A Scanning Electron Microscope Atlas of the Honey Bee*

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USDA-ARS

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HONEY BEES

(Apis mellifera L.) preceded humans on earth by 10 to 20 million years. Honey bees are one of the oldest forms of animal life still in existence from the Neolithic Age. Primeval humans gathered and ate the honey and honeycombs of wild bees, the only available sweet, as far back as 7000 B.C. Bronze Age societies celebrated preindustrial triumphs by drinking mead, probably the first intoxicating beverage, fermented from honey. In fact, the words mead and mellifera (the specific name for honey bees), which are similar in several languages, were derived from root words referring to honey bees, liquor, doctored drink, etc. In the past, words for mead, honey, and honey bee have been used interchangeably, revealing the importance placed on the alcoholic beverage derived from honey. Like honey, beeswax has been prominent in ancient folklore and mythology. In the pre-Christian era, wax was offered as a sacrifice to the gods; used in the rites of birth, circumcision, marriage, purification, and death; and used in embalming, sealing coffins, and mummification. The use of beeswax in religious candles carried over into Christian times and led to beekeeping by clergy and monks in order to ensure an adequate supply of the raw material. In the past, beeswax served as a medium of exchange and taxation; it was exacted as tribute from conquered nations and was used in writing, painting, sculpturing, and protecting works of art, as well as for illumination. Honey, beeswax, and propolis (a mixture primarily of plant resins and beeswax that bees use in nest contruction) have been used extensively in pharmacopoeia since 2700 B.C. The principal medicinal value of honey arises from its antibacterial properties when used as a wound dressing. Honey bees originated in southern Asia, probably in the region of Afghanistan. The earliest record of humans gathering honey from wild colonies is from 7000 B.C. Man first kept bees about 3000 to 4000 B.C., perhaps as early as 5000 B.C. There is no way of knowing to what extent honey bees have evolved since then; we can assume that some evolution has taken place, particularly with regard to the social organization of the colony and foraging behavior. Apis mellifem, the most widely distributed of the species of Apis, is not native to the Americas. The first record of the introduction of honey bees to the western hemisphere was in 1530 in South America. It was introduced to North America by colonists from Holland in 1638. Since bees visit a broad range of host plants and are able to conserve heat by clustering, they have become widely dispersed and are now found throughout the world. Honey bees are limited in their distribution mainly by an absence of suitable forage and/or less than 19.8 cm (7.8 inches) of rainfall annually. The scientific name, Apis mellifera, was given the honey bee by Carolus Linnaeus in 1758. It liter- ally means "the honey-carrying bee * " A more descriptive name, A. mellifica, or "the honey-mak- ing bee ' " was proposed in 1761. While this second name more accurately describes honey bees (which carry nectar but make honey), the rales governing precedence in scientific nomenclature dictate that the earlier name be retained. Nevertheless, the term A. mellifica can still be found in some bee literature. top?

BIOLOGY AND BEHAVIOR

Honey bees and their life history and products were topics of study for early philosophers, such as Aristotle, Pliny, and Virgil. Many others have studied bees throughout history. Yet, most basic knowledge of the natural history of the honey bee has been gathered only since the sixteenth century. Twentieth-century scientists have revealed the nature of honey bee sensory systems, behavior, communication, and population dynamics. For example, it is now known that while honey bees do not possess the fine-grained retinal mosaics of humans, they can navigate with precision by optically scanning the sky's polarization patterns through their ultraviolet receptors. Moreover, they easily perceive other colors and rapidly flickering patterns (as in flight at close range). Honey bees possess senses of taste and smell about as acute as those of humans and even more acute for some flavors and aromas. Other revelations are fast emerging about the flight muscle physiology of bees, their learning, memory, dances, chemical communication systems, and reproductive physiology. Although it is often more appealing to believe that bees are somehow special, honey bees are simply insects. Careful study of the literature reveals that many insects behave and function in the manner of honey bees; that is, they generate and conserve heat, raise young, forage, communicate, swarm, store provisions (some even garden), and pollinate or otherwise provide food for humans. Moreover, they do so just as efficiently as do honey bees. Honey bees may seem unique because they express all the above behavioral and physiological traits; but special combinations of traits such as these are present in other insects, in plants, and in animals, where they are equally compelling. So we must ultimately conclude that physiologically, behaviorally, and biochemically honey bees are just insects, remembering, of course, that insects themselves are quite remarkable. Although honey bees (and other bees) are often confused with their near relatives, the wasps, bees can be easily identified by their fuzzy appearance (branched body hairs), robust body, and flattened hind leg. There are more than 20 races of honey bees, the result of natural selection in their respective homelands. But only 4 principal races are important to beekeeping in the northern hemisphere: the Carniolans, Italians, Caucasians, and Dark bees. In the southern hemisphere, other races are also important. Honey bee colonies are perennial and nearly worldwide in distribution; they are distributed from the tropics to subarctic regions. This is possible because they hoard resources and because they can thermoregulate their nests, by fanning to evaporate water for cooling, by metabolizing honey to produce heat (0.1 cal per minute per bee), and by clustering to conserve the heat they produce. Other insects are capable of producing similar levels of heat energy; for bees, however, temperature regulation via clustering is the key to winter survival. Feral (wild) colonies nest in hollow trees, rock crevices, and ground holes. They seem to prefer living trees. In the northern hemisphere most nest entrances are knotholes facing southwest, undoubtedly because this is the side of the tree that weathers and cracks first. Acceptable cavities are approximately 40 L (about the size of a one-story-deep Langstroth hive), and wild colonies therein consist of about 18,000 to 20,000 bees in the most populous summer months. Unlike most other insects, bees build their nests out of their own body products, primarily wax and salivary secretions. Over the years apiculturists have gathered statistics in order to better explain the organization and activities of a colony of kept honey bees. While such figures are useful and interesting, one must keep in mind that they depend on season and locality, so extreme variations are normal. In the summer, colonies managed by a beekeeper may consist of 40,000 to 60,000 adult bees (2 to 3 times that of feral colonies). These will likely be distributed among the three castes as follows: 1 queen, 100 to 300 drones (up to 10,000 drones have been reported), 13,300 to 20,000 foraging workers, and 26,600 to 40,000 workers engaged in various hive duties such as brood rearing, comb construction, housecleaning, defense, and temperature regulation. The brood (eggs and young) in a typical colony includes 5,000 to 7,000 eggs, 7,000 to 11,000 larvae being fed, and 16,000 to 24,000 pupae in sealed cells. A single worker larva is fed approximately 1,300 meals per day for 5 days and grows to 300 times its original weight before pupation ensues (human growth is only 10 to 20 times original body weight). Three-fourths of a larva's weight is made up of fat. During brood rearing, the temperature of the brood nest is maintained at 32-35'C (90-95'F), usually 33-34'C (92-93'F). Since worker bees metabolize honey to generate the heat needed to warm the hive, honey must be present in the hive at all times. Colony humidity is also relatively constant at 48-50 +-6 6 percent relative humidity. To accomplish this bees gather water and evaporate it in the hive when atmospheric humidity in the hive is low. However, most hive humidity, including that needed for cooling, is derived from the water content of nectar and from bee metabolism. When ambient relative humidity is high the bees are apparently able, by some means, to maintain a lower level in the hive. Bee behavior is instinctive and genetically pro- grammed. Yet bees have plasticity in their central nervous system, as exhibited by their well-developed ability to learn and remember. Bees can learn in most sensory modalities (i.e., distance, sight, smell, taste, and touch). There is some evidence of a rudimentary ability to reason, such as associating flower type with reward. Bees are opportunists, as well, exploiting the most lucrative floral sources to save time and energy. Nevertheless, habituation (training) is an important part of bee behavior; bees can become accustomed to such things as frequent manipulation by beekeepers or the presence of floral sources. Bees have evolved with numerous highly specialized sensory receptors that are unevenly distributed over the head, thorax, and abdomen. In function, the head is principally sensory for sight, smell, taste, and touch. The main portion of the brain within is a coalescence of three ganglia (nerve centers) that process much of the sensory information and initiate appropriate behavioral patterns. The thorax, tightly packed with well-innervated muscles, is the locomotory center for flight, walking, and sound production. The feet and legs are believed to bear important taste and touch receptors, as well. Certainly, the ability to build hexagonal wax cells of uniform size is dependent in part on sensory receptors on the legs. In the abdomen are found digestive, circulatory, reproductive, and defensive organs, along with the wax glands. Nerve and respiratory systems are distributed throughout the body. Since the insect is encased in a hard exoskeleton, it must of necessity have specialized external sensory areas. The bee's numerous external sensory receptors inform the central nervous system about the external environment, as well as about events within the body (such as the direction in which legs and wings are moving, whether the head is up or down, if the sting is in or out, or whether the bees is in contact with food or forage). Honey bees communicate with one another both phonetically and kinetically. Tonal qualities of sounds produced by bees suggest that several 14 moods" can be communicated. The best known of their communication systems is the dance language that provides information regarding the location of a particular source of forage. Information in this dance includes distance, direction, and quality and quantity of food. The recruitment dances instinctively performed by worker bees are in fact ritualized, miniaturized versions of the foraging trip the returning bee has just taken. The recruit bee learns and practices the trip in miniature and then leaves on her own (rather than being led, as with other social insects) to the source. Several other lesserknown dances are performed by bees, and sound production by the dancing bees is an essential part of the dance activity. Bees also communicate via the aroma and taste of the products they bring back to the hive, as well as by at least 31 pheromones (chemical compounds) they produce from glands in their bodies. Honey bees have no unusual nutritional re- quirements, only a balanced diet containing carbo- hydrates, fats, proteins, minerals, vitamins, and water.'Even so, the logistics of honey bee foraging and food consumption are incredible. A typical colony may use up to 100 lb pollen for brood rearing each year; 4 million foraging trips are required to collect this quantity. A single bee may carry up to 5 million pollen grains in a single trip. Some pollen is proba- bly consumed, but most is mixed with small quanti- ties of honey or nectar and possibly salivary prod- ucts and packed into cells adjacent to the brood nest where it undergoes a chemical change to a product called bee bread. This product is stored until consumed by adult bees for conversion into glandu- lar larval food, a kind of "mother's milk " Bee bread is the principal food of the adult nurse bees. This nutrient was so named by primitive man because of its bready taste. Nurse bees eat and convert bee bread into at least two different glandular secretions, which are then fed to bee larvae. The diets of workers, queens, and drones are entirely dissimilar. Brood food recipes for each of the three castes involve differing ratios of the two glandular products (each is the product of bees of a different age); a quantity of honey is then added, the amount being caste dependent. Cannibalism of eggs and larvae, which occurs during periods of food scarcity, can preserve the colony by conserving vital nutritional elements. Under ideal conditions and depending on the plant species involved, a colony may produce 90.7 kg (200 lb) or more surplus honey. The bees visit 2.5 to 500 million flowers for the nectar from which this quantity is produced. Approximately 3.6 kg (8 lb) honey are consumed in foraging and brood rearing to produce 0.45 kg (1 lb) surplus. Estimates of energy consumption indicate that foraging bees get about 11,265,100 km (7 million flight miles) to 3.8 L (1 gal) honey. Normally bees forage no more than a 3.2- to 4.0-km (2- to 2.5-mi) radius from the hive, covering 324 to 5062 ha (8,000 to 12,500 a) but may on occasion fly up to 16.1 km (10 mi) at a speed of 19.3 to 24 km (12 to 15 mi) per hour. The farther that bees must fly from a colony to forage for nectar, the more fuel they burn and the less efficient they are at producing a surplus of honey. The top speed of a worker bee is about 29 km (18 mi) per hour. As with the production of heat mentioned earlier, honey must be present in the hive to refuel foraging bees; without it foraging ceases.top?

PRODUCTS OF THE HIVE

Since humans first began keeping bees, their principal aim has been the harvest of honey. Thus beekeeping methods have been adapted to accommodate colony behavior. Some success has been achieved in manipulation of colonies to capitalize on certain behavioral traits, but honey bees must still be considered wild, not domesticated, creatures, and honey a raw agricultural commodity. Ninety percent of the world's beekeepers live in Europe, Russia, Asia, and Africa and produce 54 percent of the world's honey by averaging 9.1 kg (20 lb) per colony. Ten percent of the world's beekeepers live in Australia and North and South America and produce 46 percent of the world honey crop by averaging 22.7 to 45.4 (50 to 100 lb) per colony. Some stingless bees (not honey bees) are kept for honey production, but the number of these colonies is comparatively small. Worldwide honey production is currently in ex- cess of 544,320 t (600,000 tons) annually. This quantity is provided by an estimated 50 million colonies kept by about 61/2 million beekeepers. The current world population is around 3,500 million people, so there are approximately 500 times more honey bees than people. Honey is elaborated from the nectar of numerous plant species but may also be produced from honeydew excretions of aphids and scale insects). Nectars vary considerably in quality and quantity, depending on the floral source. Similarly, honeys vary; some honey is nearly colorless (like water), with a light, pleasing aroma, and some is as dark as crankcase oil, with a heavy-bodied aroma. Honey from most floral sources falls between these extremes. Bees convert nectar to honey by drying it down to a moisture content of 15 to 20 percent and by adding a salivary enzyme that changes sucrose (long-chain sugar) into glucose and fructose (two short-chain sugars); honey is composed of sugars, mainly fructose and glucose. Honey also contains trace amounts of minerals, enzymes, vitamins, and colloids. Other biologically active constituents (such as hydrogen peroxide and gluconic acid) inhibit some microbial development but accelerate yeast growth. A limited number of plant sources yield nectar with toxic elements, but fortunately bees either recognize and avoid these or are able to nullify their effects. (Beekeepers avoid areas with such noxious plants.) Honey is used as a sweetener (1 part honey 1.67 parts sugar) and in baking, baby foods, confectioneries, cosmetics, meat packing, pharmaceuticals, and syrups, and for curing tobacco. Honey is often used to maintain moisture as well. In times past, it was believed to be a powerful aphrodisiac. It is served in liquid or granulated (spread) form and in the comb; limited quantities of dried honey are now available. But for bees, honey is the allpurpose food, essential for stores of body fat, for flight, and in the production of heat, humidity, and wax. Other products of the hive include pollen, brood (still eaten by some primitive cultures), propolis (bee glue), royal jelly, venom, and of course beeswax. For making beeswax, each worker bee has four pairs of wax glands on the underside of its r abdomen; these function best in 12- to 18-day-old bees, according to the needs of the colony. Both protein (pollen) and carbohydrates (honey) are required to produce beeswax; 1 lb beeswax, which contains about 450,000 wax scales, will provide enough wax to make 35,000 hexagonal cells that can store 10 kg (22 lb) honey. Thus bees consume part of their food (pollen and honey) for the purpose of converting it into nest structure -specifically cells for food storage and brood rearing. It takes 2.7 to 4.5 kg (6 to 10 lb) honey to produce 0.45 kg (1 lb) wax. Beeswax has many uses worldwide, including the production of candles, cosmetics (the largest user-industry), electronics, lubricants, leather and fabric preservatives, polishes, inks and paints, models for dentistry, and beer. A large portion of the beeswax produced is recycled to the bee industry where it is used to produce the foundation for new honeycomb and queen cell cups. World production of beeswax exceeds 9072 t (10,000 tons) annually. Propolis is used in the attachment of combs to the top and sides of the hive, as well as for filling cracks, reducing the size of the hive entrance, and embalming intruders. It is composed of plant resins gathered by worker bees, beeswax (30 to 60 percent), balm (perhaps a glandular secretion of bees or a product of honey bee digestion), as well as pollen and hive debris. In times past, varnishes responsible for the tonal quality of violins and the finishes ori other fine woods contained refined propolis. The human nutritional value of pollen and queen (royal) and worker jelly has been of great interest throughout the world. However, there is much doubt as to their real worth. These jellies, larval food synthesized from the digestion of pollen and secreted by the brood food glands of worker bees, have, like pollen, no proven attributes except as bee food. Nevertheless, both are used in various cosmetics, lotions, and dietary supplements. According to Greek mythology the infant Zeus, out of gratitude for the honey that sustained him, gave the honey bee its sting for defense. Because the bee abused this power, Zeus later decreed that the bee must die whenever the sting is used. Perhaps it is ironic that now we have developed the means to milk venom from bees and use this product in medicine. The collection and sale of bee venom is an increasingly popular although extremely limited enterprise. Presently, its greatest use is in the treatment of bee venom hypersensitivity. It is also reported as helpful in reducing the pain caused by certain types of arthritis. Commercial beekeeping has given rise to two additional hive products, namely, the queen and worker honey bees. Worker bees are packaged and sold by the pound by beekeepers who are engaged in this highly specialized form of beekeeping. Packages of worker bees and queens are frequently delivered by the postal service. A package of bees normally contains 0.9 to 1.4 kg (2 to 3 lb) of bees plus a mated queen. Packaged bees are used for establishing new colonies or for replacement of those lost through natural causes or catastrophic events. The selling of honey bee queens is a highly lucrative commercial enterprise. Queens are often advertised as being of a specific genetic origin with certain desirable attributes. These queens are used by beekeepers to requeen existing colonies in which the old queen is failing or was lost. Beekeepers may also expand their businesses with the purchase of additional queens; each new queen is installed in a new colony made by dividing an existing colony in half (the old queen heads up the parent unit).top?

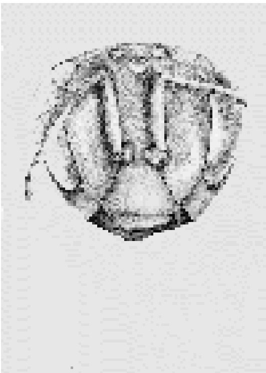
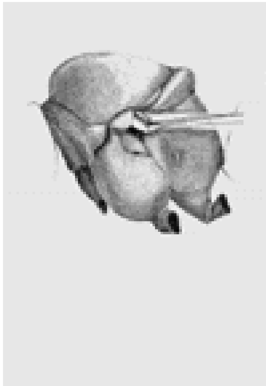
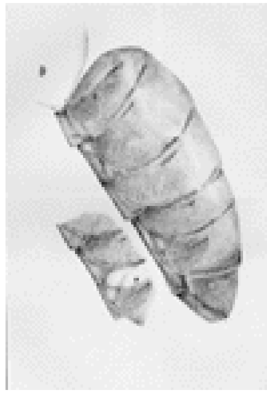
POLLINATION

Reproduction in many plant species is a sexual process analogous to that of animals. Pollen (equivalent to sperm) must find its way to the stigma (equivalent to the vagina). Flower visitors, principally bees, are essential in the transfer of pollen within and between flowers. Floral nectars and aromas attract bees and thus ensure adequate pollination and the reproductive success of the plant. The honey bee's most significant contribution to human dietary habits has been these pollination activities. Without honey bees human tables and lives would be impoverished by a general lack of fruits, vegetables, flowers, and other bee-pollinated plant products; and the human diet would be almost wholly restricted to cereals, some nuts, and the meat of wild animals. One of the world's estimated 20,000 to 30,000 living species of bees, the honey bee has become indispensable, humanity's greatest and most versatile insect benefactor. More than 90 fruit, vegetable, nut, and seed crops are partially or entirely dependent on bees for pollination, as are numerous ornamental plants and wild flowers. The value of bee-pollinated crops in the United States is estimated to be $100 million100 times the value of the honey produced. These crops represent up to one-third of the human diet in many countries. Mobile beekeepers in the United States and elsewhere can even supply bees to farmers at the time pollination is needed. Early in the year these beekeepers provide pollination services to growers in warm areas. They then move their hives into the more temperate climates, following the spring weather northward (southward in the southern hemisphere) and pollinating both orchard and field crops. When they terminate their annual trek, they collect a final large honey crop and then return home in the fall to prepare for another northward migration the following year.top?

ENEMIES OF HONEY BEES

Like other animal life, honey bees are beset by a variety of threats to their survival -disease, parasites, nest destroyers and predators. Their enemies include other insects, mites, spiders, birds (woodpeckers, bee martins, and honey buzzards), and mammals (bears, skunks, badgers, and baboons). The ever-present wax moth is a particular problem; larvae of this moth destroy the wax combs of weak colonies (and colonies kept by unwary

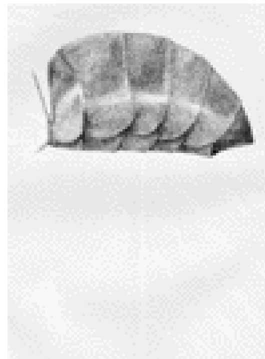
THE QUEEN

The Head **The Thorax** **The Abdomen**

Queen Info

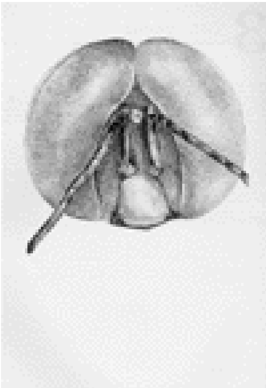
THE WORKER

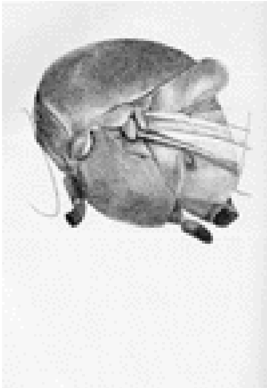


THE HEAD **THE THORAX** **THE ABDOMEN**

WORKER INFO

THE DRONE





The Head

The Thorax

The Abdomen

Drone Info

Appendix

Major Anatomical Divisions of the Honey Bee

G L 0 S S A R Y

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

ACROSOME. Caplike process at the distal end of the sperm that releases proteins and enzymes that permit the sperm nucleus to enter the egg cytoplasm

ACUMINATE. Tapering to a point

AEDEAGUS. Penis

ALINOTUM. Wing-bearing plate on the dorsal surface of the mesothorax or metathorax

ANNULATE. Furnished with or composed of rings; composed of rings of cuticle

ANTECOSTAL. Pertaining to a particular ridge on the inner side of a tergal or sternal plate that forms an attachment site for longitudinal muscles

ANTERIOR. Situated before or toward the front; opposite Of POSTERIOR

APODEME. Any cuticular ingrowth of the body wall, usually formed in a multicellular matrix such as body cuticle

APOPHYSIS. (plural, APOPHYSES) Any internal or external outgrowth of the body wall (cuticle)

AROLIUM. Median lobe of the pretarsus, arising between the bases of the claws

ARTIFACTUAL. Pertaining to any artificial accoutrements in a natural process or subject; a substance or structure not naturally present

ATRIUM. Cuticular antechamber leading from the spiracular opening to the tracheal orifice

AURICLE. Structure in the front end of the first tarsal segment of the hind leg that pushes the pollen mass up into the pollen basket of the hind tibia

AUXILIA (plural, AUXILIAE). Small plates beneath the bases of the pretarsal claws that bear the pulvilli

AXONEME. Flagellar structure (tail) of an insect sperm

BALM. See PROPOLIS

BASALARE. Pleurite (lateral sclerite) arising from the episternum, a rounded bib of exoskeleton anchoring (giving insertion to) the anterior pleural muscles of the wing

BASICONICUM. See SENSILLUM AMPULLACIUM and SENSILLUM BASICONICUM

BASISTERNUM. Principal sclerite or area of the sternum anterior to the roots of the sternal apophyses or the sternal costal suture

BASITARSUS. Proximal segment of the tarsus; the first and largest segment of the honey bee foot

BEE BREAD. Pollen stored in the comb, to which bees have added small quantities of nectar and other largely unknown products

BICONVEX. Convex or protuberant on both sides; in insect eyes, pertaining to the shape of the corneal lens of each ommatidium of the compound eye or the single lens surmounting each ocellus

BIPOLAR. Having two poles; pertaining to the most common type of sensory neuron of cuticular sense organs, one pole the distal dendrite (which is continuous with the neuronal cell body), the other (proximal) pole the origin of the axon

BLEB. Any small blisterlike projection

BROOD. Eggs, larvae, and pupae

CALCARIS. Multicellular spur set in a membranous socket (the wax spur in the honey bee)

CAMERA (noun). Curved narrow sclerite underlying the paired lobes of the arolium; (adjective) pertaming to an eye type possessing a lens that admits and refracts light to a photosensitive retina behind the lens

CAMPANIFORM. Bell-shaped, pertaining to a type of external proprioceptor (a sense organ housed under a small dome or bell-shaped cuticular elevation that consists of a single relatively large bipolar rieuron whose distal tip is embedded in modified cuticle that is displaced as the surrounding cuticle is stressed, which action is the adequate stimulus for this receptor); pertaining to a stress receptor monitoring tension developed from muscle activity, usually at joints (these strain gauges are widely distributed on the body and appendages of the honey bee)

CANNULAR. Pertaining to a small tube or carmula, usually a cuticular canal or channel

CARDO. (plural, CARDINES) Basal ring in the genitalia; more commonly, the proximal subdivision of a maxillary appendage; and in the honey bee worker a slender, cuticular, sticklike process that articulates with the lorum and stipes

CERVIX (also CERVICUM). Neck, either the connecting piece between head and thorax or the neck of the drone penis between vestibulum and bulb

CHAETICA. See SENSILLUM CHAETICUM

CHALAZA. Discrete bulbous elevation of the body wall that constricts the hair socket

CHEMORECEPTOR (also CHEMOSENSOR). Sense organ that can detect odorant molecules in air or water

CHEMOSENSOR. See CHEMORECEPTOR

CIBARIUM. Food pocket of the external or preoral mouth cavity between the base of the hypopharynx and the undersurface of the clypeus

CLYPEUS. Facial area of the cranium just above the labrum, usually separated from the frons by an epistomal suture

COMET. Aggregation of airborne drone honey bees

CONDYLE. Any process by means of which an appendage is articulated in a rounded cavity

CORNEA. Optically transparent cuticle overlying the ommatidia of the compound eye or the photoreceptors of the dorsal ocelli

CORNUTUS (plural, CORNUTI). Horn or hornlike process of the male genitalia

COSTA. Thickened anterior margin of the wing (according to wing vein nomenclature, the costa is the vein extending along the anterior margin of the wing)

COXA. Basal (most proximal) segment of the leg, the medial surface of which articulates with the body

CUTICLE (adjective, CUTICULAR). Protein-chitinous material making up the exoskeleton and lining of the foregut and hindgut

DENDRITE. Receptive portion (usually) of the nerve cell where the generator potential (stimulus) originates; also the postsynaptic region of an interneuron

DENTICLE. Small tooth or toothlike process

DIOPTRIC. Refractive, pertaining to corneal lens and cones, which are capable of bending light rays toward the rhabdomeres of underlying photoreceptor cells

DISTAL. That part of the body (or an appendage) that is farthest from the body

DORSAL. Pertaining to the upper surface; opposite of VENTRAL

DORSUM. Upper surface.

EMPODIUM. Spinelike process springing from the unguitractor of the foot

EPICRANIUM. Dorsal surface of the head

EPIMERON. Posterior division of a thoracic pleuron

EPIPLEURON. Pleural sclerite of the prothoracic segment

EPISTERNUM. Anterior and larger lateral thoracic sclerite between the sternum and the notum; the anterior sclerite of the pleuron

EPISTOMAL. Pertaining to the lower face between the mouth and eyes, or to a sclerite immediately behind or above the labrum

ESOPHAGUS. That part of the foregut that lies between the pharynx and crop

EXOCUTICLE. Primary cuticular layer, a rigid, relatively thick, structureless layer of cuticle situated between the epicuticle (outer) and endocuticle (inner) layer of the exoskeleton

EXORECEPTOR. Any receptor cells or organs that monitor and sense forms of energy that arise outside of the bee (such as light quanta and odorant molecules)

FACET. Polygonal (sometimes round in a frontal view) subdivision of corneal lens cuticle forming the outer boundaries of an ommatidium of the compound eye

FASCICLE. Bundle or cohesive group

FEMORAL. Pertaining to the femur

FEMUR. Third and usually largest (or stoutest) segment of a leg; the thigh

FIBULA. Jugal fold of the wing; also, the spur at the end of the tibia that closes over the toothed notch on the basitarsus to form an enclosed antenna cleaner

FLABELLUM (also LABELLUM). Distal lobe of the glossa (tongue)

FLAGELLUM. That portion of the antenna beyond the second segment, which may be subdivided; a whiplike process; the tail of a sperm

FLEXION. Bending in which the angle lessens between the bending components

FLEXUOUS. Having a bending quality; capable of bending

FORAMEN. Opening in the body wall to permit passage of viscera from one part to another

FORAMEN MAGNUM. Hole in the back of the head capsule that is linked with the cervix, through which passes the ventral nerve cord, esophagus, dorsal vessel, and other viscera

FOSSA. Pit or deep sulcus

FRONS. Unpaired sclerite of the head lying between the arms of the epicranial suture; the anterior portion (forehead) of the head capsule

FRONTAL. Pertaining to the front of the head or to the anterior aspect of any part

GALEA. Outer lobe of the maxilla, which in the worker honey bee is a long, thin, tapering blade

GASTER. Globular or ovoid last seven segments (two to eight) of the abdomen behind the petiole; the abdomen

GENA. Cheek, the part of the head on each side below the eyes

GLABROUS. Smooth, not hairy

GLIA. Nonexcitable cells that accompany and ensheath neurons

GLOSSA (plural, GLOSSAE). Tongue, which in the honey bee is long, densely hairy, and split posteriorly by a deep groove (the bee tongue is flexible and contractile)

GUSTATORY. Pertaining to gustation, the sensing of water-borne odorant molecules; pertaining to the sense of taste

HEMOLYMPH (also HAEMOLYMPH). Blood; in bees a solution containing a variety of nucleated cells called hemocytes possessing little or no respiratory function

HIRSUTE. Hairy

HYPOPHARYNX. Ventral portion of the stomodeal section of the alimentary canal posterior to the mouth (in the honey bee, the hypopharynx is an intergnathal lobe, spanning functional mouth and cibarium)

INFRAEPIMERON. Lower (most ventral) sclerite of the epimeron

INNERVATED. Supplied with nerves that can communicate with other body parts

INTER-. Prefix meaning between

INTERSTITIAL. Pertaining to an area between two lines or two body tissues

INTRA-. Prefix meaning within

INTRAEPIMERON. That area within an epimeron (a posterior division of a thoracic pleuron)

JOHNSTON'S ORGAN. Mechanoreceptor organ located in the second segment of the antenna (a scolopophorous organ usually consisting of some scores of bipolar neurons whose apical ends (dendrites) insert into the basal part of the third segment of the antenna; these collective, oriented nerve cells are stimulated by particular frequencies induced in the antenna when the latter comes in contact with vibrations propagated in air, water, or ground)

JUGAL. Pertaining to the area of origin of the forewing, particularly its posterior margin

LABELLUM. See FLABELLUM

LABIUM. Second maxilla; the lower lip; in the honey bee worker, a compound structure consisting of the prementurn, postmentum, labial palpi, ligular lobes, glossa, paraglossae, and various glands

LABRUM. Upper lip, covering the base of the mandibles and forming the roof of the mouth

LANCET. Swordlike cuticular process with serrated edges used for piercing by the sting apparatus

LATERAL. Pertaining to the outside margins; opposite Of MEDIAL

LIGULA. Major portion of the labium, consisting collectively of the glossa and paraglossae

LORUM. Flexible, transverse band supporting the base of the submenturn, with its extremities attached to the distal ends of the cardines (see CARDO)

MANDIBLE. One of two flattened, shovellike cuticular mouthparts in worker and queen honey bees that act as a pair of grasping organs for food ingestion and the manipulation of wax in comb building

MAXILLA (plural, MAXILLAE). Paired mouthparts for chewing and shredding located below the mandibles, consisting of a number of cuticular sclerites (galea, lacinia, stipes, cardo)

MECHANORECEPTOR. Sense organ capable of registering various mechanical (physical) perturbations that originate within or outside the insect

MEDIA. Wing vein; the fourth longitudinal vein extending from the base through approximately the middle of the wing

MEDIAL. Pertaining to the middle of something; opposite Of LATERAL

MENTUM (also PREMENTUM). Part of the tongue, the second sclerite bearing the labial palpi, paraglossae, and ligula

MESOEPISTERNUM. Mesothoracic episternum

MESOMERES. One of two medially situated, secondary lobes at the posterior end of the drone pupa, which are phallic rudiments that unite in the adults to form the aedeagus

MESONOTUM. Dorsal surface of the second or middle thoracic segment of the adult insect

MESOPEDE. Middle leg

MESOSTERNUM. Main ventral (breast) sclerite of the mesothorax

MESOTHORAX (adjective, MESOTHORACIC). Second thoracic segment

METANOTUM. Dorsal sclerite (plate) on the insect's back; on the last thoracic segment

METATHORAX (adjective, METATHORACIC). Third and last thoracic segment

MICROPYLE. Area of minute openings in the insect egg through which sperm gain entry

MICROTRICHIA. Miniature body hairs, not articulated and probably not innervated

MONOCONDYLE. Pertaining to a joint having only one condyle and thus a single point of articulation

NEURON. Nerve cell, capable of being depolarized or hyperpolarized when stimulated and conveying this transient potential change along its length

NOTUM (adjective, NOTAL). General name or suffix given to dorsal sclerites

NUMERAL. Pertaining to a particular number

OCCIPITAL. Pertaining to the occiput

OCCIPUT. Back of the head

OCCLUSOR. Muscle that closes a spiracle when it contracts partially or completely

OCELLUS. Simple eye (so-called) consisting of relatively few photoreceptor cells under one smooth biconvex lens; in honey bees, three ocelli are situated on the vertex

OLFACTORY. Pertaining to reception of air-borne odorant molecules by chemoreceptors

OMMATIDIUM (plural, OMMATIDIA). All the photoreceptor cells, dioptric apparatus, and associated pigmented glial cells of one lens facet

OPERCULUM. Cover or lid

ORIFICE. Opening, entrance, or hole.

PALP. Telopodite or lobe of a mouthpart appendage PAPILLA (plural, PAPILLAE). Minute, soft projection

PAPILLATE. Covered with small projections

PARAGLOSSA (plural, PARAGLOSSAE). One of the paired, thin, elongate lobes arising from the common ligular base on the prementum at the sides of the tongue, their concave inner surfaces clasping the base of the tongue

PARAMERE. One of the paired lateral processes or lobes of the phallobase

PECTINATE. Comblike; pertaining to the rigid incurved setae on the basal parts of the maxilla and labium or the rows of spines on the feet

PEDICEL (also PEDICELLUS). Second segment of antenna

PEG ORGAN . See SENSILLUM AMPULLACIUM and SENSILLUM BASICONICUM

PENULTIMATE. Next to last

PETIOLE. Stalk or stem; in honey bees, the greatly constricted area between the first and second abdominal segments

PHALLOBASE. Base of the phallus (penis)

PHALLOTREME. End or distal opening of the aedeagus (penis)

PHALLUS (adjective, PHALLIC). Penis

PHEROMONE. One of the biochemicals produced by various glands that have warning, aphrodisiac, trail-forming, and other functions, the chemoreception of which in insects initiates social responses and (perhaps) endocrine changes

PHoTONEGATIVE. Avoidance (behavioral) reaction to light

PHOTORECEPTOR. Cell or collection of cells, usually characterized by the presence of rhabdomeric microvilli containing visual pigment, that are specialized in the absorption of light quanta

PIPING. See QUACKING

PIT ORGAN. See SENSILLUM AMPULLACIUM and
SENSILLUM COELOCONICUM

PIT PEG. Peg sensillum arising from the base of a pit or other cuticular cavity

PLACOID. See SENSILLUM PLACODEUM

PLANTA. Sclerite forming the basal joint of the posterior tarsus, the sole of the posterior tarsal joint just proximal to the arolium, which is covered with ranks of strong spines

PLATE ORGAN. See SENSILLUM PLACODEUM

PLEURITE. Any sclerite in the pleural (lateral) portion of a body segment

PLEURON. Pleurite; also the subcoxal sclerotization above, before, and behind the coxa

POLARIZATION PATTERN. Electric vector of linearly polarized skylight, which can be perceived by ultraviolet receptors in the bee compound eye and used for navigation

POLYGONAL. Having many straight sides

PORE. Surface opening, blind-ended or continuous

POSTERIOR. Hindmost; opposite Of ANTERIOR

POSTMENTUM. Triangular, small sclerite, a constituent of the labium

POSTOCCIPUT. Extreme posterior rim of the head capsule, that portion behind the occipital suture

PREMENTUM. See MENTUM

PRESCUTUM. Anterior area of the mesonotum or metanotum between the antecostal suture and the prescutal suture

PRETARSUs. Terminal segment of the insect leg, the functional foot of the insect.

PROBOSCIS. Composite "organ" formed of the maxillae and labium, especially or only when those two appendages are brought together to form a tube through which liquids are drawn up to the mouth by the cibarial pump

PROCTIGER. Small papilla bearing the anus

PRONOTUM. Dorsal surface of the prothorax

PROPODEUM (adjective, PROPOIJEAL). First abdominal segment, which appears to be part of the thorax

PROPOLIS. Admixture of plant resin, beeswax, and other unknown products (probably glandular in origin) produced by worker bees and used for various purposes including filling cracks in the hive, glue for suspending combs, and for embalming intruders

PROPRIOCEPTOR. "Sense organs capable of continuously registering deformation (changes in length) and stress (tensions, decompressions) in
the body, which can arise from the animal's own movements, its weight or other external mechanical forces " (Lissman 1950)

PROTHORAX. First (most anterior) thoracic segment

PROTRACTOR MUSCLE. Muscle that permits an extension

PROXIMAL. Nearest the organism

PULVILLUS. Padlike structure between the tarsal claws or on the underside of the tarsal joint

PUNCTATE. Having pits or punctures

PUPATION. Metamorphosis from the larval stage to the pupal stage

PUTATIVE. Commonly accepted, reputed

QUACKING. Sound made by queen bees

RADIUS. Third of the longitudinal veins behind (or counting from) the subcosta

RAMUS (plural, RANH). Branchlike division of any structure or appendage; a cuticular, curved sclerite that forms the base of a lancet of the sting apparatus

RASTELLUM. "Little rake"; in worker honey bees, a row of closely set spines forming a comb on the distal tip of the hind tibia that functions as a portion of the pollen press

RHABDOMERE. Ranked microvilli on the medial and distal surfaces of the photoreceptor cell, an array that constitutes the photoreceptor organelle (as these photosensitive membranes contain the visual pigment)

ROYAL JELLY. Generic term for glandular products fed to bee larvae; more correctly used to identify those glandular products fed to queen larvae for the first 3 days of life

RUGOSITY. Roughness in surface texture

SCAPE. First (most proximal) segment of the antenna

SCLERITE. Any portion of the insect exoskeleton bounded by sutures

SCLEROTIZED. Process of cuticular hardening and darkening leading to tanned protein called sclerotin

SCUTELLUM. Smaller part of the alinoturn set off by the transcutal suture (fissure) through the posterior part of the Scutum

SCUTUM. Part of the alinotum sandwiched between the prescutum and mesoscutum

SENSILLUM (plural, SENSILLA). One, several, or many aggregated sense cells, usually responsive to a common modality (although some trichoid sensilla may have several olfactory receptor cells and a single mechanoreceptor cell)

SENSILLUM AMPULLACIUM. Basiconic peg organ that is covert within a long cuticular canal within the cuticle and is reported to be an olfactory receptor (see SENSILLUM BASICONICUM)

SENSILLUM BASICONICUM. Olfactory sense organ, consisting of an external small cone or peg, usually unjointed at its base, with lateral side pores that permit ingress of odorant molecules, which contact the dendrite membranes of one to several bipolar sensory neurons within the peg

SENSILLUM CHAETICUM. Hairlike (or bristlelike) sense organ whose function is to detect movement and/or olfaction

SENSILLUM COELOCONICUM. Olfactory sense organ in the form of a pit peg

SENSILLUM PLACODEUM. Platelike olfactory sensillum, abundant on the honey bee antenna

SETA (plural, SETAE). General term for cuticular hairs, which may or may not be innervated

SETOSE (also HIRSUTE). Bearing setae

SPATULATE. Rounded and/or broad at the top and slender at the base

SPERMATHECA. Sac in the female insect acting as a reservoir for sperm received from the male

SPICULE. Slender, needlelike cuticular process

SPIRACLE. Breathing pore in the exoskeleton contiguous with internal tracheae

STERNACOSTA. Internal ridge developed from the (externally visible) sternal suture; usually the bases of the sternal apophyses line up on this ridge

STERNELLUM. Area of the sternum posterior to the bases of the sternal apophyses or the sternacostal suture

STERNITE. Subdivision of a sternal plate; any one of the sclerotic components of a definitive sternum

STERNUM. General name for the ventral aspect of the organism; opposite the dorsal TERGUM

STIPES. One of the basal segments of the maxilla, the distal part of the coxal base of the maxilla and the one to which the maxillary palps and galea are affixed distally

STRIGILIS. That portion of the antenna cleaner at the distal end of the tibia that closes over the notch in the basitarsus (in some texts STRIGILIS and FIBULA are synonymous)

STYLET. Medial part of the shaft of the sting, which is flanked by the barbed lancets (the lancets and stylet combine to form a channel through which the venom is discharged)

SUBALARE. Epipleurite (of the epimeron) that provides anchorage for the posterior muscles of the wing

SUBCOSTA. Wing vein immediately behind and parallel to the costa; the second vein projecting along the leading edge of the wing

SULCUS. Furrow or groove of the cuticle

SUPRAEPIMERON. Upper sclerite of the epimeron

SUPRAEPISTERNUM. Upper sclerite of the episternum

SUTURE. Seam in the cuticle indicating the division of distinct parts of the body wall

TANGENTIAL. Pertaining to a direction oblique to the object in question

TARSOMERE. Any segment of the tarsus (foot)

TARSUS. Foot; the combined tarsomeres

TEGULA. Major, dorsally situated, triangular articular sclerite of the forewing

TELOPODITE. Distal portion of the insect limb beginning with the trochanter

TEMPORAL. Pertaining to the temples, the posterior aspect of the side of the head

TENTORIUM. Endoskeleton of the insect head; in the bee, consisting mainly of two cannular, sclerotized arms extending from the anterior tentorial pits in the epistomal suture posteriorly and upward to the posterior pits in the postoccipital sulcus, including a narrow, arched, hollow rod (tentorial bridge) that forms a bridge between the posterior ends of the bars

TERGITE. Any dorsal sclerite or part of a dorsal segment

TERGUM. Dorsal surface of any body segment, often subdivided into a number of smaller segments or sclerites

TERMINAL. Last, ultimate

TERMINALIA. Terminal or last abdominal segments, usually including the genital structures

TERMINUS. Extremity (at either end)

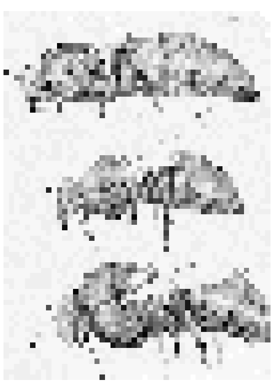
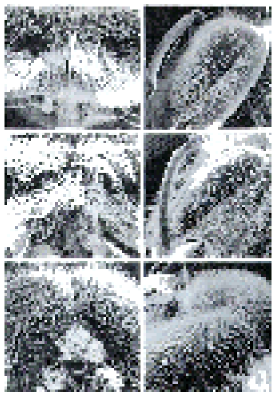
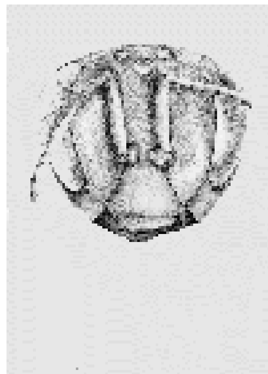
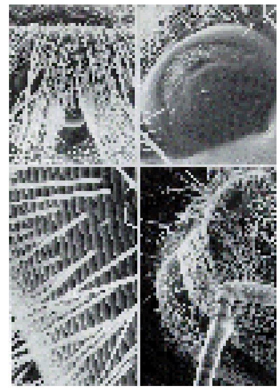
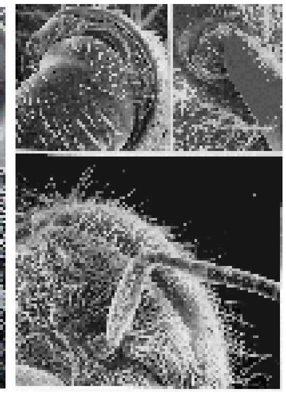
THENAR. Prominence at the base of a claw

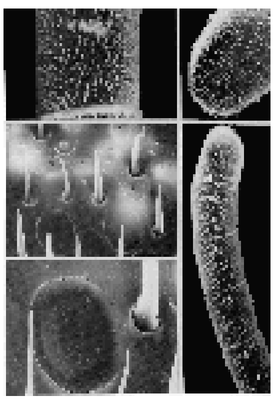
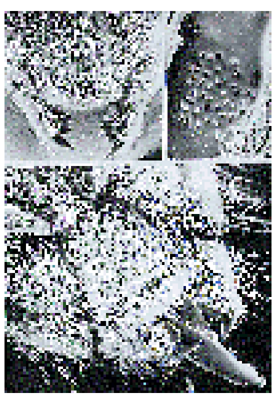
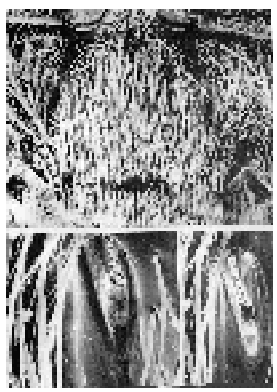
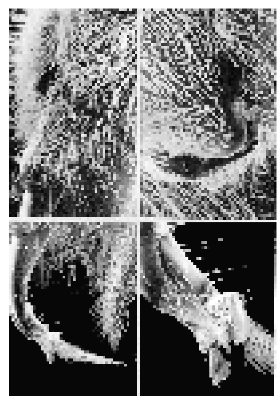
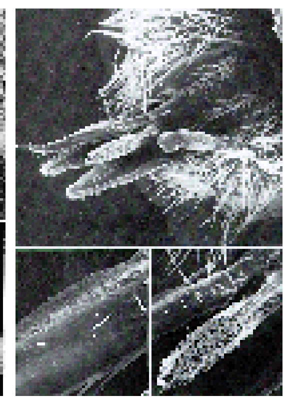
THORAX. Second body region of the insect which bears the true legs and wings

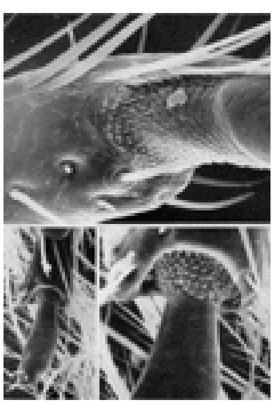
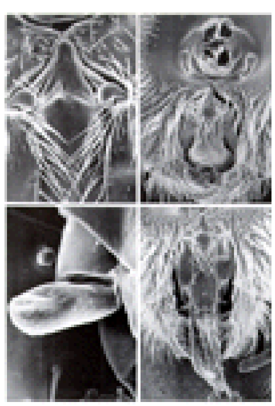
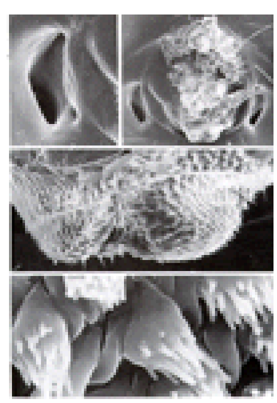
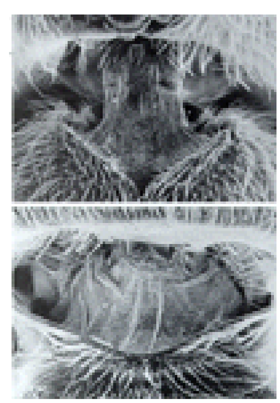
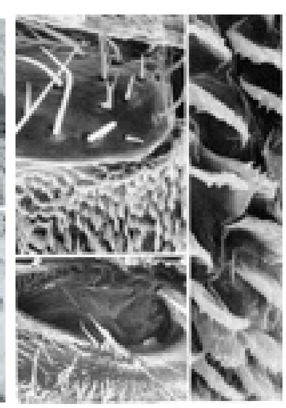
TIBIA. Fourth division of the leg, situated between the femur and the tarsus

TORMOGEN CELL. Epidermal cell that gives rise to the socket housing a seta, then later functions as

THE HEAD

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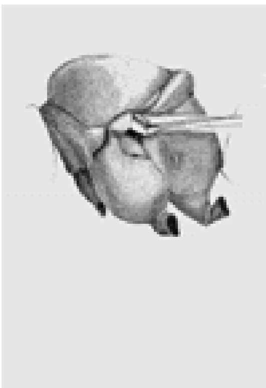

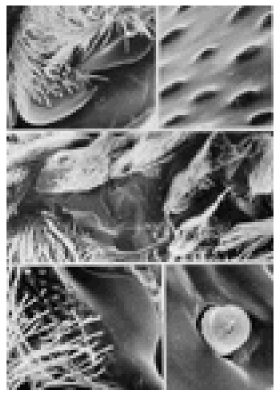
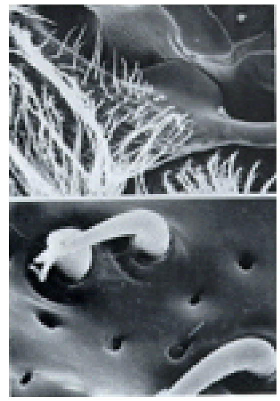
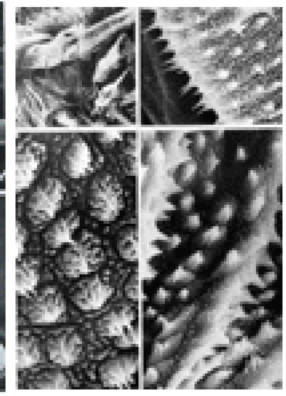

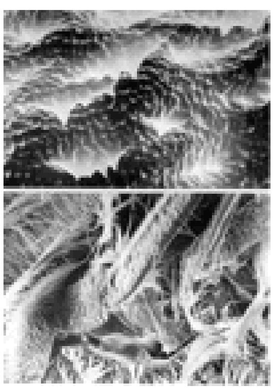

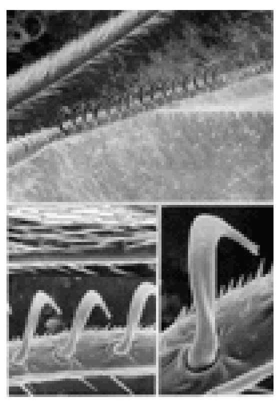

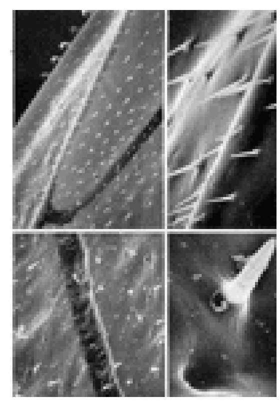

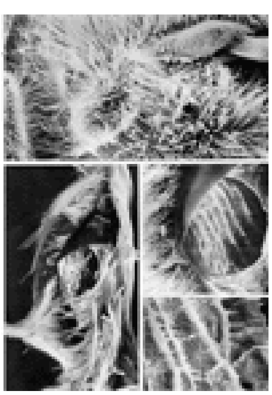
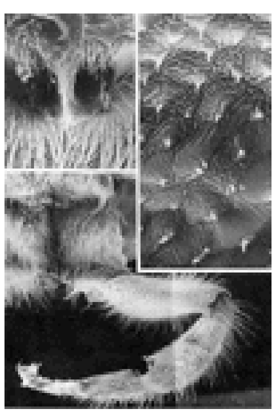
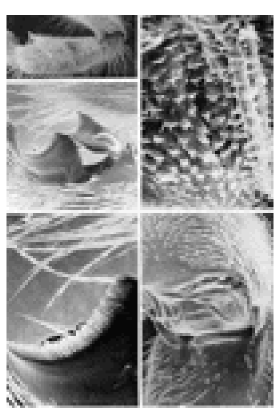
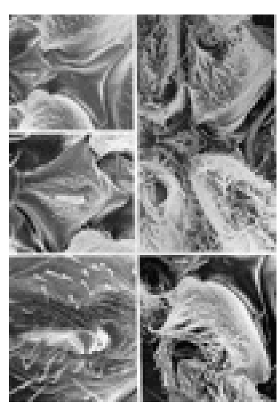


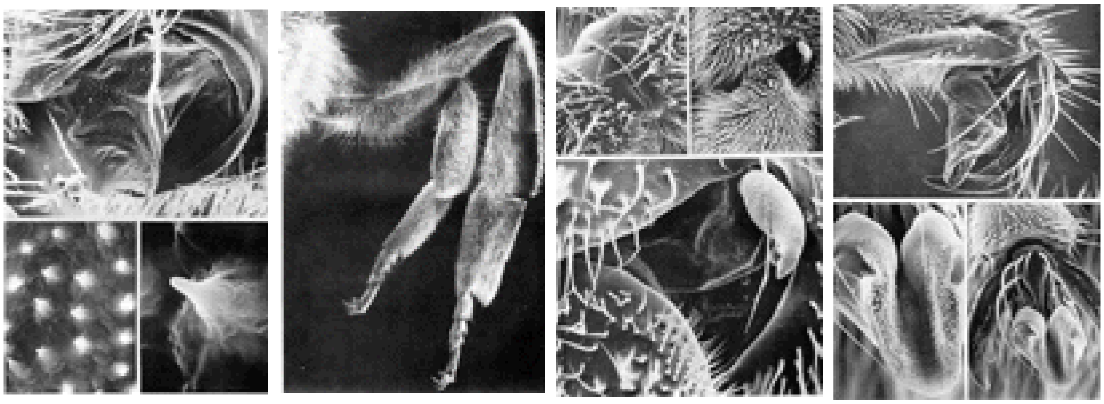

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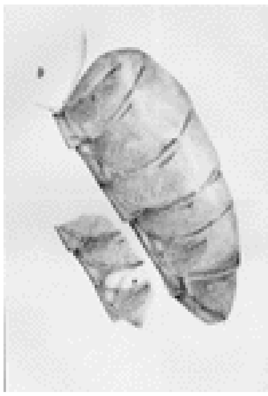
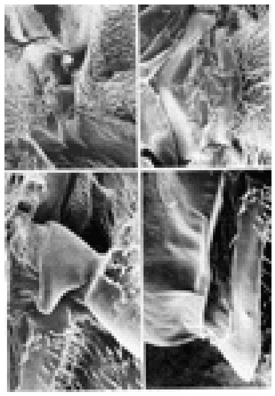
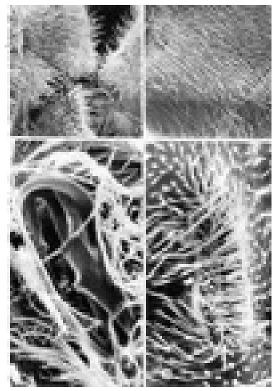
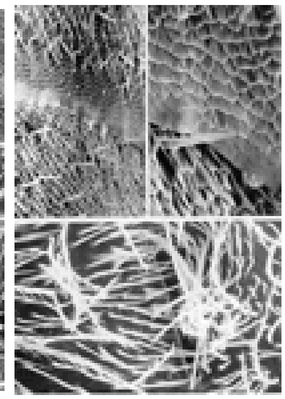
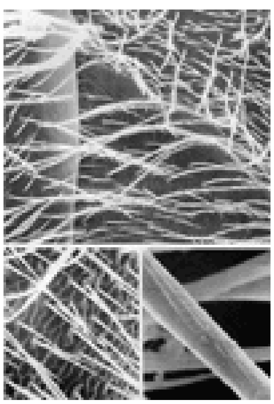
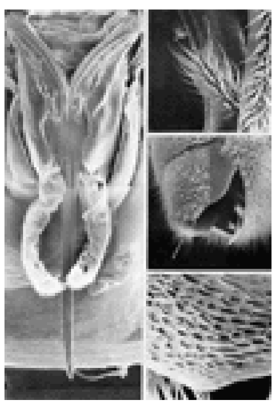
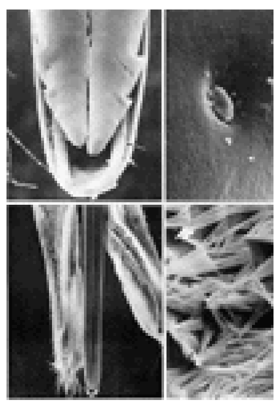
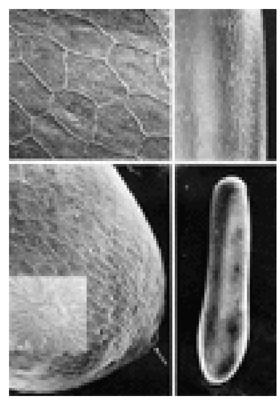



QUEENS ARE THE PRODUCT of fertilized eggs; they receive a special diet throughout larval life consisting of royal jelly for the first 3 days and a modified jelly thereafter. Caste is apparently determined by food volume and the quantity of juvenile hormone and water in the larval diet. Sixteen days are needed to complete development from the egg. When a colony of bees decides to provide itself with a new queen, several are reared. Usually, the first queen to emerge kills her sisters and, if the mother is present, disposes of her as well. After about 5 days of adulthood, the virgin queen begins a series of mating flights. As a result, a queen may mate with 6 to 18 or more drones and store 5 to 12 million quiescent sperm in a special sac in her abdomen called a spermatheca. Once this initial period of copulation is passed, the queen no longer attempts to mate. Instead, her abdomen enlarges to accommodate her fertile ovaries and she becomes an egglaying machine. A queen may live I to 2 years, although life spans in excess of 5 years have been reported. Normally, however, 60 percent of the queens die or are replaced during the first year.

Relationships between individuals within a colony may be quite complex. A new queen is usually reared within a colony from one of the many eggs produced by her mother, and thus a queen is often simultaneously a mother of some colony inhabitants and a sibling of others. As a consequence of a unique sex determination system, there are three possible levels of relationship among siblings within a colony. Those that have the same father are super sisters, those whose fathers are brothers are full sisters, and those with unrelated fathers are half sisters. Thus worker bees within a colony cannot be considered a homogeneous genetic mixture. The colony is in fact a collection of subfamilies different in genetic origin.

The queen is fed and groomed by worker attendants. Her egg-laying rate is governed by the workers, probably through the amount of food they provide her. Reported maximum egg-laying rates vary; some authorities report production in excess of 2000 eggs per day. The queen is capable of laying 2 to 3 times her body weight in eggs in a single day. A queen determines the sex of her progeny by fertilizing or withholding sperm from the egg as it passes down the oviduct (the mechanism by which a queen accomplishes this is unknown). The fertilized and unfertilized eggs are deposited correctly in worker and drone cells respectively.

Although larval diet is the single factor that governs eventual development of a queen (worker larvae receive a different larval food), there are at least 53 known characteristics that differentiate a queen from her sister workers. Notably the queen's eyes are smaller and her brain is reduced in size. Her only complex behavior seems to be that of seeking out and killing sister queens and mating.

Humans have learned to control the genetics of honey bees, and production of hybrid honey bee stock has been under way for many years. The purpose of this hybridization, as with other species, is to incorporate a number of favorable characteristics into a single genetic line. To accomplish this, methods have been developed for the instrumental insemination of queens. Completion of a successful hybrid system hinges on development of an adequate means of germ plasm (sperm or egg) storage or maintenance.

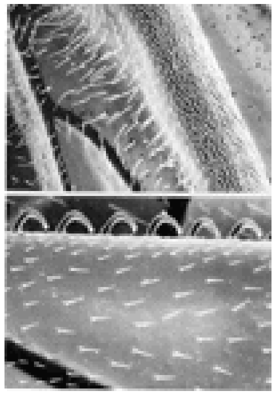
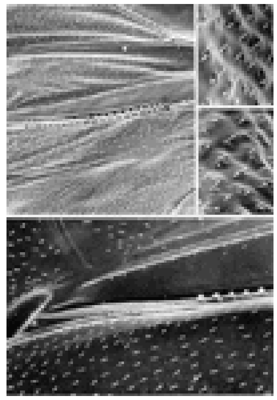
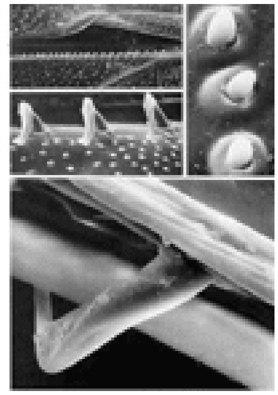
The plate layouts, determined primarily by subject matter, were created for their instructional value and to enhance reader interest. The sequence of micrograph identifications thus varies according to the location of the survey micrograph(s). Unless indicated otherwise, the micrographs are oriented so that the head is to the left, the dorsal side at the top.

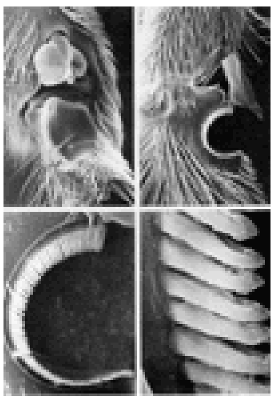
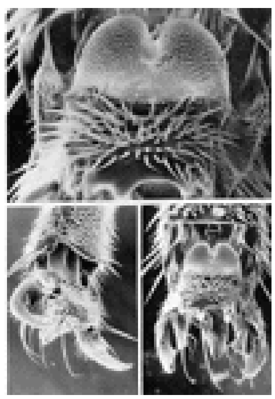
Back to THE QUEEN

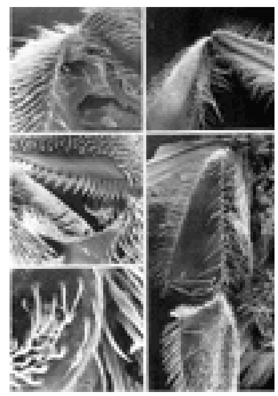
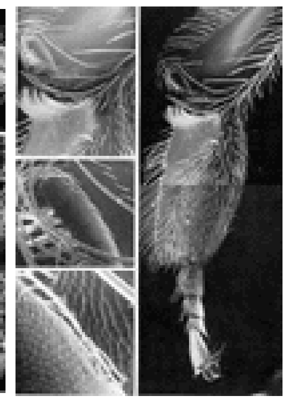
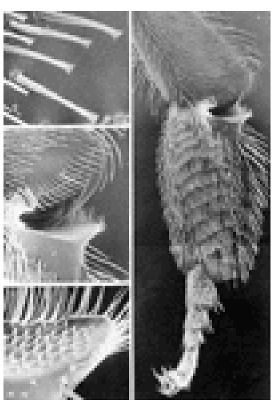
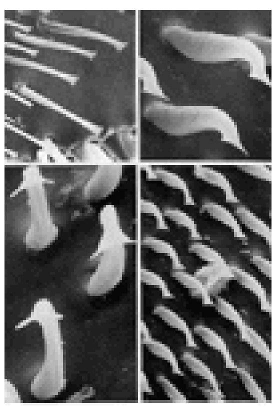
THE HEAD

BACK TO "THE WORKER"

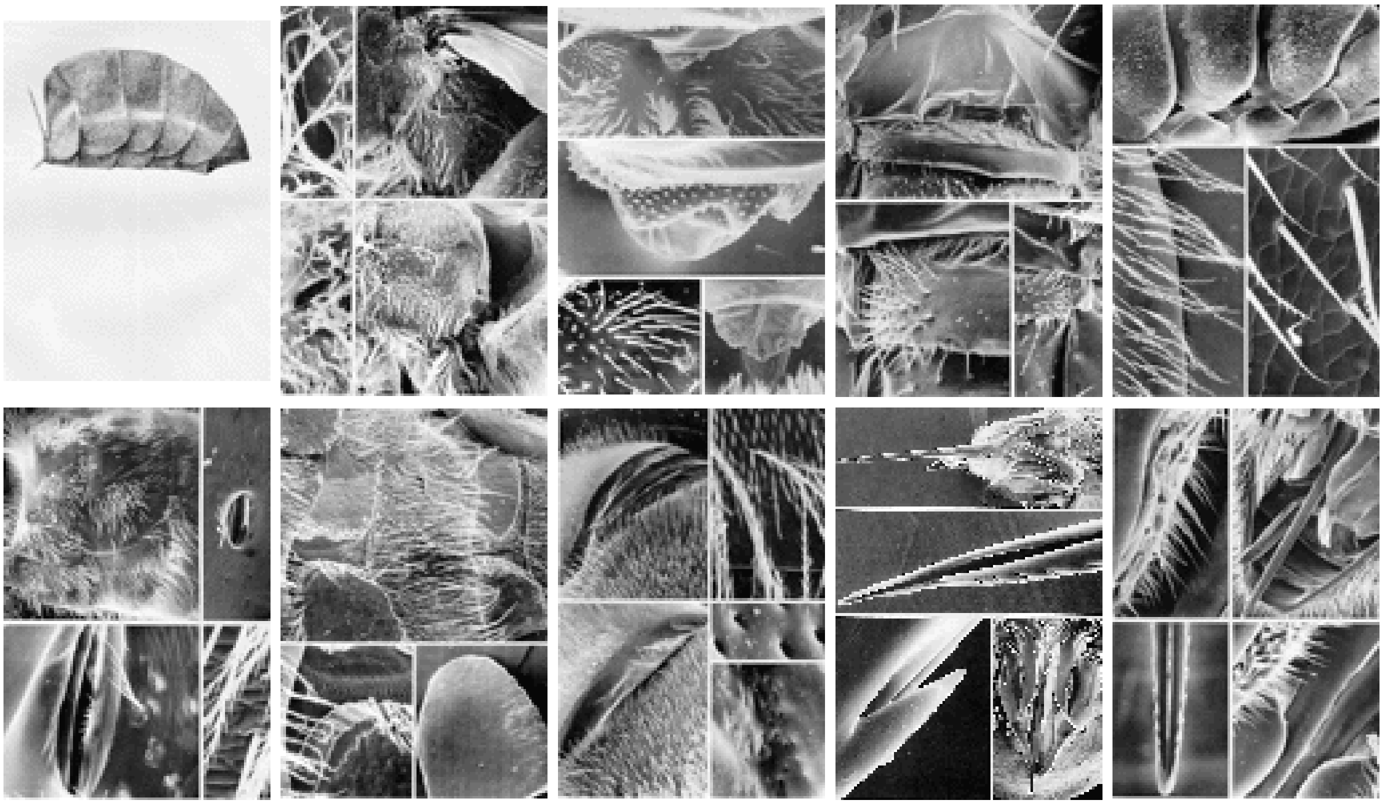
THE THROAX

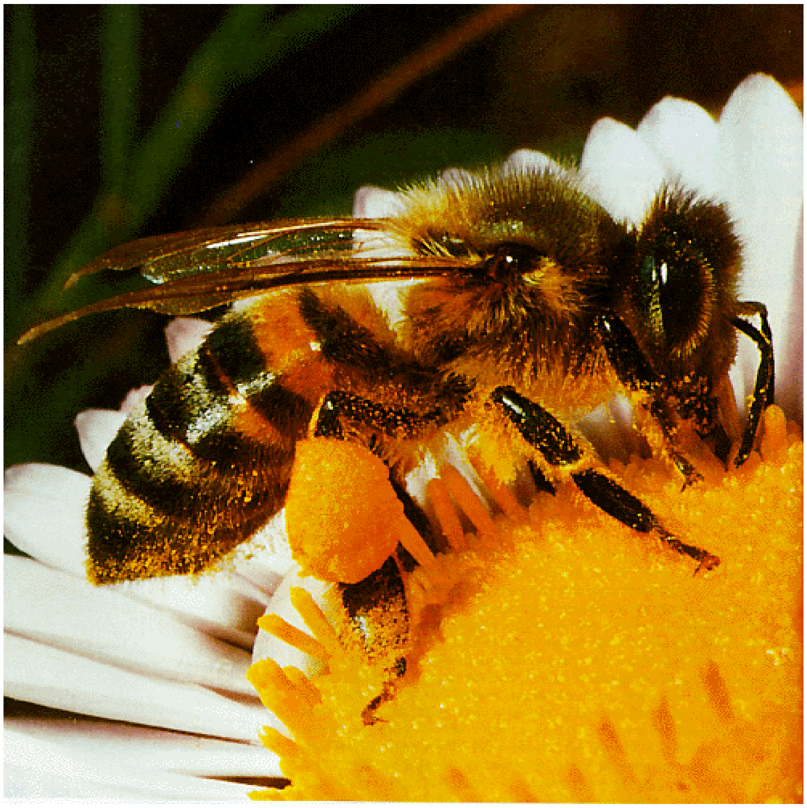





THE ABDOMEN





WORKER BEES ARE IMPERFECT FEMALES

maternally developed to provide all life support systems. Together with the sexually developed queen, also an imperfect female, the workers form the perfect female system-reproduction plus sustenance.

Worker honey bees are produced from fertilized eggs in 21 days (compared with 16 for queens). They lack fully developed sex organs as a result of a controlled diet that leads to hormonal deficiencies. However, some workers may develop functional ovaries and lay significant numbers of unfertilized eggs that develop into drones. Moreover, it is reported that worker bees in queenless colonies can produce female offspring from diploid eggs via parthenogenesis (that is, without mating). This occurs most frequently in one race of bees, which occasionally requeen colonies with worker-produced progeny.

Workers are the labor force of the colony, performing specialized duties based primarily on their age. Early in adult life they engage in hive duties such as brood rearing, comb construction, and colony defense, while late in their lives they become foragers.

Contrary to popular opinion worker bees are frequently idle, and foraging bees are highly opportunistic. Hive bees spend most of their time unproductively, and foragers prefer the most lucrative nectar and pollen sources. Although the divisions of labor are fairly clear-cut based on age, research has shown that in a worker population with an unbalanced age structure resulting from some catastrophic event, individual worker bees will adapt and assume duties that are not normal for their age. It has been shown that when bees are forced to modify their behavior in this fashion they perform less effectively than when they follow a normal sequence of development. Although the pheromones produced by the queen are necessary to maintain the integrity of the hive, worker bees are thought to control the fate of the colony by their activities, such as governing where and how many eggs the queen lays, replacing a failing queen, or ensuring the production of drones. The life span of worker bees is 4 to 6 months in the winter but only 28 to 35 days in the spring and summer.

Individual foraging bees readily discriminate between sources and normally retain a high degree of fidelity to a single source. Differences in foraging cues such as color, aroma, and taste are often subtle, but these modalities are handled with ease by the workers' sets of finely tuned receptor cells. Bees have an excellent sense of direction and time. Their chronometric powers permit them to emerge from the hive each day at the precise time a certain plant species begins to produce nectar or pollen. They also have an excellent memory, especially for odors. After one experience they can remember for 6 days; after three experiences they can remember for 2 weeks.

Honey bees forage between about 16'C (61'F) and 43'C (100'F). Honey bees are photonegative below 16'C; most plants do not even secrete nectar below 15.5'C (60'F). The honey bee eye, like that of many insects, is adapted to perceive rapid movement. This exceptional visual resolution enables bees in flight to discern the complex shapes and broken patterns of objects below, such as colored flowers against a green background. Bees have three visual pigments in each eye that permit them to see hues in the ultraviolet spectrum as well as the portion of the color spectrum (except red) visible to humans.

A bee collecting nectar normally makes 7 to 13 trips per day (the average is 10, the maximum recorded is 24), spending 27 to 45 min per trip. Flight speeds average 14.8 km (9.2 mi) per hour loaded and 13 km (8.1 mi) per hour empty. In doing so, a worker can visit as few as 5 or as many as 800 flowers in a single trip. When filled, the honey stomach can hold up to 85 percent of the weight of the bee. Bees collecting pollen usually take 6 to 10 minutes to gather a load, making 6 to 12 trips per day (the average is 10, the maximum reported is 47). On a single trip a bee will visit I to 200 flowers. The weight of a pollen load can be 20 to 33 percent of the weight of the bee. These estimates are variable, of course, and depend on the productivity of the plant source(s) involved and the needs of the colony. Research has shown that individual worker bees have an 804-km (500-mi) maximum lifetime flight limitation, determined by the exhaustion of her enzymatic mechanisms of carbohydrate metabolism.

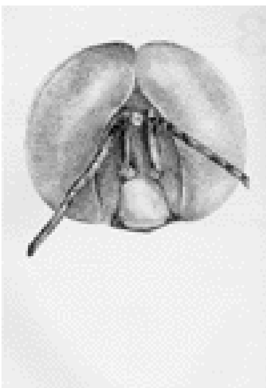
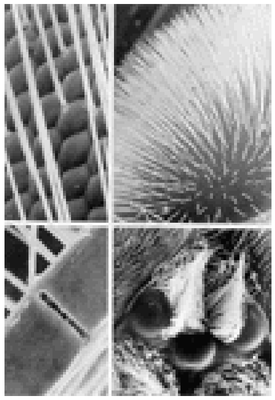
When gathering pollen, a bee often uses both mouthparts and forelegs to dislodge pollen from the flower so that she becomes dusted with pollen. She then uses tarsal brushes on the foreleg to clean her mouthparts and head. Following this she uses similar brushes on her middle legs to clean the forelegs and thorax. Then with her hind legs she cleans the wings, abdomen, and middle legs. When cleaning the middle legs the bee grasps each leg between the pollen combs of the hind legs, drawing it past the combs. Interestingly, the result is that pollen taken from the right side of the bee is deposited in the left comb and vice versa. Then to pack the pollen the bee uses the rastellum (rake) on the opposite leg to clean each comb and force the pollen into the pollen press of that leg, which squeezes it (like toothpaste from a tube) up into the pollen basket on the outside of the hind leg. Thus in the packing process, pollen is moved from one side of the body to the other and then back again.

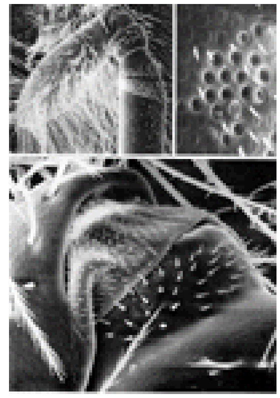
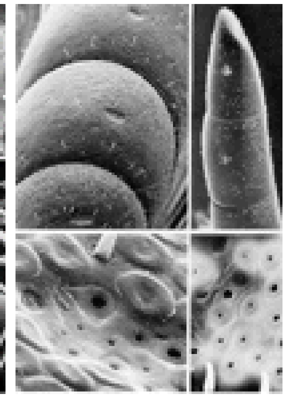
Since the tip of her sting is heavily barbed, the worker bee normally loses her sting when she impales an enemy as she attacks in self-defense or in defense of the hive. Shortly thereafter she dies as a result of a sizable loss of internal organs and tissue. If she doesn't lose her sting but empties the venom sac the worker is unable to replenish the venom. Adult worker bees must eat pollen (bee bread), grow, and mature before they have a full complement of venom. Venom gradually accumulates until the bees are about 15 days old. Hence, young bees are unable to sting effectively.

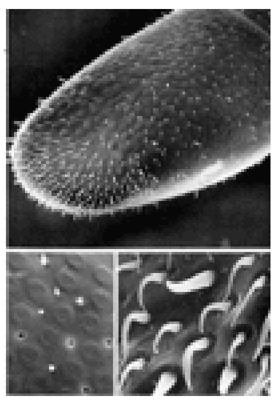
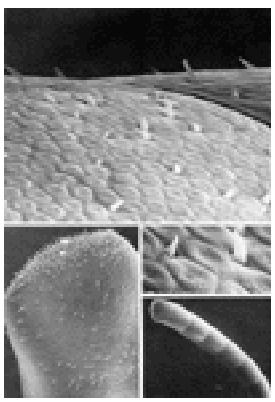
Some enemies of honey bees, such as skunks, are unaffected by large numbers of stings. Others, such as humans, may develop a hypersensitivity to the venom, which can be lethal; such people number less than 1 or 2 percent of the world population. (Recent studies have shown that most hypersensitive people do not react more intensively with each successive sting. Rather their level of reaction remains the same or decreases slightly with each event.) Normally, people who work with bees and are stung routinely eventually develop immunity to the extent that each additional sting produces only a small wheal or minimal swelling at the site of the sting.

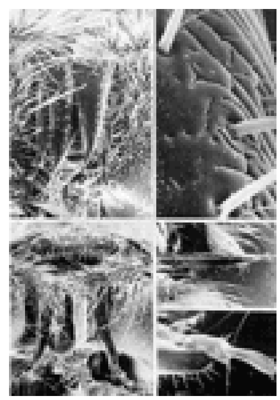
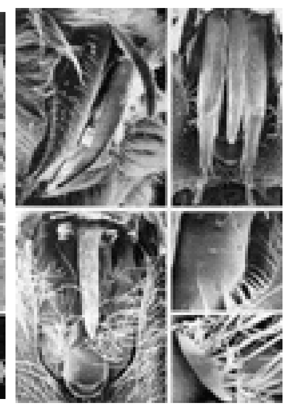
RETURN TO "THE WORKER"

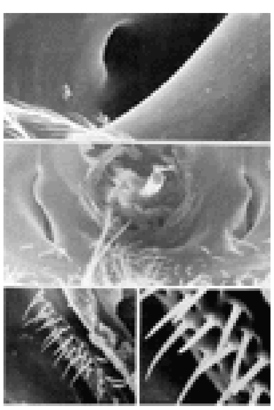
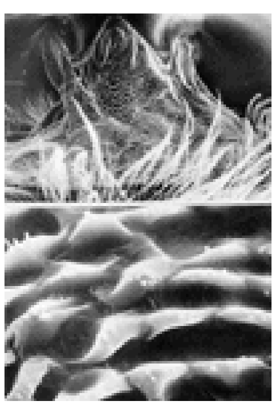
THE HEAD

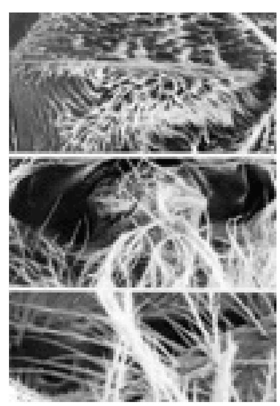



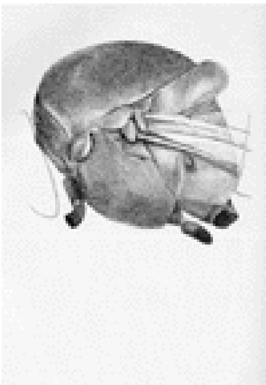



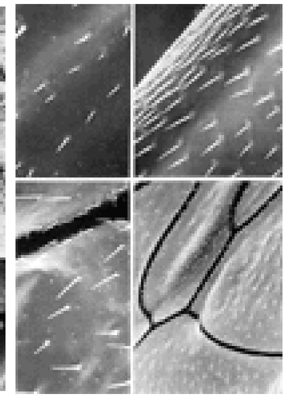
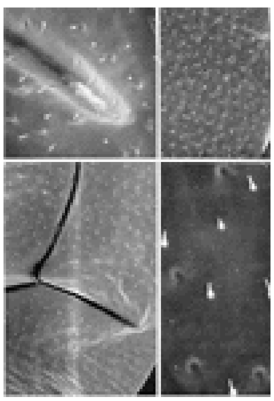
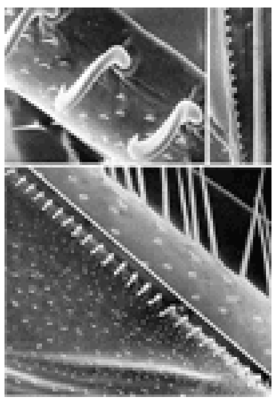
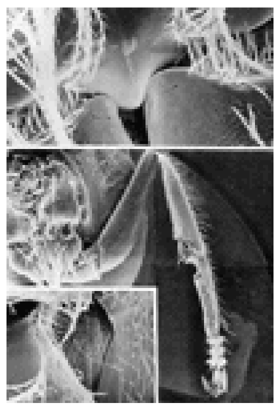
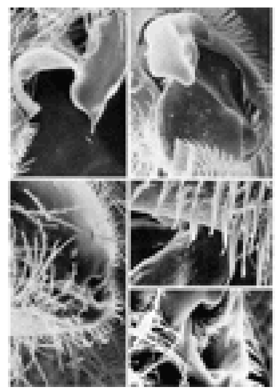
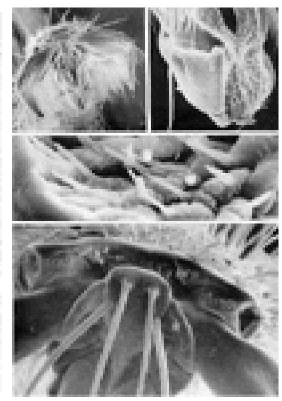
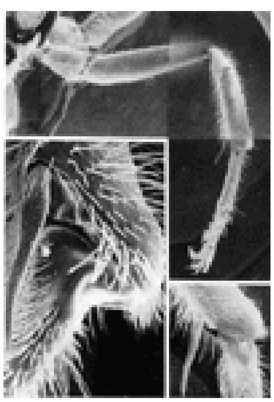



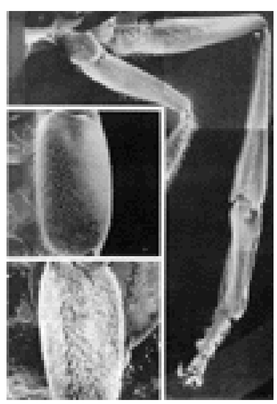
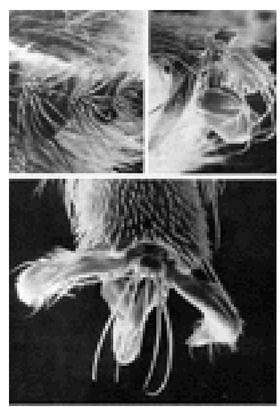



THE THORAX

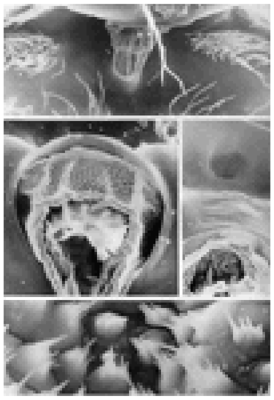
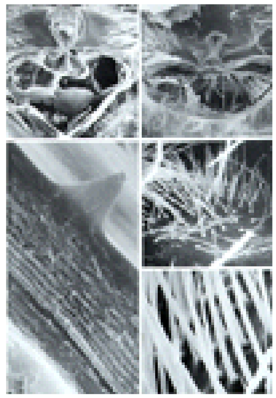


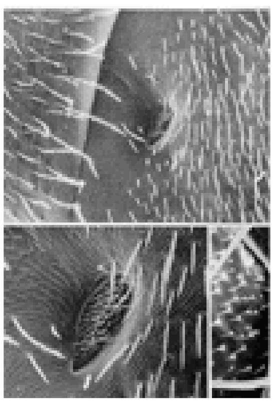
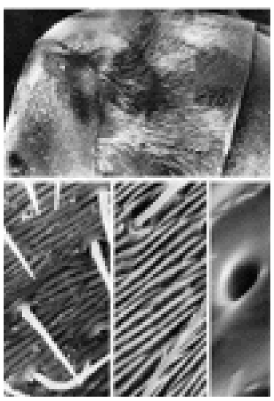
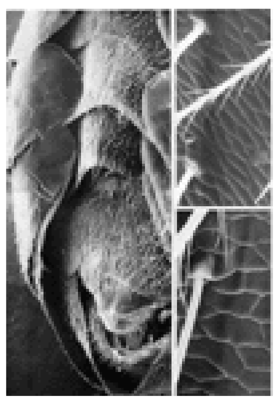


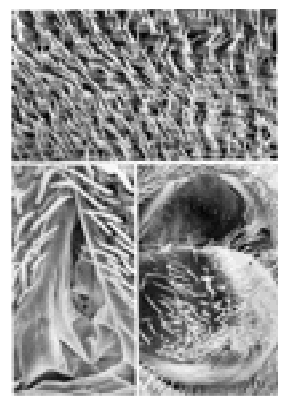








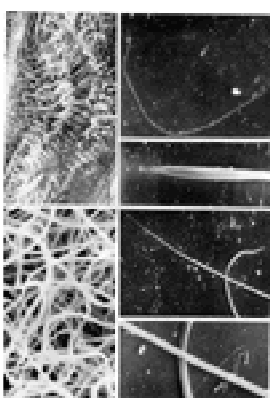



THE ABDOMEN



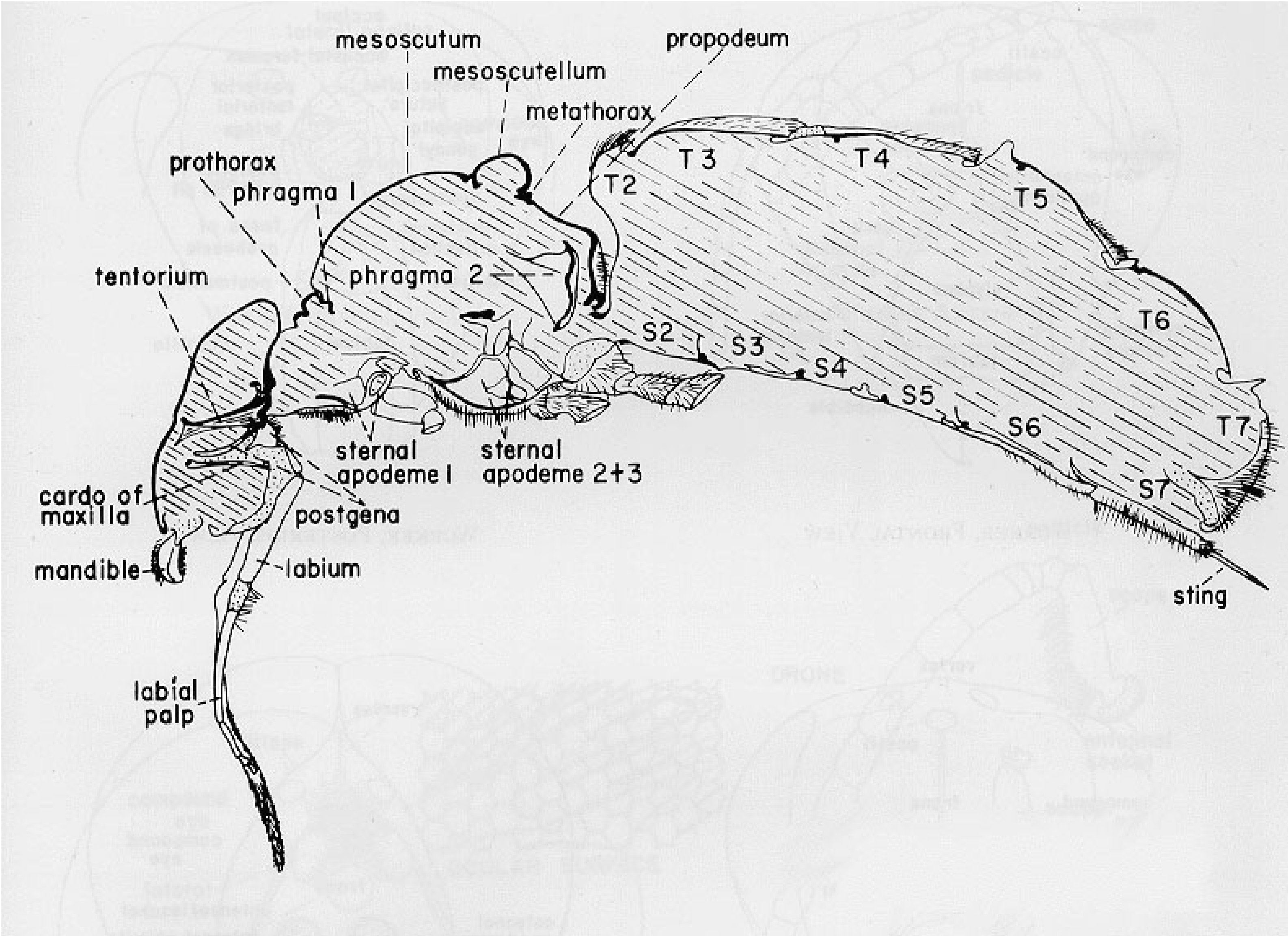
THE DRONE

DRONES ARE PRODUCED PARTHENOGENETICALLY (that is, from unfertilized eggs) and have a grand-father but no father. As a consequence, drones are haploid, having only one set of chromosomes (N =16) as opposed to two sets for queens and workers (N = 32). Development from egg to adult requires 24 days. These male honey bees, broader and heavier than queens, are defenseless, do not forage, and to a great extent are dependent on worker bees for their daily needs. Early in their adult life drones are fed by workers but later in life they feed themselves on honey stored in the hive. In cooler climates, drones are normally present only during the summer months and their life span is only about 2 :months. Late in the fall they are driven out of the hive by workers preparing for winter and eventually die due to starvation, exposure, or predation.

The drone's sole purpose for being is mating and, if successful, his reward is death. Drones have highly developed sense organs for mating. These include large eyes capable of nearly 360' vision with many ultraviolet receptors that enable a pursuing drone to silhouette the queen against skylight. Drones also have highly modified antennae for detecting the scent of the queen. They are sexually mature after 10 to 12 days and may embark on as many as 25 flights during a lifetime. Each flight lasts about 30 to 60 min.

When the weather is favorable, groups of airborne drones called comets gather to await passage of a queen on a mating flight. The congregation areas are characterized by particular air currents and landmarks. Drones locate the queen by her scent and, using their powerful wings, chase her. Eventually one catches the queen, and they copulate in flight. Air pressure from the abdominal respiratory system expels the male genitalia. An audible "pop" signals a successful mating and the demise of the drone, which falls to the ground.

Worker bees may develop functional ovaries and produce unfertilized eggs that develop into drones. These drones will be full sized if raised in drone-sized cells but much smaller if raised in worker cells. All are sexually functional.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mesoscutellum
propodeum
metathorax
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phragma 1
T2
T3
T4
T5
T6
T7
tentorium
phragma 2
S2
S3
S4
S5
S6
S7
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sternal apodeme 2+3
cardo of maxilla
postgena
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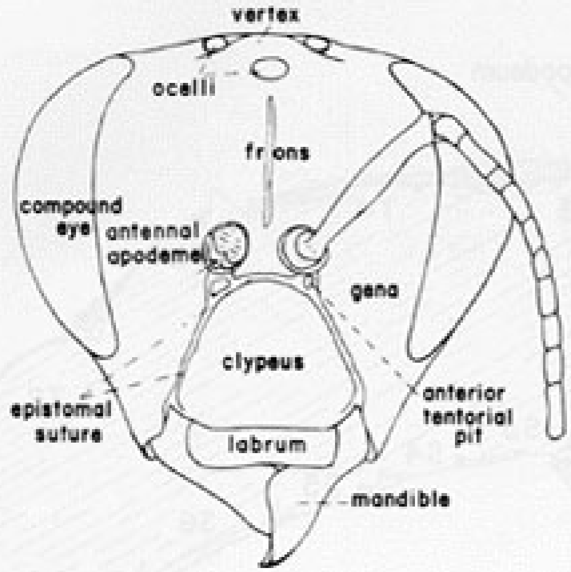
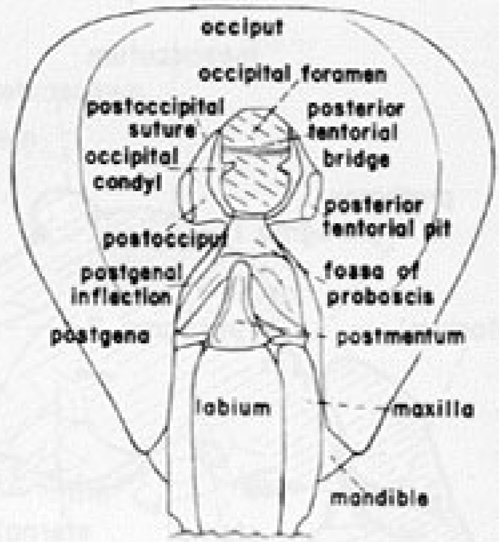
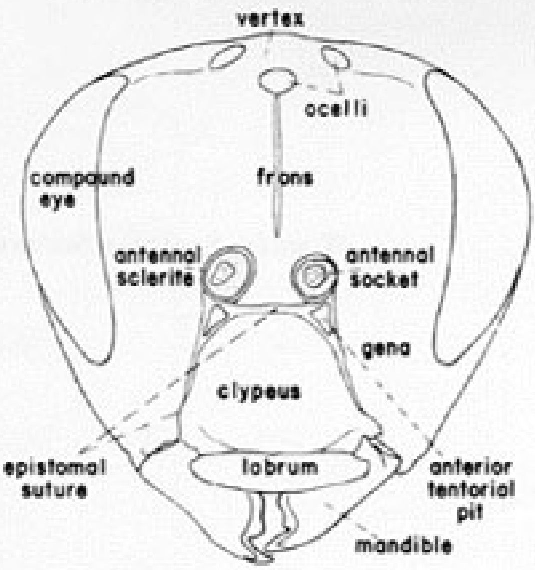
labium
labial palp
sting



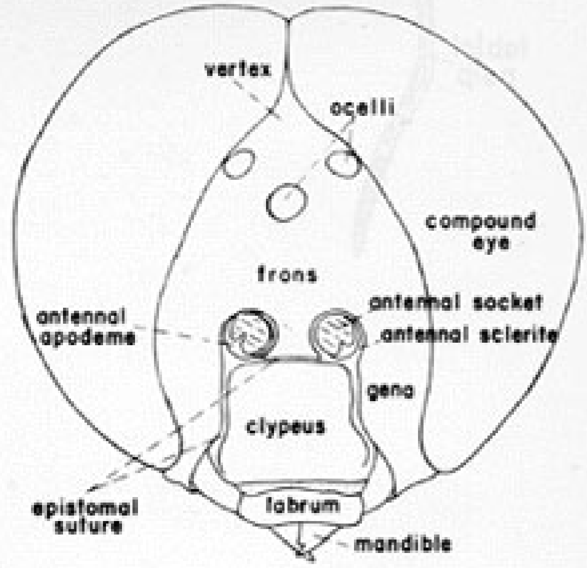
Worker, Frontal View



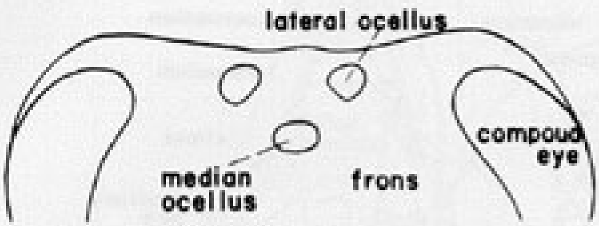
Worker, Posterior View



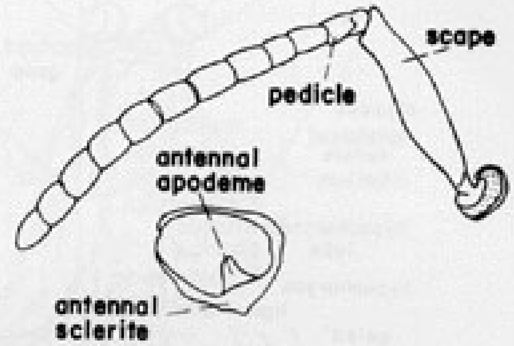
Queen, Frontal View



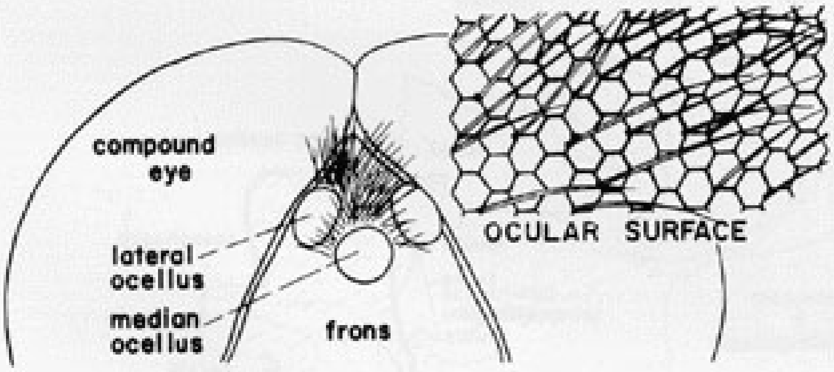
Drone, Frontal View



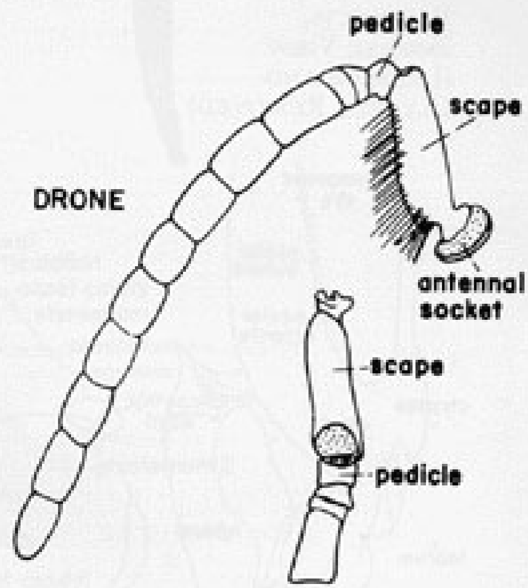
Worker, Dorsal View



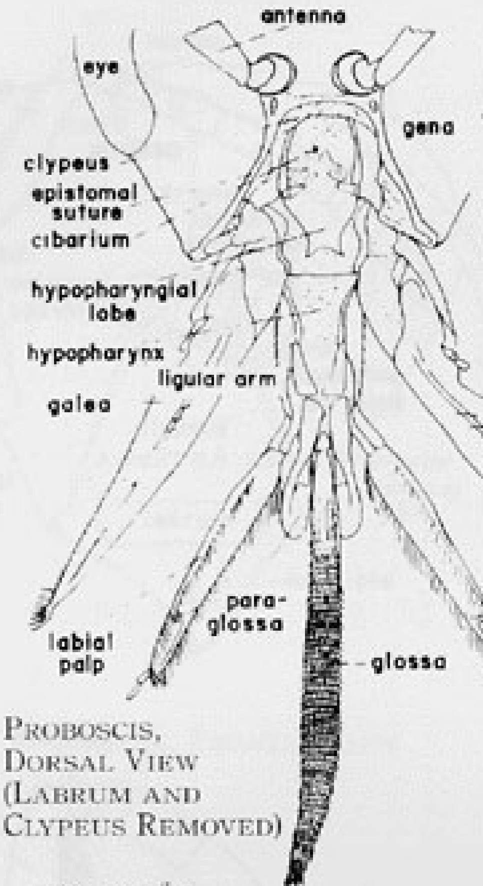
Worker Antenna



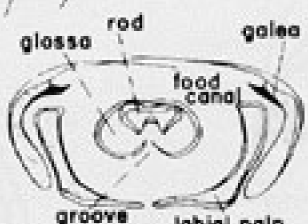
Drone, Dorsal View



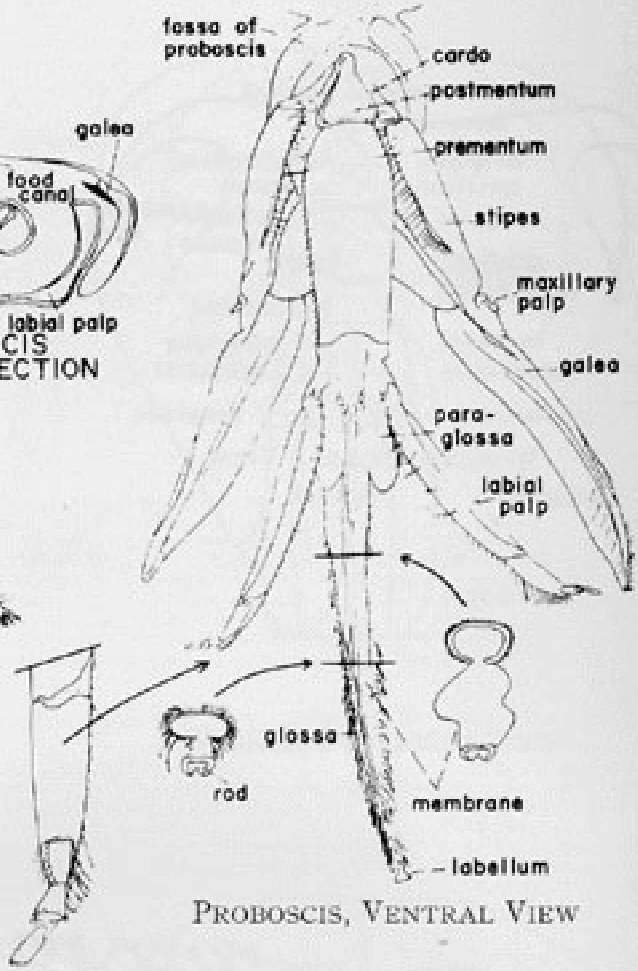
Drone Antenna



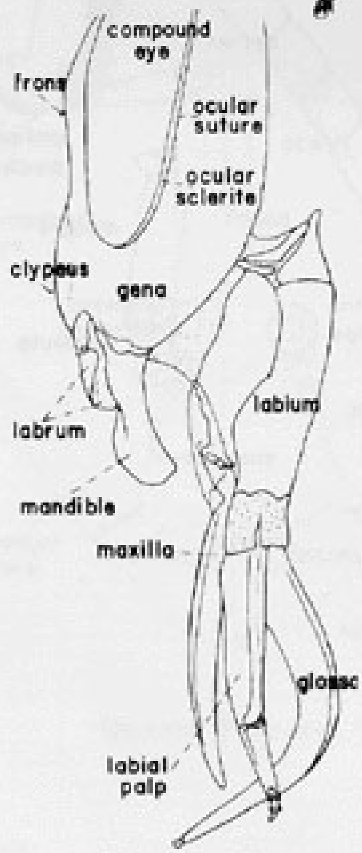
PROBOSCIS, DORSAL VIEW (LABRUM AND CLYPEUS REMOVED)



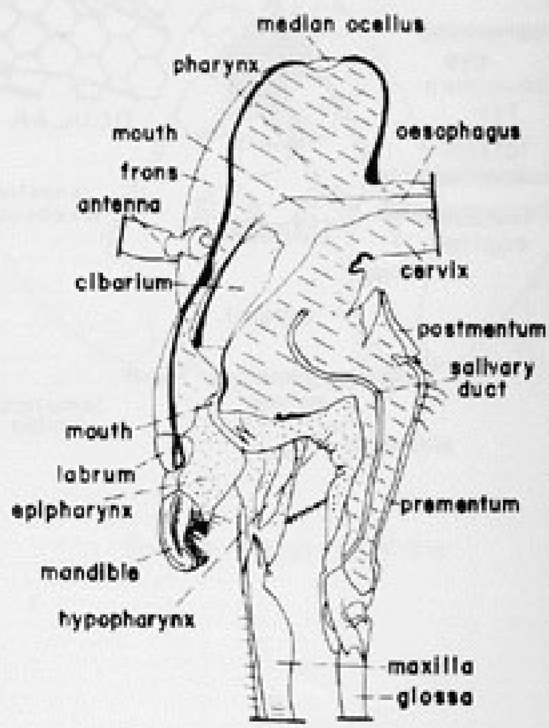
PROBOSCIS CROSS SECTION



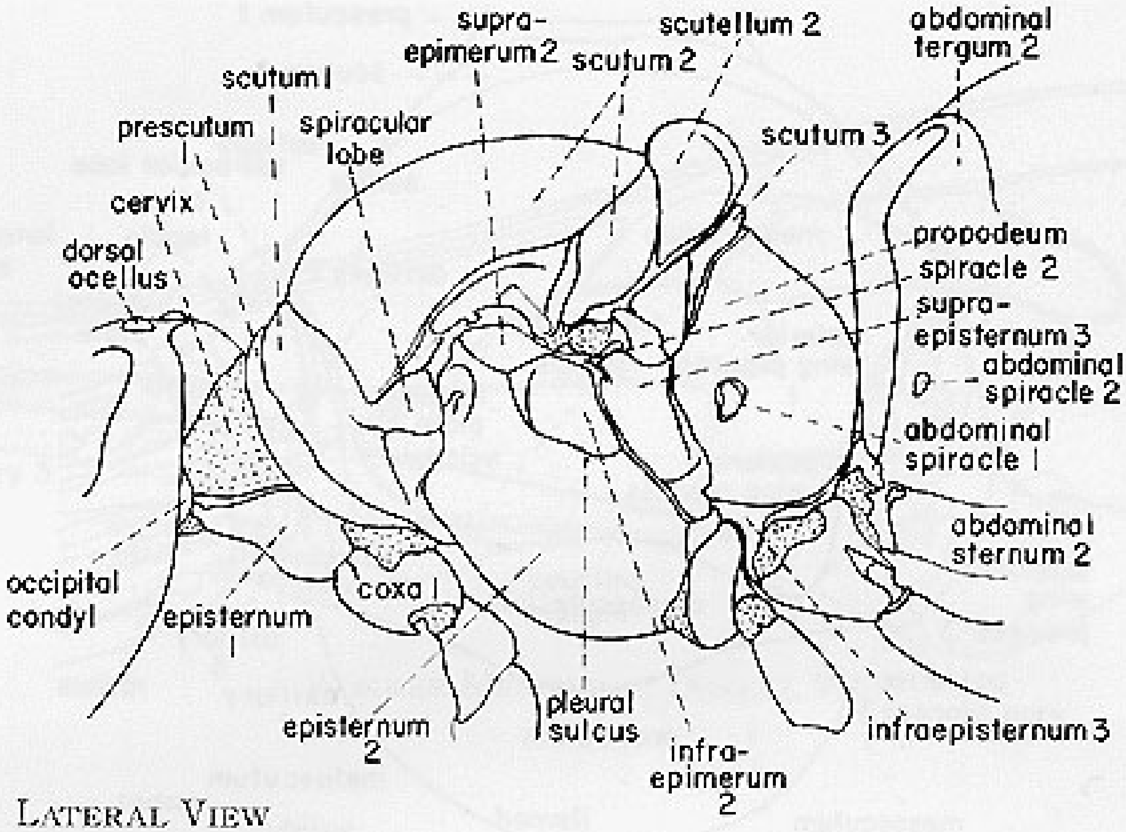
PROBOSCIS, VENTRAL VIEW



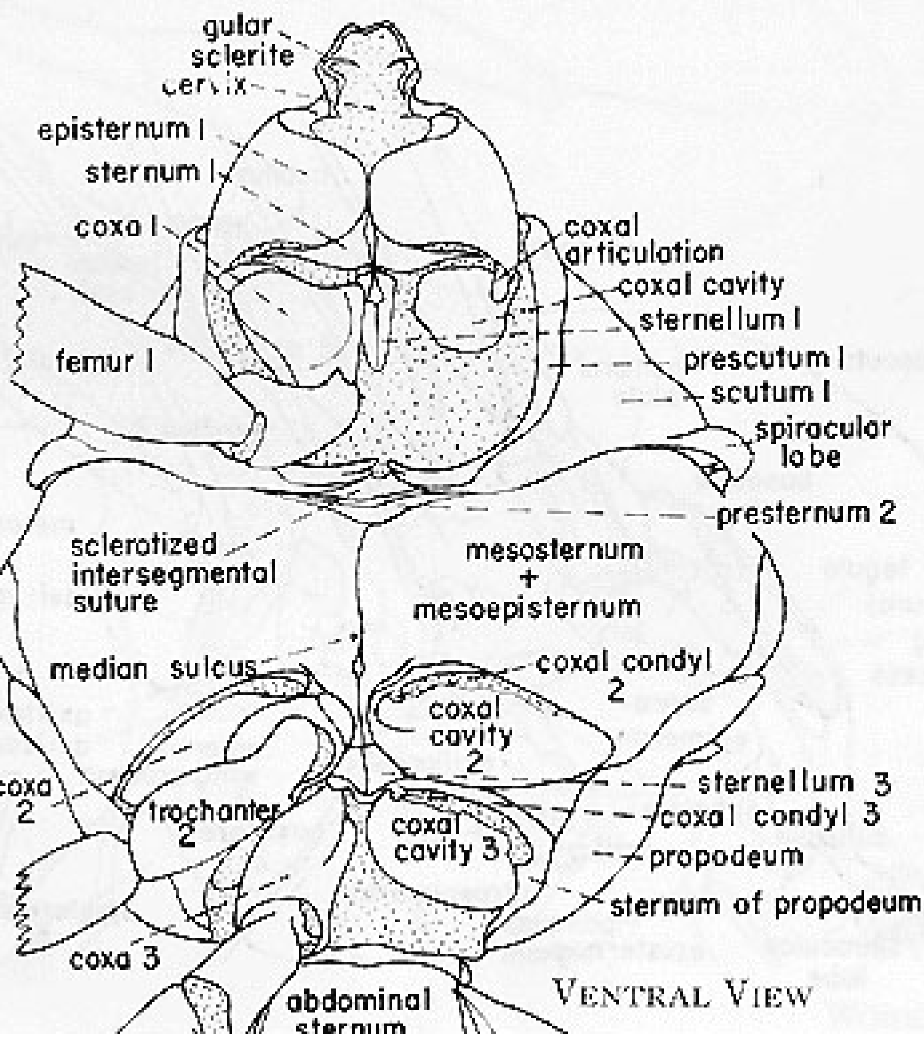
WORKER, LATERAL VIEW



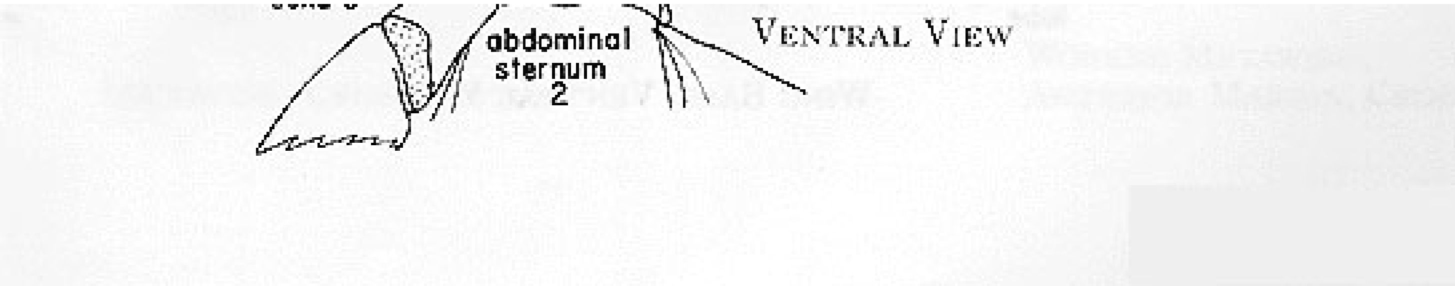
WORKER, SAGITTAL SECTION



Lateral View



Ventral View


abdominal
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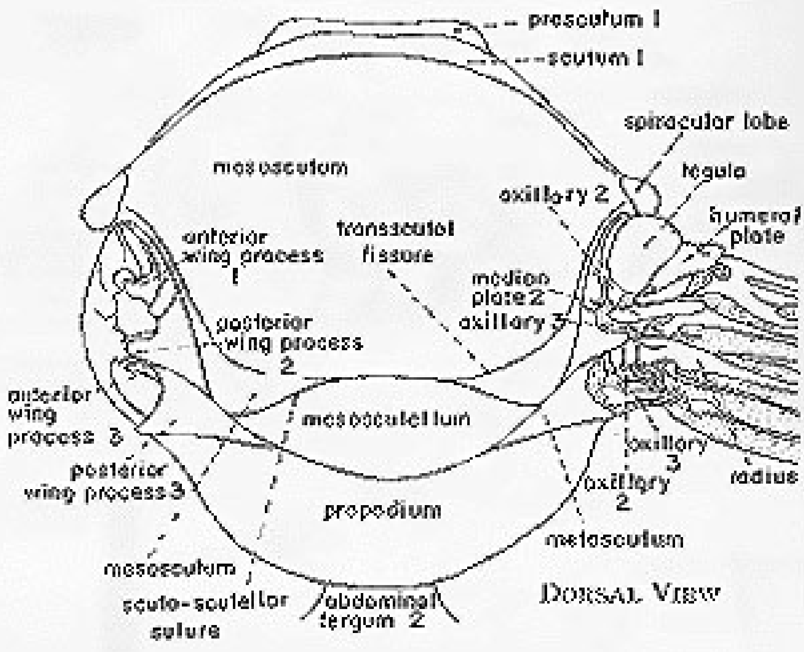
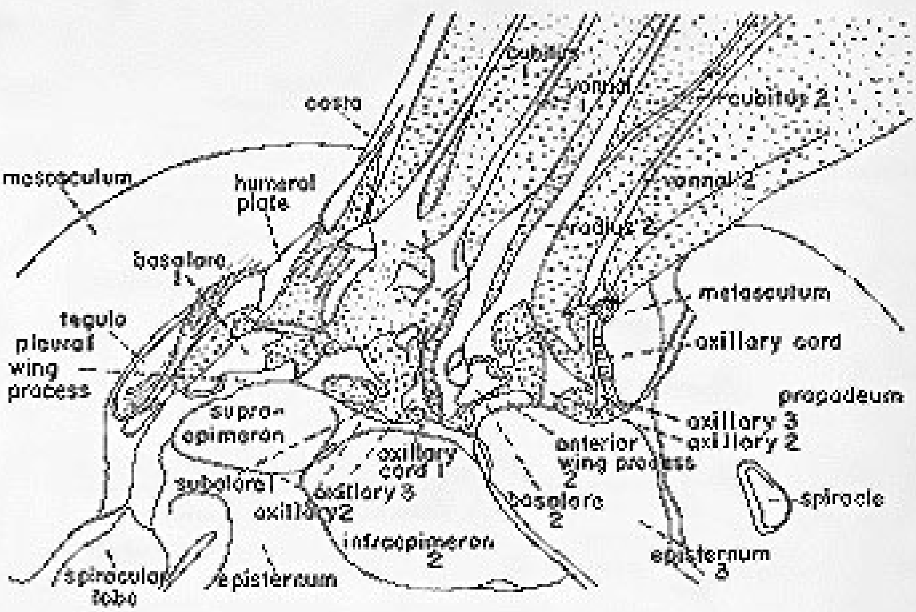
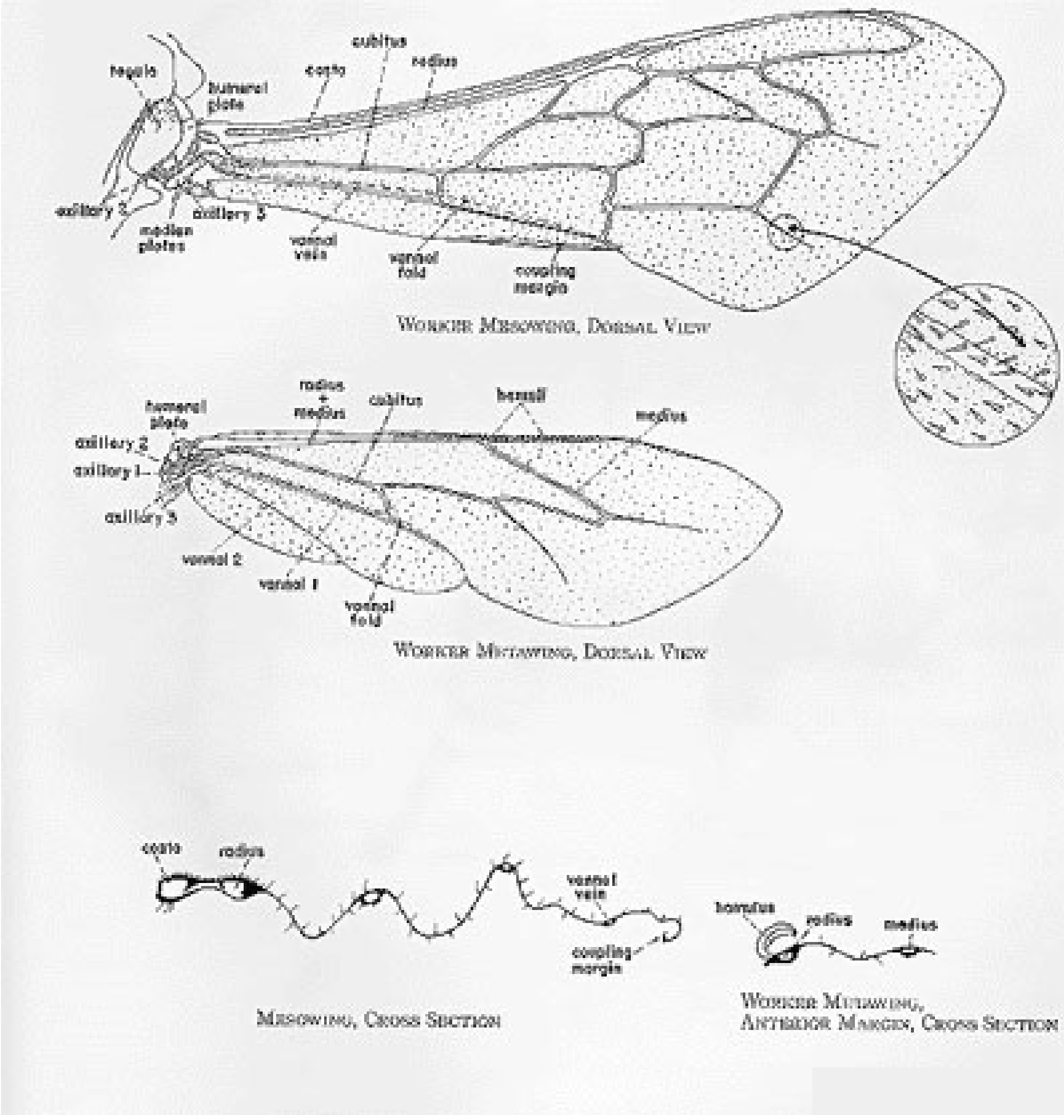
VENTRAL VIEW



DORSAL VIEW



WING BASE, VENTRAL VIEW

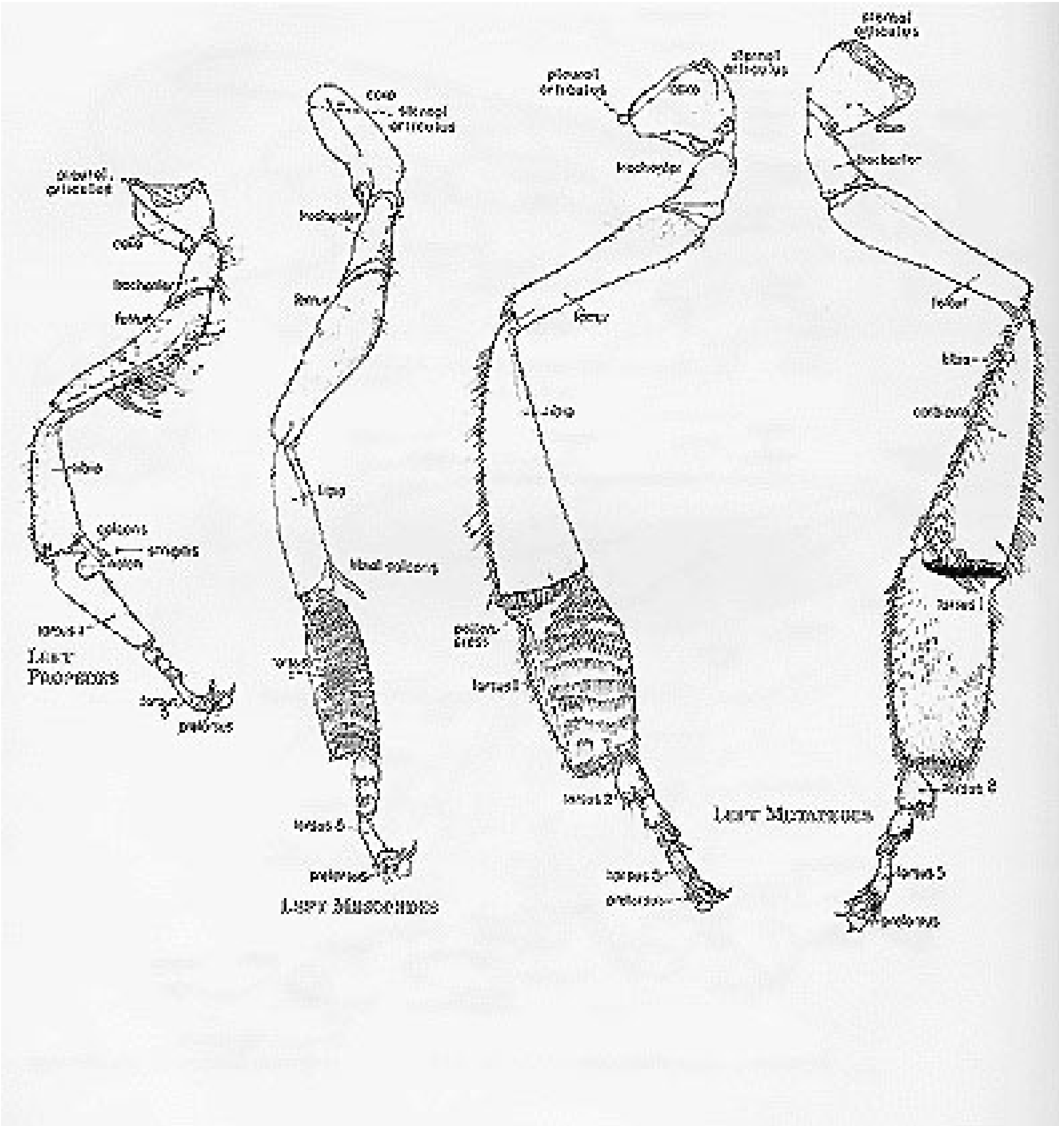


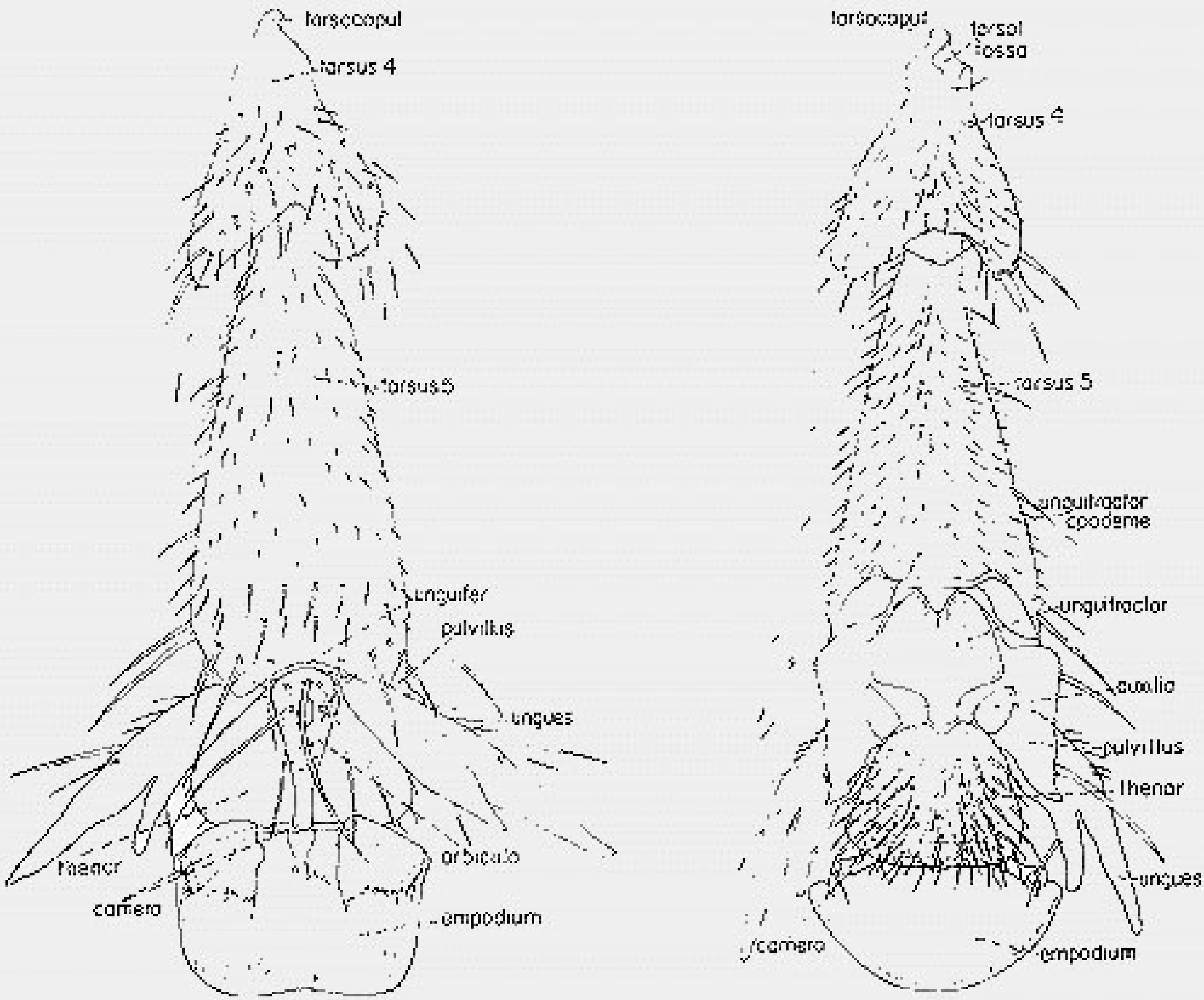
Worker Mesowing, Dorsal View

Worker Metawing, Dorsal View

Mesowing, Cross Section

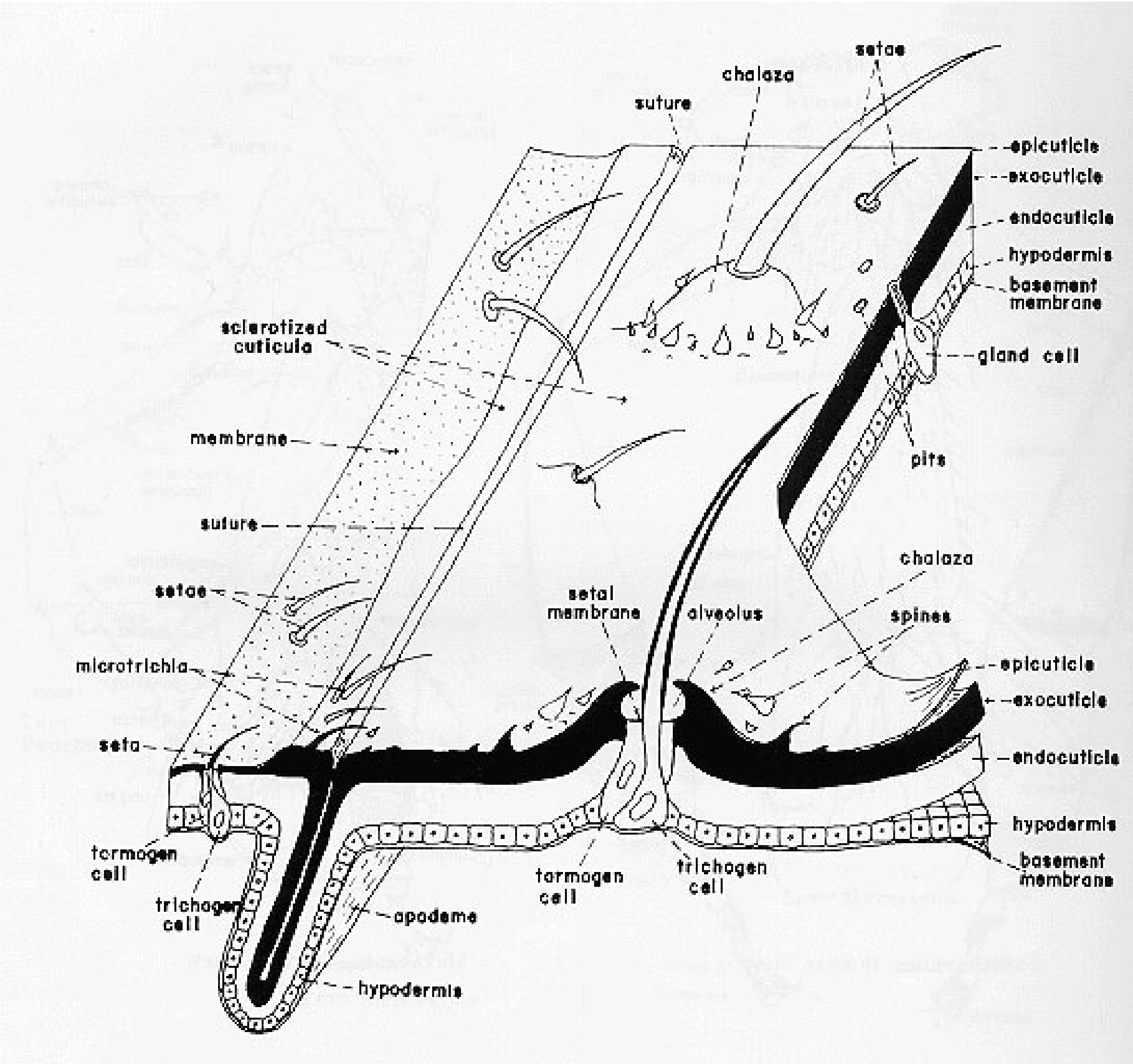
Worker Metawing, Anterior Margin, Cross Section





Metapedes, Dorsal View

Metapedes, Ventral View



setae
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chalaza
setal membrane
alveolus
spines
setae
epicuticle
microtrichia
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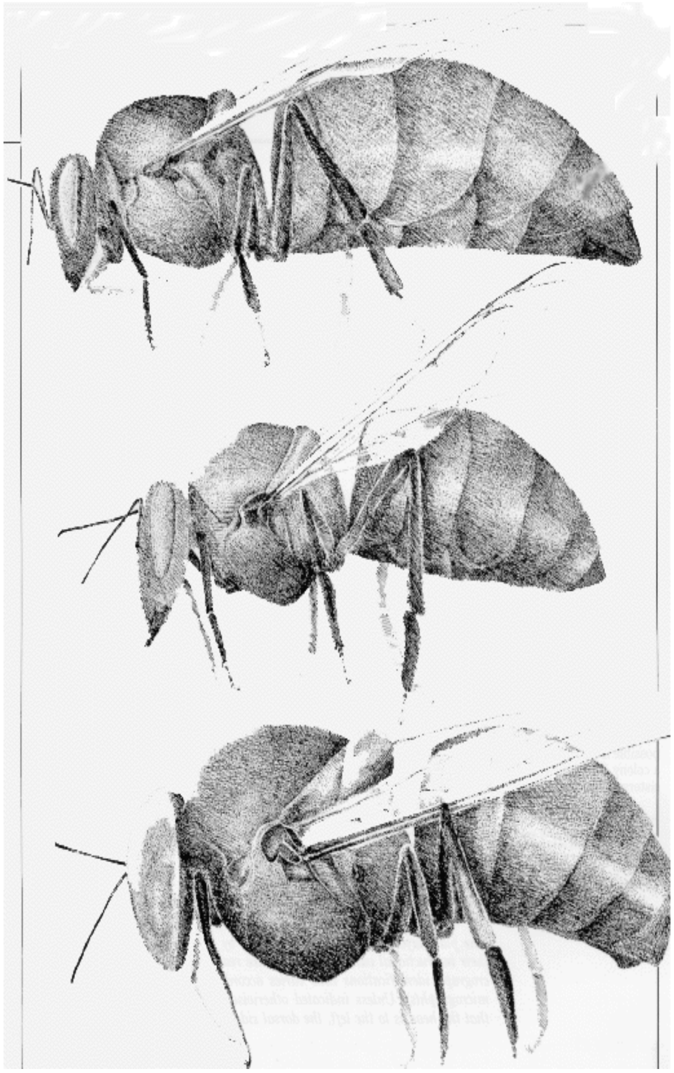


TOP TO BOTTOM: queen, worker and drone honey bees.

drawn approximatly to scale. Body hairs omitted. (X8).

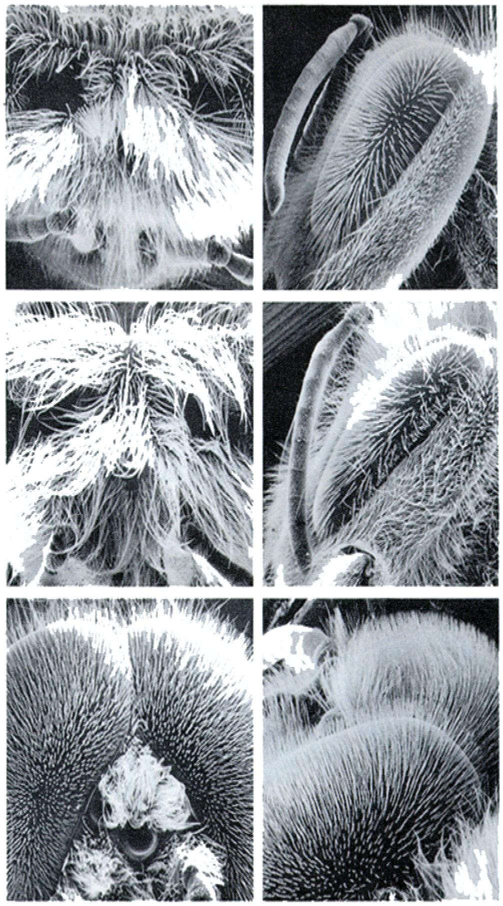


PLATE 1.2. EYES, HONEY BEE CASTES

TOP RIGHT. Worker compound eye, lateral view. The eye is surrounded by the short-haired gena (cheek). The dense, coarse, long interfacetal hairs of the eyes are apparent. (x31)

MIDDLE RIGHT. Queen compound eye, lateral view. Compare with the top right micrograph. (x31)

BOTTOM RIGHT. Drone compound eye, lateral view. This and the other views of the eyes show a sizable visual field, which is greatest in the drone. The drone bee can see forward, to the side, downward, upward, and to some extent rearward. (x 31)

TOP LEFT. Worker, vertex of head. The antennae are visible (bottom of the field) but most of the other structures are obscured by hairs. In the upper center, the circular outlines of the two lateral ocelli (but not the median ocellus) are barely visible. (x 31)

MIDDLE LEFT. Queen, vertex of head. Compare with the top left micrograph. The ocelli are obscured by hairs. (x 31)

BOTTOM LEFT. Drone, vertex of head. The two rounded eminences (top of thefield) are the dorsal sectors of the compound eyes, which are contiguous in this region. In the lower center of the field are the three ocelli (one is almost completely covered with hairs). These are located down on the face of the drone rather than in the dorsoanterior portion of the head as in the queen and worker. The dorsal bonding of the compound eyes has apparently displaced the ocelli. (x 31)

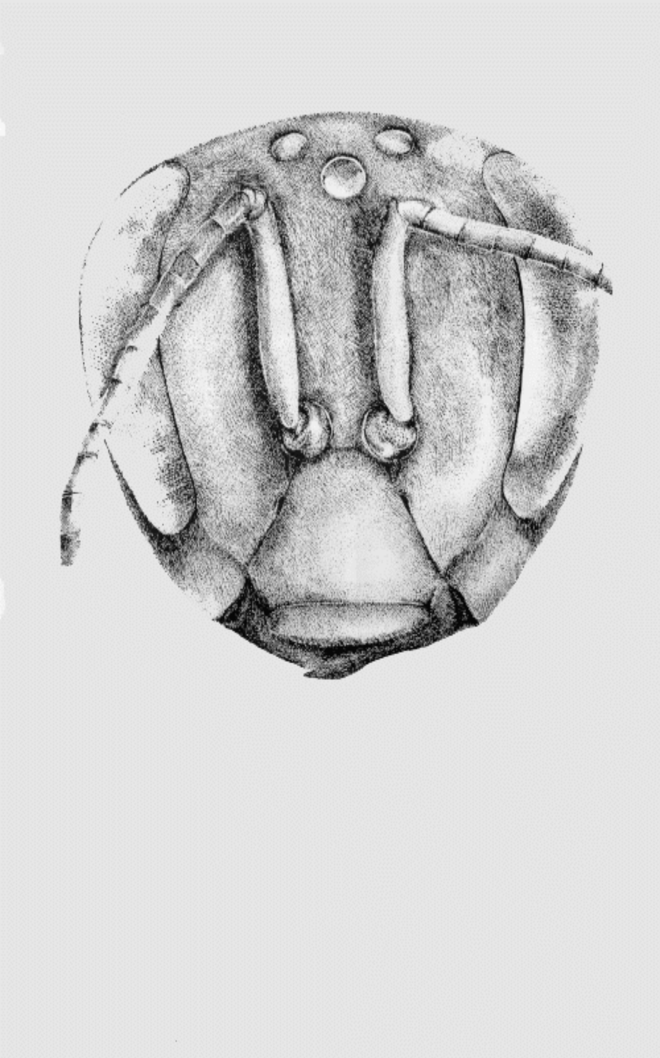


PLATE 1.3 QUEEN HEAD

Frontal View of the queen head

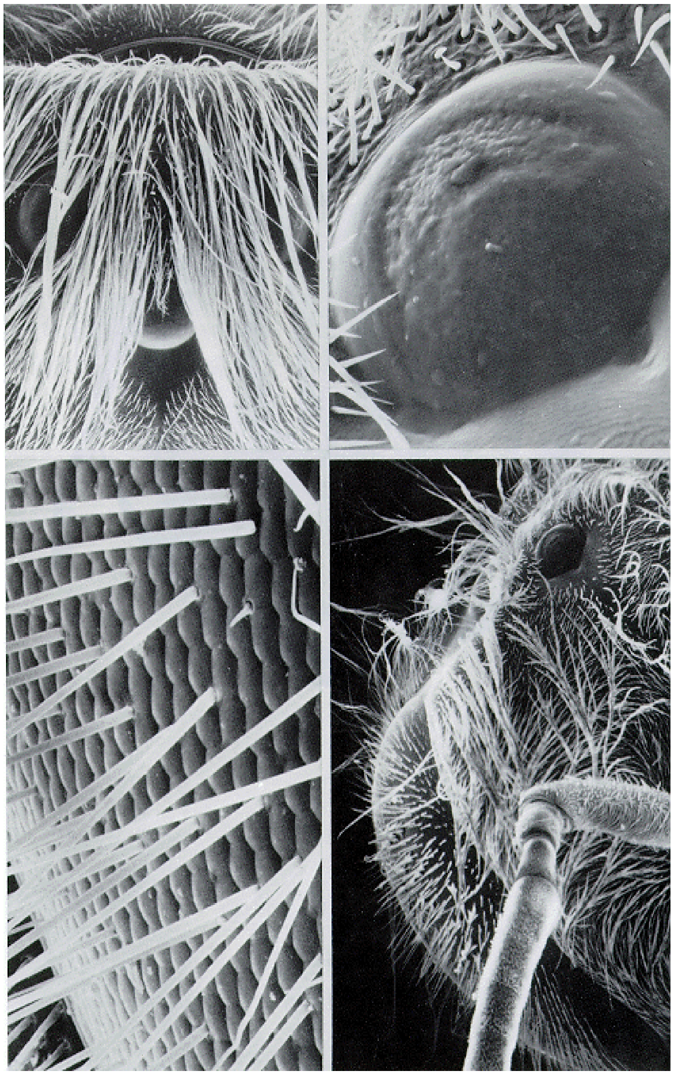


PLATE 1.4. QUEEN EYES

TOP LEFT. Trio of queen ocelli, two lateral and one median. Long body hairs drape over these socalled simple eyes. (x 58)

TOP RIGHT. Higher magnification of the median ocellus. A single lens serves as the dioptric apparatus for hundreds of underlying photoreceptor cells. The optics are such that no image is formed at the level of the photoreceptor cells. (x 600)

BOTTOM RIGHT. Survey micrograph of the queen compound eye showing its hirsute character and the glabrous median ocellus (top of the field). The lateral ocelli are obscured by the angle of view and hairs. (x 50)

BOTTOM LEFT. Interfacetal hairs, which are socketed, relatively large, and long. The depth of the focal plane is evident, as the focus is maintained over the considerable curved expanse of the eye. (x 496)

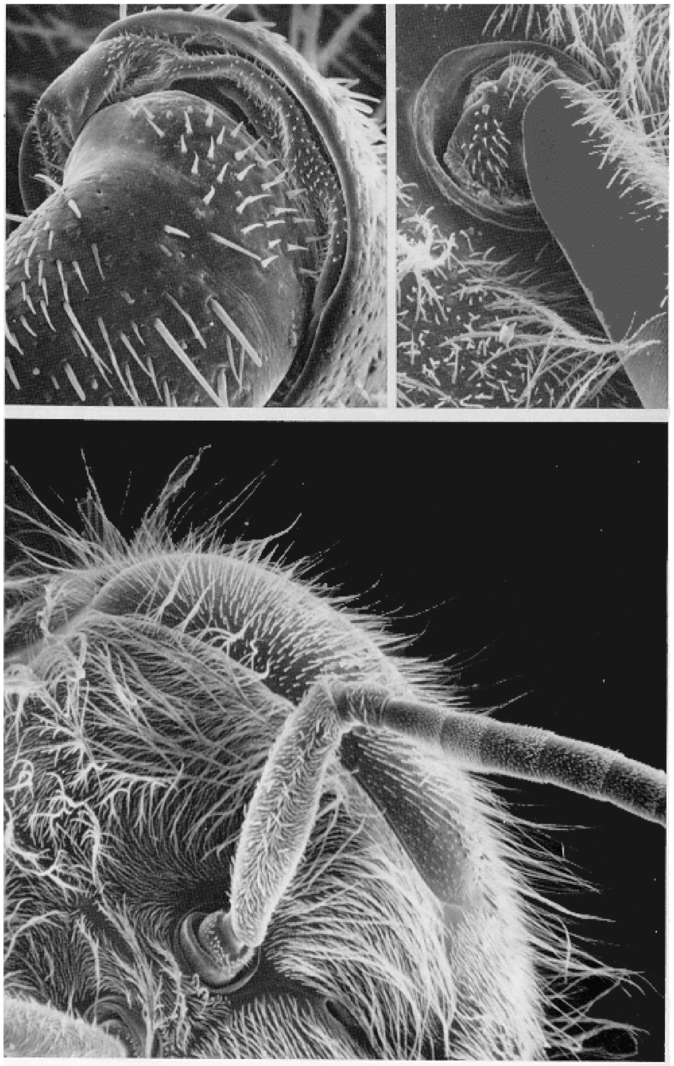


PLATE 1.5. QUEEN ANTENNA, BASE AND ELBOW

BOTTOM. Survey from the vertex of the queen head showing the hairy hemispherical compound eye with its array of interommatidial hairs. Both antennal bases are present; the left scape (first antenna segment) is the prominent short antenna segment, followed by the much longer pedicel (the first segment after the scape), and five flagellum segments follow thereafter, while six additional segments are outside this field. The flagellum moves relative to the scape by the action of two muscles that span the pedicel and insert on the first flagellum segment. (x 53)

TOP RIGHT. Base of the scape, seated within a membrane-lined socket that lies on the wall of the frons. Presumed mechanoreceptive hairs are in rows on the wall of the scape. (x 110)

TOP LEFT. Close-up of the articulation of the scape with the antenna socket. As the antenna moves, the hairs on the scape base may be differentially bent against the socket side. These hairs may be mechanoreceptors that monitor the attitude of the scape. (x 330)

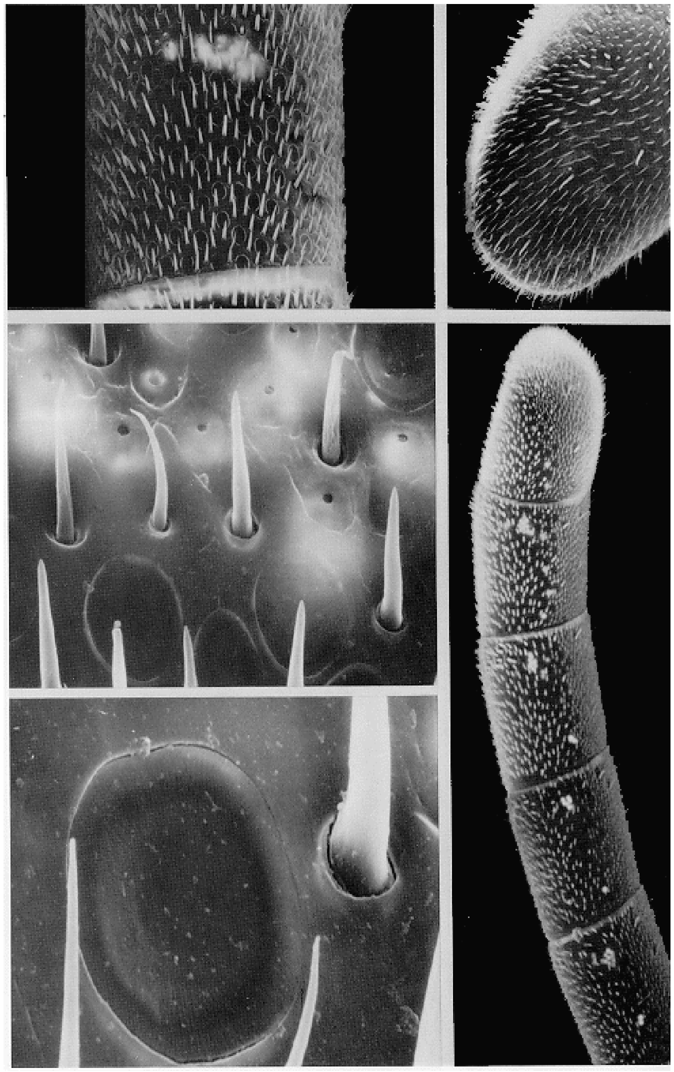


PLATE 1.6. QUEEN ANTENNA SURFACE

BOTTOM RIGHT. Last five segments of the queen antenna. The antenna surface is profusely covered with a variety of uniformly distributed sense organs. On each segment, usually at the proximal and distal border, are small clusters of pit organs, which appear as bright spots. (x 144)

TOP RIGHT. Terminal segment of queen antenna. A few stout peg organs (sensilla basiconica) and stout long pegs are seen among the majority of sensory hairs. The plate organs are not visible. (x 270)

TOP LEFT. Medial surface of the second antenna segment of the queen. A few pit organs show brightly. It is not known why these pit organs reflect more secondary electrons to the scanning electron microscope collector and therefore appear brighter. The faint circular outlines of the plate organs are visible. (x 330)

MIDDLE LEFT. Higher magnification of the surface on the penultimate segment of the queen antenna. The bright pit organs are relatively sparse but are aggregated. Placoid (plate) and trichoid (hair) sensilla surround the pit organs. (x 2,200)

BOTTOM LEFT. Close-up of a plate organ and several trichoid sensilla. The crack that extends along the outer rim of this plate organ is probably artifactual. At this magnification the subtle cuticular ribbing relief around the organ's periphery is visible. Exquisitely small pores (not visible) line these ribs and permit odorant molecules to enter and make contact with the sensory dendrites circumferentially arrayed under the plate. (x 5,500)

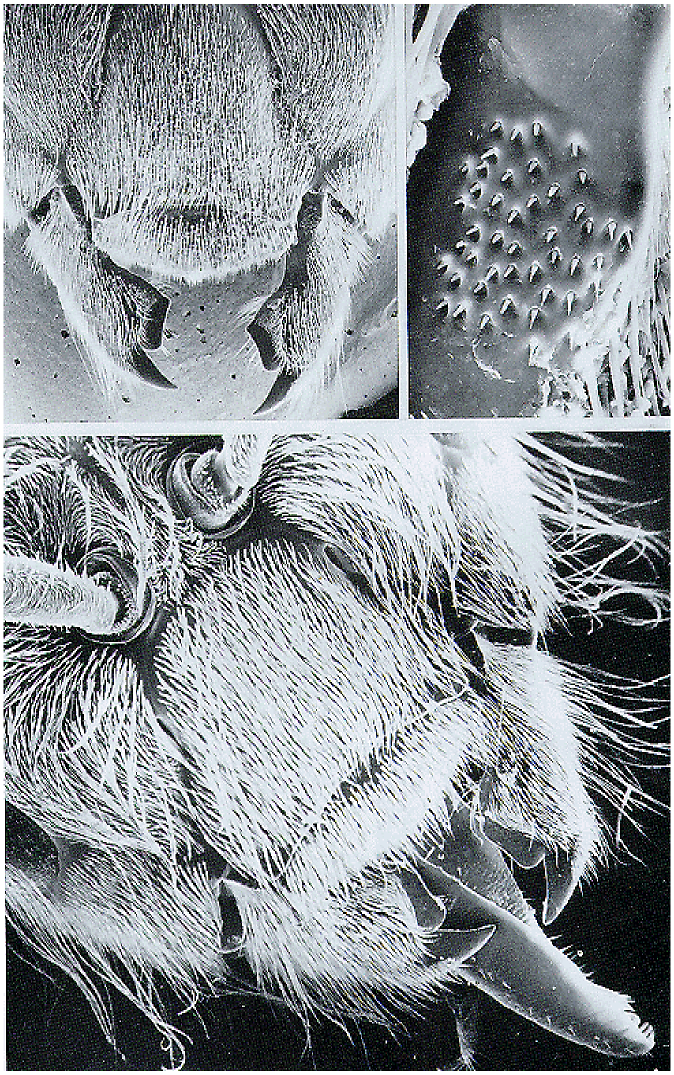


PLATE 1.7. QUEEN HEAD, ANTERIOR VIEW

BOTTOM. Queen head. At the base of the antennae and projecting downward is the roughly rectangular clypeus; extending in front of that is the smaller, largely rectangular labrum (upper lip). Both mouthparts are very hirsute. Along the lateral sides of the clypeus-labrum are the clawlike mandibles. Projecting forward from between the mandibles are the galea and behind these are the labial lobes. (x 56)

TOP LEFT. Queen mouthparts, dorsoanterior view. Here the mandibles are better outlined and part of their articulation with the genae is visible. At this viewing angle the labrum completely covers the galea and labial lobes. (x 41)

TOP RIGHT. Medioproximal surface of the mandible where it adjoins the clypeus. Over 40 small, socketed hairs (possibly mechanoreceptors) make contact with the sides of the clypeus in normal mastication. If these hairs are innervated and mechanosensory in nature, they could monitor the attitude of the mandible relative to that of the clypeus-labrum. (x 438)

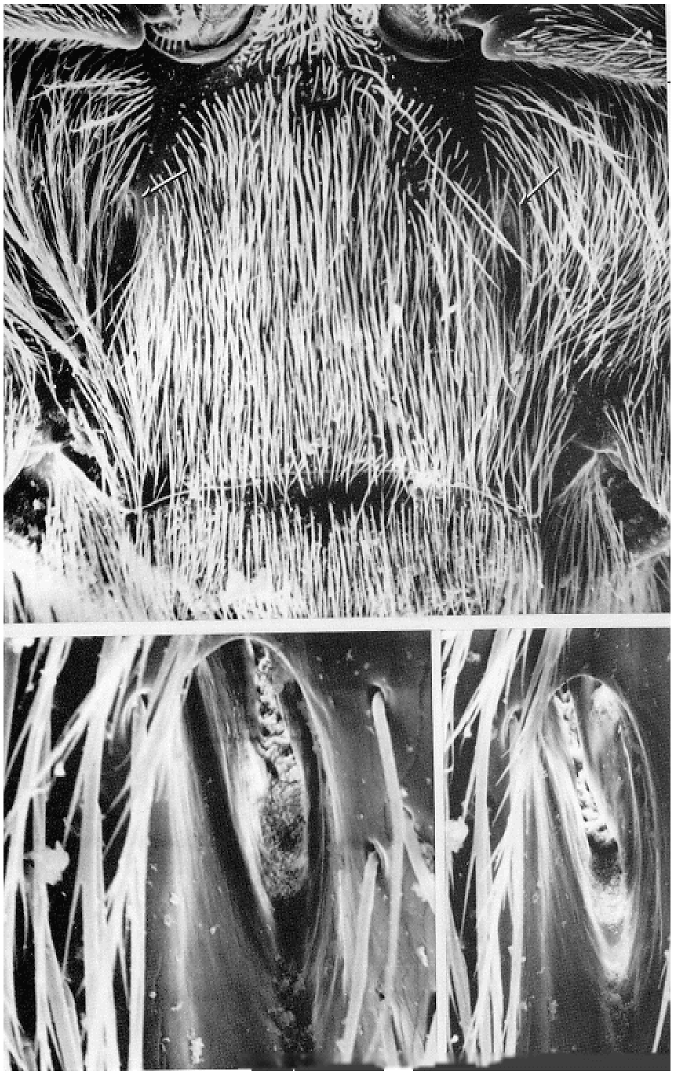


PLATE 1.8. QUEEN TENTORIAL PITS

TOP. Frontal view of antennae (top) and the clypeus with labrum (bottom). Two anterior tentorial pits (arrows), lying on the epistomal sulcus, are cannular (tubular) structures that extend inward to form part of the tentorium (internal skeleton) of the head. The latter provides general structural support and cuticular braces for muscle attachment. (x 90)

BOTTOM RIGHT. Close-up of the right anterior tentorial pit. This is one of the openings of the two hollow cuticular tubes that extend through to the posterior tentorial pits. (x 600)

BOTTOM LEFT. Higher magnification of the queen right anterior tentorial pit. (x 750)

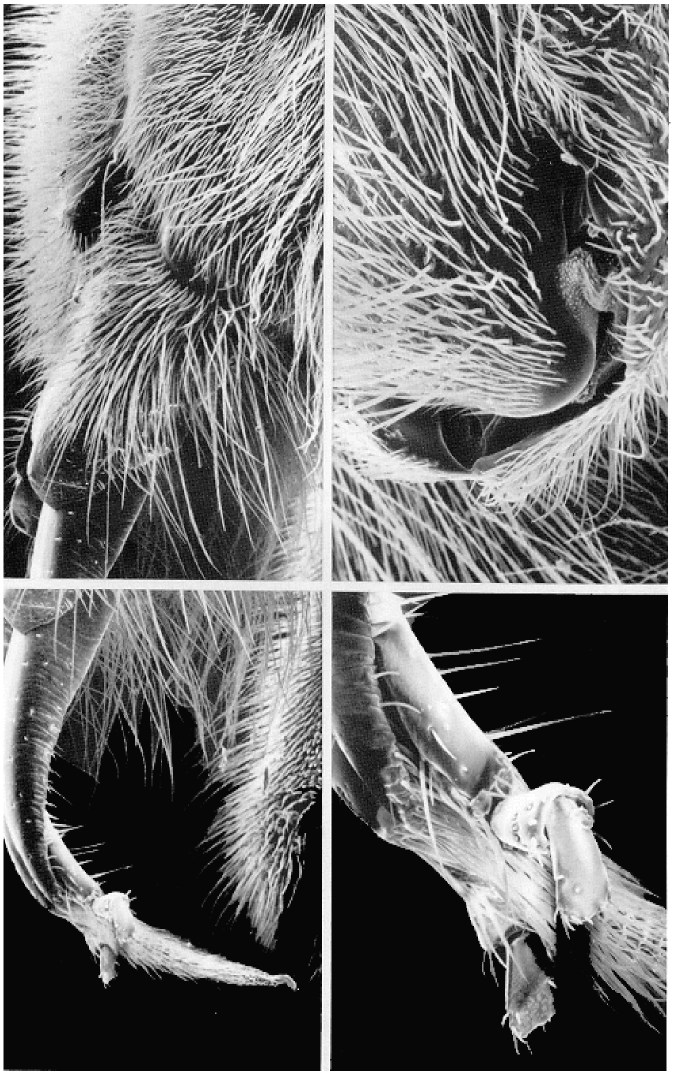


PLATE 1.9. QUEEN PROBOSCIS, LATERAL VIEW

BOTTOM LEFT. Sharply bent glossa (tongue). Over half the length of the glossa, the principal feature of this micrograph, is covered by the embracing proximal segments of the labial palps. The labial palps terminate in a pair of budlike appendages that appear to be sensory in nature. The most extended appendage is the glossa. (x 65)

BOTTOM RIGHT. Close-up of the terminus of the labial palp. Each "bud" has two segments and bears short cuticular spines and pegs, which may be sensors for taste and touch. (x 180)

TOP LEFT. Proximal portion of the glossa and labial palps. The mandibles with their naked tips incompletely cover the glossa and the hairy labrum abuts and somewhat overhangs the paraglossae. (x 65)

TOP RIGHT. Base of the mandible (bottom) where it articulates with (hinges on) the gena (top). An array of tiny cuticular denticles is visible on the intersegmental "membrane" (x 169)

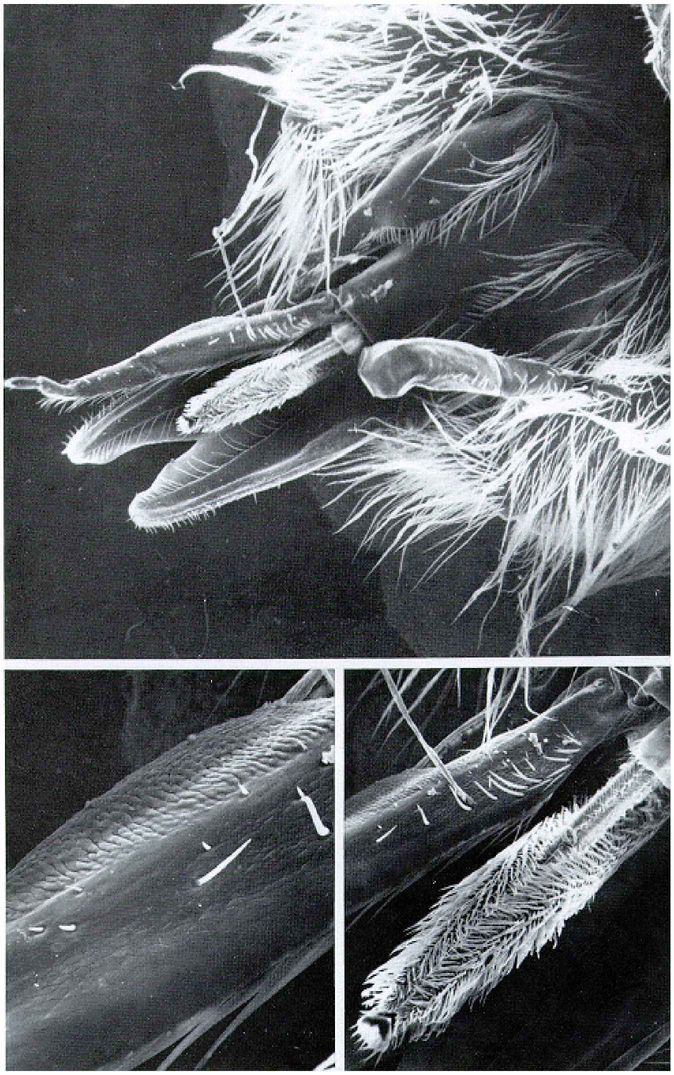


PLATE 1.10. QUEEN MOUTHPARTS, POSTERIOR VIEW

TOP. Mouthparts, posterior view. The innermost projecting piece represents the retracted glossa (tongue), which is much smaller than that of the worker. Distally the glossa is tipped by a (brightappearing) flabellum. At the base of the glossa are the bilobed paraglossae; these two pieces emanate from a flattened sclerite called the prementurn. Immediately lateral to the glossa are the two foursegmented labial palps. The one on the right of the glossa has been bent back to better display the underlying maxillary galea. When feeding, the two palps and the two galea come together to form a tube or funnel through which liquids are drawn up by the mechanical movements of the glossa and the suction created by the cibarium (not visible). (x 56)

BOTTOM RIGHT. Higher magnification of the underside of the queen glossa showing its bilobed construction, flabellum at the tip, and the sparse hairs (sensilla chaetica) of the lateral-lying labial palp. A few very short pegs (sensilla basiconica) are seen near the sensilla chaetica. Of particular interest is the high density and overlapping (at the tips) nature of the sensilla chaetica on the glossa. (x 121)

BOTTOM LEFT. Close-up of the underside of the left labial palp showing the two types of putative chemoreceptor sensilla, sensilla chaetica (the longer hairs) and sensilla basiconica (the very short but stout hairs). (x 327)

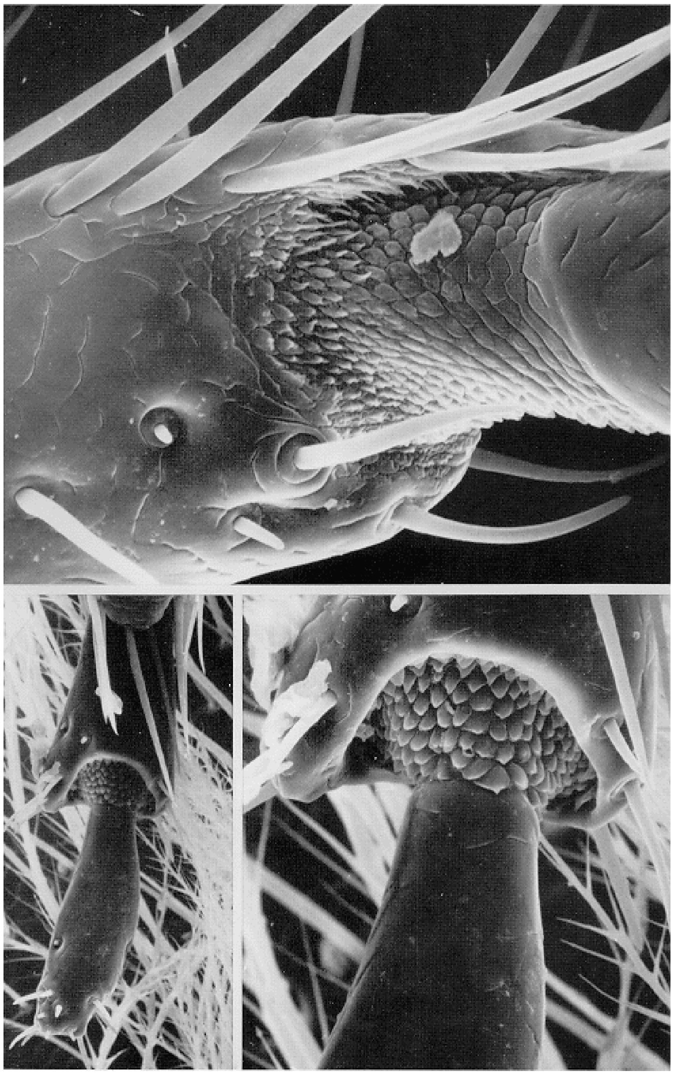


PLATE 1.11. QUEEN MOUTHPARTS , LABIAL PALP

BOTTOM LEFT TWO distalmost segments of the labial palp. Less than a dozen sense organs are at the tip. (x388)

BOTTOM RIGHT Tip of the penultiniate labial palp segment and the base of the apical segment. Chenioreceptor and/or mechanoreceptor hairs arise at the base of the distal segment. (x 1,068)

TOP Articulation between the first and second segments of the queen labial palp. Peg organs and sensilla chaetica are obvious features. Cuticular scales (probably uninnervated) are circumferentially arrayed. (x 1,333)

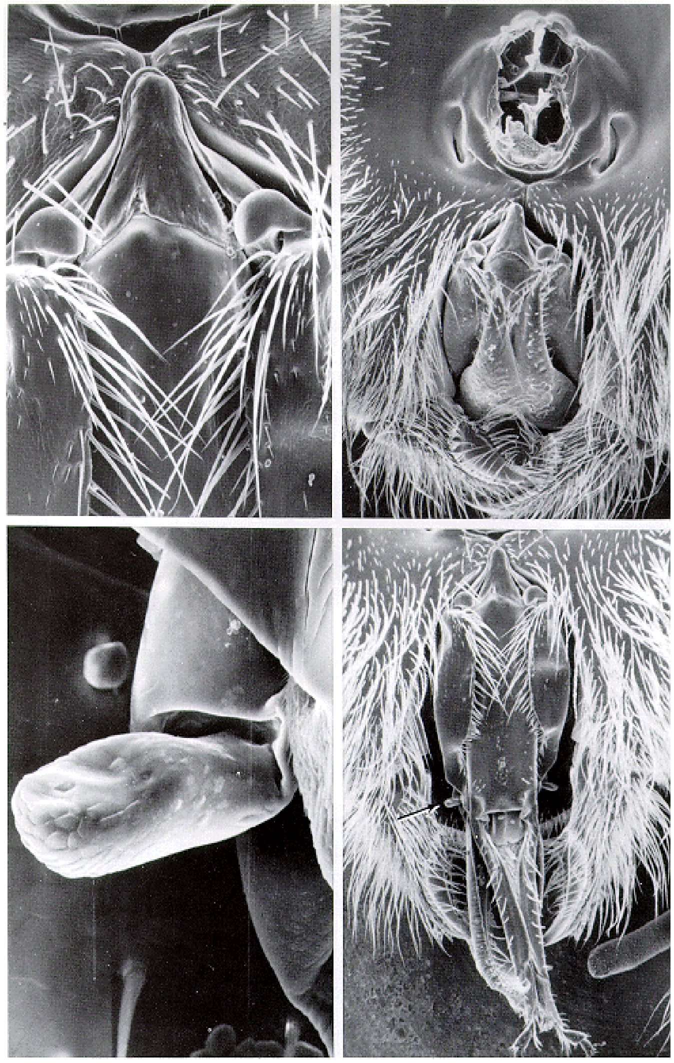


PLATE 1.12. QUEEN HEAD POSTERIOR VIEW

BOTTOM Proboscis and other mouthparts posterior view of the head. The mouthparts are extended forward. Most structures in the other micrographs of this plate are visible in this field. The arrow points to the maxillary palp. (x 40)

TOP RIGHT Head, posterior view. The large opening (lop) is the foramen magnum, to which is attached the cervix (or neck, through which pass the nerve cord, aorta, and esophagus as they span the head to the thorax). The opposing crescent-shaped apertures flanking the basal part of the foramen are the posterior tentorial pits. At the base of the foramen is the triangular postmentum, which is situated atop the bilobed prementum. Embracing the latter are the stipes and galea. Here the mouthparts are retracted beneath the head. (x 37)

TOP LEFT Higher magnification of the postmentum region. Flanking each side of the postmentum is the cardo. (x 112)

BOTTOM LEFT Maxillary palp. This largely unadorned structure is without obvious cuticular sensilla. Possibly the "blebs" are campaniform sensilla. (x 564)

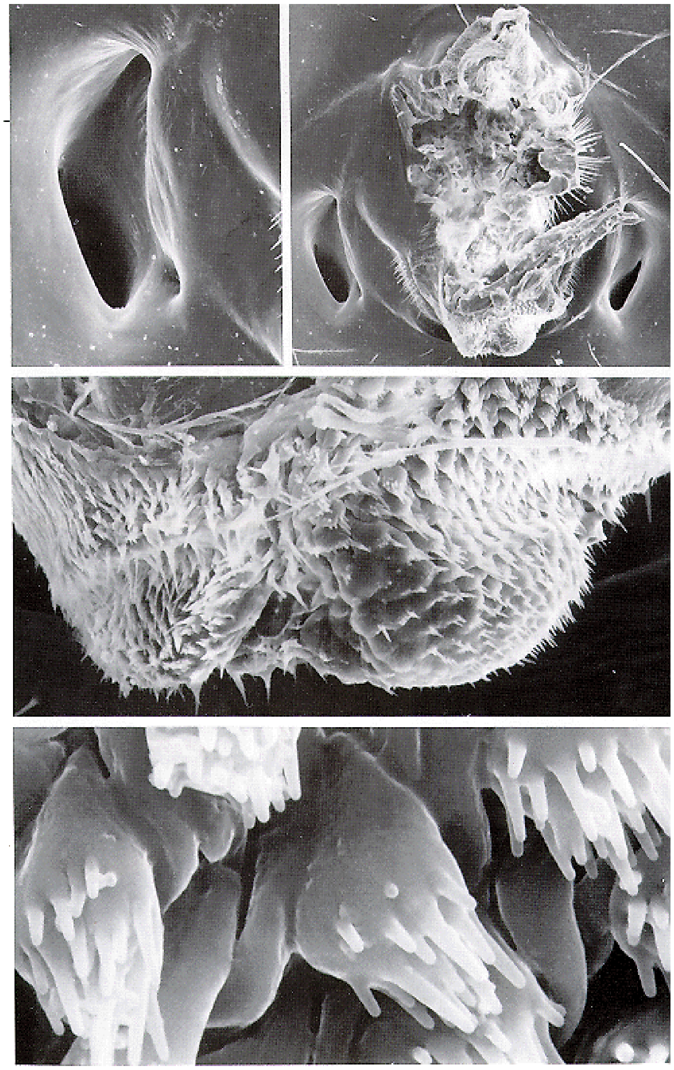


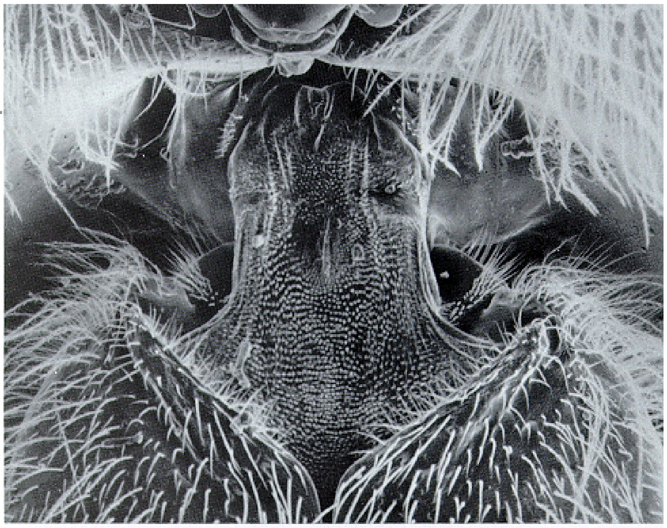
PLATE 1.13. QUEEN CERVIX, HEAD DETACHED

TOP RIGHT. Occipital foramen on the posterior of the head. This hole communicates with the cervix (neck), which in turn attaches to the prothorax. On each side of the foramen are the posterior tentorial pits, which extend to the posterior tentorial bridge within the head. Between pit and foramen is the lateral occipital sclerite with its rows of mechanoreceptive hairs. (x 66)

TOP LEFT. Close-up of the left posterior tentorial pit. At the extreme uppermost edge and below near the lower right edge of the pit are smaller depressions associated with the dorsal and ventral bridges. (x 198)

MIDDLE. Ventral aspect of the bilobed cervical membrane, which is covered with short cuticular spines. (x 540)

BOTTOM. Close-up of these cuticular spines on the bilobed portion of the cervix. Up to 20 blunt, short, fingerlike processes may emanate from each scale at its distal end. (x 5,400)



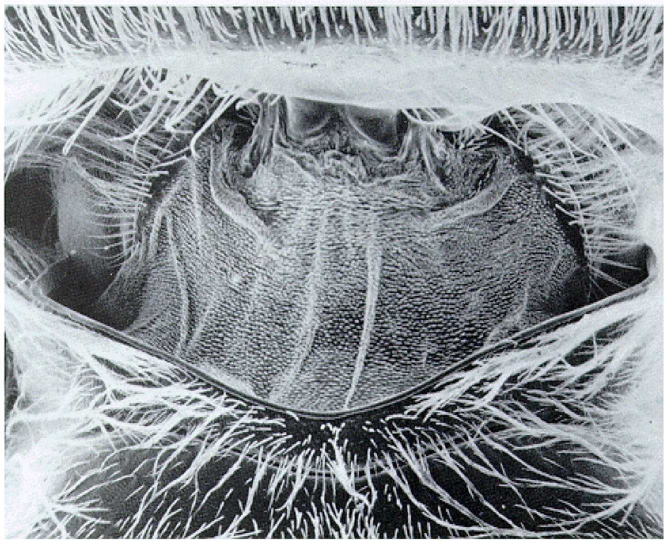


PLATE 1.14. QUEEN CERVIX

TOP Ventral cervix (neck) region showing the rather narrow and mombranous character of the cervix, which connects the head to the rounded right and left episternal plates of the thorax (bottom) The surface of the cervix is studded with circumferentially arranged, tiny cuticular scales. (x 90)

BOTTOM Dorsal cervix region. The cervix, with several folds and covered with small cuticular studs, visibly connects the prescutum of the thorax (bottom) to the occipital region of the head. (x 67)

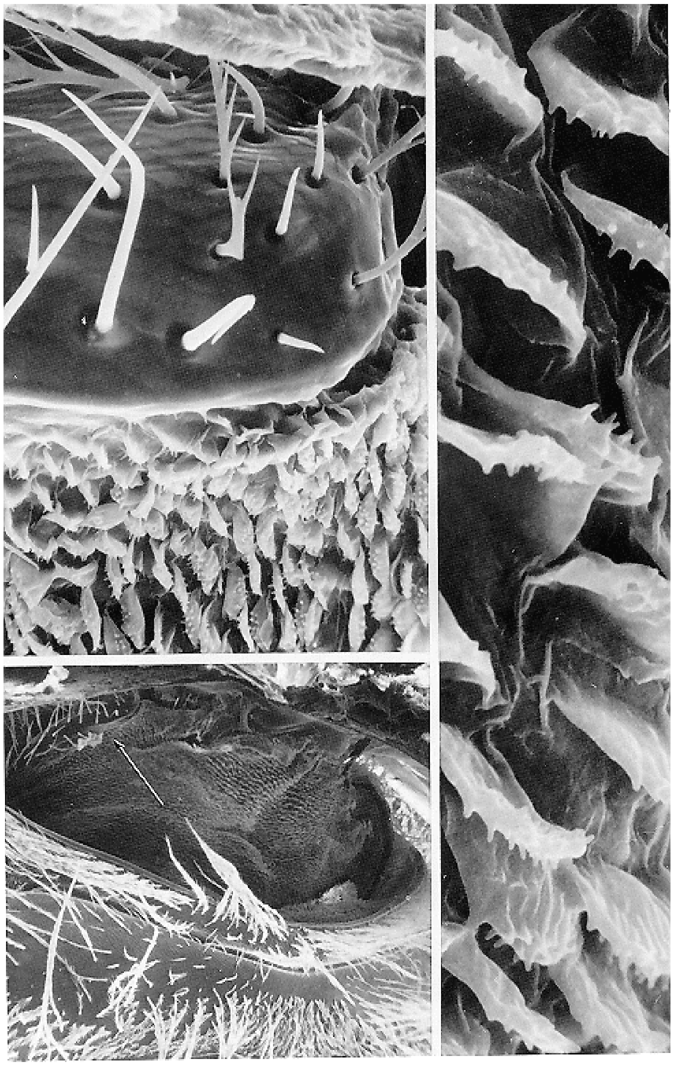


PLATE 1.15. QUEEN CERVIX, CLOSE-UP

BOTTOM LEFT Dorsoposterior view (viewed obliquely) of the postocciput of the queen where the head joins the darker-appearing membranous cervix (neck). Long body hairs cover the thorax. The arrow indicates an area further magnified in the top left micrograph. (x 84)

TOP LEFT Lateral occipital sclerite (hair plate) (arrow in the bottom left micrograph) bearing putative mechanoreceptor hairs that are bent when this plate touches the episternum of the prothorax. In bending, these hairs inform the central nervous system of the angle of the head relative to the rest of the body. (x 912)

RIGHT Higher magnification of the cuticular scales adorning the membranous cervix. The adaptive value of these scales and their short, pectinate processes is unknown at present. (x 2,200)

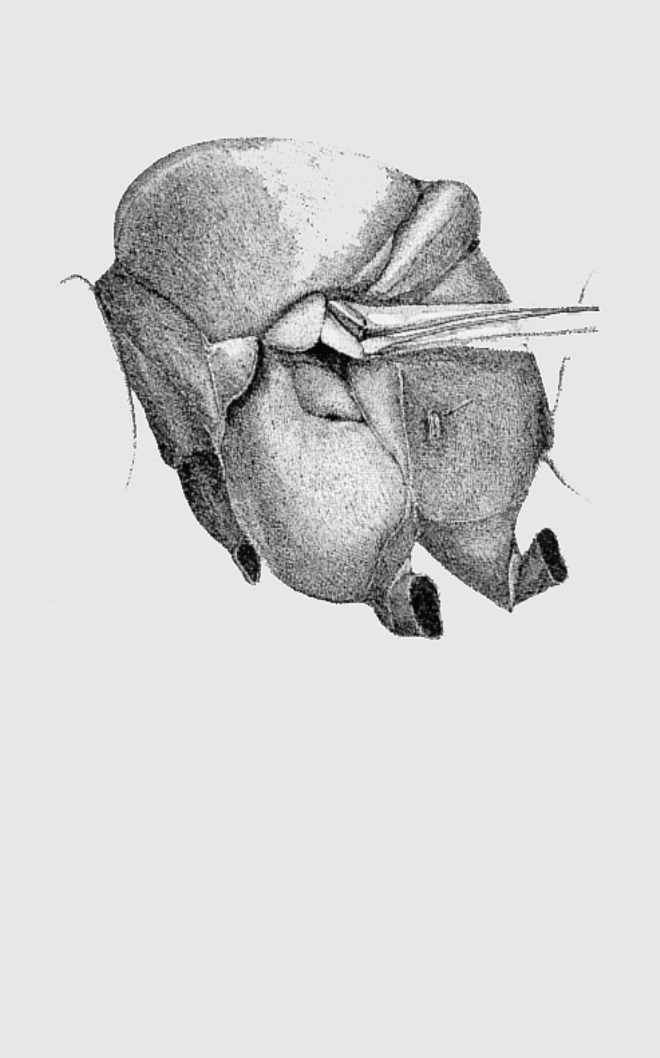


PLATE 1.16. QUEEN

QUEEN THORAX Posterior region bearing the relatively large oval spiracle (arrow) is actually the first segment of the abdomen (see also Plate 1.36) although it is broadly fused to the thorax.

PLATE 1.17. QUEEN WINGS

Photomontage of the proximal third of the forewing and its associated plates at the point of the wing's articulation with the thorax (the head Is to the top, dorsum to the right). Visible at the wing hinge area is the largest plate, the tegula, which is closest to the body. Above the tegula and to the left is the humeral plate; to the right is the median plate, which seemingly communicates with the vannal vein (the stout vein that projects approximately through the center of the wing in this viewing angle). The high density and fine character of the microtrichia covering the wing surface is evident. Despite its rather stiff appearance, the wing is remarkably flexible and resilient, capable of propelling the bee at speeds of over 20 km per hour. With their wings "disengaged" and folded back over the body, queens are able to vibrate their wing muscles to produce the sounds known as piping or quacking. (x 34)

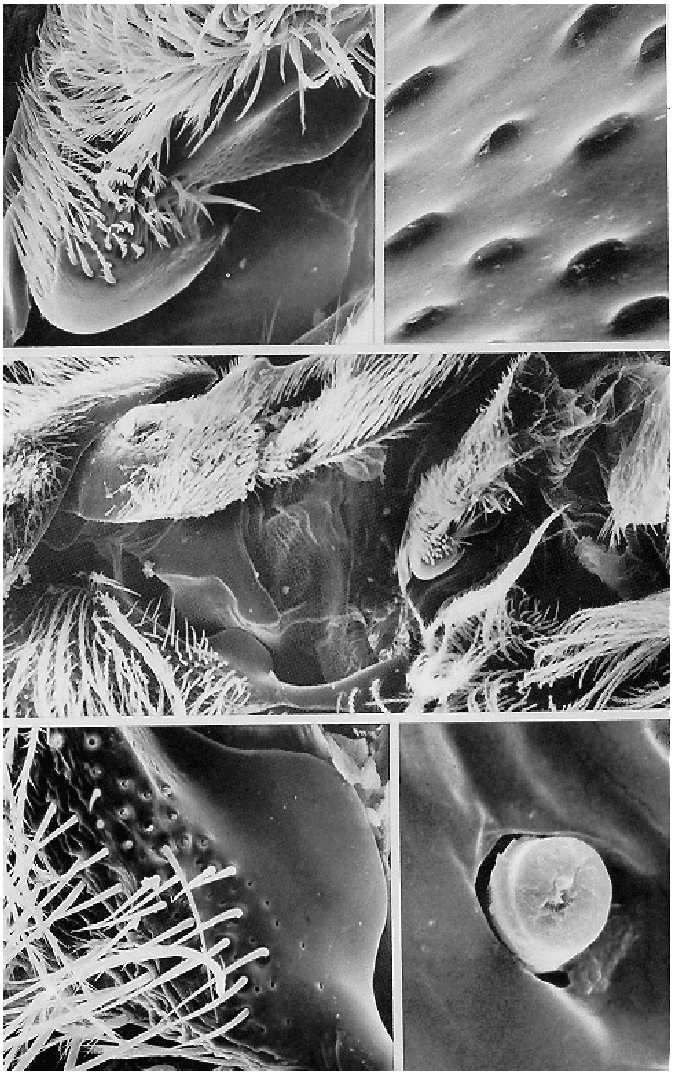


PLATE 1.18. QUEEN WING BASES

MIDDLE Wing base detail (the head is to the left). Numerous proprioceptors are evident on the various sclerotized pleural plates adjacent to the wing bases. The function of the pores that are visible is not known. (x 85)

TOP LEFT Pleural region beneath the hind wing. Many branched hairs emanate from sockets. (x432)

TOP RIGHT Higher magnification of shallow pores in the cuticle. (x 4,400)

BOTTOM LEFT. Wing sclerite with branched, acutely tipped body hairs and relatively short trichoid sensilla. The sensilla may be innervated and if so might serve as external proprioceptors. Pores are visible along the trailing margin. (x 360)

BOTTOM RIGHT Sheared trichoid. An apparent lumen is in the hair shaft. (x 5,500)

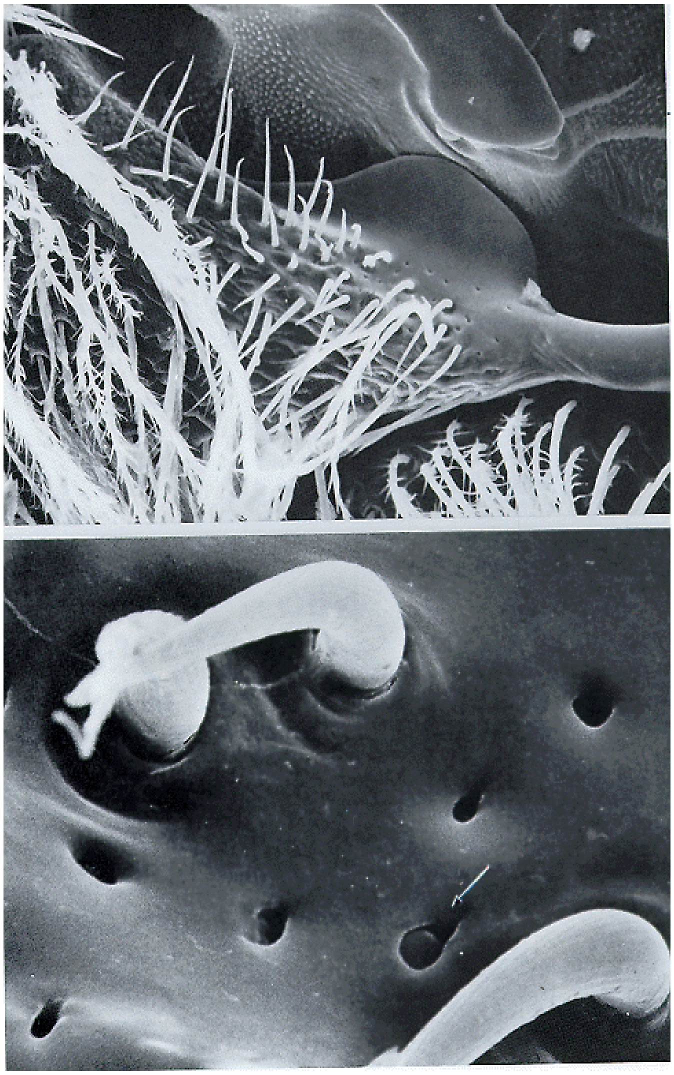


PLATE 1.19. QUEEN FOREWING BASE

TOP Forewing base showing a variety of hair types. Some functional inferences can be drawn, based on the size and position of the hairs. Short and long trichoid sensilla may have an exoreceptive function and respond (bend) to wind shear forces. The long ones may also be proprioceptive in nature if they contact the pleural surface when the wing is upright and inform the central nervous system of wing attitude. The body hairs are probably not innervated. Chemosensory pit organs are also present. Behind the pits (lop) is an axillary sclerite that articulates with a portion of the pleuron. (x270)

BOTTOM Higher magnification of the pits and short trichoids at the wing base. A pit in the lower center of the field appears to have a recessed dome (arrow) and may be a campaniform sensillum. The hair and the pit may both house sensory neurons capable of monitoring the wing flexion. (x 3,600)

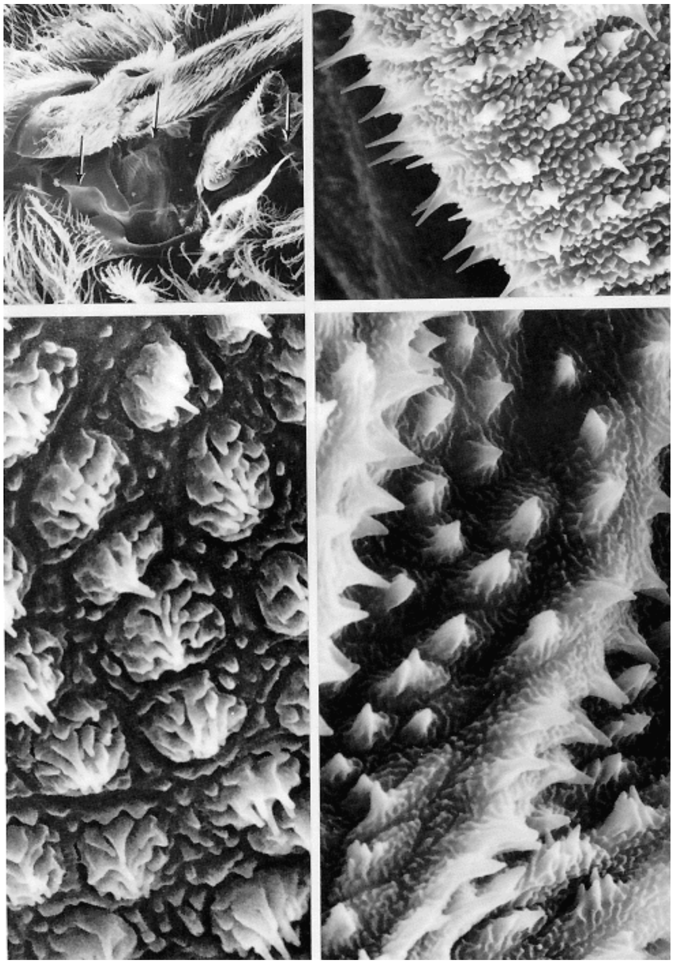


PLATE 1.20. QUEEN WING BASE MEMBRANES

TOP LEFT Forewing base and stub of the hind wing (center right of //I(, field Interesting lateral membranous areas in the middle of the field (arrows) are in higher magnification in the other three micrographs of this plate (see also Plates 1.18, 1.19, 1.21, and 1.22). (x 55)

BOTTOM LEFT Rosettelike cuticular spines at the wing base arrayed in rows with high-relief, cuticular sculpturing between these spine clusters (left arrow hi top left micrograph (x 23,400)

TOP RIGHT Pleural surface beneath the hind wing base (right arrow in top left micrograph). Acutely tipped spines rise from a surface covered with small cuticular knobs. (x 2,200)

BOTTOM RIGHT Pleural membrane at the base of the forewing (center arrow in top left micrograph) Elsewhere on the body cuticular sculpturing is characterized by more prominent (than in the top right micrograph), short, stout spines in furrows between rows of taller spines. The cuticular surface is covered with a series of low-lying ridges. (x 23,800)

PLATE 1.21. QUEEN WING ARTICULATION

BOTTOM. Articulation at the queen wing base. The leading marginal veins of the forewing and hind wing pivot from axillary sclerites and project diagonally in this micrograph. A portion of the ventral wing membrane (center of the field) possesses no hairs but rather has low-lying cuticular protrusions and multipeaked ridges (top micrograph). (x 95)

TOP. Forewing base. The underside of the wing exhibits several types of cuticular rugosites. The function of this surface relief is not known. (x 5,100)

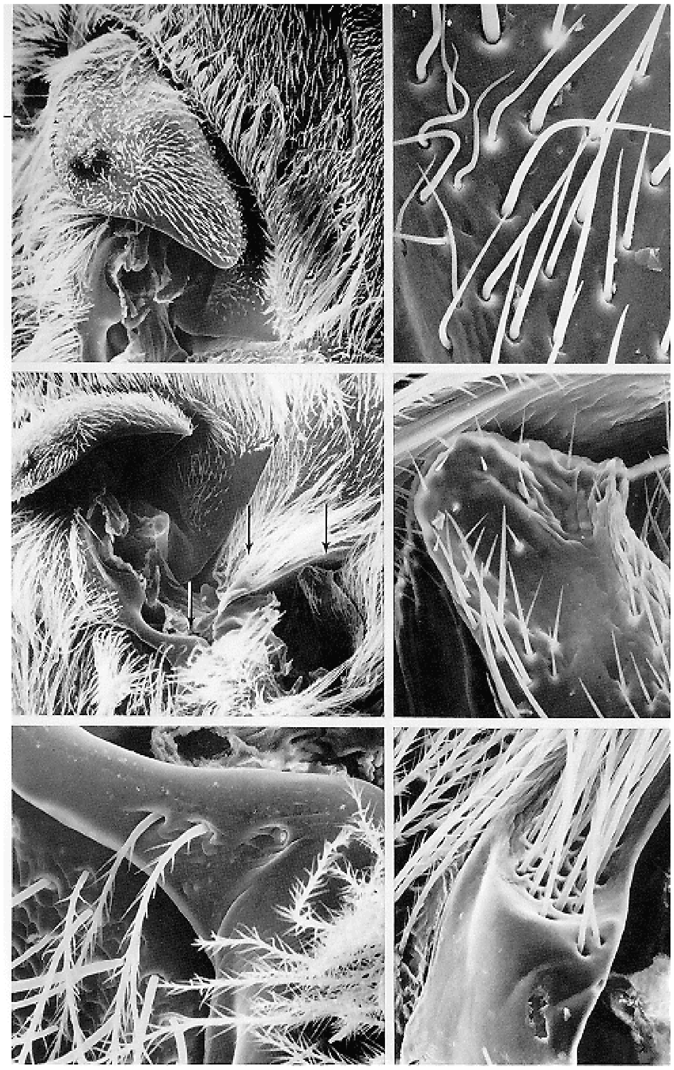


PLATE 1.22. QUEEN WING BASE SCLEROTIZED PLATES

TOP LEFT Base of the forewing (the head is to the tipper left). The hairy tegula partly covers the triangular humeral plate.

TOP RIGHT. Hair plate of socketed (presumed) mechanoreceptors on the interior edge of the humeral plate. Electron beam damage probably caused the bending and twisting of hairs. Rotational movements of the tegula and hurneral plate bend these hairs; if innervated, they could monitor such dislocations. (x 66)

MIDDLE LEFT Another view of the forewing base showing the upraised humeral plate. The arrows point to structures shown in far higher magnification cation on the bottom left, bottom right, and middle right micrographs (X 1'5 0)

BOTTOM Close-tip of the radius vein. Branched hairs emanate from this part of the wing base. Structures surrounding this vein base are visible in the middle left micrograph, indicated by the left arrow. (x 2,600)

MIDDLE RIGHT. Condylelike projection at the wing base with hairs aparentlyly in contact with the wing margin. Hairs project at different levels and angles from this knob. These hairs, if innervated, may be mechanoreceptors recording wing beat frequency and/or tension and flexion of the wings. A low-magnification view of this structure in relation to other wing structures is in the middle left micrograph (right arrow) (x 300)

BOTTOM RIGHT High-magnification view of a fascicle of about 20 socketed hairs in a cuticular protuberance at the wing base. Features adjacent to this structure are visible in the middle left micrograph (middle arrow) These hairs, if innervated, may be m echan o receptors monitoring a single kind of temporal displacement, such as the upstroke or downstroke of the wing. (x 60)

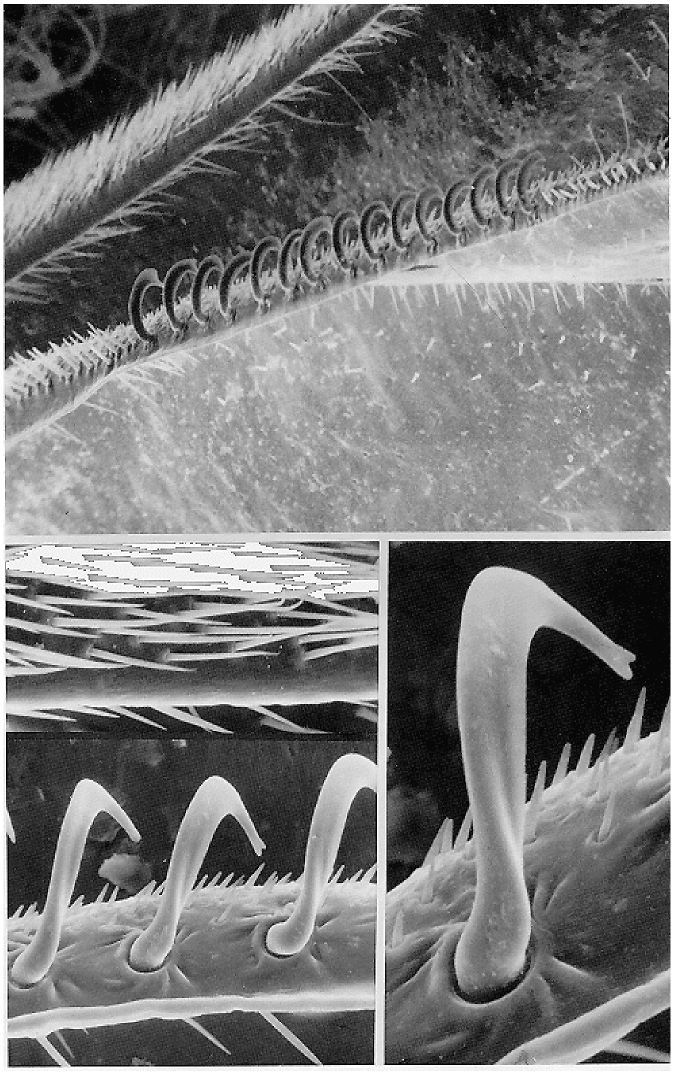


PLATE 1.23. QUEEN W1NG HOOKS

TOP. Hooks on the hind wing close to the thickened base of the articulating forewing. Particularly apparent are the hind-wing hairs on the leading edge of the hind wing (compare with peg organs of the worker, Plate 2.23). These hairs project forward and are found on either side of the 15 hooks. (x 170)

MIDDLE LEFT. Higher magnification of the trailing edge of the forewing clasped by the wing hooks in flight. The hairs adjacent to the trailing vein of the forewing are socketed and may be mechanoreceptors capable of sensing the attack angle of the wings. The bent tips of a few hairs may have been caused by electron beam damage. (x 480)

BOTTOM LEFT. Hooks on the leading edge of the hind wing, each with a slightly forked terminus. The bent and twisted nature of the hook is apparent from this angle; in three dimensions the hook extends in two directions. (x 605)

BOTTOM RIGHT. Enlargement of the middle hook in the bottom left micrograph. The socket for the hook is less pronounced than that of the worker and no peg organs are present, only socketed microtrichia that may be capable of monitoring the proximity of the wings. (x 1,210)

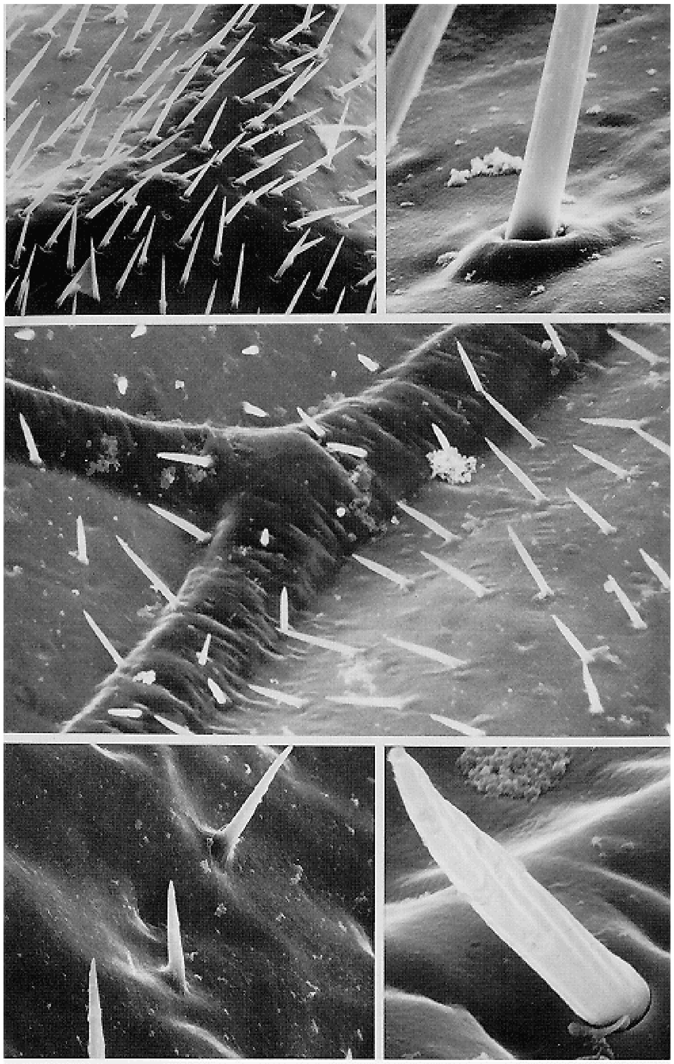


PLATE 1.24. QUEEN FOREWING SURFACE

TOP LEFT Dorsal surface of the forewing showing a dense population of short, slender, socketed hairs that may be mechanoreceptors that provide aerodynamic sense, that is, monitor the vector and magnitude of air currents over the wing surface. (x 550)

TOP RIGHT. Higher magnification of a single hair, revealing an oval rather than round socket. Presumably the hair's flexion is confined to the long axis of the oval so it can record wind in one axis only. (x 3,300)

.MIDDLE. Ventral surface of the forewing. The setae are less dense than on the dorsal surface. If innervated, some unsocketed hairs may be chemoreceptors. (x 510)

BOTTOM LEFT. Three unsocketed setae on the ventral side of the forewing. (x 1,100)

BOTTOM RIGHT. Socketed seta on the ventral side of the forewing vein. The tip can not be resolved well, but its bulbous nature suggests a terminal pore. If so, this hair is probably a chemoreceptor. (x 5,500)

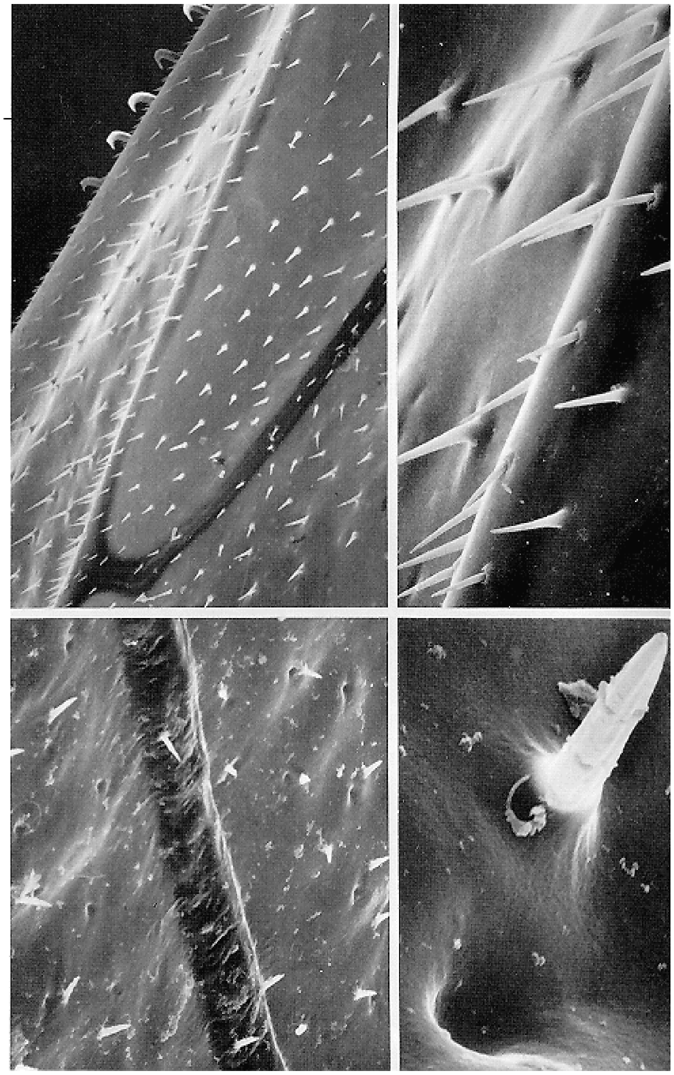


PLATE 1.25. QUEEN HIND WING SURFACE

TOP LEFT. Dorsal surface of the hind wing. Numerous hairs are evenly spaced over the surface. Wing hooks are visible on the leading edge of the wing. (x 168)

TOP RIGHT Close-up of the wing in the top left micrograph. Socketed hairs arise from the vein and nonsocketed hairs are in the membranous, interveinal area. Veins are often conduits for nerves, so the socketed hairs may be innervated and have a mechanoreceptor function. (x 800)

BOTTOM LEFT. Ventral surface of the hind wing. The sparse, scattered, nonsocketed hairs give the appearance of peg organs (sensiIla basiconica).(x 450)

BOTTOM RIGHT Higher magnification of a hair, which looks like a grooved peg, on the ventral hind wing. Such hairs may be chemoreceptors. The depression or pit (bottom) delimits the base of a hair on the opposite side of the wing. (x 4,200)

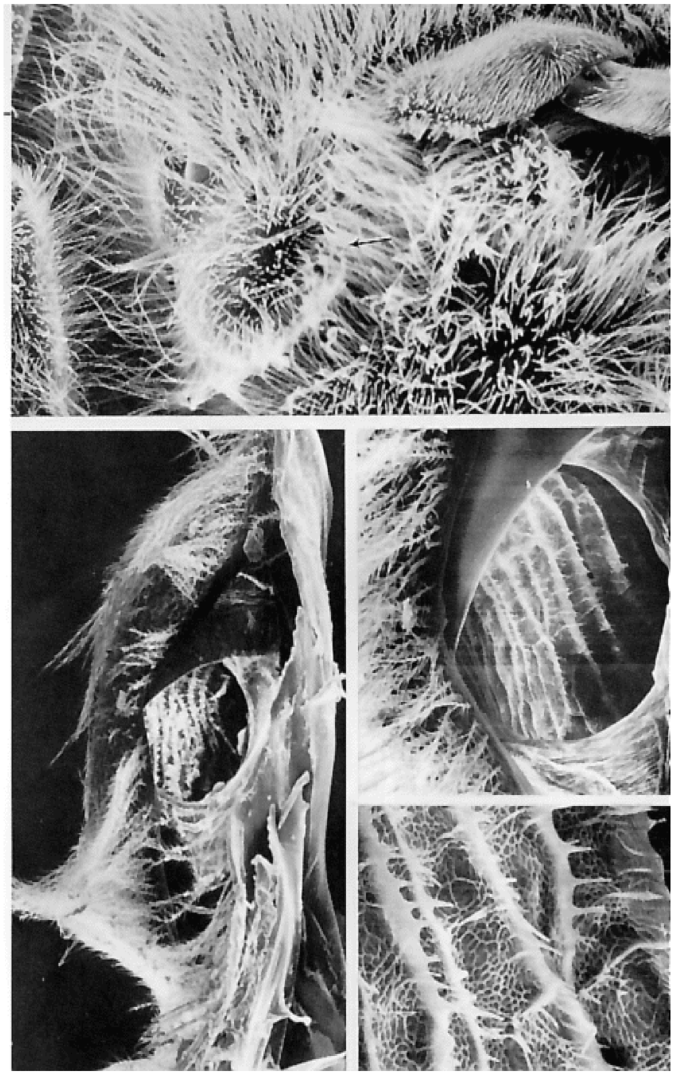


PLATE 1.26. QUEEN PROTHORACIC SPIRACLE

Top. Prothoracic spiracle, which lies beneath the spiracular lobe, or hairy plate (arrow) (the head is to the top left of this oblique view). The forewing base is visible (upper right). This spiracle is protected by the spiracular lobe and shrouded with body hairs, which must be removed, as in the other micrographs in this plate, before the spiracle and its interior can be observed. (x 56)

BOTTOM LEFT. Portion of the spiracular lobe, the atrium of this spiracle, and its immediate interior. This area is revealed when the hairs are removed from the thorax and a superficial slice of cuticle is taken from this region. (x 1,500)

MIDDLE RIGHT. Close-up of the tracheal atrium revealing the airway without any of its cuticular overcoats. The inner wall of the atrium has cuticular ridges from which project small spines or hairs, which support the integumental "pocket" concept of the atrium. The tracheal opening has been removed. (x 300)

BOTTOM RIGHT. Higher magnification of the cuticular hairs and ridges of the atrium of the prothoracic spiracle. The cuticular reticulum extends along the floor of the atrium. (x 1,200)

1.27

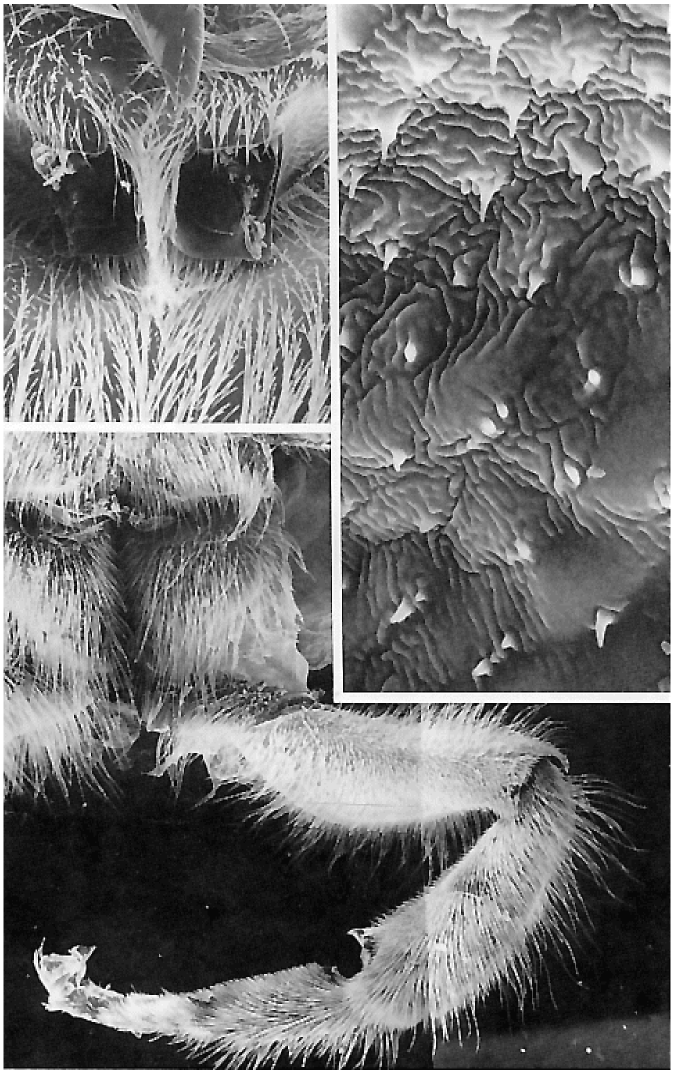


PLATE 1.27. QUEEN FORELEG

BOTTOM. Photomontage of the prothoracic leg (foreleg). The three main segments of the leg (distal to proximal) are the tarsus, tibia, and the femur (the largest of the three). At the proximal end of the tarsus (basitarsus) is the sharply notched "antenna cleaner." A closing lobe (fibula) or spur extends to partly cover the notch. In grooming, the antenna is passed repeatedly through this notch to clean the sensory hairs and plates of the antenna. (x34)

TOP LEFT Prothoracic leg bases (legs removed; head is to the top). The two empty coxal cavi ties are side by side. The tips of the maxillae (top) are situated between the coxal cavities. (x 60)

TOP RIGHT Higher magnification of the intersegmental membrane between the trochanter and femur. The irregularly furrowed character of this surface is interesting, as are the unsocketed, tiny teatlike cuticular spurs. (x 2,400)

1.28

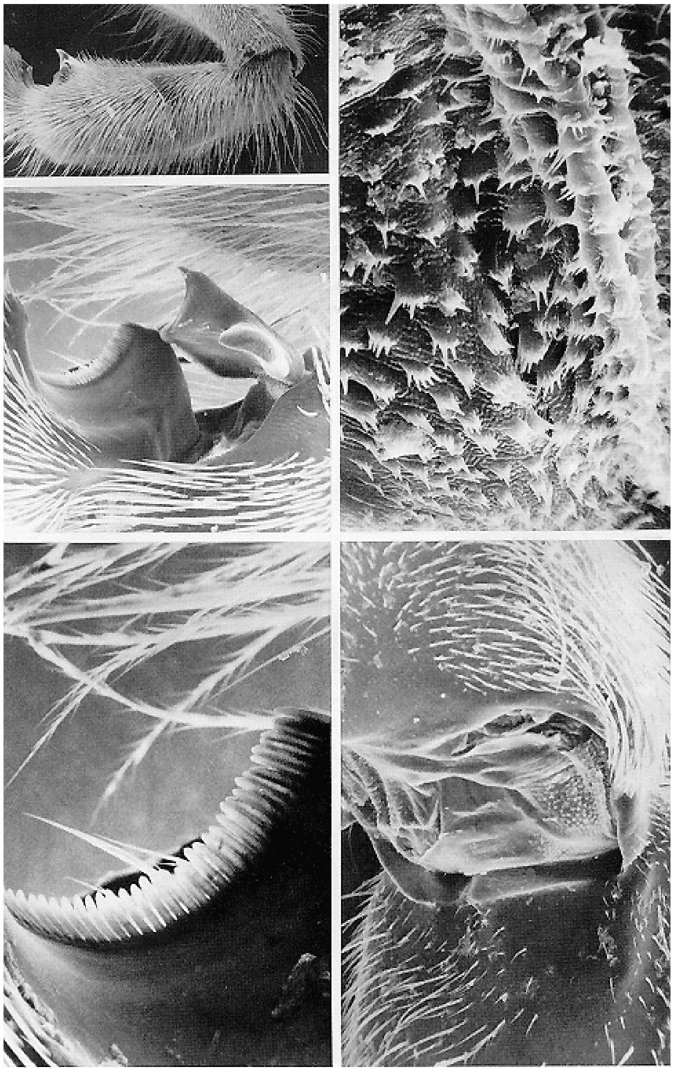


PLATE 1.28. QUEEN FORELEG, CLOSE-UP

TOP LEFT. Survey of the basal portion of the leg. The segments (from left to right) are the basitarsus, tibia, and (projecting at a 45' angle to the tibia) the femur. The "beak" at the end of the tibia is the fibula. (x 3 1)

MIDDLE LEFT. Basitarsus (left), which articulates with the tibia. The lobe on the tibia is the fibula, which closes over the haired notch for antenna cleaning. (x 120)

BOTTOM LEFT Antenna cleaner, or comb. This semicircular fringe of stiff hairs is located on the basitarsus at its junction with the tibia. The antenna is pulled past these hairs to remove debris. When the foreleg is flexed, the notch with hairs is overlaid by the short fibula, forming a cuticular circle that enables all sides of the antenna to be cleaned at once. (x 384)

BOTTOM RIGHT Posterior portion of the femur-tibla Joint of the foreleg. (x 144) close-up of the cuticular relief and the short spurs that adorn the back of the femur-tibia joint (intersegmental membrane). A comparison of this
field with the corresponding area in the bottom right micrograph shows the limited area over which this kind of cuticular ornamentation occurs. (x 168)

1.29

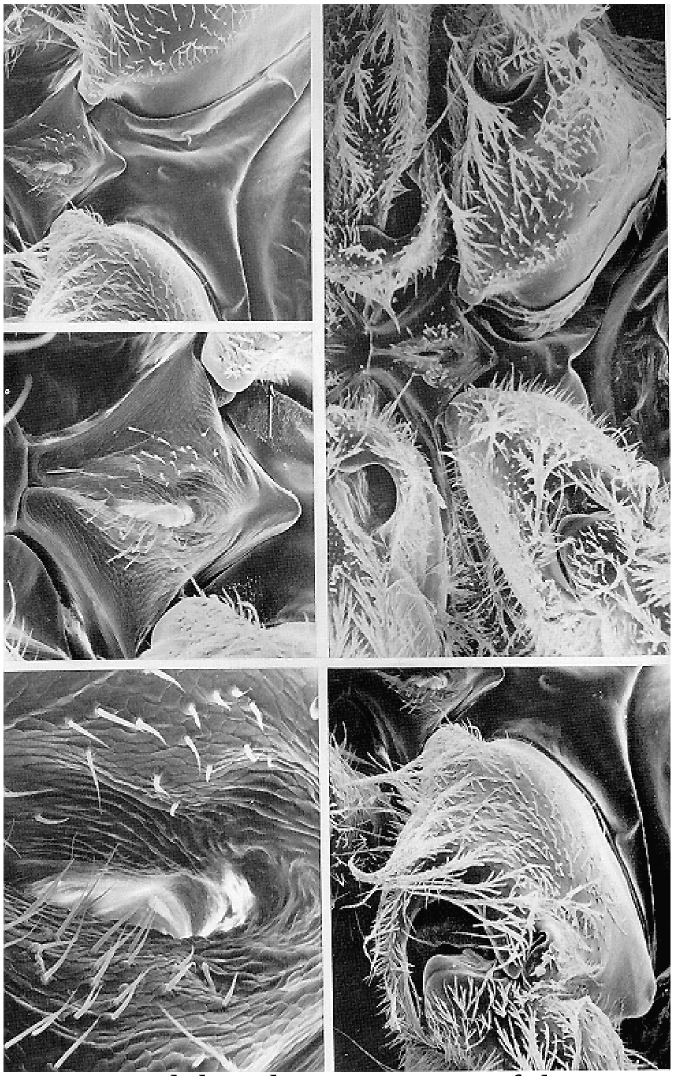


PLATE 1.29. QUEEN MIDDLE AND HIND LEG BASES

TOP RIGHT Ventral view of the middle and hind (rig t) leg bases. The coxae and trochanters of the bind (metathoracic) legs are on the right, those of the middle (mesothoracic) legs on the left. The rectangular plate between both sets of legs is the sternellum. The rhomboidal plate bounded by the four leg bases is the propodeal sternum; it is punctuated by a center apodeme. (x 47)

BOTTOM RIGHT Ventral view of the base of the metahtoracic leg. The major appendage here is the metathoracic coxa. The distal appendage that projects to the bottom of the field is the trochanter. (x 55)

TOP LEFT. Sternal sclerite situated between the metathoracic coxae. This plate is more properly called the propodeal sternum. (x 50)

MIDDLE LEFT Higher magnification of the propodeal sternum and the adjoining coxae of the mesothoracic legs.
The hair plates (arrow) at the bases of the coxae are probably mechanoreceptors monitoring leg movement. (x 100)

BOTTOM LEFT Apodeme (cuticular invagination) and the surrounding propodeal sternum. (x 300)

1.30

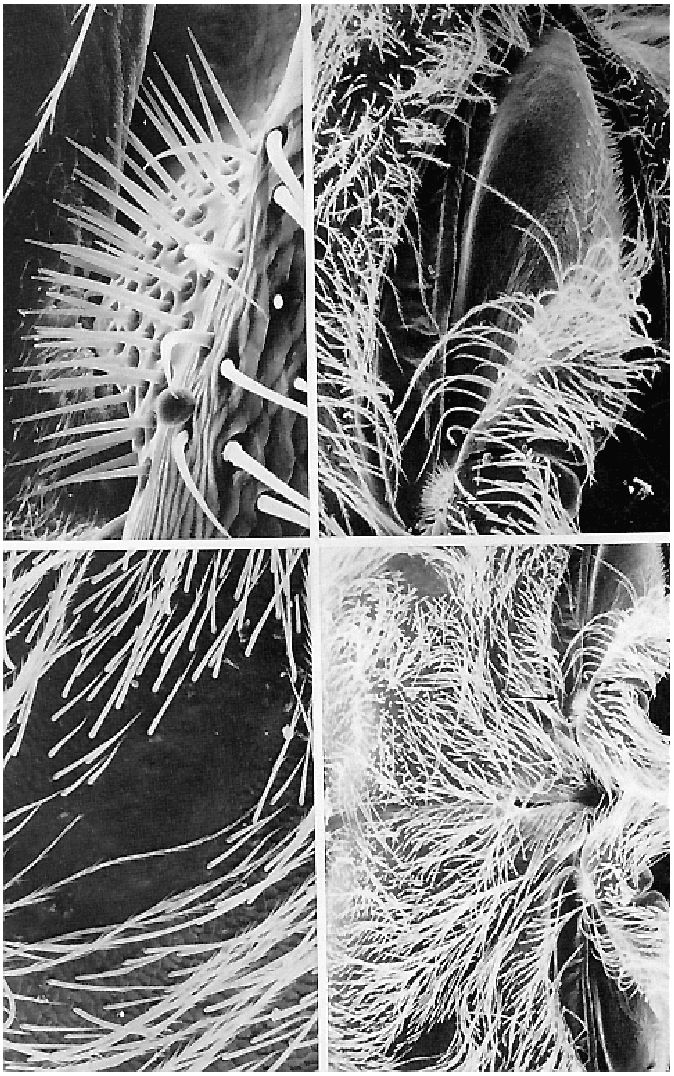


PLATE 1.30.QUEEN MIDDLE LEG BASES

BOTTOM RIGHT Thorax, ventral view. The middle (mesothoracic) coxae are on the extreme right, one above the other. The groove (line) running side to side through the middle of the field is the median sulcus. This division separates the right mesosternum and mesoepisternum from its left counterpart. The arrow points to one of the "pincushion" structures further magnified in the top right and top left micrographs. (x 40)

TOP RIGHT Higher magnification of the left coxa in the bottom right micrograph. The "eyelid" cuticular structure is an intersegmental membrane, and at the extreme basal portion of the field is a small portion of the coxal condyle. Immediately above the condyle (arrow) is the "pincushion" structure indicated by the arrow in the bottom right micrograph: this structure is even further magnified in the top left micrograph. (x 96)

TOP LEFT Forty-odd tiny setae. This may be a collection of inechanoreceptors (making up a hair plate), whose probable function is to irionitor leg loading and position by spine displacement through coxal contact with the basal margin of the mesosternum (x 664)

BOTTOM LEFT Higher magnification of one of the two hairless areas visible (at 7 and 11 o'clock) in the survey of the upper ven ter of the thorax in the bottom right micrograph. No cuticular hairs exist in this (the 7 o'clock) area nor are there any empty sockets or other indications of cuticular sensilla. Also absent is the normal cuticular relief. The function, if any, of these areas remains a mystery. (x 208)

1.31

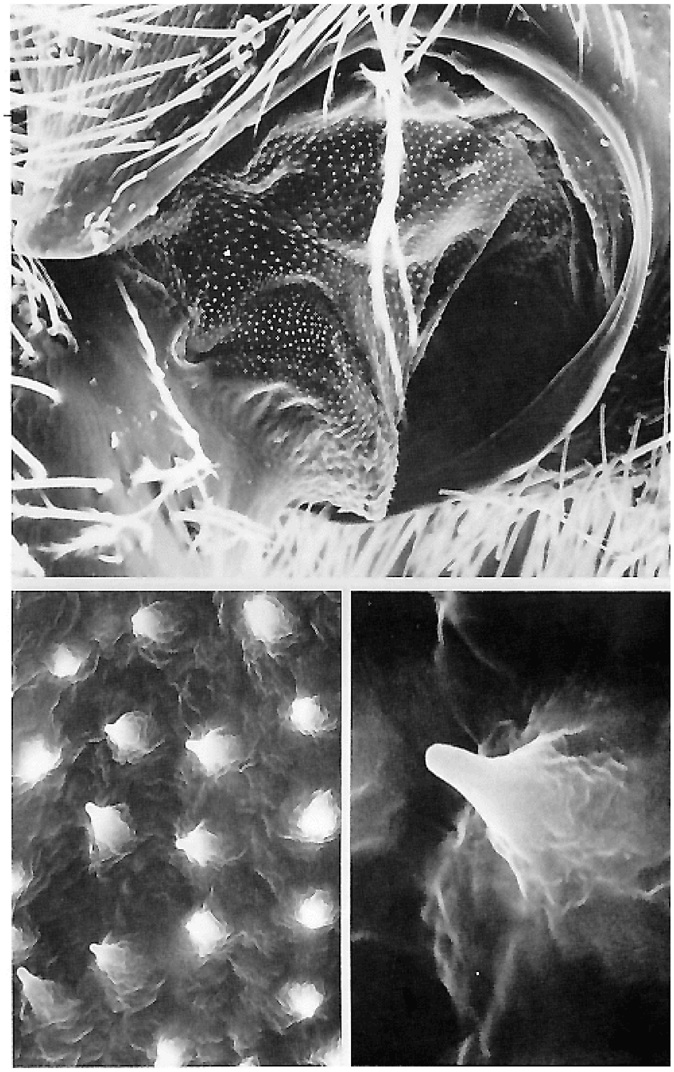


PLATE 1.31. QUEEN MIDDLE LEG BASE

TOP Close-up of the leg base and coxal cavity of the middle leg. The articulating (intersegmental) "membrane" is characteristically covered with rows of tiny spinelike processes. (x 324)

BOTTOM LEFT. Close-up of the cuticular spines arising from the intersegmental "membrane" between the mesothoracic coxa and trochanter of the queen. The linearity of the rows of these spines is apparent in this view. (x 4,800)

BOTTOM RIGHT. Close-up of one of the unsocketed spines showing its general morphology and blunt tip. (x 18,000)

1.32

PLATE 1.32. QUEEN MIDDLE AND HIND LEGS

Photomontage of the middle, or mesothoracic (left), and hind, or metathoracic (right) legs. At the leg base the first segment, the coxa, is almost completely obscured by the hairs of the mesothoracic pleurites. The next segment, the trochanter, is visible, extending (horizontally) to articulate with the larger femur. The tibia joins the femur (at the "knee") and extends downward. The mesothoracic tibia is about as wide as the femur, but the hind tibia is flattened and much broader. The second downward-projecting segment is the basal tarsomere, which is clearly much larger than the other, more distal tarsal segments. In the queen the metathoracic basal tarsomere lacks the pollen collection apparatus of its counterpart in the worker (see Plates 2.28, 2.29, 2.30, and 2.31). Four remaining tarsal segments are present; the last one (pretarsus) is elongate and bears claws. These first four tarsal segments have no muscles, but a common tendon traverses all of them and inserts into the flexor muscle of the pretarsus. (x 28)

1.33

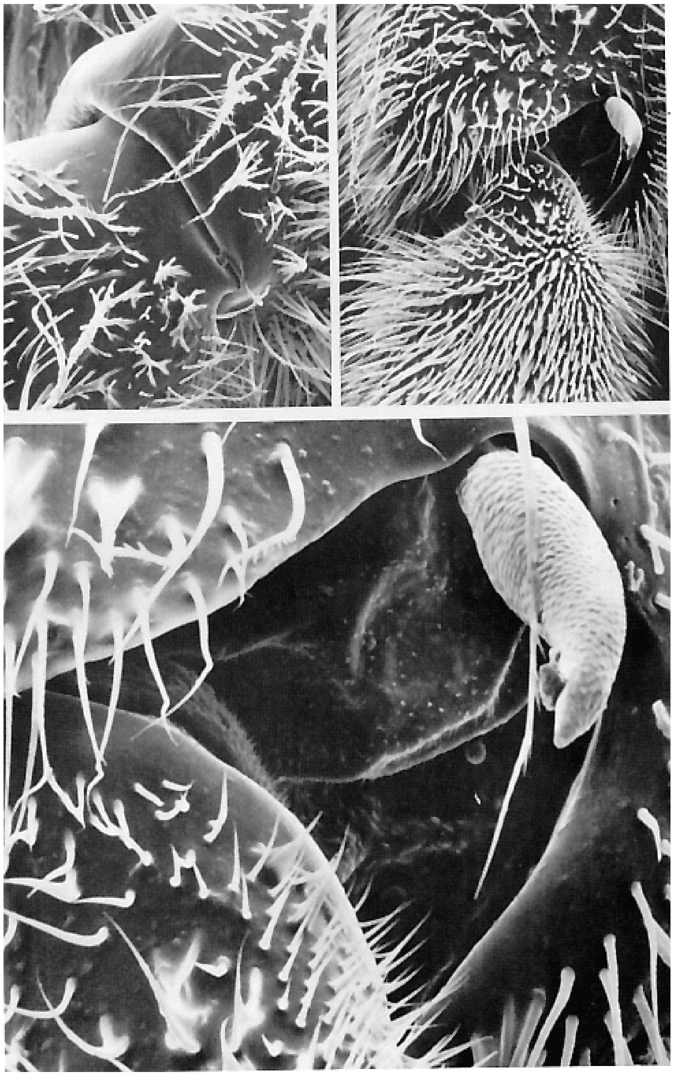


PLATE 1.33. QUEEN MIDDLE LEG

TOP LEFT Articulation between coxa and trochanter of the middle leg. (x 140)

TOP RIGHT Digitiform, scale-covered cuticular spur at the tibia-basitarsus joint. (x 31)

BOTTOM Higher magnification of the tiny spur in the top right micrograph. It appears to arise from the intersegmental membrane between the two leg segments. This miniscule, pineconelike spine may be an external proprioceptor-mechanoreceptor that monitors leg flexion or torque. The comparable appendage in worker bees is called the wax spur (see Plate 2.27). (x 360)

1.34

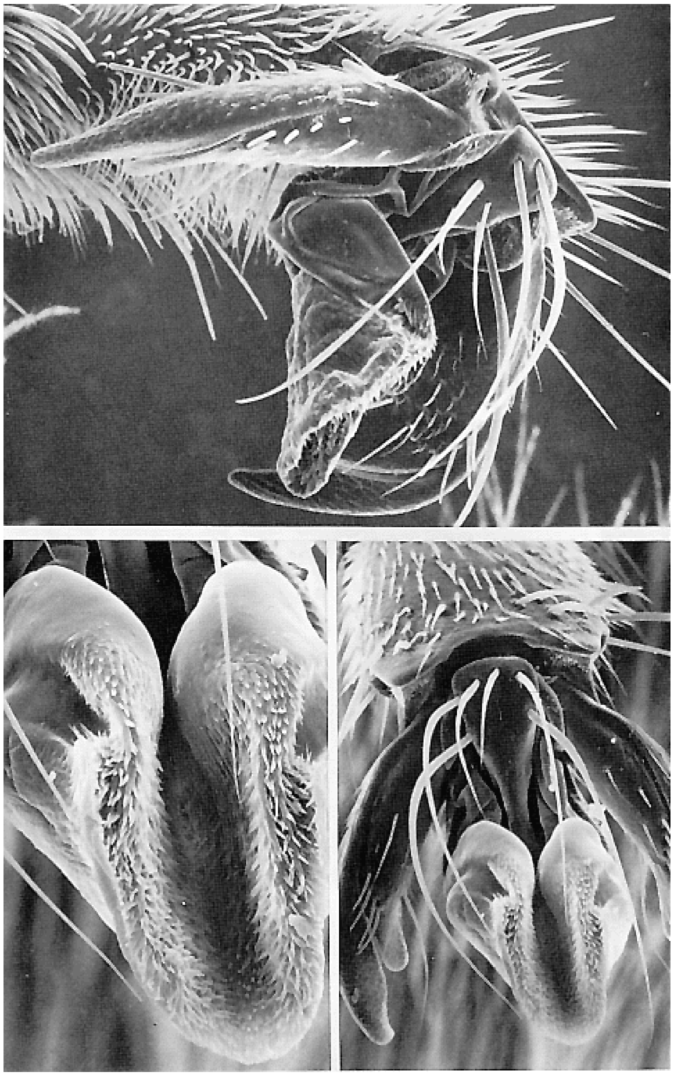


PLATE 1.34. QUEEN FOREFOOT AND HINDFOOT

TOP Pretarsus of the metathoracic (hind) leg. Its two main features are the paired claws surrounding the toung like like arolium. About a half dozen long, large, curved hairs project backward from the median sclerite. At the base of the arolium, and projecting proximally (leftward), is the planta, which is covered with spines that extend distally. The unguitractor, which is not well displayed in this field, is located to the left of the planta. The medial surface of each bilobed claw has several ranks of fine hairs and a few chaeticalike sensilla. (x270) Metathoracic pretarsus facing the viewer, dorsal side up.

BOTTOM RIGT The median sclerite is visible, along with the stout spines that issue from it. Several different forms of hair are present on the base of the last tarsal segment (top). (x 168)

BOTTOM LEFT Spiny arolium. As the claws relax, the arolium assumes the pursed shape. When the claws are active and extended, the arolium is drawn upward and spreads out between the claws. The bee uses this fleshy lobe to grip surfaces that cannot be penetrated or grasped by the claws. (x 378)

1.36

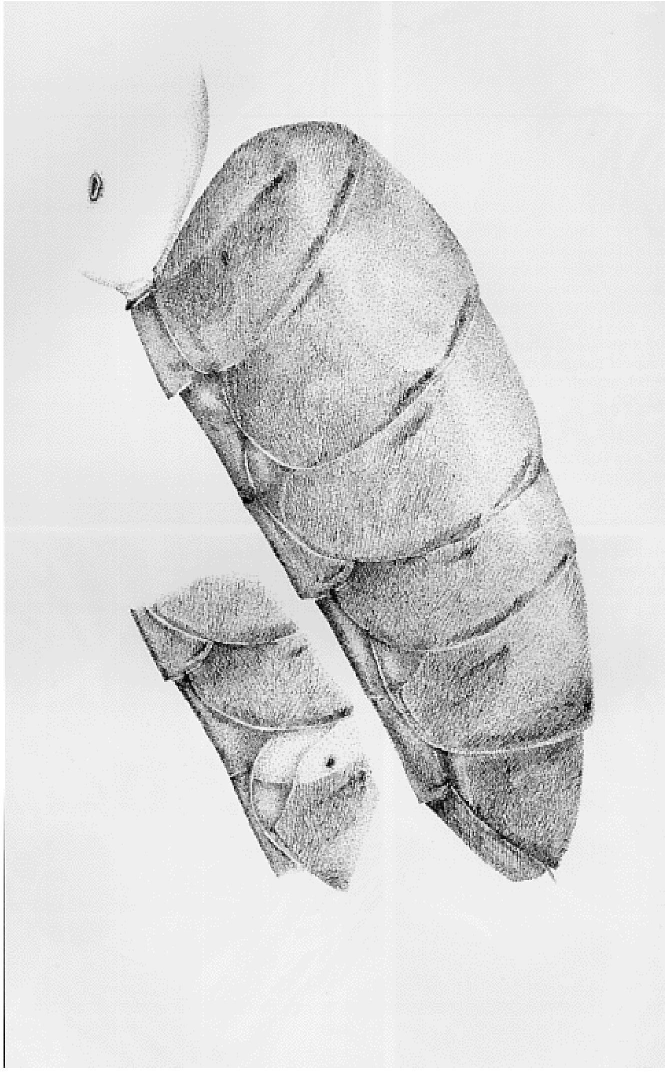


PLATE 1.36. QUEEN ABDOMEN

Gaster (abdomen), which consists of a first, rather indistinct segment (attached to the thoracic region) with a prominent spiracle, the petiole (waist), and the remaining posterior gaster segments. The dark spots indicate the relative position of spiracles on the first abdominal segment and on that portion of the abdomen behind the petiole. There is one spiracle on each side of the first seven segments (see also Plate 1.16).

1.37

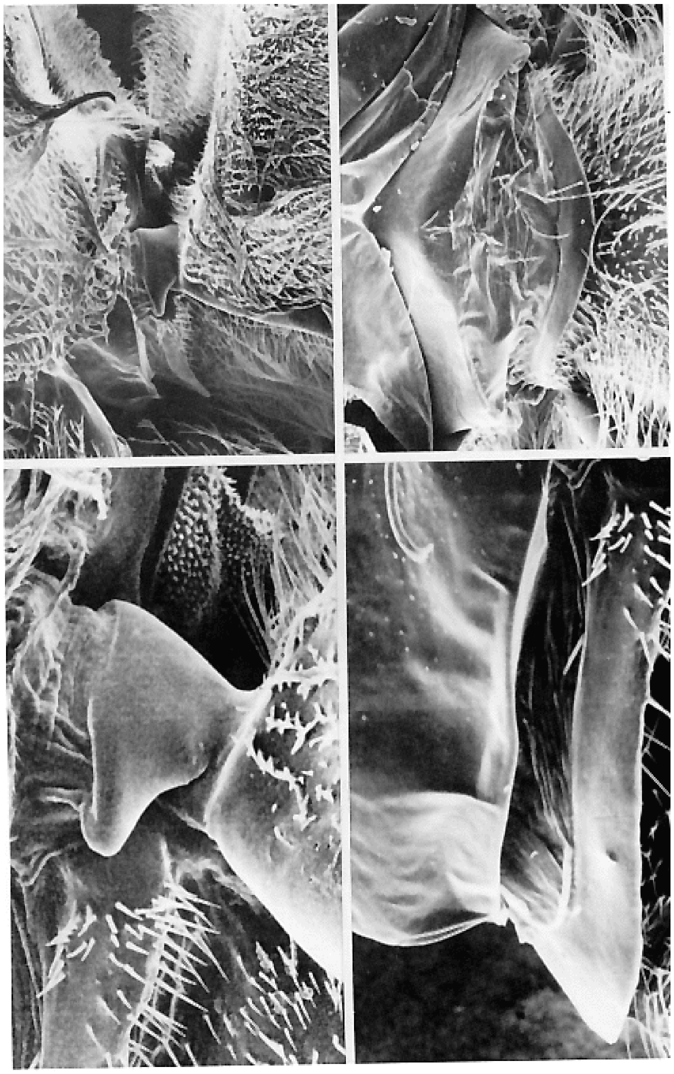


PLATE 1.37. QUEEN I- PETIOLE LATE PAL AND VENTRAL VIEWS

TOP LEFT Lateral view of the petiolar region, or "waist," the constricted area between the first and second abdominal segments. On the left is the "bump" of the propedeum (first abdominal tergal plate); on the right, across the narrow petiolar isthmus, is the second abdominal tergite. The 1, saddle" between the two segments is the membranous roof of the petiole pocket. (x 6 1)

BOTTOM LEFT Close-up of the petiole. Immediately below and on the left is the first abdominal sternite. On the right is the second abdominal sternite. (x 2 10)

TOP RIGHT Ventral view of the petiole. A membranous area divides the ringlike first abdominal sternite (left) from the cuticular ring that is the second abdominal sternite. (x 55)

BOTTOM RIGHT Petiolar region. On the right is the ringlike second abdominal sternite. Projecting leftward from that sternite is the wrinkled and flexible intersegmental membrane. (x 175)

1.38

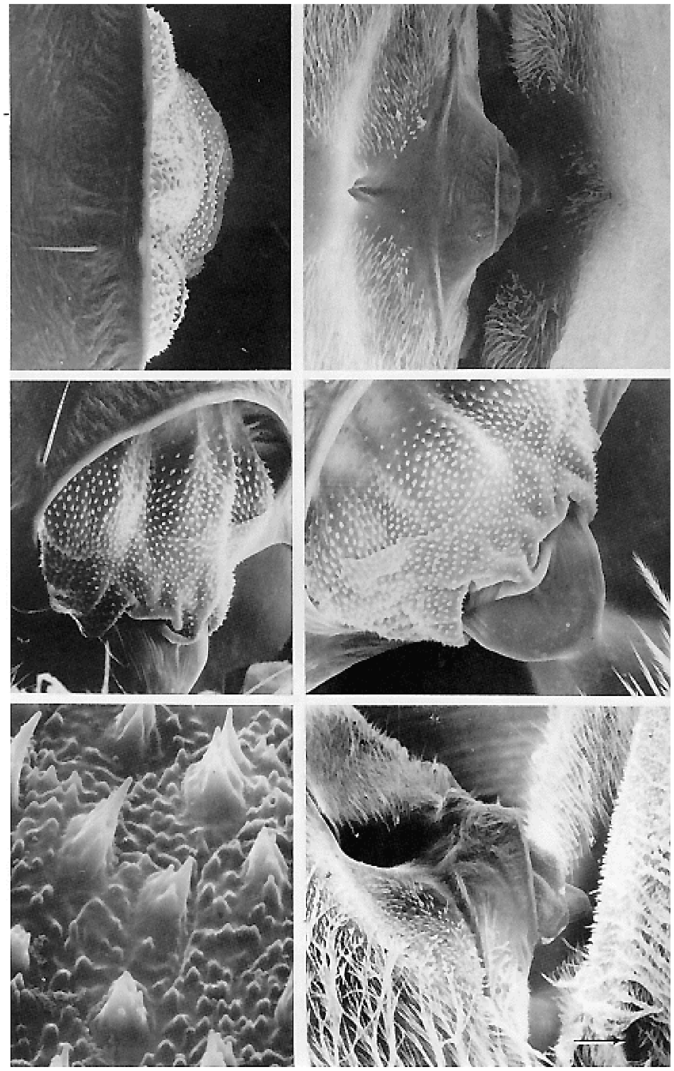


PLATE 1.38. QUEEN PETIOLE, DORSAL VIEW

TOP LEFT. Dorsal view of the essentially hairless petiole. The dark vertical sector (with one socketed cuticular hair) is the posterior portion of the mesoscutellum The intersegmental membrane spanning the propodeum and second abdominal tergite appears as a trilobed structure. (x 140)

MIDDLE LEFT. Tangential orientation of the petiole (the head is to the top). The numerous cuticular spines in the interseginental membrane are in a somewhat ordered array. (x 150)

BOTTOM LEFT. Higher magnification of the multipeaked cuticular spines on the intersegmental membrane of the petiolar region. The interspine areas have a low-lying bumpy texture. (x 2,600)

TOP RIGHT Petiolar region (the head is to the left). The propodeum has been tipped forward so that its full posterior extent is visible as it attaches to the gaster (abdomen). The slender petiolar attachment is the vital linkage that connects the spherical thorax (with the first abdominal segment) with the even more massive gaster. (x 66)

MIDDLE RIGHT. Dorsal view of the interseginental membrane of the petiolar region (the head is to the upper left). Compare this micrograph with its left side counterpart in the bottom right micrograph (x 175)

BOTTOM RIGHT Lateral view of the petiolar region. At the extreme lower right (arrow) is the dorsal portion of the second abdominal spiracle. (x 60)

1.39

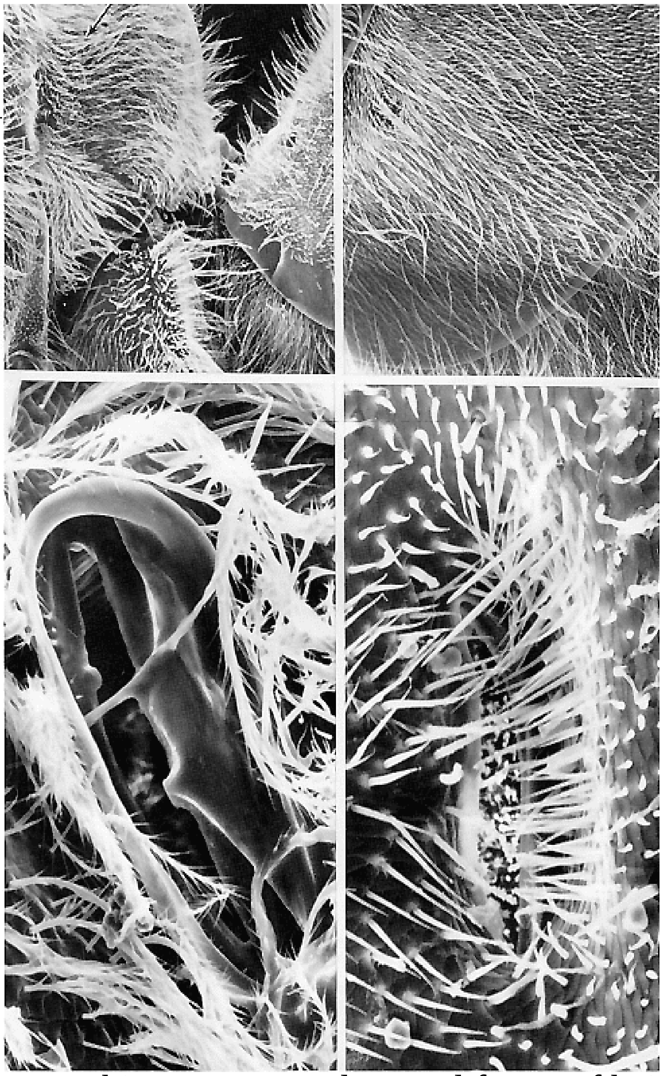


PLATE 1.39. QUEEN ABDOMINAL SPIRACLES

TOP LEFT. Survey of the pleural portion of the first and second abdominal segments. The small spiracular apertures (one per segment) (arrow) are obscured by extensive hair cover. (x31)

BOTTOM LEFT. First abdominal spiracle on the propodeal segment of the thorax. This is the largest spiracle (along with its opposite side twin). Its elevated cuticular rim surrounds a shallow atrium, and the interior rim is the true opening into the tracheae. The tracheae are closed off from the inner (interior) rim by a sizable valve, which is incompletely Seen here because of a thin film of dried material emanating from the trachea. (x 240)

TOP RIGH T. Abdominal spiracle (upper left) With difficult\,, the covert and linear character of this aperture can be made out. (x 37)

BOTTOM RIGHT. Higher magnification of aii abdominal spiracle. A cuticular hair fence of tergal orign incompletely covers this aperture, and several forms of hairs are present.
The inner wall of the atrium Is replete with very short hairs. (x 360)

1.41

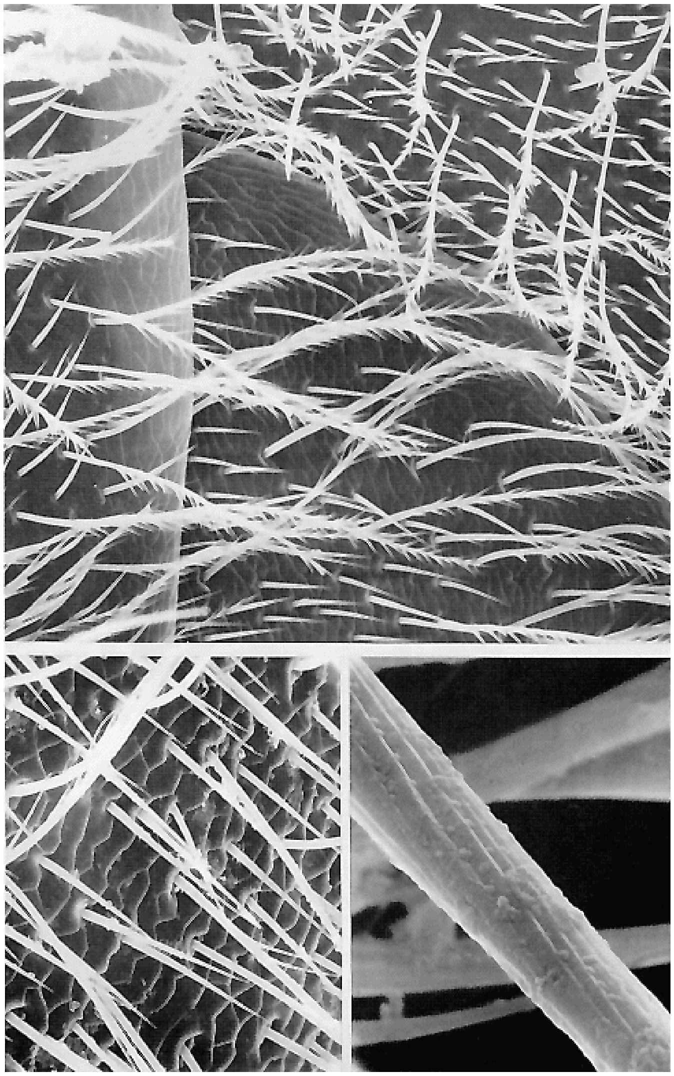


PLATE 1.41. QUEEN THORAX AND ABDOMEN, CUTICULAR HAIRS

TOP Portions of two terminal abdominal segments. Of interest is the cuticular relief that extends over these segments and the fringed and glabrous cuticular hairs that are abundant over the entire body. (x 263)

BOTTOM LEFT. Cuticle and cuticular hairs of a metathoracic pleurite. Most of these cuticular hairs are unfringed and unbranched, and the tips are sharply pointed. Some of the long branched hairs along the periphery of the abdominal tergites and sternites are attached to gland cells that may be the source of queen pheromone obtained by workers during grooming. (x 550)

BOTTOM RIGHT. Close-up of a cuticular hair shaft on an abdominal sternite. The fluted nature of the side wall is not artifactual, although the "blebs" on the shaft wall may be debris. (x 550)

1.42

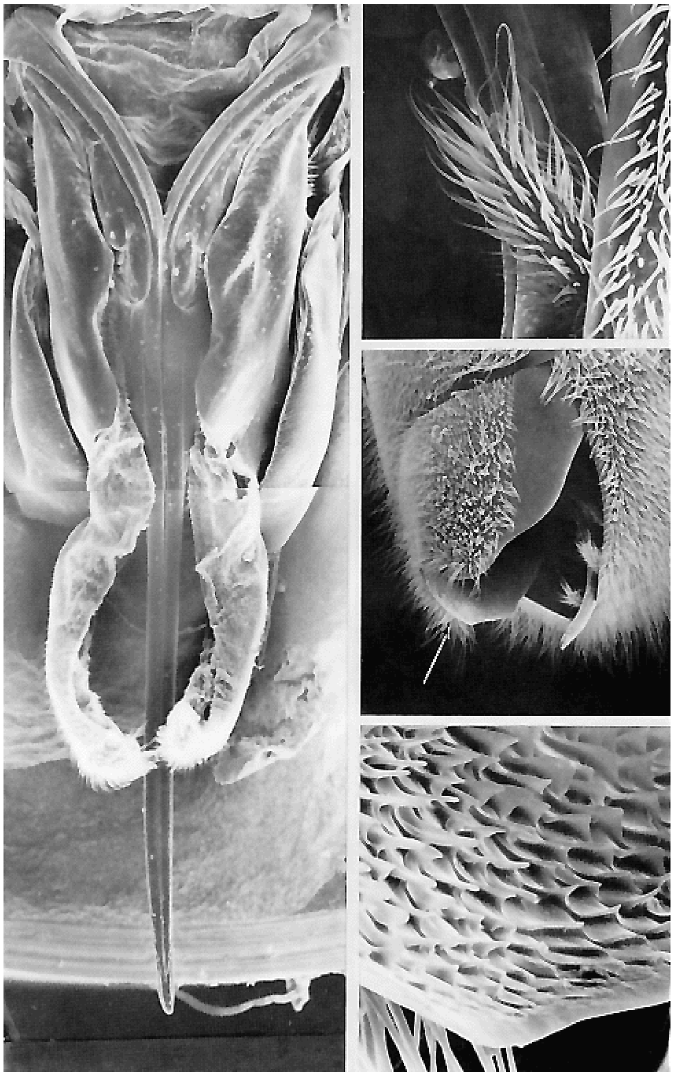


PLATE 1.42. QUEEN STING

LEFT Photomontage showing the entire ventral surface of the sting. The two barbed lancets, in close apposition, overlay the stylet trough to form the venom channel. On either side are the distorted (in specimen preparation) sheath lobes of the sting. Each sheath lobe is extended proximally from beneath an oblong plate. Medial to each plate, near the top of the montage is a forked structure; each "tine" or ramus connects proximally with a triangular plate, which in turn is associated with a quadrate plate. The latter sclerite ties alongside (to the Outside of) the oblong plate. See the Appendix, Fig. A. 1. (x 94)

MIDDLE RIGHT Lateral view of the abdominal tip. The ultimate abdominal segment seen here is number seven; the seventh tergal and sternal plates enclose most of the sting as well as segments eight to ten. The aperture through which eggs and feces pass when expelled from the body also functions as the entrance to the sting chamber. The fuzzy projections arising from the floor of the sting chamber are the tips of the sting sheath. The arrow at the bottom left of the field points to the area further magnified in the bottom right micrograph. (x 31)

BOTTOM RIGHT Medial surface of the abdominal tip (ventral sclerite) revealing myraids of stout cuticular spines (arrow in right middle micrograph) (x 62)

TOP RIGHT Higher magnification of the abdominal tip in the right middle micrograph showing the setose condition of the sting sheath at its proximal origin. (x 250)

1.43

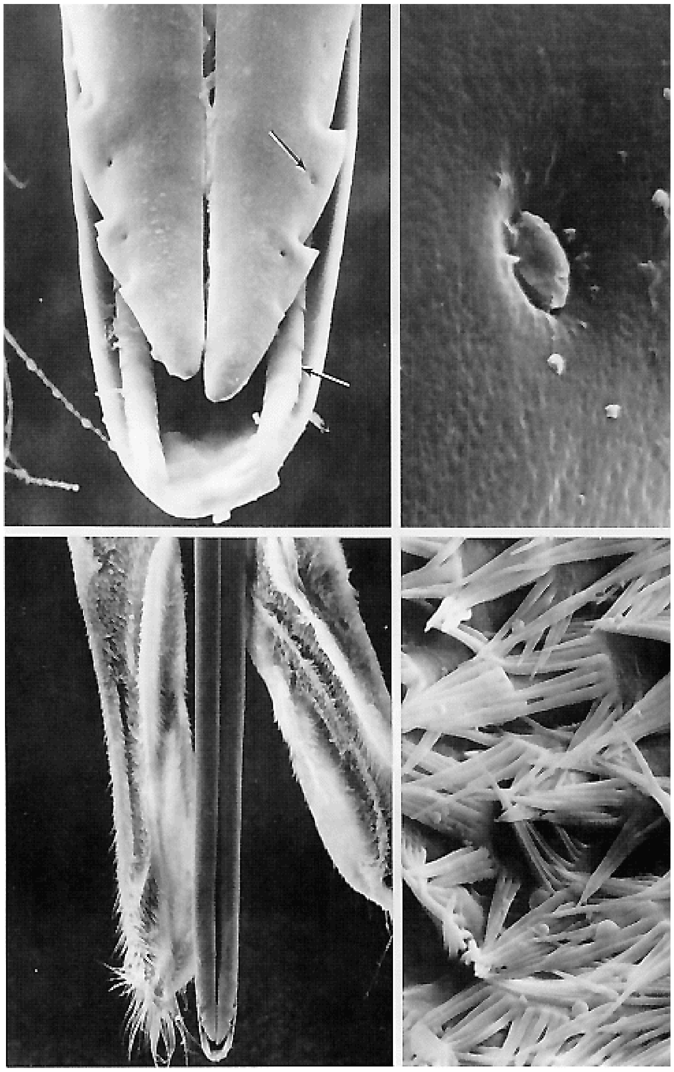


PLATE 1.43. QUEEN STING. CLOSE-UP

TOP LEFT Distal tip of the sting apparatus showing the terminus of the venom channel. Two barbed lancets in the foreground oppose each other (earlier workers reported that the queen sting had no barbs). Behind the lancets is the troughlike stylet. When stinging, the lancets slide back and forth on serrated tracks (lower arrow). The tracks form the trough at the tip of the stylet. Each thrust pulls the sting deeper into the victim. Both the track and the groove in each lancet (not visible) are serrated, probably to reduce friction. Note the small "indentations" (one per barb) (upper arrow) on the lateral margins of each lancet (see the top right micrograph). In comparison with worker barbs, the queen barbs are less formidable, which may permit the queen to sting repeatedly without loss of the sting. Other work suggests that the queen sting is covered with a surface lubricant while that of the worker is not. (x 1,040)

TOP RIGHT Highly magnified view of the indentation indicated by the upper arrow in the top left micrograph. One indentation is associated with each barb on the lancets and stylet. This structure appears to be a campaniform sensillum. If so, such a proprioceptor might monitor pressure generated by the relative depth of insertion of the sting or flexion of the lancets. (x 15,000)

BOTTOM LEFT Everted lancets of the queen. The stylet is flanked by the two hairy lobes of the sting sheath. (x 188)

BOTTOM RIGHT Masses of cuticular hair fasicles internally lining the sheath lobes. (x4,688)

1.44

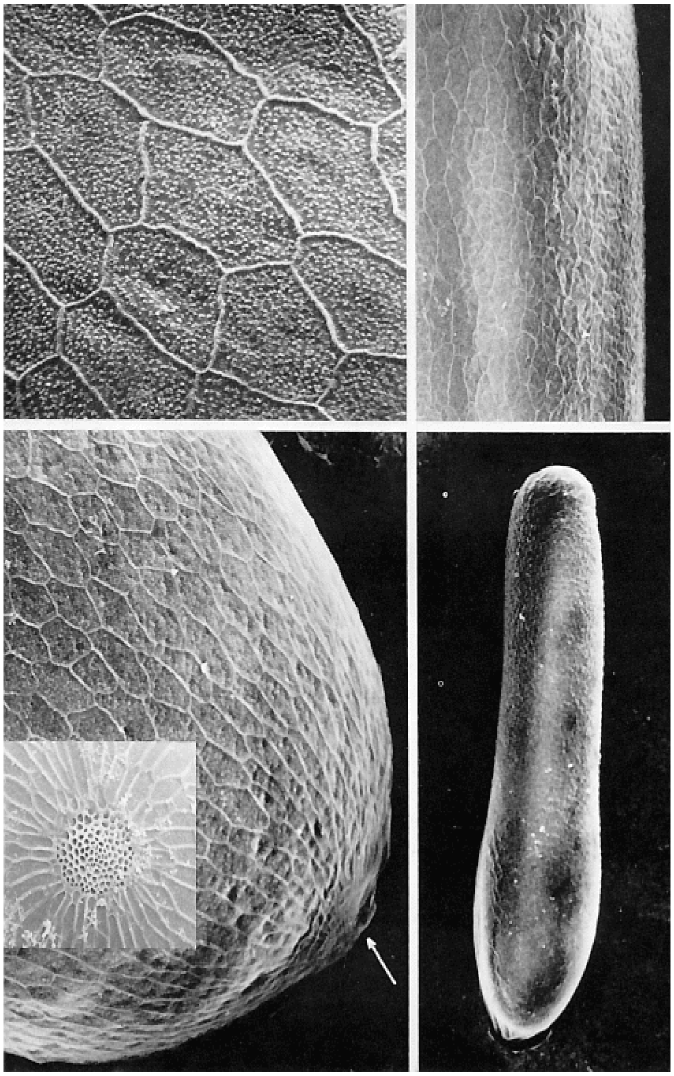


PLATE 1.44. EGG

BOTTOM RIGHT Egg produced by the queen bee. Both end,,; are rounded, and one pole seems larger than the other. At this magnification the cuticular relief characteristic for this species is barely visible, (x 110)

TOP RIGHT Higher magnification of the egg surface showing, the reticulated pattern of the cuticular ridges. (x 400)

BOTTOM LEFT Close-up of the large pole of the egg showing the linear ridge system enclosing polygonal areas of the egg surface (chorion). The arrow indicates the area further magnified in the inset. (x 600)

BOTTOM LEFT INSET. Micropyle of the egg. (x 600)

TOP LEFT. Polygonal zones on chorion. The basal chorion surface is randomly studded with minuscule, discrete bumps. (x 1,250)

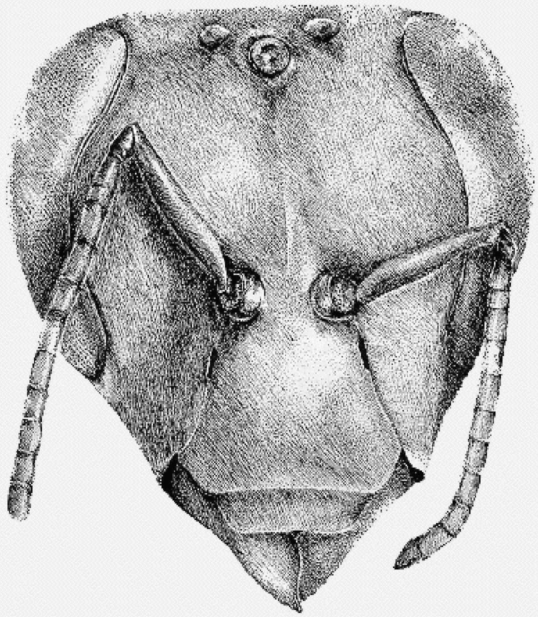


PLATE 2.1 WORKER HEAD

FRONTAL VIEW

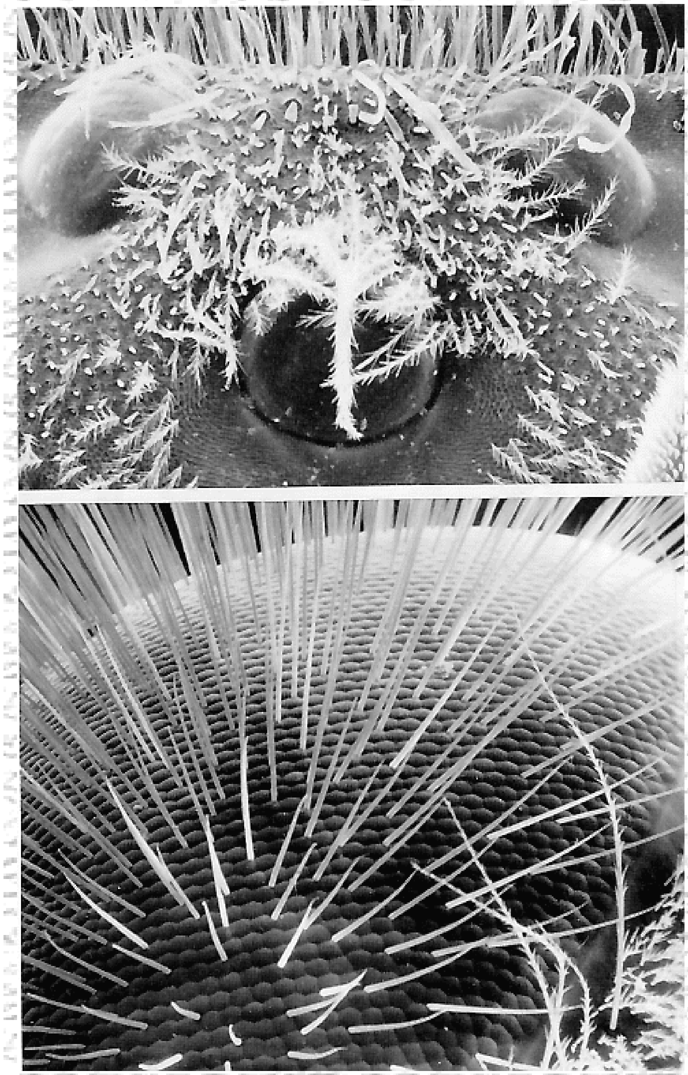


PLATE 2.2. WORKER EYES

TOP. Three ocelli (two lateral and one medial) on the dorsal portion of the head between the two compound eyes. Branched body hairs are abundant around these three photoreceptor organs. Each of the biconvex lenses refracts light to about 800 well-packed photoreceptor cells. As light monitors, these organs may regulate the start and finish of foraging activity as well as visually measure horizon versus ground to assist in maintaining level flight. (x 167)

BOTTOM. Compound eye with its thousands of facets. Under each facet are nine photoreceptor cells, all of which are color receptors and some of which are capable of analyzing polarization patterns in the skylight. The conspicuous, long, interfacetal hairs are mechanoreceptors that inform the worker of flight speed and wind direction. (x 270)

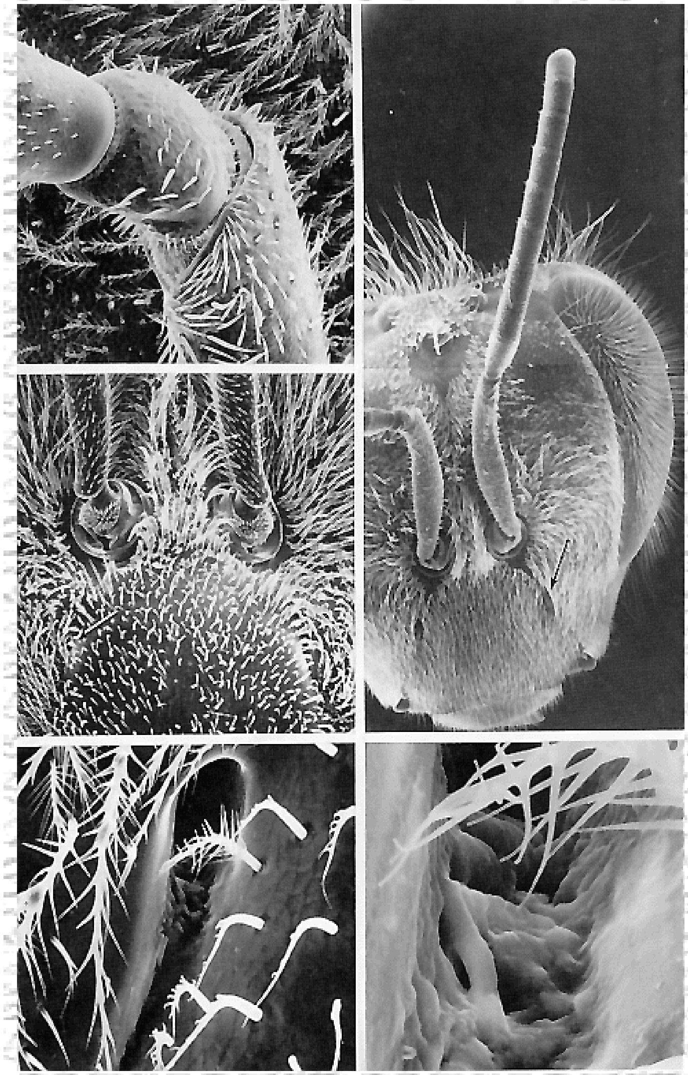


PLATE 2.3. WORKER FACE

TOP RIGHT Photomontage of frontal view of the head showing the elbowed character of the antennae. The three occlli are seen at the vertex; to the right of that cluster is the hairy compound eye. The anterior tentorial pit is near the bottom (arrow) (x 31)

MIDDLE LEFT Higher magnification of the antenna] bases. The antennal socket and sclerite enclose the bulbous base of the elongated scape (first segment) of the antenna. The basal surface is covered with rows of short (probably mechanoreceptor) hairs. Extending forward from the antennal base,; is the broad triangular clypeus. The anterior tentorial pit is visible (arrow) (x 50)

TOP LEFT Close-up of the scape-pedicellus junction (the antennal elbow). The short hairs at the base of the pedicellus may be external proprioceptors that monitor the varying angle of antennal flexion as different groups of these hairs contact and are bent against the edge of the scape at given degrees of flexion. Johnston's organ (an auditory organ) is located within the pedicel. (x 186)

BOTTOM LEFT Anterior tentorial pit. These cavities lie in the epistomal sulcus and are difficult to discern at low magnification (arrows in upper right and middle left micrographs). The pits are external manifestations of the anterior roots of the cannular tentorium, the endoskeleton of the head. (x 409)

BOTTOM LEFT Close-up of the corrugated cuticular floor and periphery of the anterior tentorial pit. (x 1,650)

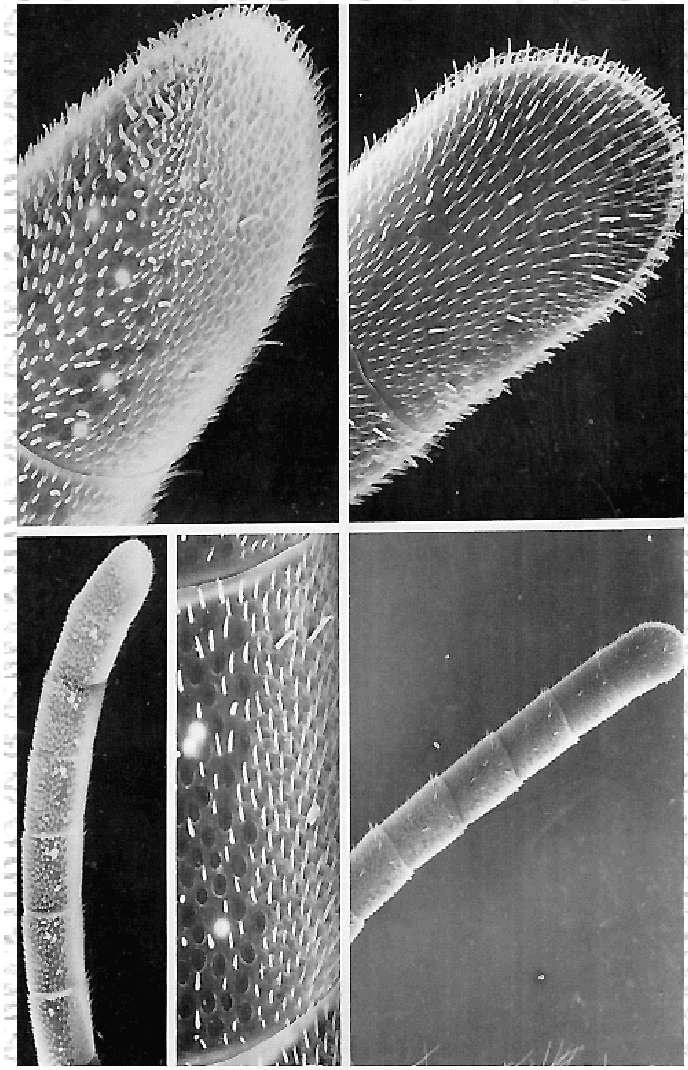


PLATE 2.4. WORKER ANTENNA

BOTTOM LEFT. Survey of the medial surface of the ultimate six (flagellar) segments. Even at this low magnification, very bright foci (denoting clustered pore sensilla) are apparent on each segment. (x 65)

BOTTOM MIDDLE. Higher magnification of the sixth antennal segment. the three bright foci are areas of' far greater secondary electron capture bv the microscope, and each bright area delimits a pore sensillum. In addition, numerous trichoid sensilla are visible on the right and many placoid sensilla are on the left. (x 702)

BOTTOM RIGHT Antenna, posterior surface. Robust trichoid sensilla are sparsely distributed among slender short trichoid sensilla. (x 65)

TOP LEFT Terminal antennal segment, dorsal view. All sensilla types known for the antenna are found here. Four pore organs are easily visible (the bright, circular spots) in the midst of many plate and trichoid seisilla (at least three types of trichoid sensilla). Electron beam damage may have caused the curled or bent trichoid sensilla. (x 390)

TOP RIGHT. Terminal antennal segment, ventral view. On this surface are 'at least three morphologically different forms of trichoid sensilla. (x 312)

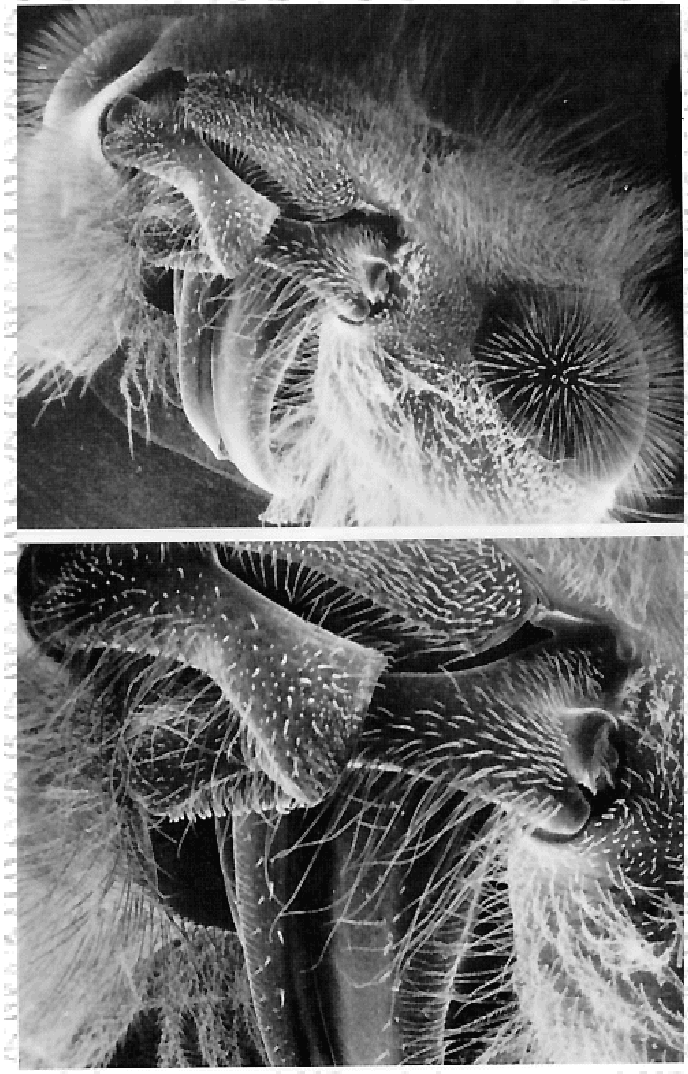


PLATE 2.5. WORKER MOUTHPARTS

TOP Tangential view of the ventral aspect of the head showing the right and left compound eyes. Most prominent are the crossed mandibles, which are laterally articulated and lie immediately beneath the oval platelike labrum. The mandibles appear to embrace the proximal portion of the glossa and surrounding galeae (of maxillae), which are folded back beneath the head. (x '03)

BOTTOM. Close-up of the sensilla and their distribution on the labrum, mandibles, and maxillae. The lateral articulation of the left mandible with the ventral margin of the gena is visible. These spatulate jaws are drawn in (toward the insect) and out. (x 85)

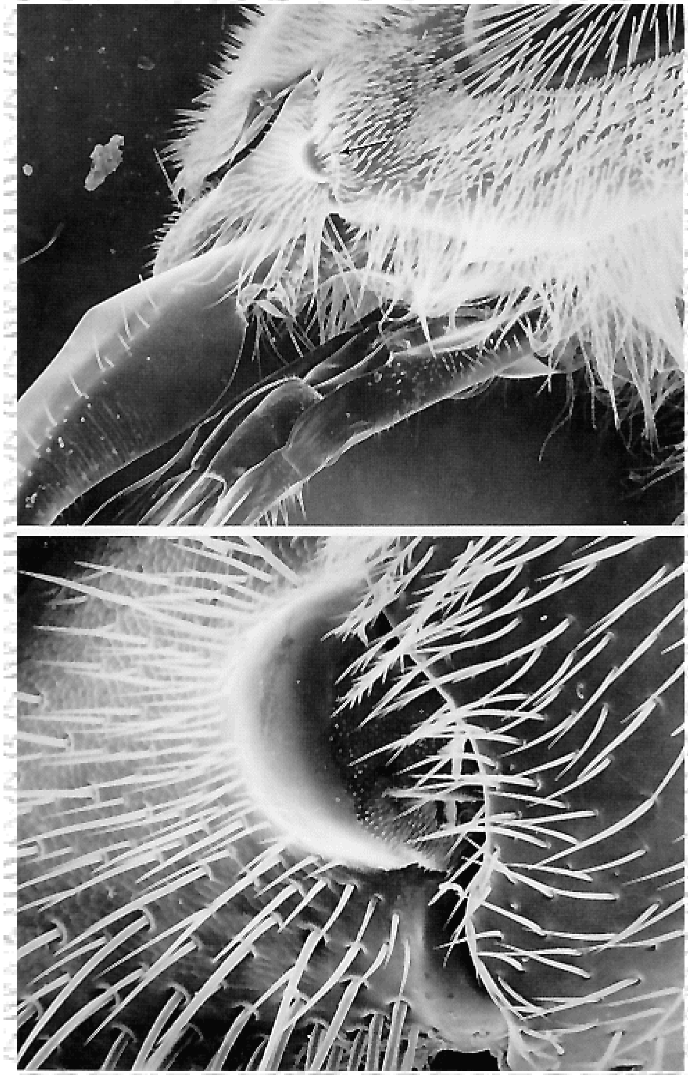


PLATE 2.6. WORKER HEAD LATERAL VIEW

TOP. Left profile of the head. The compound eye is in the tipper right corner. The relatively glabrous bladelike maxilla extends diagonally from lower left to center. Behind the makilla are the labial palps and glossa. The arrow indicates an area further magnified in the bottom micrograph. (x 55)

BOTTOM. Higher magnification of the abductor apodeme and hinge of the mandibles, which is on the dorsal margin of the mandible (arrow in top micrograph). On the right side is the gena. The posterior margin of the gena is juxtaposed with the mandible. This apodeme is seen externally as a small cuticular cavity at the lateral margin of the mandible. The cranial abductor muscle inserts into the internal cuticular inflection formed by this apodeme. Socketed proprioceptor hairs are visible on the base of the mandible. (x 335)

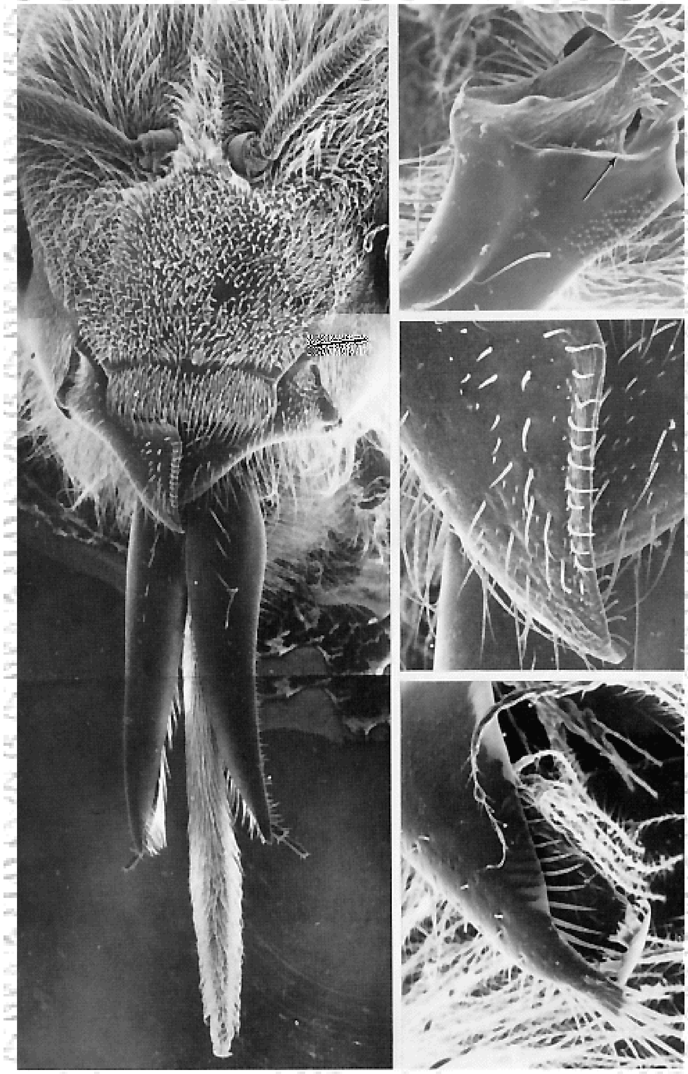


PLATE 2.7. WORKER MOUTHPARTS

TOP LEFT. Photomontage of the glossa. The glossa is extended when feeding here it is extending between the pendulous galeae, the terminal segment of the underlying labial palps are nearly covered by the galeae, and only the tips are exposed. The arrow indicates the area further magnified in the top right micrograph. (x 34)

TOP RIGHT. External opening of the mandibular gland (arrow) exposed when the mandibles are wide open. (x 100)

MIDDLE RIGHT Higher magnification of the cutting edge of the right mandible. Trichoid and basiconic sensilla are present on the exterior surface of the mandibles; these putative chemoreceptors may be gustatory in nature and assist in tasting materials that are being manipulated and chewed by the mandibles. The longer socketed hairs may be mechanoreceptors that, on contact with the other mandible, provide proprioceptive information about the degree of mandibular retraction. (x 110)

BOTTOM RIGHT Distal tip of the maxillary galea. A cluster of long, sharply pointed hairs extends from the end of the galea, and nine slender, sharp setae emanate from the mediodistal margin of this part of the maxilla. Short, peglike sensilla are sparsely posted on the lateral aspect of the galea tip. These sense organs are probably similar to the sensilla of the mandibles, and both types are likely to have similar roles in gustation and proprioception. (x 160)

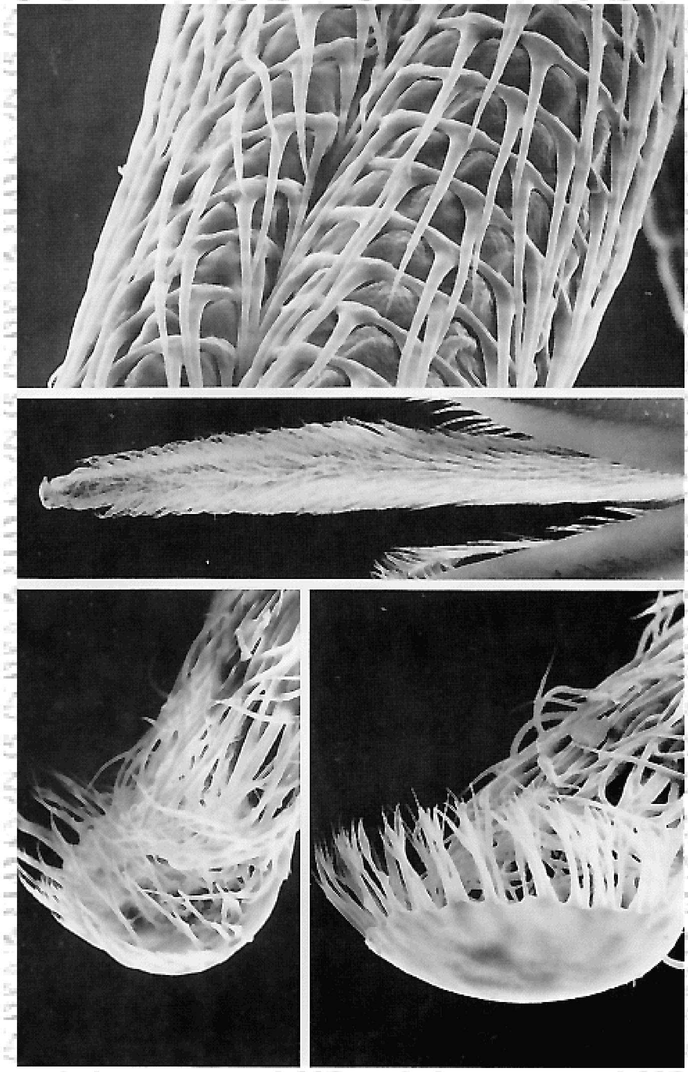


PLATE 2.8. WORKER GLOSSA

MIDDLE. Survey of the glossa projecting outward from the partial clasping of the two maxillary galea. (x 53)

TOP Bilobed glossa covered with hairs that arise from a series of cuticular rings. The intersegmental membrane intervenes between, and is overlaid by, the hairs. (x 680)

BOTTOM LEFT. Flabellum (tongue tip). The terminus, attached to the glossa by a single ventral hinge, is spatulate and tipped with branching hairs. (x 600)

BOTTOM RIGHT. Close-up of the flabellum showing its spoonlike geometry and the hair fringe around the "spoon . " The precise function of this struc- ture is unknown although it may serve as a filter for the nectar, which apparently must flow into the "spoon" before it can be imbibed by the bee. (x 650)

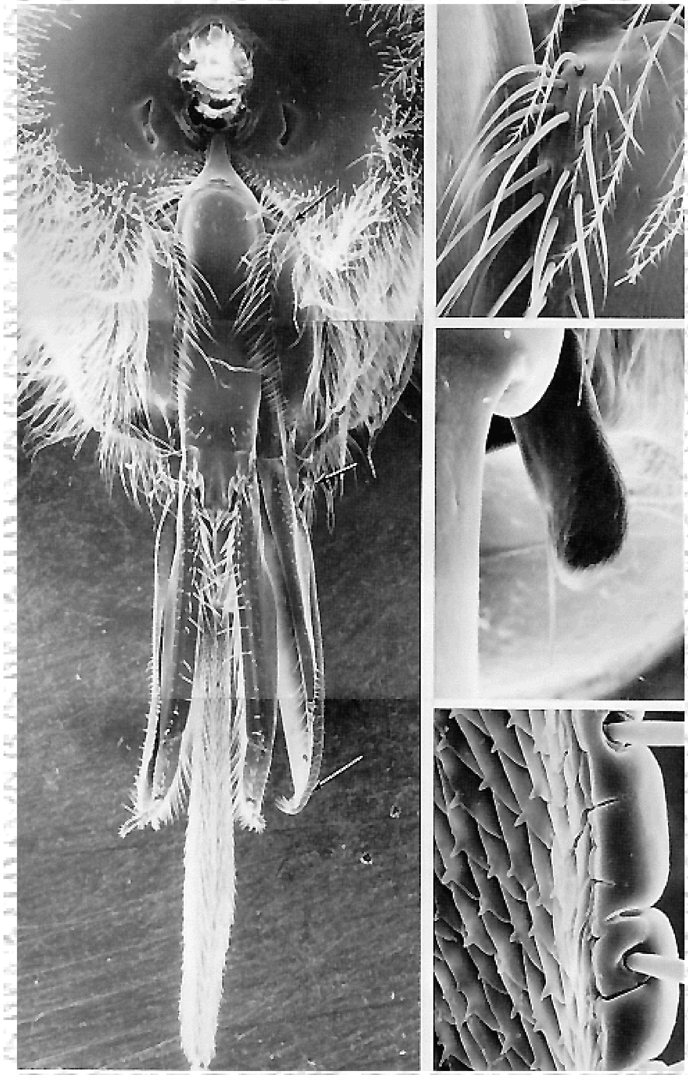


PLATE 2.9. WORKER MOUTHPARTS, POSTERIOR VIEW

LEFT Photomontage of the posterior view of the mouthparts. The occipital foramen (top of the field is still occupied by the severed tissues that pass from head to thorax. Flanking the foramen are two posterior tentorial pits. Projecting directly clown from the foramen, in the hollow (fossa of the proboscis) behind the head, are the labium and paired maxillae. The triangular piece immediately below the foramen is the postmentum. The maxillae gape, revealing the long, hairy glossa, which is half clasped by the labial palps. (Compare this micrograph with Plate 1.10, the queen mouthparts.) Lastly, the "shoulders" behind and on either side of the labium (prementum) are the mandibles. The top arrow indicates an area that is further magnified in the top right micrograph, the bottom arrow an area in the bottom right micrograph. The middle arrow points to the apical papilla of the maxillary palp, shown at higher magnification in the center right micrograph. (x 34)

TOP RIGHT Higher magnification of the prementum-mandible sector showing the branched body hairs along
with three kinds of trichoid sensilla (lop arrow In left micrograph (x 230)

MIDDLE RIGHT . Apical papilla of the maxillary palp. One slender sensilla is seen near its tip (middle, arrow in the left micrograph). (x 450)

BOTTOM RIGHT Array of spine-tipped cuticular scales (bottom arrow in left micrograph on the interior surface of the maxilla (galeae). On the lateral margin of the maxilla, relatively large socketed hairs (sensilla chaetica) arise at regular intervals. These sensors are known to be mechanoreceptors and chemoreceptors (the latter for sugar and salts). (x 1,200)

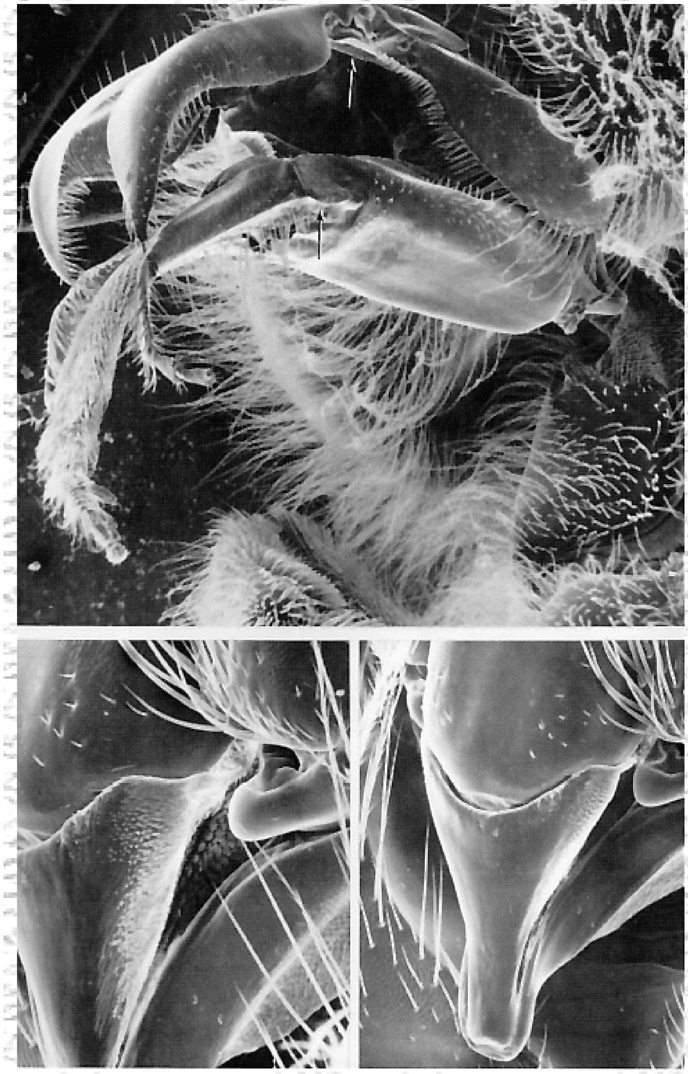


PLATE 2.10. WORKER MOUTHPARTS, ANTERIOR VIEW

TOP Survey of worker mouthparts (the compound eye and vertex of the head are cropped away at the top). Maxillae and labium appear as a twotiered awning (maxillae over labium) over the glossa. Two major segments of the maxillae are prominent. On the right is the stipes with its fringe of setae. The leftmost segments, connecting with the stipes, are the galeae with their bare-ringed (basal) and then setae-fringed margins. A pair of labial palps flanks the decumbent, elongate glossa. When not in use the glossa is retracted, merged with the labium, enclosed by the maxillae, and then folded back at the hinges (arrows) Compare this micrograph with Plate 3.8, the retracted drone mouthparts. (x60)

BOTTOM RIGHT Posterior (central) sector of the head. The principal feature is the duckbill-shaped postmentum of the labium. This sclerite points rearward toward the cervix (not visible). Above the postmentum and joining it is the prementum with its few short cuticular hairs. The cuticular "cradle" into which the postmentum fits is the lorum. (x 175)

BOTTOM LEFT Higher magnification of the near-contact zone between lorum (on the left) and postmentum (on the right). The interesting, pebblegrained inner surface of the postmentum is visible. (x 270)

PLATE 2.11. WORKER MAXILLARY PALP

BOTTOM. Survey of the anteriolateral portion of the head (upper arrow in top micrograph, Plate 2.10). The thumblike cuticular appendage in the center is the maxillary palp, which is to the right of the labium. Behind this palp (extreme lower right) is the interior surface of the mandible with its numerous hairs projecting inward. (x 432)

TOP Close-up of a hair plate containing about two dozen mechanoreceptor hairs located at the base of the maxillary palp. The hairs at the curved margin (upper right) are bent whenever the palp is moved medially so these mechanoreceptors can signal its movement and position relative to the other mouthparts. (x 2,520)

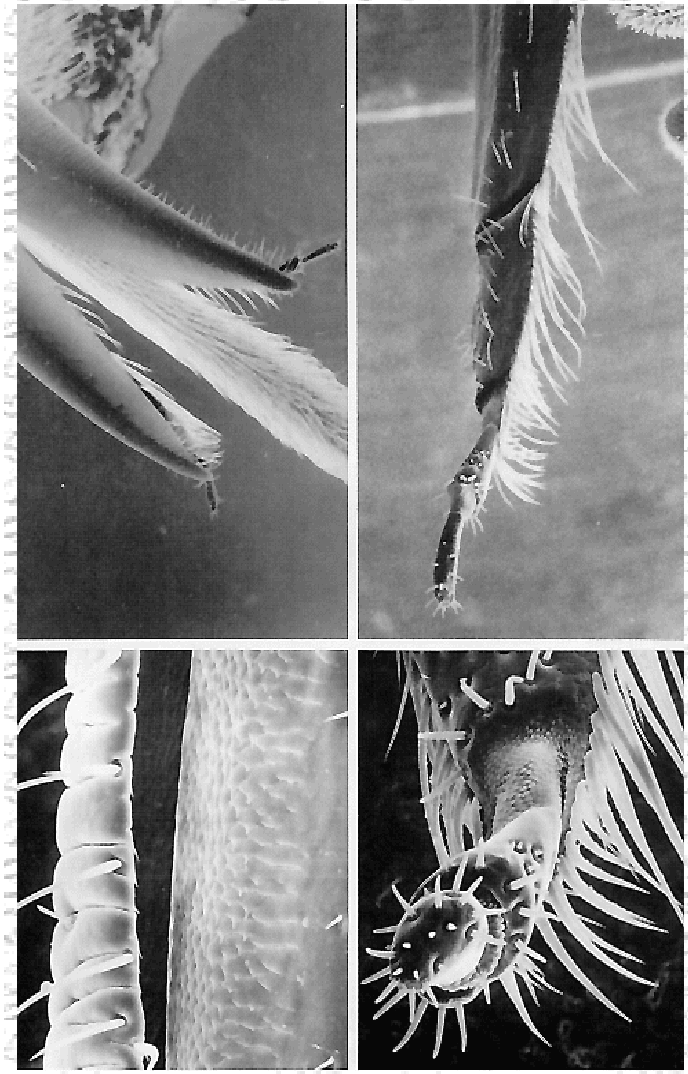


PLATE 2.12. WORKER MAXILLA AND LABIUM

TOP LEFT. Two labial palps (each partly covered by the galea of corresponding side maxilla) on each side of the very hairy glossa. (x 119)

TOP RIGHT. Four-segmented labial palp. (x 119)

BOTTOM RIGHT. Frontal view of the labial palp showing the ultimate segment with numerous sensilla. (x 372)

BOTTOM LEFT. Close-up of an annulated galea with its robust elongate trichoid sensilla. On the right is the scaly surface of the labial palp. (x 480)

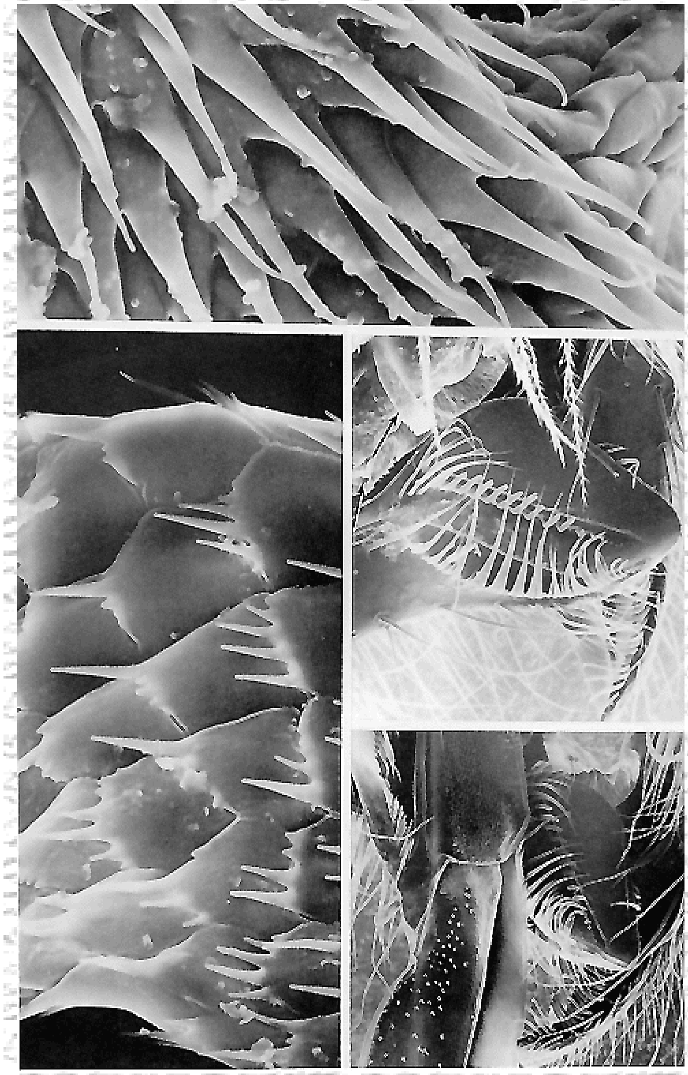


PLATE 2.13. WORKER ORAL CAVITY

BOTTOM Base of the extended proboscis, posterior view. Angling off and extending to the lower left corner is the stipes. At center is the interior surface of the left mandible. To the right of center is the right mandible, which is further magnified in the center right micrograph. (x 75)

MIDDLE RIGHT Interior surface of the partially closed mandibles. The arrows indicate areas further magnified in the top and bottom left micrographs. (x 3,200)

BOTTOM LEFT. Cuticular scales in the oral cavity (lower arrow in center right micrograph). (x3,200)

TOP Close-up of the interior surface of the oral cavity (upper arrow in center right micrograph). (x 3,200)

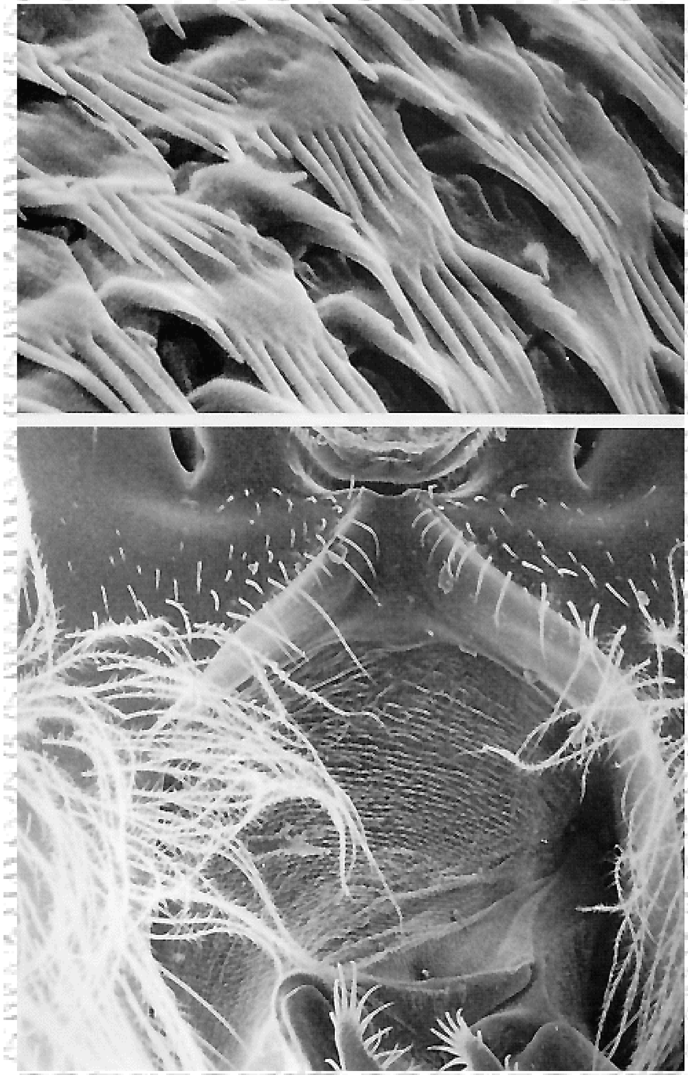


PLATE 2.14. WORKER POSTGENAL AREA

BOTTOM Ventral view of the occipital region of the head capsule. A portion of the cervix (neck) (center top) is flanked by the posterior tentorial pits. The "Gothic arch" is formed by the two postgenal inflections that surround the fossa of the proboscis. A membranous region with parallel folds Joins the postmentum (the "duckbill" at the bottom of the field). (x 108)

TOP Cuticular spines on the intersegmental membrane in the area immediately below the tip of the postmentum. (x 4,320)

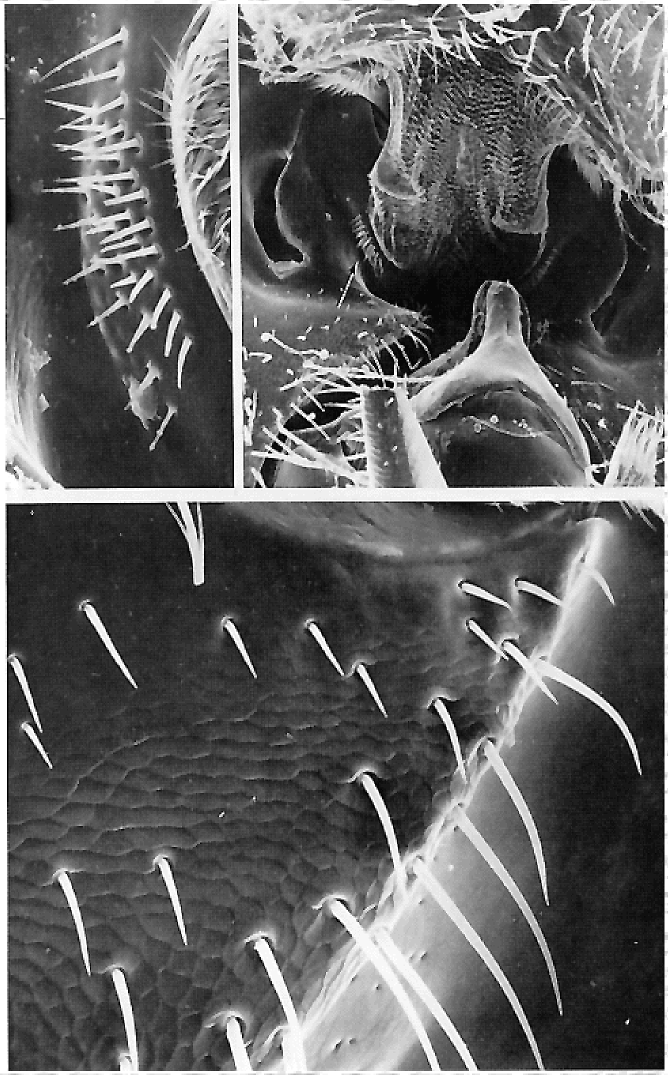


PLATE 2.15. WORKER CERVIX, VENTRAL VIEW

TOP Posterioventral view of head where the membranous cervix (neck) (covered with ranks of short spines) Joins the head. On either side of the cervix are the posterior tentorial pits. The occipital foramen (where the cervix joins the head) is flanked by two hair plates, each consisting of 30 short, trichoid sensilla (arrow) which are bent when the head turns laterally toward the cervix. These sensilla are gravity receptors. The pre- mentum extends upward, pointing to the cervix. (x 80)

TOP LEFT Close-up of the 30 socketed hairs (known mechanoreceptors that make up the left lateral occipital hair plate. These are adjacent to the cervix (arrow in top right micrograph). (x 720)

BOTTOM Posterior of the head. The hair plate is located in the ventromedial region of the head (arrow in top right micrograph). These trichoid sensilla are probably gravity receptors (and external proprioceptors) that inform the central nervous system about the attitude of the head and/ or mouthparts relative to the rest of the body. Signaling may be accomplished when the hairs contact and are bent by the postmenturn or the cervical sclerite. (x 720)

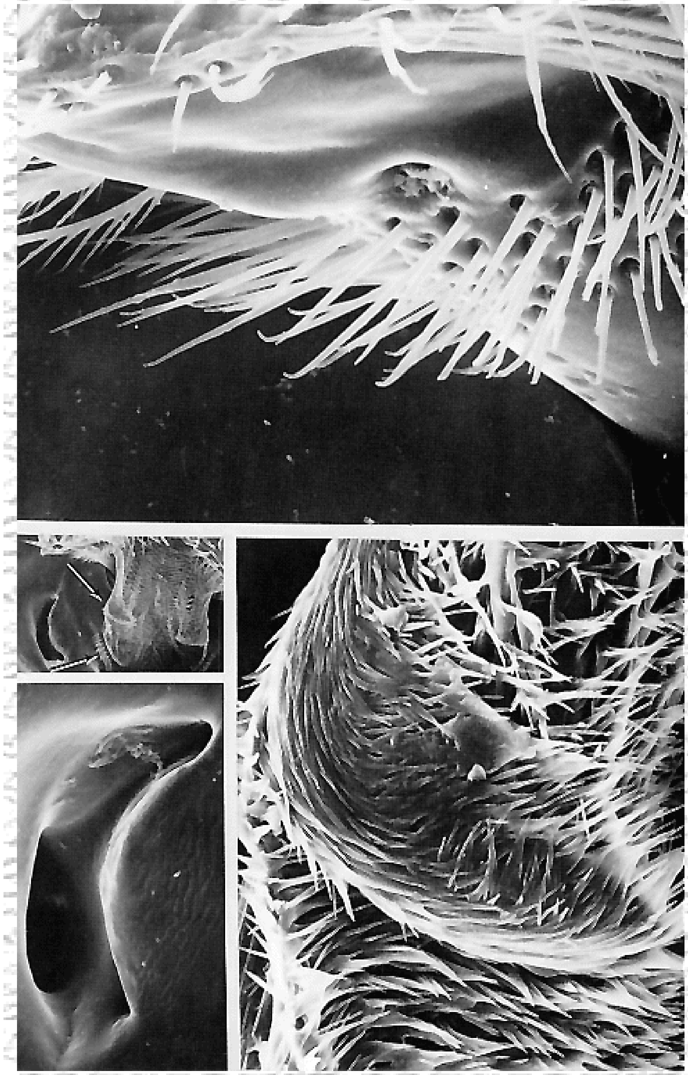


PLATE 2.16. WORKER CERVIX AND VENTRAL POSTOCCIPUT

MIDDLE LEFT. Posterior view of the head showing the cervix (neck). Oil the left is the left tentorial pit. In the right half of the field the cervical membrane connects the occipital foramen of the head to the prescutum of the thorax. The upper arrow points to the area further magnified in the bottom right micrograph; the lower arrow points to the area shown in the top micrograph. (x 68)

BOTTOM LEFT Close-up of the left tentorial pit. The large "hole" is the external manifestation of an inwardly directed posterior tentorial arm, an important constituent of the endoskeleton, or tentorium. The small cavity above leads to the cannular tentorial bridge; the smaller one below is a tube that extends ventrally inward and terminates at the occipital foramen. (x 220)

BOTTOM RIGHT Array of body hairs on the ventral portion of the cervix. These may engage the cervical hair plate on the posterior portion of the head (upper arrow in middle left micrograph) to monitor head movement (X 980)

TOP The ventral cervical hair plate on the prescutum (lower arrow in middle left micrograph). These three dozen or so socketed hairs constitute a major external proprioceptor organ that monitors head flexion. Specifically, these mechanoreceptors record the degree of ventral (downward) projection of the head as the lower part of the head touches these hairs on the "throat." (x875)

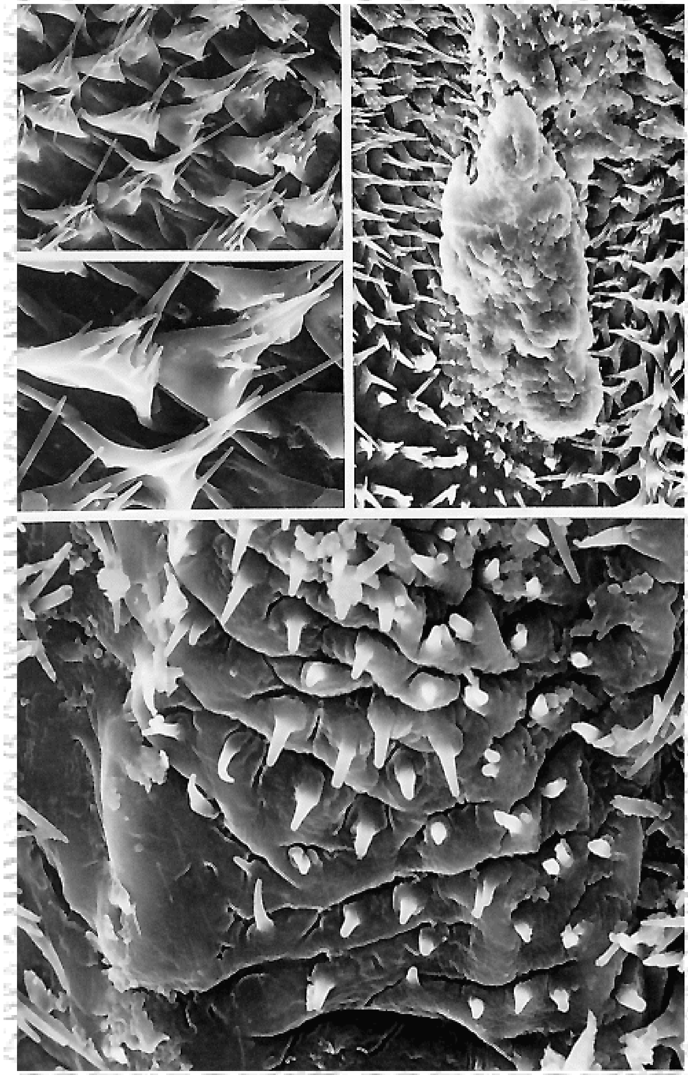


PLATE 2.17. WORKER CERVIX, VENTRAL VIEW, CLOSE-UP

TOP RIGHT Ventral cervix with an unidentified mass that may be a congealed secretion. (See also Plate 2.15, top right micrograph.) (x 910)

BOTTOM Ventral view of the cervix with the congealed mass removed The area beneath the mass is quite unlike the surface of the rest of the cervical membrane. Numerous unoriented, unsocketed, short hairs arise from nonsclerotized cuticle. (x3,060)

TOP LEFT. Ventral view showing several ranks of these triangular cuticular scales, from each of which issue about a dozen hairs of varying lengths. (x 1,320)

MIDDLE LEFT Close-up of several triangular scales showing that the longest hairs emanate fron-i the triangular apex. A slight film (probably honey) is visible at the base of some of the scales. (x 2,750)

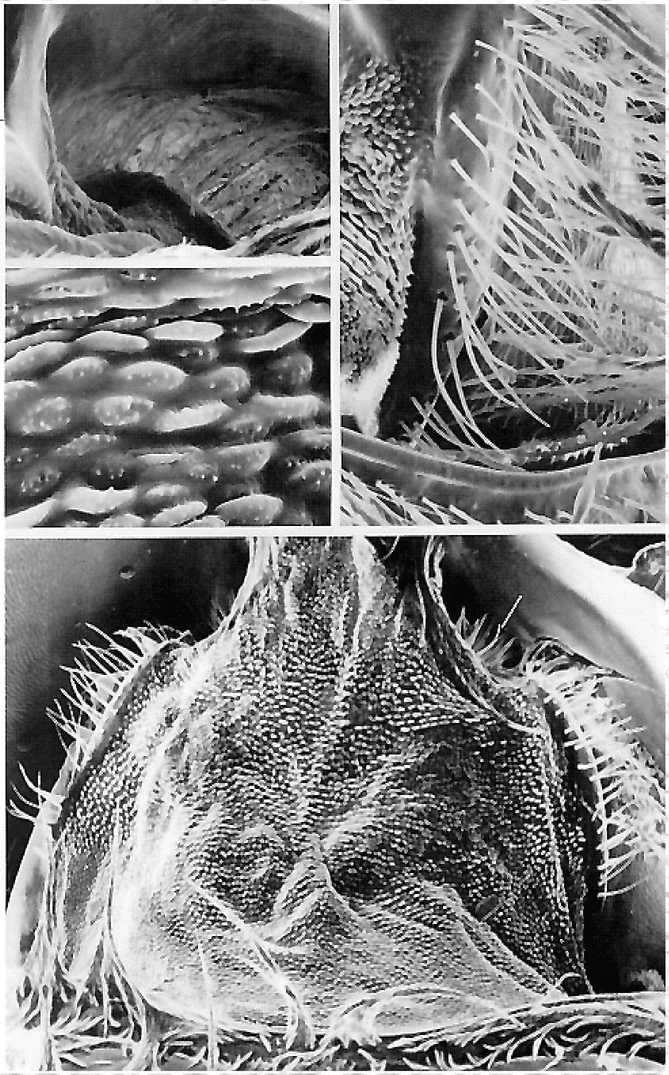


PLATE 2.18 WORKER CERVIX, DORSAL VIEW

BOTTOM Dorsal cervix (neck). The flexible, nonsclerotized membranous nature of the cervix (neck) is evident. (The neck has been stretched on this specimen.) A pair of lateral hair plates (one per side) is visible. Certain mechanoreceptor hairs in each plate are stimulated when the\- engage the back of the head (arrow) (x 94)

TOP RIGHT Lateral hair plate (the head is to the top, the thorax at the bottom). (x 225)

TOP LEFT Head, posterior view. The vaulted area in the upper region of this field is the back of the head, the basal portion the thorax. Sensory hairs situated on the curved plate engage the back of the head, (x240)

MIDDLE LEFT. Surface relief of the cervical membrane, dorsal view. The rows of small rounded tubercles have small, discrete projections arising from them. (x 1,000)

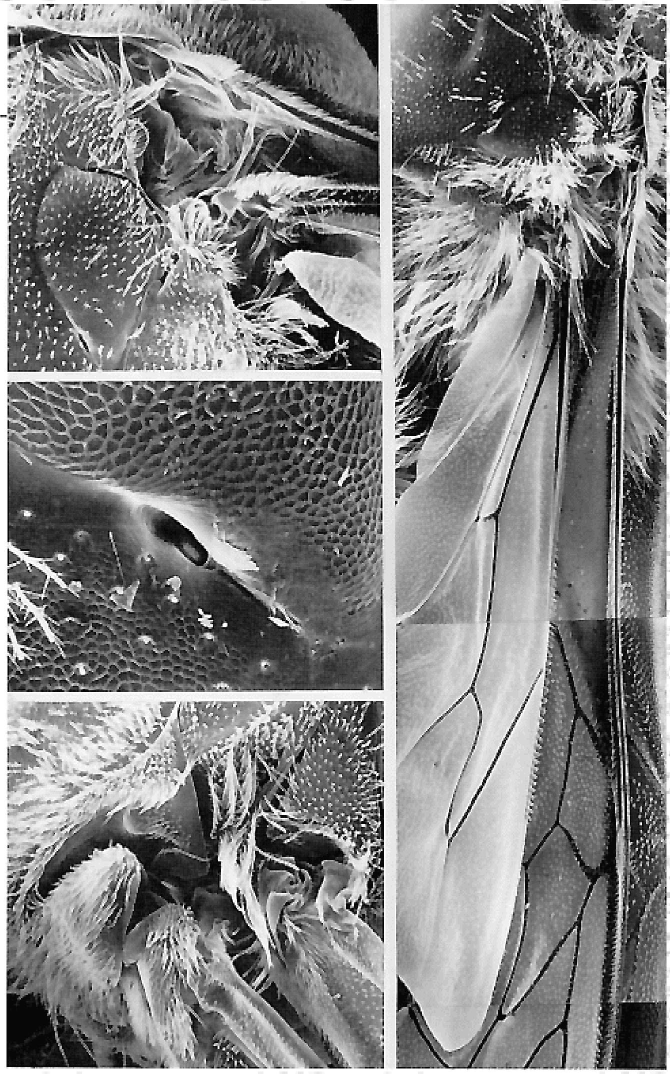


PLATE 2.20. WORKER WINGS

RIGHT. Photomontage of worker wings, a survey of most of the metathoracic (hind) wing covering a sizable fraction of the mesothoracic (fore-) wing. Most of the wing sclerites (plates at the wing base) are shrouded with hairs. (x 2 7)

TOP LEFT. Wing bases with wings folded back over the abdomen. The hairy, roughly rectangular pleurite (at 10 o'clock) is the supraepimeron; immediately below it is the intraepimeron. (x 55)

MIDDLE LEFT. Pit marking the apodeme on the pleural sulcus between the intraepimeron and episternum. (x 240)

BOTTOM LEFT. Dorsolateral view of wing sclerites with wings extended (the head is to the left). The posterior notal wing process is prominent (at 8 o clock) with the radius (wing vein) approaching the side of the process. With their wings "disengaged" and folded back over the body, bees are able to vibrate their wing muscles to produce heat and also sounds, such as those created while dancing. (x 50)

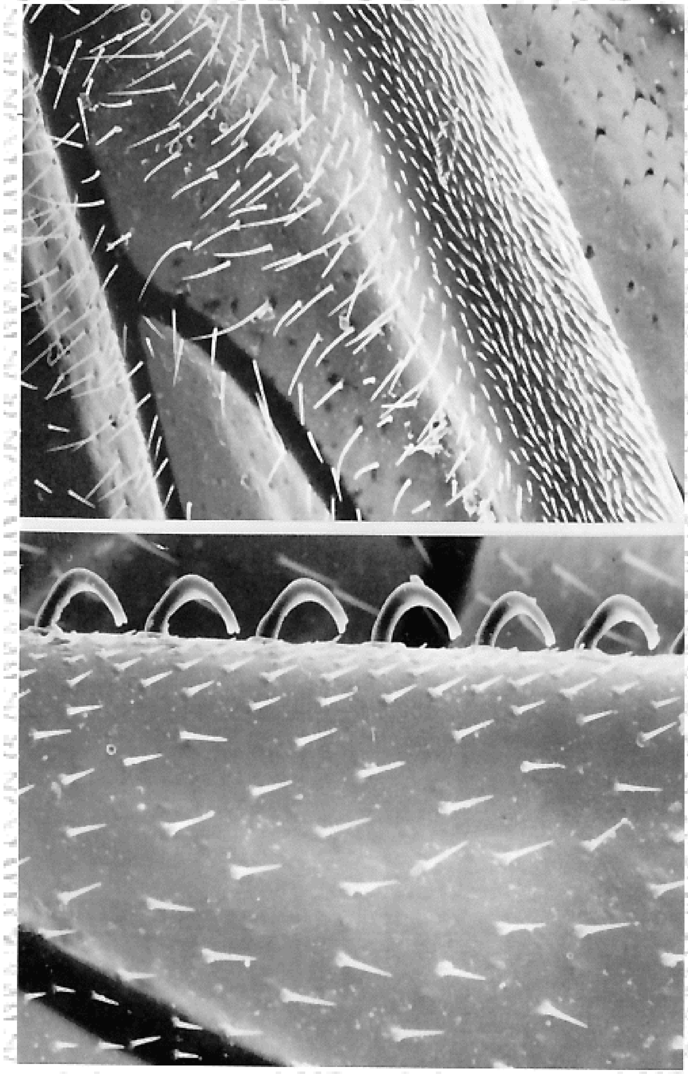


PLATE 2.21. WORKER WING SURFACE, DORSAL VIEW

TOP Leading edge and upper surface of the forewing. The costal ribs are covered with short and rnedium-length hairs. Hairs arising from ribs may be innervated because the hollow rib can acconuriodatc nerves and heiriolymph. (x 170)

BOTTOM Leading edge and upper surface of the hind wing showing the bank of hooks that connects with the curled posterior margin of the forewing. The hind-wing hooks of the worker are somewhat smaller and more angulated than those of the drone. Rows of microtrichia stud the surface of the hind wing. (x 318)

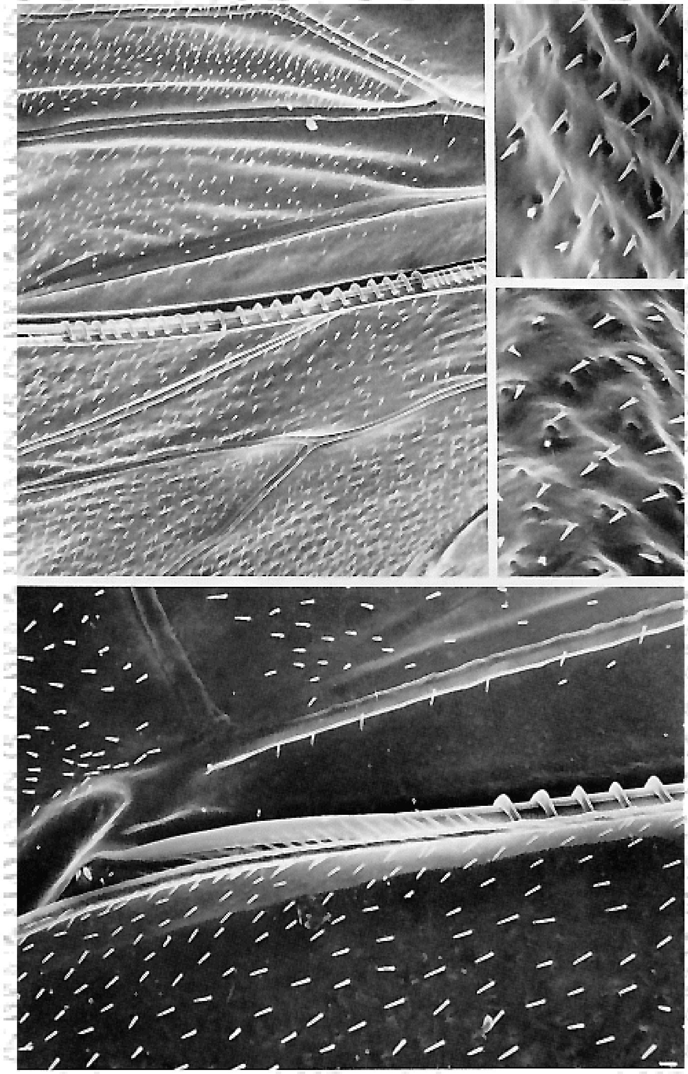


PLATE 2.22. WORKER WING SURFACE, VENTRAL VIEW

TOP LEFT Ventral wing surface in the midwing area showing the complete rank of 21 hooks engaging the posterior marginal fold of the forewing. Setal distribution patterns are evident, and a few setae arise from the wing veins. (x 70)

BOTTOM Ventral surface of the forewings (upper and hind wings (lower) hooked as in flight. The forewing posterior margin fold or curl is especially distinct (x 170)

TOP RIGHT. Setae from the ventral surface of the forewing. In this and the middle right micrograph, the wing surface is slightly wrinkled, which may be due in part to drying after death. (x 330)

MIDDLE RIGHT Higher magnification of the intervein setae from the ventral surface of the hind wing. (x 330)

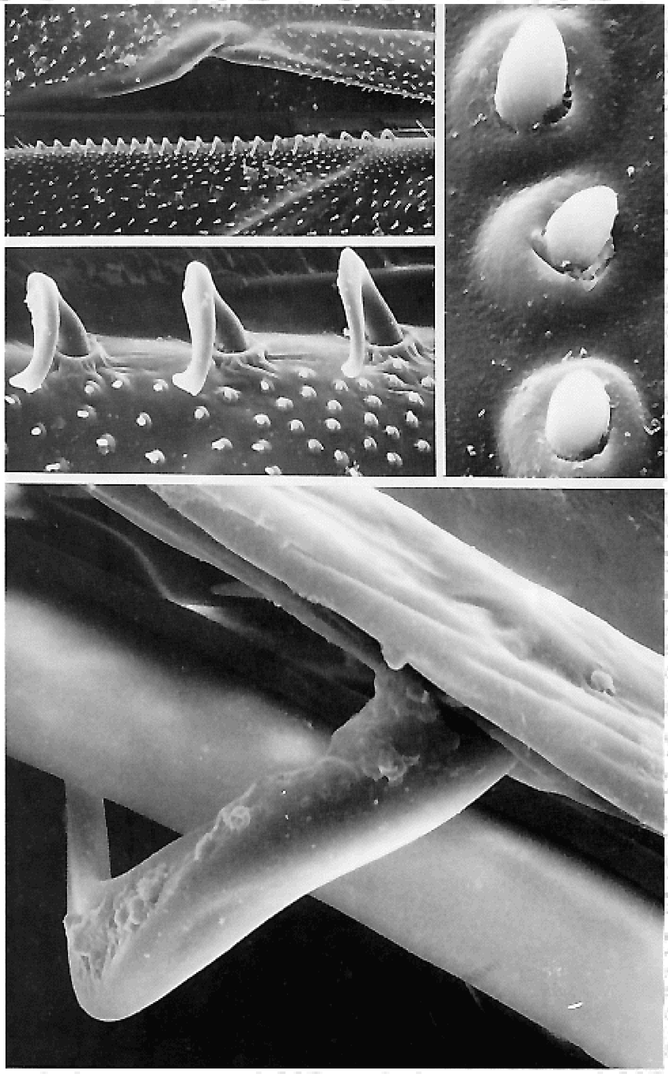


PLATE 2.23. WORKER WING HOOKS

TOP LEFT. Survey of a posterior section of the forewing (foreground) in proximity to the corresponding anterior margin (radius and media veins) of the hind wing with the hooks (hamuli) that connect both wings in flight. Microtrichia and small peg organs cover the anterior margins of the worker hind wing (while only microtrichia are noted in queens; see Plate 1.23) and on the opposing portion of the forewing. (x 77)

MIDDLE LEFT. Higher magnification of the hind wing hooks with nearby short peg organs. Hooks arise from a socket; each hook is bent twice, at the midpoint and at the tip. (x 600)

TOP RIGHT. Close-up of three peg organs. Each socket has a limited amount of free space that might permit some movement of the peg. (x 5,400)

BOTTOM. Hind-wing hook articulating with the thickened posterior margin of the forewing. Thus connected, the two wings function essentially as one, which provides a larger gliding surface. The forewing is driven while the hind wing passively trails in flight. The wing beat frequency is approximately 235 to 250 per second. (x 2,660)

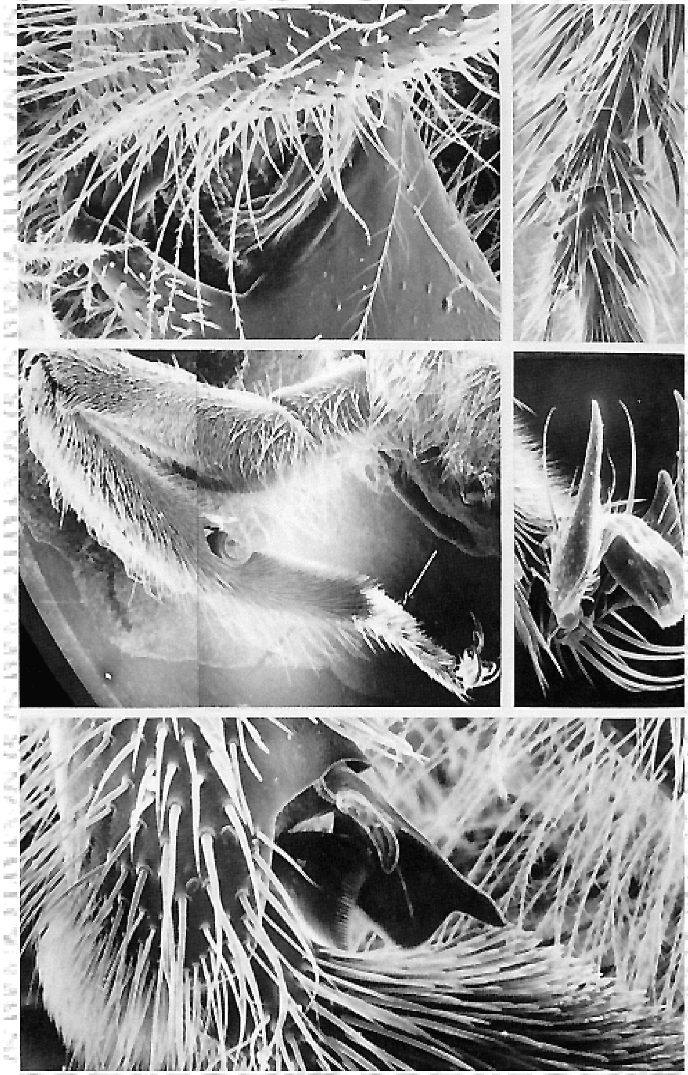


PLATE 2.24. WORKER FORELEG

MIDDLE LEFT. Photomontage of the entire leg. The deeply notched antenna cleaner is at the proximal end of the basitarsus. A stress receptor (the subgenual organ) on the interior of the tibia detects substrate vibration (sound). The arrow indicates an area further magnified in the top right micrograph. (x 3 1)

TOP LEFT Articulation between tibia and femur The wrinkled, flexible intersegmental membrane has small cuticular spines. (x 200)

BOTTOM Higher magnification of the tibia-basitarsus antenna cleaner (comb). The deep notch is on the proximal end of the basitarsus, over which lies the fibula, a thumblike spur that extends from the distal portion of the tibia. The antenna is placed in the notch and drawn past the fine comb and fibula. All castes have an antenna cleaner. (x 144)

TOP RIGHT Five tarsal segments (arrow in center left micrograph). Each of the four most proximal tarsomeres is connected via monocondylic articulations. Their concerted movement is effected by the shortening of a tendon that traverses the entire length of these segments. (x 105)

MIDDLE RIGHT Claws and the fleshy lobe (arolium) lying between the claws. Each claw has two principal points, one short and rather rounded, the other elongate and sharper. Several long and slender hairs are on each claw. (x 180)

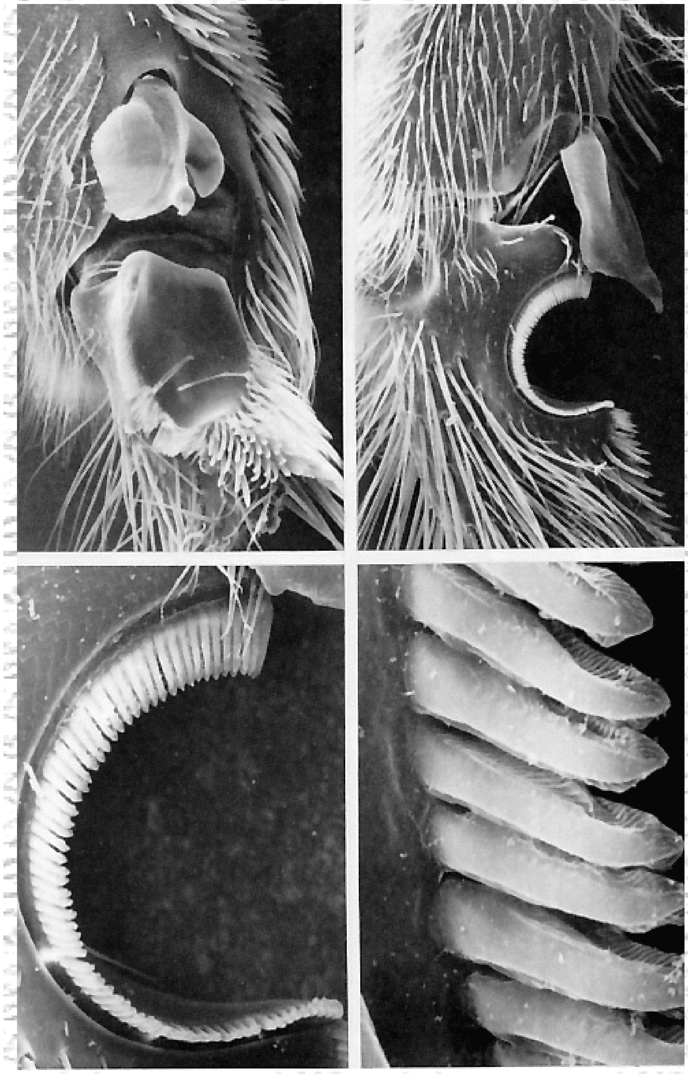


PLATE 2.25. WORKER ANTENNA CLEANER

TOP LEFT Tibia-basitarsus joint. The tangential view of the bulbous fibula (bilobed spur) from the tibia positioned over the antenna cleaner notch on the basitarsus is particularly useful because it gives another dimension to the vital grooming apparatus (previously, the fibula was described as a large, flattened spur). (x 140)

TOP RIGHT Tibia -basitarsus joint in profile. The extent of overlap be- tween the fibula and the semicircular notch on the basitarsus shows that the antenna would be almost completely surrounded by the antenna cleaner when the basitarsus is fully flexed. (x 86)

BOTTOM LEFT. "Fan" of the seventy spinelike hairs of the tarsal comb. These hairs are responsible for cleaning the outer surface of the antenna. (x 260)

BOTTOM RIGHT Tarsal hairs. The pectinate quality of the tarsal hairs is evident here. Ridges or corrugations on the medial expanse of each hair, at right angles to the long axis of the hair, give additional cleaning capacity and traction to the antenna cleaner. (x 1,560)

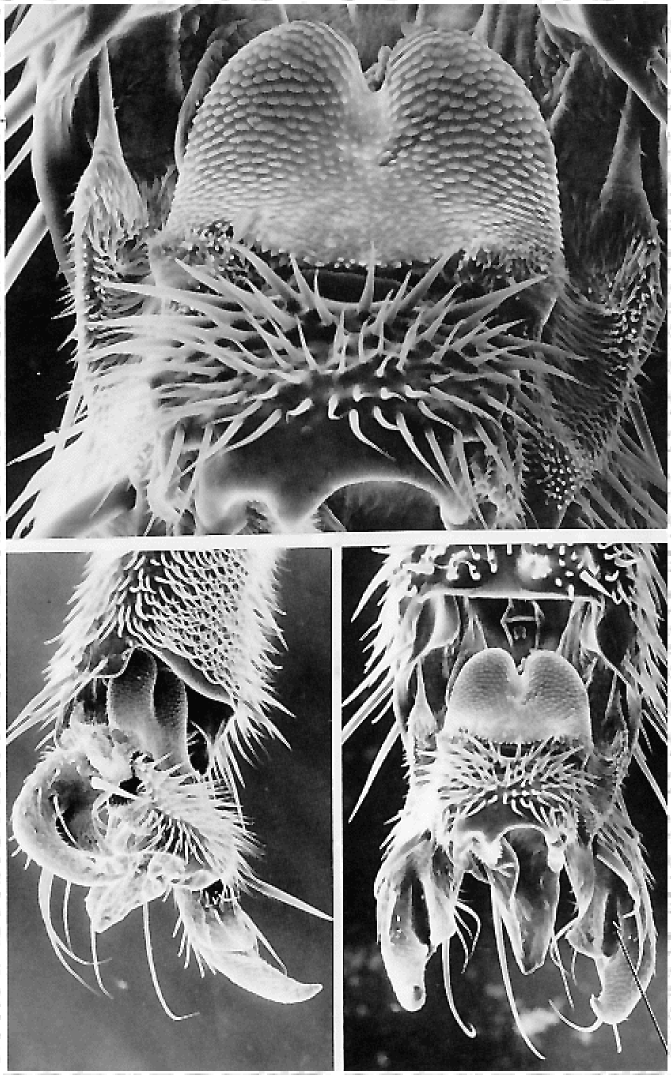


PLATE 2.26. WORKER FOOT

BOTTOM LEFT Last tarsomere and pretarsus. Claws are on either side of the wrinkled arolium. Above the arolium is the heavily bristled planta; above the planta is the unguitractor, which is without seta but has rows of low-lying cuticular scales. This structure may function like the heel of a hand, providing an Opposing surface for the claw. (x 1,50)

BOTTOM RIGHT Frontal view of the medial surface of the foot. The bilobed character of the unguitractor is better seen in this view, as well as the deep pit or fossa (arrow) at the base of the subordinate claw. (x 210)

TOP Higher magnification of the planta and unguitractor. (x 540)

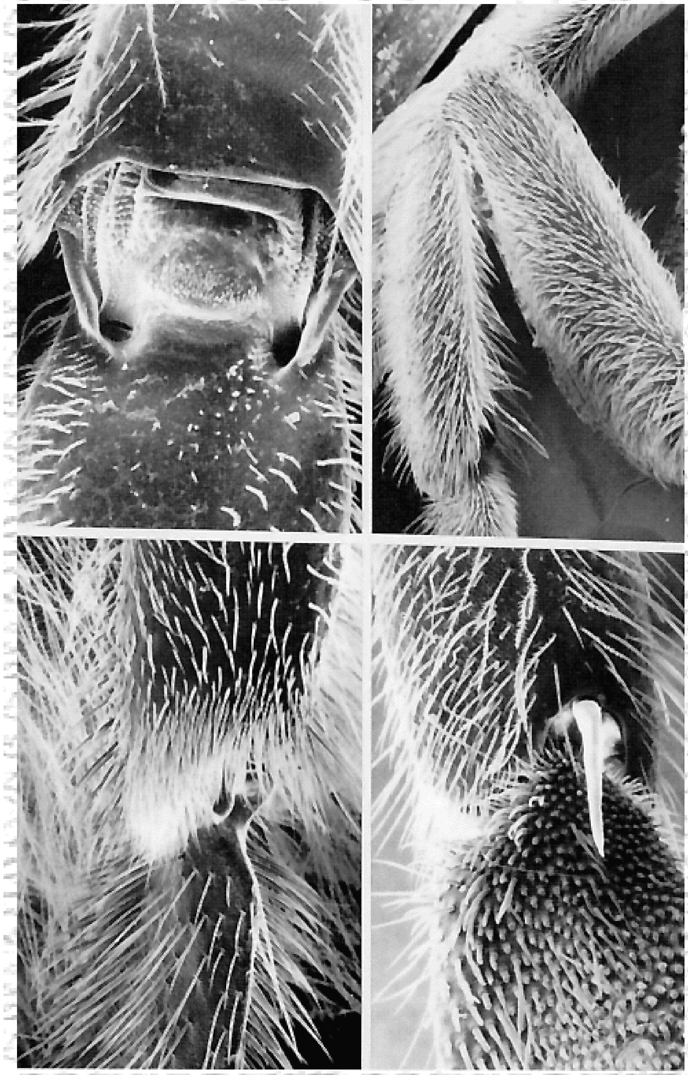


PLATE 2.27. WORKER MIDDLE LEG

TOP RIGHT Lateral view of the mesothoracic (middle) lea. The femur is to the right of the tibia, which bears [lie basitarsus. A prominent tibial spine is present at the tibia-basitarsus Joint. (x 40)

BOTTOM RIGHT Close-up of the tibia-basitarsus joint of the middle leg, the tibial spine, and the so-called (but inappropriately named) wax spur (see Plate 2.38). The setal character changes abruptly from tibia to basi-- tarsus. (x 78)

BOTTOM LEFT Femur-tibia articulation, lateral view. (x 93)

TOP LEFT. Medial view of the femur-tibia joint showing the flexible, nonsclerotized, intersegmental membrane connecting the two limbs. Many small setae stud this membrane. (x 182)

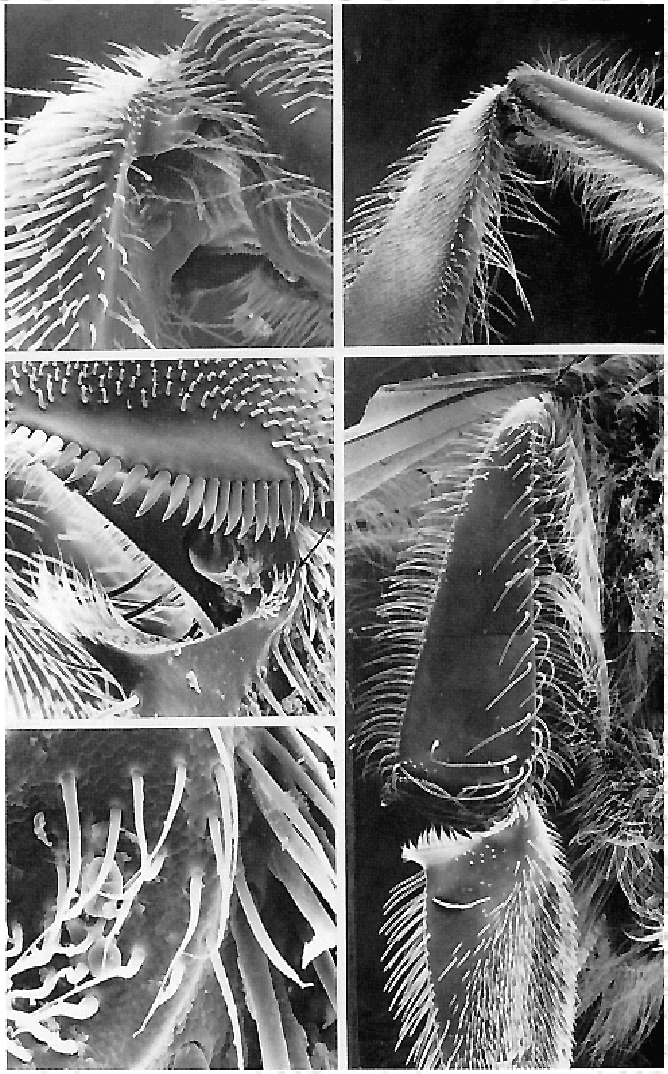


PLATE 2.28. WORKER HIND LEG

BOTTOM RIGHT. Photomontage of the hind (metathoracic) leg, lateral view. The ascending femur (on the right) articulates with the descending tibia, the base of which is the basitarsus. The pollen basket is comprised of the curved hairs surrounding the glabrous central area of the tibia. (x 31)

TOP RIGHT Medial surface of the leg showing the femur (right) and tibia (x 3 1)

TOP LEFT. Higher magnification of the femur-tibia joint (the "knee") and its connective or intersegmental membrane (see the top right micrograph). (x 150)

MIDDLE LEFT Articulation between the tibia and basitarsus showing the pollen press. The rakelike group of hairs (rastellum) projects downward from the lobe called the auricle. The arrow indicates an area further magnified in the bottom left micrograph. (x 95)

BOTTOM LEFT. Higher magnification of the hairs located at the proximal apex of the basitarsus (arrow in middle left micrograph). These may be mechanoreceptors (external proprioceptors); if so, when the rastellum contacts the basitarsus the nerves in these hairs would inform the central nervous system of the attitude of the basitarsus relative to that of the tibia and whether any pollen was being pressed (collapsed pollen grains are visible at the base of the hairs). (x 530)

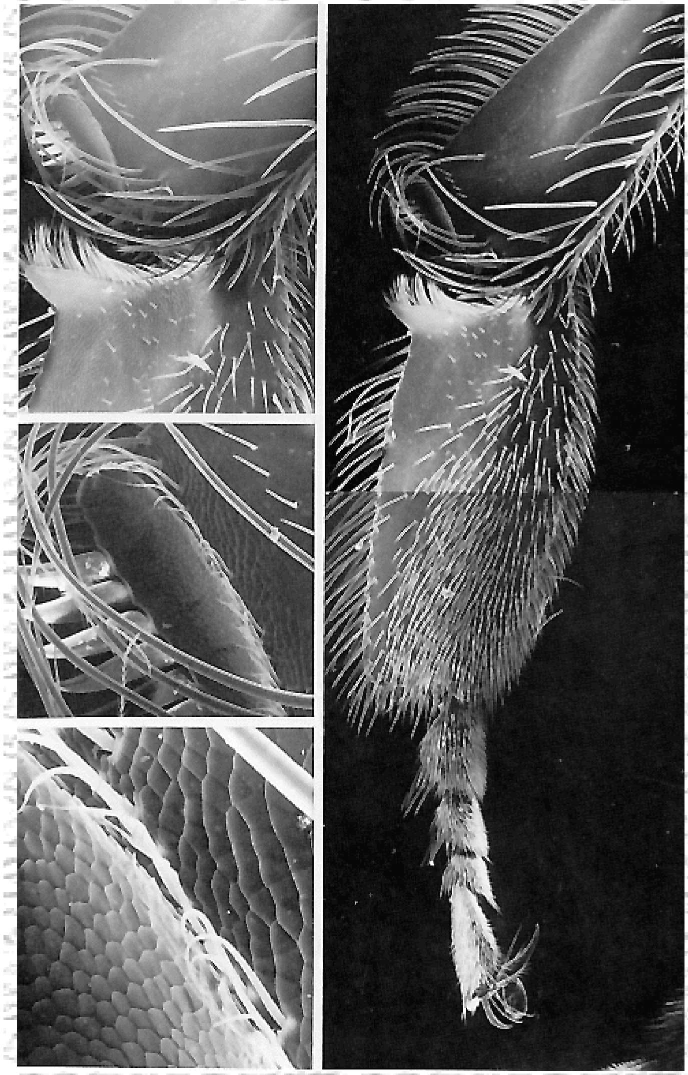


PLATE 2.29. WORKER POLLEN BASKET

RIGHT Photomontage (a continuation from Plate 2.27) showing, from top to bottom, the lateral surface of the tibia, the basitarsus, and the remaining tarsomeres. The hair arrangement on the tibia is the basis of the pollen basket. The auricle (ridge) and its hair fringe at the Junction of the tibia and basitarsus are highlighted. (x 42)

TOP LEFT Higher magnification of the auricle with its fringe of hairs. Looming above these hairs is the rank of spines of the rastellum ("little rake"). (x 62)

MIDDLE LEFT Close-up of a portion (Six spines) of the rastellum situated at the joint between tibia and basitarsus (proximal view). (x 186)

BOTTOM LEFT. Distal tibia. Fine setae extend along the auricular ridge immediately above the rastellum. Polygonal scales are evident on this ridge. (x 670)

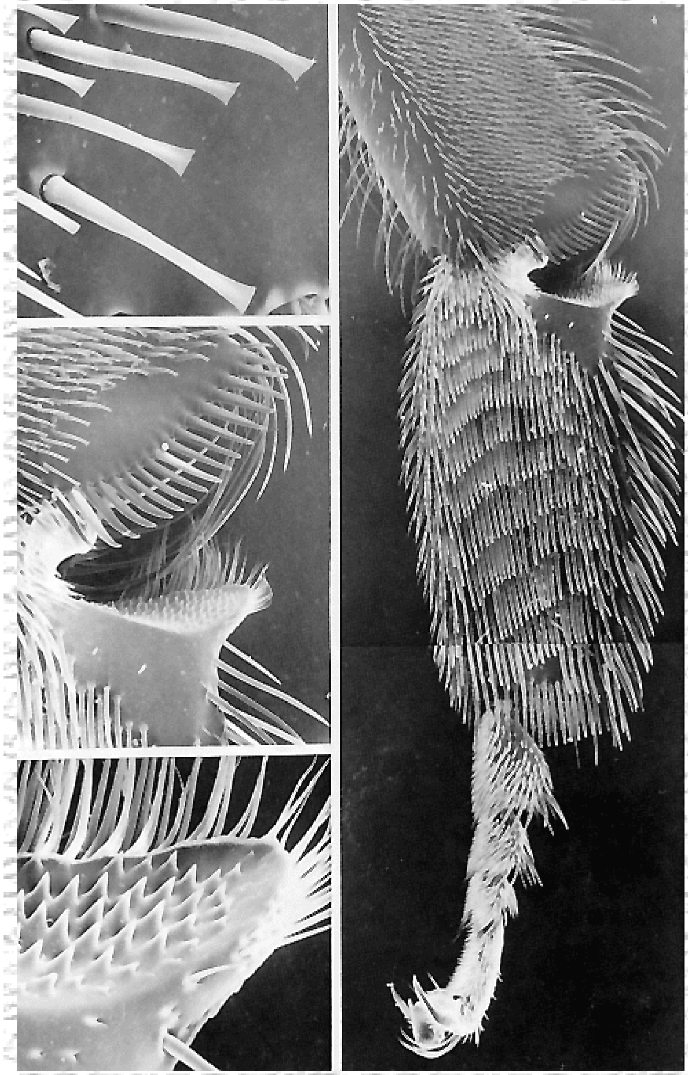


PLATE 2.30. WORKER POLLEN PRESS

RIGHT Photomontage of the metathoracic (hind) leg and its medial surface. From top to bottom are the tibia, basitarsus, and four short tarsal segments. Between the tibia and basitarsus is the flattened, notched pollen press. The ranks of hairs act as combs for grooming and pollen gathering. When the basitarsal combs are loaded to capacity with pollen, the rastellum (rake) is used to unload the comb by scraping it into the press where the pollen is compressed and transferred to the tibial baskets on the outside surface above the pollen press. Hence, pollen groomed from the right side of the body is combed from the inner surfaces of the middle and forelegs by the left hind leg, from which it is removed by the right rastelhun for deposition in the pollen basket of the same leg. The opposite sequence is used for the left side. (x 47)

MIDDLE LEFT Mediolateral view, of the pollen press. The floor of the press is edged with fine hairs, and its surface is covered with denticlelike cuticular spines or scales. Long, curved hairs from the tibia bend down and lie over the press and a picket of shorter, stiff spines (rastellum) lines the dorsomedial margin of the press.
Small mechanoreceptor hairs are visible at the leading edge of the spatulate hairs (upper left). (x 100)

TOP LEFT Hairs on the medial surface of the tibia. The flattened-tip spatulate character of these hairs contrasts markedly with the basitarsal hairs, which have serrated edges and a fairly sharp tip. The specialized hairs of the tibia may have an important function in the process of gathering and packing pollen (see Plate 2.31). (x 560)

BOTTOM LEFT Higher magnification of the sharp cuticular spines (spicules) that line the floor of the pollen press and the finer hairs that form a fringe around the press. (x 400)

2.31

PLATE 2.31. WORKER HIND TIBIA, MEDIAL SURFACE

TOP LEFT. Low-magnification view of the spatulate hairs on the inside of the tibia. (x 560)

TOP RIGHT. Higher magnification of tibial hairs. The fluted and curvaceous character of the tibial hairs is evident. (x 1,705)

BOTTOM LEFT. Higher magnification of tibial hairs showing their broad, flattened tips. (x 1,800)

BOTTOM RIGHT. Overview of tibial hairs on the hind leg. These particular hairs possess a geometry that seems ideal for holding or cradling small objects such as the pollen grain visible here. The fluted sides of the hair add surface area to enable a better grip on a pollen grain. The broad tip may be useful in combing pollen from wing surfaces. (x 750)

2.32

PLATE 2.32 WORKER ABDOMEN

Lateral view of the worker gaster (abdomen). See the discussion accompaning Plate 1.36

2.33

PLATE 2.33. WORKER ABDOMINAL SPIRACLE

TOP RIGHT Spiracular aperture (arrow), visible directly below the origin of the hind wing posterior margin. The rather triangular lateral pleurite to the left of the spiracle is the supraepisternum of the metathorax. (x 43)

TOP LEFT Close-up of the spiracular aperture and the inner longitudinal ridge that is part of the closing valve. A cuticular rim circles this, the largest of all worker spiracles. (x 350)

BOTTOM RIGHT Second abdominal spiracle (arrow) The mesothoracic and then metathoracic coxae are visible (bottom left). (x 43)

BOTTOM LEFT Second abdominal spiracle showing its overall external shape and cuticular rim. (x 350)

2.34

PLATE 2.34. WORKER PETIOLE, DORSAL VIEW

TOP Survey of the dorsal view of the petiole. At the very top is the broad posterior expanse of the propodeum. Most of the figure is filled with the anterior face of the second abdominal tergum. The petiole pocket is visible here as a small, cuticular, semicircular well that connects to a membranous petiole. (x 153)

MIDDLE Higher magnification of the elevated cupolalike area over the petiole pocket. The sparse and regular orientation of the cuticular tubercles in this membranous area is also visible. (x 680)

BOTTOM RIGHT Another view of the dorsal petiole showing the posteriorly directed membrane that extends over the propodeal cavity (x 250)

BOTTOM LEFT Lateral hair plate of the petiole. Stimulation of these mechanoreceptor hairs determines the degree of gravitational torsion of the gaster (abdomen) onto the petiole-thorax area. About three dozen large hairs and about twenty very short hairs make up this hair plate.
It is not known if all of these socketed hairs are innervated. (x 435)

2.35

PLATE 2.35 WORKER PETIOLE, VENTRAL VIEW

TOP Two hair plates, one on each side of the petiolar joint. (x 153)

BOTTOM RIGHT. Petiolar hair plate. When the second abdominal sternum in moves, certain mechanosensory hairs on this plate are contacted (and thus stimulated). These external proprioceptors monitor the movement and position of the major part of the abdomen relative to the orientation of the thorax. (x 208)

BOTTTOM LEFT Higher magnification of the right petiolar hair plates. About fifty movable (in a preferred direction) mechanosensory hairs report the gravitational pull of the abdomen on the thorax. (x 420)

2.36

PLATE 2.36. WORKER A13DOMINAL WALL

TOP Photomontage of the fourth tergite (left) followed by the three terminal tergites (fifth, sixth, and seventh). These overlie and completely conceal the corresponding pleural elements so that the related sternites (bottom) apparently make contact with the tergites. Beneath the anterior position of sternites four to seven are the wax glands. The spiracles on the last two tergites are barely visible (arrows) (x 3 1)

BOTTOM LEFT Branched hairs from the third abdominal sternite. Some of these hairs are attached to gland cells whose function in workers is unknown (see the discussion of Plate 1.41, bottom left micrograph). (x 170)

BOTTOM RIGHT. Close-up of the cuticular 11 scale" and setae (several forms) from the abdominal sclerites. (x 1, 116)

2.37

PLATE 2.37. WORKER ABDOMINAL SPIRACLES

TOP LEFT Photomontage of the abdomen showing the second and third abdominal spiracles (arrows). (x 31)

TOP RIGHT Higher magnification of the third abdominal spiracle. Cuticular hairs (two are visible) are not always present. No cuticular rim is evident. (x 384)

BOTTOM LEFT. Higher magnification of the slitlike second abdominal spiracle. Note the longitudinally disposed valve extending parallel with the elongate sides of the spiracle. A patch of very short setae is visible on the right rim of the spiracle (x 1, 118)

BOTTOM RIGHT. Close-up of the sculptured (shingled) appearance of the cuticle near the abdominal spiracles. (x 1,023)

2.38

PLATE 2.38. WORKER ABDOMEN, VENTRAL VIEW

TOP Abdominal sternites, ventral view. The glabrous surfaces are the wax " mirrors," or plates. Beneath these plates are the wax glands. Wax per- meates the mirrors and hardens into the visible wax scales from which the honey bees construct comb. The rastellum (see Plate 2.29), not the wax spur, on the hind leg is used to remove these scales when fully formed (rastellar marks are visible on the medial edges of the scales). (x 60)

BOTTOM LEFT Higher magnification of the lower left quadrant of the top micrograph showing the medial margin of the wax mirror and the adjacent wax scale. (x 136)

BOTTOM RIGHT Fully formed wax scale. (x 60)

2.39

PLATE 2.39. WORKER NASSANov GLAND

BOTTOM LEFT. Hairy sixth and the partly hairless seventh abdominal tergites. The glandular area behind the ridge is not exposed. This view complements the one in the top left micrograph, showing the entire expanse of this tergite. (x 56)

TOP LEFT. Lateral view of the last (seventh) abdominal tergum (dorsal is left). The smooth hairless area is dernarked by the strong submarginal inner ridge; above that is a margin of elevation on the tergum. At the base of this tergum, between terga. six and seven is the scent gland of Nassanov. (x 65)

BOTTOM RIGHT. Pores in the seventh tergite, from which issues the orientation (aggregation) pheromone produced by the Nassanov gland. (x 1,240)

MIDDLE RIGHT. Higher magnification of the pores in the bottom right micrograph. (x 10,000)

TOP RIGHT. Close-up of the base of the seventh tergum, which is overlapped by the sixth tergite. (x 484)

2.40s

PLATE 2.40. WORKER STING

BOTTOM RIGHT Exposed sting apparatus, ventral view. The base of the lancets extends upward into the right and left cuticular arcs (each made up of the first and second rami). At their base and extending laterally and down is the oblong plate. On the lateral margin of the plate is the quadrate plate, a shieldlike vestige of the ninth tergite. The two lobes of the sting sheath angle toward the distal lancets. (x 45)

MIDDLE. Distal tip of the sting. The serrated lancet is next to the protruding stylet. Not readily visible but present are campaniform sensilla assoclated with each barb (see also Plate 1.43, queen sting). (x 540)

TOP Photomontage of the sting, dorsal view. Visible are the first and second rami on the medial and lateral sides respectively of the doublearched extension of the triangular plate. This proximal part of the sting connects the lancets and stylet to the sting protractor muscles. A hairy lobe embraces the base of the lancets; this structure is believed to be the ventral wall of abdominal segment nine. (x 55)

BOTTOM LEFT Higher magnification of a barb on a lancet, about midway down the shaft of the lancet. (x 3,600)

2.41

PLATE 2.41. WORKER STING, RETRACTED

TOP RIGHT Sting apparatus, ventral view. Paired oblong plates straddle the lancets (exposed by dissection). On the dorsomedial surface of each oblong plate is a cleft (arrow). (x 91)

TOP LEFT. Higher magnification of the cleft in the top right micrograph. The background hairs are from a membrane thought to be the unsclerotized remains of the ventral wall of segment nine. (x 868)

BOTTOM RIGHT Higher magnification of the base of the lancets in the top right micrograph. Two flangelike medial parts of the oblong plates cover part of the lancet base. Hairs of the lobe of the ninth segment are visible (lower right). (x 650)

BOTTOM LEFT. Two lancets with barbed edges overlying the more extended stylet. (x 360)

3.1

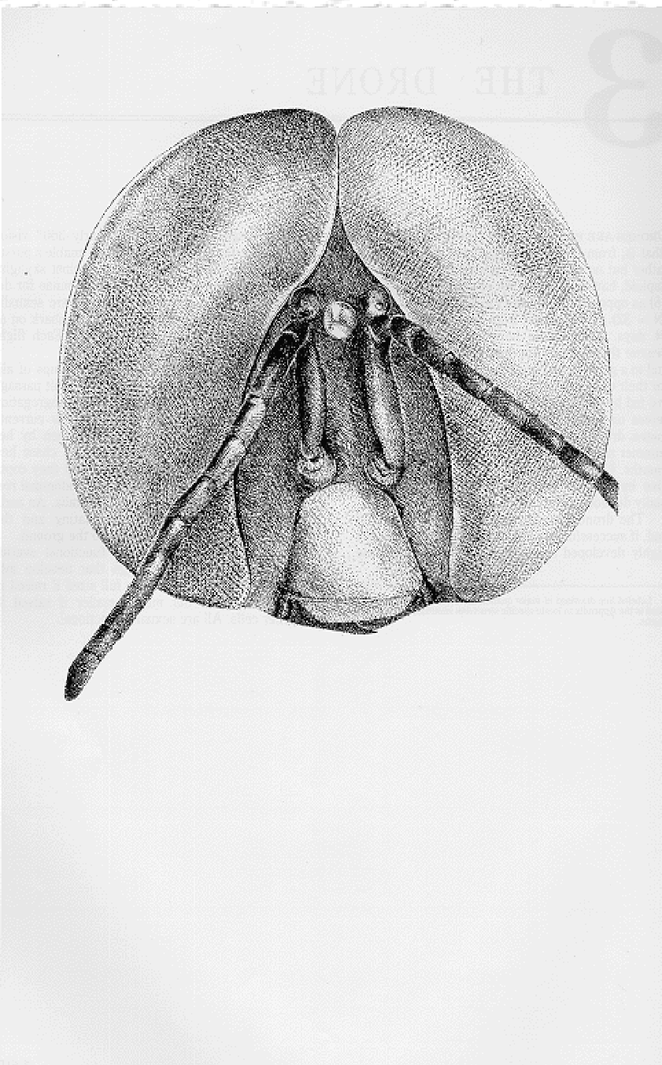


PLATE 3.1 DRONE HEAD

Frontal vie of the drone head.

3.2

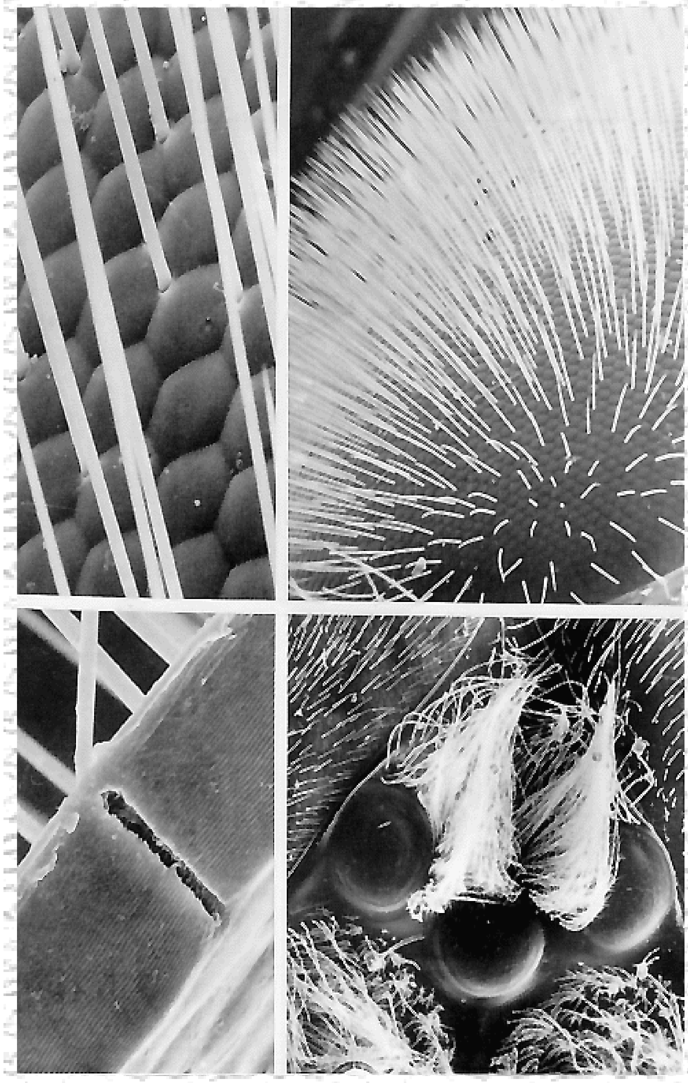


PLATE 3.2. DRONE COMPOUND AND SIMPLE EYE

TOP RIGHT. Compound eye covered with interfacetal hairs. These innervated setae arise in the interstitial space between adjacent facets of the compound eye. At the base of each hair is a single bipolar neuron. These hairs are mechanoreceptors; by bending they monitor direction of wind currents and airspeed. (x 140)

TOP LEFT. Higher magnification of the corneal surface of the compound eye showing the socketed base of each hair and the hexagonal outline of each lens facet. Lens facets at the periphery of the eye often have other frontal view geometric shapes. (x 1,400)

BOTTOM LEFT. Longitudinal section through the corneal lens of the compound eye. The deep cleft through the lens marks the boundary of one ommatidium; this recess also provides the space necessary to house the neuron and glia of the hair. The biconvex design of each lens facet and the cuticular laminations are also evident. (x 1,650)

BOTTOM RIGHT. One medial and two lateral ocelli. These three "simple" photoreceptor organs are located on the vertex of the head between the two compound eyes. Ocelli usually do not form images. These photoreceptors may monitor light levels and possibly provide input to some photoperiodically entrained circadian rhythms. No function is known for the profuse bundles of fine hairs between the ocelli. (x 60)

3.3

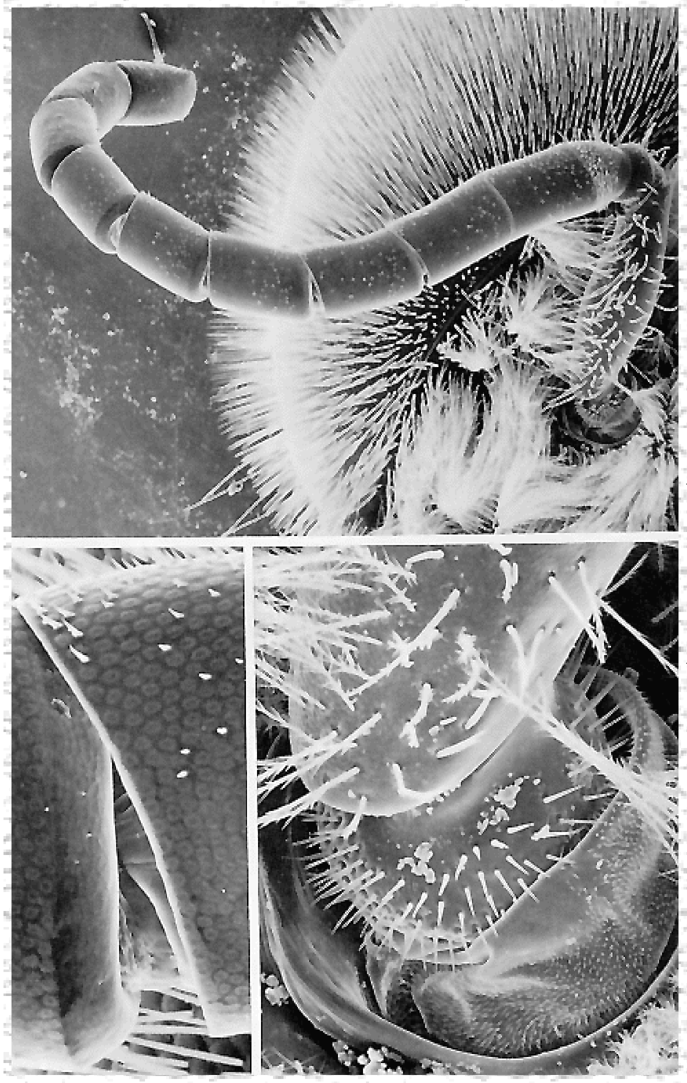


PLATE 3.3. DRONE ANTENNA AND BASE

TOP. Drone antenna. There are twelve sections of the antenna. The drone antenna has far fewer trichoid sensilla (the very short white 11 whiskers" on the flagellum) than do queen and worker antennae (see Plates 1.6 and 2.4). (x 53)

BOTTOM RIGHT Higher magnification of the antennal base showing the basal knob of the scape inserting into the membrane-lined antennal socket. Microtrichia are abundant over this "membrane." Ranks of socketed (putative) mechanoreceptor hairs completely encircle the base. (x 347)

BOTTOM LEFT Articulation between two antennal (flagellar) sections. Each subdivision (they are not true segments) fits into the succeeding one without any real articulation or musculature. The base of each annular portion inserts into a small cavity of the one behind it. Spines are absent on the intersegmental membranes. (x 304)

3.4

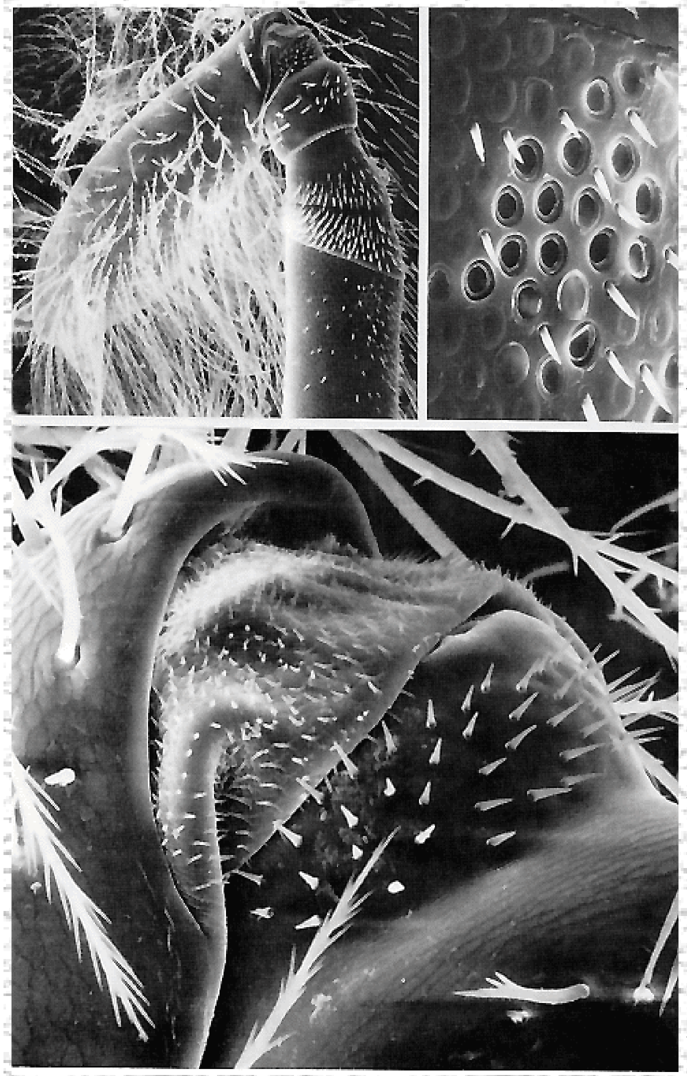


PLATE 3.4 DRONE ANTENNA

TOP Elbow dividing the antenna into a basal stalk (scape) (extending diagonally to the left) and a more flexible distal portion (projecting downward). The pedicel is the second segment of the antenna and located at the elbow (after the scape); the flagellar "segments" follow. The flagellum can be moved relative to the scape by two muscles that originate in the scape and insert in the pedicel. Flagellar "segments" do not articulate with each other, nor are muscles present between flagellar sections. (x 88)

BOTTOM Close-up of the elbow. The intersegmental membrane between scape and pedicel is studded with short, slender hairs. Some of the stouter, longer setae of the pedicel are bent as the pedicel-flagellum twists. These hairs may be proprioceptors that, when bent, report the attitude of the flagellum in space to the central nervous system. (x 720)

TOP RIGHT Higher magnification of the lateral surface of the first flagellar segment of the antenna in the top left micrograph, immediately below the pedicel-flagellum boundary. A dozen stout, socketed hairs (sensilla chaetica) are interspersed among plate organs (sensilla placodea). The center dome of these plate organs is exquisitely thin cuticle that is easily broken in specimen preparation. A few intact plate organs are visible on the periphery of the field. (x 660)

3.5

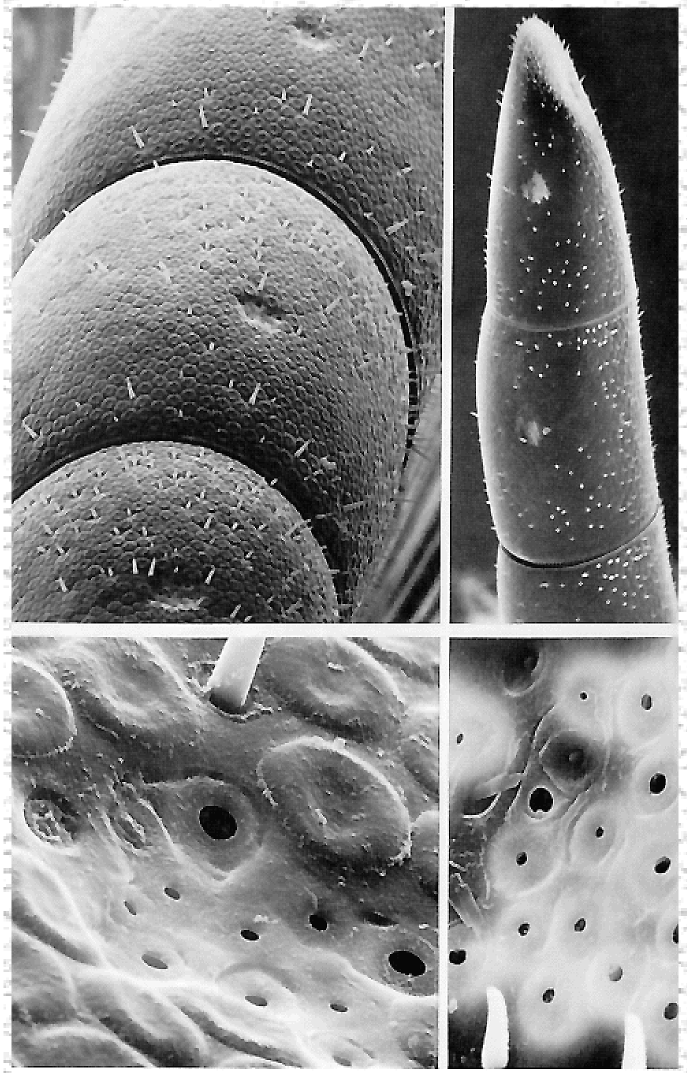


PLATE 3.5. DRONE ANTENNA Tip

TOP RIGHT Terminal three segments of the antenna. At this magnification all that is visible are peg organs and the faint, pebble-grained effect created by the profusion of plate organs. Both peg and plate organs are olfactory organs. The pits on the last two segments are really aggregations of a half dozen or so pit organs (sensilla coeloconica, sensilla ampullacia). (x 140)

TOP LEFT. Higher magnification of three antennal segments. The three sense organs (peg, pit, and plate sensilla) are more evident at this magnification. (x 420)

BOTTOM LEFT. Ten pit organs set in a cuticular depression and surrounded by plate organs. One socketed peg is visible at the top. The presence of free space at the peg base may permit the hair shaft to move; if so, this hair may be a mechanoreceptor. (x 4,200)

BOTTOM RIGHT. Cuticular depression on the antenna] segment. In this view pit organs predominate but two "pits" (at 11 o'clock) are capped; these organs may be campaniform sensilla, and if so, they must be mechanoreceptors monitoring strains of the cuticle. It is not known why this whole cuticular depression appears so bright. Even if a residual static charge at this locus attracted more gold in the shadowing process, it remains a mystery why such a charge would be preferentially located here and persist after death. (x 1,705)

3.6

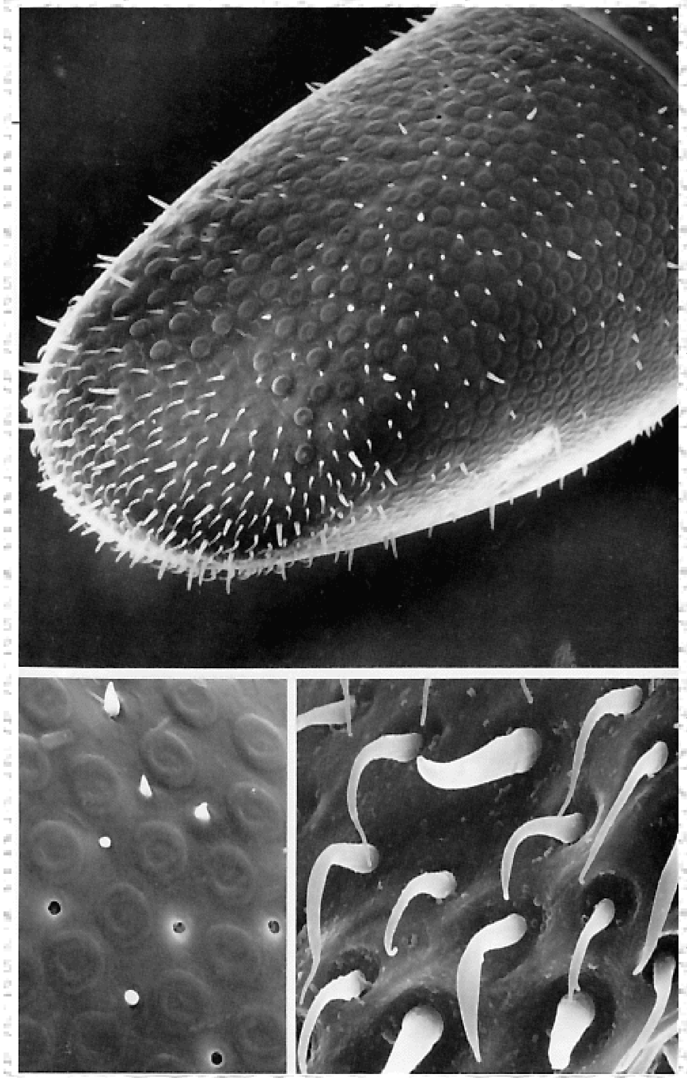


PLATE 3.6. DRONE ANTENNA TIP, VENTRAL SURFACE

TOP Low magnification of the antenna tip. At least four morphological variations of the peg organs can be resolved, and most of these are close to the antenna terminus. The plate organs are located more posteriorly and are circumferentially arranged around this segment (x 306)

BOTTOM LEFT Higher magnification of the antenna showing thick pegs, plate organs, and pit organs. Each pit organ bears a curious bright margin around its orifice. Odor molecules enter the pit as easily as they penetrate the tiny pores that radiate out in spokelike fashion on the plate organs. (x 1,100)

BOTTOM RIGHT Thick-set peg organs and more slender, curved hairs, all set in sockets. The curling tips of some of these hairs may be the result of electron beam damage. (x 3,300)

3.7

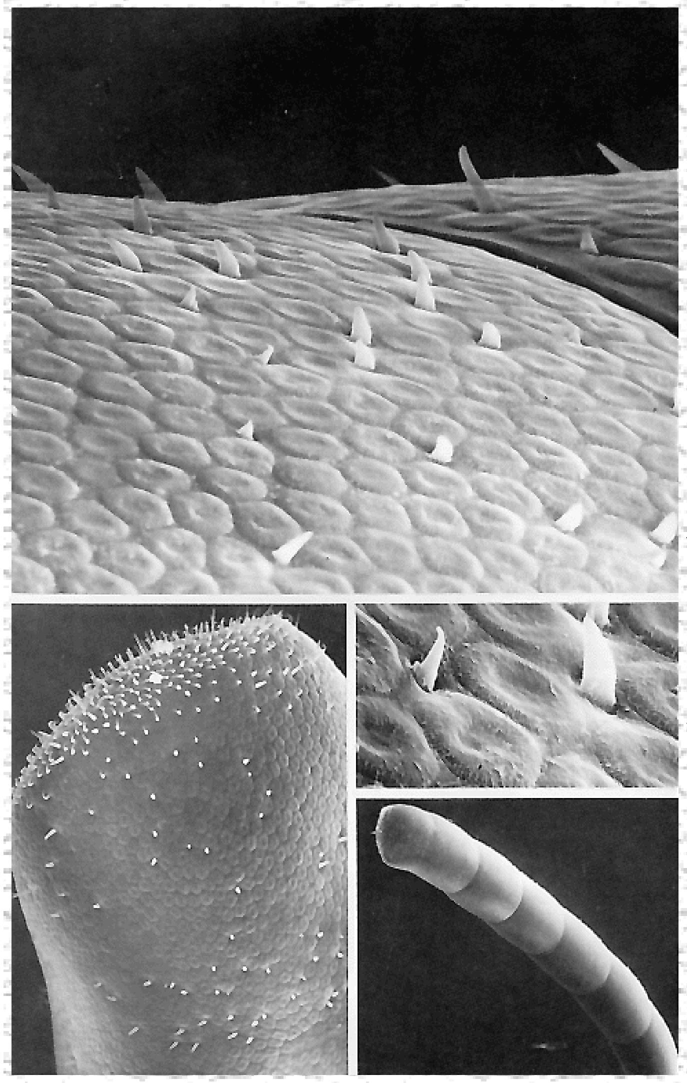


PLATE 3.7. DRONE ANTENNA SURFACE

BOTTOM RIGHT Survey of the terminal seven segments of the antenna. (x 255)

BOTTOM LEFT. Higher magnification of the tip of the antenna showing the packed, oval plate receptors (sensilla placodea) and the whiskery appearance of short peg (basiconic) sensilla and slender hairs (sensilla chaetica). There are nine distinct types of sense organs located on the worker antenna (only three types are seen in this field). Compare with Plate 2.4, worker antenna. (x 60)

TOP Higher magnification of the plate, peg, and chaetica-type receptors on the penultimate segment of the antenna. (x 1,800)

MIDDLE RIGHT Plate and peg organs on the next to last segment of the antenna. Both types are olfactory organs. (x 3,750)

3.8

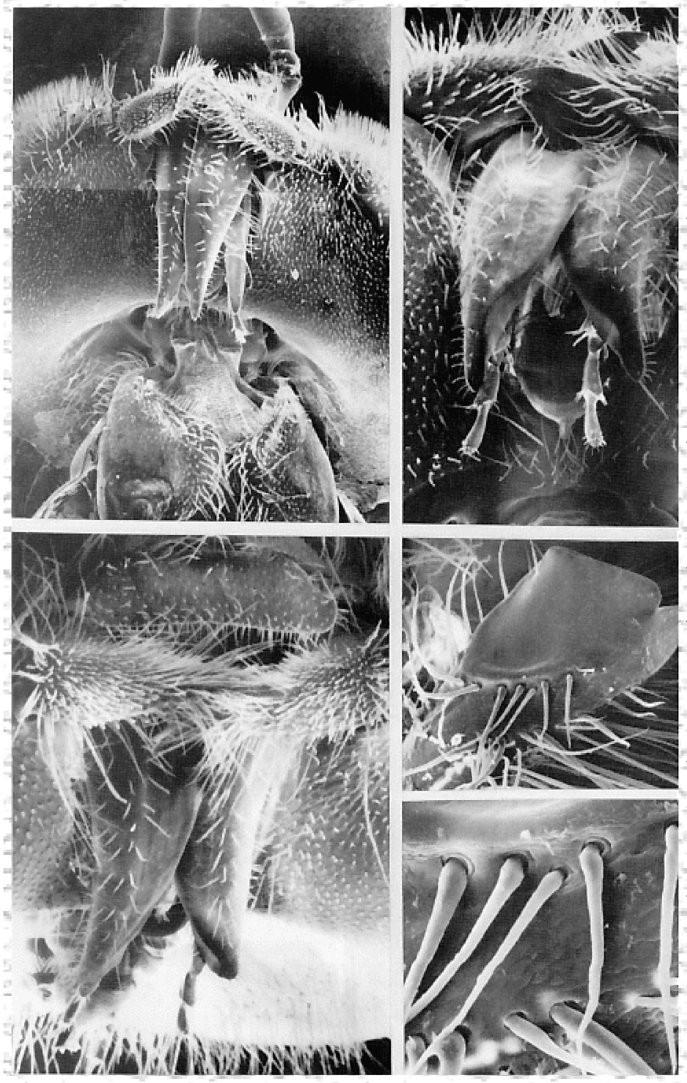


PLATE 3.8. DRONE MOUTHPARTS

TOP LEFT Photomontage of the retracted mouthparts, ventral view. In the Lipper center of the field are the incisorlike (triangular), paired galeae, and to the immediate right is one of the two labial palps. Crossed mandibles arise above and are at right angles to the galeae, with the paired antennae visible above the mandibles at this viewing angle. The upright tufts of setae on either side of the mandibles are the interfacetal hairs of the compound eyes. The cervix and paired episternal sclerites are visible below the galeae. Compare with Plates 2.7 and 2. 10, the worker mouthparts. (x 31)

TOP RIGHT Retracted mouthparts, frontal view. At this viewing angle the curved and pointed galeae partly shroud the labial paips and almost com- pletely cover the short glossa (tongue), whose terminus is visible at the Point where the galeae first cross. At the top of this figure are the hirsute, crossed mandibles. (x 65)

BOTTOM LEFT Higher magnification of the frontal view. At the very top of the field is the platelike clypeus, and successively below that are the labrum, mandibles, and galeae, which largely cover the labium with the exception of the final segments of labial palps. (x 63)

MIDDLE RIGHT Interior surface of the mandibles. Two tiers of stout, socketed hairs are on this medial surface. (x 135)

BOTTOM RIGHT Higher magnification of several hairs on the medial side of the mandible in the middle right micrograph. (x 450)

3.9

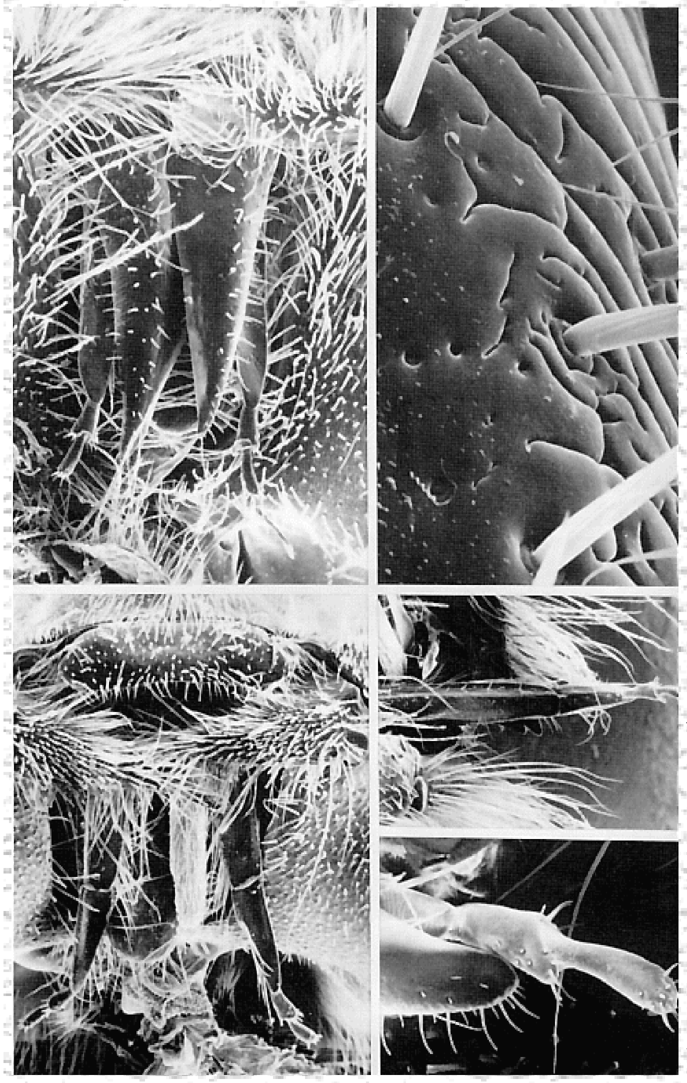


PLATE 3.9. DRONE MOUTHPARTS

TOP LEFT Drone mouthparts anterior view. The two dagger-shaped galeae overlie the paired (and somewhat splayed-out) labial palps. The relatively short glossa (tongue) is hidden from view by these mouthparts. At the top of the field hirsute mandibles extend horizontally, at right angles to the galeae and palps. (x 65)

TOP RIGHT. Close-up of the surface of a galea showing several stout, socketed hairs with fluted sides. The hairs arise from the transversely furrowed cuticle. (x 1,600)

BOTTOM LEFT. Drone mouthparts, posterior view. The very hirsute, relatively short, cylindrical glossa hangs down between the flanking labial palps. (x 55)

MIDDLE RIGHT. Distal four segments of the lablurn. (x 43)

BOTTOM RIGHT Labial palp with its few peg and trichoid sensilla. The tip of the galea is immediately below the labial palp. (x 170)

3.10

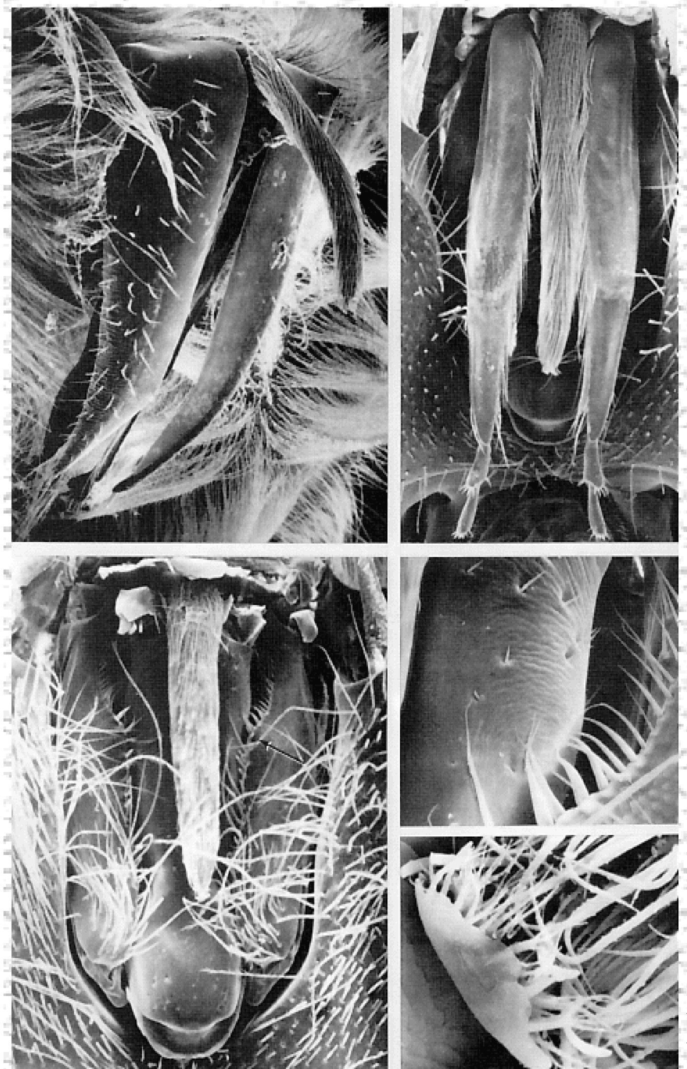


PLATE 3.10. DRONE GLOSSA

TOP LEFT. Glossa (tongue) protruding out over the retracted galeae of the maxillae. Behind the galeae and rather obscured by them are the paired labial palps. (x 63)

TOP RIGHT. Partially dissected ventral view of the relatively short glossa flanked by the four-segmented labial palps. The length of the drone glossa is less than half that of the worker. Compare with Plate 2.7. (x 65)

BOTTOM LEFT. Posterior view of the glossa, with further dissection of the mouthparts (bilateral excision of the labial palps). The short glossa hangs down between the right and left galeae, each with hairs on the medial margin. Between the galeae and partly covered by the glossa is the postmentum. The arrow points to an area further magnified in the middle right micrograph. (x 75)

MIDDLE RIGHT. Posterior view of the base of the glossa. A glimpse of the glossa is on the extreme upper left. On the right several cuticular hairs of the galea rest on the side of the postmentum (arrow in bottom left micrograph). (x 270)

BOTTOM RIGHT. Distal tip of the glossa. The expanded, spoonlike tip is called the flabellum. (x 720)

3.11

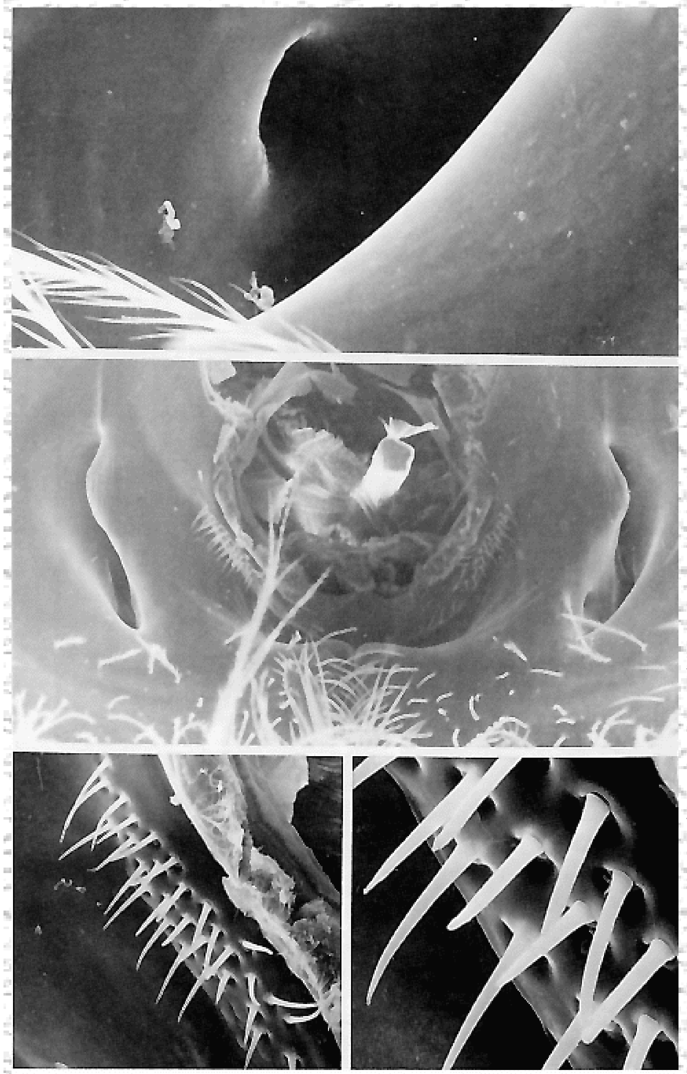


PLATE 3.11. DRONE HEAD, DETACHED, POSTERIOR VIEW

MIDDLE. Round occipital foramen ,vith sheared-off tissues protruding out of it, flanked by two crescent-shaped, posterior tentorial pits. Two ventrolaterally situated hair plates are located on the cuticular ridge immediately alongside the occipital foramen. (x 144)

BOTTOM LEFT. Entire left 28-setae hair plate. (x 550)

BOTTOM RIGHT. Higher magnification of the left hair plate showing the socketed nature of each mechanosensory hair. (x 1,760)

TOP. Small apodeme at the base of the right tentorial pit in the middle micrograph. The recess leads to the ventral postoccipital tentorial arm. (x 900)

3.12

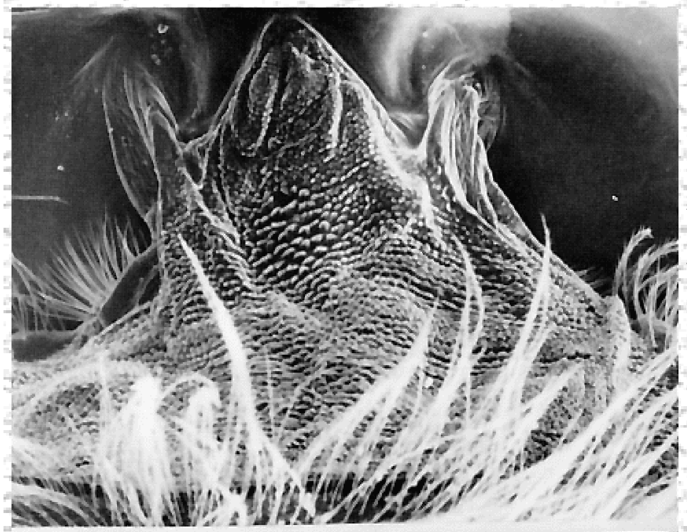


PLATE 3.12. DRONE- CERVIX, DORSAL VIEW

TOP Drone cervix (neck). In specimen preparation, the head was extended from the thorax to stretch out and show the extent of the membranous cervix. Flexuous body hairs from the pronotum are in the foreground. The lateral anchorages for this cervical membrane lie above the posterior tentorial pits, while the inedial (main) insertion is onto the run of the occipital foramen. (x 144)

BOTTOM Cuticular scales on the cervix at higher magnification. Each ellipsoidal scale shows one to eight small tubercles projecting from its dorsal surface. (x 2,700)

3.13

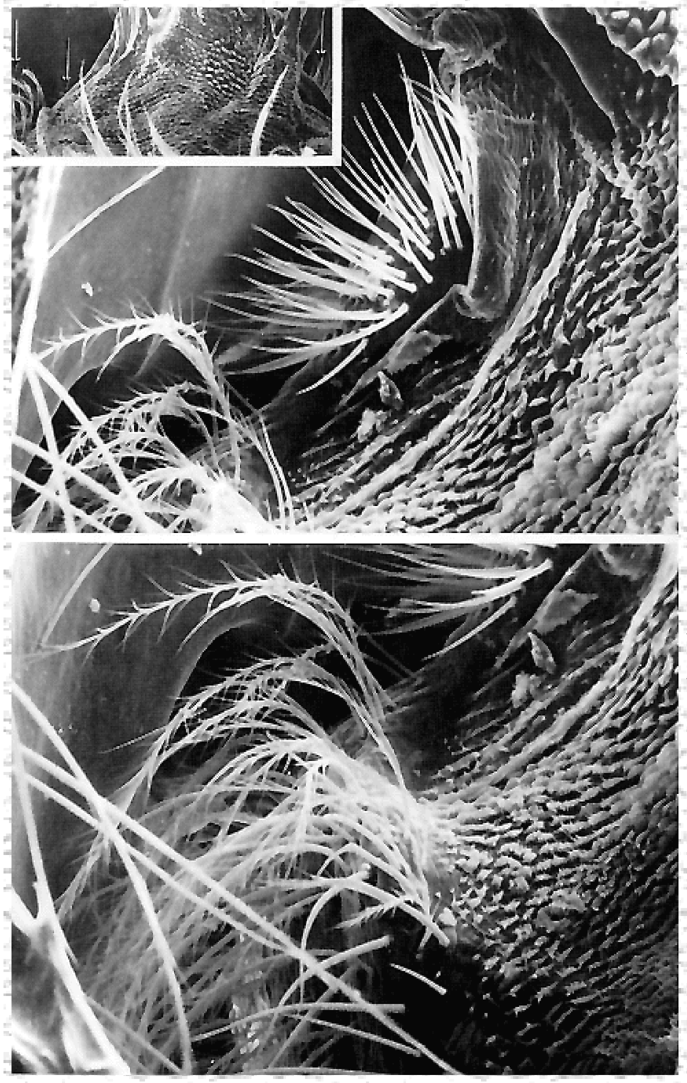


PLATE 3.13. DRONE CERVIX

TOP Dorsolateral hair plate contacting the back of the head (right and middle arrows in inset). These forty trichoid sensilla, seemingly in rows at this viewing angle, are cervical in origin while the branched hairs are from the thoracic episternum. (x 288)

TOP INSET. Survey of the whole, stretched, dorsal cervix. (x 88)

BOTTOM. Dorsolateral cervical ridge (left arrow in inset, top micrograph) extending vertically through the center of the field. The lower extremity of the dorsolateral hair plate is at the top of the field (the head is to the left). (x 360)

3.14

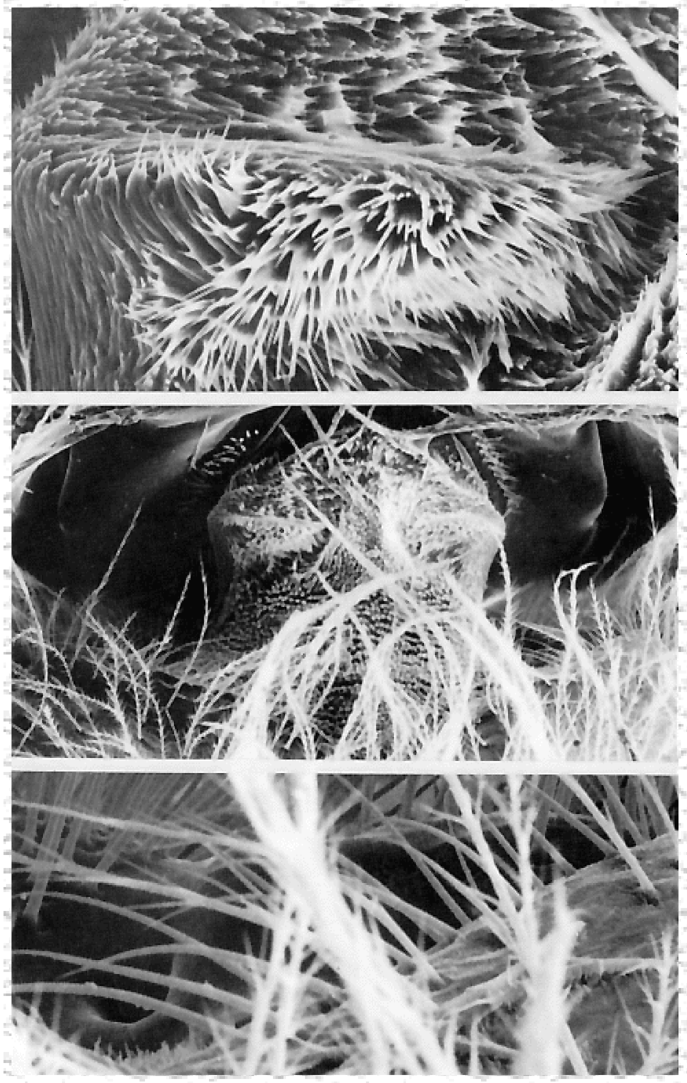


PLATE 3.14. DRONE CERVIX, VENTRAL VIEW

MIDDLE Three types of (uninnervated) cuticular ornamentation (the posterior head is to the top). The branched hairs are from the thorax; the low, elliptical scales are in the posterior half of the cervix (neck); and the taller, tufted, multipointed scales are near the occipital region. (x 144)

TOP Overall cuticular hair distribution and density of the anterior cervical tufts. (x 720)

BOTTOM Ventrolateral mechanoreceptor hair plate on the occipital process of the episternum (upper left quadrant). The cuticular "hole" (far left) may be part of an apodeme. (x 800)

3.15

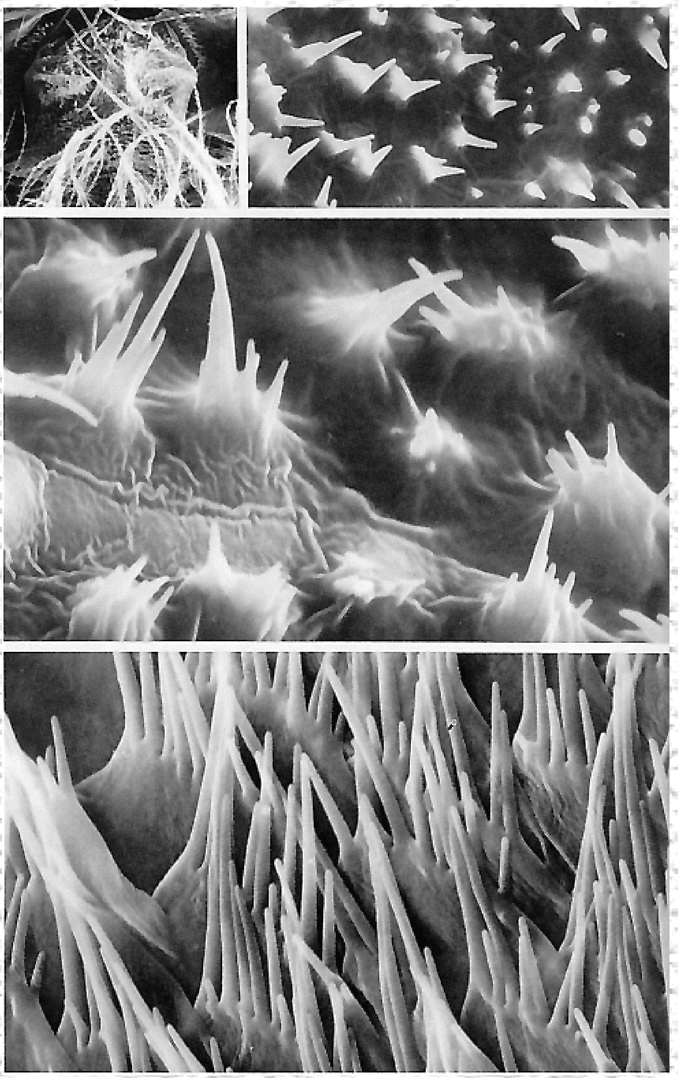


PLATE 3.15. DRONE CERVIX, VENTRAL VIEW

TOP LEFT Extended cervix (neck) (the head is to the top, the thorax to the bottom). (X 88)

TOP HIGHT Central "lobe" area on the ventral cervix. Cuticular scales III this area are for the most part solitary spines or blebs. Compare with Plate 2.17, the worker cervix. (x 2,200)

MIDDLE Cervical membrane with the cervix extended. Each cuticular scale here has five to seven spines, in several lengths. (x 3,600)

BOTTOM Cervical membrane with the neck compressed. In this condition the cuticular spines from neighboring scales mesh and seemingly overlap. (x 3,600)

3.16

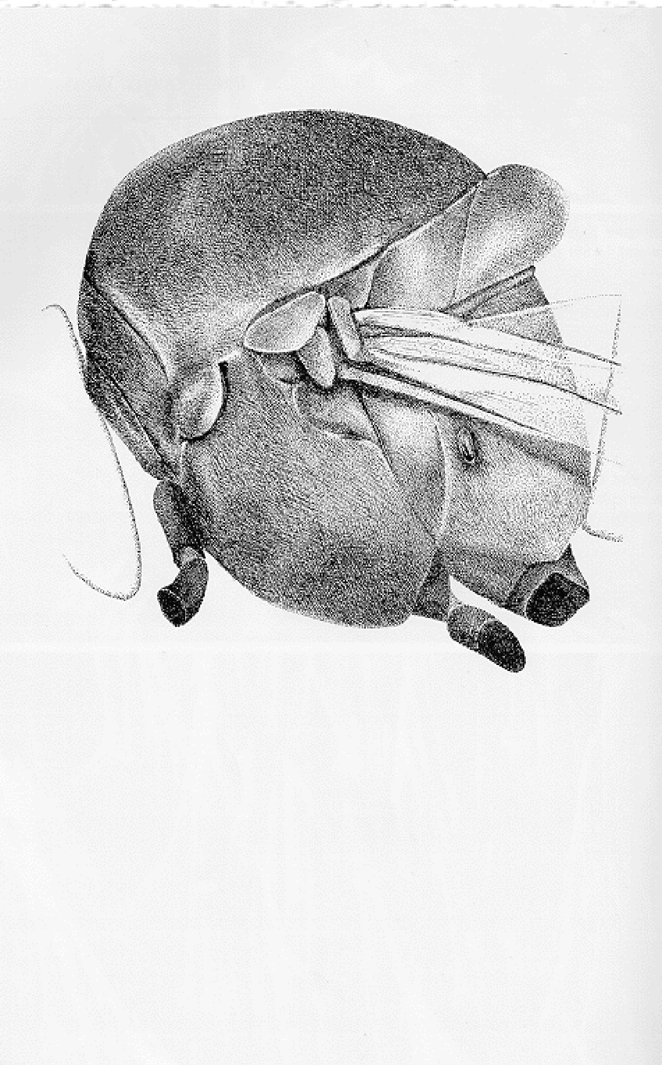


PLATE 3.16. DRONE THORAX

Lateral view of the drone thorax.

See the discussion accompaying Plate 1.16

3.17

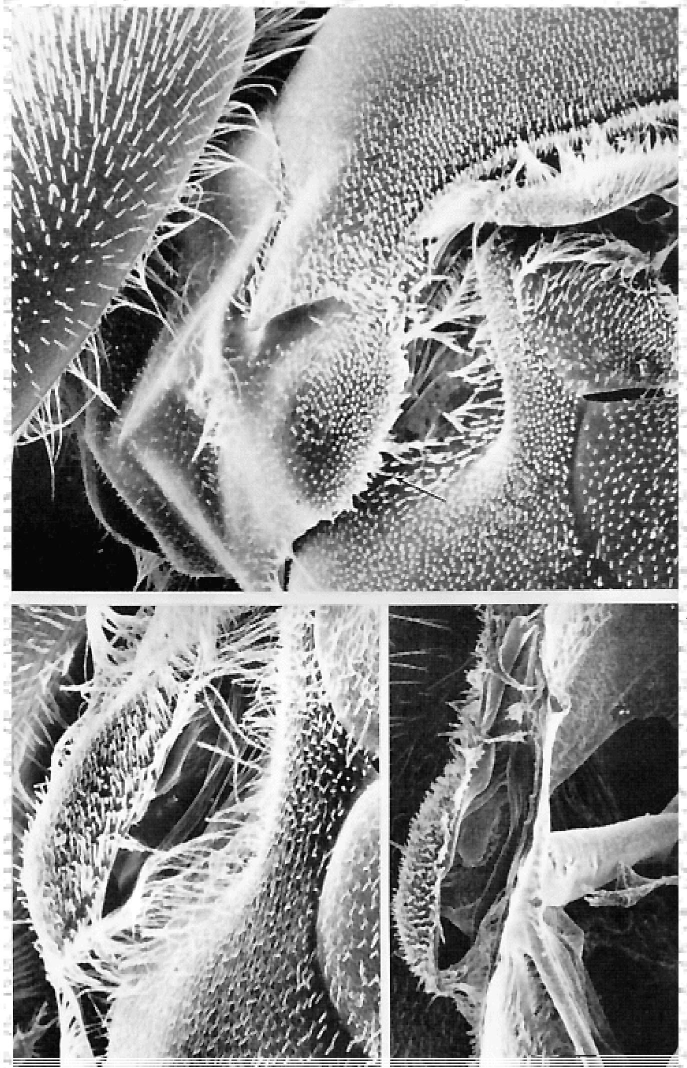


PLATE 3.17. DRONE THORACIC SPIRACLE

TOP. First thoracic spiracle somewhat concealed behind the spiracular lobe (arrow). Above the spiracle and to the right is the lateral edge of the tegula; above the tegula and clothed with short unbranched hairs is the large mesonotum. The hairy compound eye fills most of the Lipper left field. (x 56)

BOTTOM LEFT. More direct view into the first thoracic spiracle showing the valve. The lobe in the far upper right is the mesothoracic supraepimeron; the lobe immediately below is the mesothoracic intraepimeron. (x 78)

BOTTOM RIGHT. Cutaway view of the left mesothoracic spiracle. Inside the bee the trachea extends directly away from the spiracular opening. At right angles to the trachea is the occlusor muscle of the spiracle. (x 55)

3.18

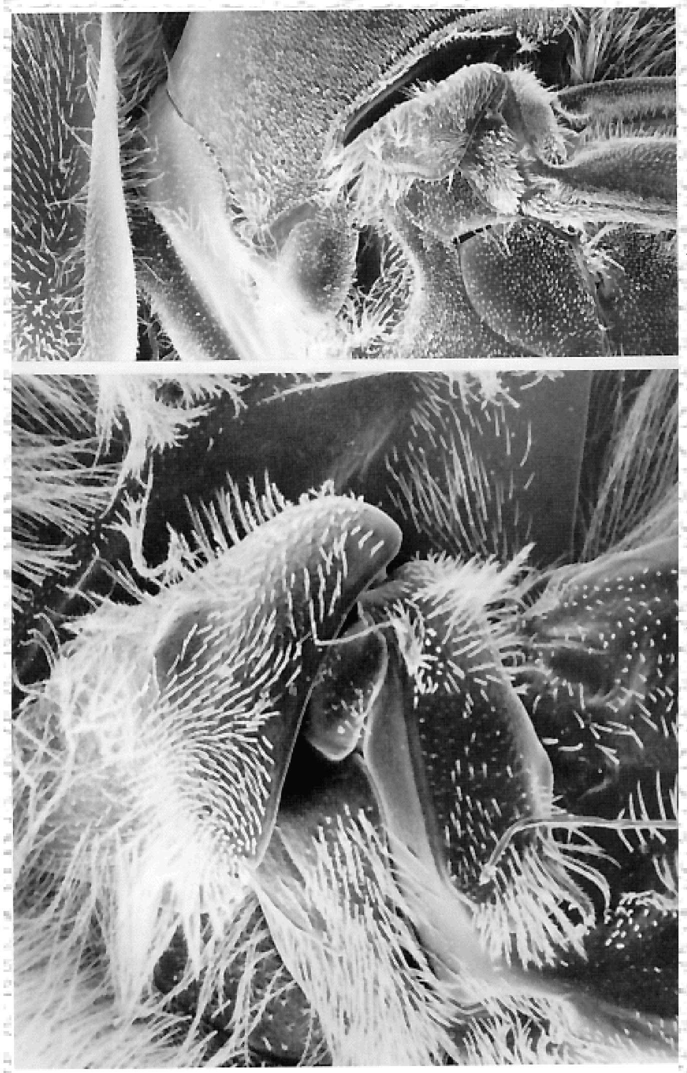


PLATE 3.18. DRONE FOREWING BASE

Top. Photomontage of the drone forewing base. At the far left is the head with the hairy compound eye. At the bottom is the spiracular lobe. Three sclerites are in descending order in the right half of the field; most dorsal is the triangular tegula, below which are the supraepimeron and infraepimeron. The pleural sulcus forms the left side margin for the latter pleurite. The main veins of the leading edge of the wing extend to the right (3 o' clock). (x 3 1)

BOTTOM. Close-up of key wing sclerites. The triangular tegula is the dominant sclerite in the left half of the field. To the right of the basal angle of the tegula is the bilobed second axillary sclerite. This plate is regarded as the pivotal sclerite of the wing base. To the right of the second axillary sclerite is a roughly trapezoidal (in outline) sclerite called the median plate. (x 100)

3.19

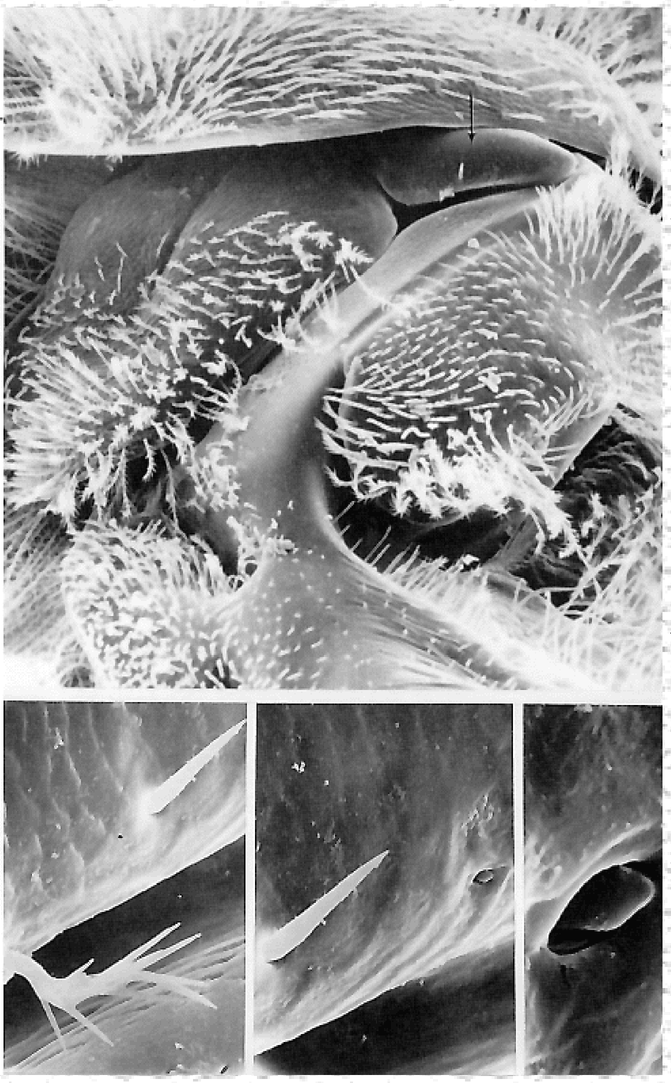


PLATE 3.19. DRONE FOREWING BASE, CLOSE-UP

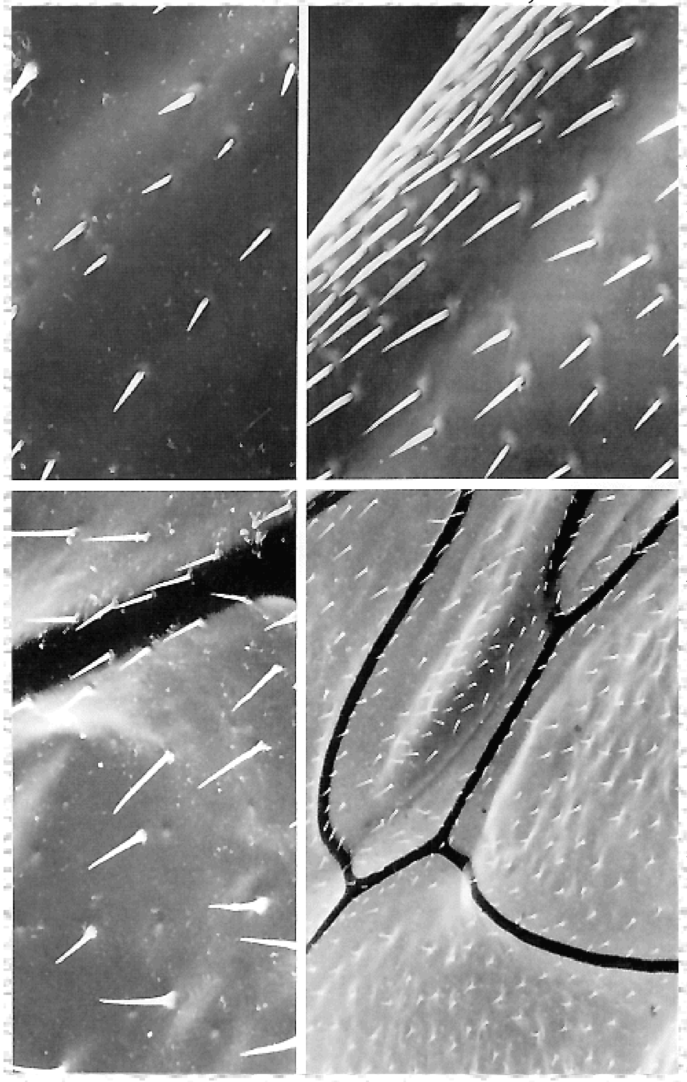
TOP. Drone forewing base (the head is to the top, dorsum to the right) (see Plate 3.18, top micrograph). The probable sensory receptors in the bottom three micrographs are located on the pleural plate (arrow). (x 190)

BOTTOM LEFT. Close-up of a uniquely branched hair and nonsocketed hair above on an area covered by cuticular scales. (x 1, 175)

BOTTOM MIDDLE. Hair in the bottom left micrograph, with the field extended to show the small peglike sensillum. (x 1,700)

BOTTOM RIGHT. Higher magnification of the cuticular "peg" in the bottom middle micrograph. The peg is unusual in that it is very flattened, rather than columnar. (x 8,500)

3.20 PLATE 3.20. DRONE WING, DORSAL SURFACE



BOTTOM RIGHT. Drone wing, dorsal surface, near the anterior wing margin and within the ultimate third of the wing. Wing veins show up as dark wide lines meandering through the wing. (x 70)

BOTTOM LEFT. Close-up of the forewing surface showing single rows of socketed setae emanating from the veins. These may be mechanoreceptors involved in monitoring wing speed. (x 280)

TOP RIGHT. Leading edge of the forewing. These setae, which project from the anteriormost vein, are socketed and may possibly be mechanoreceptors. This field is an area about two-thirds of the distance to the wing tip. (x 650)

TOP LEFT. Vein on the dorsal surface of the forewing showing several ranks of socketed hairs on either side of the wing vein. (x 720)PLATE 3.20. DRONE WING, DORSAL SURFACE

3.21

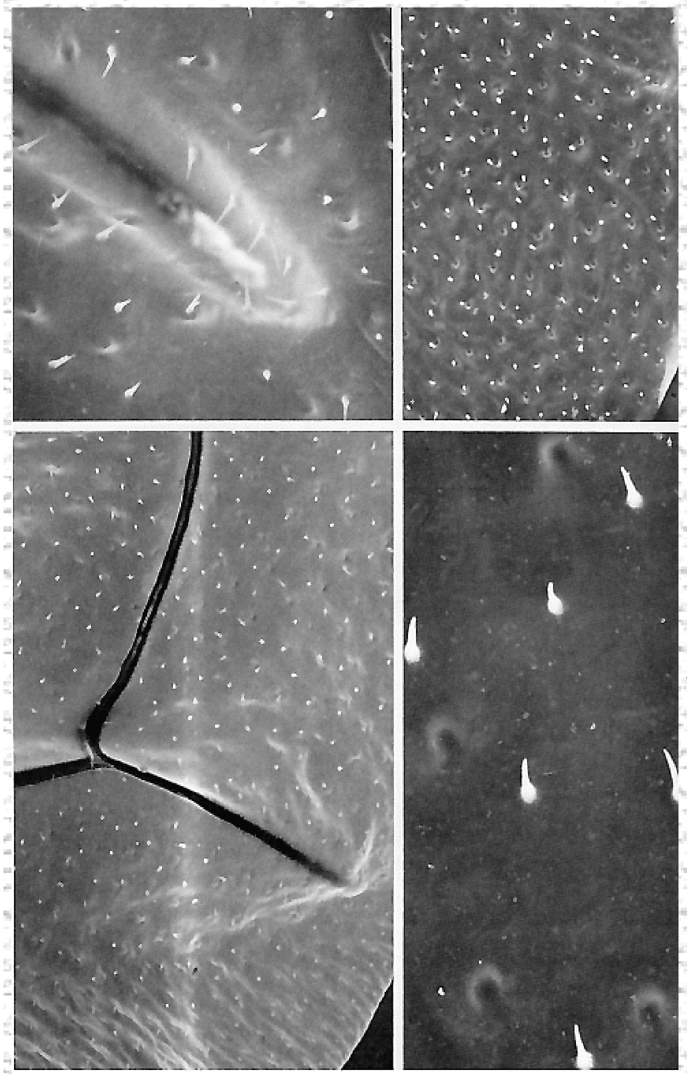


PLATE 3.21. DRONE WING, VENTRAL SURFACE

BOTTOM LEFT. Hind wing, ventral view, at low magnification. Several veins intersect in this field. (x90)

TOP LEFT Ventral view, near the tip of hind wing. Exceedingly small, cuticular spines randomly arise in this area. Some scattered pits are also visible. (x 420)

TOP RIGHT. Forewing tip, ventral view. Numerous scattered small, blunt cuticular spines are found on this surface. The pits represent the bases of the short counterpart spines arising on the reverse surface of this wing. (x 130)

BOTTOM RIGHT. Higher magnification of the ventral forewing in the top right micrograph. The spine density is 1/900 micro m^2. (x 750)

3.22

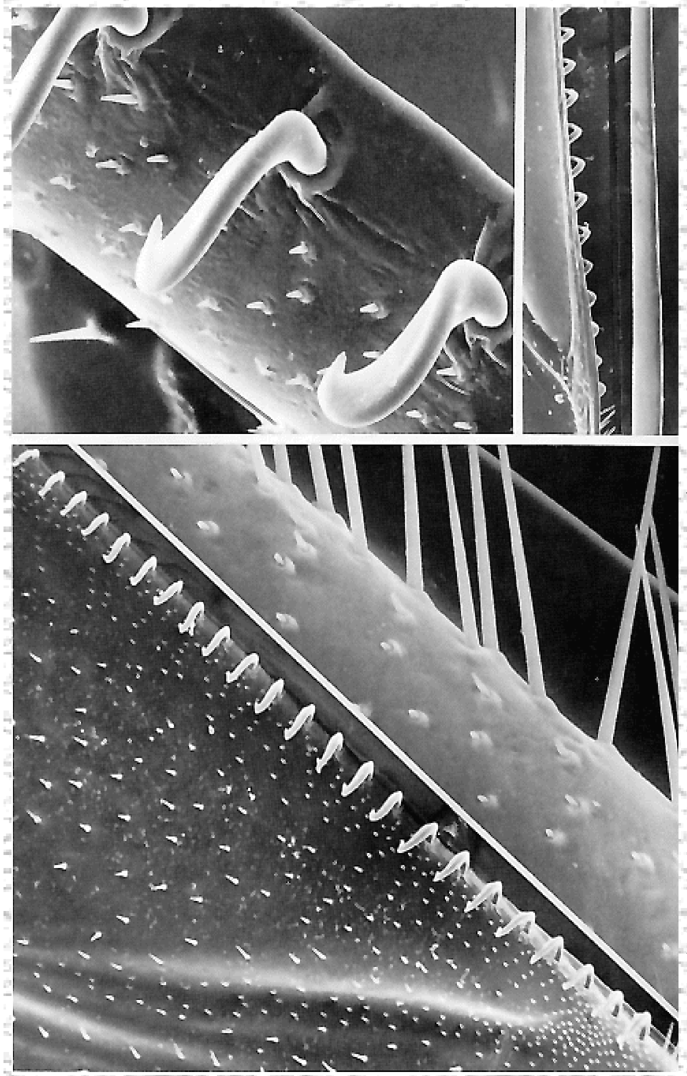


PLATE 3.22. DRONE WING HOOKS

BOTTOM LEFT. Leading edge of the hind wing The hooks engage the posterior margin of the forewing only during flight, when the forewing and hind wing beat as one. Microtrichia are abundant over the wing surface. (x 136)

BOTTOM RIGHT. Non-hook-bearing portion of the hind wing in the bottom left micrograph. Socketed hairs, both long and very short, project from this vein. (x 800)

TOP RIGHT. Photorriontage of the ventral forewing hind margin, around which the hooks engage, and the hooked leading edge of the hind wing. (x 110)

TOP LEFT. Close-up of the wing hooks. These are somewhat larger than those of the worker. Socketed small peg organs are abundant on the surface engaged by the trailing edge of the forewing. (x 720)

3.23

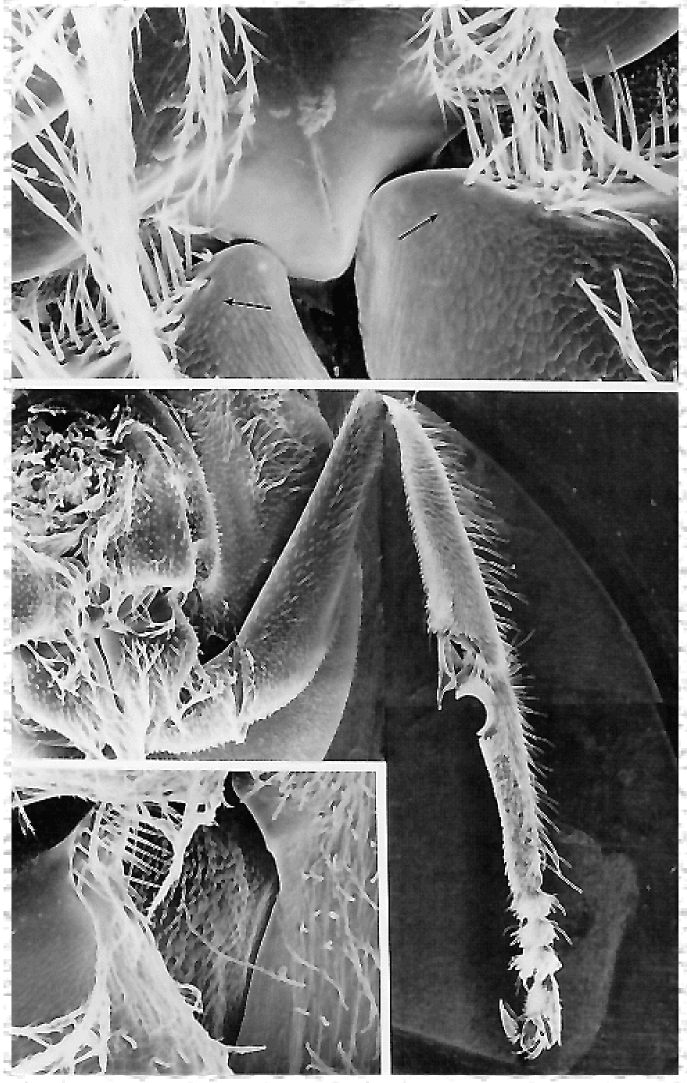


PLATE 3.23. DRONE FORELEG

MIDDLE. Photomontage of the entire left foreleg. Proximally to distally, after the coxa (first leg segment from the body) are the trochanter, femur, tibia, basitarsus (with antenna cleaner notch), three short tarsal segments, pretarsus, and claws. (x 31)

TOP. Prothorax, ventral view. Two scaled coxae (medioanterior surfaces) abut on either side to a smooth-surfaced basisternum. Mechanoreceptor hair plates of the coxae engage the lateral basisternum (arrows). (x 168)

BOTTOM LEFT Lateral edge of the coxa extending diagonally through the center of the field. A mechanoreceptor hair plate on the lateroanterior surface engages the adjacent sternum. (x 93)

3.24

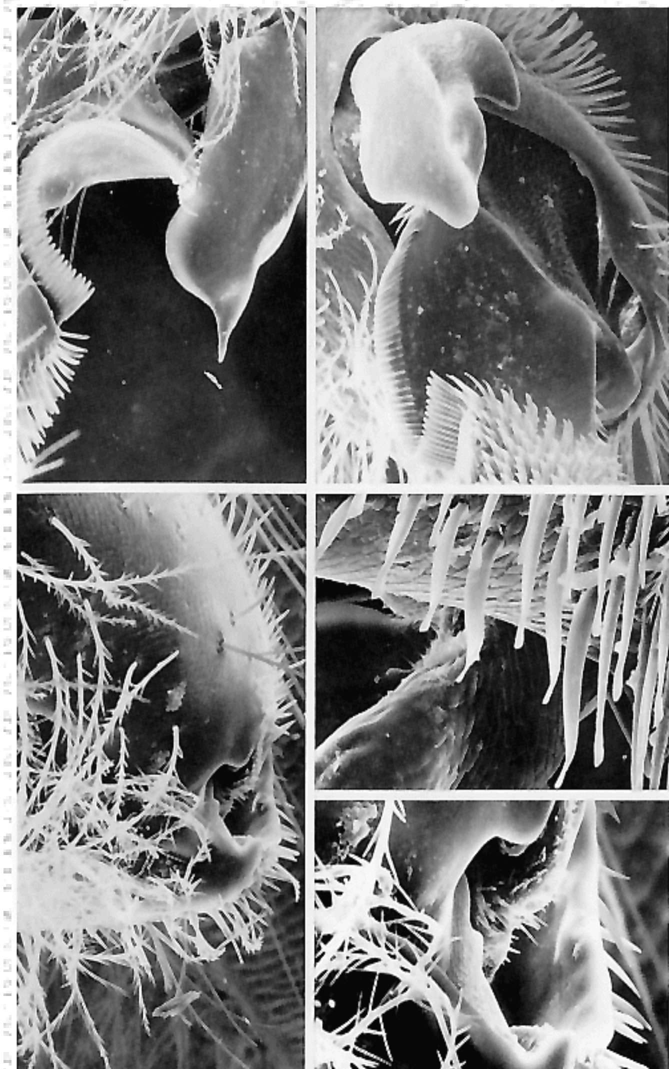


PLATE 3.24. DRONE FORELEG, CLOSE-UP

TOP LEFT. Tibia-basitarsus joint, the region of the antenna cleaning apparatus (comb). The fibula (upper right) is a clasplike spur that closes over the semicircular toothed notch (rimmed with comblike hairs). The antenna is inserted in this enclosure and drawn upward to clean debris from its cuticular receptors. The fibula fits into the proximal portion of the basitarsus to form an embrace around all antenna surfaces. (x 161)

TOP RIGHT. Dorsal view of the fibula showing the notch of the antenna cleaner. From this angle it is apparent that the fibula is contoured into several lobes to make better contact with the circular (in cross section) antenna. (x 195)

MIDDLE RIGHT Higher magnification of the tibia-basitarsus joint. A patch of unusual cuticular setae is on the tibia (see the top right micrograph). These setae have twisted blunt tips with several parallel ridges along the long axis of the hair. (x 496)

BOTTOM RIGHT. Femur-tibia joint. The intersegmental membrane is studded with short, acute cuticular spines. (x 770)

BOTTOM LEFT Femur-tibia joint. The tibia is very flexed relative to the femur. The long, straight, unbranched hairs of the compound eye are in the far background. (x 280)

3.25

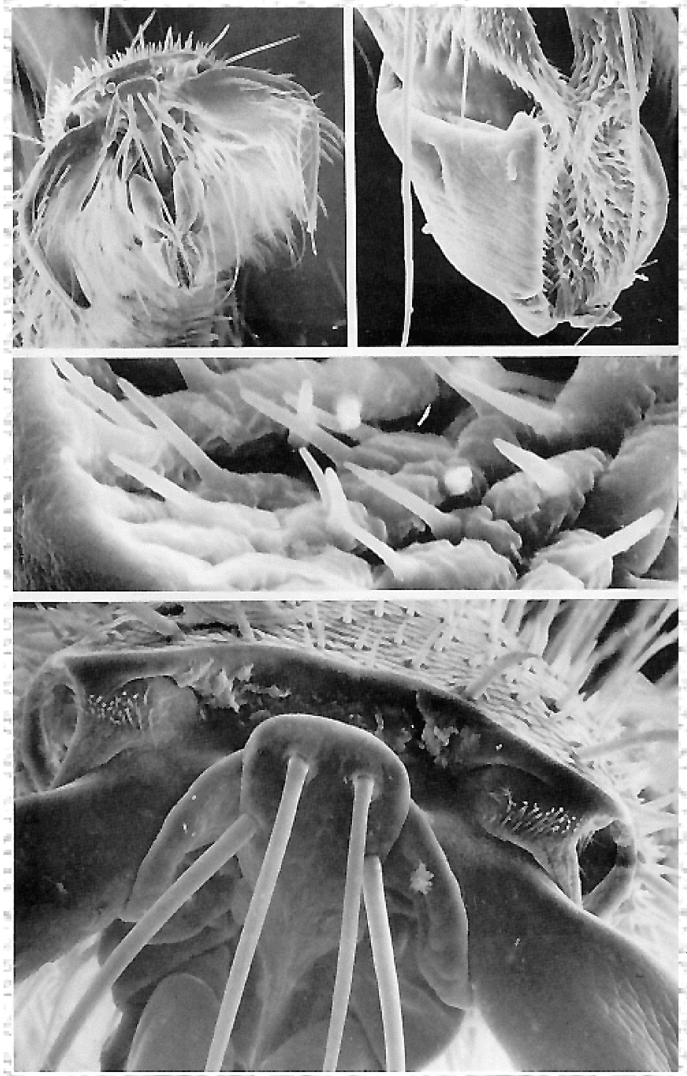


PLATE 3.25. DRONE FOREFOOT AND HIND FOOT

TOP LEFT. Survey of the hind foot. The claws are simple, unlobed, hollow hooks fringed with (probably sensory) hairs. (x 100)

TOP RIGHT. Arolium (from the hind foot) showing its hirsute medial surface and glabrous, grooved exterior (compare with Plate 1.34, the queen forefoot and hind foot). Three long spines hang down from the median sclerite above. (x 400)

MIDDLE. Higher magnification of the hairs lining the medial surface of the arolium. (x 4,250)

BOTTOM. Forefoot (prothoracic foot). In the foreground is the median sclerite, from which extend four stout, slightly curved spines. The basal portions of the right and left claws are on either side of the median sclerite. The ventrodistal margin of the fifth tarsal segment arises over the claw bases and median sclerite. Left and right sensory hair plates are evident above the claws; when the claws are raised they contact these putative mechanoreceptors to inform the drone whether its claws are extended or flexed. (x 510)

3.26

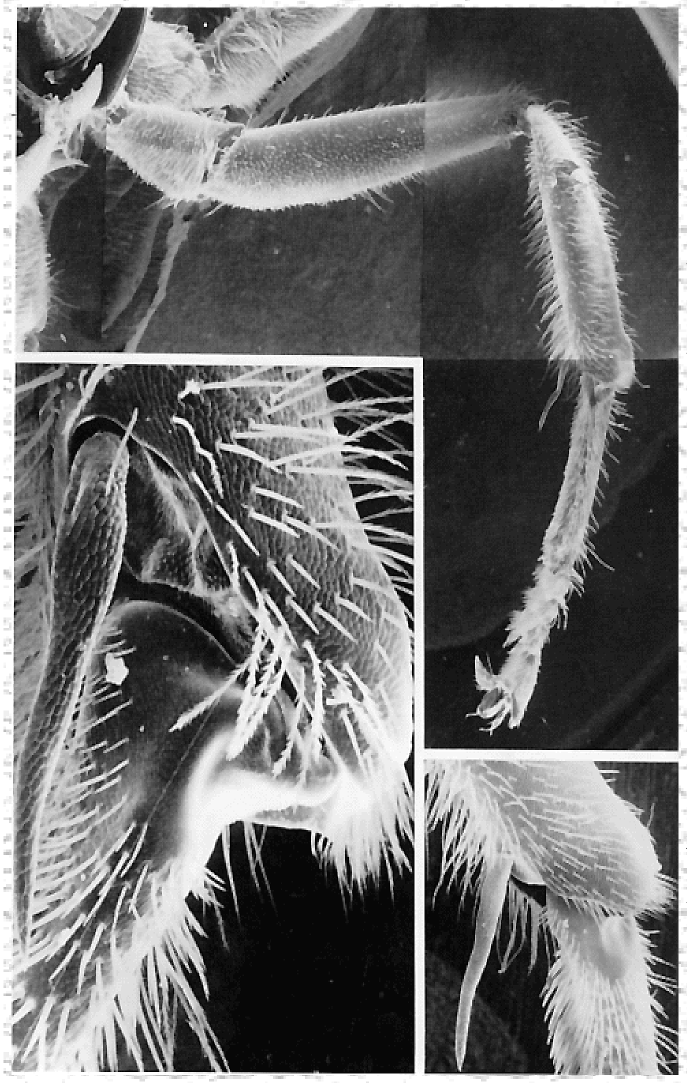


PLATE 3.26. DRONE MIDDLE LEG

TOP. Photomontage of the left middle (mesothoracic) leg. The coxa is obscured but, proximally to distally, the trochanter, femur tibia (with spine or wax spur pointed downward), basitarsus and three additional tarsomeres, and the pretarsus with claws are visible. (x 31)

BOTTOM RIGHT . tibia-basitarsus Joint. This is a monocondylic (single point) articulation. The relatively large size and stoutness of the tibial spine are evident. (x 93)

BOTTOM LEFT. Tibia-basitarsus Joint. This view and magnification make apparent the differences in the cuticular surfaces between the scalelike tibial base, the pebble-grained tibial spine, and the smooth head of the basitarsus. The two forms of setae (branched and simple trichoid) on the tibia are visible at this articulation, as well as the scales on the mtersegmental membrane at this Joint. (x 355)

3.27

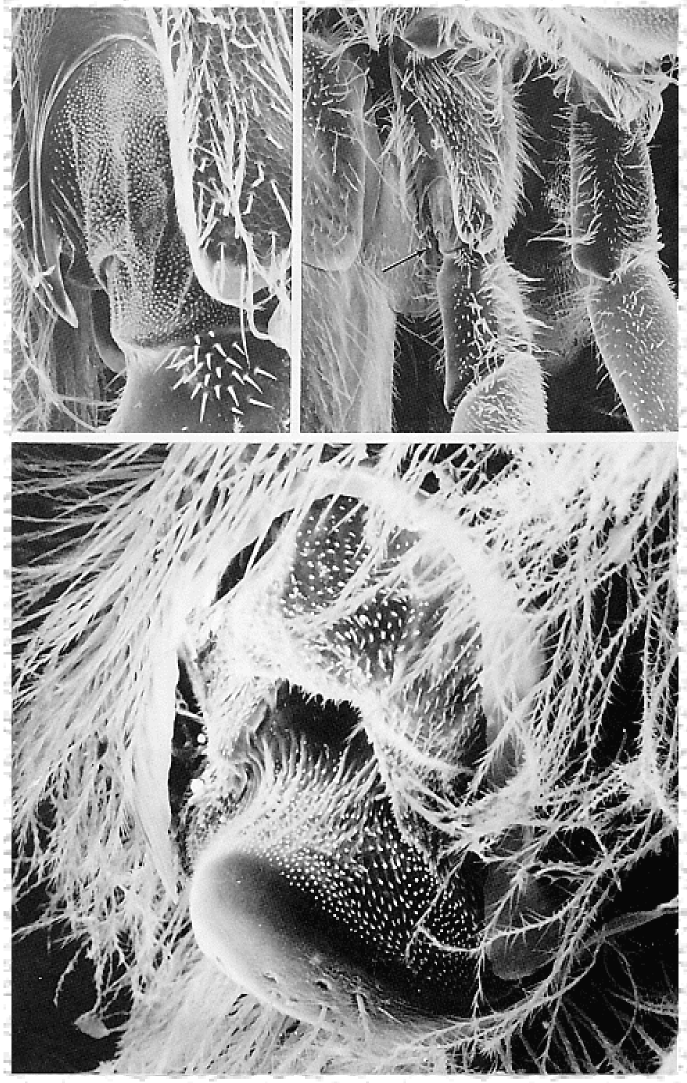


PLATE 3.27. DRONE LEG BASES

TOP RIGHT. Bases of the middle (mesothoracic) and hind (metathoracic) legs (the abdomen is to the left). In the foreground, proximally to distally, are the coxa, trochanter, and a small portion of the femur of the hind leg. The arrow indicates the trochanter-coxa Joint, which is further magnified in the bottom right micrograph. (x 60)

TOP LEFT. Scale-studded intersegmental membrane (center) covering the articulation between the hind coxa and trochanter. The proximal surface of the trochanter has about two dozen short, sharp, socketed hairs that may be mechanoreceptors that contact the coxa In the course of locomotion and inform the nervous system as to leg position. (x 240)

BOTTOM. Trochanter-coxa joint (arrow in top right micropraph (x 298)

3.28

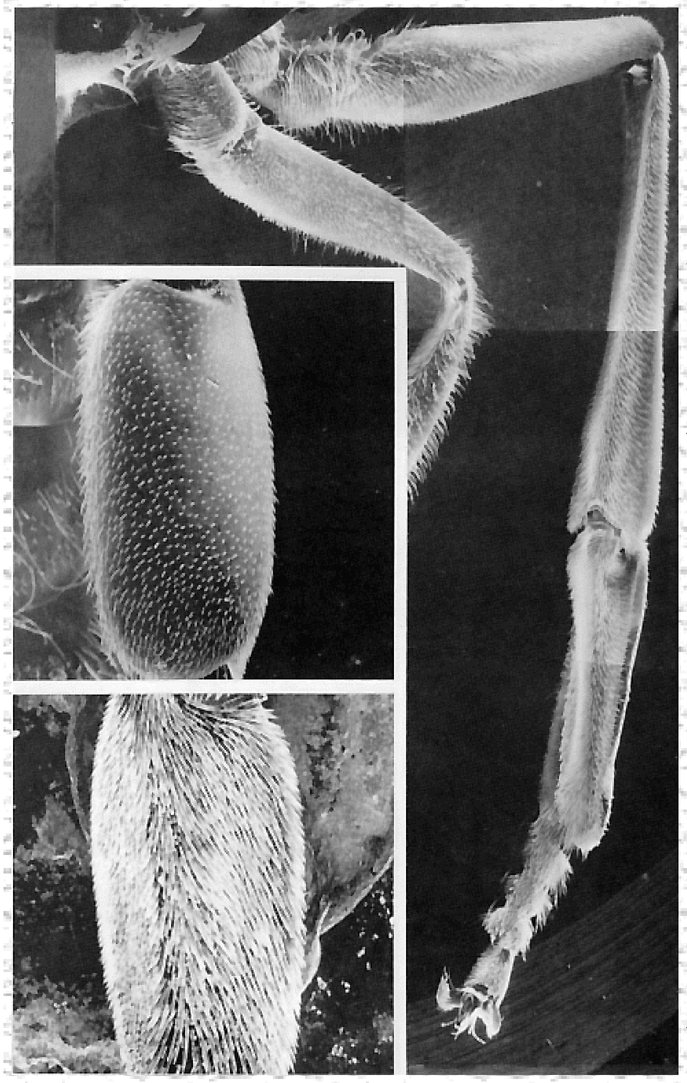


PLATE 3.28. DRONE HIND LEG

TOP. Photomontage showing entire left hind (metathoracic) leg and the coxa, trochanter, and femur of the adjacent leg. At the distal extremity of the completely exposed leg are the two claws of the pretarsal segment, followed proximally by four tarsal subsegments, the most proximal of which connects to the elongate flattened basitarsus. The basitarsus articulates with the tibia. The femur, trochanter, and coxa are in a distal to proximal succession. No pollen gathering or transfer modifications such as on these segments in 'the worker are present on the drone hind leg. Compare with Plates 2.28, 2.29, 2.30, and 2.31. (x3l)

MIDDLE LEFT. Lateral view of the metathoracic pretarsus (distal edge at the top). The setae are relatively sparse and extremely short. (x 37)

BOTTOM LEFT. Medial surface of the metathoracic pretarsus (distal edge at the top). This side is characterized by a dense pile of rather long setae. (x 34)

3.29

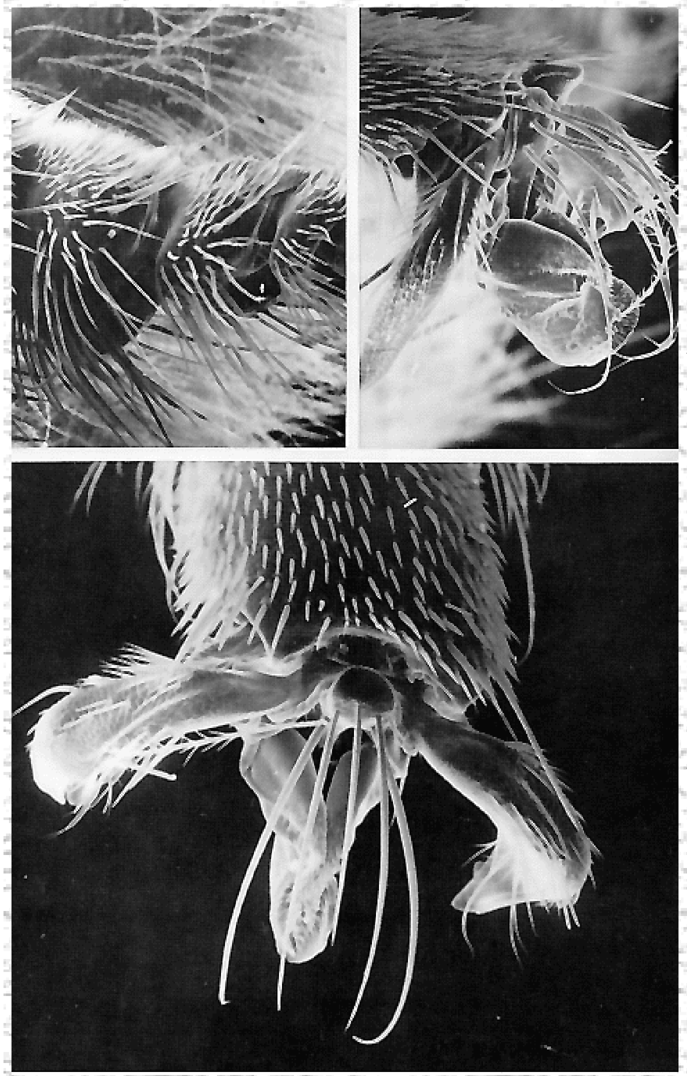


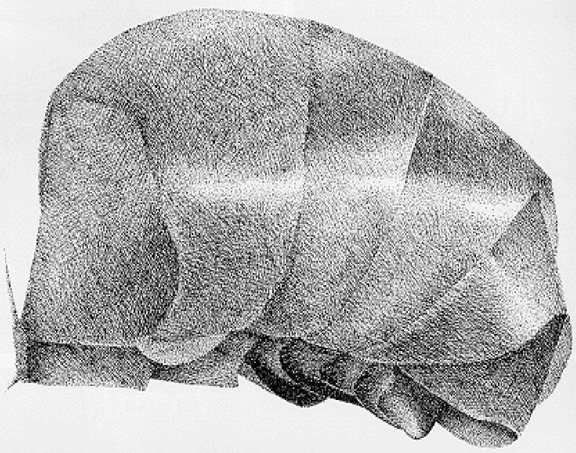
PLATE 3.29. DRONE HIND FOOT

BOTTOM. Pretarsus and fifth tarsal segment. The claws gape widely to better reveal the soft, pursed medial lobe (arolium). Five long, curved setae emanate from the median sclerite, which, in turn, articulates with the last tarsal segment. Rows of short trichold sensilla descend over the dorsum of the last tarsal segment. (x 180)

TOP LEFT. Three tarsal segments of the hind (metathoracic) foot. The planta (seen here as the upper surface, which is the best orientation for the viewer), covered with short hairs, contacts the substratum. (x 110)

TOP RIGHT. Lateral view of the pretarsus and last (fifth) tarsal segment showing the contracted nature of the arolium and the upright orientation of the medial sclerite. The five trichoid sensilla arise from the medial sclerite at different levels. (x 143)

3.30



Lateral view of the drone gaster (abdomen).

See the discussion accompaying Plate 1.36.

3.31

PLATE 3.31. DRONE PETIOLE, DORSAL VIEW

TOP. Slightly curved anterior margin of the propodeum, at the top of the field. The membranous connective of the (dorsal) petiole is in the center. (x 100)

MIDDLE LEFT. Close-up of the dorsal membranous region in the top micrograph, with the connective cut. Longitudinal wrinkles and copious scales are prominent in this region. (x 168)

MIDDLE RIGHT. Apodeme for wing muscle attachment, immediately anterior to the petiole. (x 234)

BOTTOM. Higher magnification of the cuticular scales of the dorsal membranous wall of the petiole. Five to seven spines of several lengths project from each scale. (x 3,230)

3.32

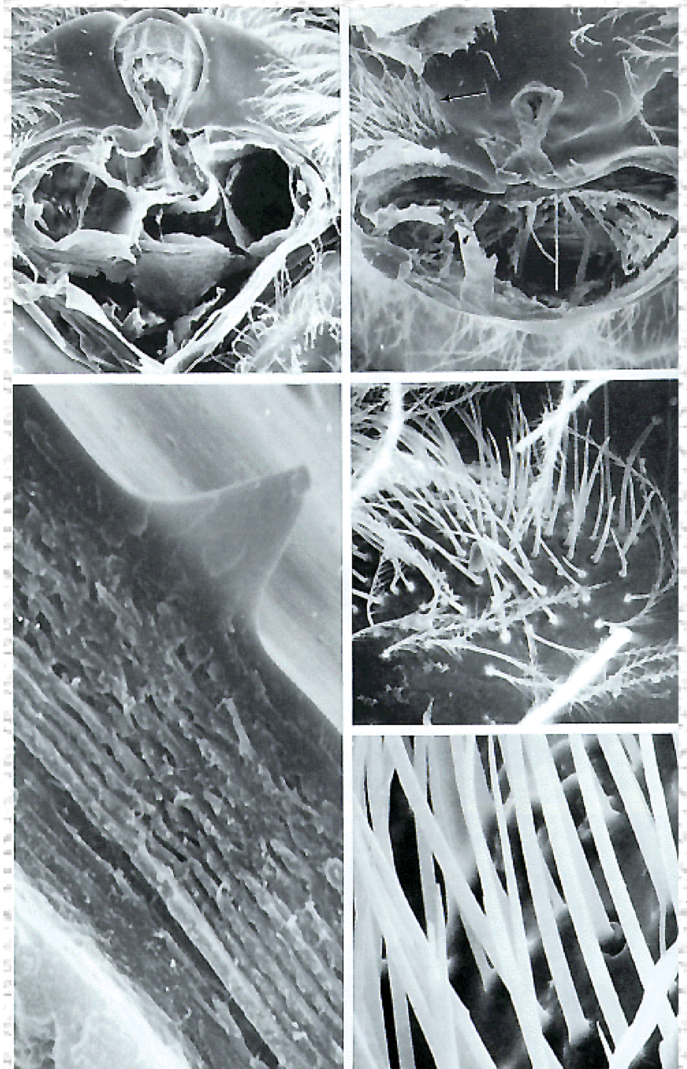


PLATE 3.32. DRONE PETIOLE, ABDOMEN DETACHED

TOP LEFT. Cross-sectional cut through the membranous petiole. The longitudinally seamed, scaly membrane (at 12 o'clock) and the thoracic cavity immediately beneath are exposed. Two sizable muscles with sheaths (at 3 and 9 o'clock) are visible; these assist in elevating the abdomen. (x 50)

TOP RIGHT. Reverse view of the top left micrograph showing the crosssectioned anterior end of the abdomen (gaster). The arrow points to the hair plate that is further magnified in the middle right micrograph. (x 50)

MIDDLE RIGHT. Dorsolateral hair plate of the petiole (arrow in top right micrograph). These mechanoreceptors monitor the gravitational pull of the gaster onto the thorax via the petiole. The socketed, unbranched hairs are mechanosensors. (x 300)

BOTTOM RIGHT. Higher magnification of the setae of the hair plate. (X 1,000)

BOTTOM LEFT. Longitudinal section through a cuticular spur in the petiolar region. The laminated appearance of the exocuticle is apparent. (x 8,640)

3.33

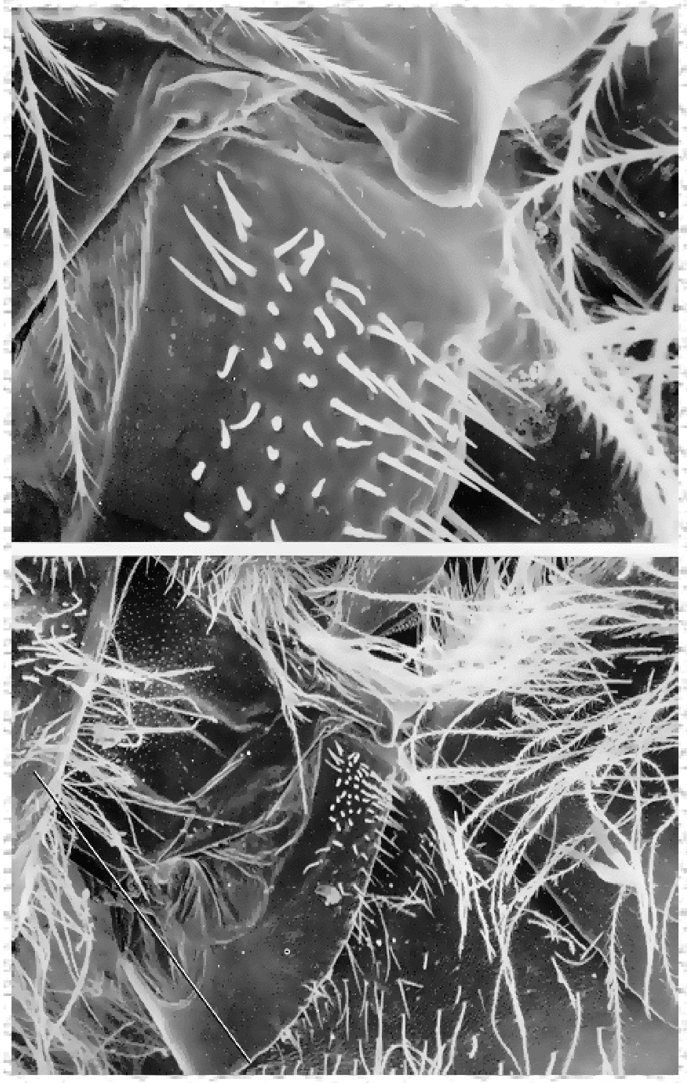


PLATE 3.33. DRONE PETIOLAR HAIR PLATE, OBLIQUE VIEW

BOTTOM. Petiole, the junction between the first and second abdominal segments. This joint ensures great flexibility of the abdomen relative to the thorax. Monitoring this movement and providing the bee with information on the alignment of the thorax to the abdomen relative to gravity are several (mechanoreceptor) hair plates that are externally placed proprioceptors. One such hair plate is visible; the setae (sensilla) probably make contact with the dorsal wall of the petiole of the first abdominal segment. The black and white diagonal bar indicates the alignment of body segments (the head is to the upper left). (x 85)

TOP. Higher magnification of the contact zone between the hair plate receptors and the dorsal petiole. These four dozen sensory hairs are arrayed in various directions, so several of them contact the petiolar protuberance at any one time at any degree of flexion, which ensures a constant monitoring of abdominal position. (x 430)

3.34

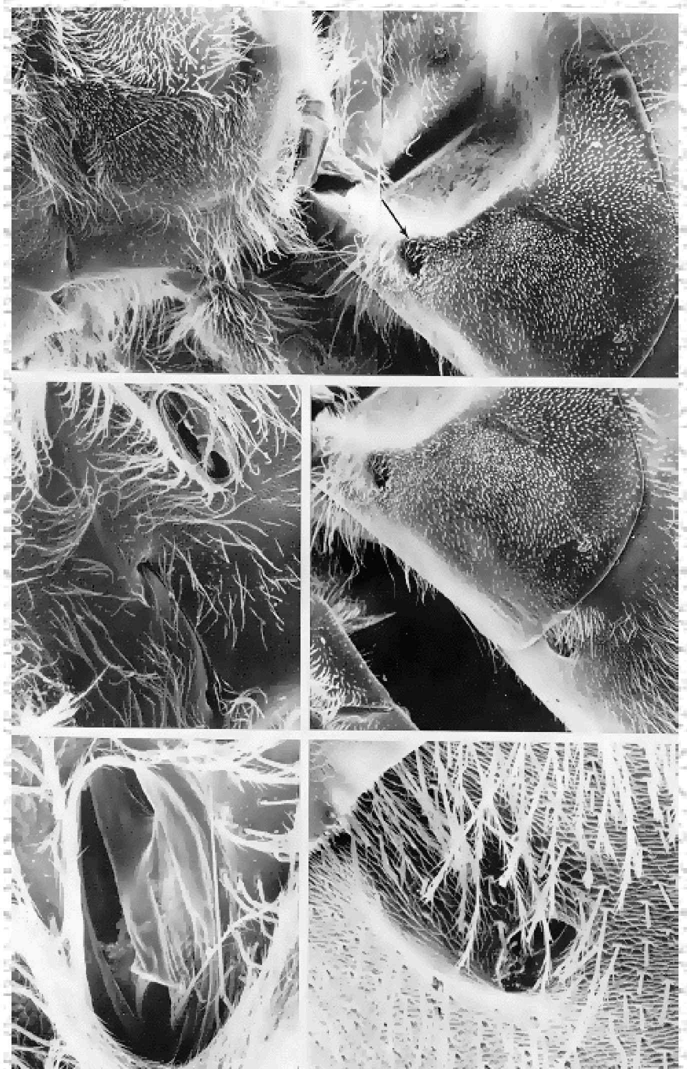


PLATE 3.34. DRONE SPIRACLES

TOP. Photomontage showing primarily the first (propodeal) and second segments of the abdomen (dorsum at the top). Spiracles are visible (arrows) on these two segments. The wings have been removed. (x 31)

MIDDLE LEFT. Spiracle on the first abdominal segment at moderate magnification. This spiracle is somewhat larger than the others, and its elongate-oval rim differs from the more rounded appearance of the succeeding spiracles. (x 63)

BOTTOM LEFT. Close-up of the first abdominal spiracle. The operculum (plate) covering this spiracle has been damaged in specimen preparation; in the intact bee this plate can be pulled down by an occlusor muscle, much like a window shade, thus shutting off this spiracle from the outside. The operculum is never completely open and its excursion is not large, so this situation permits only a minimal aperture. (x 170)

MIDDLE RIGHT. Two spiracles, one each on the second (left) and third (right) abdominal tergites. The more circular nature of these openings is evident. These spiracles are noticeably larger than those of the worker and queen. (x 3 1)

BOTTOM RIGHT. Higher magnification of the third abdominal spiracle. The circular depression in the cuticle leads to an oval pit (lower right) that connects directly to the underlying trachea via a valve mechanism capable of occluding the spiracle atrium from the trachea. The branched hairs and valvular apparatus may be barriers that keep mites from entering the trachea through this spiracle. (x 250)

3.35

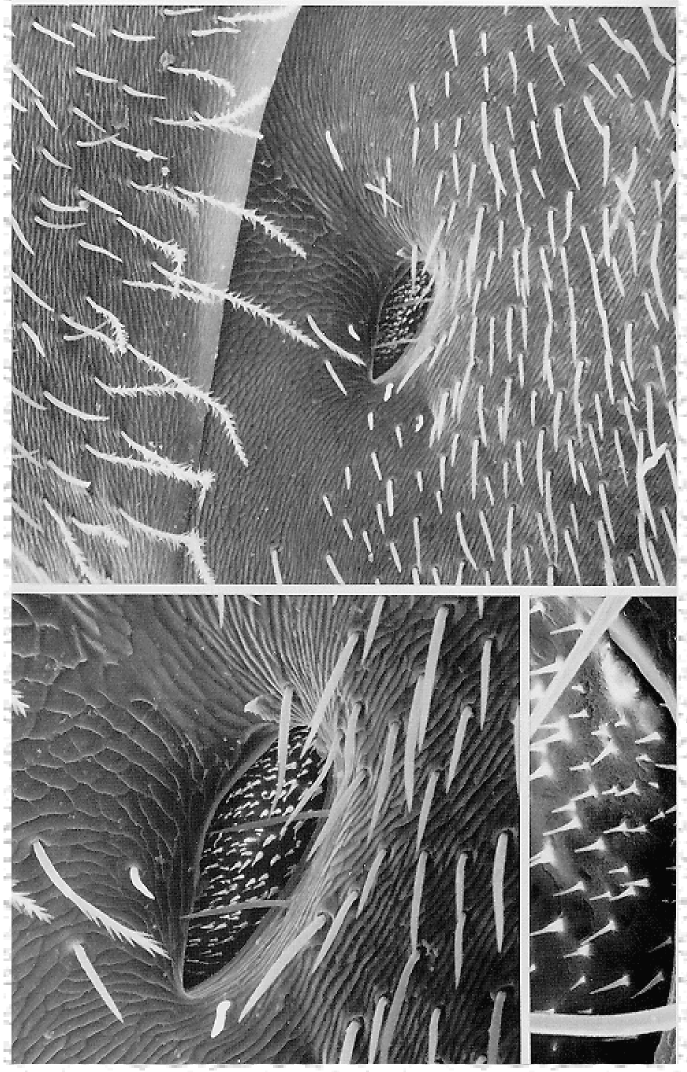


PLATE 3.35. DRONE SPIRACLES, CLOSE-UP

TOP. Survey of a portion of the second and third abdominal tergites showing the spiracle on the third. The posterior margin of the second abdominal tergite, which is sparsely covered with branched body hairs, is visible on the left. On the anterior margin of the third tergite are few setae, but the teardrop-shaped spiracular opening is surrounded by socketed hairs on its dorsal, ventral, and posterior margins. (x 175)

BOTTOM LEFT. Close-up of the spiracular opening. Inside the spiracle is the cuticular atrial wall, which bulges out somewhat and is covered with very short hairs. Atmospheric air passes over these finer setae and gains entrance to the trachea directly behind the atrium via a small channel. This canal can be opened when the muscles of its valve relax. (x 400)

BOTTOM RIGHT. Higher magnification of the small, unsocketed hairs of the medial wall of the spiracular atrium. The function of these hairs may be to remove particulate matter from the airstream. (x 800)

3.36

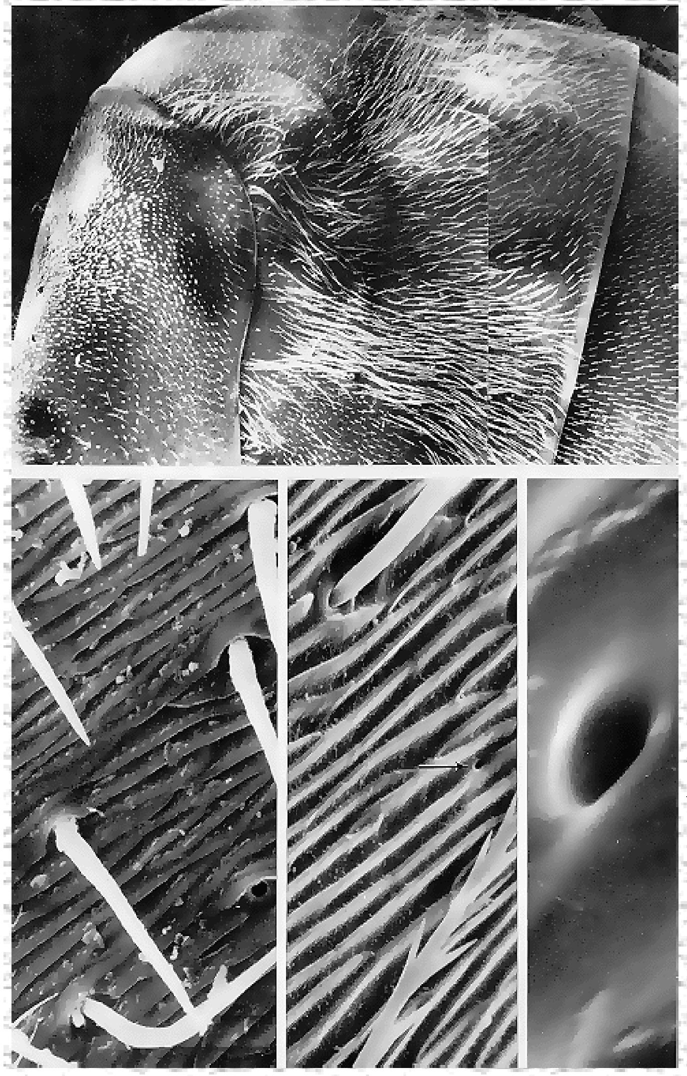


PLATE 3.36. DRONE ABDOMEN, DORSAL SURFACE

TOP. Photomontage of the dorsal portion of the left abdomen. About half of the second, third, and fourth abdominal tergites are visible in their total lateral expanse. (x 40)

BOTTOM LEFT. Higher magnification of a sector of the lateral surface of an abdominal tergite showing the furrowlike cuticular relief. Sparse, unbranched, socketed hairs are visible. The pores (at 4 and 10 o'clock) are probably orifices through which hairs once projected. (x 775)

BOTTOM MIDDLE. Highly magnified area of abdominal tergite showing both socketed smooth setae and a branched body hair. A pore is visible (arrow). (x 1,400)

BOTTOM RIGHT. Higher magnification of a cuticular pore on an abdominal tergite (arrow in bottom middle micrograph). This orifice has founded lips and no cuticular lid. (x 14,000)

3.37

PLATE 3.37. DRONE ABDOMEN, VENTRAL SURFACE

LEFT. Photomontage in low magnification of a survey view of the ventral surface of the gaster (abdomen). The terminalia are visible (bottom right of the field). The mesomeres and other parts of the male genitalia are recessed behind and beneath the terminal (tenth) abdominal sternite. In specimen preparation, the internal gut contents probably were reduced; such shrinkage would cause the abdominal sclerites to appear compressed and to overlap more than in life. (x 40)

TOP RIGHT. Higher magnification of the abdominal sternal surface showing the scalelike appearance of the epicuticle. Only branched body hairs are found in this area. (x 650)

BOTTOM RIGHT. Close-up of the scalelike cuticular sculpturing on a ventral abdominal sternite. Portions of two branched body hairs are visible. (x 1,400)

3.38

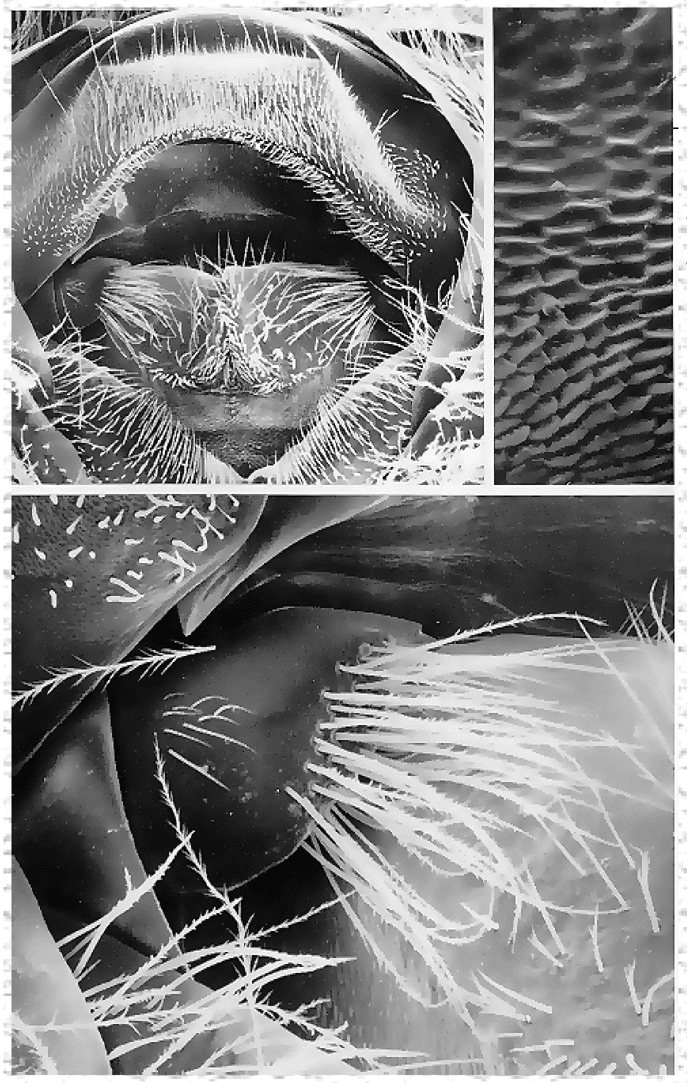


PLATE 3.38. DRONE GENITAL ORIFICE

TOP LEFT. Terminal segments of the abdomen, frontal view. Two (paired) penis valves clasp the phallotreme, in which the penis is barely visible in its inverted position. Lateral to each of the penis valves is a "bewhiskered" paramere. Dorsal and ventral to the penis valves are sectors of intersegmental membrane. Within the dorsal intersegmental membrane (left), just above the left paramere, is the greatly reduced ninth tergite. The sclerotized "roof" for these organs is called the eighth tergite; immediately below the apex of that roof is a black crescent, the anus. Just below the anus is a platelike area called the proctiger. The eighth sternite forms the ventral V-shaped enclosure for these terminalia. (x 40)

TOP RIGHT. Cuticular sculpturing of the intersegmental membrane surrounding the paramere-penis valve complex. (x 484)

BOTTOM. Higher magnification of the left paramere in the top left micrograph showing kinds of setae that arise on the parameral plate and lie over the left penis valve. Nine setae also arise from the lateral portion of the paramere. Immediately above and to the left of the paramere is the very small ninth tergite. The eighth tergite and sternite form the upper and lower diagonal sclerite margins respectively. (x 168)

3.39

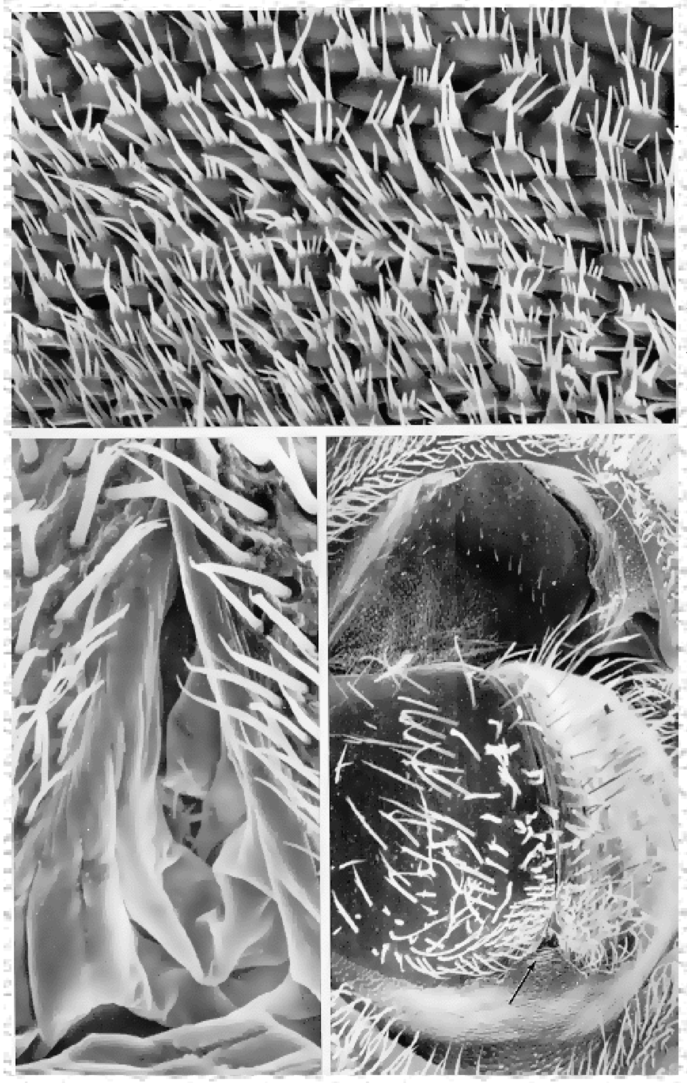


PLATE 3.39. DRONE GENITAL ORIFICE, INTERIOR VIEW

BOTTOM RIGHT. Frontal view of the terminal segments of the abdomen. Because of collapse of the last segments, the proctiger and anus are hidden under the eighth tergite, whose arched posterior margin is visible at the top of the field. The arrow points to the phallotreme, which is further magnified in the bottom left micrograph. (x 75)

BOTTOM LEFT. Phallotreme, the external opening of a deep endophallic pouch (arrow in bottom right micrograph). (x 510)

TOP. Cuticular scales on the dorsal aspect of the last (seventh) tergite. Each scale has four to six spinelike processes in essentially two size classes. (x 1,085)

3.40

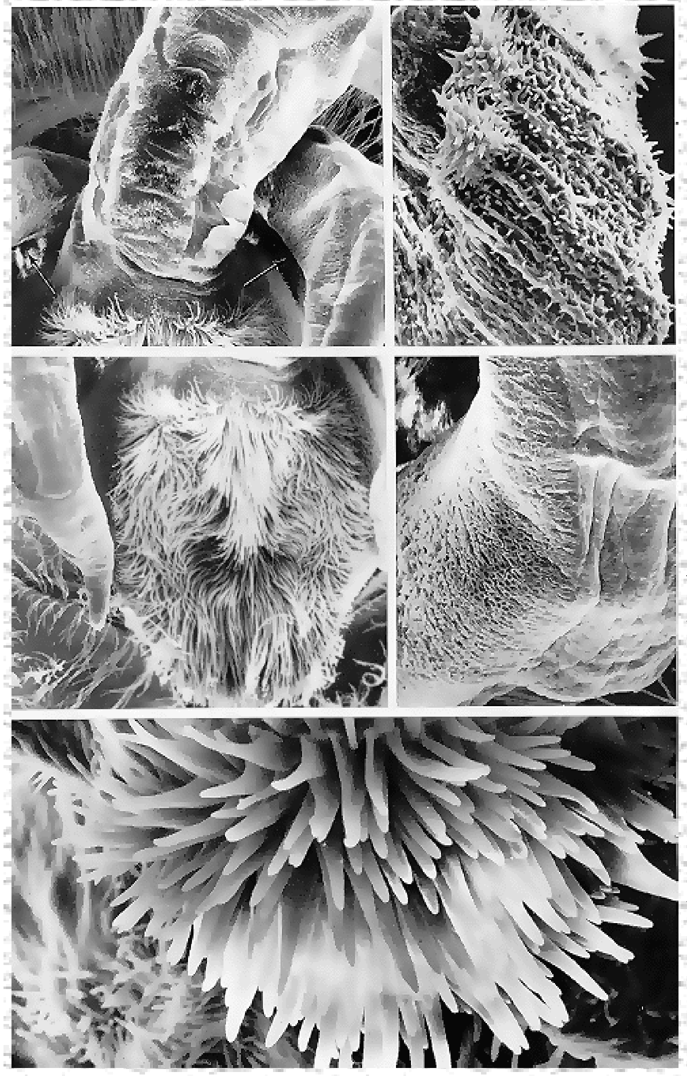


PLATE 3.40. DRONE GENITALIA

TOP LEFT. Vestibulum (bottom of the field). On either side of the vestibulum are the lateral horns or cornuti (arrows). The principal feature is the cervix of the tubelike penis. Chevronlike sclerites cover the ventral wall of the cervix. (x 3 1)

MIDDLE LEFT. Base of the genitalia, located immediately below the field in the top left micrograph. The ventral plate of the vestibulum of the penis is covered with flexuous setae. On both sides of the vestibulum are the cornuti (external genital lobes). (x 31)

BOTTOM. Tufts of spicules on the medial wall of the cervix of the penis. (x 441)

TOP RIGHT. Higher magnification of the wall surface of the male genital duct. (x 300)

MIDDLE RIGHT. Surface of the horn (cornutus). The dorsal and lateral surfaces are papillate while the ventral surface is relatively smooth with longitudinal folds. (x 100)

3.41

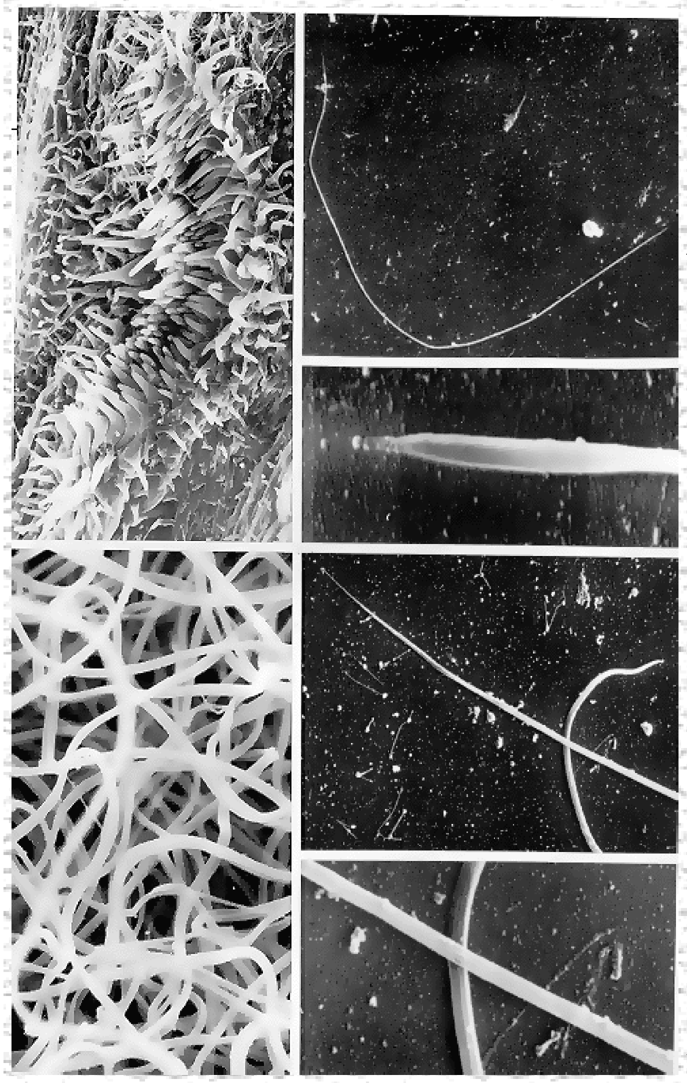


PLATE 3.41. SPERM

TOP LEFT. Floor of the cervix of the penis. Profuse small spines (spicules) line this intima. Several slender sperm are barely visible lying atop the spicules. (x 241)

BOTTOM LEFT. Massed, intertwined spermatozoa. (x 3,900)

TOP RIGHT. One entire sperm. (x 700)

UPPER MIDDLE RIGHT. One sperm head. The small nodules of the head are probably a manifestation of the acrosome. (x 16,000)

LOWER MIDDLE RIGHT. Head (right) and tail (left) of a sperm. (x 3,000)

BOTTOM RIGHT. Higher magnification of the sperm tail. The linear grooves may relate to the interspaces between adjacent peripheral microtubule singlets in the axoneme of the tail. (x 10,000)