eliminate useless structures, the origin of characters apparently in no way related to survival is of interest. I believe with Lutz (1924) that "it is to be expected that creatures possess many totally useless characters." What possible difference could it make from the standpoint of survival, for example, whether the inner margins of the eyes of a bee are parallel, diverge slightly below, or converge slightly below? Similar questions might be asked involving such characters as the distance between the antennal bases, and many of the features of the wing venation, e.g., the amount of curvature of the basal veins and of the second recurrent veins. If, as seems extremely probable, natural selection plays no direct role in determining whether a bee with a strongly curved basal vein in each forewing (e.g., *Halictus*) is more likely to survive than one with a nearly straight basal vein (e.g., *Andrena*), and if, as seems equally probable, these characteristics are not persisting remnants of features formerly important from the standpoint of survival, then why do such differences exist?

A standard answer, and one that is probably sometimes correct, is that at some time during the phylogenetic history of the group a single change or mutation affected some physiologically or morphologically functional characteristic in addition to the structure which is seemingly of no survival value to the species. Natural selection would then act upon the functional characteristic without regard for, let us say, the curvature of the basal vein. If this mutation affected a physio-

logical characteristic that determined the adaptability of individuals to different climates, different seasons, or different hosts, then we might soon have two species living in different climates, at different seasons, or on different hosts and differing from each other outwardly in the curvature of the basal vein. The accumulation by each species of additional mutations, the division of each of the species into other species, and the extinction of intermediate forms would result in the formation of two genera differing by the curvature of the basal vein among other characters.

This explanation appears to be particularly likely if we accept Goldschmidt's theory that a new species arises in a single step as a result of a great mutation which affects many characteristics of the organism.

If, on the other hand, we believe that new species usually arise as the result of the accumulation of minor mutations, then it appears possible that at least some of the characters which have no significance from the standpoint of natural selection had a different origin. It seems likely that chance mutations of no selective importance may eventually characterize a species, hence, also, the genus or higher category resulting from the subdivision of the original species. It is particularly easy to imagine this starting in isolated populations of a species, such as occur on islands, mountains, or in limited habitable areas near the margins of the range of the species. Such populations may eventually differ from one another by features that have nothing to do with natural selection but appear as a result of a different series of mutations in each isolated population. Finally, we may suggest that many of the characteristics of a species appear not to function in its favor, but they may exist so long as they do not act against it with such force as to result in extinction.

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PART 3. PHYLOGENY OF THE BEES

EARLIER CLASSIFICATIONS

IT SEEMS WORTH WHILE to review a few previous works that have contributed to the current concepts of the classification and phylogeny of bees before discussing a new interpretation. A very few students have provided the basis of modern opinions on bee classification. With the exception of the classification first proposed by Robertson, authors have laid stress in defining the higher groups of bees primarily on two sets of characters, namely, the mouthparts and the scopa. However, certain of the other characters that are valuable indicators of the relationships of bees have been pointed out by Bischoff (1934) and Grütte (1935), but neither of these authors has proposed a classification or a phylogenetic system. The result has been classifications of varying degrees of unnaturalness. Any phylogenetic study or attempt to devise a natural classification should, of course, be based upon as many characters as possible.

The classifications of Friese (1895) and others arbitrarily separated the parasitic from the nonparasitic bees. The classification of Ashmead (1899) was characterized by the large number of families, some admittedly unnatural assemblages of genera, and others (e.g., Psithyridae) relics of earlier classifications in which the primary division separated the parasitic and nonparasitic forms. Many of the genera were carelessly placed in the wrong families, partly as the result of the use of only the most superficial and long-known characters.

An entirely new and carefully considered classification of bees was proposed by Robertson (1904), modified and more conveniently presented by Viereck (1916), and followed by several American writers. Robertson observed that the seventh abdominal tergum of many female and the eighth of many male bees bears a flattened, bare, margined pygidial plate. He believed that the presence or absence of this plate was a primary character dividing bees into two great natural groups. In fact, he went so far as to suggest that the pygidialate and apygidialate bees might have arisen from pygidialate and apygidialate sphecoid wasps, respectively.

He observed that the pygidialate bees constituted a group homogeneous in comparison to the extremely diverse groups of the apygidialata. Forms with typical pygidial plates occur in Robertson's Colletidae and Hylaeidae, and remnants of such plates (without, however, the usually accompanying prepygidial fimbria) are found in his Megachilidae (*Lithurge*) and Xylocopidae (*Xylocopa*) although all these groups were placed in the apygidialata by Robertson. The majority of the sphecoid wasps possess a pygidial plate. Clearly, the pygidial area is a primitive structure in bees, which has been independently lost many times. Certain bees obviously related to pygidialate forms, as, for example, *Ericrocis* and *Oreopasites*, lack pygidial plates. It is seen that the various apygidialate groups are not closely related to one another, but rather each, as shown by numerous other characters, is most closely related to some pygidialate group. This appears to be the true explanation of the diversity which Robertson observed in the apygidialata. Here is an excellent example of the fallacy of basing a classification upon a single character! At the same time, it indicates the difficulty of building a sound classification upon a limited fauna. Had Robertson possessed a single specimen of the numerous pygidialate forms of Colletidae, he could not have proposed his classification as he did. Nevertheless, Robertson's careful work drew attention to many important characters in bee structure.

Cockerell and Robbins in 1910 published a classification of the genera occurring in Colorado.

In his classification of the Hymenoptera, Börner (1919) used primarily the mouthparts for differentiation of various groups. Groups which seem unrelated on the basis of other characters were sometimes placed together because of similarity resulting from convergence. For example, the Ceratininae and Nomadinae constituted a family by themselves in his classification.

If the new classification presented in this paper has any advantages over previous ones,

it is because of an attempt to take into consideration as much as possible of the available data. Specimens from all major faunal areas of the world and representing as many genera as possible have been studied and the visible

characters of a considerable series of genera have been recorded in part 2. No major divisions in the classification are based upon a single or even a very few characters.

PHYLOGENETIC HISTORY

The sphecoid wasps are the group of Hymenoptera most closely related to the bees, and on the basis of habits, at least, are more primitive than the bees. Indeed, morphologically speaking, this group of wasps as a unit differs from bees primarily only in the absence of branched hairs and in the slender posterior basitarsi, which are ordinarily not flattened and not broader than the following segments, as they are in the bees. A classification of the Hymenoptera should place the bees as a division of the superfamily Sphecoidea; to rank them as a superfamily separate from the Sphecoidea obscures the close relationship between these wasps and bees, unless some category higher than superfamily is employed to unite the two groups.

An examination of various sphecoid wasps seems to show that the bees did not arise from any existing group of wasps. Nevertheless, a knowledge of these wasps is frequently useful in determining whether a given structure is primitive or specialized in the bees. For example, it is obvious that the short, broad glossa of the Colletidae is more primitive than the acute glossa of the higher bees because the sphecoid wasps as well as most other Hymenoptera exhibit the former type of structure. By similar reasoning numerous characters have been judged as to degree of specialization and are placed upon the accompanying list. Only those requiring special discussion are considered at length.

The facial foveae are found in most Colletidae and Andrenidae but are lost in some representatives of each family, such as *Caulopolicana* and *Melitturga*. They are not characteristic of any other family, but in *Conanthalictus*, the African *Nomia hadrosoma* Cockerell (Halictidae), and certain species of *Exomalopsis* (Apidae) they seem to be retained as a primitive character among otherwise highly modified bees. Similar conditions exist with regard to a number of other characters. For example, the lower portions of the

pre-episternal sutures are present (except where independently lost as in *Diphaglossa* and *Nomia*) in the Colletidae and Halictidae, absent in other families except for certain Panurginae (Andrenidae) and certain Ammobatini (Apidae). The Megachilidae and Apidae are, in general, distinguishable from other bees by the subvertical metanotum and propodeum. A few genera (e.g., *Ceratina* and *Chelostoma*), however, in each of these families retain the primitive horizontal metanotum and base of the propodeum.

Facts such as these are frequently useful in determining the relationships of groups. When they are considered in connection with the numerous parallelisms described in the second portion of part 2, however, it is clear how few of the characteristics of the higher categories (e.g., families) are absolutely constant. This does not necessarily mean, however, that the classification is invalid. Such conditions, indeed, are to be expected among organisms constantly evolving and adapting themselves to varying environmental conditions.

The Andrenidae are characterized by the presence of two subantennal sutures below each antennal socket. Unless the V-shaped submentum and slender mentum, tapering basally, which together form part of the complicated folding mechanism of the proboscis, were evolved independently in the Panurginae and in the higher bees, a most improbable possibility, the inner subantennal sutures must have been lost in the Melittidae, Megachilidae, and Apidae. A cursory examination might suggest that the inner sutures are preserved in the Megachilidae and the outer in the Apidae. That such is not the case is indicated by the fact that the main anterior roots of the tentorium are involved in the formation of the outer subantennal sutures of the Andrenidae and in the formation of the only subantennal sutures of other bees. The explanation of the outward-directed upper ends

of the subantennal sutures in the Megachilidae is probably as follows. In *Anthophora* and most other bees the upper portions of the anterior roots of the tentorium meet the face along the subantennal sutures, from whose upper ends they turn outward and are attached along a line near the lower margins of the antennal sockets. The line of attachment to the face is thus strongly angulate. A mere straightening of this line of attachment, an intermediate stage of which may be seen in *Macropis*, would result in the condition found in the Megachilidae. The same facts may explain the positions of the upper ends of the subantennal sutures at the outer margins of the antennal sockets in andrenids.

A few characters seem to have appeared and then disappeared within the bees. For example, the lower lateral margins of the clypeus in the Oxaeinae and Panurginae are bent backward. Neither the colletids nor the sphecoid wasps exhibit such a character; it obviously arose in an immediate ancestor of the andrenid bees. A study of the accompanying phylogenetic tree (diagram 13) shows that the curvature must have been lost in the Andreninae, Megachilidae, Melittidae, Xylocopinae, Fideliinae, and Apinae, and either retained or regained in the Anthophorinae, in

which it is again secondarily lost in *Hemisia* and *Exomalopsis*.

In the accompanying list are found various features that appear to be useful in determining the phylogenetic history and classification of bees. On the left is indicated for each structure the condition believed to be most primitive among the bees, while on the right is indicated the derived condition or conditions. Except for the items marked by an asterisk (*), which seem to have arisen in the primitive bees but to be absent from the wasps, the characteristics indicated at the left are held in common among at least certain lower bees and at least some of the sphecoid wasps, while the alternative characters on the right are specializations of the bees, some of which, incidentally, are paralleled by certain wasps. In some cases many intermediate degrees of specialization occur between the extremes indicated in the two columns. For example, maxillary palpi with five, four, three, and two segments occur, in addition to the extremes of six and zero indicated in the list. The characters discussed in the preceding paragraphs have been omitted, because of the difficulty of suggesting their significance in a mere list.

LIST INDICATING THE DEGREE OF SPECIALIZATION OF CERTAIN CHARACTERS

PRIMITIVE	SPECIALIZED
Labrum broader than long	Labrum longer than broad
Subantennal suture directed toward inner margin of antennal socket	Subantennal suture directed toward outer margin of antennal socket
Facial foveae present	Facial foveae absent
Hypostoma free from tentorium	Hypostoma fused with tentorium
Stipes without comb on posterior distal margin	Stipes with comb, usually in a concavity, on posterior distal margin
Lacinia present	Lacinia absent
Galea short	Prepalpal portion of galea greatly elongated
Galea with comb on inner surface	Postpalpal portion of galea greatly elongated
Submentum broad, quadrate	Galea without comb on inner surface
Labial palpus with segments similar	Submentum absent
Maxillary palpus six-segmented	Submentum V-shaped, apices of arms articulating with cardines
Paraglossa short	Labial palpus with first one, two, or three segments elongate and flattened
Glossa short, truncate or emarginate	Maxillary palpus absent
First flagellar segment short	Paraglossa exceedingly long
Scutellum nearly flat, horizontal	Glossa linear, acute or terminating in a flabellum
Metanotum horizontal	First flagellar segment elongated
	Scutellum strongly convex or angulate in profile
	Metanotum vertical

PRIMITIVE

Propodeum with horizontal basal area
 Claws cleft or with inner tooth
 Middle coxa short
 Pre-episternal suture complete
 *Basitibial plate present

*Scopa on posterior legs (coxae to basitarsi)

Pterostigma large
 Notaulus long
 Second abscissa of vein M + Cu much longer than cu-v (rear wing)
 Jugal lobe of posterior wing long
 Three submarginal cells
 Wings evenly covered with hairs, not papillate
 *Prepygidial fimbria present
 Pygidial plate present
 Pseudopygidial area absent
 Volsella present
 Eighth sternum of male with pair of distal lobes, commonly themselves lobate and complex
 Penis valves not attached to penis
 Gonostyli articulated with gonocoxites
 Sting well developed

SPECIALIZED

Propodeum entirely declivous
 Claws simple (in female)
 Middle coxa elongate dorso-ventrally
 Pre-episternal suture absent
 Basitibial plate absent
 Scopa absent
 Scopa on abdominal sterna
 Scopa on posterior tibia
 Scopa modified to form a corbicula
 Pterostigma small
 Notaulus punctiform
 Second abscissa of M + Cu shorter than cu-v (rear wing)
 Jugal lobe of posterior wing short
 One submarginal cell
 Wings bare basally, papillate beyond venation
 Prepygidial fimbria absent
 Pygidial plate absent
 Pseudopygidial area present
 Volsella absent
 Eighth sternum of male without distal lobes

Penis and penis valves closely associated
 Gonostyli fused with gonocoxites
 Sting feebly developed

Examination of various bees shows that those of the tribe Paracolletini possess practically all the characters in the left-hand column of the list. The Paracolletini are consequently regarded as the most primitive group of bees. Indeed, there is nothing in their structure which would indicate that all other bees could not have been actually derived from them; we need not necessarily postulate the characters of a hypothetical common ancestor of the colletids and other bees, so closely do some genera of this group approach the structure which we would suggest for such an ancestor.

From a *Paracolletes*-like ancestor it seems possible to derive, through independent loss of the pygidial area and the scopa, as well as by other modifications, the subfamilies of the Colletidae. It is possible that the absence of the scopa in two of these subfamilies is a primitive rather than a specialized feature, but in view of the other specialized characteristics of the forms lacking scopae, this seems improbable. Certain authors (e.g., Meade-Waldo, 1923) have suggested that the hylaeine bees are quite unrelated to the colletine forms, a conclusion that might seem justified

from a study of the genera of the Northern Hemisphere alone. When the numerous genera of Australia, South America, and southern Africa are studied, many of the great differences between the two Holarctic genera (*Hylaeus* and *Colletes*) are bridged. I believe, therefore, that the Colletidae as here understood is a natural family. It is interesting to observe that the genera *Diphaglossa* and *Stenotritus* lack the lower portions of the pre-episternal sutures.

The Halictidae, as here understood (including the Dufoureae of many authors), is a relatively homogeneous family, in the recognition of which there is rarely any difficulty. These bees probably arose from some colletid-like bee, as indicated in the accompanying phylogenetic tree. There can be no doubt that the Dufoureae constitutes a distinct group within the family, but I see little justification for giving it the rank of family; such elevation of categories merely obscures the important fact that the Dufoureae and Halictinae are conspicuously far more closely related to each other than either is to any other bees.

The Andreninae, Panurginae, and Oxaeinae

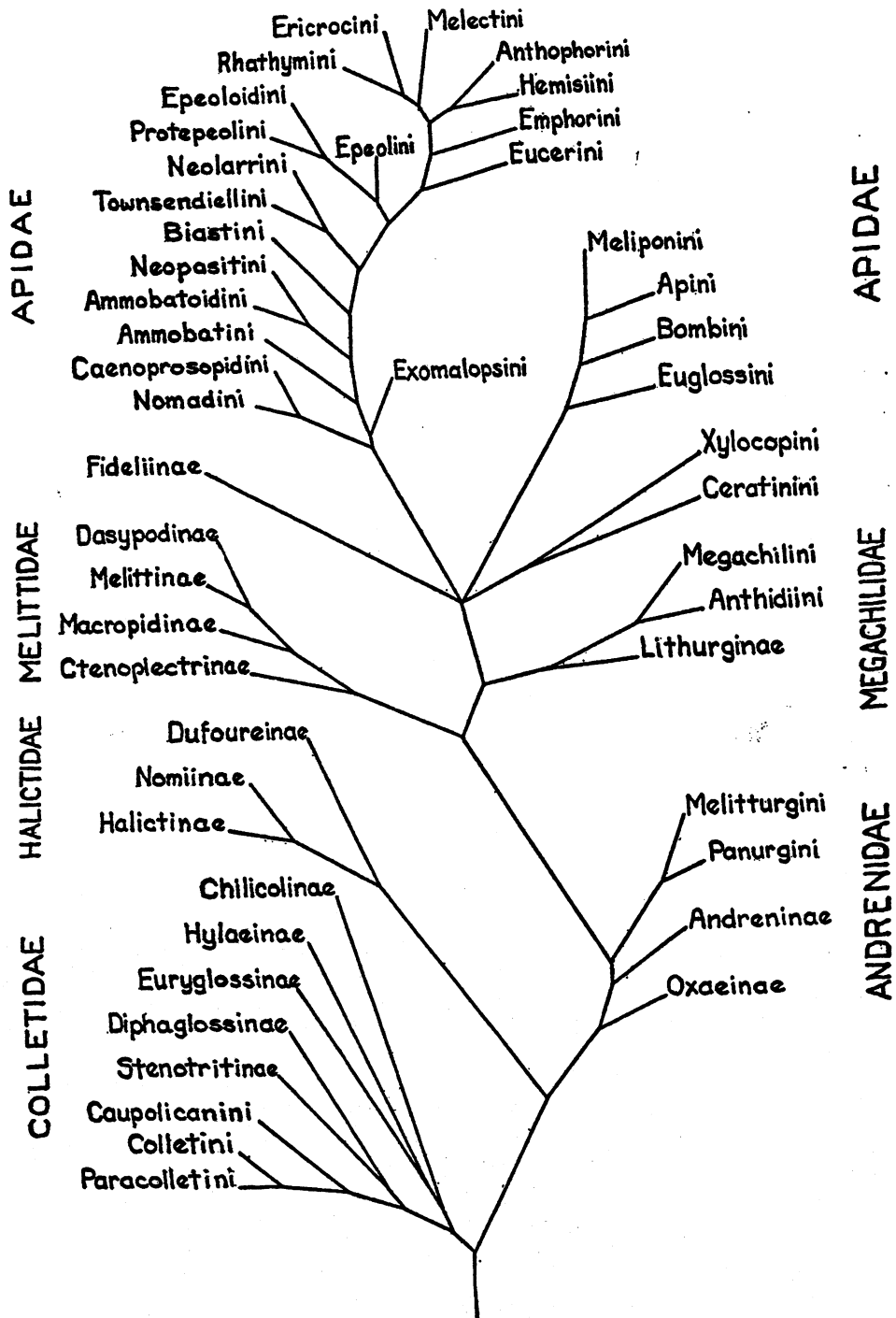


DIAGRAM 13. Phylogenetic tree suggesting relationships of the various subfamilies and tribes of bees.

are united in a single family, the Andrenidae. The homogeneity of this assemblage is indicated, for example, by the presence of two pairs of subantennal sutures. In all other bees there is but one subantennal suture beneath each antenna. It appears to me a matter of choice whether one wishes to regard the Oxaeinae as a distinct family or not. The Oxaeinae and Andreninae are more distinct than the subfamilies within other families of bees, including the Apidae in the sense in which I use it.

Primarily because the Panurginae shares with the higher families of bees the V-shaped mentum, tapering basally, I have suggested in the accompanying phylogenetic tree that the higher families arose from the Panurginae or the immediate ancestors of that group.

The classification here suggested for the Megachilidae is entirely different from that of previous authors, because *Lithurge* appears to be so different from the other genera in the family that the primary division into subfamilies should be between *Lithurge* and the others. That *Lithurge* is an ancient type is shown by its retention, in contrast to all other megachilids, of long jugal lobes of the posterior wings and of a remnant of the pygidial plate in the female and a conspicuous pygidial plate in the male. Furthermore, I believe that *Osmia* and its relatives are closely related to *Megachile*, while both of these groups are quite distinct from the anthidiine bees.

It must be set down as a good possibility that the Megachilidae arose from a primitive member of the Apidae rather than from a pre-apid stock, as suggested in the phylogenetic tree. Perhaps the megachilids arose from something resembling *Fidelia* or *Xylocopa*.

The Melittidae consists of four groups which, while clearly related, have been widely separated in previous classifications. They agree with each other in the type of mouthparts and, except for *Ctenoplectra*, in the complete lack of pre-episternal sutures and of those portions of the scrobal sutures in front of the scrobes.

The family Apidae is here understood to contain the Anthophoridae, Apidae, Bombidae, Ceratinidae, Emphoridae, Euceridae, Euglossidae, Fideiidae, Nomadidae, and Xylocopidae of certain previous authors. It

appears to me that these categories represent a unified group comparable to the previously mentioned families in distinctness and in the closeness of the relationship of the forms contained in it. To divide it into several families (without the use of a category above "family" for the whole) would result in obscuring this relationship. If it were to be divided into subfamilies, then, as may be seen from the phylogenetic tree, we might either use four names, raising each subfamily to family rank, or more than twenty, raising each tribe to family rank. If either one of these were done, the subfamilies or tribes, as the case might be, in the remainder of the families must also be raised to family rank. The six families that I have recognized appear to me to conform more nearly to the family concept currently in use in the rest of the Hymenoptera than would any less conservative classification.

The family Apidae is easily divisible into four subfamilies which, while distinct phylogenetically, are difficult to separate in a key because of convergent forms among them. The subfamilies are the Xylocopinae, Apinae, Fideiinae, and Anthophorinae. The Xylocopinae contains two very different types separated as the tribes Ceratinini and Xylocopini. Although certain authors have failed to see any resemblance between these tribes and although they are undoubtedly groups that separated long ago, I have placed them in the same subfamily because they have similar types of scopa, both lack, or virtually lack, pygidial plates and bastibial plates, both have strongly transverse anterior coxae with at least an indication of a spine directed posteriorly from the median distal angle of each, and *Xylocopa* and *Ceratina* both have a "scale" or projecting process on the outer surface of each posterior tibia, at least in the females. These structures seem to indicate a relationship between the Xylocopini and Ceratinini.

The Apinae, with the exception of the Euglossini and *Psithyrus*, are social bees. Except for the parasitic forms, all are characterized, in the worker cast at least, by the possession of corbiculae. It seems likely that the acquisition of the social habit has greatly increased the rate of evolution in these forms. Even within a single genus such as *Trigona*

there are immense variations in structure. The differences between the male genitalia of *Apis* and those of other Hymenoptera are very great, so that on this basis *Apis* might be placed very far from any other bees. However, the corbicula, the apical combs of the tibiae of the females, the absence of the hind tibial spurs, the proximity of the clypeus to the antennal bases, the short, angulate, first recurrent vein, as well as other characters prove beyond doubt the close relationship of *Melipona* and *Apis*. Many other less extreme differences occur between various social bees and, as I have said, suggest a rapid evolution correlated with the unusual habits of these insects.

The Fideliinae is a small African subfamily of Apidae. Primarily on the basis of the shape of the eighth abdominal sternum of the male, Popov (1939) placed this group among the lower bees (Colletidae and Andrenidae). However, it appears that the many resemblances of *Fidelia* to the Apidae are more than mere convergence. Undoubtedly, although specialized in many respects, *Fidelia* retains many primitive features, among which is the shape of the eighth sternum. It is another example of variation in the rate of evolution of different structures. Furthermore, there exists in many Eucerini a pair of distal lobes on the eighth sternum comparable to, but less developed than, those of *Hylaeus*, certain Panurginae, the Melittidae, and the Fideliinae.

The Anthophorinae is the largest and systematically the most difficult group of the Apidae. The nonparasitic tribes that it contains are rather easily placed in relation to each other, the Exomalopsini being clearly the most primitive. The subfamily, however, contains numerous parasitic groups. Two of these, the Melectini and Ericrocini, as shown by the slanting second abscissa of vein M+Cu in the posterior wings and by the small pterostigmata, are related to the pollen collecting Anthophorini and Hemisiini and have been placed accordingly in the phylogenetic tree. Grütte (1935) believed that *Melecta* and *Crocisa* arose from *Anthophora*. However, these two parasitic genera and their close relatives exhibit a number of characters more primitive than those of any Anthophorini and hence could not have arisen

from the latter group. In these melectine genera the pterostigmata are larger than in the Anthophorini, and the volsellae, which are absent in the latter tribe, are present. For such reasons as these, the Melectini are shown in the phylogenetic tree as arising from bees more primitive than the living Anthophorini. Linsley (1939) has suggested the possibility that *Ericrocis* may have arisen from *Hemisia* or *Epicharis* and be unrelated to *Melecta* or *Anthophora*. *Ericrocis*, however, resembles the Melectini and differs from the Hemisiini in the long first submarginal cell as compared to the second and third, the exceedingly short second abscissa of vein M+Cu of the posterior wings, the small vannal lobe of the posterior wings, the horizontal rather than arched median section of the epistomal suture, and the strongly arcuate lower portions of the epistomal suture. The other parasitic groups of the Anthophorinae, constituting the Nomadidae of authors (e.g., Linsley and Michener, 1939) are apparently very ancient and are so dissimilar from one another as well as from the nonparasitic groups that their true place in the phylogenetic system is difficult to determine. Some of these groups exhibit characters (e.g., the large pterostigmata in some) that are more primitive than those of the other Anthophorinae except the Exomalopsini. Hence the latter tribe is the only nonparasitic group from which the parasites could have arisen, and many of them are so different from any members of that tribe that there is no basis for regarding them as derived from *Exomalopsis* or any of its immediate ancestors. Grütte (1935) believed that some of the genera arose from panurgine bees, but since none possess subantennal areas, it seems that their only relation to the panurgines is their derivation from primitive Anthophorinae, the closest relatives of the Panurginae among the bees with long proboscides. As shown by the extreme diversity of the "nomadids," however, Grütte was probably correct in regarding different groups of them as having arisen independently from primitive, no longer extant, pollen collecting anthophorines. Actually there may have been fewer branches from the nonparasitic stock and more subdivisions of those few branches. Grütte's contention that the Epeolini arose from primitive *Tetralonia*-like bees, and the

Protepeolini from *Entechnia* (= *Melitoma*), is shown to be improbable by the relative sizes of the pterostigmata in these groups, the short vein cu-v in the posterior wings of *Melitoma*, the short third submarginal cell in the Epeolini, and the subequal submarginal cells in the Protepeolini (first and third elon-

gate in *Tetralonia* and *Melitoma*). We seem to have evidence for a greatly increased speed of evolution among the parasitic forms as compared with those that are not parasitic. The result has been differences in structure among the parasites so great that their phylogeny is no longer apparent.

RELATIVE ANTIQUITY OF THE FAMILIES

The distribution of groups frequently gives clues to their relative antiquity and thereby serves as a test for systems of phylogeny based on other data. The family Colletidae, which exhibits many primitive characteristics, is well represented in South America, Africa, and especially Australia where it has become diversified into dozens of genera. Except for minor intrusions, such as that of *Caupolicana* as far north as New Mexico and Arizona, only two genera of Colletidae, *Hylaeus* and *Colletes*, occur in the Holarctic region. Aside from these latter widespread genera, the family has the Panaustral type of distribution well known among primitive southern groups. Related genera are found on the widely separated southern continents, but nowhere in the connecting land areas to the north. The Halictidae is the only other family of burrowing bees well represented in Australia. The subfamily Dufoureae is absent from that region as well as other southern continents. We may well conclude that the Colletidae and Halictidae are the two oldest groups of bees, groups which reached Australia long ago when it was connected, or nearly connected, by land with other continents. In the other families of bees only a small number of genera have reached Australia. *Megachile* and *Exoneura* are represented there by many species, but they, as well as most of the other genera of long-tongued bees in Australia, are forms which nest in wood or canes and might be carried by the currents of the ocean.

South America, which was isolated from North America as well as from other continents for a long period following a connection in the early Tertiary, had apparently already acquired a fauna containing, in addition to the Colletidae and Halictidae, at least the Andrenidae, many groups of Apidae, and possibly certain Megachilidae. These families must have arisen, therefore, before the time of the submergence of the Central American isthmus, and their representatives have evidently given rise to the Oxaeinae, certain panurgines, the Euglossini, Exomalopsini, Hemisiini, Protepeolini, and probably the Emphorini.

We may, then, arrange the families from older to younger as follows: Colletidae, Halictidae, Andrenidae, Apidae, and (?) Megachilidae. Hardly enough is known of the distribution of the Melittidae to suggest its antiquity. The Colletidae and Halictidae are perhaps as old as the Cretaceous, as indicated by their distribution, but could not have arisen before the advent of flowering plants in that period. The Andrenidae and Apidae are apparently at least as old as the early Tertiary land connection between North and South America. These data agree as well as can be expected with the relative ages suggested by the phylogenetic tree presented above.

The described fossil bees are too little known morphologically and hence systematically to contribute additional information on the phylogeny or antiquity of bees.

CORRELATIONS OF BIONOMICS WITH CLASSIFICATION

The bionomics of various groups of non-parasitic bees corroborates to a certain extent the classification based on morphology. Most of the solitary bees nest in the soil. However, many Hylaeinae and Megachilidae, a few

Anthophorinae (*Clisodon*), and the Xylocopinae nest in twigs or larger pieces of wood. Only the Megachilidae among the solitary bees are disposed to use suitable cavities of any nature in which to place their nests.

Some regularly dig their own tunnels, but many seem to do so only if no others can be found. The Colletidae, Xylocopinae, and certain Megachilidae and Anthophorinae construct tunnels in which the cells are placed end to end in regular series. The Andrenidae, Dufoureae, and Melittidae dig tunnels each ending in a single cell. Then from some distance above this cell another tunnel is formed, which in its turn terminates in a cell. This process is repeated several times. The final result is a branching nest, with the branches irregular and rather long. A somewhat similar procedure must account for the nests of the Eucerini, in which several tunnels diverge from near the surface of the ground. The nests of the Halictinae consist of a main tunnel from which the cells radiate at right angles.

The cells and tunnels of the Colletidae are lined with a thin, transparent substance said to be applied by the broad glossa, while practically no other bees line their burrows similarly. In the Andrenidae, Dufoureae, Melittidae, Xylocopini, and Anthophorinae the cells but not the burrows leading to them are lined with a thin wax or varnish-like substance. The cells of the social bees are made of wax. In the Halictinae there are no cell linings. This also appears to be true of the Ceratinini. In the Megachilidae, while there are no secreted cell linings and, of course, no tunnel linings, foreign materials are usually carried in to produce highly characteristic cells. Thus most *Megachile* make the cells from pieces of leaves, *Trachusa* uses pieces of leaves cemented together with resin or gum, *Dianthidium* and *Megachile* subgenus *Chelostomoides* utilize pebbles cemented with resin, while *Anthidium* uses plant down.

The pollen masses in the cells of the Andrenidae, Halictidae, and Melittidae consist of firm spheres (or ovals in *Macropis*), upon each of which an egg is laid. In the Xylocopinae the pollen masses are similarly firm but are more elongate and flattened in shape. On the other hand, in the Colletidae, Megachilidae, and Anthophorinae the pollen is mixed with a liquid, probably nectar in the case of the first two and water in the case of the last, and forms a semiliquid mass in the bottom of each cell.

The Megachilidae are remarkable for the fact that the mature larvae spin cocoons which are provided, except in certain *Hoplitis*, with a conspicuous projecting nipple at one end. Outside of this family only a few genera make cocoons, and they are not furnished with nipples. Genera making such cocoons are *Apis*, *Bombus*, *Macropis*, *Melecta*, and *Systropha*.

In temperate climates most bees pass the winter as mature larvae in their cells, but the Halictinae and Bombini hibernate as adult females. *Apis* likewise passes the winter in the adult stage (queens and workers), but true quiescent hibernation does not occur in this genus.

This brief summary of some of the features of the bionomics of bees will serve to show that the biological characters are in some cases correlated with the structural ones. Many of them are less dependable, however, than the structural characteristics, or perhaps the most dependable biological characters remain to be recognized. For the information presented above on bee biologies I am indebted to the reviews of Malyshev (1917) and Nielson (1934), and to Mr. J. W. MacSwain.

PART 4. A CLASSIFICATION OF THE BEES

THIS SECTION PRESENTS THE SYSTEMATIC RESULTS of the comparative morphological study of the bees. The families, subfamilies, and tribes of the world and genera occurring in America north of Mexico are briefly described and included in the keys. Because of lack of material, it has been impossible to include in the keys genera not occurring in that area. However, the systematic position of many exotic genera is indicated. For the sake of brevity no attempt has been made to give long or comparative descriptions for each genus although they would be desirable; instead, certain comments on the general appearance and particularly distinctive features of each form are presented in order to facilitate identification. Characters indicated in the keys are not repeated in the descriptions.

While in this paper it has only been possible to give keys to the genera, or in some cases subgenera, references are made to useful revisional papers or papers containing keys to species of the United States and Canada. Complete citations to these papers are found in the bibliography for parts 3 and 4. The synonymies are limited, to conserve space, to citations of the original descriptions of the various generic names. Since a list of type species of all generic and subgeneric names of bees has been published by the late Grace A. Sandhouse (1943), genotypes are not indicated for synonymous and subgeneric names. Many names proposed for groups of exotic bees have been placed as synonyms or subgenera of genera occurring in the area covered by this paper. In certain instances such placement is open to question, in which case the names are omitted from the synonymies.

Because many of the characters necessarily used in the keys to the families and subfamilies are difficult to see, requiring examination of mouthparts or scraping away of hair, etc., an artificial key leading directly to the North American genera is included, using characters more easily seen than the more obscure but apparently fundamental characters of the higher categories.

The terminology of the wing veins and cells is modified from that of H. H. Ross, as

in previous portions of this paper, except that certain convenient terms are retained from older systems, thus:

Marginal cell = cell second R_1 of the forewing.

Submarginal cells = cells first R_1 , first R_2 , and second R_2 of the forewing.

Recurrent veins = veins first m-cu and second m-cu of the forewing.

Prestigma = first abscissa of vein R_1 , a small, usually thick vein immediately basad of the pterostigma of the forewing.

In all cases where the lengths of the jugal and vannal lobes of the posterior wings are compared, each is measured from the base of the wing.

In using the terms anterior and posterior in connection with legs or wings it is considered that these structures are extended at right angles to the body.

It is frequently necessary to determine the sex of bees. The antennae, with very few exceptions, are twelve-segmented in females, thirteen-segmented in males. Ordinarily six metasomal terga are exposed in females, seven in males, but the apical one in either sex may be hidden by the preapical one. Females always possess at least a rudiment of a sting, whereas males have in its place the genital capsule.

The propodeum is recognized as the first abdominal segment; thus the first metasomal segment becomes the second abdominal segment.

As in other parts of this paper, bees that live at the expense of others are termed parasites, although it is realized that some other expression, such as social parasites orinquilines, might better indicate their relations to their hosts.

KEY TO THE FAMILIES

1. Subantennal areas defined by two subantennal sutures beneath each antennal socket (fig. 91); glossa acute, short or long; labial palpi with segments similar or first alone, very rarely second also, elongate and flattened; middle coxae at least externally much shorter than distance from summits to posterior wing bases; females and many males with defined pygidial area Andrenidae

- Subantennal areas not defined, there being but one subantennal suture (figs. 1, 88), or very rarely a small triangular enclosed area below each antenna; glossa variable; labial palpi with segments similar or first two elongate and flattened, only very rarely first alone elongate; middle coxae variable in length; pygidial area present or absent 2
2. Mentum and submentum virtually absent (fig. 143); galea elongated prepalpally and evenly tapering to a slender basal point, prepalpal portion usually as long as postpalpal portion (fig. 136); labial palpi with segments similar and cylindrical in most North American species; basal vein (first abscissa of vein M) usually strongly curved in North American forms (fig. 170); pre-episternal suture usually complete (fig. 150); metanotum horizontal; middle coxae externally much shorter than distance from their summits to posterior wing bases Halictidae
- Mentum and submentum present; galea prepalpally short and not evenly tapering, prepalpal portion at least as short as, usually much shorter than, postpalpal portion (figs. 13, 137); labial palpi with segments similar or first two elongate and sheath-like; basal vein not strongly curved; pre-episternal suture, metanotum, and middle coxae variable 3
3. Glossa in females and in males of all American species rounded, truncate, bilobed, or bifid (fig. 145); submentum broad, rather elongate, not V-shaped (fig. 145); pre-episternal suture complete (fig. 152), except in the exotic subfamilies Diphaglossinae and Stenotritinae; middle coxae externally much shorter than distance from summits to posterior wing bases Colletidae
- Glossa acute, often elongate (figs. 15, 142, 143); submentum V-shaped (figs. 15, 142); pre-episternal suture present, if at all, only above scrobal suture (figs. 22, 148), except in certain exotic Ammobatini and Caenoprosopidini; middle coxae over two-thirds as long as distance from summits to posterior wing bases, except in Melittidae and a few parasitic Apidae 4
4. Labial palpi with segments similar and cylindrical (as in figs. 143, 145); galeae short; middle coxae, except in *Macropis*, much shorter than distance from summits to posterior wing bases Melittidae
- Labial palpi with first two segments elongate and sheath-like (figs. 15, 142); galeae greatly elongated (fig. 13); middle coxae, except in a few parasitic Apidae, over two-thirds as long as distance from summits to posterior wing bases 5
5. Labrum longer than broad and widened to broad articulation with clypeus (fig. 124); subantennal sutures directed toward outer margins of antennal sockets (fig. 89); two submarginal cells, usually about equal in length (fig. 167); pygidial area absent except in *Lithurge*; scopa, when present, on abdominal sterna Megachilidae
- Labrum usually broader than long (figs. 125, 127), if not, narrowed basally to short articulation with clypeus; subantennal sutures directed toward inner margins of antennal sockets (fig. 1); usually three submarginal cells (figs. 35, 165), when two, the second often much shorter than first, rarely but one closed submarginal cell; pygidial area often present; scopa, when present, on posterior legs, rarely on abdominal sterna also. Apidae

FAMILY COLLETIDAE

Labrum broader than long; subantennal areas absent or at least reduced to small triangular spaces; lower sides of clypeus not bent parallel to long axis of body; subantennal sutures directed toward inner margins of antennal sockets; facial foveae often present; stipites without combs; galeae short postpalpally and usually prepalpally, with a comb on inner side of each; submentum broad and rather elongate, not V-shaped; mentum absent or rather broad; labial palpi short, segments similar or, rarely, the first somewhat elongated and broadened; glossa short, truncate or emarginate, very rarely rounded, acute only in males of a few Australasian genera; hypostoma free from tentorium (in forms examined); pre-episternal sutures usually complete; metanotum usually horizontal; middle coxae as seen from the outside much shorter than the distance from their summits to posterior wing bases; pygidial plate present or absent; volsellae present.

The truncate or bifid glossa is the most characteristic feature of this family. Many of the genera are also distinguished from practically all other bees in having the posterior part of vein second m-cu of each forewing arcuate toward the apex of the wing.

KEY TO THE SUBFAMILIES OF COLLETIDAE

1. Jugal lobe of posterior wing small, less than one-half as long as vannal lobe; pre-episternal suture absent below scrobal suture Diphaglossinae
- Jugal lobe of posterior wing long, reaching at

- least to, and usually well beyond, middle of vannal lobe. 2
2. Pre-episternal suture absent below scrobal suture Stenotritinae
Pre-episternal suture complete (fig. 152) . . . 3
3. Cardines, prementum, and stipites unusually elongate; pre-palpal portions of galeae much long than postpalpal parts; scopa and pygidial plate absent Chilicolinae
Cardines, prementum, and stipites relatively short; prepalpal portions of galeae about as long as postpalpal parts 4
4. Clypeus elongated upward so that anterior tentorial pits lie at or below middles of lateral sections of epistomal suture, except in males having greatly enlarged antennal scapes; scopa absent; pygidial plate absent Hylaeinae
Clypeus not elongated, usually broader than long, anterior tentorial pits above middles of lateral sections of epistomal suture; scopa and pygidial plate variable. 5
5. Scopa of females present; pubescence abundant, that of thorax conspicuously plumose; three submarginal cells, or if two, they are subequal in length Colletinae
Scopa absent; pubescence sparse and very short, but feebly plumose; two submarginal cells, the second much smaller than the first. Euryglossinae

SUBFAMILY COLLETINAE

Malar areas short to moderate in length; jugal lobe of posterior wing reaching at least to middle of vannal lobe; scopa rather large.

KEY TO THE TRIBES OF COLLETINAE

1. First flagellar segment at least nearly as long as scape; vein second m-cu of forewing not arcuate outward in posterior portion but slanting basally so that it is almost parallel with Cu_1 ; distal portions of wings papillate. Caupolicanini
First flagellar segment far shorter than scape; vein second m-cu usually arcuate outward in posterior portion and at a strong angle to Cu_1 (fig. 168); distal portions of wings not papillate. 2
2. Pygidial and basitibial plates of female absent. Colletini
Pygidial and basitibial plates of female present. Paracolletini

TRIBE PARACOLLETINI

Glossa bilobed; pterostigma rather large; wings hairy throughout, not papillate; vein second m-cu at a strong angle to Cu_1 and

usually arcuate outward in posterior portion.

This tribe is Panaustral in distribution, its genera occurring in South America, Africa, and Australia. Genera included are: *Anthoglossa*, *Biglossa*, *Brachyglossula* (= *Pasiphae*), *Callomelitta*, *Dasycolletes*, *Goniocolletes*, *Lamprocolletes*, *Nomiocolletes*, *Paracolletes*, *Perditomorpha*, *Polyglossa*, *Scapter* (= *Strandiella*), and *Trichocolletes*. In all probability the tribe includes also *Andrenopsis*, *Cladocerapis*, *Euryglossidia*, *Lonchopria* (= *Bicolletes* and *Halictandrena*), *Notocolletes*, and *Phenacolletes*, genera which I have not been able to study.

TRIBE COLLETINI

Similar to the Paracolletini but females without pygidial plate, strong prepygidial fimbria, or basitibial plate; horizontal basal portion of propodeum short and provided with longitudinal carinae, often separating it into a series of pits.

This tribe appears to contain only the genus *Colletes*.

GENUS COLLETES LATREILLE

Colletes LATREILLE, 1802, *Histoire naturelle des fourmis* . . . , p. 423.

Evodia PANZER, 1806, *Kritische Revision der Insekten-fauna Deutschlands* . . . , vol. 2, p. 207.

Colletes (*Rhinocolletes*) COCKERELL, 1910, *Entomologist*, vol. 43, p. 242.

Colletes (*Philopoda*) FRIESE, 1921, *Stettiner Ent. Zeitg.*, vol. 82, p. 83.

Colletes (*Denticolletes*) NOSKIEWICZ, 1936, *Prace Nauk. Wydawnictwo Towarzystwa Nauk. Lwowie*, ser. 2, vol. 3, p. 486.

Colletes (*Puncticolletes*) NOSKIEWICZ, 1936, *ibid.*, ser. 2, vol. 3, p. 490.

GENOTYPE: *Apis succincta* Linnaeus (monobasic).

The genus *Colletes* is common in North America and widespread over the world, although absent from Australia. Our species are moderate in size, and most of them have bands of pale hair across the abdomen. In appearance they are similar to *Halictus* and some species of *Andrena* but may be distinguished at sight by one familiar with the groups of bees. The first submarginal cell is nearly as long as the next two together which are subequal in size or the third smaller (fig. 168).

The North American species having at

least some black hair on the dorsum of the thorax have been reviewed by Swenk (1908).

TRIBE CAUPOLICANINI

Glossa deeply bifid and provided with numerous long and sometimes branched hairs, as in the Diphaglossinae; pterostigma narrow, about as broad as distance from inner margin of prestigma to costal margin of wing, vein r arising from its apex; pygidial plate present in female; vein second m-cu at a large angle to Cu₁, sometimes almost parallel to it, not arcuate outward posteriorly.

As far as known this tribe contains only the primarily Neotropical genera *Caupolicana* and *Ptiloglossa*. Only the former reaches the United States, although the latter extends far into Mexico.

GENUS CAUPOLICANA SPINOLA

Caupolicana SPINOLA, 1851, in Gay, *Historia fisico . . . de Chile . . .*, Zoologica, vol. 6, p. 212.

Megacilissa SMITH, 1853, Catalogue of hymenopterous insects in the . . . British Museum, pt. 1, p. 123.

GENOTYPE: *Caupolicana gayi* Spinola, designated by Sandhouse, 1943, Proc. U. S. Natl. Mus., vol. 92, p. 534.

This is a genus of very large, robust, densely hairy bees with a very large, dense, and greatly plumose scopa in the female. The eyes of the male converge slightly toward the vertex. The second submarginal cell is much smaller than either of the others and narrowed costally, vein first m-cu nearly interstitial with first transverse cubital.

In the United States species of this genus occur only in the southernmost states, from Arizona to Florida.

SUBFAMILY STENOTRITINAE

Glossa very short, merely rounded rather than emarginate, at least in some; malar areas short; first flagellar segment much longer than scape; clypeus not elongated; ocelli of male far down on face; eyes sometimes converging above; pre-episternal sutures absent below scrobal sutures, weak above it; jugal lobe of posterior wing about three-fourths as long as vannal lobe; pterostigma narrower than distance from inner margin of prestigma to wing margin but

elongate, vein r arising at apex; wings hairy throughout, scarcely papillate distally; scopa and pygidial plate present.

This is a subfamily of large, hairy, Australian bees. The genus *Stenotritus* (= *Gastropsis*) is the only representative that I have studied, but *Ctenocolletes* and *Melitribus* are apparently also to be included.

A most remarkable feature of at least *Stenotritus pubescens* (Smith) is the presence of a small triangular area below each antennal base. These areas are demarked laterally by subantennal sutures which meet before reaching the clypeus. While these small subantennal areas may not be homologues of the areas of the Andrenidae, they may, nevertheless, be indications of the manner in which the latter arose.

SUBFAMILY DIPHAGLOSSINAE

Glossa strongly bifid, provided with numerous long hairs; malar areas long; first flagellar segment much shorter than scape; clypeus not elongated upward as in Hylaeinae; pre-episternal suture absent below scrobal suture, feeble above; jugal lobe of posterior wing considerably less than one-half as long as vannal lobe; pterostigma reduced, no broader than distance from inner edge of prestigma to costal margin of wing, vein r arising virtually from its apex; wings hairy almost throughout, not strongly papillate distally; scopa large, extending from posterior coxa to basitarsi; pygidial plate present.

These are large, robust bees with long, plumose pubescence.

This subfamily includes the South American genera *Diphaglossa* and *Policana*.

SUBFAMILY EURYGLOSSINAE

Glossa feebly bilobed; malar areas short or nearly absent; clypeus not elongated upward as in the Hylaeinae, anterior tentorial pits above the middles of the lateral sections of the epistomal suture; pre-episternal suture complete; anterior wings with two (or rarely one) submarginal cells; jugal lobe of posterior wing not greatly shorter than vannal lobe; pterostigma large, vein r arising but little beyond its middle; wings hairy throughout, not papillate distally; scopa virtually absent; pygidial plate present.

This subfamily consists of small, more or

less hairless bees which have usually been placed in the Hylaeinae. It is confined to Australia and includes *Euryglossa*, *Euryglossella*, *Euryglossomorpha*, *Euryglossina*, *Pachyprosopis*, and probably *Melittosmithia*, *Heterapoides* (= *Heterapis*), *Stilpnosoma*, and *Turnerella*.

SUBFAMILY HYLAEINAE

Glossa feebly bilobed or subtruncate; malar areas short; clypeus elongated upward, often much longer than broad, anterior tentorial pits at or below middles of lateral sections of epistomal suture; pre-episternal suture complete; anterior wings with two submarginal cells, the second much smaller than first and each receiving a recurrent vein except in *Hylaeoides*, which has a long second submarginal cell; jugal lobe of posterior wings but little exceeded by vannal lobe; wings hairy throughout, not papillate; scopa absent; pygidial plate absent.

Although some forms (e.g., *Hylaeoides*) reach a length of 15 mm. or more, most representatives of this subfamily are small. All appear nearly hairless, and most are black with rather restricted yellow markings on the head, thorax, and legs. The subfamily contains the genera *Eupalaeorhiza*, *Hylaeoides*, *Hylaeus*, *Meroglossa*, and *Palaeorhiza*. Several groups such as *Euprosopis*, *Gnathoprosopis*, and *Nesoprosopis* are closely related to *Hylaeus*, perhaps best regarded as subgenera of it. While best represented in Australia, this subfamily is almost worldwide in distribution. All American species fall in the genus *Hylaeus*, and those of the United States were revised by Metz (1911). Meade-Waldo (1923) has listed the species of this as well as of the preceding and following subfamilies.

GENUS HYLAEUS FABRICIUS

Hylaeus FABRICIUS, 1793, *Entomologica systematica* . . . , vol. 2, p. 302.

Prosopis FABRICIUS, 1805, *Systema piezatorum* . . . , p. 293.

Prosopis ASHMEAD, 1894, *Psyche*, vol. 7, p. 43.

Nesoprosopis PERKINS, 1899, *Fauna Hawaiianensis* . . . edited by D. Sharp, vol. 1, p. 75.

Prosopistemon COCKERELL, 1906, *Entomologist*, vol. 39, p. 17.

Prosopis (*Koptogaster*) ALFKEN, 1912, *Ber. Westpreussischer Bot.-Zool. Ver. Danzig*, vol. 34, p. 23.

Nothylaeus BRIDWELL, 1919, *Proc. Hawaiian Ent. Soc.*, vol. 4, p. 125.

Gnathylaeus BRIDWELL, 1919, *ibid.*, vol. 4, p. 126.

Metylaeus BRIDWELL, 1919, *ibid.*, vol. 4, p. 126.

Nothylaeus (*Anylaeus*) BRIDWELL, 1919, *ibid.*, vol. 4, p. 129.

Hylaeus (*Deranchylaeus*) BRIDWELL, 1919, *ibid.*, vol. 4, p. 136.

Hylaeus (*Nesylaeus*) BRIDWELL, 1919, *ibid.*, vol. 4, p. 147.

Prosopis (*Hoploprosopis*) HEDICKE, 1926, *Deutsche Ent. Zeitschr.*, p. 415.

Prosopis (*Barbata*) MÉHELY¹ (not Humphrey), 1935, *Naturgeschichte der Urbienen*, p. 135.

Prosopis (*Abrupta*) MÉHELY, 1935, *op. cit.*, p. 137.

Prosopis (*Pseudobranchiata*) MÉHELY, 1935, *op. cit.*, p. 139.

Prosopis (*Navicularia*) MÉHELY, 1935, *op. cit.*, p. 140.

Prosopis (*Auricularia*) MÉHELY (not Blainville), 1935, *op. cit.*, p. 147.

Prosopis (*Cingulata*) MÉHELY, 1935, *op. cit.*, p. 149.

Prosopis (*Fasciata*) MÉHELY, 1935, *op. cit.*, p. 150.

Prosopis (*Dentigera*) MÉHELY, 1935, *op. cit.*, p. 151.

Prosopis (*Imperfecta*) MÉHELY, 1935, *op. cit.*, p. 154.

Prosopis (*Campanularia*) MÉHELY (not Lamarck), 1935, *op. cit.*, p. 157.

Prosopis (*Pectinata*) MÉHELY, 1935, *op. cit.*, p. 161.

Prosopis (*Trichota*) MÉHELY, 1935, *op. cit.*, p. 169.

Prosopis (*Lambdopsis*) MÉHELY, 1935, *op. cit.*, p. 171.

Prosopis (*Spatularia*) MÉHELY (not van Deventer), 1935, *op. cit.*, p. 175.

Prosopis (*Mehelya*) POPOV (not Csiki), 1939, *Compt. Rendus (Doklady) Acad. Sci. U.R.S.S.*, new ser., vol. 25, p. 167.

Prosopis (*Paraprosopis*) POPOV, 1939, *ibid.*, new ser., vol. 25, p. 169.

Prosopis (*Spatulariella*) POPOV, 1939, *ibid.*, new ser., vol. 25, p. 169.

Hylaeus (*Metziella*) MICHENER, 1942, *Jour. New York Ent. Soc.*, vol. 50, p. 273.

¹ I have not seen Méhely's "Naturgeschichte der Urbienen," but according to Sandhouse (1943) he designated no genotypes for his subgenera, which are therefore invalid under article 25c of the International Rules of Zoological Nomenclature. If this decision is followed, the names will be credited to Popov, 1939, *Compt. Rendus (Doklady) Acad. Sci. U.R.S.S.*, new ser., vol. 25, pp. 167-169.

Hylaeus (*Cephalylaeus*) MICHENER, 1942, *ibid.*, vol. 50, p. 273.

Mehelyana SANDHOUSE, 1943, Proc. U. S. Natl. Mus., vol. 92, p. 569.

GENOTYPE: *Apis annulata* Linnaeus, designated by Latreille, 1810, *Considérations générales . . . des insectes*, p. 438.

A proposal has been put before the International Commission on Zoological Nomenclature suggesting that *Hylaeus* be set aside in favor of *Prosopis*, more common in current European use. *Hylaeus*, however, has been in more or less frequent use ever since 1793, and is in general use in the United States. Hence it seems best to continue to use that name for the present.

While there are many Old World groups of *Hylaeus*, the species occurring in the United States fall into but five subgenera, separated as follows (key based entirely on males).

KEY TO THE NEARCTIC SUBGENERA OF *Hylaeus*

1. Scape of antenna at least as broad as long, greatly enlarged; anterior tentorial pits above middles of lateral margins of clypeus *Cephalylaeus*
Scape of antenna not greatly enlarged; anterior tentorial pits near middles of lateral margins of clypeus 2
2. Apical process of ninth sternum bare, not or scarcely bifid; apical lobes of eighth sternum rather small, neither pectinate nor deeply emarginate; gonocoxites scarcely broadened basally 3
Apical process of ninth sternum (in North American forms) bifid and nearly always hairy; apical lobes of eighth sternum large, outer margin pectinate or with a deep emargination; gonocoxites expanded basally 4
3. Apical process of ninth sternum considerably shorter than disk of sternum, acute. *Metsiella*
Apical process of ninth sternum as long as disk of sternum, truncate or a little emarginate apically *Prosopis*
4. Apical lobe of eighth sternum with a number of small processes so that outer margins are pectinate; pubescence present on both anterior and posterior parts of lobes. *Hylaeus, sensu stricto*
Apical lobes of eighth sternum not pectinate, but outer margins each with a deep emargination, pubescence usually confined to the narrow process anterior to emargination *Paraprosopis*

SUBFAMILY CHILICOLINAE

Glossa bilobed, the lobes short and rounded; proboscis elongate much as in *Halictus*, cardines, stipites, and prementum very long, and prepalpal portions of galeae several times as long as postpalpal portions; malar areas somewhat elongate; entire head often more or less oval; clypeus longer than broad, although with anterior tentorial pits below its middle; pre-episternal suture complete; anterior wings with two submarginal cells, second much smaller than first, each receiving a recurrent vein; jugal lobe of posterior wings but little exceeded by vannal lobe; wings hairy throughout, not papillate; scopa and pygidial plate absent.

This Neotropical subfamily includes the genus *Chilicola* and no doubt *Oediscelis* (= *Hylaeosoma*) and *Idioprosopis*. Cockerell's genus *Xeromelissa* possibly belongs here, although it more likely represents a distinct subfamily.

FAMILY ANDRENIDAE

Labrum broader than long; subantennal areas defined by sutures (fig. 91); epistomal suture angulate at lower ends of each of the four subantennal sutures; lateral margins of clypeus below anterior tentorial pits usually concave; lower sides of clypeus bent backward more or less parallel to long axis of body (except in many species of *Andrena*), but clypeus not strongly protuberant; facial foveae usually present; stipites without combs; galeae short prepalpally and usually so postpalpally, often with a comb on inner side of each; mentum and submentum variable; labial palpi short, the segments similar or first segment elongated and flattened, very rarely first two segments elongated; glossa short or long, acute, without a flabellum; hypostoma fused to tentorium in rear fourth to three-fourths of their lengths; pre-episternal sutures absent to distinct below scrobal sutures; metanotum horizontal; middle coxae short as seen externally, far shorter than distance from summits to posterior wing bases; jugal lobe of posterior wing at least nearly three-fourths as long as vannal lobe; basitibial and pygidial plates present in females; volsellae present.

The most characteristic feature of this family is the presence of the defined sub-

antennal areas (fig. 91). These are most conspicuous in species with extensive yellow facial markings in which the sutures stand out as black lines. In other forms it is often necessary to scrape away a little hair below the base of one antenna in order to see the rather feeble sutures.

This family is divisible into three very distinct subfamilies.

KEY TO THE SUBFAMILIES OF ANDRENIDAE

1. Marginal cell with apex pointed on the costal margin of the wing or very narrowly rounded (fig. 169); mentum with sides subparallel Andreninae
Marginal cell truncated or with apical portion bent away from costal margin of wing; mentum variable 2
2. Pterostigma virtually absent; mentum and submentum absent as distinct sclerites; apices of posterior femora of female enlarged and flattened to form a plate associated with, and similar to, basitibial plate Oxaeinae
Pterostigma moderate to large in size; mentum tapering basally; submentum V-shaped; apices of posterior femora unmodified Panurginae

SUBFAMILY ANDRENINAE

Facial foveae large (fig. 91) and usually covered with minute hairs giving a golden or reddish brown sheen in females, but in males foveae absent or virtually undefined and not clothed with minute hairs; first flagellar segment rarely a little more than half as long as scape, usually much shorter; submentum more or less plate-like, transverse, but because it is produced posteriorly in the middle of the distal margin for the reception of base of mentum, it closely approaches V-shaped condition of long-tongued bees; maxillary palpi six-segmented; segments of labial palpi cylindrical, similar to one another; glossa usually short, acute; pre-episternal sutures absent below scrobal sutures; pterostigma moderate to large in size; marginal cell longer than distance from apex to wing tip; scopa present from coxae to basitarsi of posterior legs; male gonostyli absent or fused with gonocoxites.

This family is represented by the great, primarily Holarctic genus *Andrena* and by two small genera of doubtful distinctness found in the deserts of California.

KEY TO THE GENERA OF ANDRENINAE

1. Pterostigma almost always broader than distance from inner margin of prestigma to costal margin of wing and at least half as long as distance from its apex to apex of marginal cell (fig. 169); male gonocoxites each with a dorsal lobe or angle (sometimes reduced as in *A. crataegi* and *A. solitaria*) so that the subcontiguous basal portions of the gonocoxites are at least one-fourth and usually one-half the length of the gonocoxites. *Andrena*
Pterostigma as broad as distance from inner margin of prestigma to costal margin of wing and less than one-half as long as distance from its apex to apex of marginal cell; male gonocoxites not as in *Andrena* 2
2. Male gonocoxites with dorsal lobes very large and extending apically so as nearly to obscure, from above, the small, delicate, lateral, basally constricted and apically spatulate homologues of the apical lobes of *Andrena*; posterior trochanter of female with numerous long, more or less curled hairs. *Megandrena*
Male gonocoxites with dorsal lobes absent, apical portions not flattened and thin but slender and thickly sclerotic; subcontiguous basal portions of gonocoxites less than one-fourth as long as gonocoxites; posterior trochanters of female with pubescence straight, not unusually long *Ancylandrena*

GENUS ANDRENA FABRICIUS

Andrena FABRICIUS, 1775, *Systema entomologiae* . . . , p. 376.

Anthrena ILLIGER, 1801, *Mag. Insektenkunde*, vol. 1, p. 127.

Melittidia GUÉRIN-MÉNEVILLE, 1830, in *Du-perry. Voyage autour du monde* . . . sur . . . La Coquille, . . . , *Zool.*, vol. 2, pt. 2, p. 270.

Anthocharessa GISTEL, 1850, *Isis (Encycl. Zeitschr.)*, no. 6, p. 82.

Campylogaster DOURS, 1873, *Rev. Mag. Zool.*, ser. 3, vol. 1, p. 286.

Biareolina DOURS, 1873, *ibid.*, ser. 3, vol. 1, p. 288.

Melandrena PÉREZ, 1890, *Actes Soc. Linnéene Bordeaux*, vol. 44, p. 170.

Hoplendrena PÉREZ, 1890, *ibid.*, vol. 44, p. 170.

Simandrena PÉREZ, 1890, *ibid.*, vol. 44, p. 174.

Holandrena PÉREZ, 1890, *ibid.*, vol. 44, p. 176.

Scapteroides GRIBODO, 1894, *Bull. Soc. Ent. Italiana*, vol. 26, p. 112.

Melittidia DALLA TORRE, 1896, *Catalogus hymenopterorum*, vol. 10, p. 99.

Parandrena ROBERTSON, 1897, *Trans. Acad. Sci. St. Louis*, vol. 7, p. 337.

Callandrena COCKERELL, 1898, *Trans. Amer.*

Ent. Soc., vol. 25, p. 186.

Micrandrena ASHMEAD, 1899, Trans. Amer. Ent. Soc., vol. 26, p. 89.

Iomelissa ROBERTSON, 1900, Trans. Acad. Sci. St. Louis, vol. 10, p. 50.

Trachandrena ROBERTSON, 1902, Trans. Amer. Ent. Soc., vol. 28, p. 189.

Ptilandrena ROBERTSON, 1902, *ibid.*, vol. 28, p. 192.

Opandrena ROBERTSON, 1902, *ibid.*, vol. 28, p. 193.

Pierandrena ROBERTSON, 1902, *ibid.*, vol. 28, p. 193.

Diandrena COCKERELL, 1903, Psyche, vol. 10, p. 75.

Andrena (*Gonandrena*) VIERECK, 1917, Trans. Amer. Ent. Soc., vol. 43, p. 390.

Andrena (*Scrapieropsis*) VIERECK, 1922, Occas. Papers Boston Soc. Nat. Hist., vol. 5, p. 42.

Andrena (*Conandrena*) VIERECK, 1924, Canadian Ent., vol. 56, p. 20.

Andrena (*Dactylandrena*) VIERECK, 1924, *ibid.*, vol. 56, p. 20.

Andrena (*Tropandrena*) VIERECK, 1924, *ibid.*, vol. 56, p. 21.

Andrena (*Platandrena*) VIERECK, 1924, *ibid.*, vol. 56, p. 21.

Andrena (*Andrenella*) HEDICKE, 1933, Mitt. Zool. Mus. Berlin, vol. 19, p. 210.

Andrena (*Charitandrena*) HEDICKE, 1933, *ibid.*, vol. 19, p. 210.

Andrena (*Chrysandrena*) HEDICKE, 1933, *ibid.*, vol. 19, p. 211.

Andrena (*Cnemidandrena*) HEDICKE, 1933, *ibid.*, vol. 19, p. 212.

Andrena (*Euandrena*) HEDICKE, 1933, *ibid.*, vol. 19, p. 212.

Andrena (*Glyphandrena*) HEDICKE, 1933, *ibid.*, vol. 19, p. 213.

Andrena (*Gymnandrena*) HEDICKE, 1933, *ibid.*, vol. 19, p. 213.

Andrena (*Lepidandrena*) HEDICKE, 1933, *ibid.*, vol. 19, p. 215.

Andrena (*Leucandrena*) HEDICKE, 1933, *ibid.*, vol. 19, p. 215.

Andrena (*Plastandrena*) HEDICKE, 1933, *ibid.*, vol. 19, p. 217.

Andrena (*Poecilandrena*) HEDICKE, 1933, *ibid.*, vol. 19, p. 218.

Andrena (*Schizandrena*) HEDICKE, 1933, *ibid.*, vol. 19, p. 218.

Andrena (*Taeniandrena*) HEDICKE, 1933, *ibid.*, vol. 19, p. 219.

Andrena (*Zonandrena*) HEDICKE, 1933, *ibid.*, vol. 19, p. 220.

GENOTYPE: *Apis helvola* Linnaeus, designated by Viereck, 1912, Proc. U. S. Natl. Mus., vol. 42, p. 613.

This is one of our most abundant genera of bees, both in species and individuals. Several attempts have been made to define subgenera, but none are satisfactory. A careful study of a very great number of species will be necessary before this can be properly done. Certain of the subgenera, however, are rather distinctive and these are here briefly characterized.

Iomelissa, consisting of a single species oligolectic on the flowers of violets, may be recognized by the elongate and unusually hairy glossa. *Callandrena*, *Diandrena*, and *Parandrena*, frequently but seemingly unjustifiably regarded as distinct genera, have but two submarginal cells, thus differing from other groups. *Diandrena* consists of blue or green bees, without yellow on the face of the male and with the head and thorax dull as a result of fine roughening. *Callandrena* and *Parandrena* are black. *Callandrena* (from Lower California) differs from *Parandrena* in the presence of a large yellow area on the clypeus and on the paraocular areas in both sexes, and the reduced pterostigma, approaching that of *Ancylandrena* and *Megandrena*. Its genitalia, however, are as in typical *Andrena*. The species of *Trachandrena* have the basal area of the propodeum large, defined, and strongly roughened and the posterior margins of the abdominal terga very broadly depressed. The very numerous remaining species of *Andrena* comprise several subgenera, which will probably be definable when adequately studied.

Keys to species of certain areas or to certain groups of species have been given by Robertson (1902a), Bruner (1903), Viereck (1916), Atwood (1934), Linsley (1938), Lanham (1941), and others.

GENUS ANCYLANDRENA COCKERELL

Andrena (*Ancylandrena*) COCKERELL, 1930, Pan-Pacific Ent., vol. 7, p. 5.

GENOTYPE: *Andrena* (*Ancylandrena*) *heterodoxa* Cockerell = *A. atoposoma* Cockerell (monobasic).

This genus is represented by two species, one as yet undescribed, found in the arid parts of California. These are forms with black integument and much pale hair; clypeus of male black, but paraocular areas yellow below. In both this and the following

genus the scopa of the tibiae and the rather unusually short basitarsi consists of long hairs, much less compact than in *Andrena*.

GENUS *MEGANDRENA* COCKERELL

Andrena (*Megandrena*) COCKERELL, 1927, Pan-Pacific Ent., vol. 4, p. 42.

GENOTYPE: *Andrena* (*Megandrena*) *enceliae* Cockerell (monobasic).

This genus is represented by a single species found in the California desert. It is 13 to 16 mm. in length, with black integument (except for the yellow clypeus and lower parts of the paraocular areas in the male) and long white hair forming even, broad, abdominal fasciae.

SUBFAMILY PANURGINAE

Facial foveae, when present, much smaller than in Andreninae, not clothed with fine hairs, and frequently distinct in males as well as in females; submentum V-shaped; mentum tapering basally; labial palpi frequently with first segment much elongated; maxillary palpi usually six-segmented but reduced in some species of *Perdita*; pterostigma usually rather large; marginal cell, which is usually not longer than distance from apex to apex of wing, usually obliquely truncate apically but sometimes merely bent away from wing margin; scopa primarily confined to posterior tibiae and basitarsi; male gonostyli commonly distinct from gonocoxites.

KEY TO THE TRIBES OF PANURGINAE

1. With three submarginal cells, the first about as long as second; facial foveae absent in female; eyes of male strongly convergent above Melitturgini
- With two submarginal cells, or if with three first much longer than second; facial foveae present in female; eyes of male but little, if at all, convergent above. Panurgini

TRIBE MELITTURGINI

This tribe is represented by the single Old World genus *Melitturga* (often incorrectly called *Melitura*). It exhibits many similarities to the Neotropical Oxaeinae; the antennae are very short, although the first flagellar segment is longer than the scape; the eyes are strongly convergent above and the ocelli placed far down on the face near

the antennal bases in the males; the facial foveae are absent, at least in the females. The pterostigma is small, although not absent as in the Oxaeinae. The first two segments of the labial palpi are elongated and slightly flattened.

TRIBE PANURGINI

This is a tribe represented by a number of genera and is found in all the continents except Australia. The first flagellar segment is much shorter than the scape, eyes not, or but little, convergent above, ocelli near summit of head, facial foveae present in females and many males; pterostigma moderate to large in size, none, or only the first, of the labial palpal segments elongated and flattened.

In addition to the North American genera listed below, this tribe includes such forms as *Acamptopoeum* (= *Liopoeum*), *Camplopoeum*, *Epimethia*, *Liphanthus*, *Meliturgula*, *Parafriesea* (? = *Calliopsis*), *Parapsaenythia*, *Poecilomeliitta*, *Rhopitulus*, and probably *Anthrenoides*.

KEY TO THE NORTH AMERICAN GENERA OF PANURGINI

1. With three submarginal cells, second quadrate. *Psanythia*
With two submarginal cells, or if with three as in some *Perdita*, second small, triangular, petiolate. 2
2. Last submarginal cell much shorter than first and but little longer than broad . . . *Perdita*
Second submarginal cell as long as or but little shorter than first, much longer than broad . 3
3. Inner subantennal sutures longer than width of subantennal areas; gonostyli at least not greatly exceeded by penis valves; pterostigma considerably broader than prestigma. 4
Inner subantennal sutures shorter than, or at most as long as, width of subantennal areas; gonostyli reduced, if distinct greatly exceeded by penis valves; pterostigma slender, rarely broader than distance from inner margin of prestigma to costal margin of wing 5
4. First recurrent vein approximately interstitial with first transverse cubital; body minutely roughened between fine punctures; seventh abdominal sternum of male heavily sclerotic with a shallow apical emargination, the margin of which is thickened *Panurginus*
First recurrent vein considerably distad of first transverse cubital; body shining between

- rather coarse punctures; seventh abdominal sternum of male thin, submembranous, with median apical cleft *Pseudopanurgus*
5. Anterior margin of clypeus with at least a slight convexity medially overhanging the subapical groove in which a row of hairs arises; abdominal terga with yellow or white integumental fasciae or maculations and without conspicuous pubescent fasciae . *Nomadopsis*
Anterior margin of clypeus not convex medially, except in female of *Hypomacrotera callops* (Cockerell), the subapical groove being open and often giving rise to but few hairs; abdomen without pale integumental maculations 6
6. Pterostigma from base to vein r but little longer than prestigma; distance from apex of pterostigma to costal end of truncation of marginal cell about equal to distance from latter point to wing tip; abdominal terga with apical pubescent fasciae; middle tarsi of male usually longer than hind tarsi. . . *Calliopsis*
Pterostigma from base to vein r nearly twice length of prestigma; distance from apex of pterostigma to costal end of truncation of marginal cell much longer than distance from latter point to wing tip; abdominal terga without pubescent fasciae; middle and hind tarsi of male about equal in length
. *Hypomacrotera*

Campiopoeum semirufum Cockerell was described from Texas in 1937. It appears to be based on a specimen of *Pseudopanurgus abdominalis* (Cresson). *Campiopoeum* as now restricted is an Old World genus.

GENUS PSAENYTHIA GERSTAECKER

Psaenythia GERSTAECKER, 1868, Arch. Naturgesch., vol. 34, p. 111.

Protandrena COCKERELL, 1896, Ann. Mag. Nat. Hist., ser. 6, vol. 18, p. 91; COCKERELL, 1896, Canadian Ent., vol. 28, p. 184.

Protandrena (*Austrandrena*) COCKERELL, 1906, Psyche, vol. 13, p. 37.

GENOTYPE: *Psaenythia philanthoides* Gerstaecker, designated by Sandhouse, 1943, Proc. U. S. Natl. Mus., vol. 92, p. 592.

This is our only genus of Panurgini exhibiting three large submarginal cells, although the African *Meliturgula* and *Poecilomelitta* resemble it in this respect. The South American groups *Anihrenoides* and *Parapsaenythia* probably should be included in *Psaenythia*. The genus is divisible into at least two sub-

genera, *Psaenythia*, *sensu stricto*, occurring in South America and having yellow abdominal markings and coarsely serrate posterior tibial spurs, and *Protandrena*, occurring in Mexico and the Great Plains and Rocky Mountains of the United States and westward to Arizona, with the abdomen entirely black and the posterior tibial spurs finely serrate. *Psaenythia*, *sensu stricto*, also is distinguished by the presence of a longitudinal carina on the inner surface of the posterior femur. On this carina or ridge arises a fringe of long hairs, and behind it the surface of the femur is smooth and shining.

Our species of this genus are rather coarsely punctate, black, usually with yellow markings on the face, thorax, and legs. The pterostigma is rather large and usually exhibits a distinct angle in its margin between vein r and the apex. The inner subantennal sutures are considerably longer than the width of the subantennal plates.¹ There is no median convexity in the distal margin of the clypeus as in *Nomadopsis*. The facial foveae are slender, broadest above and tapering below, smaller in the males than in the females. The pre-episternal suture is present far below the scrobal suture.

GENUS PANURGINUS NYLANDER

Panurginus NYLANDER, 1848, Notiser Sällskapet Fauna Flora Fennica, vol. 1, p. 223.

Greeleyella COCKERELL, 1904, Entomologist, vol. 37, p. 235.

Birkmania VIERECK, 1909, Proc. Ent. Soc. Washington, vol. 11, p. 50.

GENOTYPE: *Panurginus niger* Nylander (monobasic).

This is a Holarctic genus of slender bees, often with yellow areas on the clypeus and legs in the males. The facial foveae are broadly linear and low on the face in the females, inconspicuous or absent in males. The pre-episternal sutures are absent.

The American species of the genus were revised by Crawford (1926), and a group of them by Michener (1935).

¹ Certain small South American species usually placed in this genus have short subantennal plates and usually exceptionally long male antennae. These are to be included in the genus *Liphanthus*.

GENUS *PSEUDOPANURGUS* COCKERELL

Pseudopanurgus COCKERELL, 1897, Canadian Ent., vol. 29, p. 290.

Anthemurgus ROBERTSON, 1902, Canadian Ent., vol. 34, p. 321.

Protandrenopsis CRAWFORD, 1903, Canadian Ent., vol. 35, p. 337.

Heterosarus ROBERTSON, 1918, Ent. News, vol. 29, p. 91.

GENOTYPE: *Panurgus aethiops* Cresson, by original designation.

This genus has a distribution similar to that of *Psaenythia*, but is much more common and more widely distributed in North America, being represented by many species in the Rocky Mountain area and by a few species ranging as far as the Atlantic and Pacific coasts. It is divisible into three subgenera, of which only *Heterosarus* is known in South America. Although a few species of *Pseudopanurgus* have the abdomen red, most are black with varying yellow markings on the face, thorax, and legs, especially of the males.

KEY TO THE SUBGENERA OF *Pseudopanurgus*

1. Segments of labial palpi subequal in length. *Anthemurgus*
First segment of labial palpus much longer than others 2
2. First segment of labial palpus much longer than following segments together; rather large forms, females robust *Pseudopanurgus, sensu stricto*
First segment of labial palpus about as long as following segments together; small, slender forms *Heterosarus*

The species of the last subgenus superficially resemble *Panurginus* and have been placed in that genus by Cockerell and others.

GENUS *NOMADOPSIS* ASHMEAD

Nomadopsis ASHMEAD, 1898, Psyche, vol. 8, p. 285.

Spinoliella ASHMEAD, 1899, Trans. Amer. Ent. Soc., vol. 26, p. 84.

Spinoliella (Claremontiella) COCKERELL, 1933, Pan-Pacific Ent., vol. 9, p. 26.

GENOTYPE: "*Perdita*" *zonalis* Cresson, *lapsus calami* for *Calliopsis zonalis* Cresson, by original designation.

This is a rather large genus of moderate-sized to small bees, black with usually extensive yellow or white maculations. It is found

in the western half of the United States and thence southward into at least the more arid parts of South America.

The North American species of the genus have, since their separation from *Calliopsis*, usually been placed in the genus *Spinoliella* Ashmead. The type of that genus is a South American form apparently closely related to our species. Failure to use the name *Nomadopsis* for our forms is entirely a result of an error in citing the type species. Cresson long ago described a species in the genus *Perdita* and another in the genus *Calliopsis* under the specific name *zonalis*. Ashmead, in 1898 (Psyche, vol. 8, p. 285), named *Nomadopsis* and cited as its type *Perdita zonalis* Cresson. Clearly from his description he intended to write *Calliopsis zonalis* Cresson, and Ashmead himself made this correction the next year (Psyche, vol. 9, p. 375) when he cited the type of *Nomadopsis* as *C. zonalis*. It has been said that Ashmead's specimens were in reality *Spinoliella euxantha* Cockerell, but this probably cannot be proved. Hence the type of *Nomadopsis* must be regarded as *Calliopsis zonalis* Cresson.

GENUS *PERDITA* SMITH

Perdita SMITH, 1853, Catalogue of hymenopterous insects in the . . . British Museum, pt. 1, p. 128.

Macrotera SMITH, 1853, *op. cit.*, pt. 1, p. 130.

Cockerellia ASHMEAD, 1898, Psyche, vol. 8, p. 284.

Philoxanthus ASHMEAD, 1898, *ibid.*, vol. 8, p. 285.

Macroteropsis ASHMEAD, 1899, Trans. Amer. Ent. Soc., vol. 26, p. 85.

Perdita (Pentaperdita) COCKERELL AND PORTER, 1899, Ann. Mag. Nat. Hist., ser. 7, vol. 4, p. 415.

Perdita (Tetraperdita) COCKERELL AND PORTER, 1899, *ibid.*, ser. 7, vol. 4, p. 415.

Perdita (Geoperdita) COCKERELL AND PORTER, 1899, *ibid.*, ser. 7, vol. 4, p. 415.

Perdita (Perditella) COCKERELL, 1899, Psyche, vol. 8, p. 312.

Glossoperdita COCKERELL, 1916, Jour. Ent. Zool., vol. 8, p. 43.

Perdita (Alloperdita) VIERECK, 1917, Bull. Amer. Mus. Nat. Hist., vol. 37, p. 241.

Zaperdita ROBERTSON, 1918, Ent. News, vol. 29, p. 91.

Perdita (Lutsiella) COCKERELL (not Enderlein), 1922, Amer. Mus. Novitates, no. 47, p. 1.

Xerophasma COCKERELL, 1923, *ibid.*, no. 66, p. 1.

Perdita (*Cockerellula*) STRAND, 1932, Folia Zool. Hydrobiol., vol. 4, p. 196.

GENOTYPE: *Perdita halictoides* Smith (monobasic).

This is a North American genus containing many species of minute or moderate-sized bees. Species are few in the eastern states but numerous in the arid west. They exhibit great morphological differences, and many subgeneric and generic names have been proposed for the variants. However, as yet no satisfactory subgeneric classification has been given. Some forms (*Macrotera* and *Macroteropsis*) with a long, slender pterostigma but little broader than the prestigma and similar in shape to that of *Calliopsis* perhaps represent a genus distinct from the numerous forms with very large pterostigmata. The facial foveae are usually rather low on the face, linear in females and linear, punctiform, or absent in males. The pre-episternal suture is absent below the scrobal suture.

The species of this genus were revised by Cockerell (1896), and a list of the forms was given by the same author in 1911. Extensive unpublished manuscripts on the genus have been written by Timberlake. *Xerophasma* is little more than a nocturnal *Perdita* with large ocelli and three submarginal cells as in the subgenus *Alloperdita*.

GENUS CALLIOPSIS SMITH

Calliopsis SMITH, 1853, Catalogue of hymenopterous insects in the . . . British Museum, pt. 1, p. 128.

Calliopsis (*Verbenapis*) COCKERELL AND ATKINS, 1902, Ann. Mag. Nat. Hist., ser. 7, vol. 10, p. 44.

Calliopsis (*Perissander*) MICHENER, 1942, Jour. New York Ent. Soc., vol. 50, p. 275.

GENOTYPE: *Calliopsis andreniformis* Smith, by designation of Ashmead, 1899, Trans. Amer. Ent. Soc., vol. 26, p. 85.

This is a genus having the abdomen rather broad and flattened as in *Nomadopsis* rather than slender as in *Panurginus*. Rather extensive yellow or white markings are found on the face, thorax, and legs. There are not a great many species, but they occur from coast to coast in North America. The South American genus *Parafriesea*, to judge by the single female specimen before me, is probably a mere subgenus of *Calliopsis*.

The subgenus *Verbenapis* differs from other species of *Calliopsis* by the very long galeae, long basal segment of the labial palpi, and the hairs of the front tarsi of the female which are used to draw pollen from the slender flowers of *Verbena*. The subgenus *Perissander* is distinguished by the exceedingly long middle tarsi and the distorted and infuscated wing apices of the male.

GENUS HYPOMACROTERA COCKERELL AND PORTER

Hypomacrotera COCKERELL AND PORTER, 1899, Ann. Mag. Nat. Hist., ser. 7, vol. 4, p. 418.

GENOTYPE: *Hypomacrotera callops* Cockerell and Porter, by original designation.

This small genus, found in the southwestern United States, is black with certain pale areas on the face and legs and often with the abdomen of the female largely red. The tips of the wings of the males are infuscated.

SUBFAMILY OXAEINAE

The Oxaeinae contains a few very large Neotropical bees, ranging north as far as the southwestern United States. As already stated this group has many points of similarity to the Melitturgini.

Facial foveae absent; ocelli low on face, near antennal bases; first flagellar segment as long as scape, others very short; inner orbits of males strongly converging above; mentum and submentum absent as distinct sclerites; basal segment of labial palpi flattened and elongated; pre-episternal suture absent below scrobal suture; pterostigma virtually absent; marginal cell narrow, longer than distance from apex to wing tip, apex bent away from wing margin; three submarginal cells, third largest, second shortest on posterior margin; distal part of wing strongly papillate; scopa abundant from coxa to basitarsus; male genital capsule tapering basally so that gonobase is small.

This subfamily contains but two genera, *Oxaea* and *Protoxaea*. In the former the maxillary palpi are wanting. In the latter they are long and six-segmented. *Protoxaea* is the only genus occurring in the United States.

GENUS PROTOXAEA COCKERELL AND PORTER

Protoxaea COCKERELL AND PORTER, 1899, Ann. Mag. Nat. Hist., ser. 7, vol. 4, p. 410.

GENOTYPE: *Megacilissa gloriosa* Fox, by original designation.

These are large, hairy, fast flying bees, found in southern parts of the United States from Texas to Arizona, and thence southward through Mexico.

FAMILY HALICTIDAE

Labrum broader than long, or if not, as in females of some groups, apex produced to form a broad, acutely pointed process (figs. 125, 126); subantennal areas absent; lower sides of clypeus not bent back parallel to long axis of body; subantennal sutures directed toward inner margins of antennal sockets (except in *Systropha*, etc.); facial foveae ordinarily absent; stipites without combs; galeae without combs, elongated prepally, not postpally, the pre-palpal portion of each tapering evenly to an acute base; mentum and submentum absent; labial palpi ordinarily with segments similar and cylindrical, rarely with first one, two, or three segments much elongated; glossa acute, usually short, without flabellum; hypostoma fused with tentorium for its entire length; pre-episternal sutures usually complete; metanotum horizontal (fig. 150); middle coxae with exposed parts much shorter than distance from summits to posterior wing bases (fig. 150); basitibial plate usually present in females except in parasitic genera; jugal lobe of posterior wings much more than half as long as vannal lobe; pygidial plate present in females; volsellae present.

This distinctive family is easily recognized by the long prepalpal parts of the galeae, and by the absence of mentum and submentum. The more common American forms may be distinguished by the strong arcuation or angulation of the first abscissa of vein M (fig. 170), the three submarginal cells, and the complete pre-episternal suture.

KEY TO THE SUBFAMILIES OF HALICTIDAE

1. Clypeus short, ordinarily not longer than labrum which is broadly rounded or truncate at apex; clypeus seen in profile ordinarily rounded and protuberant beyond level of the nonprotuberant supraclypeal area; antennal sockets usually well below middle of face Dufoureae
- Clypeus longer than labrum, the apex of which in females is often provided with broad, pointed process; clypeus seen in profile not strongly convex and not protuberant beyond level of supraclypeal area 2

2. Pre-episternal suture conspicuous and complete (fig. 150); first submarginal cell ordinarily longer than third when three are present; supraclypeal area convex and protuberant seen in profile Halictinae
- Pre-episternal suture absent or inconspicuous below scrobal suture; first and third submarginal cells subequal in length; supraclypeal area but little protuberant Nomiinae

SUBFAMILY HALICTINAE

Clypeus as seen in profile but little convex and not protuberant much beyond the level of the convex supraclypeal area; clypeus longer than labrum, which in females is commonly provided with a broad, pointed apical process; antennal sockets not, or but little, below middle of face; first abscissa of vein M (basal vein) strongly arcuate; scopa, when present, usually very extensive and found on posterior trochanters, femora, tibiae, and basitarsi; prepygidial fimbria usually divided by a longitudinal line without hairs or with only appressed hairs.

In a few genera of this subfamily the glossa is elongated and variously modified; the labial palpi, however, are not elongated as they are so often in the Dufoureae. While this is a world-wide subfamily, most of the genera occur in America. In addition to the North American genera listed below it includes *Acanthalictus*, *Caenohalictus*, *Chlerogas*, *Corynura*, *Diagonozus*, *Echthralictus*, *Eupestersia*, *Gastrohalictus*, *Lucasiellus* (= *Lucasius*), *Megalopta*, *Neocorynura* (= *Cacosoma*), *Nesohalictus*, *Nomioides*, *Oxyhalictus*, *Paragapostemon*, *Parasphecodes*, *Patellapis*, *Pseudagapostemon*, *Rhinotula*, *Rhopalictus*, *Rivalisia*, *Sudila* (= *Ceylonicola*), *Temnosoma*, *Thrinchostoma*.

KEY TO THE NEARCTIC GENERA OF HALICTINAE

1. Posterior tibiae as long as posterior tarsal segments together; head and thorax brilliant blue or green; abdomen of female green or brown or black, that of male yellow with transverse black (or dark blue) bands; second and third submarginal cells each receiving a recurrent vein *Agapostemon*
- Posterior tibiae as long as first two to four tarsal segments together; if brilliantly metallic as above, first recurrent vein (first m-cu) interstitial with or distad of first r-m. 2
2. Vein first m-cu interstitial with or received be-

- yond first r-m; brilliant metallic green or blue throughout 3
- Vein first m-cu received basad of first r-m (fig. 170), so that second and third submarginal cells each receive a recurrent vein (rarely first r-m absent, so that there are but two submarginal cells); black or dull metallic green or blue, sometimes with abdomen red. 4
3. Second and third abdominal terga with apical fringe of simple bristles, each of which arises from a puncture; tegulae large, subtruncate posteriorly, inner posterior angle nearly right angular; inner hind tibial spurs of female pectinate; labrum rounded at apex *Augochloropsis*
- Second and third abdominal terga unfringed or second only fringed with plumose hairs, their margins impunctate; tegulae moderate in size, rounded posteriorly; inner hind tibial spurs of female serrate; labrum produced to a triangular, acute process . . . *Augochlora*
4. Scopa absent; prepygidial fimbria of female reduced, not divided by longitudinal line; head and thorax coarsely punctate, dorsum of propodeum especially coarsely rugose; head and thorax black, not at all metallic, abdomen usually red, clypeus and legs not marked with yellow *Sphecodes*
- Scopa present in female; prepygidial fimbria ordinarily divided by longitudinal line; head and thorax more finely punctate, dorsum of propodeum more finely rugose, wrinkled, or striate; head and thorax sometimes slightly metallic; abdomen usually black; clypeus and legs of males sometimes marked with yellow. 5
5. Middle tibial spurs coarsely serrate with eight to ten large teeth; sixth abdominal tergum of female with a pair of apical dorsal lobes forming a deep, narrow notch between them; prepygidial fimbria not divided by a line; posterior margin of fifth abdominal sternum of male produced to large, flat plate. *Xeralictus*
- Middle tibial spurs very finely serrate; sixth abdominal tergum without a pair of dorsal apical lobes; prepygidial fimbria usually divided by a line; fifth abdominal sternum of male unmodified 6
6. Abdominal terga with subapical bands of pale pubescence; veins second r-m and second m-cu not weak *Halictus*
- Abdominal terga without subapical bands of pale pubescence, although often with basal bands of pale tomentum or pubescence; veins second r-m and second m-cu in female conspicuously fainter and narrower than other wing veins *Lasioglossum*

GENUS AGAPOSTEMON GUÉRIN-MÉNEVILLE

Agapostemon GUÉRIN-MÉNEVILLE, 1844, Iconographie du règne animal de G. Cuvier . . . , Insectes, vol. 3, p. 448.

GENOTYPE: *Apis femoralis* Guérin-Ménéville (monobasic).

This is a genus of rather large bees (8 to 14 mm. long) in which at least the head and thorax are brilliant metallic green or blue. In addition to the characters mentioned in the key, the marginal cell is narrowly truncate and conspicuously appendiculate; veins second r-m and second m-cu are strong as in *Halictus*, the inner hind tibial spurs of the female have a very few large teeth, the basitibial plate is obsolete, and the posterior surface of the propodeum is surrounded by a strong carina. The posterior femora of the males are frequently dilated. In the long posterior tibiae this genus resembles the otherwise very different Australian halictine bee, *Parasphecodes*.

Species of *Agapostemon* are found throughout most of North America. The species of the United States were revised by Sandhouse (1936).

GENUS AUGOCHLOROPSIS COCKERELL

Augochlora (*Augochloropsis*) COCKERELL, 1897, Canadian Ent., vol. 29, p. 4.

Augochloropsis (*Paraugochloropsis*) SCHROTKY, 1906, Zeitschr. Hymen. Dipt., vol. 6, p. 312.

GENOTYPE: *Augochloropsis subignita* Cockerell = *Augochlora ignita* Smith, by original designation.

The North American species of this genus are 10 to 13 mm. in length, more robust and more finely punctate than species of *Agapostemon* and larger than species of *Augochlora*. The marginal cell is narrowly truncate and feebly appendiculate, veins second r-m and second m-cu are strong as in *Halictus*, the basitibial plate is obsolete, and the posterior surface of the propodeum is not surrounded by a carina.

Like *Augochlora* this is a primarily Neotropical genus. It occurs in the United States only east of the Rocky Mountains and in Arizona. The species of this genus occurring in the United States have been revised by Sandhouse (1937).

GENUS AUGOCHLORA SMITH

Augochlora SMITH, 1853, Catalogue of hymenopterous insects in the . . . British Museum, pt. 1, p. 73.

Oxystoglossa SMITH, 1853, *op. cit.*, pt. 1, p. 83.

Odontochlora SCHROTKY, 1909, Rev. Mus. La Plata, vol. 16 (ser. 2, vol. 3), p. 141.

Augochlorella SANDHOUSE, 1937, Jour. Washington Acad. Sci., vol. 27, p. 66.

GENOTYPE: *Halictus purus* Say, designated by Cockerell, 1923, Ann. Mag. Nat. Hist., ser. 9, vol. 11, p. 448.

This genus includes the smallest of our brilliantly metallic Halictinae. The veins second r-m and second m-cu are strong as in *Halictus*, the basitibial plate of the female is defined, and the posterior surface of the propodeum is not surrounded by a carina.

KEY TO THE SUBGENERA OF *Augochlora*

1. Mandibles of female bidentate apically; second flagellar segment of male longer than first; preoccipital carina meeting hypostomal carinae; marginal cell narrowly truncate and appendiculate . . . *Augochlora*, *sensu stricto*
Mandibles of female with large, rounded, inferior tooth and smaller superior one; second flagellar segment of male subequal to first in length; preoccipital carina not reaching hypostomal carinae; marginal cell pointed . . . *Augochlorella*

These subgenera have been treated as distinct genera by Sandhouse (1937) who revised the species occurring in the United States. Many other species of *Augochlora* are found in the American tropics.

GENUS HALICTUS LATREILLE

Halictus LATREILLE, 1804, Nouveau dictionnaire d'histoire naturelle . . . , vol. 24, p. 182.

Seladonia ROBERTSON, 1918, Ent. News, vol. 29, p. 91.

Odontalictus ROBERTSON, 1918, *ibid.*, vol. 29, p. 91.

Halictus (Monilapis) COCKERELL, 1931, Ann. Mag. Nat. Hist., ser. 10, vol. 7, p. 529.

GENOTYPE: *Apis quadricincta* Fabricius, designated by Richards, 1935, Trans. Roy. Ent. Soc. London, vol. 83, p. 170.

This genus may be distinguished from all other Halictinae by the presence of subapical fasciae of pale pubescence on the abdominal terga. The marginal cell is pointed, but the apex slightly bent away from the wing margin and minutely appendiculate (fig. 170). The

basitibial plate of the female is present, and the inner hind tibial spurs of the female are coarsely serrate.

The species of this genus may be divided into two poorly differentiated subgenera, both found throughout the United States as well as in much of the Old World.

KEY TO THE AMERICAN SUBGENERA OF *Halictus*

1. At least some greenish or bluish reflections on head and thorax; length usually under 7 mm.; seventh sternum of male with median depression *Seladonia*
Entirely black, without metallic reflections; length over 7 mm.; seventh sternum of male without depression . . . *Halictus*, *sensu stricto*

Robertson's genus *Odontalictus* is to be included in the subgenus *Halictus*, *sensu stricto*, as here defined. The North American species of *Halictus* were revised by Sandhouse (1941).

GENUS LASIOGLOSSUM CURTIS

Lasioglossum CURTIS, 1833, British entomology . . . , vol. 10 [if bound as published in 16 vols.], pl. 448.

Hemihalictus COCKERELL, 1897, Canadian Ent., vol. 29, p. 288.

Sphecodogastra ASHMEAD, 1899, Trans. Amer. Ent. Soc., vol. 26, p. 92.

Paralictus ROBERTSON, 1901, Canadian Ent., vol. 33, p. 229.

Dialictus ROBERTSON, 1902, *ibid.*, vol. 34, p. 48.

Evyllaes ROBERTSON, 1902, *ibid.*, vol. 34, p. 247.

Chloralictus ROBERTSON, 1902, *ibid.*, vol. 34, p. 248.

Curtisapis ROBERTSON, 1918, Ent. News, vol. 19, p. 91.

GENOTYPE: *Lasioglossum tricingulum* Curtis = *Melitta xanthopus* Kirby (monobasic).

This genus may be distinguished from others by the faint distal veins of the forewings of the females. The marginal cell is pointed, not, or only minutely, appendiculate; the basitibial plate of the females is usually present. The species of this genus vary from 5 to nearly 12 mm. in length.

Lasioglossum is almost world-wide in distribution and found throughout the United States.

The genus is here used in a different sense from that of previous authors. It has usually been regarded either as a synonym of *Halictus* or, if separated generically or subgenerically from *Halictus*, the groups known as *Chloralictus*.

tus, *Evyllaes*, etc., have likewise been separated. However, in view of the weak distal veins of the wings, the absence of apical bands on the terga, etc., in *Lasioglossum* as here used, it seems that the relationships are more clearly indicated by the present arrangement. Furthermore, the various subgenera of *Lasioglossum* separated below, with the possible exception of the subgenera *Lasioglossum*, *sensu stricto*, and *Paralictus*, intergrade to a certain extent.

KEY TO THE SUBGENERA OF *Lasioglossum*

1. Vein first r-m in female strong like the more basal wing veins; rather large forms, usually black although *L. pavonotum* is strongly green *Lasioglossum*, *sensu stricto*
Vein first r-m in female weak, as are second r-m and second m-cu, rarely absent; large to small forms 2
2. Black, nonmetallic species; inner hind tibial spurs of female variable; large to small forms 3
Dull green species; inner hind tibial spurs of female with a few long teeth; primarily small forms 4
3. Scopa sparse, consisting of a row of simple bristles on trochanters and lower edges of femora, shorter bristles on upper part of femora, and some long, nearly simple hairs on inner sides of tibiae . . . *Sphecodogastra*
Scopa normal, largely plumose 6
4. Labrum of female with apex broadly rounded; mandibles of female simple; scopa reduced. *Paralictus*
Labrum of female with the usual apical process; mandibles of female dentate; scopa normal 5
5. With two submarginal cells *Dialictus*
With three submarginal cells *Chloralictus*
6. With two submarginal cells *Hemihalictus*
Normally with three submarginal cells *Evyllaes*

Hemihalictus is represented by a single species, apparently differing from *Evyllaes* only in the absence of vein first r-m. *Dialictus* consists of a few species differing from the large subgenus *Chloralictus* by the same character. *Evyllaes* and *Chloralictus* will fall as synonyms of *Hemihalictus* and *Dialictus*, respectively, if this character is not regarded as subgeneric in value. *Sphecodogastra* includes not merely *L. texanum* (Cresson), a form with unusually large ocelli, but also *L. aberrans* (Crawford), *galpinseae* (Cockerell), and apparently *oenotherae* (Stevens).

GENUS *XERALICTUS* COCKERELL

Xeralictus COCKERELL, 1927, Pan-Pacific Ent., vol. 4, p. 41.

GENOTYPE: *Xeralictus timberlakei* Cockerell (monobasic).

In this genus the labrum of the female, while obtusely angulate apically, does not bear a true process; the labrum of the male bears a median basal tubercle; the glossa is about ten times as long as broad; the mandibles of the male are very large and curiously angulate. The posterior margins of the abdominal terga lack pubescent fasciae. The distal veins of the forewing in the female are as strong as the others, not weak as in *Lasioglossum*, the marginal cell is pointed on the wing margin, three submarginal cells are present, basitibial plates are present in the female, the pygidial plate is partly exposed in the female, and the scopa, while well developed on the tibiae and basitarsi, is reduced on the trochanters and femora.

Xeralictus is known from a single species from the deserts of southern California.

GENUS *SPHECODES* LATREILLE

Sphecodes LATREILLE, 1804, Nouveau dictionnaire d'histoire naturelle . . . , vol. 24, p. 182.

Dichroa ILLIGER, 1806, Mag. Insektenkunde, vol. 5, p. 46.

Sabulicola VERHOEFF, 1890, Ent. Nachr., vol. 16, p. 328.

Drepanium ROBERTSON, 1903, Ent. News, vol. 14, p. 103.

Proteraner ROBERTSON, 1903, *ibid.*, vol. 14, p. 103.

Sphecodium ROBERTSON, 1903, *ibid.*, vol. 14, p. 104.

Machaeris ROBERTSON, 1903, *ibid.*, vol. 14, p. 104.

Dialonia ROBERTSON, 1903, *ibid.*, vol. 14, p. 104.

Sphecodes (*Callosphecodes*) FRIESE, 1909, Ann. Hist. Nat. Mus. Natl. Hungarici, vol. 7, p. 182.

GENOTYPE: *Sphex gibba* Linnaeus (monobasic).

This is a genus parasitic primarily upon species of *Halictus* and *Lasioglossum*. Males of certain species are difficult to distinguish from those of *Lasioglossum* but are more coarsely roughened, particularly on the propodeum, lack metallic reflections and yellow markings on the face and legs. The distal wing veins are strong, as in *Halictus*, and the basitibial plates of the female are obsolete.

Robertson has proposed a number of generic names for species ordinarily placed in *Sphecodes*; these names have usually been regarded as subgeneric in rank. Our species of the genus are so imperfectly known, however, that a satisfactory key to the subgenera cannot be made at the present time. *Sphecodes* is almost world-wide in distribution and found throughout the United States.

SUBFAMILY NOMIINAE

Clypeus seen in profile but little convex and not protuberant beyond level of more or less flat supraclypeal area; clypeus much longer than labrum; antennal sockets but little, if any, below level of middle of face. First abscissa of vein M commonly slightly bent, sometimes strongly so as in the Halictinae; scopa usually large and extending from posterior trochanters to basitarsi; prepygidial fimbria not divided by a longitudinal line.

In addition to *Nomia*, this subfamily includes the genera *Crocisaspidia*, *Crinoglossa*, *Meganomia*, *Reepenia*, and *Steganomus* (= *Cyathocera*).

The subfamily is represented in North America only by the genus *Nomia*. The other genera are found in the Old World.

GENUS NOMIA LATREILLE

Nomia LATREILLE, 1804, Nouveau dictionnaire d'histoire naturelle . . . , vol. 24, p. 182.

Nitocris RAFINESQUE, 1815, Analyse de la nature . . . , p. 123.

Eunomia CRESSON (not Hübner), 1875, in Report upon geographical and geological explorations and surveys west of the one hundredth meridian . . . Geo. M. Wheeler . . . , vol. 5, zool., p. 722.

Nomia (*Paranomia*) FRIESE (not Conrad), 1897, Festschr. Fünftzig. Bestehene Ver. Schlesische Insektenkunde, Breslau, p. 48.

Epinomia ASHMEAD, 1899, Trans. Amer. Ent. Soc., vol. 26, p. 88.

Dieunomia COCKERELL, 1899, Entomologist, vol. 32, p. 14.

Pseudapis KIRBY, 1900, Bull. Liverpool Mus., vol. 3, p. 15.

Hoplonomia ASHMEAD, 1904, Jour. New York Ent. Soc., vol. 12, p. 4.

Stictonomia CAMERON, 1905, Rec. Albany [South Africa] Mus., vol. 1, p. 192.

Nomia (*Macronomia*) COCKERELL, 1917, Ann. Durban Mus., vol. 1, p. 468.

Nomia (*Nomiapis*) COCKERELL, 1919, Proc. U. S. Natl. Mus., vol. 55, p. 208.

Nomia (*Acunomia*) COCKERELL, 1930, Amer. Mus. Novitates, no. 433, p. 11.

GENOTYPE: *Andrena curvipes* Fabricius (monobasic).

Many morphologically very different forms are included in *Nomia*, which may eventually be divided into several genera. Since the majority of the species occur in the Old World and specimens of most of them are not now available to me, it has seemed best to follow current practice in interpreting *Nomia* in the broad sense.

Species of the genus *Nomia* are found in many parts of the United States, but in any one locality very few occur.

KEY TO THE AMERICAN SUBGENERA OF *Nomia*

1. First abscissa of vein M (basal vein) strongly curved (as in *Halictus*); abdominal terga without green bands. *Curvinomia*
First abscissa of vein M but slightly curved; abdominal terga with or without green bands 2
2. Last antennal segments of male broad and flat; posterior basitarsi of male much longer than posterior tibiae; abdominal terga without green bands *Dieunomia*
Last antennal segments of male not broader than preceding segment; posterior basitarsi of male but little if any longer than tibiae; abdominal terga with or without green bands 3
3. At least certain abdominal terga with brilliant green or bluish green apical bands; distance from apex of pterostigma to apex of marginal cell greater than distance from latter point to wing tip *Acunomia*
Abdominal terga without green or blue bands; distance from apex of pterostigma to apex of marginal cell but little longer than distance from latter point to wing tip . . . *Epinomia*

The subgenus *Nomia*, *sensu stricto*, is restricted to the Old World. *Curvinomia*, new subgenus (type, *Nomia californiensis* Michener), differs from other American forms and resembles numerous African and Australian species as yet unplaced subgenerically in the curvature of the basal abscissa of vein M of the forewing. Unfortunately *Curvinomia* is unknown in the male. *Paranomia*, new name, is proposed for *Paranomia* Friese (not Conrad, 1860). The type is *Nomia chalybeata* Smith. Until additional material has been studied, the American species usually in-

cluded in *Paranomia* will be placed in *Acunomia*.

The most important papers on the North American species of *Nomia* are by Cockerell (1910) and Cockerell and Blair (1930).

SUBFAMILY DUFOUREINAE

Clypeus convex as seen in profile, protuberant beyond level of supraclypeal area, conspicuously short, ordinarily not longer than the labrum, the apex of which is broadly rounded or truncate; scopa largely confined to posterior tibiae and basitarsi; prepygidial fimbria not divided as in most Halictinae.

In this group the glossa and labial palpi are frequently elongated and the basal segments of the latter sometimes flattened.

In addition to *Dufourea* (and *Halictoides*) this subfamily includes the Old World genera *Rophites* (= *Rhophites*) and *Systropha* and the small New World genera *Conanthalictus* and *Micralictoides*. Furthermore, it very likely includes the Palearctic groups *Morawitzia* and *Trilia*.

The genus *Rophites* (with the subgenus *Rhophitoides*) is distinguished from the others by the elevated pygidial plate in the male. *Rhophitoides* differs from other groups in the subfamily by having the clypeus considerably longer than the labrum. *Systropha* resembles *Conanthalictus* in having three submarginal cells and plumose scopal hairs but is much larger with the male antennae greatly modified.

KEY TO THE AMERICAN GENERA OF DUFOUREINAE

1. With three submarginal cells *Conanthalictus*
 With two submarginal cells 2
2. Distance from apex of pterostigma to apex of marginal cell almost always at least as great as distance from apex of marginal cell to wing tip; ninth abdominal sternum of male without a spiculum but with a pair of basal lobes; penis valves large, elevated above bases of gonocoxites. *Dufourea*
 Distance from apex of pterostigma to apex of marginal cell less than distance from apex of cell to wing tip; ninth abdominal sternum of male with median basal angle (a blunt spiculum) but without pair of basal lobes; penis valves but little elevated above bases of gonocoxites *Micralictoides*

GENUS CONANTHALICTUS COCKERELL

Halictus (*Conanthalictus*) COCKERELL, 1901, Ent. News, vol. 12, p. 209.

? *Sphecodosoma* CRAWFORD, 1907, Jour. New York Ent. Soc., vol. 15, p. 182.

Conanthalictus (*Phaceliapis*) MICHENER, 1942, Jour. New York Ent. Soc., vol. 50, p. 277.

GENOTYPE: *Halictus conanthi* Cockerell (monobasic).

This is a genus of minute black or metallic greenish or bluish bees with the abdomen sometimes red. The body surface is exceedingly finely and closely punctate, giving it a dull satiny appearance. The pubescence is sparse, not forming conspicuous abdominal fasciae. Marginal cell longer than distance from apex to wing tip; first submarginal cell nearly as long as second and third together.

This genus is divisible into two or three subgenera. In *Conanthalictus*, *sensu stricto*, from Texas and New Mexico the head is considerably longer than broad, while in the Californian *Phaceliapis* the head is broader than long. Crawford's genus *Sphecodosoma* from Texas is apparently another subgenus of *Conanthalictus*, resembling *Conanthalictus*, *sensu stricto*, in the elongate head but differing in the linear glossa, ten times as long as broad. I have not seen specimens of *Sphecodosoma*.

GENUS MICRALICTOIDES TIMBERLAKE

Dufourea (*Micralictoides*) TIMBERLAKE, 1939, Ann. Ent. Soc. Amer., vol. 32, p. 397.

GENOTYPE: *Halictoides ruficaudus* Michener, by original designation.

This is a small genus, containing three known species of small bees, all from California. The females in particular are difficult to distinguish from *Dufourea*. The ninth sternum of the male exhibits a much more primitive condition in *Micralictoides* than in *Dufourea*. It is interesting to note that *Systropha* agrees with *Dufourea* in this character.

The species of this genus were reviewed by Bohart (1942).

GENUS DUFOUREA LEPELETIER

Dufourea LEPELETIER, 1841, Histoire naturelle des insectes, hyménoptères, vol. 2, p. 227.

Halictoides NYLANDER, 1848, Notiser Sällskapet Fauna Flora Fennica, vol. 1, p. 195.

Halictoides (*Epihalictoides*) COCKERELL AND PORTER, 1899, Ann. Mag. Nat. Hist., ser. 7, vol. 4, p. 420.

Halictoides (*Parahalictoides*) COCKERELL AND PORTER, 1899, *ibid.*, ser. 7, vol. 4, p. 420.

Conohalictoides VIERECK, 1904, Ent. News, vol. 15, p. 245.

Neohalictoides VIERECK, 1904, *ibid.*, vol. 15, p. 261.

Cryptohalictoides VIERECK, 1904, *ibid.*, vol. 15, p. 261.

Mimulapis BRIDWELL, 1919, Proc. Hawaiian Ent. Soc., vol. 4, p. 162.

Beiheliella COCKERELL, 1924, Ent. News, vol. 35, p. 169.

Halictoides (*Cephalictoides*) COCKERELL, 1924, Psyche, vol. 31, p. 244.

GENOTYPE: *Dufourea minuta* Lepeletier, designated by Richards, 1935, Trans. Roy. Ent. Soc. London, vol. 83, p. 172.

This Holarctic genus is exceedingly variable, the posterior abdominal sterna and the legs of the male in most species being highly modified. There are such great differences in structure among the species of *Dufourea*, particularly the males, that a subdivision of the genus into various subgroups seems desirable. However, no satisfactory division has yet been proposed, nor have characters for separating the subgenera in the females been found. Tentatively I recognize two subgenera, but the subgenus *Halictoides* still contains very diverse elements.

KEY TO THE SUBGENERA OF *Dufourea*

1. Seventh sternum of male thickened, much modified, usually with an elevated apical process *Halictoides*
Seventh sternum of male not modified, apex thin and rounded . . . *Dufourea*, *sensu stricto*

Mimulapis, separated as a distinct genus by Timberlake, appears to be merely a highly modified *Halictoides*.

FAMILY MELITTIDAE

Labrum broader than long; subantennal areas absent; subantennal sutures directed, except sometimes at their upper ends, toward inner margins of antennal sockets; lower sides of clypeus not, or but little, bent backward; clypeus not protuberant; facial foveae absent; stipites and galeae both without combs, the galeae short prepalpally and usually so postpalpally; submentum V-shaped; mentum tapering basally; labial palpi with segments similar to one another, cylindrical; glossa short or long, acute; pre-episternal and scrobal sutures usually absent, the former always absent below the latter; metanotum horizon-

tal or subhorizontal; middle coxae short as seen externally, much shorter than distance from their summits to posterior wing bases; scopa confined to posterior tibiae and basitarsi, although trochanters and femora are hairy; basitibial plates and pygidial plate present in female; volsellae present.

KEY TO THE SUBFAMILIES OF MELITTIDAE

1. Inner hind tibial spur much broadened basally and throughout its length provided with a comb of very many long fine teeth; scrobal suture present in front of mesepisternal scrobe; pterostigma hardly twice as long as broad; marginal cell bent gradually away from wing margin for nearly half length of cell Ctenoplectrinae
Inner hind tibial spur unmodified; scrobal suture absent in front of mesepisternal scrobe; pterostigma more than twice as long as broad; marginal cell bent away from wing margin, if at all, only apically 2
2. Pterostigma broad, its margins based of vein r conspicuously converging basally; posterior basitarsi of female as broad as tibiae, of male robust and less than half as long as tibiae; jugal lobe of posterior wing more than half as long as vannal lobe . . . Macropidinae
Pterostigma slender, its margins based of vein r almost always scarcely converging basally; posterior basitarsi more slender than tibiae (except in male *Haplomellita*) and more than half as long as tibiae; jugal lobe of posterior wing usually not over half as long as vannal lobe 3
3. With three submarginal cells; jugal lobe of posterior wing nearly half as long as vannal lobe (rarely three-fourths as long); posterior basitarsi shorter than tibiae. . . Melittinae
With two submarginal cells; jugal lobe of posterior wings variable but usually less than half as long as vannal lobe; posterior basitarsi variable Dasypodinae

SUBFAMILY MELITTINAE

Pre-episternal suture and scrobal suture in front of mesepisternal scrobe absent; three submarginal cells, second much the smallest, first largest; marginal cell longer than distance from apex to wing tip, apex very narrowly rounded, on wing margin, distitarsi unusually large.

In this Holarctic and African subfamily the species are of moderate size, black, with the abdomen provided with pale pubescent fasciae, giving the aspect of certain species of

Halictus and *Andrena*. The genera included are *Melitta*, *Melittoides*, and *Notomelitta*, of which only the first occurs in America.

GENUS *MELITTA* KIRBY

Melitta KIRBY, 1802, Monographia apum Angliae . . . , vol. 1, p. 117.

Cilissa LEACH, 1812, in Brewster's Edinburgh Encyclopaedia, vol. 9, p. 154.

Kirbya LEPELETIER (not Robineau-Desvoidy), 1841, Histoire naturelle des insectes, hyménoptères, vol. 2, p. 145.

Melitta (*Brachycephalapis*) VIERECK, 1909, Proc. Ent. Soc. Washington, vol. 11, p. 47.

? *Dolichochile* VIERECK, 1909, *ibid.*, vol. 11, p. 49.

GENOTYPE: *Melitta tricineta* Kirby, designated by Richards, 1935, Trans. Roy. Ent. Soc. London, vol. 83, p. 172.

This genus consists of *Andrena*-like bees with abdominal fasciae of pale pubescence. The species are rare but have been collected from coast to coast in North America. A few species are also known from Eurasia and Africa.

Dolichochile, doubtfully reduced here to the rank of a subgenus of *Melitta*, may be recognized by the very long mandibles with a rounded tooth near the middle and by the long malar space. The subgenus is known from a single female specimen from New Jersey. *Brachycephalapis* is apparently not distinguishable as a subgenus from *Melitta*.

SUBFAMILY DASYPODINAE

Pre-episternal suture entirely absent, as is scrobal suture in front of mesepisternal scrobe; second submarginal cell somewhat shorter than first; marginal cell pointed almost on wing margin and longer than distance from its apex to wing tip; scopa consisting of long, simple hairs.

The members of this subfamily are non-metallic, usually with rather abundant pale pubescence forming fasciae on the abdominal terga.

Included in this widely distributed subfamily are *Dasypoda* and apparently *Eremaphanta* from the Eurasian region, *Haplomelita*, *Samba*, and perhaps *Rediviva* from Africa, and the African and North American *Hesperapis*. The last-named genus alone occurs in the North American fauna.

GENUS *HESPERAPIS* COCKERELL

Hesperapis COCKERELL, 1898, Canadian Ent., vol. 30, p. 147.

Zacesta ASHMEAD, 1899, Trans. Amer. Ent. Soc., vol. 26, p. 73.

Panurgomia VIERECK, 1909, Proc. Ent. Soc. Washington, vol. 11, p. 48.

Halictoides (*Amblyapis*) COCKERELL, 1910, Ann. Mag. Nat. Hist., ser. 8, vol. 5, p. 362.

Capicola FRIESE, 1911, Zool. Jahrb., Abt. Syst. Geogr. Biol., vol. 30, p. 672.

Capicola (*Rhinochaetula*) FRIESE, 1912, Arch. Naturgesch., vol. 78, div. A, pt. 5, p. 185.

GENOTYPE: *Hesperapis elegantula* Cockerell (monobasic).

This is a genus represented by numerous species in the southwestern United States and by one extending as far north as North Dakota. It is abundant in South Africa, and it seems not unlikely that the recently described *Eremaphanta* Popov from Turkestan is the same genus. The abdomen is much flattened, the scopa usually sparse and made up of much shorter hairs than in *Dasypoda*.

KEY TO THE AMERICAN SUBGENERA OF *Hesperapis*

1. Male robust, with form of a female; its flagellum short with segments mostly broader than long. 2
Male slender; its flagellum long with segments longer than broad. *Panurgomia*
2. Galea of maxilla only twice as long as broad *Amblyapis*
Galea of maxilla much more than twice as long as broad. *Hesperapis*, *sensu stricto*

Amblyapis was described as a dufourea bee, but specimens at hand show clearly that it is a dasypodine.

SUBFAMILY MACROPIDINAE

Pre-episternal suture entirely absent, scrobal suture present only behind mesepisternal scrobe; two submarginal cells of subequal length; marginal cell slightly longer than distance from its apex, which is pointed very near the wing margin, to wing tip; pygidial plate of male strongly elevated and parallel-sided.

This subfamily contains only the genus *Macropis*.

GENUS *MACROPIS* KLUG

Megilla FABRICIUS, 1805, Systema piezatorum . . . , p. 328.

Macropis KLUG, 1809, in Panzer, Faunae insectorum Germaniae initia . . . , pt. 107, no. 16.

Macropis (*Paramacropis*) POPOV, 1936, Ann. Mus. Civico Storia Nat. Genova, vol. 59, p. 287.

GENOTYPE: *Megilla labiata* Fabricius (monobasic).

This Holarctic genus is represented in the United States by a few species found in the eastern, central, and northern states. They are black with some pale pubescence and with yellow areas on the face in the male. All our species belong to the subgenus *Macropis*, *sensu stricto*, having the gonostyli deeply bifid.

Although *Megilla* is isogenotypic with *Macropis* and has priority over it, it has virtually never been used in this sense. I follow Benson, Ferrière, and Richards (1937) in requesting the placement of *Macropis* on the *nomina conservanda* list.

SUBFAMILY CTENOPECTRINAE

Scrobal and upper parts of pre-episternal sutures evident; two submarginal cells; marginal cell considerably longer than distance from its apex to wing tip; jugal lobe of posterior wings about half as long as vannal lobe; posterior basitarsi of female nearly as broad as tibiae; pygidial plate of male absent, that of female narrow apically, greatly broadened basally.

This subfamily contains only the genus *Ctenoplectra*, found from Australia and Africa to China.

FAMILY MEGACHILIDAE

Labrum longer than broad, broadened basally to form a long line of articulation with clypeus; subantennal areas absent; subantennal sutures directed toward outer margins of antennal sockets (fig. 89); lower sides of clypeus not bent backward parallel to long axis of body; facial foveae absent; hypostoma free from tentorium; first flagellar segment much shorter than scape; stipites with or without combs; galeae short prepalpally, long postpalpally, without combs; submentum V-shaped; mentum tapering basally; labial palpi with first two segments elongated and flattened, sheath-like, first segment usually shorter than second; glossa linear, with a flabellum; pre-episternal suture and scrobal suture in front of mesepisternal scrobe absent;

metanotum usually vertical, sometimes subhorizontal; middle coxae elongate, at least half, and usually much more than half, as long as distance from summits to hind wing bases; pterostigma small; submarginal cells two, second as long, or nearly as long, as first (fig. 167); marginal cell pointed or narrowly rounded at apex, which is usually a little bent away from costal margin of wing and nearer to wing tip than to base of cell; basitibial plates absent; scopa, when present, confined to abdominal sterna; pygidial plate usually absent; penis valves more or less fused to penis.

This is a large and morphologically rather uniform group of bees. Nonparasitic females are easily recognized by the position of the scopa. All forms may be recognized by the form of the labrum and the direction taken by the subantennal sutures.

KEY TO THE SUBFAMILIES OF MEGACHILIDAE

1. Jugal lobe of posterior wing about three-fourths as long as vannal lobe; tibiae coarsely spiculate on outer surfaces; male with pygidial plate, female with slender remnant thereof in the form of large spine, flattened dorsally. Lithurginae
- Jugal lobe of posterior wings less than half as long as vannal lobe; tibiae not spiculate; pygidial area entirely absent. Megachilinae

SUBFAMILY LITHURGINAE

Face of female elevated below antennal sockets; epistomal suture absent between the widely separated anterior tentorial pits; mandibles in both sexes short and robust, tridentate, the middle tooth longer and more elevated than the others; stipites without combs; metanotum about one-eighth as long as scutellum; coarse spiculae of tibiae arranged in two longitudinal rows on fore and middle legs, scattered on posterior legs; posterior basitarsi slender, parallel-sided, about as long as posterior tibiae; second abdominal tergum unusually small, posterior margin broadly rounded; terga two to seven of male exposed and unmodified.

This subfamily contains only the genus *Lithurge*.

GENUS LITHURGE LATREILLE

Lithurge LATREILLE, 1825, Familles naturelles du règne animal . . . , p. 463.

Lithurgus BERTHOLD, 1827, Latreille's natürliche Familien des Thierreichs, p. 467.

Lithurgopsis FOX, 1902, Ent. News, vol. 13, p. 138.

GENOTYPE: *Centris cornuta* Fabricius (monobasic).

This is a genus of rather hairy bees with pale fasciae across the abdomen, superficially resembling *Megachile*. The American species, which have long proboscides and visit chiefly cactus flowers, belong to the subgenus *Lithurgopsis*, having arolia in the males. In typical Old World *Lithurge*, *sensu stricto*, arolia are absent in both sexes. *Lithurge* occurs across the southern part of the United States from the Atlantic to the Pacific.

The United States species of this genus were reviewed by Mitchell (1938).

SUBFAMILY MEGACHILINAE

Face of female very rarely elevated below antennal sockets; epistomal suture complete; mandibles variously toothed, apical tooth longest, preapical tooth not elevated; stipites with or without combs; posterior basitarsi much shorter than tibiae; second abdominal tergum large, with the posterior margin usually straight, so that base of abdomen lacks compressed aspect of *Lithurge*; abdomen of male with fewer unmodified sterna than in *Lithurge*.

KEY TO THE TRIBES OF MEGACHILINAE

1. Inner margin of pterostigma from its base to base of radial vein not much, if any, longer than width of pterostigma; claws of female cleft or at least with an inner tooth. Anthidiini
- Inner margin of pterostigma from its base to base of radial vein much longer than width of pterostigma; claws of female simple Megachilini

TRIBE ANTHIDIINI

In this tribe, which occurs in all the major continents, there is usually at least some pale integumental maculation, and the posterior margin of the scutellum is usually vertical or even overhanging, at a distinct angle to the dorsal surface.

In addition to the genera listed below, this tribe includes *Afrostelis*, *Anthodiocetes*, *Archanthidium*, *Hypanthidium*, *Pachyanthidium*,

Proanthidium, *Serapista* (= *Serapis*), *Euasapis*, *Odontostelis*, and *Parevaspis*. The last three genera are probably best regarded as subgenera of *Stelis*.

KEY TO THE NEARCTIC GENERA OF ANTHIDIINI

1. Metanotum with a median spine; axillae produced to angles; second submarginal cell shorter than first, first transverse cubital transverse to wing; scopa absent. . . *Dioxys*
Metanotum simple; axillae rounded in American forms; second submarginal cell usually at least as long as first, first transverse cubital oblique 2
2. Arolia absent; mandibles of female with five or more close-set, conical teeth 3
Arolia present; mandibles of female with not more than four teeth 4
3. Seventh abdominal tergum of female with a large median emargination; second recurrent vein distad of second transverse cubital by several vein widths *Callanthidium*
Seventh abdominal tergum of female not emarginate medially; second recurrent vein but little distad of second transverse cubital (fig. 167) *Anthidium*
4. Subantennal sutures more or less strongly arcuate outward, especially below; scutellum produced to a sharp truncation considerably overhanging metanotum and propodeum *Anthidiellum*
Subantennal sutures straight; scutellum rounded, not produced to overhang metanotum and propodeum. 5
5. Posterior lobe of pronotum with its carina greatly expanded forward to form a lamella whose anterior margin usually lies in front of anterior margin of mesoscutum; posterior coxae each with a tooth, largest in males *Dianthidium*
Posterior lobe of pronotum, if carinate, with anterior margin of carina behind anterior margin of mesoscutum; posterior coxae not dentate 6
6. Scopa absent; eighth abdominal tergum of male but little exerted, rounded apically. . . *Stelis*
Scopa present in female; eighth abdominal tergum of male more or less modified with processes or at least a shallow emargination 7
7. Posterior lobe of pronotum with considerably produced lamella; mandibles of female terminating in long oblique margin; second recurrent vein usually distad of second transverse cubital by several vein widths. . *Paranthidium*
Posterior lobe of pronotum with carina, if present, not produced to a lamella; mandibles of female with tridentate, not strongly oblique,

- apex; second recurrent vein interstitial with second transverse cubital or distad of it by only one or two vein widths 8
8. Abdominal terga with yellow or white fasciae which are almost always unbroken but usually gradually narrowed medially; maxillary palpi three-segmented . . . *Heteranthidium*
- Body entirely black except for clypeus and paraocular areas of male; maxillary palpi five-segmented *Trachusa*

GENUS TRACHUSA PANZER

Trachusa PANZER, 1804, Faunae insectorum Germaniae initia . . . , pt. 86, nos. 14, 15.

Diphysis LEPELETIER, 1841, Histoire naturelle des insectes, hyménoptères, vol. 2, p. 307.

GENOTYPE: *Trachusa serratulae* Panzer = *Apis byssina* Panzer, designated by Sandhouse, 1943, Proc. U. S. Natl. Mus., vol. 92, p. 605.

This genus of moderate-sized bees lacks carinae on the posterior lobes of the pronotum.

In North America species of the genus occur in California, Arizona, and Sonora. There is one Eurasian species. The species were reviewed by Michener (1941a).

GENUS HETERANTHIDIUM COCKERELL

Heteranthidium COCKERELL, 1904, Ent. News, vol. 15, p. 292.

GENOTYPE: *Anthidium dorsale* Lepeletier, by original designation.

This is a genus of moderate-sized to large, showy bees. The posterior lobes of the pronotum are either with or without a transverse carina on each.

This genus is widely distributed but not common in the United States. Our species have been revised by Schwarz (1926).

GENUS DIANTHIDIUM COCKERELL

Anthidium (*Dianthidium*) COCKERELL, 1900, Ann. Mag. Nat. Hist., ser. 7, vol. 5, p. 412.

GENOTYPE: *Anthidium curvatum* Cockerell (not Smith) = *Dianthidium sayi* Cockerell, by original designation.

Dianthidium is distinguished from all other anthidiines by the hind coxal spines of the male and the form of the pronotal lobes. There is a strong carina separating the anterior from the lateral faces of the mesepisterna. The maxillary palpi are two-segmented. The bees of this genus are usually

rather small, and they are more cylindrical in body form than is *Anthidium*.

This widely distributed genus occurs throughout the United States. The species of this and the following genus have been reviewed by Schwarz (1926a).

GENUS PARANTHIDIUM COCKERELL AND COCKERELL

Dianthidium (*Paranthidium*) COCKERELL AND COCKERELL, 1901, Ann. Mag. Nat. Hist., ser. 7, vol. 7, p. 50.

Paranthidium (*Mecanthidium*) MICHENER, 1942, Jour. New York Ent. Soc., vol. 50, p. 278.

GENOTYPE: *Anthidium perpictum* Cockerell, by original designation.

The anterior faces of the mesepisterna are not separated from the lateral faces by a carina or are separated from them only by a weak and irregular carina; the maxillary palpi are three-segmented.

This genus is found in the eastern and central United States, westward as far as Arizona and south far into Mexico. It is not the same as *Paraanthidium* Friese.

Our species of this genus are divisible into two subgenera. *Paranthidium*, *sensu stricto*, consists of rather small, yellow and black forms with the aspect of *Dianthidium*, and with the median lobe of the eighth tergum of the male relatively short and the second recurrent vein much distad of the second transverse cubital. The subgenus *Mecanthidium* consists of much larger forms, sometimes without yellow markings, with the median lobe of the eighth tergum of the male much elongated and beak-like and the second recurrent vein distad of the second transverse cubital by only two or three vein widths.

GENUS ANTHIDIELLUM COCKERELL

Anthidium (*Anthidiellum*) COCKERELL, 1904, Bull. So. California Acad. Sci., vol. 3, p. 3.

Anthidium (*Cerianthidium*) FRIESE, 1923, Die europäischen Bienen (Aphidae), vol. 3, p. 204.

GENOTYPE: *Anthidium strigatum* Panzer, by original designation.

This is a genus of small, robust bees with conspicuous yellow integumental markings and unusually coarse punctation. The subantennal sutures are more or less arcuate. The maxillary palpi are two-segmented. A strong carina separates the anterior from the lateral

face of the mesepisternum and is continued as a carina across each posterior lobe of the pronotum. The front and middle tibiae and tarsi are provided with long fringes of hair; the middle basitarsi are much shorter than the middle tibiae, unlike other pollen collecting anthidiine bees. The second recurrent vein is considerably distad of the second transverse cubital, as in *Dianthidium* and *Paranthidium*.

This genus is widely distributed over the world and is found over most of the United States except in the north. The species of the genus have been reviewed by Schwarz (1926a).

GENUS ANTHIDIUM FABRICIUS

Anthidium FABRICIUS, 1805, *Systema piezatorum* . . . , p. 364.

GENOTYPE: *Apis manicata* Linnaeus, designated by Latreille, 1810, *Considérations générales* . . . des insectes, p. 439.

The genus *Anthidium* contains robust, black bees with conspicuous yellow or white integumental maculations, at least on the abdomen. The maxillary palpi are two-segmented. The posterior lobes of the pronotum lack carinae, and the anterior face of the mesepisternum is not separated from the lateral face by a carina.

Anthidium is widespread in distribution, being well represented throughout most of the United States. Keys to many American species of the genus have been presented by Schwarz (1927).

GENUS CALLANTHIDIUM COCKERELL

Callanthidium COCKERELL, 1925, *Proc. California Acad. Sci.*, ser. 4, vol. 14, p. 365.

GENOTYPE: *Anthidium illustre* Cresson, by original designation.

Although closely related to *Anthidium* and resembling that genus in structure, the large bees of the genus *Callanthidium* are quite distinctive in appearance. The abdominal fasciae are regularly and narrowly broken medially but not elsewhere. The posterior lobes of the pronotum in the females each have a weak transverse carina. Unlike *Anthidium*, the penis valves greatly exceed the claspers in length.

This small genus is confined to the western United States.

GENUS STELIS PANZER

*Stelis*¹ PANZER, 1806, *Kritische Revision der Insekten-faune Deutschlands* . . . , vol. 2, p. 246.

Gyrodroma ILLIGER, 1807, *Mag. Insektenkunde*, vol. 6, p. 198.

Gymnus SPINOLA, 1808, *Insectorum liguriae species novae aut rariores* . . . , vol. 2, p. 9.

Ceraplastes GISTEL, 1848, *Naturgeschichte des Thierreichs*, p. x.

Stelidomorpha MORAWITZ, 1875, *Imp. Obshchestvo* . . . Moskva, [Izv. Obshch. Liubitelei estestvoznaniia . . . , Moscow], vol. 19, p. 131.

Chelynia PROVANCHER, 1888, *Additions et corrections* . . . faune entomologique du Canada . . . hyménoptères, p. 322.

Stelis (*Protostelis*) FRIESE, 1895, *Die Bienen Europas*, vol. 1, p. 25.

Melanostelis ASHMEAD, 1898, *Psyche*, vol. 8, p. 283.

Stelidium ROBERTSON, 1902, *Canadian Ent.*, vol. 24, p. 323.

Microstelis ROBERTSON, 1903, *Trans. Amer. Ent. Soc.*, vol. 29, p. 170.

Stelis (*Pavostelis*) SLADEN, 1916, *Canadian Ent.*, vol. 48, p. 313.

Stelis (*Heterostelis*) TIMBERLAKE, 1941, *Jour. New York Ent. Soc.*, vol. 49, p. 125.

Stelis (*Stelidina*) TIMBERLAKE, 1941, *ibid.*, vol. 49, p. 131.

GENOTYPE: *Apis aterrima* Panzer (not Christ) = *Apis punctulatissima* Kirby (monobasic).

The species of this genus vary greatly in appearance, some being black and yellow as in *Anthidium*, some entirely black, some metallic blue or green, with or without yellow or white maculations. Some forms superficially resemble very closely certain species of *Osmia*. *Stelis* differs from most of the pollen gathering anthidiines by having the middle basitarsus considerably shorter than the middle tibia. The genus is widely distributed over the world and found throughout the United States, but it is rarely common. The species of *Stelis* are parasitic upon other megachilids, such as *Anthidium*, *Ashmeadiella*, *Hoplitis*, and *Osmia*. The subgenus *Stelis*, *sensu stricto*, having pointed axillae, does not occur in America. *Odontostelis*, *Euaspsis*, and *Parevaspis*, genera not occur-

¹ *Trachusa* Jurine, 1801, *Erlangen Litteratur-Zeitung*, vol. 1, p. 164 (see Morice and Durrant, 1914, *Trans. Ent. Soc. London*, p. 426), is isogenotypic with *Stelis* but has been invalidated by opinion no. 135 of the International Commission of Zoological Nomenclature.

ring in the United States, are questionably distinct from *Stelis*.

KEY TO THE NEARCTIC SUBGENERA OF *Stelis*

1. Second recurrent vein interstitial with, or distad of, second transverse cubital; posterior lobes of pronotum usually each with a transverse carina 2
 Second recurrent vein received by the second submarginal cell considerably basad of second transverse cubital; posterior lobes of pronotum without or with but feeble transverse carinae 5
2. Base of propodeum abruptly declivous without horizontal basal pitted area; lateral margins of axillae strongly convex, not continuing on same arc as margin of scutellum; apical margin of fourth sternum of male broadly and shallowly emarginate and provided with a fringe of long hairs; large black forms with abundant yellow maculations. . . *Heterostelis*
 Base of propodeum with subhorizontal pitted basal zone; lateral margins of axillae continued in same curve as posterior margin of scutellum; apical margin of fourth sternum of male variable 3
3. Transverse carina of posterior pronotal lobe extending mesad of lateral margin of mesoscutum; anterior face of mesepisternum separated from lateral face by weak carina; posterior margin of fourth sternum of male not fringed, with median notch through which shows a pair of black teeth arising from following sternum, the margin of which is fringed; coarsely punctured black forms, usually with yellow maculations. . *Protostelis*
 Transverse carina of posterior lobe of pronotum not extending mesad of lateral extremity of mesoscutum; anterior and lateral faces of mesepisternum not separated by a carina; posterior margin of fourth sternum of male fringed, not notched, following sternum not toothed; comparatively finely punctate forms 4
4. Small black forms less than 6 mm. in length, with restricted pale maculations on abdomen; posterior lobes of pronotum without transverse carinae. *Microstelis*
 Larger species, over 6 mm. in length, black or metallic blue, without pale maculations; posterior lobes of pronotum each with a transverse carina *Pavostelis*
5. Fourth abdominal sternum of male with strong depression in posterior part, margin of sternum elevated slightly on either side of depression; posterior basitarsi of female broadest subapically; seventh abdominal tergum of female with strong longitudinal ridge; seventh

- abdominal sternum of female tridentate at apex, median tooth largest . . *Melanostelis*
 Fourth abdominal sternum without depression, margin slightly elevated and produced medially; posterior basitarsi of female parallel-sided; seventh abdominal tergum and sternum of female little modified, apices pointed, rounded, subtruncate, or feebly bilobed. . 6
6. Posterior basitarsi more than half as broad as posterior tibiae; black or metallic forms without pale maculations on head and thorax, with or without such markings on abdomen; base of propodeum narrowly slightly more horizontal and coarsely punctate than rest of propodeum. *Chelynia*
 Posterior basitarsi less than half as broad as posterior tibiae; nonmetallic forms with pale markings at least on abdomen; base of propodeum variable 7
7. Base of propodeum with narrow horizontal pitted zone; head and thorax with pale maculations; tegulae black, usually with pale spots *Stelidium*
 Base of propodeum nearly vertical and usually coarsely punctured as in *Chelynia*; head and thorax immaculate; tegulae ferruginous *Stelidina*

GENUS *DIOXYS* LEPELETIER AND SERVILLE

Dioxys LEPELETIER AND SERVILLE, 1825, Encyclopédie méthodique, histoire naturelle . . insectes, vol. 10, p. 109.

Paradioxys MOCSÁRY, 1894, Természetrájsi Füzetek, vol. 17, p. 35.

Hoplospites ASHMEAD, 1898, Psyche, vol. 8, p. 284.

Chrysopheon TITUS, 1901, Canadian Ent., vol. 33, p. 256.

GENOTYPE: *Trachusa cincta* Jurine (monobasic).

This is a genus of moderate-sized black bees, usually with apical fasciae of pale, plumose hairs on the abdominal terga. The abdomen of the female in many species is partly red and is produced to a usually broadly rounded apex. The sting is greatly reduced. The mandibles are bidentate in both sexes; the labrum is several times as long as broad. Each posterior lobe of the pronotum bears a transverse carina, and there is a strong carina separating the anterior from the lateral faces of the mesepisterna. Arolia are absent.

This genus, parasitic on other megachilids, is Holarctic in distribution. In America it occurs in the Rocky Mountain and western states. *Aglaopis* is said by Meade-Waldo to be a synonym of *Dioxys*, but the original de-

scription does not indicate this, as it states that the labrum is short.

Dioxys is perhaps deserving of distinction as a separate tribe.

TRIBE MEGACHILINI

In this tribe there is no pale integumental maculation comparable to that so common in the Anthidiini. The abdominal pattern, often present, results from bands of pale hairs. Except in certain parasitic forms, the posterior portion of the scutellum is separated by no sharp angle from the dorsal surface.

In addition to the genera found in North America, this tribe includes *Androgynella*, *Berna*, *Gronoceras*, *Heriadopsis*, *Noteriades*, *Stenosmia*, and *Thaumatosoma*. The genera having arolia were reviewed by Michener (1941).

KEY TO THE AMERICAN GENERA OF MEGACHILINI

1. Arolia absent; seventh tergum of male with a strongly elevated preapical ridge which is frequently toothed or notched and sometimes formed into a group of long spines; eighth tergum of male hidden or largely so. 2
- Arolia present; seventh tergum of male without such a preapical ridge, the spines, teeth, or notches, if present, usually being apical; eighth tergum of male sometimes hidden, more often exposed 3
2. Eyes hairy in American species; axillae each produced to conspicuous tooth; posterior surface of scutellum separated from dorsal surface by distinct angle; apex of abdomen attenuated, sixth segment of male provided with several long spines; scopa absent. *Coelioxys*
- Eyes bare; axillae not angulate; scutellum rounded in profile; apex of abdomen not attenuate, seventh segment without long spines; scopa present *Megachile*
3. Thorax elongate, mesoscutellum seen in profile but feebly convex, metanotum convex and constituting part of dorsal surface of thorax, so that in profile a line tangent to the convexities of the mesoscutum and mesoscutellum would nearly touch metanotum; propodeum with rather distinct horizontal basal zone; shortest distance between tegulae usually but little, if any, greater than length of mesoscutum; pterostigma broader than distance from inner edge of prestigma to costal margin of wing and longer than prestigma 4
- Thorax short, mesoscutellum seen in profile conspicuously convex, metanotum flattened or convex, on posterior declivity of thorax, so that in profile a line tangent to the convexities of the mesoscutellum and mesoscutum would not closely approach metanotum, and that part of metanotum nearest such a line is its anterior margin, not a median convexity; propodeum ordinarily entirely declivous; shortest distance between tegulae greater than length of mesoscutum; pterostigma but little, if any, broader than distance from inner edge of prestigma to costal margin of wing, often as short as prestigma 9
4. Second abdominal tergum with anterior face consisting of large concavity separated from dorsal surface by strong carina; posterior lobes of pronotum each with strong transverse carina *Heriades*
- Second abdominal tergum with anterior face sulcate or shallowly concave, not separated from dorsal face by a carina; posterior lobes of pronotum not carinate 5
5. First recurrent vein nearly interstitial with first transverse cubital (may be a short distance either side of it); shortest distance between tegulae considerably greater than length of mesoscutum *Formicapis*
- First recurrent vein considerably distad of first transverse cubital; shortest distance between tegulae but little, if any, greater than length of mesoscutum 6
6. Suture between mesothoracic and metathoracic pleura practically straight in long median portion; clypeal truncation of female produced and overhanging base of labrum; face below antennae in male covered with short, fine, appressed pubescence. *Robertsonella*
- Suture between mesothoracic and metathoracic pleura arcuate; anterior margin of clypeus not much produced beyond base of labrum; face of male with the usual long pubescence 7
7. Male with but six exposed metasomal terga; clypeus of female very short and broad, produced to a slender median apical horn *Chelostomopsis*
- Male with seven exposed terga; clypeus of female not greatly modified. 8
8. Posterior coxae each with longitudinal carina on inner ventral angle; labial palpi with third segment flattened and connate with second, so that there is but one small cylindrical segment. *Chelostoma*
- Posterior coxae not carinate; labial palpi with third segment cylindrical, similar to fourth. *Prochelostoma*

9. Anterior face of mesepisternum shining, nearly impunctate, separated from lateral face by weak carina; second abdominal tergum with anterior face consisting of broad, shining concavity; seventh abdominal tergum of male quadridentate. *Ashmeadiella*
Anterior face of mesepisternum not separated by a carina or abrupt change in sculpture from lateral face; second abdominal tergum with anterior face shallowly concave or sulcate. 10
10. Parapsidal lines punctiform or short oval, at most three times as long as broad; seventh tergum of male without tooth on posterior margin at each side; almost always metallic forms 11
Parapsidal lines linear; seventh tergum of male often with tooth on posterior margin at each side; rarely metallic forms . . . 12
11. Posterior coxae each with longitudinal carina on inner ventral angle; parapsidal lines slightly elongated; carina separating propodeum from lower part of metapleuron arched in Nearctic species . . *Diceratosmia*
Posterior coxae not carinate; parapsidal lines punctiform; carina separating propodeum from lower part of metapleuron straight. *Osmia*
12. Second abdominal tergum with anterior face flat or slightly convex except for longitudinal median sulcus, not separated from horizontal dorsal surface by a line or carina, except sometimes for short distance across summit of sulcus; body usually elongate. 13
Second abdominal tergum with anterior face broadly and shallowly concave, almost always separated from dorsal surface by transverse impressed line or feeble carina; body usually short and robust. . . *Anthocopa*
13. Posterior coxae each with longitudinal carina on inner ventral angle; proboscis short, galeae and first two segments of labial palpi furnished with numerous strong hairs, apices of which are hooked or wavy. *Proteriales*
Posterior coxae not carinate, rarely with an impunctate line replacing the carina (but sometimes with a ventral carina whose distal end turns toward the outer rather than the inner side of the apex of the coxa); proboscis long, without unusual hairs. *Hoplitis*

GENUS PROCHELOSTOMA ROBERTSON

Prochelostoma ROBERTSON, 1903, Trans. Amer. Ent. Soc., vol. 29, p. 167.

GENOTYPE: *Heriades philadelphi* Robertson, by original designation.

This and the next genus include our most slender species of Megachilidae. They are small, black forms, with or without abdominal fasciae.

Prochelostoma contains a single species, found in the eastern United States.

GENUS CHELOSTOMA LATREILLE

Chelostoma LATREILLE, 1809, Genera crustaceorum et insectorum . . . , vol. 4, p. 161.

Gyrodroma THOMSON (not Illiger), 1869, Opuscula Ent., vol. 1, p. 22.

GENOTYPE: *Apis maxillosa* Linnaeus = *Apis florissomnis* Linnaeus (monobasic).

This genus occurs in the Palearctic region and on the Pacific coast of the United States. Our species were revised by Michener (1938a). The structure of the labial palpi of this genus is unique among megachilids.

GENUS CHELOSTOMOPSIS COCKERELL

Chelostomopsis COCKERELL, 1925, Proc. California Acad. Sci., ser. 4, vol. 14, p. 205.

Raphidostoma COCKERELL, 1936, Pan-Pacific Ent., vol. 12, p. 133.

GENOTYPE: *Chelynia rubifloris* Cockerell, by original designation.

A single small black species with narrow abdominal fasciae is included in this genus. It is found in the Pacific coast states.

GENUS HERIADES SPINOLA

Heriades SPINOLA, 1808, Insectorum liguriae species novae aut rariores . . . , vol. 2, p. 7.

Trypetes SCHENCK (not Schönherr), 1859, Jahrb. Ver. Naturk. Herzogthum Nassau, vol. 14, p. 32.

Neotrypetes ROBERTSON, 1918, Ent. News, vol. 29, p. 91.

Heriades (Physostetha) MICHENER, 1938, Ann. Ent. Soc. Amer., vol. 31, p. 523.

GENOTYPE: *Apis truncorum* Linnaeus, designated by Latreille, 1810, Considérations générales . . . des insectes, p. 439.

The bees of this genus are small, black, and coarsely punctate. The abdominal fasciae, except laterally, consist of a single row of plumose hairs on the extreme apical margins of the terga. Each posterior coxa has a longitudinal carina on its inner ventral angle. The eighth tergum of the male is hidden. The American species were reviewed by Michener (1938).

This Holarctic and Ethiopian genus is found throughout the United States. Typical *Heriades* with acute axillae does not occur in America.

KEY TO THE AMERICAN SUBGENERA OF *Heriades*

1. Carinae of mandibles of female separated except apically; second abdominal sternum of male large and produced to a rounded or pointed apex; sixth sternum of male with broad apical emargination; seventh sternum of male with fine subapical hairs *Neotrypetes*
Carinae of mandibles of female united basally; second sternum of male short, truncate apically; sixth sternum of male with small, apical median emargination; seventh sternum of male with two short subapical rows of stout spines *Physostetha*

GENUS *ASHMEADIELLA* COCKERELL

Ashmeadiella COCKERELL, 1897, Ent. News, vol. 8, p. 197.

Titusella COCKERELL, 1906, Bull. Amer. Mus. Nat. Hist., vol. 22, p. 445.

Ashmeadiella (Arogochila) MICHENER, 1939, Amer. Midland Nat., vol. 22, p. 58.

Ashmeadiella (Corythochila) MICHENER, 1939, *ibid.*, vol. 22, p. 74.

Ashmeadiella (Chilosima) MICHENER, 1939, *ibid.*, vol. 22, p. 78.

Ashmeadiella (Cubitognatha) MICHENER, 1939, *ibid.*, vol. 22, p. 81.

GENOTYPE: *Heriades opuntiae* Cockerell, by original designation.

Ashmeadiella is a genus of small or moderate-sized bees with the usual narrow abdominal fasciae. The integument is black, the abdomen sometimes largely red. The genus, which was recently revised by Michener (1939), is confined to North America and is abundant only in the southwestern states.

KEY TO THE SUBGENERA OF *Ashmeadiella*
FEMALES

1. Total length of outer side of mandible, measured along lower carina, at most twice as long as scape; mandibles tridentate; clypeus punctate, produced, and truncate *Ashmeadiella, sensu stricto*
Total length of outer side of mandible more than twice as long as scape; clypeus very rarely both produced and truncate, if produced variously rounded or lobed . . . 2

2. Mandibles ordinarily with four or more teeth . 3
Mandibles ordinarily with two or three teeth . 4
3. Apices of mandibles greatly broadened, distance from first tooth to inner apical angle at least one-half length of mandible; clypeus short, its apex somewhat lobate, not, or hardly, produced beyond a line connecting lower ends of eyes *Titusella*
Apices of mandibles not broad, distance from first to fourth tooth distinctly less than one-half length of mandible; clypeus produced beyond a line between lower ends of eyes, its apex broadly rounded *Chilosima*
Apices of mandibles not broad, distance from first to fourth tooth distinctly less than one-half length of mandible; clypeus produced but little beyond line between lower ends of eyes, apex variously lobed, lateral angles large *Corythochila*
4. Mandibles bidentate, slender, elbowed; clypeus short, anterior margin straight, not produced; surface of clypeus impunctate, upper margin strongly elevated. *Cubitognatha*
Mandibles tridentate, more robust, not elbowed; clypeus produced and usually variously lobate; surface of clypeus punctate, upper margin not elevated *Arogochila*

MALES

1. Mandibles tridentate *Chilosima*
Mandibles bidentate 2
2. Lateral margins of seventh tergum distinctly and rather evenly convex throughout, lateral teeth broad, nearly right angular
 *Corythochila* and *Arogochila*
Lateral margins of seventh tergum straight, sinuate, or only slightly convex, lateral teeth with apices acute *Ashmeadiella*,
 *sensu stricto*, *Cubitognatha*, and *Titusella*

GENUS *FORMICAPIS* SLADEN

Formicapis SLADEN, 1916, Canadian Ent., vol. 48, p. 271.

GENOTYPE: *Formicapis clypeata* Sladen (monobasic).

The single species contained in this genus is small and black, with much the aspect of *Chelostomopsis*. Its relationships, however, are probably with *Hoplitis* and *Robertsonella*, as shown by the presence of a minute tooth at each side of the seventh tergum of the male. The clypeus of the female is provided with a broad, snout-like, apical projection. *Formicapis* is found from Alaska to the mountains of Colorado.

GENUS ROBERTSONELLA TITUS

Robertsonella TITUS, 1904, Jour. New York Ent. Soc., vol. 12, p. 22.

GENOTYPE: *Robertsonella gleasoni* Titus = *Heriades simplex* Cresson, by original designation.

This is another genus which, in spite of certain characters indicating a relationship to *Chelostomopsis*, is perhaps most closely related to *Hoplitis*. It is represented by two or three rather rare, small, black species with narrow abdominal fasciae, and is found from California to the Atlantic coast states.

GENUS HOPLITIS KLUG

Hoplitis KLUG, 1807, Mag. Insektenkunde, vol. 6, p. 225.

Andronicus CRESSON, 1864, Proc. Ent. Soc. Philadelphia, vol. 2, p. 384.

Alcidamea CRESSON, 1864, *ibid.*, vol. 2, p. 385.

Monumetha CRESSON, 1864, *ibid.*, vol. 2, p. 387.

Osmia (*Ctenosmia*) THOMSON, 1872, Hymenoptera Scandinaviae, vol. 2, p. 233.

Osmia (*Liosmia*) THOMSON, 1872, *op. cit.*, vol. 2, p. 233.

Osmia (*Tridentosmia*) SCHMIEDEKNECHT, 1886, Apidae Europaeae . . . , vol. 2, p. 887.

Hoplitella COCKERELL (not Levensen), 1910, Canadian Ent., vol. 42, p. 169.

Hoplitina COCKERELL, 1913, *ibid.*, vol. 45, p. 34.

Chlorosmia SLADEN, 1916, Canadian Ent., vol. 48, p. 270.

Autochelostoma SLADEN, 1916, *ibid.*, vol. 48, p. 270.

GENOTYPE: *Apis adunca* Panzer (monobasic).

Found throughout the United States, this Holarctic and Ethiopian genus consists of moderate-sized to small, slender bees. It is in need of subgeneric revision, but the most outstanding features of the American subgenera are indicated below. *Chlorosmia* consists of brightly metallic forms. All others are non-metallic. In *Alcidamea* the last flagellar segment of the male is produced, curved, and sharply pointed. In *Monumetha* the last flagellar segment is not pointed, but the whole flagellum of the male is somewhat flattened, and the scape is swollen. The face of the male is covered with short, appressed, silvery pubescence. In *Andronicus* flagellar segments two to five are greatly dilated in the male. *Hoplitina* consists of small forms with unmodified antennae and with the abdomen at least partly red. *Hoplitis*, *sensu stricto*, and

several other subgenera are confined to the Old World.

GENUS PROTERIADES TITUS

Proteriades TITUS, 1904, Jour. New York Ent. Soc., vol. 12, p. 25.

Chelostoma (*Cephalapis*) COCKERELL, 1910, Ann. Mag. Nat. Hist., ser. 8, vol. 5, p. 23.

GENOTYPE: *Heriades semirubra* Cockerell, by original designation.

Proteriades is a genus of small, nonmetallic bees with the base of the abdomen red. The several species of the genus are known only from California, although they are probably found also in neighboring states. They are apparently confined in pollen collecting to flowers of *Cryptantha*.

GENUS ANTHOCOPA LEPELETIER AND SERVILLE

Anthocopa LEPELETIER AND SERVILLE, 1825, Encyclopédie méthodique, histoire naturelle . . . insectes, vol. 10, p. 314.

Phyllotoma DUMÉRIEUX, 1860, Mém. Acad. Sci. Inst. Imp. France, vol. 31, p. 842.

Pseudosmia RADOSZKOWSKI, 1872, Horae Soc. Ent. Rossicae, vol. 8, p. 18.

Osmia (*Hoplosmia*) THOMSON, 1872, Hymenoptera Scandinaviae, vol. 2, p. 233.

Osmia (*Erythrosomia*) SCHMIEDEKNECHT, 1886, Apidae Europaeae . . . , vol. 2, p. 886.

Osmia (*Furcosmia*) SCHMIEDEKNECHT, 1886, *op. cit.*, vol. 2, p. 888.

Osmia (*Atoposmia*) COCKERELL, 1935, Pan-Pacific Ent., vol. 11, p. 50.

Anthocopa (*Eremosmia*) MICHENER, 1943, Ann. Ent. Soc. Amer., vol. 36, p. 66.

Anthocopa (*Hexosmia*) MICHENER, 1943, *ibid.*, vol. 36, p. 74.

Anthocopa (*Phaeosmia*) MICHENER, 1943, *ibid.*, vol. 36, p. 77.

Anthocopa (*Xerosmia*) MICHENER, 1943, *ibid.*, vol. 36, p. 81.

GENOTYPE: *Apis papaveris* Latreille (monobasic).

This is a group of rather robust, nonmetallic or feebly metallic bees of small to moderate size. For a more complete discussion of the differences between *Anthocopa* and the closely related genus *Hoplitis*, see Michener (1941). The North American species of *Anthocopa* have been revised by Michener (1943). The genus is found in Africa, Eurasia, and in North America from the Rocky Mountains westward.

KEY TO THE AMERICAN SUBGENERA OF *Anihocopa*

MALES

1. Mandibles tridentate 2
Mandibles bidentate 3
2. Proboscis long, when folded reaching well behind anterior coxae; posterior coxa with carina along inner ventral angle feeble . . .
. *Atoposmia*
Proboscis short, when folded hardly reaching anterior coxae; posterior coxae each with a conspicuous carina along inner ventral angle.
. *Eremosmia*
3. Maxillary galeae and labial palpi furnished with stiff hairs with hooked apices; eighth tergum largely exposed with a large transverse sulcus medially and three long teeth apically *Xerosmia*
Maxillary galeae and labial palpi without hooked hairs; eighth tergum but little, if at all, exposed, not tridentate. 4
4. Posterior coxae each with strong longitudinal carina on inner ventral angle; clypeus with truncation much longer than distance from its end to lateral angle of clypeus; black, without metallic luster *Phaeosmia*
Posterior coxae with inner ventral carinae feeble; clypeal truncation concave, shorter than distance from its end to lateral angle of clypeus; body with feeble metallic luster.
. *Hexosmia*

FEMALES

1. Maxillary galeae and first two segments of labial palpi furnished with stiff, hooked hairs *Xerosmia*
Maxillary palpi and galeae without hooked hairs 2
2. Proboscis long, when folded reaching well behind anterior coxae; posterior coxa with carina along inner ventral angle feeble . . .
. *Atoposmia*
Proboscis short, when folded hardly reaching anterior coxae; posterior coxae with carinae along inner ventral angles variable . . . 3
3. Body with a feeble metallic luster; posterior coxae with inner ventral carinae weak . . .
. *Hexosmia*
Body black, without metallic luster; posterior coxae each with strong carina on inner ventral angle 4
4. Mandibles more than four times as long as shortest breadth (length measured from apex to lower basal angle) *Eremosmia*
Mandibles less than four times as long as shortest breadth *Phaeosmia*

GENUS *DICERATOSMIA* ROBERTSON

Diceratosmia ROBERTSON, 1903, Trans. Amer. Ent. Soc., vol. 29, p. 166.

GENOTYPE: *Osmia quadridentata* Cresson = *Osmia conjuncta* Cresson, by original designation.

The species of this small Holarctic genus that are found in the United States are rather coarsely punctate and dull metallic blue.

GENUS *OSMIA* PANZER

Osmia PANZER, 1806, Kritische Revision der Insekten-fauna Deutschlands . . . , vol. 2, p. 230.

Amblys ILLIGER, 1807, Mag. Insektenkunde, vol. 6, p. 198.

Osmia (*Ceratosmia*) THOMSON, 1872, Hymenoptera Scandinaviae, vol. 2, p. 232.

Osmia (*Helicosmia*) THOMSON, 1872, *op. cit.*, vol. 2, p. 233.

Osmia (*Aceratosmia*) SCHMIEDEKNECHT, 1886, Apidae Europaeae . . . , vol. 2, p. 885.

Osmia (*Melanosmia*) SCHMIEDEKNECHT, 1886, *op. cit.*, vol. 2, p. 885.

Osmia (*Chalcosmia*) SCHMIEDEKNECHT, 1886, *op. cit.*, vol. 2, p. 886.

Nothosmia ASHMEAD, 1899, Trans. Amer. Ent. Soc., vol. 26, p. 75.

Acanthosmioides ASHMEAD, 1899, *ibid.*, vol. 26, p. 76.

Osmia (*Pachyosmia*) DUCKE, 1900, Ber. Naturwiss.-med. Ver. Innsbruck, vol. 25, p. 6.

Centrosmia ROBERTSON, 1903, Trans. Amer. Ent. Soc., vol. 29, p. 165.

Gnathosmia ROBERTSON, 1903, *ibid.*, vol. 29, p. 165.

Xanthosmia ROBERTSON, 1903, *ibid.*, vol. 29, p. 166.

Monilosmia ROBERTSON, 1903, *ibid.*, vol. 29, p. 166.

Leucosmia ROBERTSON, 1903, *ibid.*, vol. 29, p. 166.

Cephalosmia SLADEN, 1916, Canadian Ent., vol. 48, p. 270.

GENOTYPE: *Apis bicornis* Linnaeus = *Apis rufa* Linnaeus, designated by Latreille, 1810, Considérations générales . . . des insectes, p. 439.

This is a large Holarctic genus of robust species most of which are metallic. They are found throughout the United States. Our species have recently been revised by Sandhouse (1939), and the following key is based upon that presented by her.

KEY TO THE AMERICAN SUBGENERA OF *Osmia*

1. Malar space at least nearly as long as pedicel, bearing a small depression in female; middle

- femora of male each with a projection on lower margin *Osmia, sensu stricto*
Malar space almost absent, lacking depression; middle femora of male without projections. . 2
2. Terga two to six with subapical fimbriae of plumose hairs; clypeus of female with two small median tufts of hair on margin in addition to usual large tufts; apical margin of fifth sternum of male thickened and lateral portions transversely sulcate . . *Chalcosmia*
Terga two to six with apical impunctate bands, or if hairs reach near margins, they are simple; clypeal truncation of female with only the usual two tufts of hair; apical margin of fifth sternum of male neither thickened nor transversely sulcate laterally 3
3. Labrum considerably longer than wide; metanotum anteriorly with median horizontal portion; clypeus of female sparsely punctate to nearly impunctate; apical margin of third and usually of fourth sterna truncate *Cephalosmia*
Labrum but little longer than broad; metanotum declivous throughout; clypeus of female densely punctured; apical margin of third sternum of male usually convex, of fourth usually emarginate 4
4. Black, or, if dark blue, head of female much broader than thorax, clypeal margin thickened and male with lateral margins of sixth and seventh terga reflexed and middle tarsal segments modified *Melanosmia*
Strongly metallic, without above combination of characters 5
5. Mandibles constricted a short distance from base, widened to apical margin which is about twice (female) or one and one-half (male) times as wide as narrow part; second sternum of male with at least longitudinal median band of bristles, usually an elevated median process *Acanthosmioides*
Mandibles narrow at base, apical margin not so wide as in *Acanthosmioides*; second sternum of male not modified as above . *Nothosmia*

GENUS MEGACHILE LATREILLE

*Megachile*¹ LATREILLE, 1802, Histoire naturelle des fourmis . . . , p. 434.

Anthophora FABRICIUS (not Latreille), 1805, Systema piezatorum . . . , p. 372.

Chalicodoma LEPELETIER, 1841, Histoire naturelle des insectes, hyménoptères, vol. 2, p. 309.

Megachile (Eutricharaea) THOMSON, 1872, Hymenoptera Scandinaviae, vol. 2, p. 228.

¹ Schulz (1906, Spolia hymenopterologica, p. 64) spelled this name *Megalochila* and made comparable changes in the spelling of its compounds.

Gnathocera PROVANCHER (not Kirby), 1882, Nat. Canadien, vol. 13, p. 232.

Megachile (Paramegachile) FRIESE, 1899, Die Bienen Europas, vol. 5, p. 34.

Megachile (Eumegachile) FRIESE, 1899, *op. cit.*, vol. 5, p. 36.

Megachile (Pseudomegachile) FRIESE, 1899, *op. cit.*, vol. 5, p. 36.

Chelostomoides ROBERTSON, 1901, Canadian Ent., vol. 33, p. 231.

Ceratias ROBERTSON (not Kroyer), 1903, Trans. Amer. Ent. Soc., vol. 29, p. 168.

Oligotropus ROBERTSON (not Oken), 1903, *ibid.*, vol. 29, p. 168.

Gnathodon ROBERTSON, 1903, *ibid.*, vol. 29, p. 168.

Xanthosarus ROBERTSON, 1903, *ibid.*, vol. 29, p. 168.

Anthemois ROBERTSON, 1903, *ibid.*, vol. 29, p. 168.

Cyphopyga ROBERTSON, 1903, *ibid.*, vol. 29, p. 169.

Sayapis TITUS, 1905, Proc. Ent. Soc. Washington, vol. 7, p. 154.

Megachile (Creightonella) COCKERELL, 1908, Entomologist, vol. 41, p. 146.

Amegachile FRIESE, 1909, Die Bienen Afrikas, p. 326.

Megachile (Delomegachile) VIERECK, 1916, State [Connecticut] Geol. Nat. Hist. Survey, Bull. 22, p. 745.

Sarogaster ROBERTSON, 1918, Ent. News, vol. 29, p. 92.

Megachile (Hackeriapis) COCKERELL, 1922, Ann. Mag. Nat. Hist., ser. 9, vol. 10, p. 267.

Megachiloides MITCHELL, 1924, Jour. Elisha Mitchell Sci. Soc., vol. 40, p. 154.

Megachile (Archimegachile) ALFKEN, 1933, Kownia, vol. 12, p. 56.

Megachile (Litomegachile) MITCHELL, 1934, Trans. Amer. Ent. Soc. (for 1933), vol. 59, p. 301.

Megachile (Leptorachis) MITCHELL, 1934, *ibid.*, vol. 59, p. 301.

Megachile (Argyropile) MITCHELL, 1934, *ibid.*, vol. 59, p. 302.

Megachile (Neomegachile) MITCHELL, 1934, *ibid.*, vol. 59, p. 302.

Megachile (Cressoniella) MITCHELL, 1934, *ibid.*, vol. 59, p. 302.

Megachile (Xeromegachile) MITCHELL, 1934, *ibid.*, vol. 59, p. 302.

Megachile (Phaenosarus) MITCHELL, 1934, *ibid.*, vol. 59, p. 303.

Megachile (Pseudocentron) MITCHELL, 1934, *ibid.*, vol. 59, p. 303.

Megachile (Acentron) MITCHELL, 1934, *ibid.*, vol. 59, p. 303.

Megachile (*Melanosarus*) MITCHELL, 1934, *ibid.*, vol. 59, p. 303.

Megachile (*Derotropis*) MITCHELL, 1936, *ibid.*, vol. 62, p. 118.

GENOTYPE: *Apis centuncularis* Linnaeus, designated by Curtis, 1828, *British entomology* . . . , vol. 5 [if bound as published in 16 vols.], pl. 218.

A large genus, *Megachile* consists of moderate-sized, black (i.e., nonmetallic) bees, commonly with fasciae of pale pubescence on the abdomen. The anterior face of the mesepisternum is not separated from the lateral face by a carina, nor are the posterior lobes of the pronotum carinate. The anterior face of the second abdominal tergum is concave, but the concavity is not margined by a carina. In the male the eighth tergum is partly visible, and sterna two to four or two to five are exposed.

The type species here given is not that first designated, for Latreille in 1810 regarded *Apis muraria* Retzius as the genotype. However, since that species is the type of the well-known genus or subgenus *Chalicodoma*, which would become a synonym of *Megachile* if Latreille's designation were upheld, it has seemed best to follow the Curtis designation, as have Benson, Ferrière, and Richards (1937). Should the International Commission of Zoological Nomenclature uphold Latreille's designation, the subgenus *Megachile*, *sensu stricto*, of the following key becomes *Anthemois*.

Species of *Megachile* are found throughout the United States and may be separated into subgenera by the following key, modified from that of Mitchell, who has recently revised the North American forms of this large genus.

KEY TO THE SUBGENERA OF *Megachile*
OCCURRING NORTH OF MEXICO

MALES

1. Abdomen with three exposed sterna; body slender *Chelostomoides*
- Abdomen with four exposed sterna; body commonly more robust 2
2. Mandibles lacking inferior projection . . . 3
- Mandibles with inferior projection 4
3. Small slender species with short pubescence; apical abdominal terga not conspicuously tomentose; disk of seventh tergum above carina subhorizontal *Neomegachile*
- Larger, more robust species with long erect pubescence; fifth and sixth terga densely covered with pale tomentum; disk of seventh tergum above carina vertical *Cressoniella*
4. Carina or transverse ridge of seventh tergum usually with a definite median emargination, sometimes obscured by lateral denticulation 5
- Carina or transverse ridge of seventh tergum without median emargination, though often denticulate or serrate 18
5. Front coxal spines vestigial or absent *Megachile*, *sensu stricto*
- Front coxae each with a large spine 6
6. Middle tibial spurs absent 7
- Middle tibiae each with the usual apical spur 10
7. Mandibles tridentate; middle basitarsi conspicuously protuberant beneath *Xanthosarus*
- Mandibles quadridentate; middle basitarsi not protuberant beneath 8
8. Mandible with median sharp angle or tooth on the lower margin; posterior face of front femur sharply carinate above; middle tibia with spur-like apical projection *Pseudocentron*
- Mandible without median ventral angle; posterior face of front femur not carinate above; middle tibia without spur-like apical projection, although often angulate or protuberant 9
9. Middle tibiae dilated apically; front basitarsi not much produced apically, subequal in length to segments two to five together *Acentron*
- Middle tibiae not dilated apically, inner margin with slight angle just before apex; front basitarsi much produced apically, length along posterior margin not much exceeding length of second segment *Melanosarus*
10. Middle coxae each with long slender spine *Xanthosarus*
- Middle coxae not spined 11
11. Front basitarsi dilated, usually brightly colored 12
- Front basitarsi simple, usually dark in color 13
12. Mandibles tridentate; abdomen rather long and slender, parallel-sided; claws usually each with a sharp basal tooth *Sayapis*
- Mandibles quadridentate; abdomen rather short and robust; claws without basal teeth. *Delomegachile*
13. Mandibles distinctly quadridentate . . . 14
- Mandibles tridentate 15
14. Seventh tergum with apical margin (not carina) with four conspicuous teeth; front coxae more or less pubescent anteriorly and

- without a patch of red bristles anterior to each spine *Argyropile*
 Seventh tergum with apical margin without conspicuous teeth; front coxae bare anteriorly, with a dense patch of red bristles anterior to each spine . . . *Delomegachile*
15. Seventh tergum with morphological apical margin (not carina) without evident teeth; sixth tergum usually conspicuously pale tomentose 16
 Seventh tergum with apical margin with either median or lateral teeth or both; sixth tergum with, at most, inconspicuous pale tomentum across base 17
16. Seventh tergum with carina or transverse ridge entire laterad of the definite median emargination; mandible with indistinct tooth between the definite apical and median teeth *Leptorachis*
 Seventh tergum with carina usually denticulate laterally, median emargination inconspicuous; mandibles definitely tridentate (Palearctic subgenus, introduced into United States). *Eutricharaea*
17. Eighth tergum produced medially to conspicuous spine-like projection; lateral teeth of apical margin of seventh tergum conspicuous, median ones not evident; fifth tergum entirely lacking pale tomentum . . *Sayapis*
 Eighth tergum not conspicuously protuberant medially; apical margin of seventh tergum with evident, although small, median and lateral teeth, median pair carinate, lateral ones acute; sixth tergum often with narrow band of pale tomentum basally *Litomegachile*
18. Fifth sternum with small but distinct median tubercle on apical margin; large robust species, front tarsi broadly dilated but only slightly excavated anteriorly. *Phaenosarus*
 Fifth sternum not tuberculate 19
19. Proboscis very long, second segment of labial palpi 1.7 to 4 times length of first *Megachiloides*
 Proboscis shorter, second segment of labial palpi at most 1.5 times length of first. . 20
20. Second segment of labial palpi at least slightly longer than first; sixth sternum with a robust, basal, median, apically directed spine-like projection *Derotropis*
 First and second segments of labial palpi subequal in length; sixth sternum usually lacking in a basal median projection *Xeromegachile*
- Abdomen cordate or ovoid 3
2. Mandibles with a cutting edge between the two median teeth; claws each with a sharp basal tooth; basal grooves of abdominal terga not fasciate; apex of seventh tergum gradually concave; maxillary palpi neither densely nor conspicuously pubescent *Sayapis*
 Mandibles lacking definite cutting edge; claws without sharp basal teeth; basal grooves of abdominal terga often fasciate; maxillary palpi densely pubescent; seventh tergum usually abruptly concave or grooved apically. *Chelosiomoides*
3. Mandibles with five well-defined teeth. . . 4
 Mandibles with three or four teeth, or obscurely five-dentate 7
4. Mandibles with two apical teeth separated from three inner ones by rather long cutting edge; middle basitarsi as long as middle tibiae; robust black species. . *Melanosarus*
 Mandibular teeth not grouped as above; middle basitarsi usually somewhat longer than middle tibiae; species with pale abdominal fasciae 5
5. Abdomen more ovoid; emargination between second and third mandibular teeth as deep as, or deeper than, that between third and fourth *Megachile, sensu stricto*
 Abdomen more cordate; emargination between second and third mandibular teeth much shallower than that between third and fourth 6
6. Seventh tergum broad and short, broadly rounded apically, with pubescence erect nearly to tip; seventh sternum not at all protruding beyond apex of tergum *Xanthosarus*
 Sixth tergum rather long, apex narrowly rounded or subtruncate, pubescence of apical half appressed; seventh sternum slightly exceeding the tergum. *Phaenosarus*
7. Mandibles tridentate, with two apical teeth and a very long cutting edge extending to the inner angle *Derotropis*
 Mandibles distinctly or obscurely quadridentate, without a long cutting edge as in *Derotropis*. 8
8. Proboscis very long, second segment of labial palpus 1.7 to 4 times as long as first; third mandibular tooth vestigial, a short cutting edge between it and inner angle. *Megachiloides*
 Proboscis of usual length, second segment of labial palpus but little, if any, longer than first; mandibles distinctly quadridentate. 9
9. Innermost mandibular tooth either rounded or broadly and sharply truncate, not acute.

FEMALES

1. Abdomen parallel-sided; narrow, slender species 2

-10
Innermost mandibular tooth acute12
10. Small forms (9 mm. or less) with short pubescence; abdomen rather acutely pointed; pubescence of seventh tergum appressed in large part; with short, suberect hairs visible toward base in profile . . . *Neomegachile*
Larger forms (12 mm. or more) with much longer and denser pubescence; seventh tergum with abundant erect pubescence visible in profile11
11. Lateral ocelli considerably nearer to posterior edge of vertex than to eyes; innermost mandibular tooth broadly truncate. . . .
..... *Cressoniella*
Lateral ocelli usually nearer to eyes than to edge of vertex but, if not, innermost mandibular tooth rounded . . . *Delomegachile*
12. Abdominal sterna with definite pale apical fasciae beneath scopa. . . . *Eutricharaea*
Abdominal sterna lacking apical fasciae. .13
13. Emargination between third and fourth mandibular teeth slightly angulate, giving an approach to the five-toothed condition; pubescence of seventh tergum mostly or entirely appressed14
Emargination between third and fourth mandibular teeth evenly concave15
14. Abdomen more ovoid; seventh tergum distinctly concave in profile; clypeal margin with median incurved area
..... *Megachile*, *sensu stricto*
Abdomen more cordate; seventh tergum at most but slightly concave in profile, usually straight; clypeal margin straight.
..... *Litomegachile*
15. Seventh tergum distinctly concave in profile.16
Seventh tergum straight in profile18
16. Seventh tergum with no erect hairs visible in profile, uniformly and entirely covered with fine pale tomentum *Argyropile*
Seventh tergum with abundant erect pubescence visible in profile17
17. Clypeal margin denticulate . . *Delomegachile*
Clypeal margin entire *Litomegachile*
18. Seventh sternum largely bare or but thinly pubescent, usually with bare rim or ridge extending beyond or above apical fringe of short hairs19
Seventh sternum densely pubescent, without apical bare rim or ridge. . *Xeromegachile*
19. Apical rim of seventh sternum not reflexed upward or forward20
Apical rim of seventh sternum reflexed upward or forward *Argyropile*
20. Third mandibular tooth acute, an incomplete cutting edge between it and second tooth.

- *Pseudocentron*
Third mandibular tooth truncate, without a cutting edge between it and second tooth.21
21. Apical rim of seventh sternum very inconspicuous; cheeks narrower than eyes, vertex very narrow behind eyes and lateral ocelli; third mandibular tooth broadly truncate. .
..... *Leptorachis*
Apical rim of seventh sternum definite and rather conspicuous; cheeks below subequal in width to eyes; vertex broader behind eyes and ocelli. *Acentron*

GENUS COELIOXYS LATREILLE

Coelioxys LATREILLE, 1809, *Genera crustaceorum insectorum* . . . , vol. 4, p. 166.

Paracoelioxys GRIBODO, 1884, *Bull. Soc. Ent. Italiana*, vol. 16, p. 274.

Paracoelioxys RADOSZKOWSKI (not Gribodo), 1893, *Horae Soc. Ent. Rossicae*, vol. 27, p. 53.

Coelioxys (*Liothyrapis*) COCKERELL, 1911, *Proc. U. S. Natl. Mus.*, vol. 40, p. 246.

GENOTYPE: *Apis conica* Linnaeus = *Apis quadridentata* Linnaeus, designated by Latreille, 1810, *Considérations générales . . . des insectes*, p. 439.

This is a genus of coarsely punctate, black bees, usually with conspicuous abdominal fasciae of pale hairs. The abdomen is conical, tapering from the second segment, giving the species of the genus a very distinctive appearance. The anterior face of the mesepisternum is separated from the lateral face by a strong carina, and the posterior lobes of the pronotum each bear a transverse carina. The anterior face of the second abdominal tergum is strongly concave and usually margined by a carina. In the male, sterna two to five only are exposed, and the eighth tergum is hidden.

This widely distributed genus, which is parasitic on species of *Megachile*, may be found in any part of the United States. Keys to the species found in this country have been presented by Cockerell (1925) and Crawford (1914).

FAMILY APIDAE

Labrum usually broader than long, attached by rather short margin to clypeus (thus forms with the labrum long may be distinguished from the *Megachilidae*); subantennal areas absent; subantennal sutures directed toward inner margins of antennal sockets; lower sides of clypeus frequently

bent back parallel to long axis of body; facial foveae almost always absent; stipites with or without combs; galeae elongate postpalpally, short prepalpally, without combs; submentum V-shaped; mentum tapering basally; labial palpi with first two segments elongate and flattened, first segment at least as long as second; glossa linear, usually with a flabellum; pre-episternal suture almost always absent below scrobal suture and present above it; middle coxae elongate, except in a few parasitic forms; basitibial plates present in many; scopa when present on posterior tibiae and basitarsi, rarely on an abdominal sterna as well; pygidial area variable; volsella usually absent.

This is the largest family of bees, and it contains elements which have often been placed in several separate families, largely on the basis of the presence or absence of the pygidial plate, a character which is unfortunately unreliable, being frequently and independently lost in different groups of bees.

KEY TO THE SUBFAMILIES OF APIDAE

1. Scopa of female on abdominal sterna as well as on posterior legs; clypeus not protuberant, lateral portions as seen from below not parallel to long axis of body; pygidial plate absent (Africa) Fideiinae
 Scopa of female (except in parasitic forms in which it is absent) confined to posterior legs; clypeus and pygidial plate variable 2
2. Scopa of female, when present, forming a corbicula on each posterior tibia, except in queens of Meliponini; inner apical margins of posterior tibiae of nonparasitic females, except in queens of Meliponini and in *Trigona*, subgenus *Lestrimelitta*, provided with a row of stiff setae; pygidial plate absent. Apinae
 Scopa of female not forming a corbicula; inner apical margins of posterior tibiae bare or hairy, without comb of stiff setae; pygidial plate frequently present 3
3. Pygidial plate present in nearly all females and most males; clypeus almost always protuberant so that lateral portions seen from below are bent posteriorly and lie parallel to long axis of body; anterior coxae usually but little broader than long. Anthophorinae
 Pygidial plate absent, represented in some females by a flat-topped apical spine hidden in a dense pygidial fimbria; clypeus not protuberant, lateral portions seen from beneath but little bent backward and more nearly

transverse than longitudinal; anterior coxae transverse Xylocopinae

Because of the modifications and variability of the various parasitic groups, it is impossible to run certain of these bees through the preceding key to the subfamilies of Apidae. Therefore, certain additional information is here presented to aid in the determination of forms occurring in the United States.

In the Apinae the distance between the costal ends of the two recurrent veins is at least nearly twice as great as the length of the second recurrent vein and is longer than the first recurrent. This combination of characters is found elsewhere in the Apidae in some Exomalopsini of the Anthophorinae, a group having well-developed pterostigmata, in contrast to all the Apinae of the United States.

Except in *Hemisia* and a very few other genera in which the clypeus has apparently been secondarily flattened, all the Anthophorinae have a protuberant clypeus with the lower parts of the sides bent back parallel to the long axis of the body. They differ thus from the Xylocopinae, in which the clypeus is relatively flat. The clypeus of the Xylocopinae is further distinctive in that those portions of the epistomal suture between the anterior tentorial pits and the dorso-lateral angles of the clypeus are subparallel to one another, while below the pits the clypeus broadens abruptly. In the Anthophorinae the margins of the clypeus generally converge upward to the dorso-lateral angles.

SUBFAMILY FIDEIINAE

This curious African subfamily has been placed by Popov among the lower families of bees (Colletidae, Andrenidae) because of the form of the eighth abdominal sternum of the male, which bears a pair of complex apical lobes similar to those of most Colletidae. The numerous characteristics of the mouthparts and the configuration of the thorax are as in the Apidae. The mandibles of the female are broad and bilobed apically. The marginal cell is much shorter than the distance from its apex to the wing tip, and the apical portion of the cell is bent away from the costal margin of the wing; there are three submarginal cells. The basitibial plates are absent.

This subfamily contains the genus *Fidelia*,

upon which the above comments are based, and no doubt also *Parafidelia*.

SUBFAMILY ANTHOPHORINAE

This is a large group of bees containing many very diverse elements. It is, nevertheless, apparently a monophyletic unit. The reason for the diversity appears to be that repeatedly in the course of evolution parasitic forms have been produced from different non-parasitic groups. The rate of evolution among the parasitic forms, most of which have previously been placed in a polyphyletic assemblage called the Nomadidae, has been very rapid, so that their relationships are often difficult to determine. Even the male genitalia have been profoundly modified in connection with the specialization of the female abdomen associated with the parasitic habit. The North American genera of the parasitic groups of the Anthophorinae (except the Melectini and Ericrocini) were revised by Linsley and Michener (1939). The species of the nonparasitic ones are listed by Lutz and Cockerell (1920).

The tribes of the Anthophorinae may be separated as follows:

KEY TO THE TRIBES OF ANTHOPHORINAE

1. Labrum (except in certain African Ammobatini) more than one and one-half times as long as broad 2
Labrum usually broader than long, sometimes slightly longer than broad. 5
2. Middle coxae much shorter than distance from summits to posterior wing bases; body coarsely punctured with patches of squamiform pubescence; each submarginal cell receiving a recurrent vein. 3
Middle coxae at least nearly as long as distance from their summits to posterior wing bases; body finely punctate without patches of squamiform hairs; both recurrent veins received by second submarginal cell . . . 4
3. Labrum one and one-half times as long as broad; pre-episternal groove extending well below scrobal suture. Caenoprosopidini
Labrum twice as long as broad; pre-episternal suture not extending below scrobal suture. Neopositini
4. Pygidial plate of female absent or feebly defined; seventh sternum of female produced to simple or notched apex; eyes of males not convergent above Ammobatini
Pygidial plate of female well defined; seventh sternum of female broadly emarginate apically, lateral lobes multispinose; eyes of male converging above . . . Ammobatoidini
5. Second abscissa of vein M+Cu of posterior wing less, usually much less, than twice as long as the oblique cu-v and not over one-half as long as vein M (fig. 35); distal parts of wings usually strongly papillate, basal parts usually with bare areas 6
Second abscissa of vein M+Cu of posterior wings at least nearly twice as long as the transverse or somewhat oblique cu-v and rarely much shorter than vein M (as in fig. 189); wings usually pubescent throughout and but feebly papillate apically . . 13
6. Jugal lobe of posterior wing about half as long as vannal lobe; scopa consisting of long, coarsely plumose hairs 7
Jugal lobe of posterior wing at most a little over one-third as long as vannal lobe; scopa of female absent or consisting of simple hairs, or at least with long simple hairs intermixed among shorter plumose ones. 9
7. Pterostigma small, not wider than distance from inner margin of prestigma to costal margin of wing 8
Pterostigma large, elongate, wider than distance from inner margin of prestigma to costal margin of wing. Exomalopsini
8. Marginal cell longer than distance from apex to wing tip; first submarginal cell longer than either of the others, second shortest; mandibles simple Emphorini
Marginal cell as long as, or usually considerably shorter than, distance from apex to wing tip; second submarginal cell longer on posterior margin than either of the others, third usually shortest; mandibles dentate. Hemisiini
9. Wings hairy throughout, not papillate; marginal cell as long as, or longer than, distance from its apex to wing tip 10
Wings bare, or largely so, papillate apically; marginal cell commonly shorter than distance from apex to wing tip 11
10. Claws cleft or with inner median tooth; scopa present in female. Exomalopsini
Claws neither cleft nor toothed but with broad inner basal lobe; scopa absent. Rhathymini
11. Second abscissa of vein M+Cu of posterior wings shorter than cu-v, sometimes virtually absent; posterior angle of mandible beneath middle of lower end of eye; scopa absent; claws with large inner basal lobe or tooth. 12
Second abscissa of vein M+Cu of posterior wings about as long as cu-v (fig. 35); posterior angles of mandibles beneath posterior

- margins of eyes; scopa present in female; claws of male cleft, of female with median tooth on inner side. Anthophorini
12. Marginal cell considerably exceeding last submarginal cell; middle tibial spur large, bifid, or multidentate apically; male gonostyli short, broad; pygidial plate not, or poorly, defined. Eucrocini
Marginal cell not, or scarcely, exceeding last submarginal cell; middle tibial spurs unmodified; male gonostyli elongate, not greatly flattened; seventh abdominal tergum of female with pygidial plate. Melectini
13. Paraglossae as long as first two segments of labial palpi together; jugal lobe of posterior wings about half as long as vannal lobe; antennae of males commonly much elongate; scopa present. Eucerini
Paraglossae much shorter than first segment of labial palpi; jugal lobe of posterior wings usually less than half as long as vannal lobe; antennae of males not unusually elongate; scopa frequently absent. 14
14. Marginal cell at most but little larger than pterostigma, truncate apically; one or two submarginal cells, second, when present, much wider than long. Neolarrini
Marginal cell far larger than pterostigma; two or three submarginal cells, if but two, second usually at least as long as broad. 15
15. Scape, excluding basal bulb, less than twice as long as broad; seventh tergum of female without pygidial plate, apical margin broadly concave; two submarginal cells. Biastini
Scape, excluding basal bulb, more than twice as long as broad; seventh tergum of female usually with pygidial plate, not broadly concave apically; two or three submarginal cells. 16
16. With but two submarginal cells, second much shorter than first and receiving only the second r-m, or sometimes first r-m very near its base; seventh sternum of female broadly emarginate, lobes at either side of emargination armed with a series of large, spine-like setae. Townsendiellini
With three submarginal cells, or if two, second at least nearly as long as first and receiving both recurrent veins (except very rarely in *Nomada*, in which marginal cell is pointed on wing margin, unlike Townsendiellini); seventh sternum of female not broadly emarginate, although sometimes with spine-like setae. 17
17. Mesepisternum entirely nearly vertical, rising from immediately in front of middle coxae as seen in profile; scopa absent. Osirini
- Mesepisternum with the usual horizontal area in front of middle coxae, except in a few Neotropical Exomalopsini. 18
18. Arolia unusually large, capitate, in North American forms nearly as long as claws, or longer; pygidial plate absent in both sexes, in female represented by narrow, flat process; scopa absent. Protepeolini
Arolia much shorter than claws, if somewhat elongate; scarcely capitate; pygidial plate present in females and most males; scopa present or absent. 19
19. Inner margins of eyes strongly converging above in males; sixth abdominal sternum of female elongate, produced posteriorly, semi-tubular, apex rounded and without spines; pygidial plate of male narrowed basally, spatulate; scopa absent. Epeoloidini
Inner margins of eyes subparallel or converging below; sixth abdominal sternum of female not elongated, apex rounded, bilobed, or produced to two long spinose processes; pygidial plate of male not narrowed basally; scopa present or absent. 20
20. Anterior coxae quadrate, the trochanters arising from their outer distal angles so that they are far apart; axillae each produced to an acute angle or spine; sixth abdominal sternum of female largely invaginated, with disk reduced and lateral distal portions produced to form a pair of long, slender, dentate or spinose processes; scopa absent. Epeolini
Anterior coxae somewhat triangular, trochanters (except in *Paranomada*) arising close to one another from apices of coxae; axillae usually rounded; sixth abdominal sternum of female not much invaginated, the disk not greatly reduced, spinose processes, if present, short or mere lobes; scopa present or absent. 21
21. Pterostigma small, short, extending but little beyond base of vein r; jugal lobe of posterior wing one-third to one-half as long as vannal lobe; scopa present. Ancylini
Pterostigma large, elongate, extending well beyond base of vein r; jugal lobe of posterior wings variable in size; scopa present or absent. 22
22. Scopa present in females; hairs of body rather abundant, many of them plumose. Exomalopsini
Scopa absent; hairs of body short and sparse, relatively few plumose. Nomadini

TRIBE EXOMALOPSINI

This is a primarily Neotropical group of moderate-sized to small, robust, or slender

bees. The scopa consists, at least in part, of strongly plumose hairs. The maxillary palpi are rather long, usually six-segmented. The pterostigmata are large, elongate, usually extend much distad of base of vein r, and each is at least as broad as, and usually broader than, distance from inner margin of prestigma to wing margin. The marginal cell is at least a little longer than the distance from its apex to wing tip; the apex of the cell is either abruptly or gradually bent away from the wing margin and pointed or narrowly rounded. There are two or three submarginal cells, if three, second usually distinctly shorter than the others. The jugal lobe of each posterior wing varies from one-fourth to over one-half as long as the vannal lobe. The basitibial plates are present, at least in females. The posterior legs of the male are commonly enlarged and modified. Arolia are present except in *Tetrapedia* (= *Fiorentinia*) and *Caenonomada* (= *Chacoana*), which genera have broadly pectinate inner hind tibial spurs and lack the outer spurs in the male.

This tribe is unusual in that the character of hind wing venation mentioned in couplet 5 of the accompanying key to the tribes, while elsewhere excellent in distinguishing groups, is here variable and unreliable as a tribal character. Hence the *Exomalopsini* run out in more than one place in the key. The majority of forms and all those occurring in the United States run to 22 in the key.

Genera included in this tribe are *Ancyloscelis*, *Caenonomada*, *Chaetostetha*, *Chalepogenus* (= *Desmotetrapedia*), *Chalepogenoides*, *Exomalopsis*, *Lanthanomelissa*, *Protomeliturga*, *Tapinotaspis*, and *Tetrapedia*. The Asiatic genus *Ctenoapis* (= *Pararhophites*) appears also to belong to the *Exomalopsini*, although its distribution would favor its placement in the closely related *Ancylini*. Study of additional material may show that these two tribes should be united. The much-reduced pterostigmata of a few species of *Exomalopsis* (e.g., *compactula* Cockerell) lend weight to this idea.

KEY TO THE GENERA OF EXOMALOPSINI
OCCURRING NORTH OF MEXICO

1. Marginal cell much longer than distance from its apex to wing tip, bent gradually from wing margin; posterior legs of male much enlarged *Ancyloscelis*

Marginal cell but little longer than distance from its apex to the wing tip, bent abruptly from wing margin so that apex of cell is obliquely truncate; posterior legs of male rarely enlarged or modified . . . *Exomalopsis*

GENUS *EXOMALOPSIS* SPINOLA

Exomalopsis SPINOLA, 1853, Mem. Accad. Sci. Torino, ser. 2, vol. 13, p. 89.

Anthophorula COCKERELL, 1897, New Mexico Coll. Agr. . . . , Agr. Exp. Sta., bull. 24, p. 44.

Diadasiella ASHMEAD, 1899, Trans. Amer. Ent. Soc., vol. 26, p. 64.

Epimonispractor HOLMBERG, 1903, An. Mus. Nac. Buenos Aires, ser. 3, vol. 2, p. 426.

Exomalopsis (*Pachycerapis*) COCKERELL, 1922, Amer. Mus. Novitates, no. 47, p. 4.

GENOTYPE: *Exomalopsis fulvopilosa* Spinola = *E. aureopilosa* Spinola, designated by Taschenberg, 1883, Berliner Ent. Zeitschr., vol. 27, p. 82.

This is a rather large genus of small, hairy, robust bees. The lower lateral portions of the clypeus are gently curved backward, not strongly bent back as in most *Anthophorinae*. The clypeus of the male is yellow or white in some species, and some have but two submarginal cells. The subgenus *Pachycerapis* was erected for forms in which the middle portion of the flagellum of the male is serrate beneath and the posterior tibiae of the male enlarged.

This is a primarily Neotropical genus, which extends as far north as Nebraska and central California. No species are known east of Mississippi.

GENUS *ANCYLOSCELIS* LATREILLE

Ancyloscelis LATREILLE, 1829, in Cuvier, Règne animal, 2d ed., vol. 5, p. 355.

Dipedia FRIESE, 1906, Flora og Fauna, vol. 8, p. 92.

GENOTYPE: *Ancylosceles ursinus* Haliday, first species to be included.

This genus, like *Exomalopsis*, consists of small bees. They are, however, less conspicuously hairy than *Exomalopsis* and have, as a rule, more conspicuous and narrower abdominal fasciae. The clypeus is strongly bent posteriorly at the sides below.

This chiefly Neotropical genus is very rare in the United States but has been found in Texas, southern Colorado, and Arizona. The North American species of the genus have been revised by Michener (1942).

TRIBE ANCYLINI

This is a small Palaearctic tribe of moderate-sized, robust bees similar to the New World Exomalopsini. The scopa, at least in *Ancyla*, is large and consists of plumose hairs. The maxillary palpi are long, six-segmented. The pterostigma is but little broader than the distance from the inner margin of the prestigma to the wing margin, is at most twice as long as broad, and extends relatively little beyond the base of vein r. The marginal cell is about as long as, or a little longer than, the distance from its apex to the wing tip; its apical portion is narrowly rounded or pointed and bent gradually away from the wing margin. There are three submarginal cells, the first and third subequal in length on the posterior side, the middle one but little shorter. The males lack pygidial plates and have the posterior legs more or less enlarged.

This tribe includes *Ancyla* and *Tarsalia*.

TRIBE NOMADINI

This is a large group of parasitic bees. As in other parasitic Anthophorinae the scopa is absent, the basitibial plates are absent, and the jugal lobes of the posterior wings are very small. The pterostigma is rather large, almost always considerably broader than the distance from the inner margin of the prestigma to the costal wing margin. The marginal cell is conspicuously longer than the distance from its apex to the wing tip and pointed or narrowly rounded. The pygidial plate is present in both sexes. The seventh sternum of the female is subtruncate to bilobed at the apex, which is provided with a few to many coarse, spine-like setae.

Nomada is abundant in the Old World as well as in the New, although the Nomadini as a group are predominantly American. In addition to the genera found north of Mexico, the tribe includes the Neotropical *Hypochrotaenia* (? = *Nomadosoma*) and *Kelita* (= *Herbstiella*), and probably other South American genera such as *Brachynomada* and *Polybiapis*. *Kelita* from Chile is of particular interest, being closely related to the Californian *Hesperonomada*, agreeing even in the hairy process of the sixth sternum of the female but differing in the somewhat reduced pterostigma and the pointed tip of marginal cell slightly bent away from the wing margin. The "*Herbstiella*"

described from California by Hicks is a *Stelis* of the subgenus *Stelidina*.

KEY TO THE GENERA OF NOMADINI
OCCURRING NORTH OF MEXICO

1. Thorax strongly dorso-ventrally compressed so that its greatest width is nearly twice its height; integument smooth, polished, practically impunctate; flagellum short, intermediate segments broader than long; coxae strongly lamellate externally in female *Paranomada*
Thorax normally convex, its greatest width about equal to its height; integument distinctly punctured (vertex and mesoscutum rarely almost impunctate); flagellum usually with intermediate segments at least as long as broad; coxae usually not lamellate externally 2
2. Mandibles with anterior and posterior basal angles almost equally distant from eye; antennal scape flattened; maxillary palpi not over one-half as long as galeae, with three to six free segments; sixth abdominal sternum of female produced posteriorly as broad, acute, or rounded, hairy process; seventh abdominal sternum of female with two small, slender apical lobes provided on inner margins with a few coarse setae; gonostyli of male rather long and slender 3
Mandibles with anterior basal angle more distant from eye than posterior basal angle; antennal scape not, or scarcely, flattened; maxillary palpi over one-half as long as galeae with six free segments; sixth abdominal sternum of female truncate or bilobed posteriorly; seventh abdominal sternum of female subtruncate or with two broad, well-separated lobes provided with coarse, spine-like setae; gonostyli of male short and robust. 5
3. Apex of marginal cell narrowly rounded and slightly bent from wing margin; maxillary palpi with three or four segments
. *Triopasites*
Apex of marginal cell acute, on wing margin; maxillary palpi with five or six segments. . 4
4. With two submarginal cells; maxillary palpi with five free segments; flagellar segments of male slightly longer than broad; middle coxae shorter than distance from their summits to hind wing bases . . . *Hesperonomada*
With three submarginal cells; maxillary palpi with six segments; most flagellar segments of male broader than long; middle coxae as long as distance from summits to hind wing bases. *Melanomada*
5. Abdomen with distinct transverse pubescent

fasciae; lateral lobes of second abdominal tergum appressed to second sternum; seventh abdominal sternum of female bilobed, the lobes margined with a row of spine-like setae; marginal cell narrowly rounded at apex, which is slightly separated from wing margin *Hexepeolus*
 Abdomen without pubescent fasciae; lateral lobes of second abdominal tergum projecting as transparent ventral flaps in dried specimens; seventh abdominal sternum of female with spine-like setae apically but not, or only feebly, bilobed; marginal cell acutely pointed on wing margin. *Nomada*

GENUS *NOMADA* SCOPOLI

Nomada SCOPOLI, 1770, Annus IV, Historiconaturalis, p. 44.

Nomadita MOCSÁRY, 1894, Természetrájsi Füzetek, vol. 17, p. 37.

Nomada (*Heminomada*) COCKERELL AND ATKINS, 1902, Ann. Mag. Nat. Hist., ser. 7, vol. 10, p. 42.

Nomada (*Micronomada*) COCKERELL AND ATKINS, 1902, *ibid.*, ser. 7, vol. 10, p. 44.

Gnathias ROBERTSON, 1903, Canadian Ent., vol. 35, p. 173.

Cephen ROBERTSON, 1903, *ibid.*, vol. 35, p. 174.

Centrias ROBERTSON, 1903, *ibid.*, vol. 35, p. 174.

Phor ROBERTSON, 1903, *ibid.*, vol. 35, p. 174.

Holonomada ROBERTSON, 1903, *ibid.*, vol. 35, p. 174.

Xanthidium ROBERTSON (not Ehrenberg), 1903, *ibid.*, vol. 35, p. 174.

Nomada (*Nomadula*) COCKERELL, 1903, Proc. Acad. Nat. Sci. Philadelphia, vol. 55, p. 611.

GENOTYPE: *Apis ruficornis* Linnaeus, designated by Curtis, 1832, British entomology . . . , vol. 9 [if bound as published in 16 vols.], pl. 419.

This is a genus of slender, wasp-like bees, usually red, black and red, or black and yellow in color. The first submarginal cell is nearly as long as the next two together (rarely the second transverse cubital, and still more rarely the first transverse cubital is absent).

The distribution of this large genus is primarily Holarctic, although a few species are found in the continents of the Southern Hemisphere. In the United States, species and individuals are rather numerous almost everywhere. For the most part they are parasitic on *Andrena*, but certain European species, at least, parasitize halictids, panurgines, and anthophorines.

No satisfactory keys have been prepared

for the separation of the rather large and well-defined subgenera of *Nomada*. The most distinctive subgenus is *Gnathias*, which differs from the others in having bidentate rather than simple mandibles.

GENUS *HEXEPEOLUS* LINSLEY AND MICHENER

Hexepeolus LINSLEY AND MICHENER, 1937, Pan-Pacific Ent., vol. 13, p. 77.

GENOTYPE: *Hexepeolus mojaviensis* Linsley and Michener, by original designation.

These rather robust bees have the aspect of an epeoline rather than a nomadine, but the structure is very similar to that of *Nomada*, agreeing with that genus even in the short gonostyli, large spatha, and angulate inner dorsal margins of the gonocoxites of the male. The color is black, often with the abdomen red, and conspicuous white markings result from bands of pubescence.

The two known species of this genus occur in the arid parts of California and are suspected of being parasitic on *Ancylandrena*.

GENUS *PARANOMADA* LINSLEY AND MICHENER

Paranomada LINSLEY AND MICHENER, 1937, Pan-Pacific Ent., vol. 13, p. 82.

GENOTYPE: *Paranomada nitida* Linsley and Michener, by original designation.

This is a curious genus, having wing venation similar to that of *Nomada*. The middle coxae are unusually widely separated, and the precoxal sutures are directed strongly forward to the midventral line so that the metapseudosternal area is provided with a large, anterior, triangular process. The maxillary palpi are short, four- to five-segmented. The abdomen has transverse pubescent fasciae on the posterior margins of the terga.

This genus is represented by two species, one known from Arizona and Lower California, the other from the former area alone. Their hosts are unknown.

GENUS *HESPERONOMADA* LINSLEY

Hesperonomada LINSLEY, 1939, Pan-Pacific Ent., vol. 15, p. 5.

GENOTYPE: *Hesperonomada melanantha* Linsley, by original designation.

This is a genus of small, slender bees with the appearance of small species of *Nomada*. The male is black, while the abdomen of the

female is largely red. *Hesperonomada* differs from *Nomada*, in addition to the characters mentioned in the key, by the reduced spatha (male genitalia figured by Linsley and Michener, 1939) and the emarginate base of the ninth sternum of the male (spiculum absent or modified in form), and by the large, pilose, pseudopygidial area and the ill-defined, hairy pygidial plate of the female.

The only known species of this genus occurs in California. Its hosts are unknown.

GENUS *TRIOPASITES* LINSLEY

Triopasites LINSLEY, 1939, Pan-Pacific Ent., vol. 15, p. 8.

GENOTYPE: *Triopasites timberlakei* Linsley, by original designation.

Although closely related to *Hesperonomada*, the species of *Triopasites* are robust and resemble in appearance *Oreopasites*. The male is black, while the female has a red abdomen. This genus differs from *Hesperonomada*, in addition to the characters indicated in the key, in the large middle coxae and the blunt rather than acute process of the sixth sternum of the female. The male genitalia are similar to those of *Hesperonomada*, but the gonostyli are shorter and rather broadly flattened. There are ordinarily three submarginal cells (first much shorter than next two together), but in some specimens the last two are united so that there are but two. As in *Melanomada* most of the flagellar segments of the male are broader than long.

Two or three species of this genus are now known from southern California, Arizona, and Lower California.

GENUS *MELANOMADA* COCKERELL

Nomada (*Melanomada*) COCKERELL, 1903, Proc. Acad. Nat. Sci. Philadelphia, vol. 55, p. 587.

GENOTYPE: *Nomada grindeliae* Cockerell, by original designation.

This genus is closely related to *Hesperonomada* and *Triopasites* but differs from both in the shining and largely impunctate vertex and mesoscutum. The coxae of the female are lamellate, somewhat as in *Paranomada* but not to so extreme a degree. This is also true of at least one (undescribed) species of *Triopasites*. The antennal scapes are not so strongly flattened as in *Triopasites*

and *Hesperonomada*. The male genitalia are very similar to those of *Hesperonomada*. The lobes of the seventh sternum of the female are more elongate and slender than in *Hesperonomada*, and the pygidial and pseudopygidial areas are about as in that genus. The apical process of the sixth sternum of the female is broad and blunt. As with related genera, the female is black with the abdomen red, the male entirely black or with the abdomen but feebly reddish.

The one or two species of this genus are known from Texas and Nebraska.

TRIBE CAENOPROSOPIDINI

This is a small, parasitic, Neotropical tribe with the appearance of the Neopasitini, to which it is perhaps related. The antennae arise far below the middle of the face as in *Neopasites*. The pterostigmata are large, extending about as far distad as basad of the base of vein r. The marginal cell is slightly longer than the distance from its apex to the wing tip, and the apex is rather abruptly bent from the wing margin so that it is narrowly obliquely truncate. The jugal lobes of the posterior wings are small. The seventh sternum of the female is much elongated and slender, hidden except for a pair of slender apical points, which are close together as in those Ammobatini in which the apical process of this sternum is not simple. In the female the sixth tergum lacks a longitudinal ridge and does not cover the large seventh tergum, which is emarginate apically and lacks a pygidial plate.

Only *Caenoprosopis*, of which I have studied but one female specimen, is known to belong to this tribe. The complete preepisternal groove is as in certain Ammobatini. The large pterostigmata suggest the Nomaadini.

TRIBE OSIRINI

This tribe, like the preceding, consists of small, slender, Neotropical, parasitic bees. The scopa and basitibial plates are absent, and the jugal lobe of the posterior wing is very small. The pterostigmata are as large as in *Nomada*, and the marginal cell is much longer than the distance from its apex to the wing tip and pointed on the wing margin. There are three submarginal cells, the first longer than the other two. The female, at

least, is provided with a pygidial plate. The seventh sternum of the female is greatly elongated, pointed at the apex, without spine-like setae, the margins curled upward to form a tubular guide for the immense sting which in repose is turned anteriorly above the abdomen. The male genitalia (according to Popov) are elongated as in *Neopasites*, the gonostyli indistinguishably fused to the gonocoxites.

As far as known this tribe includes only the genus *Osiris*, no species of which is known to occur within the United States.

TRIBE AMMOBATINI

As in other parasitic tribes, the scopa is absent. In most of the genera the labrum is much longer than broad. However, in some species of certain African genera (e.g., *Morgania*) the labrum is a little broader than long. Yet such forms are clearly related to *Ammobates* as shown by the unusually long and broad middle coxae, produced seventh sternum of the female with a simple or notched apex, and no coarse, spine-like setae. This tribe is further characterized by the obliquely truncate marginal cell, which is slightly shorter than the distance from its apex to the wing tip. The second submarginal cell is usually about as large as the first and receives both recurrent veins. The pterostigma is of moderate size, extending beyond the base of vein r. The jugal lobes of the posterior wings are very small, and the basitibial plates are absent.

This primarily Holarctic and Ethiopian tribe contains a single Nearctic genus, *Oreopasites*. Old World genera included are *Ammobates* (= *Phileremus*), *Morgania*, *Omachthes*, and *Pasites*, and apparently *Caesarea*, *Melanempis*, *Parammobatodes*, *Pasitomachthes*, *Pseudodichroa*, *Pseudopasites*, and *Sphedodopsis*.

GENUS OREOPASITES COCKERELL

Oreopasites COCKERELL, 1906, Bull. Amer. Mus. Nat. Hist., vol. 22, p. 442.

GENOTYPE: *Oreopasites scituli* Cockerell (monobasic).

This is a genus of small black bees, usually with the abdomen red, occurring from the Rocky Mountains to the Pacific coast. The species are parasitic in the nests of *Nomadop-*

sis. A revision of the genus was published by Linsley (1941).

TRIBE NEOPASITINI

This tribe consists of small bees, parasitic on anthophorines and panurgines. The scopa is absent, as are the basitibial plates. The jugal lobes of the posterior wings are very small. The marginal cell is but little, if any, shorter than the distance from its apex to the wing tip, and its apical portion is narrowly rounded and bent away from the wing margin. The second submarginal cell is much smaller than the first and receives but one recurrent vein. The pterostigma is intermediate in size between that of the *Ammobatini* and the *Ammobatoidini* and tapers considerably beyond the base of vein r. As in the *Ammobatoidini* the seventh sternum of the female is broadly emarginate apically, the lobes on either side of the emargination provided with a group of stiff setae. The pygidial plate is present in the female, although hidden by the sixth tergum which bears a longitudinal median ridge. The male genitalia are remarkable in that the penis valves are fused with the penis as in the *Megachilidae*. The gonostyli are fused with the gonocoxites.

The genera *Neopasites* and *Schmiedeknechtia* are included in this tribe. The first of these occurs in North America, the second in the Palaearctic region.

GENUS NEOPASITES ASHMEAD

Neopasites ASHMEAD, 1898, Psyche, vol. 8, p. 284.

Holcopasites ASHMEAD, 1899, Trans. Amer. Ent. Soc., vol. 26, p. 82.

Neopasites (*Trichopasites*) LINSLEY, 1942, Pan-Pacific Ent., vol. 18, p. 127.

Neopasites (*Odontopasites*) LINSLEY, 1942, *ibid.*, vol. 18, p. 128.

GENOTYPE: *Phileremus fulviventris* Ashmead (not Cresson) = *Neopasites eamia* Cockerell, by original designation.

This is a genus of small black bees, usually with the abdomen partly red, parasitic, as far as known, on species of *Calliopsis*. The body surface is coarsely and closely punctured, in contrast to most of our other parasitic Anthophorinae. The genus *Neopasites* is

found from Arizona and North Dakota eastward to the Atlantic coast.

The subgenera may be separated by the following key, based on that of Linsley:

1. Eyes clothed with erect pubescence 2
Eyes bare; median and lateral ocelli separated by less than twice their diameters; supra-antennal area closely, coarsely punctured *Neopasites*, *sensu stricto*
2. Sides of face at margin of clypeus with broad tooth; median and lateral ocelli separated by less than twice their diameters; supra-antennal area closely, coarsely punctured
Sides of face at margin of clypeus not toothed; median and lateral ocelli small, separated by at least three times their diameters; supra-antennal area polished, impunctate
Trichopasites

TRIBE AMMOBATOIDINI

In this group of moderately large bees the pterostigma is much smaller than in the Ammobatini, being narrower than the distance from the inner margin of the prestigma to the wing margin. Unlike related tribes, the first flagellar segment is elongate, although shorter than the scape. The male genitalia are small, rather elongate, the gonostyli indistinguishably fused with the gonocoxites. The Ammobatoidini are apparently most closely related to the Neopositini, although entirely different from that group in appearance.

This Palaearctic tribe includes only the genus *Ammobatoides* (= *Phiarius*), which is parasitic on *Melitturga*.

TRIBE BLASTINI

This Holarctic tribe consists of small black bees with the abdomen of the female or of both sexes sometimes red. Unlike other small "pasitine" bees the mandibles have an inner subapical tooth. The scopa is absent. The antennae of both sexes are twelve-segmented. The basitibial plates are absent and the jugal lobes of the posterior wings very small. The marginal cell is about as long as, or a little longer than, the distance from its apex to the wing tip and is bent away from the wing margin and rounded at the apex. The second submarginal cell is at least two-thirds as long as the first and receives both recurrent veins. The pterostigma is scarcely broader than the

distance from the inner margin of the very short prestigma to the wing margin. The seventh sternum of the female is broadly emarginate apically, the lobes on either side of the emargination being terminated with a group of stiff, spine-like setae. The male genitalia are broad with distinct gonostyli. A pygidial plate is present in the male.

This tribe contains two closely related genera, the Palaearctic *Biastes* and the Nearctic *Gnathopasites*. The characters given by Linsley and Michener (1939) for separating these genera were erroneous because of the inadequate descriptions of *Biastes*. *Biastes* agrees with the description given by Linsley and Michener for *Gnathopasites*, except that the penis valves of the male much exceed the rather small gonostyli. Furthermore, *Biastes*, unlike *Gnathopasites*, is coarsely punctate as is *Neopasites*, and the disk of the seventh sternum of the female in *Biastes* is reduced to a transverse bar, according to Grütte (1935).

GENUS GNATHOPASITES LINSLEY AND MICHENER

Neopasites CRAWFORD (not Ashmead), 1916, *Insecutor Inscitiae Menstruus*, vol. 4, p. 136.

Gnathopasites LINSLEY AND MICHENER, 1939, *Trans. Amer. Ent. Soc.*, vol. 65, p. 272.

Gnathopasites (*Micropasites*) LINSLEY, 1942, *Pan-Pacific Ent.*, vol. 18, p. 130.

GENOTYPE: *Phileremus fulviventris* Cresson, by original designation.

As yet this genus has not been found outside of California, and nothing is known of its habits. The genus is divided into two subgenera by Linsley.

KEY TO THE SUBGENERA OF *Gnathopasites*

1. Maxillary palpi elongate, four-segmented; second submarginal cell of anterior wing a little shorter than first; larger forms
Gnathopasites, *sensu stricto*
- Maxillary palpi short, with one or two free segments; second submarginal cell of anterior wing as long as first; smaller species
Micropasites

TRIBE TOWNSENDIELLINI

This tribe is probably related to the Neolarrini but because of the very different wing venation (marginal cell rounded at apex, far larger than pterostigma, shorter or longer than distance from its apex to wing tip, second submarginal cell not exceedingly

short although markedly shorter than first); the broadly emarginate seventh abdominal sternum of the female with lobes laterad of emargination bearing coarse, spine-like setae; and the presence of a large pygidial plate in the male, it seems best to separate it from that group. The male gonostyli are fused with the gonocoxites, but the genitalia are not elongated as in the *Neopositini*. This tribe contains only the genus *Townsendiella*.

GENUS TOWNSENDIELLA CRAWFORD

Townsendiella CRAWFORD, 1916, *Insecutor Inscitiae Menstruus*, vol. 4, p. 138.

Townsendiella (*Xeropasites*) LINSLEY, 1942, *Pan-Pacific Ent.*, vol. 18, p. 130.

Townsendiella (*Eremopasites*) LINSLEY, 1942, *ibid.*, vol. 18, p. 131.

GENOTYPE: *Townsendiella pulchra* Crawford (monobasic).

This genus consists of small black species with the abdomen sometimes red. Much of the body or at least bands on the abdominal segments are pruinose. Species of *Townsendiella* occur in the southwestern United States and northwestern Mexico; one species is suspected of being parasitic on *Hesperapis*.

KEY TO THE SUBGENERA OF *Townsendiella*

1. Maxillary palpi six-segmented; antennal flagellum of more or less uniform diameter . . . 2
- Maxillary palpi with four free segments; antennal flagellum distinctly thickened beyond the middle; first submarginal cell nearly twice as long as second *Xeropasites*
2. Anterior wings more than one and one-half times as long as thorax; marginal cell longer than distance from apex to wing tip; first submarginal cell but little longer than second; first recurrent vein received near base of second submarginal cell *Townsendiella*, *sensu stricto*
- Anterior wings less than one and one-half times as long as thorax; marginal cell much shorter than distance from apex to wing tip; first submarginal cell nearly twice as long as second; first recurrent vein usually received near apex of first submarginal cell . . . *Eremopasites*

TRIBE NEOLARRINI

This is a Nearctic tribe of small parasitic bees lacking a scopa. The maxillary palpi are long, six-segmented. The scape, as in the *Blastini*, is less than twice as long as broad, excluding the basal bulb. The wing venation

is reduced, the truncated marginal cell being at most but little larger than the pterostigma, which is as broad as distance from inner margin of prestigma to costal wing margin, and the second submarginal cell, when present, being very short and receiving only the second recurrent vein. The jugal lobe of the posterior wing is small. The basitibial plates are absent. The male is without a pygidial plate, but the eighth tergum is produced to a short, bare process. The seventh sternum of the female has a rather narrow apical emargination, and the lobes on either side of it are without coarse, spine-like setae. The male gonostyli are distinctly articulated to the gonocoxites.

This tribe contains but one genus, *Neolarra*.

GENUS NEOLARRA ASHMEAD

Neolarra ASHMEAD, 1890, *Bull. Colorado Biol. Assoc.*, no. 1, p. 8.

Phileremulus COCKERELL, 1895, *Psyche* (supplement), vol. 7, p. 9.

GENOTYPE: *Neolarra pruinosa* Ashmead (monobasic).

The members of this genus are usually minute bees, no doubt parasitic in the nests of *Perdita*. They are black, often with the abdomen at least partly red, and are more or less covered with short, appressed, pale pubescence, giving them a pruinose appearance. They are most abundant in the southwestern deserts but extend eastward at least to Tennessee. The species have been recently revised by Michener (1939a).

KEY TO THE SUBGENERA OF *Neolarra*

1. Axillae produced to distinct angles; but one submarginal cell and one recurrent vein *Phileremulus*
- Axillae rounded; usually with two submarginal cells and two recurrent veins *Neolarra*, *sensu stricto*

TRIBE PROTEPEOLINI

This is a tribe of moderate-sized, rather robust, parasitic bees which are black, variously maculated with areas of short, dense, pale pubescence. The maxillary palpi are short, with two to four segments. The pterostigma is of moderate size, much broader than distance from inner margin of prestigma to wing margin, and extending well beyond

base of vein r. The marginal cell is about as long as the distance from its apex to the wing tip, and the apex is bent away from the wing margin. The three submarginal cells are about equal in length on their posterior margins. The wings of some (*Isepeolus*) are strongly papillate and largely hairless. The seventh sternum of the female is bluntly pointed apically, without spine-like setae, and the lateral margins are curved upward so that the apical part of the sternum is sub-tubular as in the Epeoloidini and the Osirini.

The Protepeolini contains the Neotropical *Isepeolus*, the Sonoran *Protepeolus*, and probably also the Neotropical *Leiopodus*. It is possible that *Isepeolus*, with largely bare, papillate wings, long first flagellar segment, and freely articulated male gonostyli should be placed in a separate tribe.

GENUS PROTEPEOLUS LINSLEY AND MICHENER

Protepeolus LINSLEY AND MICHENER, 1937, Pan-Pacific Ent., vol. 13, p. 75.

GENOTYPE: *Protepeolus singularis* Linsley and Michener, by original designation.

In this genus the seventh abdominal tergum of the female is unusually small and bears a flat, median, apical process, on either side of which is a row of stiff setae.

Protepeolus is represented by two or three species found in New Mexico, Arizona, and northern Mexico. Their hosts are unknown.

TRIBE EPEOLINI

This tribe contains small to rather large bees whose bodies are usually marked with patches of short, appressed, squamiform pubescence which is usually white, sometimes brilliantly metallic. The pterostigma is parallel-sided, usually narrower than the distance from the inner margin of the pterostigma to the wing margin, and extends but little beyond the base of vein r. The marginal cell is about as long as the distance from its rounded apex to the wing tip. There are usually three submarginal cells, the first being considerably longer than either of the others. The jugal lobe of the posterior wing is small, and the basitibial plates are absent. A pygidial plate is present in both sexes, and a pseudopygidial area is more or less well developed in the female.

Although including the Holarctic genus *Epeolus*, this tribe is primarily Neotropical. Genera unquestionably to be placed in it are *Doeringiella*, *Epeolus*, *Thalestria*, and *Triepeolus*. *Odyneropsis* probably belongs in the same tribe, although I have not been able to study specimens of that genus.

KEY TO THE GENERA OF EPEOLINI OCCURRING NORTH OF MEXICO

1. Pseudopygidial area of female usually at least half as long as broad, sloping posteriorly, clothed with coarse, dark, erect setae; seventh abdominal sternum of female consisting of two slender parallel rods connected by a transverse bar (remnant of disk) and rods armed apically with coarse, curved, spine-like setae; marginal cell as long as, or longer than, distance from apex to wing tip, apex narrowly rounded; maxillary palpi usually with two free segments . . . *Triepeolus*
Pseudopygidial area of female transverse, usually on same plane as rest of tergum, clothed with silvery pubescence; seventh abdominal sternum of female with large disk, provided with a pair of converging, curving, dentate, apical processes; marginal cell usually shorter than distance from apex to wing tip, apex broadly rounded; maxillary palpi usually with one free segment *Epeolus*

GENUS EPEOLUS LATREILLE

Epeolus LATREILLE, 1802, Histoire naturelle des fourmis . . . , p. 427.

Diepeolus GRIBODO, 1894, Bull. Soc. Ent. Italiana, vol. 26, p. 80.

Pyrhhomelecta ASHMEAD, 1899, Trans. Amer. Ent. Soc., vol. 26, p. 66.

Argyroselenis ROBERTSON, 1903, Canadian Ent., vol. 35, p. 284.

GENOTYPE: *Apis variegata* Linnaeus (monobasic).

The genus *Epeolus* consists of small or moderate-sized, largely black bees with conspicuous areas of short, appressed, pale pubescence. This is a widely distributed genus, at least in the Holarctic region. Its species are parasitic in the nests of *Colletes*. *Pyrhhomelecta* is based on an exceedingly coarsely punctate species with a long sting and probably is a valid subgenus, while *Argyroselenis* is merely an ordinary *Epeolus* with two free segments in the maxillary palpi.

GENUS *TRIEPEOLUS* ROBERTSON

Triepeolus ROBERTSON, 1901, Canadian Ent. vol. 33, p. 231.

Triepeolus (*Synepeolus*) COCKERELL, 1921, Amer. Mus. Novitates, no. 23, p. 6.

GENOTYPE: *Epeolus concavus* Cresson, by original designation.

The species of this genus, largely confined to North and South America, have the aspect of *Epeolus* but are usually larger. They are parasites of *Melissodes* and perhaps other Eucerini. While most abundant in the western states, species of the genus occur throughout the United States. *Synepeolus* is based on a species with but two submarginal cells.

TRIBE *EPEOLOIDINI*

This is a group of moderate-sized black bees with the abdomen partly red in one species. The wing venation and shape of the seventh sternum of the female suggest a relationship with the *Protepeolini*. From that tribe the *Epeoloidini* differ, in addition to the characters given in the key, by the absence of patches of short appressed pubescence, the pubescence being long and beautifully plumose; by the slightly smaller pterostigma, which is but little broader than the distance from the inner margin of the prestigma to the wing margin; and by the small claws. The male genitalia are broad, the penis valves exceeding the claspers, the styli not free but fused to the gonocoxites.

This tribe is represented, as far as known, only by the Holarctic genus *Epeoloides*.

GENUS *EPEOLOIDES* GIRAUD

Epeoloides GIRAUD, 1863, Verhandl. Zool.-Bot. Gesellsch. Wien, vol. 13, p. 45.

Viereckella SWENK, 1907, Ent. News, vol. 18, p. 298.

GENOTYPE: *Epeoloides ambiguus* Giraud = *Apis coecutiens* Fabricius (monobasic).

This genus is represented by very few species, only two of which are known in North America, and none west of the Rocky Mountains. The European species is parasitic on *Macropis*.

TRIBE *EMPHORINI*

This is one of the tribes of large, pollen collecting Anthophorinae. The head, seen

from directly in front, unlike that of other large Anthophorinae, is gently convex above with the ocelli in front of the summit of the vertex. The clypeus of the male is black, rarely white or yellow. The first flagellar segment is often somewhat elongated but is shorter than the scape. The wings are hairy throughout and feebly papillate apically as in the Eucerini. The pterostigma is reduced, being no broader than the distance from the inner margin of the prestigma to the wing margin, although frequently tapering well beyond the base of vein r. The marginal cell is gradually bent away from the wing margin near the narrowly rounded or pointed apex as in the Eucerini. The posterior legs of the male are usually somewhat enlarged. The pygidial plate is absent in the male, the eighth tergum ending in a pair of spines or lobes.

In addition to the character of posterior wing venation given in the key, this tribe differs from the Eucerini in the short paraglossae, the form of the head, the absence of a pygidial plate in the male, and the short antennae of the male.

The *Emphorini* is an American tribe and contains *Ptilothrix* and apparently *Energonus*, *Teleutemnesta*, and *Leptometria*, all South American genera, in addition to those mentioned below.

KEY TO THE GENERA OF *EMPHORINI*
OCCURRING NORTH OF MEXICO

1. Arolia very small or absent; branches of scopal hairs not at right angles to axes of hairs *Emphor*
Arolia present, rather long and slender; branches of scopal hairs projecting at right angles to axes of hairs 2
2. Proboscis very long, in repose reaching base of abdomen *Melitoma*
Proboscis of normal length, usually not reaching beyond first coxae in repose *Diadasia*

GENUS *EMPHOR* PATTON

Emphor PATTON, 1879, Bull. U. S. Geol. Geogr. Survey Terr., vol. 5, p. 476.

GENOTYPE: *Melissodes bombiformis* Cresson, by original designation.

This genus, which is closely related to the South American *Ptilothrix*, contains one or two large species of bees with the head and thorax covered with pale pile and the abdomen largely black. The posterior legs of the

male are unusually large, and the projections of the eighth tergum of that sex are rather large and approximate at their bases.

Emphor is found in North America primarily east of the Mississippi River.

GENUS *MELITOMA* LEPELETIER AND SERVILLE

Melitoma LEPELETIER AND SERVILLE, 1828, Encyclopédie méthodique, histoire naturelle . . . insectes, vol. 10, p. 529.

Entechnia PATTON, 1879, Bull. U. S. Geol. Geogr. Survey Terr., vol. 5, p. 476.

Meliphila SCHROTTKY, 1902, An. Mus. Nac. Buenos Aires, vol. 7 (ser. 2, vol. 4), p. 310.

GENOTYPE: *Melitoma euglossoides* Lepeletier and Serville (monobasic).

In this genus of moderate-sized bees the abdominal terga are covered, at least in part, with short, appressed pubescence. The eighth abdominal tergum of the male is armed with a pair of small, widely separated spines.

Melitoma ranges from South America northward into the eastern and central United States as far as North Dakota. It is unknown west of the Rocky Mountains. Holmberg's genus *Energoponus* is apparently close to, if not a synonym of, *Melitoma*.

GENUS *DIADASIA* PATTON

Diadasia PATTON, 1879, Bull. U. S. Geol. Geogr. Survey Terr., vol. 5, p. 475.

Dasiapis COCKERELL, 1903, Ann. Mag. Nat. Hist., ser. 7, vol. 12, p. 450.

Coquillettapis VIERECK, 1909, Proc. Ent. Soc. Washington, vol. 11, p. 47.

GENOTYPE: *Melissodes enavata* Cresson, by original designation.

Diadasia is a genus of moderate-sized to large, robust bees, frequently with distinct abdominal fasciae of pale pubescence. The projections of the eighth abdominal tergum of the male are often rather broad lobes. This genus is distributed from South America to our western states, where it is represented by numerous species. In North America it does not occur east of Alberta, Kansas, and Texas. Timberlake (1941) has given a key to the species of the United States and Canada.

A few species with the clypeus of the male yellow or white have been placed in *Dasiapis*. The South American groups named *Leptomietria* and *Teleutemnesta* are apparently close to, if not synonyms of, *Diadasia*.

TRIBE *EUCERINI*

This is one of the largest tribes of Anthophorinae. Like the Emphorini it contains large, pollen collecting bees. The clypeus of the male is usually at least partly yellow or white. The first flagellar segment in the female and in some males is nearly as long as the scape. The epipharynx is large, compressed, and curled distally. The wings are hairy throughout and scarcely papillate apically. The marginal cell is as long as, or longer than, the distance from its apex to the wing tip; the apex is narrowly rounded and bent gradually away from the wing margin. North American genera all have three submarginal cells, the first and third longer than the second. While the second abscissa of vein M+Cu of the posterior wings is usually nearly twice as long as cu-v, the latter vein is commonly rather oblique, thus approaching the condition found in the Emphorini. The pterostigma is reduced, tapering but little, if at all, beyond the base of vein r. The posterior legs of the male are only rarely enlarged or modified. Arolia are present. The male in forms occurring in the United States has distinct pygidial and basitibial plates.

Although this tribe is represented in the Old World by such genera as *Eucera*, *Tetralonia*, and *Tetraloniella* and apparently by *Eucara*, *Melissina*, and *Thygatina*, the majority of the genera are restricted to the Western Hemisphere. Aside from those occurring north of Mexico, these include *Ecplectica*, *Holmbergiapis*, *Melissoptila*, *Svastra*, *Thygater* (= *Macroglossapis*), *Thyreothremma*, and perhaps *Nectarodiaeta*. One species of *Eucera* was described long ago from the United States, but it has not been since recognized and is presumably wrongly attributed to this country. The curious South American genus *Canephorula* (= *Canephora* = *Corbicula*) resembles the Eucerini in its long paraglossae, but on the basis of other characters may have to be placed in a new tribe or subfamily. I have seen no specimens of this genus.

The genera of the Eucerini occurring in the United States and Canada may be distinguished by the following key. The female of *Martinapis*, although included in a key to species of *Melissodes* by Cockerell, has never

been sufficiently described to make its inclusion in this key possible.

KEY TO THE NEARCTIC GENERA OF EUCERINI

1. Labrum at most twice as broad as long, apical margin (except in *Tetralonia*) subtruncate, often notched medially; clypeus greatly protuberant, so that seen from the side its lower end lies a distance equal to width of eye in front of lower anterior eye margin; lateral extremity of clypeus considerably separated from eye margin (except in male *Tetralonia*); anterior mandibular articulation considerably in front of lower anterior eye margin; anterior margin of clypeus, seen from front, much below lower ends of eyes. 2
 Labrum usually more than twice as broad as long, apical margin broadly rounded, sometimes with median notch; clypeus only moderately protuberant, lower end seen from side less than width of eye in front of eye; lateral extremity of clypeus closely approaching eye; anterior mandibular articulation scarcely in front of lower anterior eye margin; anterior margin of clypeus, seen from front, scarcely below lower ends of eyes 5
2. Marginal cell scarcely longer than distance from its apex to wing tip; maxillary palpi six-segmented; scopa dense, in Nearctic species consisting of simple hairs or hairs which are plumose only basally; antennae of male much elongated, flagellar segments mostly much more than three times as long as broad *Tetralonia*
 Marginal cell distinctly longer than distance from its apex to wing tip; maxillary palpi with four or five segments; scopa thin, the hairs with long branches; antennae of male shorter, flagellar segments mostly three times as long as broad or less 3
3. Mandibles each with a submedian angle on outer side; apex of clypeus trilobate, median lobe notched; first submarginal cell scarcely longer than second on posterior side; inner tooth of posterior claws at most one-fourth as long as outer *Cemolobus*
 Mandibles entire on outer surfaces; margin of clypeus entire; first submarginal cell markedly longer than second; inner tooth of posterior claws at least one-half as long as outer 4
4. Inner margins of mandibles untoothed except apically; mandibles of male bidentate at apex with inner subapical angle (thus almost tridentate); first flagellar segment of male much shorter than other segments; seventh abdominal segment of male simple laterally. *Peponapis*
 Inner margins of mandibles with tooth about one-fourth of distance from base to apex; mandibles of male simple or bidentate apically; first flagellar segment of male considerably longer than other segments; seventh abdominal segment of male with a tooth or angle at each side. *Xenoglossa*
5. Males. 6
 Females. 10
6. First flagellar segment at least nearly as long as second; antennae not reaching beyond posterior end of thorax 7
 First flagellar segment very much shorter than second; antennae commonly reaching beyond posterior end of thorax 8
7. Last antennal segment curved and produced to a point; antennae black; maxillary palpi four-segmented, last segment short. *Anthedonia*
 Last antennal segment simple; antennae yellow; maxillary palpi five-segmented, or four-segmented with last segment not greatly shorter than third . . . *Martinapis*
8. Eighth abdominal sternum with combs of long curved setae on outer margins of lateral apical lobes; abdomen feebly metallic; maxillary palpi five-segmented. . . *Florilegus*
 Eighth abdominal sternum without combs of setae; abdomen not metallic; maxillary palpi three- to six-segmented. 9
9. Male gonostyli shorter than gonocoxites, not abruptly bent; maxillary palpi usually four-segmented with last segment small, sometimes three-segmented. *Melissodes*
 Male gonostyli as long as gonocoxites, rather abruptly bent downward a little before the middle; maxillary palpi five- or six-segmented. *Xenoglossodes*
10. Scopal hairs virtually simple (with minute very short branches). *Anthedonia*
 Scopal hairs conspicuously plumose, at least basally 11
11. Scopa rather slender, hairs sparsely plumose basally; maxillary palpi five-segmented; abdomen feebly metallic . . . *Florilegus*
 Scopa large, hairs densely plumose; maxillary palpi three- to six-segmented; abdomen not metallic. 12
12. Maxillary palpi five- to six-segmented *Xenoglossodes*
 Maxillary palpi usually four-segmented, rarely three-segmented. *Melissodes*

GENUS TETRALONIA SPINOLA

Macrocera LATREILLE (not Meigen), 1810, *Considérations générales . . . des insectes*, p. 339.

Tetralonia SPINOLA, 1838, Ann. Soc. Ent. France, vol. 7, p. 538.

Synhalonia PATTON, 1879, Bull. U. S. Geol. Geogr. Survey Terr., vol. 5, p. 473.

Eusynhalonia ASHMEAD, 1899, Trans. Amer. Ent. Soc., vol. 26, p. 63.

Synalonia ROBERTSON, 1905, Trans. Amer. Ent. Soc., vol. 31, p. 365.

GENOTYPE: *Eucera antennata* Fabricius = *Apis malvae* Rossi, designated by Latreille, 1810, Considérations générales . . . des insectes, p. 439 (for *Macrocera*).

The bees of the genus *Tetralonia* are rather robust and somewhat similar in appearance to *Melissodes* but the males usually have thicker antennae. The first flagellar segment is much shorter than the others. The claws of the posterior legs in the male are usually slightly asymmetrical. In many, but not all, of the Old World species the scopa consists of plumose hairs, while in American forms it usually contains only simple hairs. This is a widespread genus, occurring in the Holarctic and Ethiopian regions and found in most parts of the United States.

GENUS *XENOGLOSSA* SMITH

Xenoglossa SMITH, 1854, Catalogue of hymenopterous insects in the . . . British Museum, pt. 2, p. 315.

GENOTYPE: *Xenoglossa fulva* Smith (monobasic).

This is a genus of large bees, frequently covered with fulvous pile. The gonostyli of the male are at least nearly as long as the gonocoxites and lack the abrupt bend basad of the middle which is characteristic of *Peponapis*, *Anthedonia*, and *Xenoglossodes*.

Throughout much of the United States and southward into South America, species of this genus may be found visiting the flowers of Cucurbitaceae.

GENUS *PEPONAPIS* ROBERTSON

Peponapis ROBERTSON, 1902, Canadian Ent., vol. 34, p. 324.

GENOTYPE: *Macrocera pruinosa* Say, by original designation.

The bees of this genus are closely related to *Xenoglossa* and have similarly restricted pollen collecting habits but are usually smaller. The male gonostyli are at least as

long as the gonocoxites and bent abruptly downward before the middle.

Peponapis is found from coast to coast in the United States.

GENUS *CEMOLOBUS* ROBERTSON

Cemolobus ROBERTSON, 1902, Canadian Ent., vol. 34, p. 324.

GENOTYPE: *Xenoglossa ipomoeae* Robertson, by original designation.

This genus is related to *Xenoglossa* and *Peponapis*, but the mandibles and clypeus are remarkably modified. The male antennal flagellum is unusually slender, the first segment longer than the others. The seventh abdominal sternum of the male is greatly expanded laterally. The gonostyli of the male are longer than the gonocoxites and considerably contorted. The maxillary palpi are four- to five-segmented.

This genus is known from a single species which has been found only east of the Mississippi River.

GENUS *MELISSODES* LATREILLE

Melissodes LATREILLE, 1829, in Cuvier, Règne animal, 2d ed., vol. 5, p. 354.

Epimelissodes ASHMEAD, 1899, Trans. Amer. Ent. Soc., vol. 26, p. 63.

GENOTYPE: *Melissodes fonscolombi* Romand, first species to be included.

With the possible exception of *Tetralonia*, this is our largest and most common genus of Eucerini. The mandibles in both sexes are simple with a small, inner, subapical angle (rarely bidentate). The claws of the posterior legs of the male are normally slightly asymmetrical, the inner one being longer with a shorter inner tooth than the outer. The pygidial plate of the male has a small preapical notch at each side. The seventh abdominal tergum of the male is almost always dentate laterally, the eighth and sixth usually so. The eighth sternum of the male is rather weakly sclerotic, although the lateral apical lobes are complexly shaped.

Species of *Melissodes* occur throughout much of North and South America.

GENUS *XENOGLOSSODES* ASHMEAD

? *Tetraloniella* ASHMEAD, 1899, Trans. Amer. Ent. Soc., vol. 26, p. 61.

Xenoglossodes ASHMEAD, 1899, *ibid.*, vol. 26, p. 63.

GENOTYPE: *Melissodes albata* Cresson, by original designation.

Xenoglossodes is very closely related to *Melissodes*, of which it is perhaps only a subgenus, differing chiefly by the characters indicated in the key. The structure of the male gonostyli is similar to that of *Peponapis*, but the two genera do not appear to be closely related.

Xenoglossodes of the western and central United States is very similar to the Palaearctic *Tetraloniella*. Since adequate material of *Tetraloniella* is not available, I have retained the name *Xenoglossodes*. In spite of the fact that page priority is not binding, *Tetraloniella* will replace *Xenoglossodes* if New and Old World forms are congeneric, because the former name has been used for our American species whenever *Tetraloniella* and *Xenoglossodes* have been considered synonymous.

GENUS *ANTHEDONIA* MICHENER

Anihedon ROBERTSON (not Agassiz), 1900, Trans. Acad. Sci. St. Louis, vol. 10, p. 53.

Anihedonia MICHENER, 1942, Jour. New York Ent. Soc., vol. 50, p. 282.

Abda SANDHOUSE, 1943, Proc. U. S. Natl. Mus., vol. 92, p. 521.

GENOTYPE: *Melissodes compta* Cresson, by original designation.

This group is closely related to *Melissodes*, having similar maxillary palpi, claws, pygidial plate, etc. The male gonostyli are as long as the gonocoxites and abruptly bent inward a little before the middle. The eighth abdominal sternum of the male is rather weakly sclerotic, as in *Melissodes*, but the lateral lobes are broadly rounded, not complexly angulate.

Anihedonia is found from the eastern states nearly to the Rocky Mountains.

GENUS *FLORILEGUS* ROBERTSON

Florilegus ROBERTSON, 1900, Trans. Acad. Sci. St. Louis, vol. 10, p. 53.

GENOTYPE: *Melissodes condigna* Cresson, by original designation.

This is also a *Melissodes*-like genus; the mandibles of the male are bidentate apically

and have in addition a small, preapical, inner angle, while those of the females are simple. The eighth sternum of the male is much thickened and heavily sclerotic apically. The male gonostyli are shorter than the gonocoxites and expanded apically.

In the United States this genus occurs only east of the Rocky Mountains, but it extends southward into the Neotropical region.

GENUS *MARTINAPIS* COCKERELL

Martinella COCKERELL (not Jousseaume), 1903, Ann. Mag. Nat. Hist., ser. 7, vol. 12, p. 450.

Martinapis COCKERELL, 1929, Entomologist, vol. 62, p. 19.

GENOTYPE: *Melissodes luteicornis* Cockerell (monobasic).

The single known species of this genus from the deserts of New Mexico and California resembles *Melissodes* in form, but the maxillary palpi are less reduced, the marginal cell is somewhat longer, the first flagellar segment of the male is longer, the teeth at the sides of the seventh abdominal tergum of the male are small, and the sixth and eighth terga are without lateral teeth. The eighth sternum of the male is entirely different from that of *Melissodes*, being strongly sclerotized, each of the apical lobes being itself divided into two large lobes, the distal ones of which are curled basally and expanded apically where they are clothed with numerous short black hairs. The male gonostyli are as long as the gonocoxites, expanded subapically, where they are clothed with black hair, and exceedingly slender beyond expanded portions. The claws of the posterior legs of the male are symmetrical, the inner tooth of each less than half as long as the outer.

The female of *Martinapis* has never been properly described, and no specimens have been available to me.

It seems possible that this genus is a synonym of the South American *Ecplectica*.

TRIBE *ANTHOPHORINI*

This is another tribe of moderate-sized to large, pollen collecting Anthophorinae. The clypeus of the male is usually pale. The first flagellar segment is often elongated, sometimes as long as the scape (fig. 17). The wings are largely bare and strongly papillate apically. The pterostigma is small, usually one

and one-half times as long as broad and ending at the base of vein r (fig. 35). The marginal cell is slightly shorter than the distance from its apex to the wing tip, rounded at its apex; first submarginal cell usually slightly longer than the subequal second and third cells on posterior margin. The jugal lobe of the posterior wing is usually a little over one-third as long as the vannal lobe; the scopa is not large, consisting of simple, or but slightly plumose, hairs, with some plumose hairs intermixed in some cases. Arolia are present in the American forms but are absent in *Asaropoda*. The eighth tergum of the male is usually bilobed, without a pygidial plate.

This widespread tribe includes the genera *Anthophora*, *Emphoropsis*, *Asaropoda*, *Habropoda*, *Pachymelus*, and *Heliothila* (= *Saropoda*). Only the first two of these genera occur in America.

KEY TO THE AMERICAN GENERA OF ANTHOPHORINI

1. Third submarginal cell nearly as broad on costal side as on posterior side (fig. 35); apex of labrum usually broadly subtruncate, margin thickened or deflexed; maxillary palpi with last three segments together scarcely, if any, longer than second, sixth sometimes absent so that there are but five segments; distal portions of penis valves much thickened; spatha absent; gonocoxites not broadly expanded below bases of gonostyli, which are often reduced and fused with the gonocoxites. *Anthophora*
- Third submarginal cell narrowed about one-third toward costal side; apex of labrum rounded, margin not thickened; maxillary palpi with last three segments together much longer than second; distal portions of penis valves thin; spatha present, although small; gonocoxites expanded as broad, thin plates below bases of the freely articulated gonostyli. *Emphoropsis*

GENUS ANTHOPHORA LATREILLE

Podalirius LATREILLE, 1802, Histoire naturelle des fourmis . . . , p. 430.

Anthophora LATREILLE, 1803, Nouvelle dictionnaire d'histoire naturelle, vol. 18, p. 167.

Lasius PANZER (not Fabricius), 1804, Faunae insectorum Germanicae initia . . . , pt. 86, no. 16.

Clisodon PATTON, 1879, Bull. U. S. Geol. Geogr. Survey Terr., vol. 5, p. 479.

Podalirius (*Amegilla*) FRIESE, 1897, Die Bienen Europas, vol. 3, p. 18.

Podalirius (*Paramegilla*) FRIESE, 1897, *op. cit.*, vol. 3, p. 18.

Anthophoroides COCKERELL AND COCKERELL, 1901, Ann. Mag. Nat. Hist., ser. 7, vol. 7, p. 48.

Anthemoessa ROBERTSON (not Agassiz), 1905, Trans. Amer. Ent. Soc., vol. 31, p. 372.

Anthophora (*Micranthophora*) COCKERELL, 1906, Trans. Amer. Ent. Soc., vol. 32, p. 66.

Alphenella BÖRNER, 1919, Biol. Zentralbl., vol. 39, p. 168.

Melea SANDHOUSE, 1943, Proc. U. S. Natl. Mus., vol. 92, p. 526.

GENOTYPE: *Megilla pilipes* Fabricius = *Apis acervorum* Linnaeus, designated by Latreille, 1810, Considérations générales . . . des insectes, p. 439.

This large genus of robust, fast flying bees is found throughout the United States and in all the continents except South America.

While *Podalirius* antedates *Anthophora*, a proposal is before the International Commission on Zoological Nomenclature recommending that the former name be rejected in favor of the latter. This seems highly desirable in view of the extensive literature that has grown around the names *Anthophora* and *Anthophoridae*.

Anthophora is undoubtedly divisible into a number of subgenera, but as they have not yet been properly defined, only a few of the more distinctive ones found in North America can be distinguished here. *Clisodon* [containing the Holarctic *Anthophora furcata* (Panzer) and its subspecies] has tridentate rather than bidentate or simple mandibles, and the basitibial plates of the female are sharply pointed below rather than rounded as in other *Anthophora*. It differs further from other anthophorids in that it nests in wood or stems, a fact which lends weight to its recognition as a genus. *Micranthophora* consists of small species with the abdomen largely covered with appressed pale pubescence, and the clypeus of both sexes commonly with an apical transverse yellow or white band. *Amegilla* is a subgenus consisting of moderate-sized bees with apical white integumental bands on the abdominal terga.

GENUS EMPHOROPSIS ASHMEAD

Emphoropsis ASHMEAD, 1899, Trans. Amer. Ent. Soc., vol. 26, p. 60.

Meliturgopsis ASHMEAD, 1899, *ibid.*, vol. 26, p. 62.

GENOTYPE: *Habropoda floridana* Smith, desig-

nated by Cockerell and Cockerell, 1901, Ann. Mag. Nat. Hist., ser. 7, vol. 7, p. 48.

The members of this genus have almost exactly the aspect of certain of the rather large species of *Anthophora*. In addition to characters mentioned in the key, *Emphoropsis* differs from *Anthophora* in the slightly longer marginal cell, which is more narrowly rounded apically. The genus is widely distributed in the Nearctic region, but is not confined to that area as the literature would indicate. A specimen from Formosa is clearly an *Emphoropsis*, agreeing with our species in its genitalia as well as in other structures. *Habropoda* is distinguished by the spinose anterior coxae, enlarged and modified posterior basitarsi, etc., in the male. It seems likely that many Old World species described as *Habropoda* are in reality *Emphoropsis*.

A key to the American species is given by Cockerell (1905).

TRIBE HEMISIINI

This is a tribe of large, robust, pollen collecting Anthophorinae. The clypeus of the male is usually yellow or white. The first flagellar segment is often longer than the rather short scape. The wings are conspicuously papillate apically and usually partly bare. The pterostigma is exceedingly small, shorter even than in *Anthophora*. The marginal cell is rather broadly rounded apically; in forms occurring in America north of Mexico it is bent rather abruptly from the wing margin, giving it an obliquely truncated appearance. The posterior legs of the male are not enlarged. The scopa is exceedingly large and dense. Arolia are absent. The apex of the eighth tergum of the male is rounded or feebly bilobed, and the male lacks a pygidial plate.

This chiefly Neotropical tribe contains the genera *Epicharis* and *Hemisia*. Only the latter occurs north of Mexico.

GENUS HEMISIA KLUG

Hemisia KLUG, 1807, Mag. Insektenkunde, vol. 6, p. 227.

Trachina KLUG, 1807, *ibid.*, vol. 6, p. 226.

Ptilotopus KLUG, 1810, Mag. Gesellsch. Naturf. Fr. Berlin, vol. 4, p. 31.

Grundlachia CRESSON (not Pfeiffer), 1865, Proc. Ent. Soc. Philadelphia, vol. 4, p. 195.

Heterocentris COCKERELL, 1899, Entomologist, vol. 32, p. 14.

Centris (*Melanocentris*) FRIESE, 1900, Ann. K. K. Naturhist. Hofmus. Wien, vol. 15, p. 244.

Centris (*Rhodocentris*) FRIESE, 1900, *ibid.*, vol. 15, p. 244.

Centris (*Cyanocentris*) FRIESE, 1900, *ibid.*, vol. 15, p. 244.

Centris (*Poecilocentris*) FRIESE, 1900, *ibid.*, vol. 15, p. 244.

Paracentris CAMERON, 1903, Trans. Amer. Ent. Soc., vol. 29, p. 235.

GENOTYPE: *Apis haemorrhoidalis* Fabricius, designated by Cockerell, 1906, Trans. Amer. Ent. Soc., vol. 32, p. 105.

This is a large genus of fast flying bees ranging from South America to the arid southwestern United States and to southern Florida. It is the *Centris* of authors. The name *Centris* is unfortunately transferred to the Euglossini where it replaces *Eulaema*. This is because Latreille's genotype designation (1810, *Considérations générales . . . des insectes*, p. 439) has been ruled invalid by opinion number 136 of the International Commission of Zoological Nomenclature, Latreille having mentioned two species in his type list. The next genotype for *Centris* is that of Blanchard (1840, *Histoire naturelle des insectes*, vol. 3, p. 405) who fixed *Apis dimidiata* Fabricius, a species belonging to the genus usually called *Eulaema*, as the type.

TRIBE MELECTINI

The Melectini, a tribe of large parasitic bees, are found in the Old World and in North America. The clypeus of the male is black. The first flagellar segment is not unusually elongated. The pterostigma is several times as long as broad, larger than in *Anthophora*, but narrow and not tapering beyond the base of vein r. The marginal cell is shorter than the distance from its apex to the wing tip, broadly rounded apically. There are usually three submarginal cells, the first usually longer than either of the others. The jugal lobe of the hind wing is very small, and the basitibial plates are absent. Arolia are present or absent. The eighth tergum of the male is usually feebly bilobed or bispinose, without a pygidial plate, but in *Zacosmia* and *Brachymelecta* such a plate is well defined. The seventh sternum of the female is some-

what produced, with the margins upturned to form a semitubular guide for the sting.

The tribe includes *Thyreus* (= *Crocisa*) and probably *Callomelecta* and *Protomelissa* in addition to the genera listed below.

The American Melectini were revised by Linsley (1939).

KEY TO THE AMERICAN GENERA OF MELECTINI

1. Anterior wings with three submarginal cells; pubescence of abdomen erect or with patches of depressed hairs. 2
Anterior wings with two submarginal cells; abdomen densely covered with appressed pubescence. *Brachymelecta*
2. Marginal cell scarcely longer than the pterostigma; maxillary palpi with one free segment; flagellum of male greatly thickened, intermediate segments several times as broad as long; pygidial plate present in male *Zacosmia*
Marginal cell much longer than pterostigma; maxillary palpi four- to six-segmented; flagellum of male with intermediate segments at most twice as broad as long; pygidial plate absent in male. *Melecta*

GENUS MELECTA LATREILLE

Melecta LATREILLE, 1802, Histoire naturelle des fourmis . . . , p. 427.

Symmorpha KLUG, 1807, Mag. Insektenkunde, vol. 6, p. 227.

Pseudomelecta RADOSZKOWSKI, 1865, Horae Soc. Ent. Rossicae, vol. 3, p. 55.

Bombomelecta PATTON, 1879, Bull. U. S. Geol. Geogr. Survey Terr., vol. 5, p. 370.

Melecta (*Melectomimus*) LINSLEY, 1939, Ann. Ent. Soc. Amer., vol. 32, p. 448.

Melecta (*Xeromelecta*) LINSLEY, 1939, *ibid.*, vol. 32, p. 450.

Melecta (*Melectomorpha*) LINSLEY, 1939, *ibid.*, vol. 32, p. 451.

GENOTYPE: *Apis punctata* Fabricius = *Andrena armata* Panzer (not Gmelin), designated by Latreille, 1810, Considérations générales . . . des insectes, p. 439.

These are large, robust bees which differ from *Zacosmia* as well as from the Ericrocini in the possession of arolia. The genus is parasitic in the nests of *Anthophora*. In North America species are found throughout the west, but none is known east of the Mississippi River. In the Palearctic region the genus is widely distributed.

The following key to the subgenera of *Melecta* is modified from Linsley (1939).

KEY TO THE AMERICAN SUBGENERA OF *Melecta*

1. Dorsal lobes of scutellum each acute or armed with a tooth or spine; wings lightly infuscated or mottled. 2
Dorsal lobes of scutellum rounded; wings blackish. *Xeromelecta*
2. Mandibles with inner margin edentate or unidentate; scutellar lobes acute or armed with a dorsal spine; thorax and usually second abdominal tergum with long, erect pubescence; marginal cell rounded at apex; outer flagellar segments of male at most a little wider than long. 3
Mandibles with inner margin bidentate; scutellar lobes each with posterior tooth; thorax and second abdominal tergum with patches of appressed pale pubescence; marginal cell subtruncate at apex; outer flagellar segments of male considerably broader than long. *Melectomorpha*
3. Mandibles with inner margin unidentate; maxillary palpi five-segmented or with a short sixth segment; scutellar lobes acute or armed with a stout spine exceeded by surrounding pubescence; second abdominal tergum clothed with erect pale hair; pygidial plate slender apically, not covering its tergum. *Melecta, sensu stricto*
Mandibles with inner margin edentate or with a very feeble tooth; maxillary palpi six-segmented, last segment nearly as long as fifth; scutellar lobes each armed with a slender curved spine as long as surrounding pubescence; second abdominal tergum without pale hairs; pygidial plate of female broad, covering exposed dorsal surface of seventh tergum. *Melectomimus*

GENUS BRACHYMELECTA LINSLEY

Brachymelecta LINSLEY, 1939, Ann. Ent. Soc. Amer., vol. 32, p. 458.

GENOTYPE: *Melecta mucida* Cresson, by original designation.

This genus is known from a single specimen from Nevada. *B. mucida* is a small species, thus resembling *Zacosmia*, but the male flagellum is not swollen as in that genus, its segments mostly being but little broader than long. The male has a pygidial plate and the marginal cell is apparently very small, characters also indicating a relationship with *Zacosmia*.

GENUS ZACOSMIA ASHMEAD

Zacosmia ASHMEAD, 1898, Psyche, vol. 8, p. 282.

Micromelecta BAKER, 1906, Invertebrata Pacifica, vol. 1, p. 143.

GENOTYPE: *Melecta maculata* Cresson, by original designation.

The species of this genus are moderate-sized, robust forms, probably parasitic in the nests of *Anthophora* of the subgenus *Micranthophora*.

Zacosmia is found from New Mexico and Alberta to the Pacific coast states. But two species are known.

TRIBE RHATHYMINI

It has seemed necessary to place the anomalous Neotropical genus *Rhathymus* in a tribe by itself. It appears to be closely related to the Ericrocini, agreeing with that group in its wing venation except for the slightly larger pterostigma which tapers slightly beyond the base of vein r. The marginal cell is unusually long, as in *Acanthopus*. However, the wings are hairy and without papillae, and the middle tibial spurs are not modified as in the Ericrocini. Arolia, not found in the Ericrocini, are present in *Rhathymus*. The male gonostyli are of a modified broad squamiform type, similar to that of the Ericrocini. As in the Melectini, the seventh tergum of the female bears a conspicuous pygidial area, and the lateral margins of the seventh sternum are upturned to form a guide for the sting.

TRIBE ERICROCINI

This is a primarily Neotropical tribe which includes a number of genera usually placed near *Melecta*. Whether the Ericrocini is directly related to the Melectini or arose from a pollen collecting group (such as the Hemisini) different from that from which the Melectini were derived remains in doubt. In addition to the characters pointed out in the key, the Ericrocini may be distinguished from the Melectini by the sharp, carinate spine at the apex of each middle tibia. In the Melectini the middle tibiae, if provided with an apical spine at all, lack the strong carina extending upward from the apex of the spine. The maxillary palpi in the Ericrocini are absent or have but one short free segment.

The tribe includes *Acanthopus*, *Ctenischelus*, *Cyphomelissa*, *Epiclopus*, *Ericrocis*, *Eurytis*, *Mesochaira*, *Mesonychium*, *Mesoplia* (= *Melissa*), and *Oxyndys*. Of these only *Ericrocis* occurs within the United States. The others are found in Central and South

America. It is to be noted that several of the names in the above list have been placed in synonymy by certain authors.

GENUS ERICROCIS CRESSON

Ericrocis CRESSON, 1887, Trans. Amer. Ent. Soc. (suppl.), p. 131.

GENOTYPE: *Crocisa* ? *lata* Cresson (monobasic).

The bees of this genus have the body form of a robust *Melecta*, with conspicuous white markings formed by patches of depressed pubescence, thus somewhat resembling *Melecta* of the subgenus *Melectomorpha*.

The few species of *Ericrocis* are found in the arid southwestern states and in northern Mexico. They were revised by Linsley (1939). It has been suspected that *Ericrocis* is a parasite of *Hemisia*, and this may indeed be the case, but Dr. E. G. Linsley and Mr. J. W. MacSwain have recently taken specimens from the nests of *Anthophora linsleyi* Timberlake.

SUBFAMILY XYLOCOPINAE

This subfamily contains two very distinct elements which might well be placed as separate subfamilies. They may be separated as follows:

KEY TO THE TRIBES OF XYLOCOPINAE

1. Pterostigma virtually absent (fig. 166); distal parts of wings strongly papillate; metanotum vertical; large forms with much coarsely plumose hair. XYLOCOPINI
- Pterostigma large; wings not papillate; metanotum horizontal; small forms with but little pubescence. CERATININI

TRIBE CERATININI

This is a group of small, rather slender bees. The mandibles are very broad basally, then abruptly narrowed to the slender, subparallel-sided, apical portions. The wing surfaces are hairy throughout, not papillate. The marginal cell is broad, longer than the distance from its apex to the wing tip, and considerably bent from the wing margin apically. The jugal lobe of each hind wing is one-third to one-half as long as the vannal lobe. The apex of the seventh tergum of the female is produced to a small, sharp, median point.

In addition to *Ceratina* this tribe includes *Allodape*, *Allodapula*, *Eucondylops*, *Exoneura*,

Exoneuridia, *Manuelia*, and *Neoceratina*. The only North American genus is *Ceratina*.

GENUS CERATINA LATREILLE

Clavicera LATREILLE, 1802, Histoire naturelle des fourmis . . . , p. 433.

Ceratina LATREILLE, 1802, Histoire naturelle . . . des crustacés et des insectes, vol. 3, p. 380.

Pithitis ILLIGER, 1807, Mag. Insektenkunde, vol. 6, p. 198.

Zadontomerus ASHMEAD, 1899, Trans. Amer. Ent. Soc., vol. 26, p. 69.

Ceratina (*Ceratinidia*) COCKERELL AND PORTER, 1899, Ann. Mag. Nat. Hist., ser. 7, vol. 4, p. 406.

Ceratina (*Crewella*) COCKERELL, 1903, Ann. Mag. Nat. Hist., ser. 7, vol. 12, p. 202.

Ceratina (*Chloroceratina*) COCKERELL, 1918, Philippine Jour. Sci., vol. 13, p. 143.

Ceratina (*Callooceratina*) COCKERELL, 1924, Proc. Ent. Soc. Washington, vol. 26, p. 77.

GENOTYPE: *Hylaeus albilabris* Fabricius = *Apis cucurbitina* Rossi (monobasic).

Our species of this genus are black, or dark metallic blue or green, often with restricted pale yellow markings on the clypeus, pronotal lobes, and legs.

KEY TO THE NEARCTIC SUBGENERA OF *Ceratina*

1. Maxillary palpi five-segmented; black, non-metallic forms. *Ceratina*, *sensu stricto*
- Maxillary palpi six-segmented; metallic blue or green forms. *Zadontomerus*

In North America species of *Zadontomerus* (often emended to *Zaodontomerus*) are more abundant than those of *Ceratina*, *sensu stricto*. American species of the genus were revised by Michener (1936).

Clavicera has priority over *Ceratina* and is isogenotypic with it but has not been used since 1802. It has, therefore, been recommended by Benson, Ferrière, and Richards (1937) that the name *Clavicera* be suppressed.

TRIBE XYLOCOPINI

The Xylocopini consists of very large, robust bees. The wings are elongate, papillate distally. The marginal cell is very slender, much longer than the distance from its apex, which is bent from the wing margin, to the wing tip (fig. 16). The jugal lobe of the hind wing is much shorter than the vannal lobe. The basitarsi are fully as long as the corresponding tibiae. The apex of the seventh tergum of the female is produced to a flat-

topped spine, largely hidden in a dense mass of hair.

This tribe includes *Mesotrichia* and *Lestis* in addition to the widespread genus *Xylocopa*.

GENUS XYLOCOPA LATREILLE

Xylocopa LATREILLE, 1802, Histoire naturelle des fourmis . . . , p. 432.

Xylocopa LATREILLE, 1802, Histoire naturelle . . . des crustacés et des insectes, vol. 3, p. 379.

Platynopoda WESTWOOD, 1840, in Jardine, Naturalist's library, vol. 26, Entomology, vol. 6, p. 271.

Audinetia LEPELETIER, 1841, Histoire naturelle des insectes, hyménoptères, vol. 2, p. 203.

Schönherria LEPELETIER, 1841, *op. cit.*, vol. 2, p. 207.

Xylocopa (*Nyctomelitta*) COCKERELL, 1929, Ann. Mag. Nat. Hist., ser. 10, vol. 4, p. 303.

Xylocopa (*Biluna*) MA, 1938, Rec. Indian Mus., vol. 40, p. 276.

Xylocopa (*Ctenopoda*) MA (not McAtee and Malloch), 1938, *ibid.*, vol. 40, p. 285.

Xylocopa (*Nodula*) MA, 1938, *ibid.*, vol. 40, p. 290.

Xylocopa (*Zonohirsuta*) MA, 1938, *ibid.*, vol. 40, p. 300.

Xylocopa (*Orbitella*) MA (not Douville), 1938, *ibid.*, vol. 40, p. 305.

Xylocopa (*Proxylocopa*) HEDICKE, 1938, Deutsche Ent. Zeitschr., p. 192.

Xylocopa (*Alloxylocopa*) MA, 1939, Lingnan Sci. Jour., vol. 18, p. 155.

Xylocopa (*Bomboixylocopa*) MA, 1939, *ibid.*, vol. 18, p. 155.

Xylocopa (*Maiella*) MICHENER, 1942, Jour. New York Ent. Soc., vol. 50, p. 282.

Xylocopa (*Ctenoxylocopa*) MICHENER, 1942, *ibid.*, vol. 50, p. 282.

Baana SANDHOUSE, 1943, Proc. U. S. Natl. Mus., vol. 92, p. 530.

Euryapis SANDHOUSE, 1943, *ibid.*, vol. 92, p. 551.

GENOTYPE: *Apis violacea* Linnaeus, designated by Latreille, 1810, Considérations générales . . . des insectes, p. 439. Although Latreille mentions two names in designating the genotype, they are synonymous and the designation should be considered valid.

Since the spelling *Xylocopa* has had virtually universal usage since 1802, it is hoped that it will be placed on the *nomina conservanda* list. In this event *Xilocopa* will be rejected.

This genus of large, black, slightly metallic, or yellowish brown bees is found throughout

the tropical and warm temperate regions of the world. Several species are found in the southern half of the United States, and a few reach the northern states in certain areas. Ackerman (1916) revised the species of the United States.

SUBFAMILY APINAE

This subfamily includes all the social bees and, in addition, the tribe Euglossini, which is evidently related to them. Certain subfamily characters, in addition to those noted in the key, are indicated in the paragraph following the key to the subfamilies of the Apidae. In all Apinae the first flagellar segment is much shorter than the scape, the wings are hairy throughout, and the basitibial plates are absent.

The North American species of this subfamily are listed by Lutz and Cockerell (1920).

KEY TO THE TRIBES OF APINAE

1. Posterior tibial spurs absent; jugal lobe of posterior wing present; labrum three to four times as broad as long; marginal cell open or with veins evanescent distally or, if complete, reaching to within one-third or less of its length from wing tip 2
- Posterior tibial spurs present; jugal lobe of posterior wing absent or much reduced; labrum at most twice as broad as long; apex of marginal cell separated from wing tip by a distance equal to at least half length of cell 3
2. Marginal cell open (or its veins weak) distally, tapering from broad base; pterostigma of moderate to large size, extending well beyond base of vein r; claws of female simple; eyes bare, sparsely hairy in some queens; sting reduced. Meliponini
- Marginal cell complete, parallel-sided for a large part of its length; pterostigma minute, not tapering beyond base of vein r; claws cleft; eyes densely hairy; sting well developed. Apini
3. Proboscis reaching at least to base of abdomen in repose; scutellum produced posteriorly to a sharp transverse carina overhanging metanotum and propodeum; posterior tibiae of male swollen with a deep hairy fossa on apical half of posterior margin Euglossini
- Proboscis in American forms not reaching behind middle coxae; scutellum rounded; posterior tibiae of male neither swollen nor fossate. Bombini

TRIBE EUGLOSSINI

This Neotropical tribe consists of usually large and often brilliantly metallic bees. They are unique among the Apoidea in possessing an extra buttress on the outer side of each anterior tentorial root, resulting in a depression on each paraocular area extending from near the antennal base toward the eye. The clypeus is strongly protuberant, its lower lateral parts bent backward. The epistomal suture is arched upward close to the antennal bases, and its lower lateral portions are abruptly bent outward nearly to the horizontal. The labrum is as long as broad or slightly shorter. The posterior tibiae of the females of nonparasitic genera are greatly broadened and largely concave externally. Arolia are absent. The pterostigma is small, not tapering beyond the base of vein r.

This tribe contains the pollen collecting genera *Eufriesia* (= *Eumorpha*), *Euglossa*, and *Centris* (= *Eulaema*), and their parasites *Exaerete* (= *Chrysantheda*) and *Aglae*. Only *Euglossa* is known to occur in the United States.

GENUS EUGLOSSA LATREILLE

Euglossa LATREILLE, 1802, Histoire naturelle des fourmis . . . , p. 436.

Plusia HOFFMANNSEGG (not Hübner), 1817, Zool. Mag., vol. 1, p. 52.

Cnemidium PERTY (not Goldfuss), 1833, Delectus animalium articulorum . . . Brasiliam . . . , p. 148.

GENOTYPE: *Apis cordata* Linnaeus (monobasic).

This is a genus of brilliant metallic green, blue, red, or golden bees with a small tuft of black pubescence on the posterior part of the scutellum. A single species has been recorded from Brownsville, Texas.

TRIBE BOMBINI

This tribe includes only the bumblebees and their parasites. They are moderate-sized to large, hairy bees. The clypeus is slightly protuberant, its lower lateral portions being slightly bent backward. The malar area is long. The labrum is about twice as broad as long. The pterostigma is small, not tapering beyond the base of vein r.

All species found in the United States are normally black with bands or areas of yellow or white or sometimes red pubescence. The

New World species of this tribe were revised by Franklin (1912, 1913), while Frison (1927) has presented a discussion of the bumblebees found in America north of Mexico.

KEY TO THE GENERA OF BOMBINI

1. Female with a corbicula on each posterior tibia; seventh abdominal tergum of female without much long pubescence and curved downward; posterior tibiae of male flattened and shining externally; male gonocoxites and gonostyli blackish, very strongly sclerotic, gonostyli but little exceeding gonocoxites *Bombus*

Females without corbiculae; seventh abdominal tergum of female hairy, not strongly down-curved; posterior tibiae of male somewhat convex externally, not strongly shining; male gonocoxites and gonostyli brown, moderately strongly sclerotic, gonostyli extending far beyond apices of gonocoxites. *Psithyrus*

GENUS BOMBUS LATREILLE

Bombus LATREILLE, 1802, Histoire naturelle des fourmis . . . , p. 437.

Bremus PANZER, 1804?¹ Faunae insectorum Germanicae initia . . . , pt. 85, no. 21.

Bombus (Kallobomus) DALLA TORRE, 1880, Der Naturhistoriker,² vol. 2, p. 40.

Bombus (Chromobomus) DALLA TORRE, 1880, *ibid.*, vol. 2, p. 40.

Bombus (Leucobomus) DALLA TORRE, 1880, *ibid.*, vol. 2, p. 40.

Bombus (Megabomus) DALLA TORRE, 1880, *ibid.*, vol. 2, p. 40.

Bombus (Melanobomus) DALLA TORRE, 1880, *ibid.*, vol. 2, p. 40.

Bombus (Pyrobomus) DALLA TORRE, 1880, *ibid.*, vol. 2, p. 40.

Bombus (Rhodobomus) DALLA TORRE, 1880, *ibid.*, vol. 2, p. 40.

Bombus (Thoracobomus) DALLA TORRE, 1880, *ibid.*, vol. 2, p. 40.

Bombus (Poecilobomus) DALLA TORRE, 1882, Ber. Naturwiss.-med. Ver. Innsbruck, vol. 12, p. 23.

Bombus (Callobomus) DALLA TORRE, 1896, Catalogus Hymenopterorum . . . , vol. 10, p. 503.

Bombus (Pyrrhobomus) DALLA TORRE, 1896, *op. cit.*, vol. 10, p. 503.

Bombias ROBERTSON, 1903, Trans. Amer. Ent. Soc., vol. 29, p. 176.

¹ See Sandhouse (1943, p. 532) for a discussion of the relative dates of publication of *Bombus* and *Bremus*.

² Zeitschrift zur Verbreitung naturwissenschaftlicher, insbesondere naturhistorischer Kenntnisse . . . , Herausgegeben von F. K. Knauer, etc., Vienna.

Bombus (Pratobomus) VOGT, 1911, Sitzber. Gesellsch. Naturf. Fr. Berlin, p. 49.

Bombus (Agrobomus) VOGT, 1911, *ibid.*, p. 52.

Bombus (Terrestribomus) VOGT, 1911, *ibid.*, p. 55.

Bombus (Hortobomus) VOGT, 1911, *ibid.*, p. 56.

Bombus (Cullumanobomus) VOGT, 1911, *ibid.*, p. 57.

Bombus (Lapidariobomus) VOGT, 1911, *ibid.*, p. 58.

Bombus (Sibiricobomus) VOGT, 1911, *ibid.*, p. 60.

Bombus (Subterraneobomus) VOGT, 1911, *ibid.*, p. 62.

Bombus (Soroensibomus) VOGT, 1911, *ibid.*, p. 63.

Alpinobomus SKORIKOV, 1914, Rev. Russe Ent., vol. 14, p. 123.

Mendacibomus SKORIKOV, 1914, *ibid.*, vol. 14, p. 125.

Alpigenobomus SKORIKOV, 1914, *ibid.*, vol. 14, p. 128.

Bombus (Diversobomus) SKORIKOV, 1914, *ibid.*, vol. 14, p. 406.

Bombus (Confusibomus) BALL, 1914, Ann. Soc. Ent. Belgique, vol. 58, p. 78.

Bombus (Pomobomus) KRÜGER, 1917, Ent. Mitt., vol. 6, p. 65.

Bombus (Odontobomus) KRÜGER, 1917, *ibid.*, vol. 6, p. 65.

Bombus (Anodontobomus) KRÜGER, 1917, *ibid.*, vol. 6, p. 65.

Bombus (Uncobomus) KRÜGER, 1917, *ibid.*, vol. 6, p. 65.

Bombus (Sulcobomus) KRÜGER, 1917, *ibid.*, vol. 6, p. 66.

Bombus (Mastrucatobomus) KRÜGER, 1917, *ibid.*, vol. 6, p. 66.

Mucidobomus SKORIKOV, 1922, Bull. Sta. Régionale Protectrice Plantes Petrograd, vol. 4, p. 149.

Volucellobomus SKORIKOV, 1922, *ibid.*, vol. 4, p. 149.

Nevadensibomus SKORIKOV, 1922, *ibid.*, vol. 4, p. 149.

Mucidobomus (Exilobomus) SKORIKOV, 1922, *ibid.*, vol. 4, p. 150.

Agrobomus (Adventoribomus) SKORIKOV, 1922, *ibid.*, vol. 4, p. 150.

Agrobomus (Laesobomus) SKORIKOV, 1922, *ibid.*, vol. 4, p. 150.

Agrobomus (Tricornibomus) SKORIKOV, 1922, *ibid.*, vol. 4, p. 151.

Kozlovibomus SKORIKOV, 1922, *ibid.*, vol. 4, p. 152.

Fervidobomus SKORIKOV, 1922, *ibid.*, vol. 4, p. 153.

Fervidobomus (Rubicundobomus) SKORIKOV, 1922, *ibid.*, vol. 4, p. 154.

Rufipedibombus SKORIKOV, 1922, *ibid.*, vol. 4, p. 156.

Alpigenobombus (*Fraternobombus*) SKORIKOV, 1922, *ibid.*, vol. 4, p. 156.

Alpigenobombus (*Funebribombus*) SKORIKOV, 1922, *ibid.*, vol. 4, p. 157.

Alpigenobombus (*Coccineobombus*) SKORIKOV, 1922, *ibid.*, vol. 4, p. 157.

Alpigenobombus (*Robustobombus*) SKORIKOV, 1922, *ibid.*, vol. 4, p. 157.

Bremus (*Boopobombus*) FRISON, 1927, Trans. Amer. Ent. Soc., vol. 53, p. 62.

Bremus (*Separatobombus*) FRISON, 1927, *ibid.*, vol. 53, p. 64.

Bombus (*Orientalibombus*) RICHARDS, 1929, Ann. Mag. Nat. Hist., ser. 10, vol. 3, p. 378.

Bombus (*Obertobombus*) REINIG, 1930, Zeitschr. Morph. Ökol., vol. 17, p. 107.

Bremus (*Senexibombus*) FRISON, 1930, Treubia, vol. 12, p. 3.

Bombus (*Nobilibombus*) SKORIKOV, 1933, Mushi, vol. 6, p. 62.

Bremus (*Pressibombus*) FRISON, 1935, Rec. Indian Mus., vol. 37, p. 342.

Bombus (*Tanguitobombus*) PITTIONI, 1939, Zool., Anz., vol. 126, p. 201.

GENOTYPE: *Apis terrestris* Linnaeus (monobasic).

This genus includes the common bumblebees. They form colonies which, in temperate and arctic regions, break up in the winter. Species are found throughout the Holarctic region and south through South America to Tierra del Fuego.

GENUS PSITHYRUS LEPELETIER

Psithyrus LEPELETIER, 1832, Ann. Soc. Ent. France, vol. 1, p. 372.

Apathus NEWMAN, 1834, Ent. Mag., vol. 2, p. 404.

Psithyrus (*Laboriopsithyrus*) FRISON, 1927, Trans. Amer. Ent. Soc., vol. 53, p. 69.

Psithyrus (*Ashtonipsithyrus*) FRISON, 1927, *ibid.*, vol. 53, p. 69.

Psithyrus (*Fernaldaepsithyrus*) FRISON, 1927, *ibid.*, vol. 53, p. 70.

Psithyrus (*Eopsithyrus*) POPOV, 1931, Eos, vol. 7, p. 134.

Psithyrus (*Metapsithyrus*) POPOV, 1931, *ibid.*, vol. 7, p. 135.

Psithyrus (*Allopsithyrus*) POPOV, 1931, *ibid.*, vol. 7, p. 136.

GENOTYPE: *Apis rupestris* Fabricius, designated by Curtis, 1833, British entomology . . . , vol. 10 [if bound as published in 16 vols.], pl. 468.

These bees have virtually the same aspect

as those of the genus *Bombus*, in whose nests they are parasitic. There is no worker caste as in *Bombus*.

TRIBE MELIPONINI

This Pantropical tribe consists of moderate-sized to minute bees, forming long-lived colonies. As in *Apis* the epistomal suture is arched upward close to the antennal sockets, and the clypeus is not protuberant. The ninth sternum of the male is virtually absent, being represented, if at all, by a narrow, longitudinal, weakly sclerotic band beneath the genitalia. The eighth sternum is rather narrow, having the form characteristic of the ninth in most bees.

The Neotropical genus *Melipona* and the Pantropical genus *Trigona* are included in this tribe. Such groups as *Tetragona* and *Lestrimelitta* are probably best regarded as subgenera of *Trigona*. No representatives of this tribe are known in the United States or northern Mexico.

TRIBE APINI

This tribe, originally confined to the Old World, is unique among bees in the form of the male genitalia, in which the gonostyli, gonocoxites, and penis valves are greatly reduced and apparently replaced in function by an immense and complicated penis. This condition, however, does not indicate that the tribe is not rather closely related to the Meliponini, a group having the usual type of genitalia. Relationship with the Meliponini is indicated by certain characters mentioned under that tribe and in the key to the tribes, and in addition by the very short and angulate first recurrent vein, the swollen scutellum, the rather long malar space, etc. The ninth sternum of the male is either absent or represented by the large plate attached to the posterior margin of the eighth sternum. In other bees the ninth sternum lies above the eighth; this plate may, therefore, represent merely a subdivision of the eighth, especially in view of the reduction of the ninth in the Meliponini.

The Apini contains only the genus *Apis*.

GENUS APIS LINNAEUS

Apis LINNAEUS, 1758, Systema naturae, 10th ed., p. 343.

Apiarus RAFINESQUE, 1815, *Analyse de la nature* . . . , p. 123.

Megapis ASHMEAD, 1904, *Proc. Ent. Soc. Washington*, vol. 6, p. 120.

Micrapis ASHMEAD, 1904, *ibid.*, vol. 6, p. 122.

GENOTYPE: *Apis mellifica* Linnaeus = *Apis mellifera* Linnaeus, designated by Latreille, 1810, *Considérations générales . . . des insectes*, p. 439.

This genus is represented in America only by the common, introduced honey bee.

ARTIFICIAL KEY TO THE GENERA OF BEES OF AMERICA NORTH OF MEXICO

1. Forewings with three submarginal cells (fig. 165) 2
- Forewings with two (rarely one) submarginal cells (fig. 167) 61
- 2(1). Marginal cell at least three-fourths as long as cell first M (figs. 165 to 170), or if not (as in *Nomada*) then considerably longer than distance from its apex to wing tip 3
- Marginal cell at most two-thirds as long as first M and not, or scarcely, longer than distance from apex to wing tip (fig. 35) 52
- 3(2). Head and thorax brilliant metallic blue or green (as in *Chrysis*) 4
- Body black or but slightly metallic 7
- 4(3). Proboscis long, apex in repose reaching at least to base of abdomen; second submarginal cell as long as first . *Euglossa*
- Proboscis short, apex not reaching fore coxae in repose; second submarginal cell shorter than first 5
- 5(4). First recurrent vein interstitial with, or distad of, second transverse cubital . 6
- First recurrent vein basad of second transverse cubital *Agapostemon*
- 6(5). Second and third abdominal terga each with apical fringe of simple bristles arising from punctures. *Augochloropsis*
- Second and third abdominal terga not fringed, impunctate on margins, or second with fringe of plumose hairs *Augochlora*
- 7(3). First recurrent vein interstitial with first transverse cubital *Caupolicana*
- First recurrent vein distad of first transverse cubital 8
- 8(7). Tibial spurs absent on posterior legs . *Apis*
- Tibial spurs present on posterior legs . 9
- 9(8). Second submarginal cell, along posterior margin, at least as long as first . . . 10
- Second submarginal cell, along posterior margin, shorter than first 14
- 10(9). Marginal cell considerably shorter than distance from its apex to wing tip *Hemisia*
- Marginal cell longer than distance from its apex to wing tip. 11
- 11(10). Posterior basitarsi longer than tibiae; second submarginal cell greatly narrowed toward marginal cell (fig. 166) *Xylocopa*
- Posterior basitarsi shorter than tibiae; second submarginal cell at least half as broad on anterior as on posterior side . 12
- 12(11). Ocelli far down on face close to antennal bases *Protoxaea*
- Ocelli near summit of vertex 13
- 13(12). Posterior tibiae of female each with a large, shining, concave corbicula surrounded by long hairs; male gonostyli but little exceeding gonocoxites *Bombus*
- Posterior tibiae of female convex and hairy; male gonostyli much exceeding gonocoxites *Psithyrus*
- 14(9). Jugal lobe of posterior wing very small; scopa of female absent 15
- Jugal lobe of posterior wing at least one-third as long as vannal lobe; scopa present in female 19
- 15(14). Integument almost entirely polished and impunctate; thorax flattened, greatest width nearly twice height. *Paranomada*
- Integument at least largely punctate; thorax not unusually flattened . . . 16
- 16(15). Apical portion of marginal cell slightly bent away from wing margin . . . 17
- Apical portion of marginal cell on wing margin 18
- 17(16, 77). Over 8 mm. in length; abdominal terga with apical pubescent fasciae *Hexepeolus*
- Under 6 mm. in length; abdominal terga pubescent laterally, not fasciate *Triopasites*
- 18(16). Vertex and mesoscutum largely impunctate; middle coxae as long as distance from summits to hind wing bases *Melanomada*
- Vertex and mesoscutum ordinarily punctate; middle coxae shorter than distance from summits to hind wing bases *Nomada*
- 19(14). Jugal lobe of posterior wings at least nearly three-fourths as long as vannal

- lobe; labial palpi with segments similar or first alone elongated20
- Jugal lobe of posterior wings at most a little over one-half as long as vannal lobe; labial palpi (except in *Melitta*) with first two segments elongate and flattened, last two small and cylindrical30
- 20(19). Marginal cell obliquely truncate, extreme apex well separated from costal margin of wing *Psaenythia*
Marginal cell pointed or narrowly rounded apically, apex at or near wing margin21
- 21(20). Second recurrent vein distinctly arcuate outward in its posterior portion (fig. 168) *Colletes*
Second recurrent vein not arcuate outward in its posterior portion, frequently straight (figs. 169, 170)22
- 22(21). Clypeus short, antennal bases far below middle of face *Conanthalictus*
Clypeus of usual shape, antennal bases near middle of face23
- 23(22). Third submarginal cell at least three-fourths as long as first; posterior basitarsi of male at least as long as tibiae; metanotum about as long as dorsal area of propodeum and covered with dense short pubescence *Nomia*
Third submarginal cell usually less than two-thirds as long as first; posterior basitarsi of male shorter than tibiae; metanotum usually shorter than dorsal area of propodeum, its pubescence similar to that of scutellum24
- 24(23). Basal vein (first abscissa of M) strongly arcuate or subangulate (fig. 170); facial foveae absent27
Basal vein straight or feebly arcuate (fig. 169); facial foveae present in female (fig. 91)25
- 25(24). Pterostigma more than half as long as distance from apex to apex of marginal cell (fig. 169) *Andrena*
Pterostigma less than half as long as distance from its apex to apex of marginal cell26
- 26(25). Male gonocoxites with large basal lobes nearly obscuring from above the slender, spatulate, apical lobes; posterior trochanters of female with long, curled hairs *Megandrena*
Male gonocoxites without dorsal lobes; posterior trochanters of female with straight hair of moderate length *Ancylandrena*
- 27(24). Abdominal terga with apical pubescent bands *Halictus*
Abdominal terga without, or with only basal, pubescent bands28
- 28(27). Middle tibial spurs coarsely serrate with eight to ten large teeth . . . *Xeralictus*
Middle tibial spurs finely pectinate, appearing simple under low magnifications29
- 29(28, 106). Coarsely punctate, dorsal area of propodeum extremely coarsely rugose; scopa absent; abdomen commonly red *Sphecodes*
More finely punctate, dorsal area of propodeum finely rugose or striate; scopa present in female; abdomen rarely red *Lasioglossum*
- 30(19). Apical portion of marginal cell on wing margin *Melitta*
Apical portion of marginal cell bent away from wing margin31
- 31(30). Small, slender, sparsely pubescent forms; horizontal part of propodeum nearly as long as subvertical part seen in profile; clypeus not protuberant. *Ceratina*
Robust bees with abundant pubescence; propodeum entirely declivous or with horizontal portion much shorter than vertical; clypeus usually protuberant32
- 32(31). Second abscissa of vein M+Cu of posterior wings less, usually much less, than twice as long as cu-v and rarely over half as long as vein M (as in fig. 35); male without pygidial plate33
Second abscissa of vein M+Cu of posterior wings at least nearly twice as long as cu-v and rarely much shorter than M (as in fig. 189); male with pygidial plate35
- 33(32). Arolia absent *Emphor*
Arolia large34
- 34(33). Proboscis in repose reaching base of abdomen *Melittoma*
Proboscis rarely reaching beyond front coxae in repose. *Diadasia*
- 35(32). Pterostigma of moderate size, about twice as long as prestigma, and extending nearly as far beyond base of vein r as basad of it, or, if small, then marginal cell is obliquely truncate at apex . . .36
Pterostigma small, little, if any, longer than prestigma and only rarely extending much beyond base of vein r; marginal cell bent gradually from wing margin37
- 36(35). Marginal cell much longer than distance from apex to wing tip and bent grad-

- usually from wing margin . . . *Ancyloscelis*
 Marginal cell little longer than distance
 from apex to wing tip, bent rather
 abruptly from wing margin so that it
 usually appears obliquely truncate . . .
 *Exomalopsis*
- 37(35). Apex of clypeus trilobate, median lobe
 notched *Cemolobus*
 Apex of clypeus truncate 38
- 38(37). Males 39
 Females 46
- 39(38). First flagellar segment at least nearly as
 long as second; flagellum of moderate
 length or somewhat elongate in *Martinapis* 40
 First flagellar segment much shorter than
 second; flagellum usually elongate,
 commonly reaching beyond propodeum 42
- 40(39). Antennae almost entirely bright yellow;
 gonostyli each ending in a very slender
 process *Martinapis*
 Antennae black or dark brown; male
 gonostyli without slender apical processes 41
- 41(40). Last antennal segment curved and produced
 to a point; maxillary palpi short,
 four-segmented *Anthedonia*
 Last antennal segment unmodified; maxillary
 palpi longer, five-segmented
 *Xenoglossa*
- 42(39). Labrum about twice as broad as long;
 clypeus strongly protuberant, so that,
 seen from the side, its anterior margin
 is as far in front of the lower anterior
 eye margin as width of eye and well below
 lower end of eye; maxillary palpi
 with five to six segments 43
 Labrum usually more than twice as broad
 as long; clypeus less protuberant so that,
 seen from side, its anterior margin is not
 so far in front of lower anterior eye
 margin as width of eye and little below
 lower end of eye; maxillary palpi three-
 to six-segmented 44
- 43(42). Marginal cell scarcely longer than distance
 from its apex to wing tip; male
 antennae very long *Tetralonia*
 Marginal cell distinctly longer than distance
 from its apex to wing tip; male
 antennae not greatly elongated
 *Peponapis*
- 44(42). Abdomen slightly metallic . . . *Florilegus*
 Abdomen black, nonmetallic 45
- 45(44). Maxillary palpi with three or four segments *Melissodes*
 Maxillary palpi with five or six segments *Xenoglossodes*
- 46(38). Scopal hairs simple or with only exceedingly
 short branches 47
 Scopal hairs plumose, at least basally . 48
- 47(46). Malar area exceedingly short, mandible
 nearly reaching eye; maxillary palpi
 four-segmented *Anthedonia*
 Malar area larger; maxillary palpi six-
 segmented *Tetralonia*
- 48(46). Malar area exceedingly short, mandible
 nearly reaching eye; anterior mandibular
 condyle scarcely in front of anterior
 eye margin 50
 Malar area larger; anterior mandibular
 condyle considerably in front of eye
 margin 49
- 49(48). Inner margin of mandible with tooth near
 base *Xenoglossa*
 Inner margin of mandible without basal
 tooth *Peponapis*
- 50(48). Abdomen slightly metallic . . . *Florilegus*
 Abdomen black, nonmetallic 51
- 51(50). Maxillary palpi three- to four-segmented
 *Melissodes*
 Maxillary palpi five- to six-segmented . .
 *Xenoglossodes*
- 52(2). Second submarginal cell small, triangular,
 petiolate on side toward marginal cell
 *Perdita*
 Second submarginal cell not unusually
 small, not petiolate 53
- 53(52). Marginal cell exceeded by third submarginal
 cell 54
 Marginal cell exceeding third submarginal
 cell 55
- 54(53). Arolia present; marginal cell much longer
 than pterostigma *Melecta*
 Arolia absent; marginal cell about as long
 as pterostigma *Zacospia*
- 55(53). Middle tibial spur bifid or tridentate
 apically *Ericrocis*
 Middle tibial spur with simple apex . . 56
- 56(55). Wings largely bare, papillate apically;
 vein cu-v of posterior wings oblique and
 little, if any, shorter than second abscissa
 of M + Cu (fig. 35) 57
 Wings pubescent, only feebly papillate;
 vein cu-v of posterior wings transverse
 and about half as long as second abscissa
 of M + Cu 58
- 57(56). Third submarginal cell considerably narrower
 on marginal cell than on posterior side
 *Emphoropsis*
 Third submarginal cell scarcely, if at all,
 narrower on marginal cell than on posterior
 side (fig. 35) *Anthophora*
- 58(56). First submarginal cell on posterior side
 about as long as second and third
 together; axillae angulate 59

- First submarginal cell on posterior side much shorter than second and third together; axillae rounded60
- 59(58, 69). Pseudopygidial area of female transverse, clothed with short, silvery pubescence; marginal cell usually shorter than distance from its apex to wing tip *Epeolus*
- Pseudopygidial area of female usually at least half as long as broad, with dark pubescence; marginal cell as long as, or longer than, distance from apex to wing tip *Triepeolus*
- 60(58). Arolia at least nearly as long as claws; eyes of male not converging above. *Protepeolus*
- Arolia much shorter than claws; eyes of male strongly converging above. *Epeoloides*
- 61(1). Portion of marginal cell on costal margin of wing little, if any, longer than pterostigma; apex of marginal cell broadly truncate62
- Portion of marginal cell on costal margin of wing at least nearly one and one-half times as long as pterostigma; apex of marginal cell variable63
- 62(61). Jugal lobe of posterior wing less than one-fourth as long as vannal lobe; body partly covered with appressed scale-like hairs *Neolarra*
- Jugal lobe of posterior wing about three-fourths as long as vannal lobe; body without dense appressed pubescence *Perdita*
- 63(62). Second submarginal cell little, if any, more than half as long as first; first recurrent vein received by first submarginal cell or interstitial with, or but little beyond, first transverse cubital. 64
- Second submarginal cell at least nearly as long as first and, except in *Formicapis* and *Panurginus*, receiving first recurrent vein67
- 64(63). Jugal lobe of posterior wing more than three-fourths as long as vannal lobe *Hylaeus*
- Jugal lobe of posterior wing less than one-fourth as long as vannal lobe65
- 65(64). Apical portion of marginal cell on wing margin *Nomada*
- Apical portion of marginal cell rounded away from wing margin66
- 66(65). Labrum much longer than broad; coarsely punctate forms. *Neopasites*
- Labrum broader than long; finely punctate forms. *Townsendiella*
- 67(63). Axillae produced posteriorly to an angle on either side of scutellum68
- Axillae rounded posteriorly70
- 68(67). Marginal cell much longer than distance from apex to wing tip.69
- Marginal cell scarcely, if any, longer than distance from apex to wing tip59
- 69(68). Eyes hairy; metanotum without median spine *Coelioxys*
- Eyes bare; metanotum with median spine *Dioxys*
- 70(67). Outer surfaces of tibiae with numerous coarse bare spiculi (weak on posterior legs of male); mandibles tridentate, median tooth largest *Lithurge*
- Outer surfaces of tibiae not, or weakly, spiculate, or, if rather strongly so, with a bristle arising from the apex of each spicule; mandibles variable, if tridentate, distal tooth largest71
- 71(70). Jugal lobe of posterior wing less, usually much less, than two-thirds as long as vannal lobe (fig. 167), except rarely in *Hesperapis*72
- Jugal lobe of posterior wing at least three-fourths as long as vannal lobe (as in figs. 169, 170)103
- 72(71). Marginal cell measured from apex of pterostigma to point where it bends away from wing margin shorter than distance from apex of cell to wing tip73
- Marginal cell thus measured at least as long as distance from apex to wing tip, cell frequently not bending away from wing margin76
- 73(72). Jugal lobe of posterior wing at least one-third as long as vannal lobe *Exomalopsis*
- Jugal lobe of posterior wing less than one-fourth as long as vannal lobe.74
- 74(73). Marginal cell not, or scarcely, exceeding second submarginal cell. *Brachymelecta*
- Marginal cell exceeding second submarginal cell75
- 75(74). Labrum much longer than broad; marginal cell obliquely truncate at apex *Oreopasites*
- Labrum much broader than long; marginal cell rounded at apex. *Gnathopasites*
- 76(72). Clypeus somewhat protuberant, lower parts of its sides bent back on either side of base of labrum so that they are nearly parallel with long axis of body; scopa absent.77
- Clypeus with lower parts scarcely bent back on either side of labrum, or, if so, only as a continuation of general curva-

- ture of clypeal margin; scopa usually present in females79
- 77(76). Apical portion of marginal cell slightly bent from wing margin17
- Apical portion of marginal cell pointed on wing margin78
- 78(77). Mandibles with anterior articulation more distant from eye than posterior articulation. *Nomada*
- Mandibles with articulations equidistant from eye *Hesperonomada*
- 79(76). Pterostigma at least nearly half as long as distance from its apex to apex of marginal cell; scopa on posterior legs. .80
- Pterostigma at most one-third as long as distance from its apex to apex of marginal cell; scopa, when present, on abdominal sterna.81
- 80(79). Posterior basitarsi of both sexes more slender than, and nearly as long as, posterior tibiae. *Hesperapis*
- Posterior basitarsi of male less than half as long as tibiae, of female conspicuously shorter than, and as broad as, tibiae. *Macropis*
- 81(79). Abdomen with yellow or white (rarely red) integumental markings82
- Abdomen without integumental markings88
- 82(81). Arolia absent83
- Arolia present84
- 83(82). Seventh abdominal tergum of female with large median emargination; second recurrent vein usually distad of second transverse cubital by several vein widths *Callanthidium*
- Seventh abdominal tergum of female not broadly emarginate medially; second recurrent vein usually scarcely distad of second transverse cubital (fig. 167) *Anthidium*
- 84(82). Scutellum produced to sharp truncation posteriorly *Anthidiellum*
- Scutellum rounded, not produced.85
- 85(84). Posterior lobes of pronotum each with a large lamella extending forward to a line in front of anterior margin of mesoscutum *Dianthidium*
- Posterior lobes of pronotum without such a lamella, although frequently strongly carinate or with a small lamella.86
- 86(85). Scopa absent; eighth abdominal tergum of male small, usually rounded posteriorly, but little modified *Stelis*
- Scopa of female present; eighth abdominal tergum of male larger with processes or emarginations.87
- 87(86). Posterior lobes of pronotum with carina elevated as a small to moderate-sized lamella; apical margin of mandible of female elongate, oblique. *Paranthidium*
- Posterior lobes of pronotum with carinae unmodified or absent; apical margin of mandible of female not strongly oblique *Heteranthidium*
- 88(81). Arolia absent *Megachile*
- Arolia present89
- 89(88). Parapsidal lines punctiform or at most about three times as long as broad; usually metallic forms.90
- Parapsidal lines linear; rather rarely metallic forms91
- 90(89). Posterior coxae each with longitudinal carina on inner ventral angle; parapsidal lines slightly elongate. *Diceratomia*
- Posterior coxae not carinate; parapsidal lines punctiform *Osmia*
- 91(89). Inner margin of pterostigma from base to vein r but little longer than width of pterostigma; claws cleft in both sexes92
- Inner margin of pterostigma from base to vein r considerably longer than width of pterostigma; claws simple in female, cleft in male94
- 92(91). Scopa absent; eighth abdominal tergum of male but little exserted, rounded posteriorly *Stelis*
- Scopa present in female; eighth abdominal tergum of male more or less modified, much produced, or at least with an emargination93
- 93(92). Posterior lobe of pronotum with strong transverse lamella . . . *Paranthidium*
- Posterior lobe of pronotum without carina or lamella *Trachusa*
- 94(91). Base of propodeum with narrow horizontal zone set off by a carina from posterior surface and traversed by carinae breaking it into a series of large pits. *Heriades*
- Base of propodeum, if horizontal, neither pitted nor set off from posterior face by a carina.95
- 95(94). First recurrent vein nearly interstitial with first transverse cubital (may be a short distance on either side of it). *Formicapis*
- First recurrent vein considerably distad of first transverse cubital96
- 96(95). Propodeum with rather distinct horizontal basal zone; metanotum on dorsal surface of thorax, highest at median convexity97
- Propodeum without or with much slanting

- horizontal basal zone; metanotum on posterior face of thorax, highest at anterior margin 100
- 97(96). Suture between mesepisternal and metepisternal pleural regions with a practically straight median section; clypeal truncation of female overhanging base of labrum; face of male with short, appressed, silvery pubescence
 *Robertsonella*
 Suture between mesepisternal and metepisternal pleural regions arcuate; anterior margin of clypeus of female scarcely overhanging base of labrum; face of male with usual long pubescence 98
- 98(97). Clypeus of female short with long median horn; male with but six exposed metasomal terga *Chelostomopsis*
 Clypeus of female without a horn; male with seven exposed terga 99
- 99(98). Posterior coxae each with longitudinal carina on inner ventral angle; labial palpi with third segment flattened and connate with second *Chelostoma*
 Posterior coxae not carinate; labial palpi with third segment cylindrical, similar to fourth *Prochelostoma*
- 100(96). Anterior face of mesepisternum shining, separated by weak carina from punctate lateral face; seventh abdominal tergum of male quadridentate
 *Ashmeadiella*
 Anterior face of mesepisternum not separated from lateral face by carina or abrupt change in sculpture; seventh abdominal tergum of male not quadridentate 101
- 101(100). Second abdominal (first metasomal) tergum with anterior face flat or convex with longitudinal sulcus . . 102
 Second abdominal tergum with anterior face shallowly concave and almost always separated from dorsal face by a carina, impressed line, or abrupt change in sculpture. . . *Anthocopa*
- 102(101). Proboscis short; galeae and first two segments of labial palpi covered with hooked or wavy-tipped bristles. *Proteriades*
 Proboscis of usual length without such bristles *Hopliis*
- 103(71). Apex of marginal cell pointed on wing margin or only narrowly rounded and scarcely bent from wing margin. 104
 Apex of marginal cell subtruncate or conspicuously bent from wing margin 107
- 104(103). Clypeus short, about as long as labrum; antennae usually inserted well below middle of face 105
 Clypeus of usual shape, ordinarily considerably longer than labrum; antennae inserted near middle of face 106
- 105(104). Distance from apex of pterostigma to apex of marginal cell almost always at least as great as distance from apex of cell to wing tip . . *Dufourea*
 Distance from apex of pterostigma to apex of marginal cell less than distance from apex of cell to wing tip *Micralictoides*
- 106(104). Basal vein (first abscissa of M) of forewing gently curved or straight (fig. 169) *Andrena*
 Basal vein strongly arcuate or subangulate (fig. 170) 29
- 107(103). Abdomen with yellow or white integumental bands or maculations.
 *Nomadopsis*
 Abdomen black or red, without pale integumental maculations . . . 108
- 108(107). Pterostigma much broader than distance from inner margin of prestigma to wing margin. 109
 Pterostigma about as broad as distance from inner margin of prestigma to wing margin 110
- 109(108). First recurrent vein approximately interstitial with first transverse cubital *Panurginus*
 First recurrent vein much distad of first transverse cubital . *Pseudopanurgus*
- 110(108). Distance from base of pterostigma to base of vein r but little longer than prestigma; abdominal terga with apical pubescent fasciae . *Calliopsis*
 Distance from base of pterostigma to base of vein r nearly twice length of prestigma; abdominal fasciae absent *Hypomacrotera*

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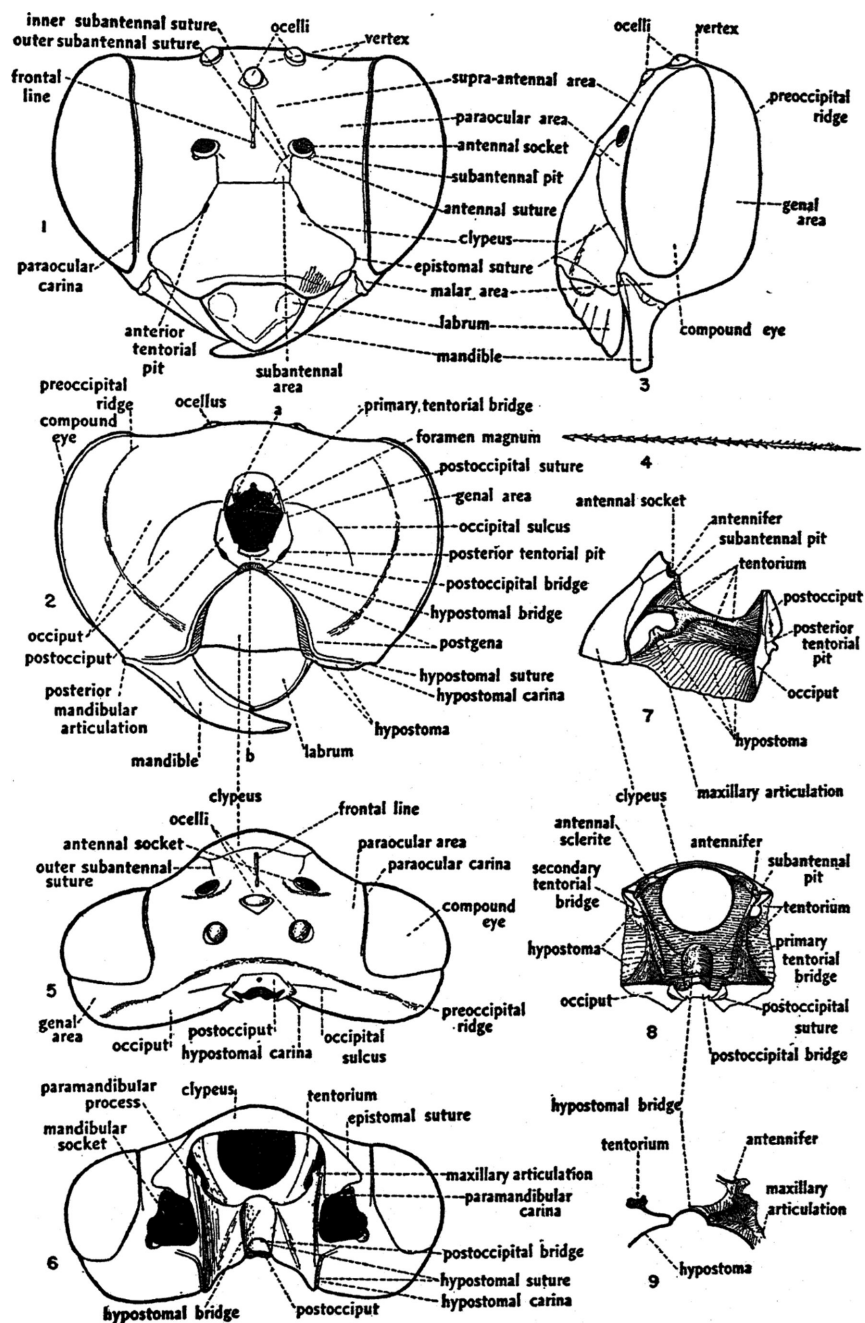
EXPLANATION OF TEXT FIGURES

Most of the figures were drawn with the aid of a camera lucida. With a few exceptions, comparable parts of different bees are drawn to the same scale, as shown by the following indications of magnifications:

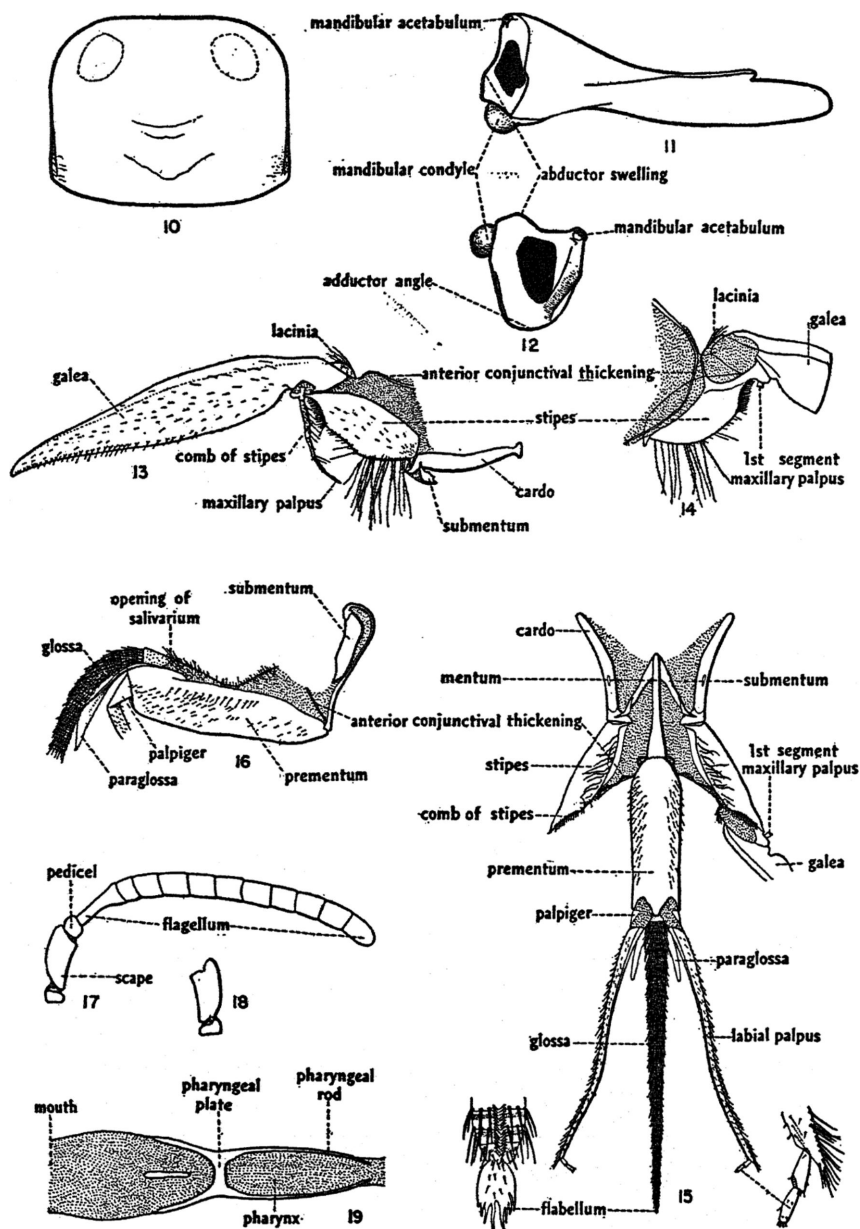
Figures 1-3, 5-9, 14, 16, 17, 20-23, 29-34, 51-80, 88-124, 128, 135, 137, 140-142, 144, 146, 149-153, 161, 162, and 177-229 are magnified about ten times, except for those of *Xylocopa*, which are magnified about eight times.

Figures 10-12, 24-28, 81-87, 127, 130, 138, 145, 154-157, 163, 237-242, and 245-246 are magnified about 24 times.

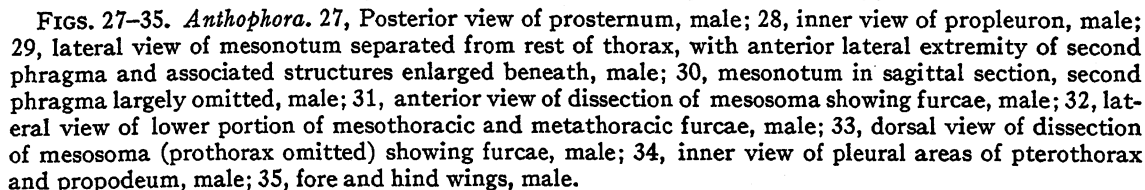
The species illustrated in figures 1-87 is *Anthophora edwardsii* Cresson. The species illustrated in figures 88-246 are *Colletes fulgidus* Swenk, *Anthidium atripes* Cresson, *Halictus farinosus* Smith, *Andrena mimetica* Cockerell, *Xylocopa orpifex* Smith, and *Bombus vosnesenskii* Radoszkowski.

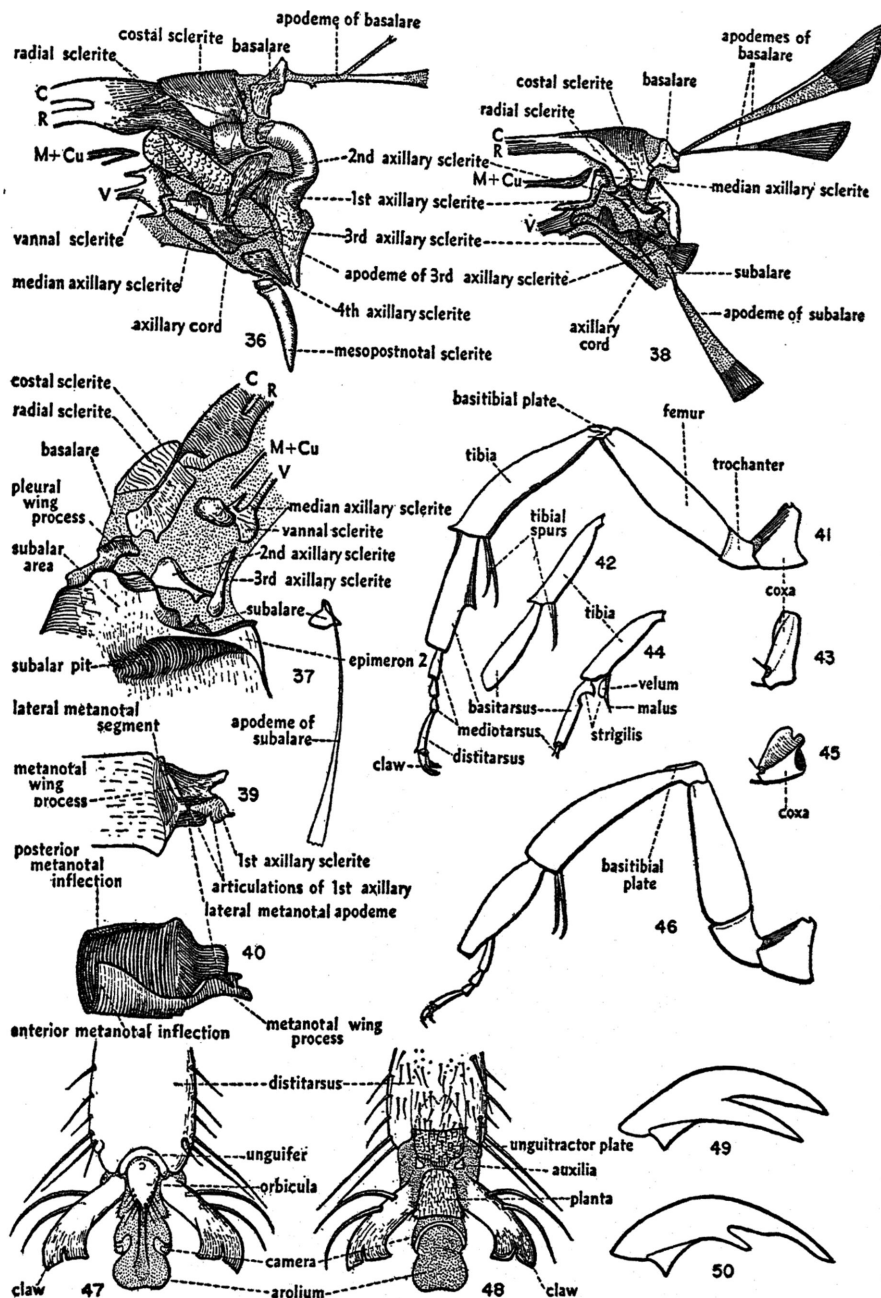


FIGS. 1-9. *Anthophora*. 1, Anterior view of head, female; 2, posterior view of head with one mandible removed, female; 3, lateral view of head, female; 4, hair from lateral part of vertex; 5, dorsal view of head, female; 6, ventral view of head with mouthparts removed, female; 7, lateral view of dissection of head showing tentorium, male; 8, dorsal view of dissection of head showing tentorium, male; 9, cross section of tentorium through hypostomal bridge showing, on the right, structures visible anteriorly, omitting anterior wall of head capsule.

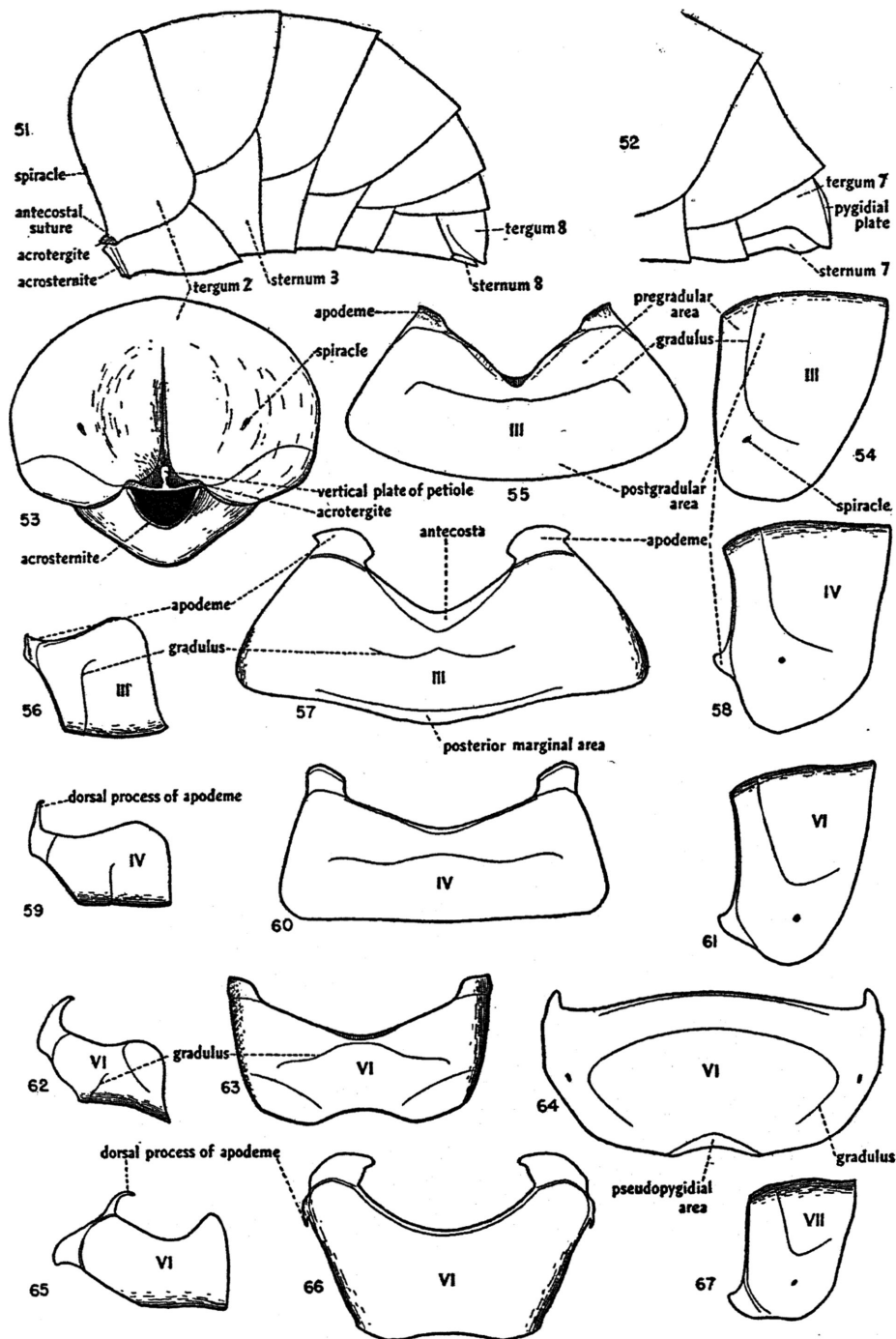


FIGS. 10-19. *Anthophora*. 10, Labrum, male; 11, inner view of mandible, female; 12, base of mandible, female; 13, outer surface of maxilla showing lateral extremity of submentum, male; 14, inner view of middle portion of maxilla, male; 15, posterior view of labium and bases of maxillae, male; 16, lateral view of labium, apices of glossa and labial palpi omitted, male; 17, under surface of antenna, male; 18, upper surface of antennal scape, male; 19, pharynx, showing pharyngeal plate, male.

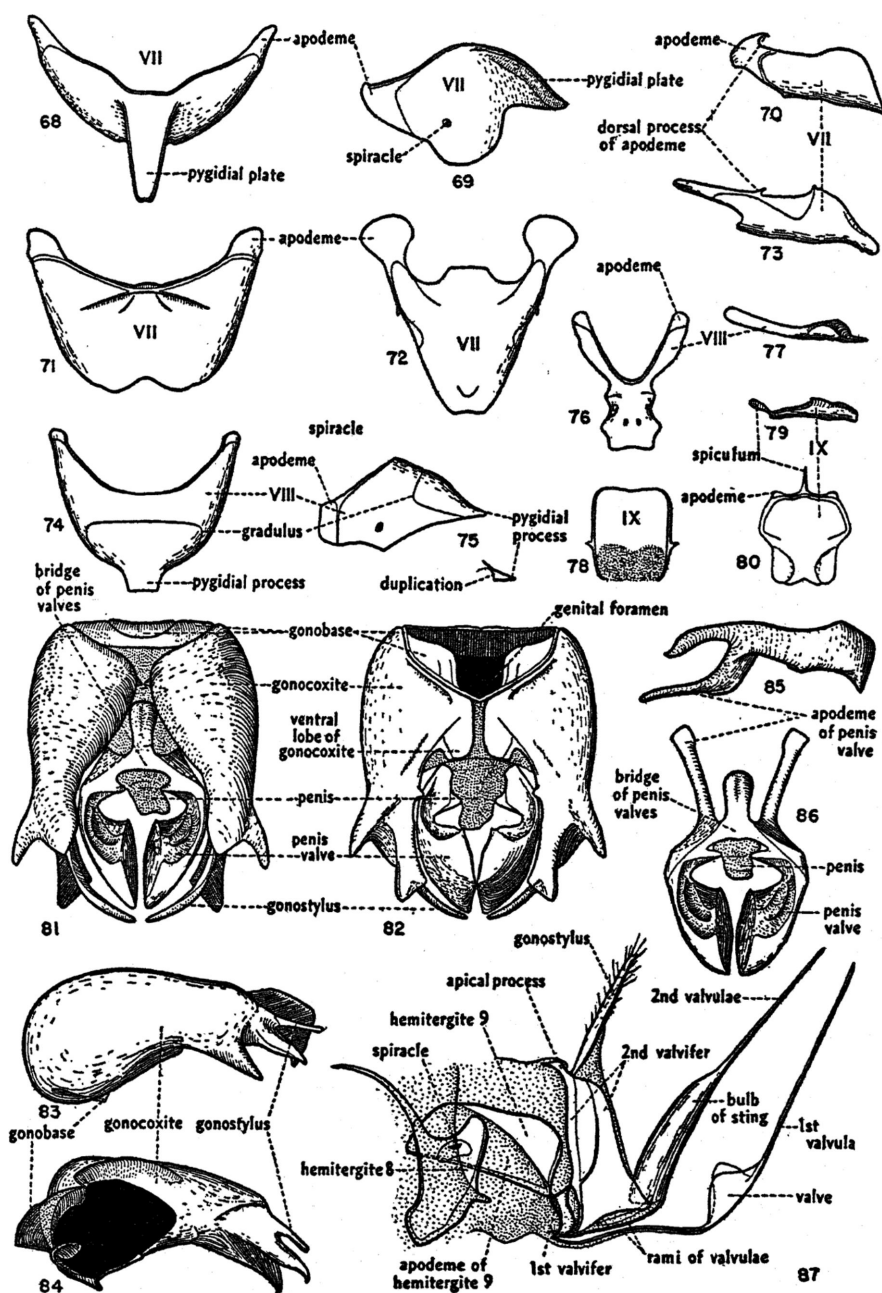




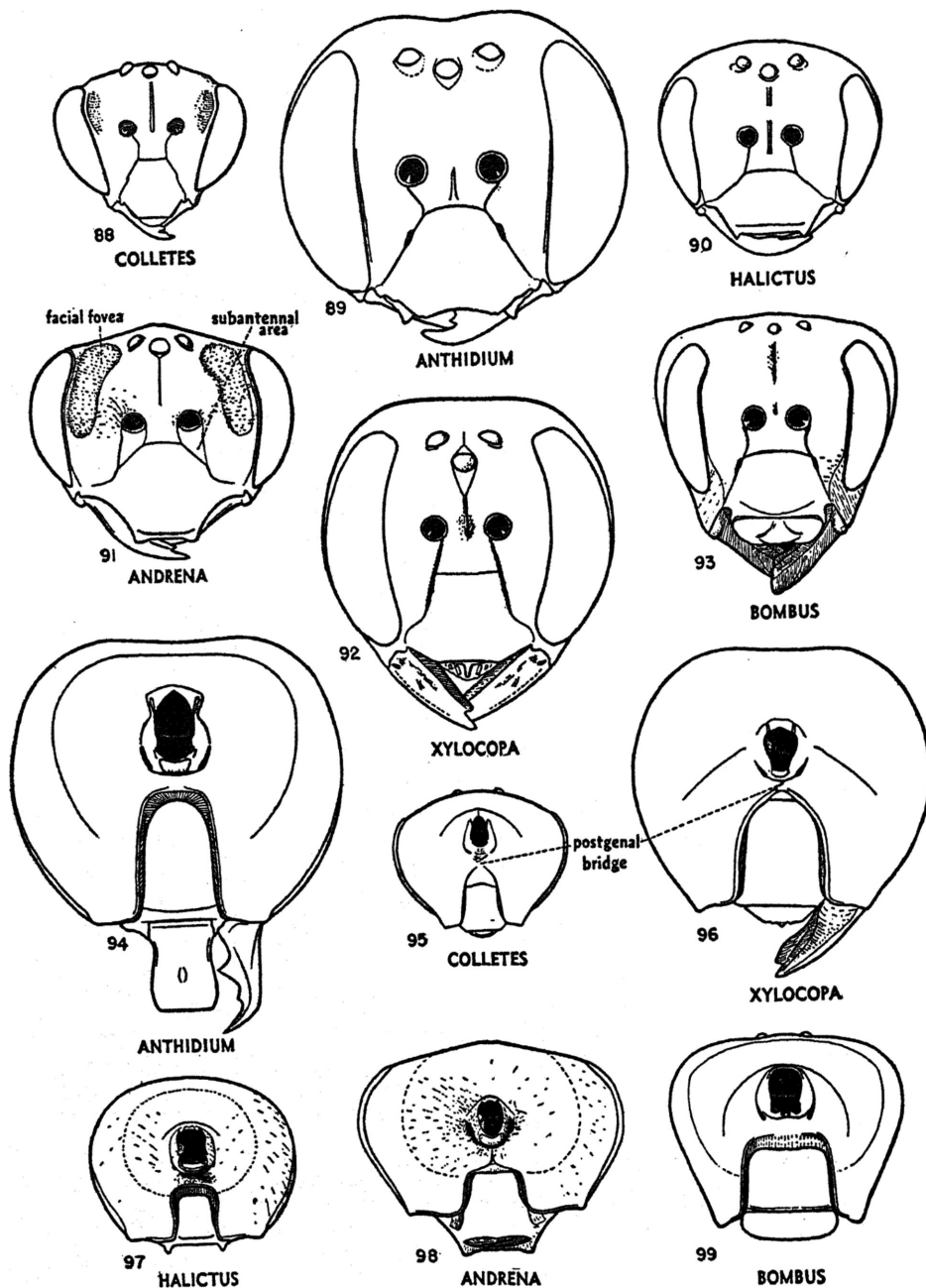
FIGS. 36-50. *Anthophora*. 36, Dorsal view of anterior wing base and mesopostnotal sclerite, male; 37, ventral view of anterior wing base and summit of mesopleuron, showing only those sclerites which project on the ventral surface of the membrane of the wing base, also inner view of subalare showing its apodeme, male; 38, dorsal view of posterior wing base, male; 39, 40, dorsal and ventral views of lateral extremity of metanotum, male; 41, inner view of posterior leg, male; 42, inner view of middle tibia and basitarsus, male; 43, inner view of middle coxa, male; 44, inner view of anterior tibia and basitarsus, male; 45, inner view of anterior coxa, male; 46, inner view of posterior leg, female; 47, dorsal view of apex of tarsus, male; 48, ventral view of apex of tarsus, male; 49, inner view of claw, male; 50, inner view of claw, female.



FIGS. 51-67. *Anthophora*. 51, Lateral view of metasoma, male; 52, lateral view of apex of metasoma, female; 53, anterior view of second abdominal segment, male; 54, lateral view of third abdominal tergum, male; 55, 56, ventral and lateral views of third abdominal sternum, male; 57, ventral view of third abdominal sternum, female; 58, lateral view of fourth abdominal tergum, male; 59, 60, lateral and ventral views of fourth abdominal sternum, male; 61, lateral view of sixth abdominal tergum, male; 62, 63, lateral and ventral views of sixth abdominal sternum, male; 64, dorsal view of sixth abdominal tergum, female; 65, 66, lateral and ventral views of sixth abdominal sternum, female; 67, lateral view of seventh abdominal tergum, male.

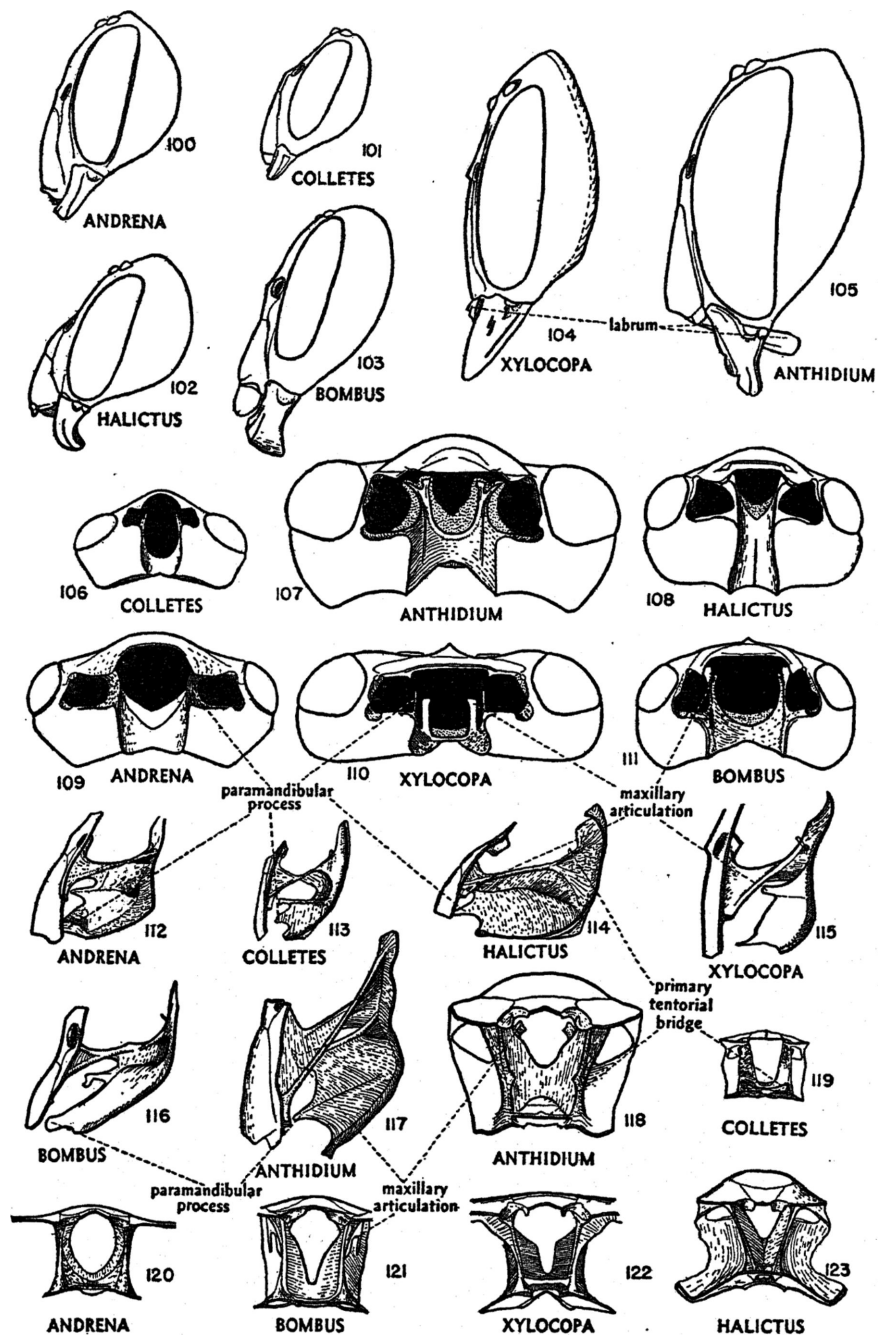


FIGS. 68-87. *Anthophora*. 68, 69, Dorsal and lateral views of seventh abdominal tergum, female; 70, 71, lateral and ventral views of seventh abdominal sternum, male; 72, 73, ventral and lateral views of seventh abdominal sternum, female; 74, dorsal view of eighth abdominal tergum, male; 75, lateral view of eighth abdominal tergum with sagittal section of pygidial process, male; 76, 77, ventral and lateral views of eighth abdominal sternum, male; 78, dorsal view of ninth abdominal tergum, male; 79, 80, lateral and ventral views of ninth abdominal sternum, male; 81, 82, 83, dorsal, ventral, and lateral views of genitalia, male; 84, inner view of gonopod, penis valve removed, male; 85, 86, lateral and dorsal views of penis valves, male; 87, lateral view of sting and associated structures, female.



FIGS. 88-99. Anterior view of head of: 88, *Colletes*, male; 89, *Anthidium*, male; 90, *Halictus*, female; 91, *Andrena*, female; 92, *Xylocopa*, female; 93, *Bombus*, worker.

Posterior view of head of: 94, *Anthidium*, male; 95, *Colletes*, male; 96, *Xylocopa*, female; 97, *Halictus*, female; 98, *Andrena*, female; 99, *Bombus*, worker.

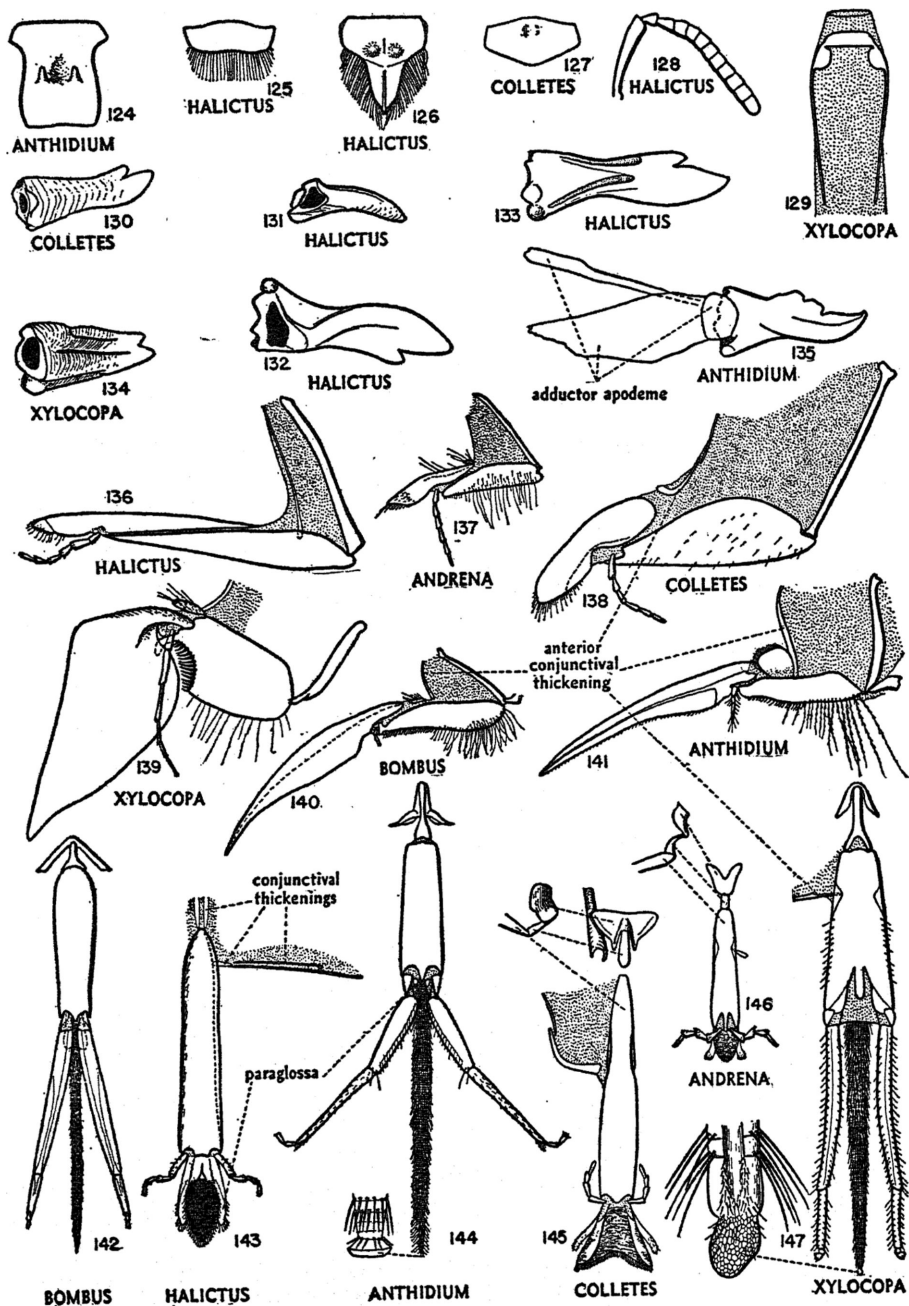


FIGS. 100-123. Lateral view of head of: 100, *Andrena*, female; 101, *Colletes*, male; 102, *Halictus*, female; 103, *Bombus*, worker; 104, *Xylocopa*, female; 105, *Anthidium*, male.

Ventral view of head with mouthparts removed of: 106, *Colletes*, male; 107, *Anthidium*, male; 108, *Halictus*, female; 109, *Andrena*, female; 110, *Xylocopa*, female; 111, *Bombus*, worker.

Lateral view of dissection of heads showing tentorium of: 112, *Andrena*, female; 113, *Colletes*, male; 114, *Halictus*, female; 115, *Xylocopa*, female; 116, *Bombus*, worker; 117, *Anthidium*, male.

Dorsal view of dissection of head showing tentorium of: 118, *Anthidium*, male; 119, *Colletes*, female; 120, *Andrena*, female; 121, *Bombus*, worker; 122, *Xylocopa*, female; 123, *Halictus*, female.



FIGS. 124-147. Labrum of: 124, *Anthidium*, male; 125, *Halictus*, male; 126, *Halictus*, female; 127, *Colletes*, female.

Antenna of: 128, *Halictus*, female.

Pharynx, showing pharyngeal plate of: 129, *Xylocopa*, female.

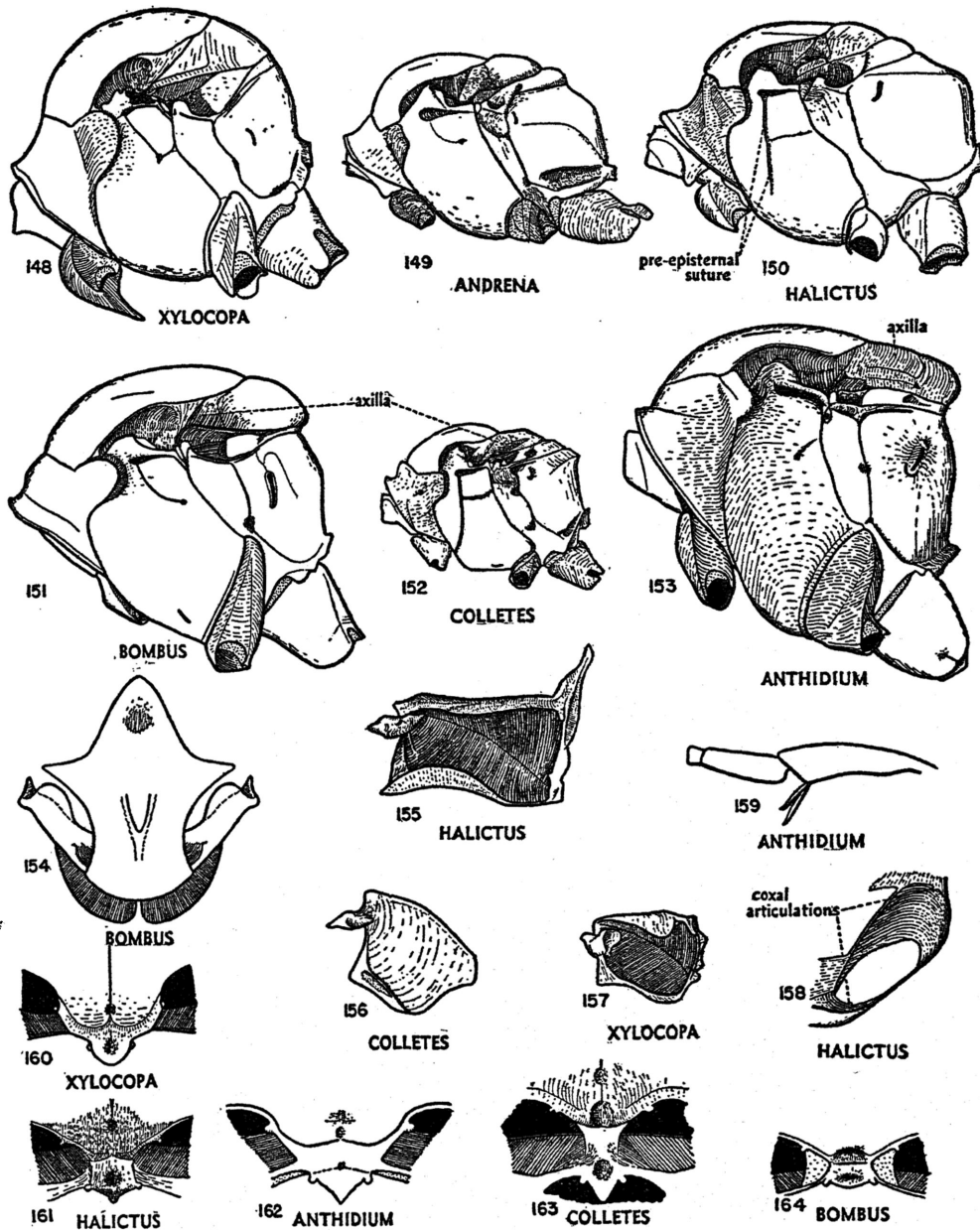
Inner view of mandible of: 130, *Colletes*, male; 131, *Halictus*, male; 132, *Halictus*, female.

Outer view of mandible of: 133, *Halictus*, female.

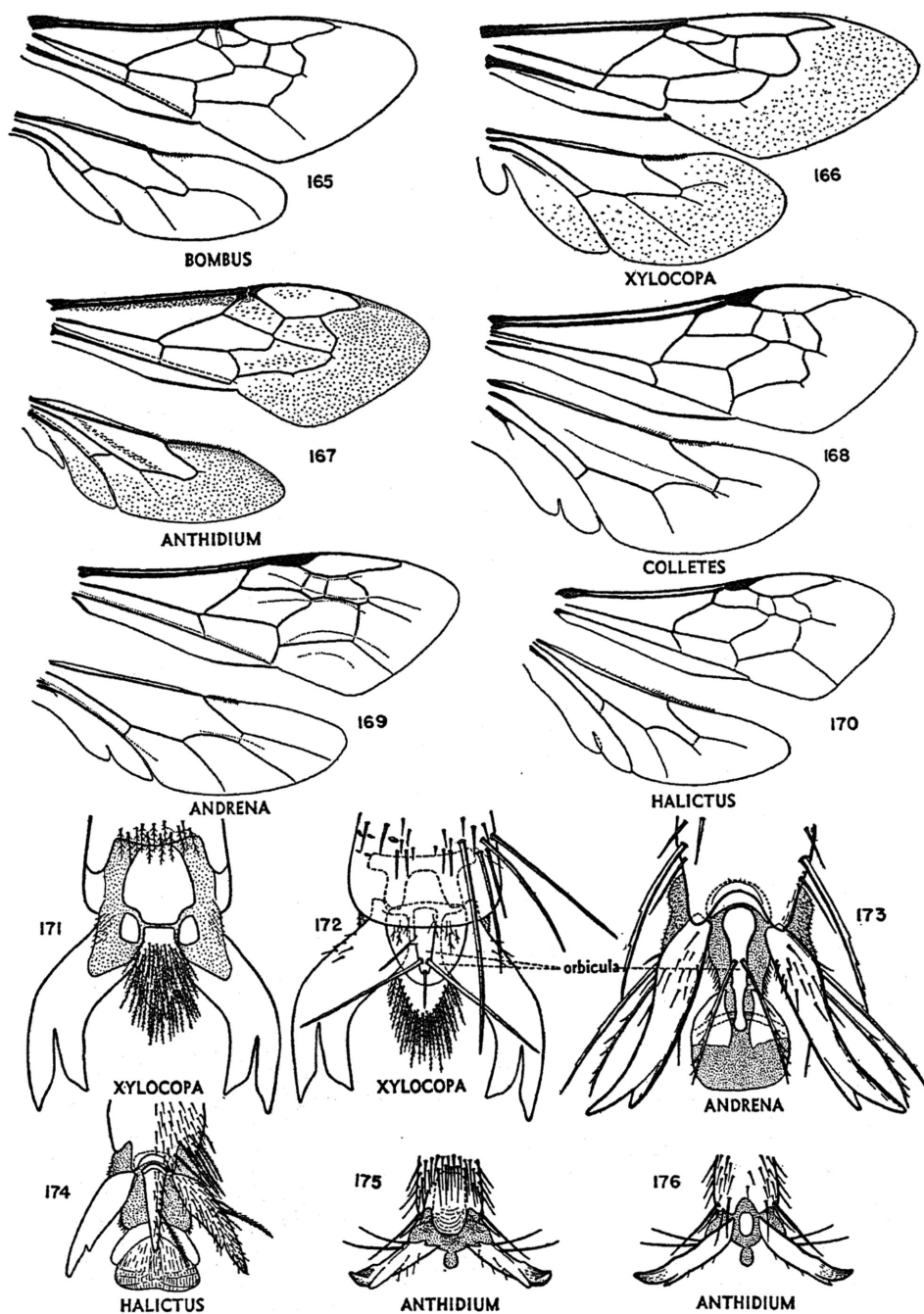
Inner view of mandible of: 134, *Xylocopa*, female; 135, *Anthidium*, male.

Outer view of maxilla of: 136, *Halictus*, male; 137, *Andrena*, female; 138, *Colletes*, male; 139, *Xylocopa*, female; 140, *Bombus*, worker; 141, *Anthidium*, male.

Posterior view of labium (with lateral views of bases and enlargements of flagella in some) of: 142, *Bombus*, worker; 143, *Halictus*, male; 144, *Anthidium*, male; 145, *Colletes*, male; 146, *Andrena*, female; 147, *Xylocopa*, female.

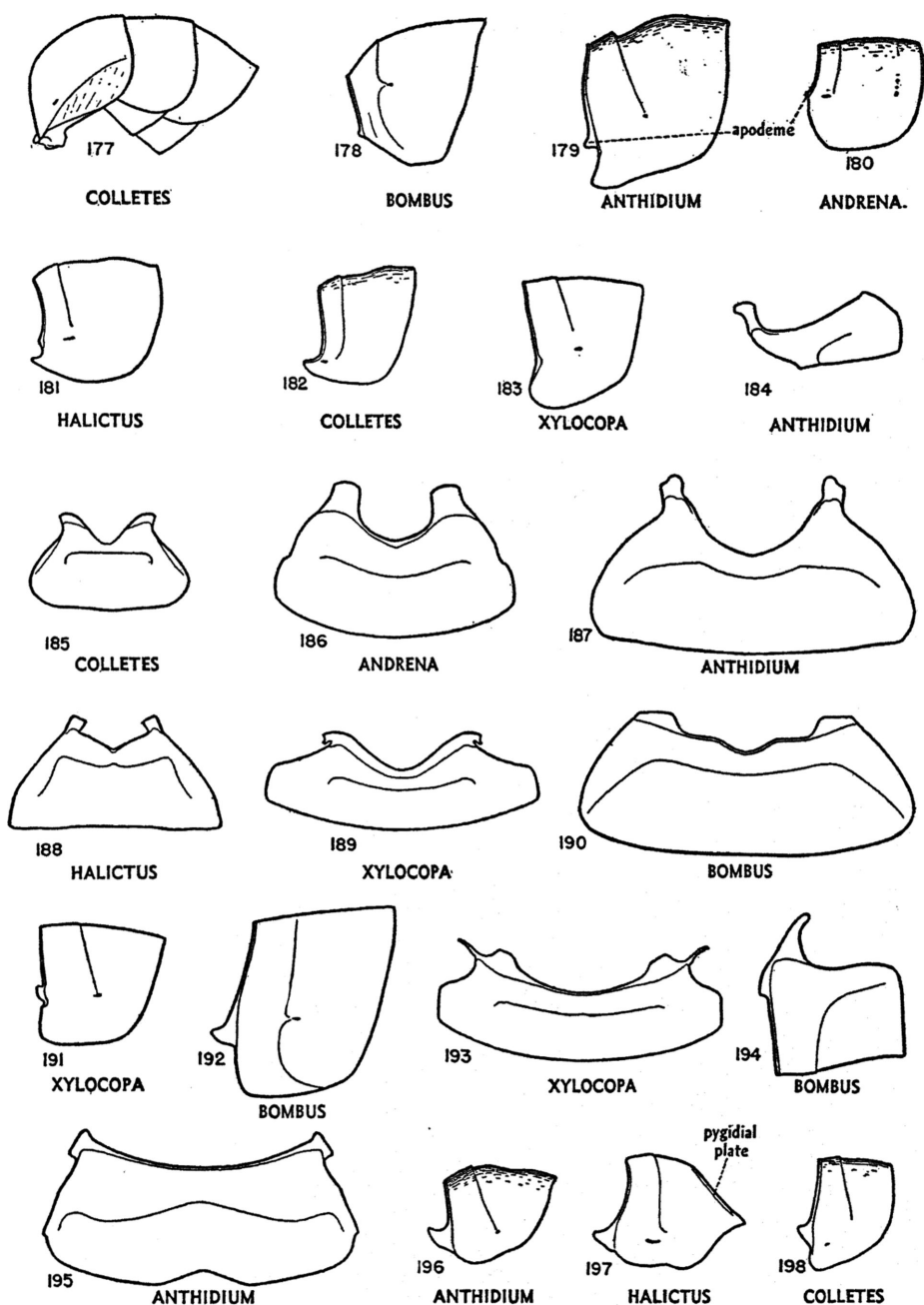


FIGS. 148-164. Lateral view of mesosoma of: 148, *Xylocopa*, female; 149, *Andrena*, female; 150, *Halictus*, female; 151, *Bombus*, worker; 152, *Colletes*, male; 153, *Anthidium*, male.
 Ventral view of prosternum of: 154, *Bombus*, worker.
 Inner view of propleuron of: 155, *Halictus*, female; 156, *Colletes*, female; 157, *Xylocopa*, female.
 Middle coxal cavity seen from within of: 158, *Halictus*, female.
 Posterior tibia and first two tarsal segments of: 159, *Anthidium*, female.
 Ventral view of posterior portion of thorax of: 160, *Xylocopa*, female; 161, *Halictus*, female; 162, *Anthidium*, male; 163, *Colletes*, female; 164, *Bombus*, worker.

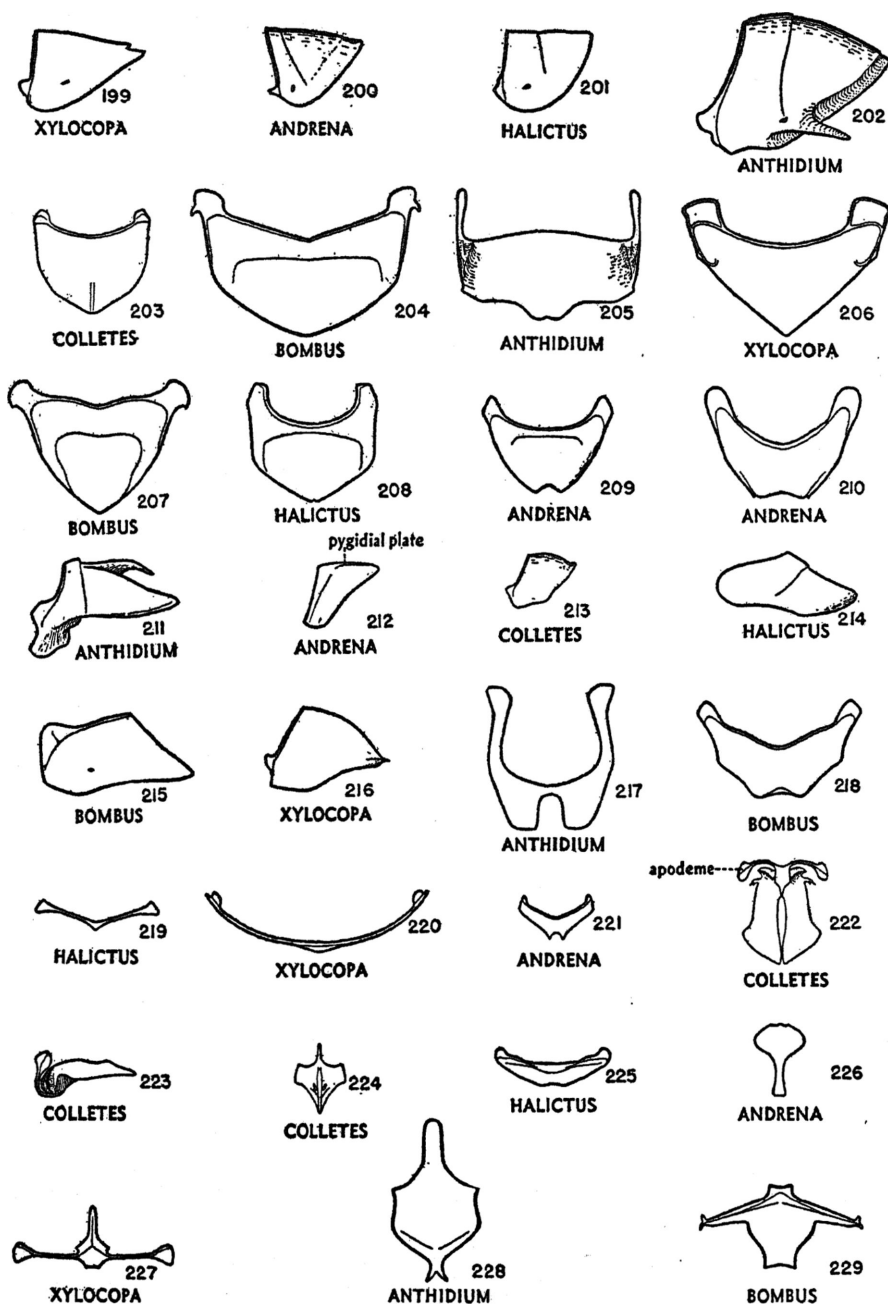


FIGS. 165-176. Wings of: 165, *Bombus*, worker; 166, *Xylocopa*, female; 167, *Anthidium*, male; 168, *Colletes*, female; 169, *Andrena*, female; 170, *Halictus*, female.

Apices of tarsi of: 171, 172, ventral and dorsal, *Xylocopa*, male; 173, dorsal, *Andrena*, female; 174, dorsal, *Halictus*, female; 175, 176, dorsal and ventral, *Anthidium*, male.



FIGS. 177-198. Lateral view of second to fourth abdominal segments of: 177, *Colletes*, male. Lateral view of third abdominal tergum of: 178, *Bombus*, worker; 179, *Anthidium*, male; 180, *Andrena*, female; 181, *Halictus*, female; 182, *Colletes*, male; 183, *Xylocopa*, female. Lateral view of third abdominal sternum of: 184, *Anthidium*, male. Ventral view of third abdominal sternum of: 185, *Colletes*, male; 186, *Andrena*, female; 187, *Anthidium*, male; 188, *Halictus*, female; 189, *Xylocopa*, female; 190, *Bombus*, worker. Lateral view of fourth abdominal tergum of: 191, *Xylocopa*, female; 192, *Bombus*, worker. Ventral view of fourth abdominal sternum of: 193, *Xylocopa*, female. Lateral view of fifth abdominal sternum of: 194, *Bombus*, worker. Ventral view of fifth abdominal sternum of: 195, *Anthidium*, male. Lateral view of sixth abdominal tergum of: 196, *Anthidium*, female; 197, *Halictus*, female; 198, *Colletes*, male.



FIGS. 199-229. Lateral view of sixth abdominal tergum of: 199, *Xylocopa*, female; 200, *Andrena*, female.

Lateral view of seventh abdominal tergum of: 201, *Halictus*, male; 202, *Anthidium*, male.

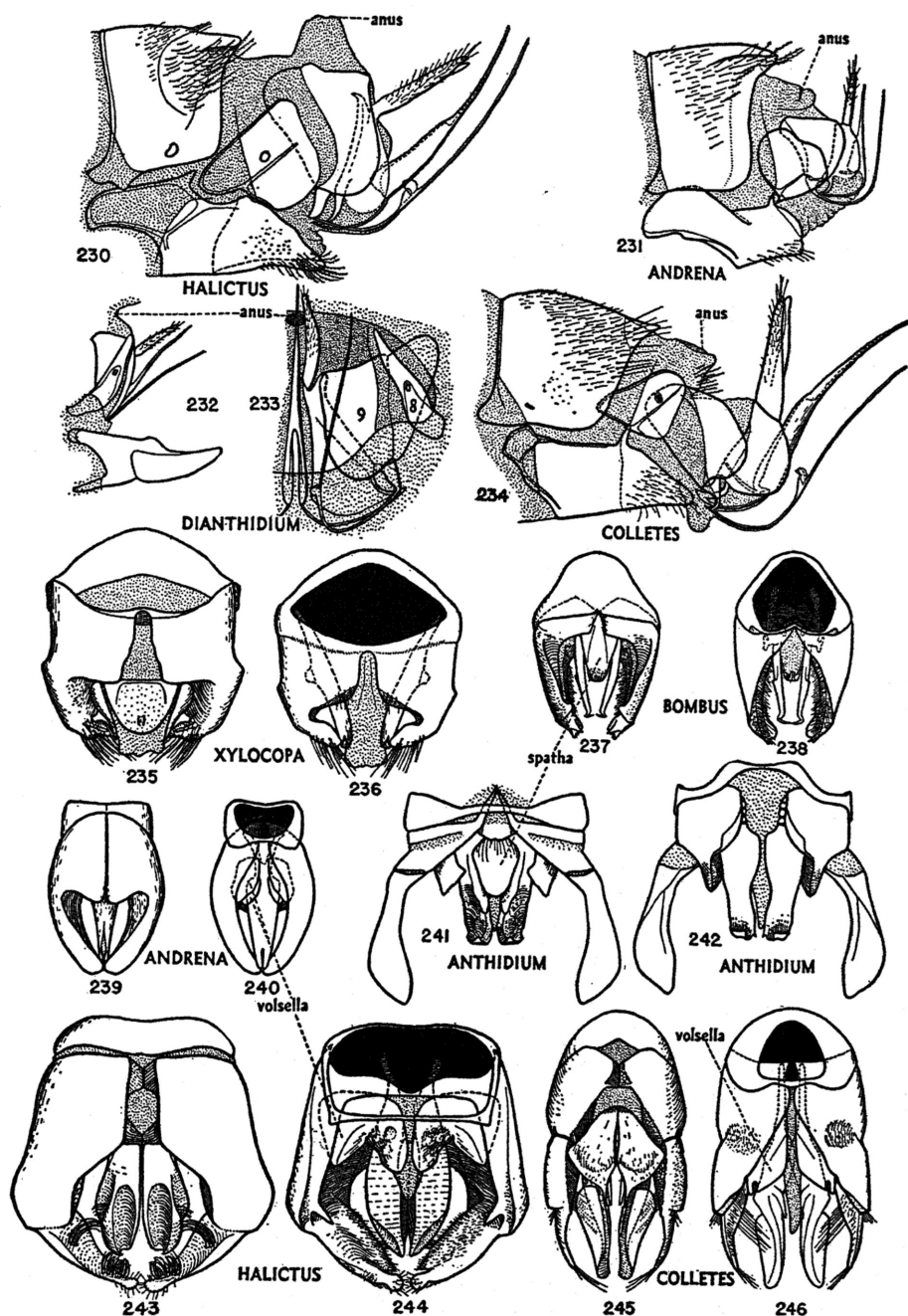
Ventral view of seventh abdominal sternum of: 203, *Colletes*, male; 204, *Bombus*, male; 205, *Anthidium*, male; 206, *Xylocopa*, female; 207, *Bombus*, worker; 208, *Halictus*, male; 209, *Andrena*, male; 210, *Andrena*, female.

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Ventral view of ninth abdominal sternum of male of: 224, *Colletes*; 225, *Halictus*; 226, *Andrena*; 227, *Xylocopa*; 228, *Anthidium*; 229, *Bombus*.



FIGS. 230-246. Lateral view of sting and associated structures of female of: 230, *Halictus*; 231, *Andrena*; 232, *Dianthidium sayi* Cockerell.

Posterior view of sting and associated structures of female of: 233, *Dianthidium sayi* Cockerell.

Lateral view of sting and associated structures of female of: 234, *Colletes* sp?

Genitalia of male (first view for each genus is dorsal, second ventral): 235, 236, *Xylocopa*; 237, 238, *Bombus*; 239, 240, *Andrena*; 241, 242, *Anthidium*; 243, 244, *Halictus*; 245, 246, *Colletes*.

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