

Foreword

This monograph is the culmination of approximately 38 years of collecting and research on the taxonomy of our native bees. Interest in this group was first incited during my employment in the North Carolina Department of Agriculture, where one of the projects was the compilation of the list of insect species known to occur in North Carolina. The list of bee species accumulated at that time (1920) was quite small, including only about 60 names, and many of these records were obtained from the literature rather than from collections made by the personnel of the Department. Initial collections resulted in many additions to this list, but with a considerable proportion unidentifiable, due either to the inadequate keys then available, or to the numerous apparently undescribed species that were found. This presented a challenge, and as a result, this group of insects has become my chief interest and an expanded knowledge of the group a primary objective.

Beginning with these earlier experiences, my associates have influenced my life and professional development. Certain of these stand out in memory as having been especially influential, and for whatever has been accomplished, some of the credit, at least, belongs to them. The head of the Division of Entomology at that time was Franklin Sherman. Aside from the regulatory, extension and economic research activities then carried on by the Division, his main interest was the compilation of the North Carolina insect list, and in consequence, he gave enthusiastic support and encouragement to this study of our bee fauna. C. S. Brimley was in the employ of the Division, devoting his time to this list. He was a naturalist of the old school, largely self-taught, with broad interests and extensive knowledge of such diverse groups as birds, reptiles, amphibians, moths, flies, wasps and many other groups of insects. He was a philosopher as well, and in him was found a close friend and a companion on many collecting excursions throughout North Carolina. In 1922, J. C. Crawford joined the Division, coming from the U. S.

National Museum. He was an experienced taxonomist and had done considerable work on the systematics of bees, as well as other groups. From this association was derived much of value, including a better understanding of certain of the basic principles of taxonomy. Many of the ideas and techniques acquired at this time influenced my work during the later years.

I joined the teaching staff of the Department of Zoology and Entomology at North Carolina State College in 1925. The late Z. P. Metcalf, Head of the Department, was an authority on the Order Homoptera and an enthusiastic taxonomist with a worldwide reputation. To him I am deeply indebted for assistance and words of advice, for encouragement and support, and for new ideas and techniques. The association lasted for more than thirty years, until his death, and throughout this period complete freedom was enjoyed in the performance of teaching duties and research activities. In this assignment the summer months were available for research and for advanced study. This included studies at Bussey Institute of Harvard University where the research was carried on under the direction of W. M. Wheeler and C. T. Brues. This association with these two outstanding teachers served to augment my interest and enthusiasm for taxonomic research.

During this period one of the genera of bees, *Megachile*, was selected for special attention. A revision of the North American species was prepared and published, with some attention given to the species of some of the other regions of the world. However, all collecting was general, so far as the bees are concerned, and much material was accumulated, with distribution and host records included. While this collecting was in progress, a bibliography was being compiled. A photographic method of copying the literature, using 35 mm. film, was developed before it came into the general use it has today.

During this time, also, keys for the identification of the species of all bee genera

were gradually developed and perfected. These have reached a state of completion which suggests the desirability of their publication, even though new records are still being made and new species discovered. Actual completion of such a comprehensive study as this one is a "will-o'-the-wisp," and there comes a time when it is best to publish what has been accomplished, in order to make the results available to other workers. It is hoped that publication of these keys and descriptions will facilitate more intensive studies of the taxonomy of bees, as well as ecological, biological and economic studies of all of the included groups.

One very important phase of this research has been the study of type collections in the United States, Canada and England. I am indebted to many individuals in various institutions for assistance in the location of type specimens, for providing facilities for their examination, and for freedom of access to the collections. Among those that should be named are Herbert F. Schwarz at the American Museum of Natural History in New York; I. H. H. Yarrow at the British Museum (Natural History) in London; G. C. Varley of the Hope Museum at Oxford, England; H. H. Ross, B. D. Burks and Milton W. Sanderson at the Illinois Natural History Survey in Urbana, Illinois; E. T. Cresson, Jr., James A. Rehn and H. J. Grant, Jr. at the Academy of Natural Science of Philadelphia; Noel M. Comeau at the Provincial Museum at Quebec; the late Nathan Banks, Joseph Bequaert and Wm. L. Brown, Jr. at the Museum of Comparative Zoology at Harvard University; and C. F. W. Muesebeck, the late Grace Sandhouse, and Karl V. Krombein at the U. S. National Museum in Washington, D. C. I am especially indebted to K. W. MacArthur at the Public Museum of Milwaukee, Wisconsin, and H. G. Rodeck at University of Colorado Museum, for lending several type specimens, and to Harvey B. Lovell of the University of Louisville for sending the entire type collection of his father, the late John H. Lovell. Through the cooperation of Arthur Humes, of the Department of Biology of Boston University, and at the suggestion of Wm. L. Brown, Jr., several of the Viereck types of *Andrena* formerly in the collection of the Boston Society of Natural History, that were temporarily lost, have been found and are now in the Museum of Comparative Zoology.

A large amount of undetermined material was received from several of these same institutions as well as from a number of others. Such collections have been received from Henry Dietrich and Howard E. Evans at Cornell University; T. H. Hubbell and U. N. Lanham at the University of Michigan; Roland Fischer at Michigan State College; J. N. Knull at Ohio State University; H. E. Milliron at the University of Minnesota; Herbert Knutson at the University of Rhode Island; J. T. Medler at the University of Wisconsin; B. Elwood Montgomery and Leland Chandler at Purdue University; Howard V. Weems, Jr., Frank W. Mead and Roger A. Morse of the Florida State Plant Board; and D. L. Wray of the North Carolina Department of Agriculture. Personal collections have been received from Henry K. Townes, G. E. Bohart, Karl V. Krombein, R. R. Snelling, H. F. Howden and wife Ann, C. D. Michener, and extensive amounts of unidentified materials from R. R. Dreisbach of Midland, Michigan, and the late P. W. Fattig of Emory University. The author is indebted to Mrs. Sylva G. Martin of South Miami, Florida for the gift of a considerable proportion of the collection of her father, the late S. Graenicher.

Several taxonomic specialists have given valuable assistance. P. H. Timberlake, of Riverside, California identified all of the material in the genus *Perdita*, which he is revising, and described all of the new species which were discovered in the eastern collections. I am grateful for his assistance and for the promptness of his attention to the material and to publication of the new names, making them available for this work. W. P. Stephen, now at Oregon State College, revised the genus *Colletes* while pursuing graduate studies at the University of Kansas. All of our eastern material was submitted to him for study. Similarly, Wallace E. LaBerge, now at Iowa State College, revised the genus *Melissodes* while at the University of Kansas, and our eastern material was sent to him also. Currently (April, 1958) A. F. Shinn is making a revisional study of *Calliopsis* at the University of Kansas and has our material of the few species of this genus that occur east of the Mississippi.

In addition to assisting in type studies at the U. S. National Museum and furnishing collected materials, Karl V. Krombein

has read portions of this manuscript and has tested the more comprehensive keys. As a result he has been able to make helpful and constructive criticisms. Similar constructive criticism has also been received from David A. Young, Frank E. Guthrie, Maurice H. Farrier, Walter M. Kulash, and Clyde F. Smith, associates in the Department of Entomology at North Carolina State College.

I am indebted to Mrs. Violet Quay and Miss Mary Oliver Ellington for a portion of the illustrations.

Also I wish to express my appreciation to the Administrative Officers of North Carolina State College for their sympathetic attitude toward this research and for the provision of funds, without which the work would not have been possible. Throughout the many years of my association with Z. P. Metcalf, there existed in the Department of

Zoology and Entomology, a "climate" conducive to research activities, and this has continued to the present time under the chairmanship of Clyde F. Smith. This same sympathetic attitude is evident in the succession of higher administrative officials, and the moral and financial support of D. B. Anderson, Chairman of the Division of Biology, Roy L. Lovvorn, Director of the Experiment Station, D. W. Colvard, Dean of the School of Agriculture, and C. H. Bostian, Chancellor of the College is here acknowledged with appreciation.

Finally I wish to acknowledge my debt to the *National Science Foundation* for funds to support this work and to provide for its publication, and I am appreciative of the helpful suggestions, first of Rogers McVaugh and later of A. C. Smith and David D. Keck, in the performance of their functions as successive Program Directors for Systematic Biology.

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Introduction

Materials and Methods

The superfamily Apoidea of the order Hymenoptera comprises the group of insects commonly called bees. The group is closely allied to the sphecoid wasps, with many characters common to both. In some schemes of classification that have been proposed (Comstock, 1940), they are combined into one superfamily, the Sphecoidea. In most recent texts, however, such as Brues, Melander & Carpenter (1954); Borror and DeLong (1954); and in the recently published catalog by Muesebeck, Krombein, Townes, *et al* (1951); the Apoidea is recognized as a superfamily group, separate from the Sphecoidea. As a matter of convenience, the separation of the two seems desirable, but the fact that the sphecoid wasps are much more closely related to the bees than they are to the vespoid wasps or any of the other Hymenoptera should not be overlooked.

The bee fauna of the Eastern United States has hitherto not been fully described. Many species new to science will be described in this monograph, and doubtless others will still remain to be discovered by collectors in the future. Furthermore, many species are known in only one sex, and only more intensive collecting, field observations, or studies of the biology will make it possible to discover the unknown sex or to correlate the two when they have been described under separate names. There is a current interest in biological and ecological studies of bees, but with respect to the total number of known species it is an almost virgin field, with a relatively small proportion in which any studies at all have been published. A review of this field of research has been published by Linsley (1958). There is a considerable fund of host plant data, largely from the works of Charles Robertson, J. C. Crawford, John H. Lovell and S. Graenicher, but there is much yet to be learned. The importance and significance of flower records, in the collection of bees, can

hardly be overemphasized. Most of the present generations of specialists in the group are keeping such records, but most of the earlier collected specimens lack any reference to host and specimens of bees collected by specialists in other groups often lack such data.

Bees are essential to our economy, being the chief pollinating agents of the flowering plants. They have a relation not only to agriculture, but to the conservation of wildlife and game management, and constitute an important element in the various ecologic factors that combine to form our environment. Thus the production of fruit crops such as apples, pears, melons, cucumbers, grapes, dewberries, huckleberries and strawberries, as well as cotton and various seed crops such as alfalfa, several clovers, vetch, onion, asparagus, buckwheat and celery, are dependent upon a sufficient population of bees, either the domesticated honey bee or some of our native, wild, solitary or social species.

Much reliance often is placed upon the honey bee in agricultural production, to compensate for a lessened effectiveness or unreliability of the native bee species. The growth of agricultural crops creates an artificial environment which often is unfavorable to the development of the large populations of native bees that are needed for adequate crop plant pollination. Nesting areas of solitary bees are plowed up, brush and weeds are cleared from roadsides and ditch banks, woods are cut or burned over and the underbrush eliminated. The plant population which extensive acreages of a crop represents is abnormally large, being a pure stand of a species which probably did not develop as such in its original native habitat. Thus its insect enemies tend to multiply, being relieved of one of the most important limiting factors, that of food supply. With bees, however, it seems possible that the availability of nesting sites is more of a limiting factor than food sup-

ply, which may be a partial explanation for the dearth of native bees in many crop areas. Fortunately in many cases the introduction of honey bees offers a rather simple solution to this problem, and there has not been too much concern about the lessened numbers of native bee species which seems to be in evidence. Some studies, however, indicate that native bees are more effective pollinating agents than the honey bee with respect to certain crops, such as alfalfa. Studies have been in progress for some time concerning possible means of amplifying populations of certain leafcutter bees and alkali bees in the alfalfa seed-producing areas.

The native bee fauna probably is much more important than the honey bee in the conservation of wild life and game management, even though many wild colonies of honey bees occur in most wooded areas. Game birds, such as quail and turkey, the song birds, and many of the mammals depend to a considerable extent upon the fruits of various native plants, and such plants have a much closer ecological relationship to the native bee fauna than have most crop plants.

Bees constitute a group of considerable size, with about 700 species listed from the eastern United States by Muesebeck, Krombein, Townes, *et al* (1951). There is much variety of form, size, color and habit within the group, with social types, represented by the honey bee and the bumble bees, and solitary types which include the large majority of species. Among these solitary species are ground burrowing and woodboring forms, as well as a considerable number which use any burrows, borings, or other types of cavities that may be available. There are also many cuckoo or parasitic species which invade the nests of pollen-collecting types to lay their eggs, making no other provision for their young.

The fact that our knowledge of bees as a group is inadequate is not the only difficulty to be encountered in attempts at identification of species or determination of any possible economic effect or ecologic significance. Comprehensive or adequate keys to the species of many of the included genera are not in existence, and the descriptions of a considerable proportion of the known

species are widely scattered in the literature. Moreover, descriptions when available are often so brief or incomplete that they are of little value in making reliable identifications. This common inadequacy of descriptions should not be taken as implying any inadequacy on the part of the workers, but is more to be considered a reflection of the degree of development of this field of science at the time these workers were active. It is quite possible, if not probable, that the work of this present generation will be found to be quite deficient in certain respects by workers in the future.

Objectives

This is a faunal study of the bees of the United States east of the Mississippi River. It is comprehensive with respect to the coverage of the group, including all the families, genera and species of bees, but is limited geographically, so that no generic or other group is covered completely unless it has these same geographic limitations.

The primary objective is to facilitate identification, and to that end simplicity of keys is sought. Thus all keys are artificial and are not intended as an expression of phylogeny. The use of couplets of contrasting characters is strictly adhered to, and the most conspicuous characters available are employed, sometimes to the exclusion of more obscure features which may be of greater phylogenetic significance.

The rather detailed descriptions and the figures should serve as a check respecting the correctness of identifications made by the use of the keys.

Geographic Area

The states of Wisconsin, Illinois, Kentucky, Tennessee and Mississippi, and all others east of this tier are included in this work. This arbitrary division is approximately the 92nd meridian and all of these states lie to the east of the Mississippi River. In large part, it is the Austral Region, but the Canadian in the Boreal Zone is included, and at the southern end of Florida the subtropical region is reached.

Collecting Techniques

In collecting bees, nets and killing bottles, of course, are essential items of equipment. The writer has found that a relatively short-handled net with a ring not more than 12 inches in diameter is preferable to a longer-handled or larger net. A smaller net with the shorter handle can be swung more rapidly than a larger one, an essential feature in catching many of the bees that have rapid flight. Because collecting on trees or high bushes necessitates a reasonably long handle, it is an advantage to have a jointed or telescoping handle, or to have a longer substitute handle or net.

The collector should have a considerable number of killing bottles so that specimens collected from various plant species that may be in bloom at the same time may be kept separate. It is well to have a vasculum or plant press so that plant specimens which are needed for identification may be collected. In addition, pill boxes for the temporary reception of collected materials and pinning boxes in which they may be pinned while still in the field are also an advantage.

Collecting often requires considerable patient watching of plants in bloom in order to observe some of the rapidly flying insects that visit them. This is particularly true of many of the males which may not be visiting the bloom for feeding purposes but rather are looking for the females. In such case they rarely alight on the bloom, and they can only be collected by sudden and swift sweeps of the net. Sweeping of the flower heads of relatively dense patches of flowering plants will sometimes yield good results, but often such movements will result in driving off some of the bees in advance of the collector.

It is essential that the killing bottles be kept as clean as possible. A small amount of absorbent material in the bottle will prevent the accumulation of enough moisture to mat the pubescent covering of the specimens. This is especially important in collecting bees because these insects often regurgitate nectar while dying in the cyanide gas. The writer uses shell vials of about an inch in diameter. Number 4 neoprene or rubber stoppers are used. A 14 mm. hole is bored through the center of the stopper, and a 1-gram lip vial is fitted into the hole with

the open end downward. The vial is partially filled with calcium cyanide or sodium cyanide, plugged with a wad of cotton, and the charged stopper is put into the shell vial. The cyanide may be slow to act at first, but after a few specimens have been placed in the killing bottle it will become effective. Sodium cyanide will remain active for a longer period than the calcium cyanide, but otherwise the two are equally effective. Rubber stoppers are much to be preferred over those of cork for they do not crack, and their pliability is an added advantage. When the cyanide becomes inactive the vials can be emptied easily and a fresh charge installed. Granular cyanide is used, with no plaster of Paris or any other material other than the cotton plug.

Preparation of Specimens

In pinning specimens it is quite important that the central area of the scutum be avoided so far as possible. If the pin is placed to one side of the center, the sculpture of this area is not destroyed. Very small specimens can be cemented to points or directly to the side of the pin. When cementing to the pin, the specimen is placed on its left side with the head downward and the legs toward the left. A small amount of cement is placed at the proper point on the pin which is then pressed firmly to the side of the specimen, holding the head of the pin in the right hand. Thus the specimen will be cemented on the left side of the pin with the head directed forward. Before specimens have completely dried and hardened it is desirable to pull the proboscis out into an extended position and to spread the mandibles apart so that the dentition and the features of the labrum beneath may be observed. It may be necessary to straighten out the legs, so that they do not cover the lateral or ventral surfaces of the thorax and thus obscure the surface features of these parts. While male specimens are still fresh and pliable, the genital armature should be pulled out into an exposed position. The hidden apical sternal plates of the abdomen of the males also are of considerable importance.

Collection data on the record labels should include the locality, date of collection, name of collector, and whenever possible, the generic identification of the plant upon which it was collected. The specific identity of the plant host seems to be less important,

but sometimes is of significance. However, identification of species in some genera of plants, such as *Rubus*, *Aster*, *Solidago* and others, is difficult even for many botanists, and in such groups especially, specific identity is of slight importance.

If any specimens are collected at some unusual time of day, as early in the morning or at dusk, or if they are found in light traps or at baits, such information should be included on the record label.

Source of Materials

Much of the material upon which this study is based was collected by the writer, largely in North Carolina. Of all the eastern states, probably it has the most diverse climatic and ecologic conditions, such as to duplicate to a considerable degree conditions from Maine to Florida along the entire Atlantic Coast. At the highest elevations extensions of the Canadian Zone are met, while along the coast the Austroriparian Zone extends to North Carolina and Virginia. Only the southern tip of Florida with its possible West Indian affinities, seems unrelated to North Carolina faunistically.

Collecting has been done also in Maine, Massachusetts, Illinois, West Virginia, South Carolina, Georgia and Florida. Many records have been obtained through the study of collections that have been sent to the author for identification. These have included much material from New England, Eastern Canada, New York, Michigan, Wisconsin, Minnesota, Illinois, Indiana, Ohio, Maryland, Virginia, West Virginia, Tennessee, Georgia and Florida, with lesser amounts from the remaining states east of the Mississippi.

Type collections that have been studied include the Frederick Smith collections in the British Museum and in the Hope Museum at Oxford University; the Provancher collection in the Provincial Museum of Quebec; the Cresson collection in the Philadelphia Academy of Science, the Robertson collection in the Illinois Natural History Survey; and types of Cockerell, Viereck, Crawford and others in the United States National Museum; the American Museum of Natural History in New York; the Museum of Comparative Zoology at Harvard; the Connecticut Agricultural Experiment Station and the Public Museum of Milwau-

kee. The Lovell types temporarily are in the possession of the author. A few of the Linnaean, Fabrician and Vachal types have also been studied.

Taxonomic Methods

All existing keys and published descriptions were used, of course, in the initial stages of this study. Later these were supplemented by examination of the types, and the identity of most of the species so far recorded in the East has been verified by comparison of specimens with the types.

As the work progressed, more and more forms came to hand which were in need of name and description. These were temporarily assigned numbers in lieu of names, and keys were constructed to include these along with all the previously known species. These provisional keys were especially useful in the study of type collections, as the types could be traced through the key and then compared with the forms to which they appeared to run. If, in this comparison, the degree of similarity was such as to indicate their common identity, the specimens were made homotypes and served as a means of comparison in type studies of other collections.

The finished keys, as they are presented in the following pages, were produced from these provisional keys by a process of development and testing, followed by revision and retesting until a workable key was achieved. Most of them have been in a process of development for a period of several years.

In large genera, such as *Andrena*, the species are separated out in one comprehensive key, even though subgeneric groupings of these species have been proposed. The limits of these subgenera sometimes are poorly defined, and the characters separating them are often difficult to observe or interpret. Well defined subgeneric groups may eventually be recognized as valid genera, but such modifications of the classification are dependent upon revisional and extensive studies of these large genera throughout their range.

All included species, both old and new, are described as completely as seems necessary to establish identity, with the aid of the keys. The redescription of older species is desirable because of the frequent in-

adequacy of the original descriptions, and new species, of course, are described of necessity. The desirability of including descriptions of species which have been described in recent years and are in consequence relatively complete might be questioned, but it is believed that the advantage gained is worth the extra space. Having these descriptions included results in a self-sufficient work, relieving its users of the necessity of referring to other publications, which is a marked advantage in consideration of the extent of the literature that otherwise would be involved.

Illustrations of significant structural details are very useful, and figures showing these features are provided as a part of the description for most species. In males, the genital armature and telescoped seventh and eighth sternal plates are important in this regard. This necessitates dissecting these parts out of the specimen and mounting them in some manner as to facilitate their observation. Of the various methods which the writer has used, the technique described seems to give the best results.

Specimens are first relaxed by leaving them in a moist chamber for a period of 12-24 hours. Very old and dry specimens may take as much as 48 hours to relax sufficiently to manipulate with safety, but usually it is sufficient to leave them in the chamber over night. After relaxing, the terminal segments of the abdomen are removed and placed in a saturated solution of KOH. This is not heated, but the parts are left in the cold solution for 12-24 hours. Overnight is usually enough. This clears the structures sufficiently without softening or distorting them. After this clearing process, they are separated with dissecting needles under a microscope and cemented on a card point, on the pin with the specimen.

Detailed collection records are given only for the new species, while the general geographic distribution and seasonal occurrence are given for all previously described species. The flower-visiting habits also are given, as far as they are known.

The list of bibliographic references under each genus and species includes only those of some taxonomic, biologic or ecologic significance. The reference to the original description, is always included, as are the references to most synonyms. Articles which merely list the species are not included.

Ecology

Bees are closely related ecologically to the flowering plants, and some knowledge of the details of this relationship is essential for a reasonably complete survey of bee species for any given area. In general, the native flowering plants will have the more interesting or unusual insect visitors, as there is more likely to be a close ecological association between these native plants and the native wild bees that visit them. In contrast, introduced plants are more likely to be visited by the more generalized species of bees which visit a wide range of host plants. Likewise, those introduced bees that have survived are likely to be generalized forms that visit a wide range of food plants. Such species are much more likely to be equipped for survival in the new environment than specialized forms that have a limited range of host plants. Many of our native bees visit only one or a limited number of closely related plant species, such as a few closely related species forming a single genus. In consequence, they are limited in their distribution to the range of the host plants. Also, since they are dependent upon the flowers, they are limited seasonally by the blooming period of the plants. Thus, flight periods are apt to be brief and geographic distribution limited.

The availability of nesting sites, also, is a limiting factor in the distribution of bees, and as a consequence such physiographic features as character of the soil, degree and direction of slope, drainage, amount and distribution of rainfall, etc. have some bearing on the occurrence of bees. On favorable sites relatively dense populations may build up, especially in those groups that are gregarious. It is probably true also that many species range but a short distance from the nesting area. Thus there are marked variations in relative abundance from one locality to another, even though the host plants may be generally available.

Climate of course is important, limiting as it does the geographic distribution of both the host plants and the bee visitors. But within the geographic limits of this distribution, the day-to-day or hour-to-hour weather conditions can be very limiting, so far as any success in the collection of many species is concerned. Many bees cease activity in the absence of sunshine, or will

remain inactive as long as the weather is too cool or windy.

Time of day is important, for with most species activity is most marked through the middle four or five hours of the day. To this, however, there are exceptions as there are a very few species that are nocturnal, crepuscular or matinal, or time their flight to coincide with a brief period early in the day when the host flowers are open, as shown by *Pyrrhopappus carolinianus* (Walt.) DC. and its bee visitor, *Hemihalicus lustrans* Ckll.

Thus it can be seen that to meet with success in the collection of some of the more specialized bees it is necessary to find a combination of conditions that includes the host plant in bloom, adjacent to or in the near vicinity of some favorable nesting site, within the distribution limits of the species, during the daily active period of flight, and in warm, calm, sunny weather.

Generalized bees that visit a wide range of host plants tend to be in flight for much longer periods of time than the specialized forms and are usually much more widely and generally distributed. It is these forms which are in flight through most of the midsummer period, and it seems possible that some of them have more than a single generation during a season. The specialized more restricted species tend to fly either in the spring or in the fall and probably have only a single generation.

Morphology

With regard to general structure, the terminology adopted by Michener (1944) is followed, although without strict adherence. Some of the terms he has proposed, while certainly logical, are different from those used for comparable parts in other insect orders, and their use is avoided here for that reason. So far as possible figures are used in place of, instead of as supplements to, printed descriptions. Only where some additional explanation is desirable is any space devoted to discussion of the parts illustrated.

The three body regions are designated the *head*, *thorax* and *abdomen*, in accordance with the terminology in the orders other than the Hymenoptera. Michener (1944, p. 167) uses the terms *mesosoma* and *metasoma* for the thorax and abdomen, since in all the Clistogastra the morpho-

logical first abdominal segment is fused with the metathorax and is known as the *propodeum*. Thus the middle body region includes four segments, rather than the usual three of other insects, and the abdomen conversely includes only the segments 2-8. These terms, however, are limited in their application to the ants, wasps, bees and related insects. It seems better to employ the older and more generally used terms in a work which it is hoped will have general usage. In numbering the abdominal segments, also, the propodeum will be disregarded as representing the first, but instead the morphological segment 2, will be considered the basal one.

A lateral view of *Andrena* (fig. 1) and a front view of the head (fig. 2) show the general external characteristics. Most of the features illustrated are useful in furnishing specific or key characters in one or another of the groups of bees, and an explanation of certain of them is desirable.

The *foveae* (fig. 2) are shallow depressed areas on the front of the head and are present in the females of the Andrenidae and most of the Colletidae. They are poorly developed in the males of these two families and are lacking in all of the other groups.

The *subantennal sutures* have some significance in classification but are rather unsatisfactory as key characters as they are so frequently obscured by the dense pubescence of the face. Only in the Andrenidae are both the outer and inner pairs represented, the inner pair apparently being much reduced or absent in all other groups. Because of this they are rarely used in the keys or mentioned in the descriptions.

The *antennae*, as in the higher groups of wasps, are 12-segmented in the females and 13-segmented in the males. Usually sexual dimorphism is so marked in the bees that there is no problem in distinguishing the sexes, but where the similarity is considerable, as in some of the parasitic groups, this difference in the number of antennal segments is helpful. The apical ten or eleven segments form the flagellum, and the relative lengths of these segments, especially of the basal one, is of considerable value as a key character.

When, as in some groups, the eye is closely approximate to the base of the mandible, there is no distinct *malar space*. It

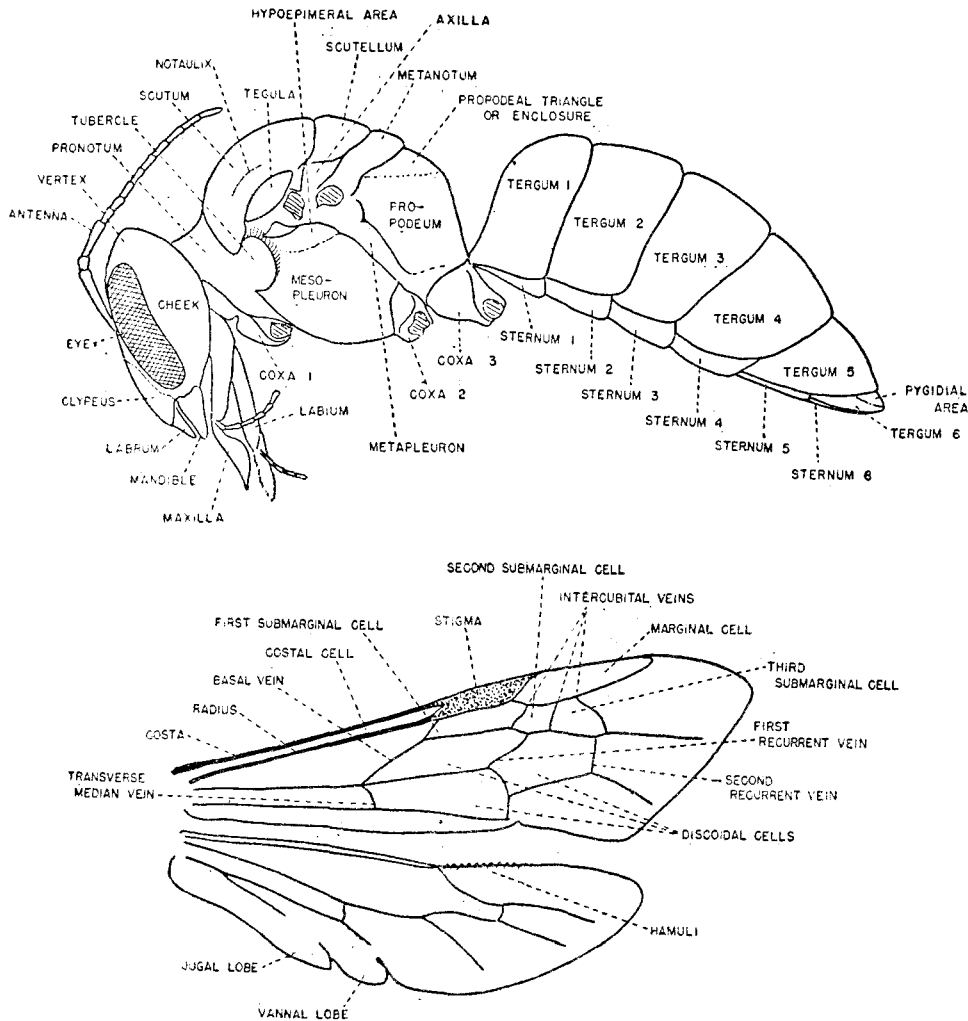


Figure 1—Morphological features and wing venation of bees.

is extensive in most of the social bees, as well as in a few other unrelated solitary species.

The *labrum* and *mandibles* are relatively simple generalized structures, not markedly different from those of more primitive insects, but they show a rather wide range in form and in relative proportions. The remaining appendages forming the proboscis, the *maxillae* and *labium*, are especially significant in the recognition of the families of bees; hence the importance of having them pulled out into a visible position while the insect is still fresh and pliable. In the more primitive groups (e.g.,

Colletidae) there is a close resemblance of these structures to those in the wasps, with a broadly truncate or bifid glossa, a 4-segmented labial palpus and a 6-segmented maxillary palpus (see *Colletes*, in fig. 3). In the structurally more specialized bees the glossa becomes acute and more or less elongated, the lacinia becomes reduced in size, the number of segments of the maxillary palpus is reduced, and various other modifications may be found. The labium and maxillae are united basally by the V-shaped submentum (lorum) which is attached on each side apically to the tip of the cardo.

The posterior surface of the head below is occupied by a deep excavation, the *proboscival fossa*, into which the proboscis fits when retracted. The margins of this fossa are formed by the *hypostomal carinae* which are quite conspicuous and furnish useful distinctive specific characters in several groups.

The thorax is similar to that of the sphecoïd wasps, with a collar-like *pronotum*, the posterior margin of which is produced on each side to form a rounded *tubercle*. The *propodeum* commonly exhibits four distinct surfaces; one dorsal, one posterior, and two lateral. In many species or groups these surfaces are delimited by marginal carinae, and the dorsal surface is further characterized by striations, reticulations or other sculpturing which are of considerable taxonomic importance.

The legs in most females differ from those of the other Hymenoptera chiefly in the broadening of the hind tibiae and basitarsi and, to some degree, the mid basitarsi also. Along with the expansion of these parts there has been a development of pollen-collecting hairs which are borne on the hind legs in all groups except the Megachilidae where they are found on the ventral surface of the abdomen. The basitarsi in some groups equal or even exceed their tibiae in length, so that there are three large and conspicuous leg segments instead of the usual two (femur and tibia). Since males collect no pollen, these leg features are lacking, with all segments usually quite slender and wasp-like. In parasitic species, moreover, both sexes are wasp-like in appearance, for in these the females have lost their pollen-collecting organs.

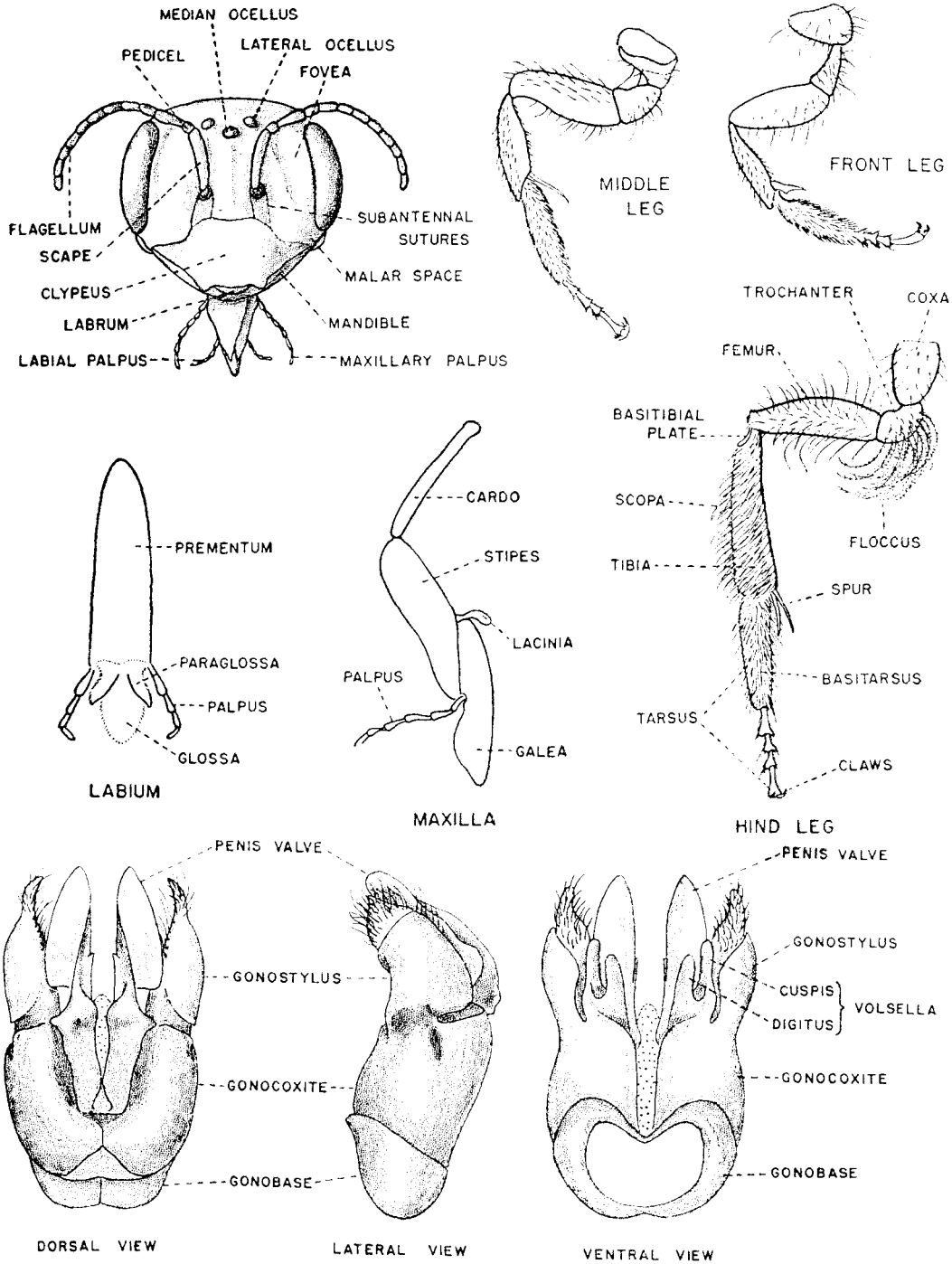
Two forms of pollen-collecting organs are found in bees. In all of our non-parasitic solitary species they are composed of localized brushes of hairs, and the resulting organ is known as a *scopa*. Usually these scopal hairs are more elongate and spine-like than the other body hairs, and they may either be simple and unbranched or more or less densely plumose. The social bees, in the family Apidae, have a more specialized structure, called the *corbicula* or "pollen-basket." In such bees the outer surface of the hind tibia is bare and highly polished and is surrounded by a marginal fringe of hairs, forming the basket. An analogous form is found in some of the

more primitive solitary bees, such as *Colletes* and *Andrena*, in which the lateral surfaces of the propodeum have a fringe of elongate hairs along the upper margin, while the central area of these surfaces is nearly or quite devoid of pubescence. Thus a basket is formed into which the pollen is packed, and this is known as the *propodeal corbicula*. In the genus *Andrena* a more or less dense and plumose tuft of elongate curved hairs on the hind trochanters is called the *trochanteral floccus*.

The wings (fig. 1) exhibit a considerable range of variation between genera and the other higher categories but are commonly of little help in the separation of species within the genus. Important differences include the number of submarginal cells (two or three), the relative size of the stigma, the size and form of the marginal cell, the form of the basal vein and 2nd recurrent vein, and the relation of the recurrent veins to the submarginal cells. In the hind wing the relative size of the jugal and vannal lobes, and the relative lengths of some of the abscissae of the veins are of significance in separating some of the superspecific categories.

Excluding the propodeum, the abdomen includes six well defined segments in the female and seven in the male. Each segment is composed of a dorsal, strongly arched tergum and a relatively flat, ventral sternum. There are no pleural plates. In many groups, the 6th tergum of the female and the 7th of the male bear a triangular apical plate, the *pygidial plate*.

The segments beyond the 6th in the female and 7th in the male are retracted and much reduced and modified apparently to form a portion of the reproductive structures. Thus remnants of the 7th and 8th tergal plates are associated with the sting in the female, while in the male the retracted 8th segment is composed of a tergum and sternum between which the genital armature lies. In some groups, such as *Megachile*, there is a further retraction of some of the other sternal plates. This results in an arching of the abdomen posteriorly, since there are more exposed terga than sterna. These hidden sterna become more or less markedly modified and conceivably have an accessory reproductive or copulatory function. They are significant taxonomically, and it is necessary sometimes to extract and mount them for ob-



MALE GENITAL ARMATURE

Figure 2—Structural details of head, mouthparts and legs in *Andrena*, and male genital armature in *Colletes*.

ervation before accurate identifications are possible. The genital armature, also, is important, hence the desirability of pulling it out into an exposed position. This is not always sufficient, however, as structural details are sometimes difficult to observe unless the part is removed and is at least partially cleared in caustic potash.

The sting is composed of two pairs of valvulae which represent appendages of the retracted 7th and 8th segments, and a pair of styli which are accessory appendages of the 8th.

With respect to the male genital armature, the terminology of Michener (1944) will be followed (fig. 2). This will result in some changes in the terms employed in several of the included groups where the terminology of Snodgrass and others has been used in the past.

Classification

The close relationship of the bees to the sphecoid wasps, indicated by the similarity in the form of the prothorax, has been pointed out. The mouthparts also, at least in the more primitive bees, are quite similar to those of the wasps. The essential difference between the bees and wasps is that relating to the food stores provided for the immature stages. Correlated with this difference are the mechanisms adapting the two groups to the collection and storage of two contrasting types of food materials.

Wasps are carnivorous, and while some nectar is fed to the young in some of the social forms, they rely mainly on insects or spiders which the adults either kill or paralyze and store in the nests. Bees in contrast, feed their larvae on pollen or nectar, or on a combination of both, and the females have developed various structural modifications adapting them to the collection of pollen and nectar. Chief among these modifications is the branching of the body hairs, an increase in the density of the hairy covering, a broadening of certain of the segments of the hind legs, and the development of special organs for the collection and transportation of pollen.

These features are most readily seen in the females of non-parasitic species. Males take no part in the nest construction or food storage activities. Lack of function in these respects is reflected in the structure in that these distinctive modifications are

lacking or are poorly developed. Parasitic or inquiline species likewise display a reduction in degree of development of these characters, and many bees with such habits are very wasp-like in appearance and can be easily mistaken for wasps.

The most reliable of these bee-like characters is the plumose condition of the body hairs, which all bees show to some degree. Somewhere on the upper surface of the thorax these branched hairs will be found, even if they are lacking on all other parts of the body, but the plumose condition is sometimes hard to see without high magnification and the best of lighting. Usually, there will be other characters indicating the identity even of the most wasp-like bees. All of the parasitic species in the families Magachilidae, Anthophoridae and Apidae, have elongate and highly specialized mouthparts which are quite unlike those of the wasps. Since all but one of the genera of parasites belong in these families, the difficulties are not as great as they might seem. However, when the mouthparts are retracted and covered in large part by the labrum and mandibles, these wasp-like bees may be confusing. Males of the non-parasitic bees are not so difficult to recognize, as most of them have a much more copious covering of body hairs than is to be found in any of the wasps.

The marked difference in function of the two sexes in most bees is correlated with a distinct and often extreme difference in structure, and the resulting dimorphic condition of most bee species constitutes a major problem in bee taxonomy. Rarely can the two sexes of a species be associated by evident visible characters. The description of one usually will not serve for the other, and more often than not entirely different characters must be employed in the construction of keys. Thus it is necessary in most genera to devise separate keys for the sexes. Each sex is best described as a separate entity, without regard to the other.

Deviating somewhat from the classification proposed by Michener (1944), eight families of bees are recognized in this work. These are the Colletidae (bifid-tongued bees), Melittidae and Andrenidae (ground bees), Halictidae (sweat bees and others), Megachilidae (leaf-cutter and mason bees), Anthophoridae (long-tongued solitary bees), Xylocopidae (carpenter bees), and Apidae (social bees).

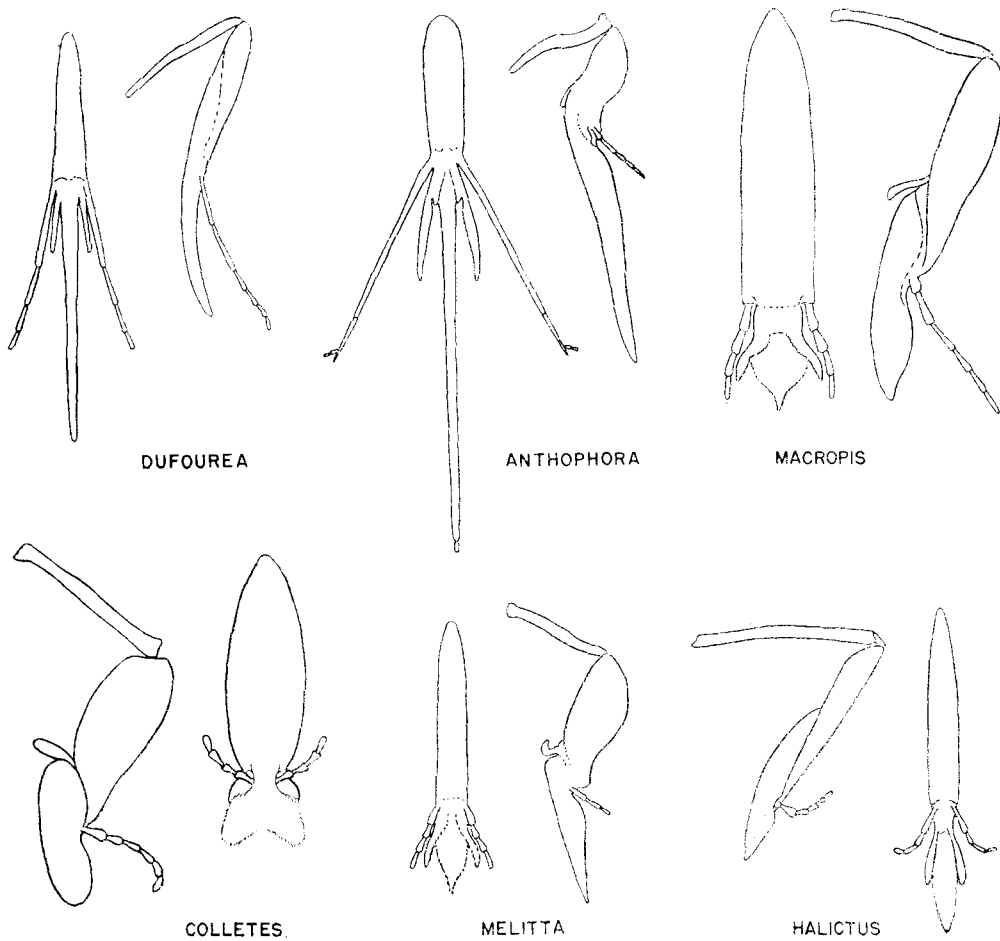


Figure 3—Form of labium and maxilla in representative genera of bees.

In the classification of bees, the most significant structures are the wings and the mouthparts. Three basic forms are recognized in the mouthparts; first, the primitive type in which the glossa is obtuse, truncate or bilobed, as in the family Colletidae (fig. 3, *Colletes*); second, the glossa short and acutely pointed, with the labial palpi of four more or less equal segments, as in the Andrenidae (fig. 2), Melittidae and Halictidae (fig. 3, *Macropis*, *Halictus* and *Melitta*) and third, the glossa much elongated and slender, the labial palpi with the 1st and 2nd segments also elongated, but with the 3rd and 4th very short and inconspicuous, as in the Megachilidae and Anthophoridae (fig. 3, *Anthophora*). In the

Halictidae, *Dufourea* is exceptional in having a much elongated glossa, similar to that in *Anthophora*. The labial palpi, however, are unlike those in the long-tongued bees, and in the lack of both the mentum and submentum of the labium it resembles the other genera in that family.

The chief differences in the front wings are with regard to the number of submarginal cells. In all of the Megachilidae there are only two submarginals (fig. 4, *Megachile*), while in the Xylocopidae, Apidae, and all but one small genus of the Anthophoridae there are three (fig. 4, *Holcopasites*; fig. 5, *Xylocopa*, *Nomada*, *Anthophora* and *Bombus*). In a few of the Halictidae there are two (fig. 4, *Hemihalictus*), but

most of the halictids have three (fig. 5, *Halictus* and *Nomia*). In the other families (i.e. Colletidae, Andrenidae and Melittidae) both conditions are found in about equal proportions. Other characters useful in recognition of the family groups are the shape of the clypeus and labrum, the presence or absence of a distinct pygidial plate at the tip of the abdomen, and the relation of the tip of the marginal cell to the costal margin of the wing.

The location and character of the pollen-carrying organs also is significant. It may be logical to assume that in the ancestral form the pollen collecting hairs were rather generally distributed over the body. Thus, in those bees which are more primitive in some other respects, it is also true that there is a more general distribution of these pollen-carrying hairs. In *Colletes* for instance, which is quite primitive in the character of the mouthparts as well as in various other ways, and in *Andrena*, also quite generalized, the pollen collecting hairs are found on the lateral faces of the propodeum, on the trochanters, femora and tibiae of the hind legs and pollen grains cling to a considerable degree to the pubescence of the ventral surface of the abdomen.

In the more specialized groups the distribution of these hairs is more limited. Thus they form a scopa on the femora and tibiae of the hind legs in most halictids and also in *Caupolicana*, a genus related to *Colletes*. In the Melittidae, Xylocopidae and most of the Anthophoridae, the distribution has "progressed", in comparison with the halictids, and the scopa is found on the hind tibiae and basitarsi. In the Megachilidae it is located on the venter of the abdomen, with the hind legs bearing only very short and nonfunctional hairs, at least with regard to the transportation of pollen. In the panurgine genera of the Andrenidae the pollen load is carried entirely on the hind tibiae. In the Apidae the tibial scopa is replaced by the corbicula. The ultimate in these specializations involves the complete loss of these collecting organs, as in all of the parasitic groups. This holds true as well in *Hylaeus*, a colletid genus in which the pollen is carried internally.

The degrees of specialization of the pollen collecting apparatus thus could be listed

as below, beginning with the more generalized:

1. Scopal hairs on propodeum, hind trochanters, femora and tibiae—*Colletes* & *Andrena*
2. Scopal hairs on hind femora & tibiae—*Caupolicana*, Halictidae
3. Scopal hairs on venter of abdomen—Megachilidae
4. Scopal hairs on hind tibiae only—Panurginae
5. Scopal hairs on hind tibiae and basitarsi—Melittidae, Anthophoridae & Xylocopidae
6. Tibial scopa modified to form corbicula—Apidae
7. Scopal hairs lost—*Hylaeus* & all parasitic genera

This arrangement of families and genera should not be taken to represent a phylogenetic sequence. *Hylaeus*, *Colletes* and *Caupolicana* appear to be related to each other even though they illustrate different degrees of specialization of these pollen-carrying organs. Parasitic types are found in the Halictidae, Megachilidae, Anthophoridae and Apidae.

Satisfactory keys to the higher categories of insects, and probably of other living organisms also, often are difficult to devise. In a natural classification, the more significant differences between the more inclusive groups are often obscure or difficult to observe or to interpret. Furthermore, characters or conditions upon which we base our classification often are subject to exceptions in some of the lower groups or species which should be included. In the bees most writers have placed much reliance on the condition of the mouthparts, and a relatively simple key to the families can be prepared using these structures.

Unfortunately, such a key is very difficult to use, for the mouthparts usually are hidden beneath the labrum and closed mandibles. A specimen must be relaxed, the mandibles spread apart and the proboscis pulled out into a visible position in order to see them. With materials that have been in a dried condition for any length of time, this often is very difficult to do without damaging the specimen, and may sometimes prove to be practically impossible.

Moreover, it is impractical if any large amount of material is involved. Also the risk of damage to a unique or type specimen often is too great.

Thus it is very desirable to employ characters that are readily visible, so far as possible, in constructing keys to these larger groups. The key below has been pre-

pared to that end. Wing characters usually are clearly visible and are significant in the classification of these higher categories. Some of the differences however, such as the presence of two or three submarginal cells, are subject to some variation within some of the family groups. As a result, this key to the families is somewhat longer than

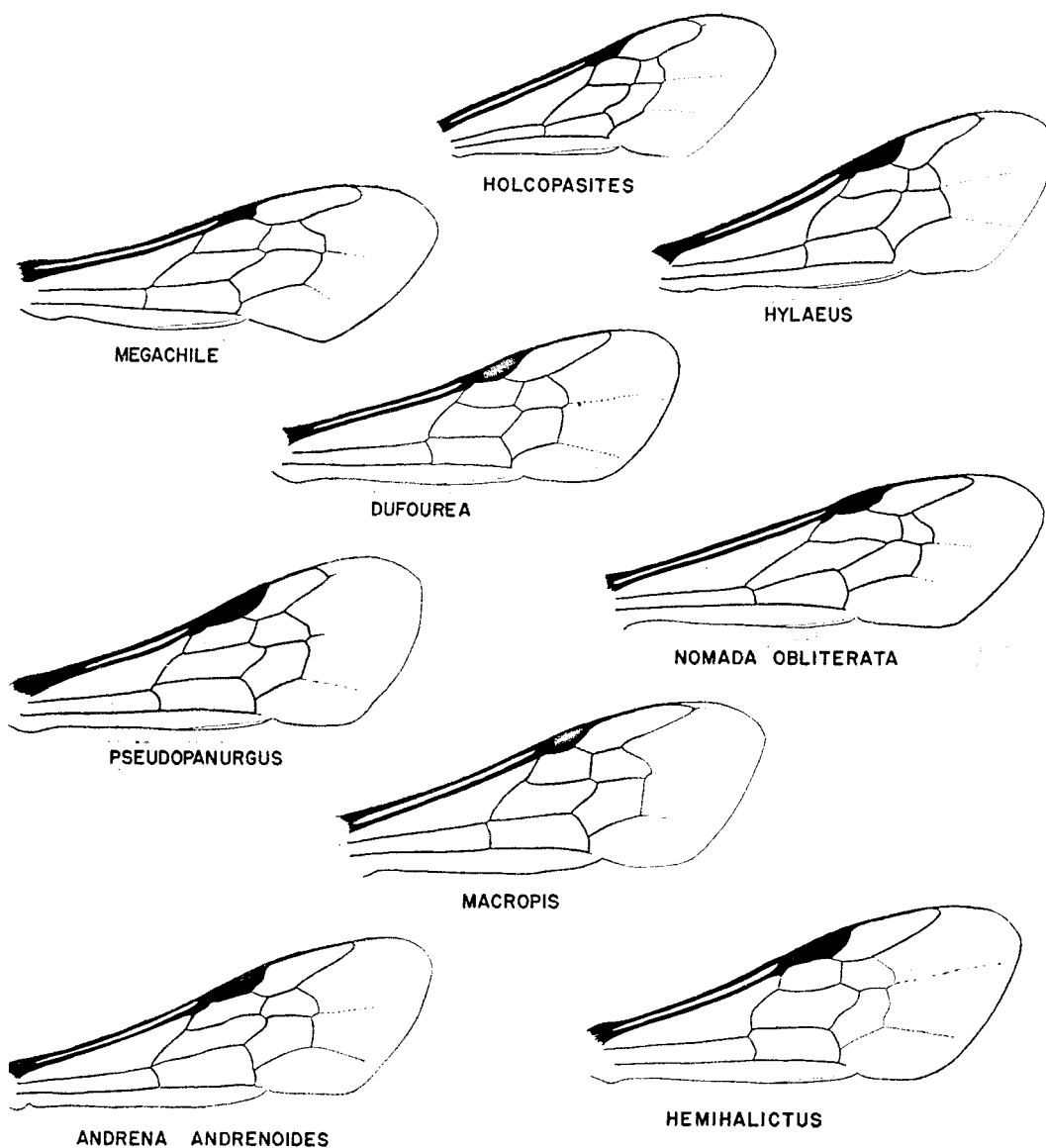


Figure 4—Venation of front wing in representative genera of bees.

might be thought necessary, since these characters are not entirely constant. The character of the mouthparts in each group is included but is given a secondary or supporting position. It will be possible in most cases to run a specimen through the key to the proper family without seeing them. Included in the key is one andrenid genus, *Protoxaea*, which has not yet been found in the eastern United States. Should it appear in any collections made in the eastern United States, it should be possible to recognize it in this key. Also, since most of the other genera of bees that are not represented in the eastern states are not as atypical within their families as *Protoxaea* in the Andrenidae, it is hoped that this key will make it possible to run any nearctic materials to the proper family.

KEY TO FAMILIES

1. Front wing with basal vein strongly arched; glossa acute, usually short; labrum usually hidden by mandibles when closed, but if exposed, then much broader than long; pygidial plate poorly developed or absent Halictidae
Basal vein very nearly straight; or if somewhat arched, then labrum large and fully exposed when mandibles are closed; glossa variable 2
2. Front wing with no more than two submarginal cells 3
Front wing with three submarginal cells 9
3. Two submarginal cells always present; marginal cell transversely or obliquely truncate at tip; glossa acute, usually short Andrenidae
Marginal cell rounded or acute apically, or if truncate and very short, then but one submarginal cell present 4
4. First recurrent vein entering first submarginal cell, or interstitial with first intercubital vein 5
First recurrent vein entering second submarginal cell 6
5. First recurrent vein entering first submarginal cell; pygidial plate present; glossa slender and elongate Anthophoridae (*Neotarra*)
First recurrent vein interstitial or nearly with first intercubital vein; pygidial plate absent; glossa short, obtuse; small black bees, usually with yellow face marks Colletidae (*Hylaeus*)
6. (4). Marginal cell usually rounded apically, but if acute, then tip bent away from costa; glossa slender and elongate; females of nonparasitic forms with scopa on venter of abdomen Megachilidae
Marginal cell acute or narrowly rounded apically, only slightly bent away from costa, if at all; females with scopa on hind pair of legs. 7
7. Antennae in female located below mid line of face; face in male without yellow maculations Halictidae (*Dufourea*)
Antennae located at or slightly above mid line of face; clypeus in male yellow 8
8. Facial foveae present in female; basitibial plate well developed on hind tibia of male; first submarginal cell considerably longer than second Andrenidae
Facial foveae absent; basitibial plate poorly developed on hind tibia of male; first and second submarginal cells subequal in length Melittidae (*Macropis*)
- 9 (2). Second recurrent vein recurved posteriorly toward outer margin of wing, or first recurrent vein interstitial with first intercubital vein; glossa short and obtuse or bifid Colletidae
Second recurrent vein more nearly straight; first recurrent vein entering second submarginal cell, or interstitial with second intercubital vein; glossa acute 10
10. Malar space distinct, usually extensive; pygidial plate absent; females of nonparasitic genera with tibial corbicula Apidae
Malar space lacking, or if at all evident, then pygidial plate well developed; females of nonparasitic genera with tibial scopa 11
11. Clypeus strongly convex, more or less enclosing the labrum laterally, this fully exposed when mandibles closed and nearly as long as broad; pygidial plate usually present 12
Clypeus less strongly convex, the labrum usually partially or entirely covered by the closed mandibles; pygidial plate present or absent 13
12. Basal segment of flagellum equal to the next 5 (female) or 6 (male) combined; glossa relatively short; basal segments of labial palpus short; scopal hairs on

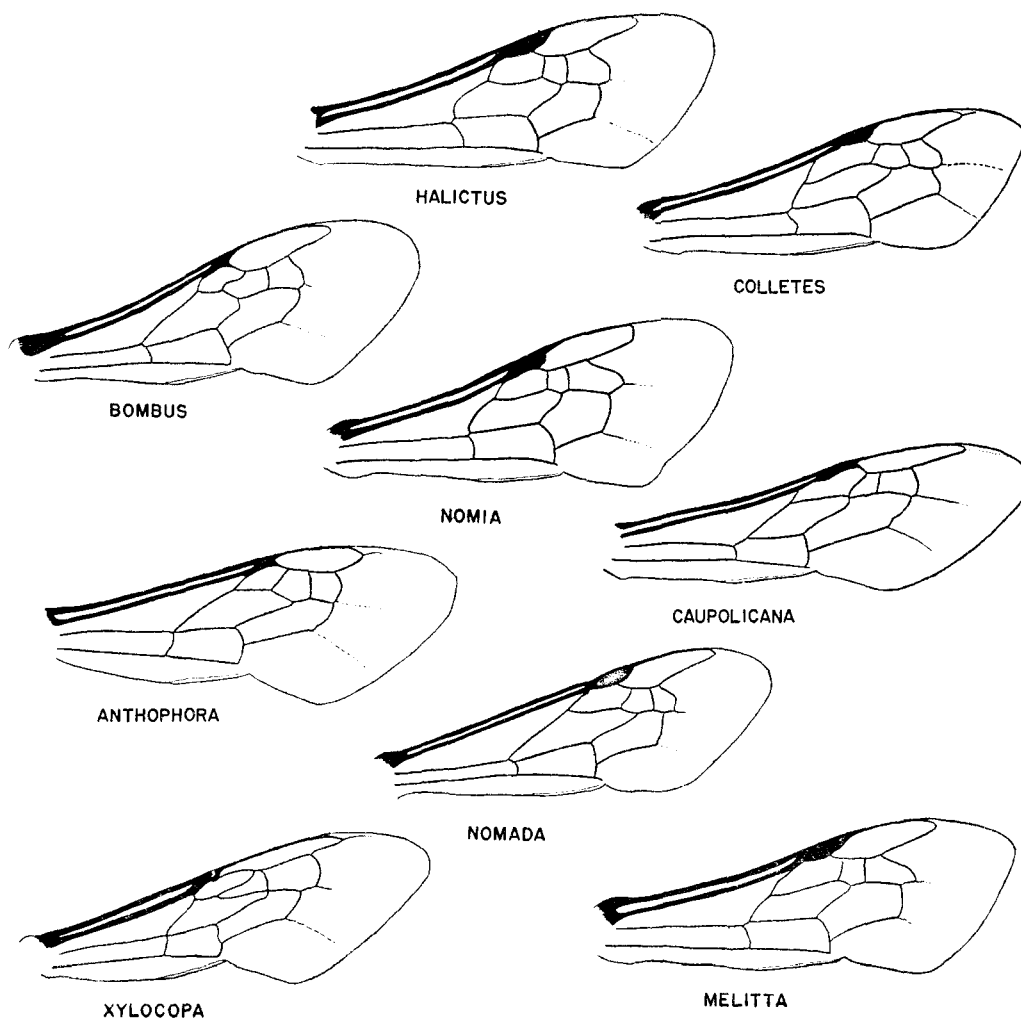


Figure 5—Venation of front wing in representative genera of bees.

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| <p>hind coxae, trochanters, femora and tibiae Andrenidae (<i>Protoxaea</i>)
 Basal segment of flagellum no more than equal to the next 4 combined (usually much shorter); glossa slender and elongate; segments 1 and 2 of labial palpi much elongated; scopal hairs on hind tibiae and basitarsi Anthophoridae</p> <p>13 (11). Facial foveae present in female; basitibial plate well developed on hind tibia of male Andrenidae
 Facial foveae absent in female; basitibial plate not or poorly developed in male 14</p> | <p>14. Pygidial plate well developed; first submarginal cell about equal to second and third combined Melittidae (<i>Melitta</i>)
 Pygidial plate usually absent, but if at all evident, then first submarginal cell no longer than the third alone 15</p> <p>15. Second submarginal cell more nearly triangular, with the two intercubital veins approximate anteriorly; glossa slender and elongate Xylocopidae
 Second submarginal cell quadrangular, about as broad as long, the two intercubital veins nearly or quite parallel; glossa short and acute Halictidae (<i>Nomia</i>)</p> |
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