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(WITH 33 PLATES)

BY

R. E. SNODGRASS

Bureau of Entomology and Plant Quarantine
U. S. Department of Agriculture



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I. MORPHOLOGY OF THE MALE GENITALIA OF INSECTS

The study of the external genitalia of male insects has reached a stage at which its current theories should be required to pass a thorough physical examination, or be retired on the ground of incompetence. The facts concerning the ontogeny and the adult structure of the male genital organs are now sufficiently known to permit of tentative generalizations on the homology of the major parts from one order of insects to another. The phylogenetic origin and evolution of the organs, however, is still obscure, and none of the theories that have been proposed as to the primitive nature and possible relation of the genital rudiments to preexisting structures is consistent with all the facts that must be considered in an attempt to solve the problem.

The work here presented is a contribution from the Division of Insect Identification, Bureau of Entomology and Plant Quarantine, United States Department of Agriculture, and the writer is indebted for most of the material used and for all the determinations of species to the various specialists in Hymenoptera of the taxonomic staff of the Bureau.

The paired coelomic sacs of primitive arthropods undoubtedly opened by means of coelomoducts discharging through coelomopores on the mesal aspects of the bases of the segmental appendages, as do the embryonic coelomic sacs of Onychophora, and their persisting remnants, the nephridia. Any pair of coelomic sacs and their ducts that became specialized as genital outlets, therefore, opened primarily also on the bases of a corresponding pair of appendages. This primitive condition (fig. 1 A) is retained in many modern arthropods, as in numerous Crustacea and Diplopoda. The particular pair of coelomic sacs that have become genital ducts pertains to different somites in different arthropod groups, and may be different in the two sexes within a group. *Primary paired genital ducts, therefore, are homologous only where they open on homologous somites.* Among the Crustacea and Diplopoda having the genital apertures on the bases of the legs, the male ducts usually open through a pair of small penial processes (fig. 1 A, *Pen*) on the mesal surfaces of the genital coxae. In some species in each of these groups, however, and in Onychophora and Symphyla, the ends of the ducts appear to have migrated mesally from the appendage bases to the venter of the genital segment, where they open through a common median orifice or on a single median penis (B, *Pencn*).

With the insects, evidence from embryogeny and from the adult relation of the vasa deferentia to the nerves of the eleventh abdominal

segment shows that the primary genital ducts of the male must have opened on the *tenth* segment of the abdomen. In early embryonic stages of certain Orthoptera the terminal mesodermal ampullae of the ducts lie within the vestigial appendages of the tenth segment (fig. 1 C, *Appd*). This primary relation of the ducts to the appendages clearly suggests that the mesodermal vasa deferentia of primitive insects opened on the bases of the tenth pair of abdominal limbs, where probably, as in many adult Crustacea and Diplopoda (fig. 1 A), they discharged through small penes located on the mesal surfaces of the coxopodites.

Paired penes giving exit individually to the genital ducts occur among the Hexapoda in Protura, Ephemeroptera, and in certain Dermaptera. The penes of Ephemeroptera appear to belong to the tenth abdominal segment (see Snodgrass, 1936; Qadri, 1940). They may be supposed to be either the stumps of former appendages of this segment that primarily contained the outlets of the ducts, or a pair of true penes that have persisted after the disappearance of the appendages. Inasmuch as in some ephemeropterid species the penes are united in a single median organ containing the outlets of both ducts, the second supposition may be the more plausible, since a median union of the penes takes place in some Crustacea and Diplopoda. The paired genital organs of Dermaptera assume an adult structure quite different from that in Ephemeroptera, but according to Qadri (1940) they have the same origin from a pair of penis lobes of the tenth segment that give exit individually to the paired genital ducts. The paired penes of Protura would appear to have no homology with those of Ephemeroptera and Dermaptera because they pertain to the eleventh abdominal segment.

The single median genital organ of the male usually present in insects other than members of the three groups mentioned above is developed in a manner different from that of the production of a median penis by the union of a pair of primitive penes. This second type of median genital organ, distinguished by the writer as the *phallus*, is formed by the union of a pair of primary genital lobes that at no time in their known history contain the outlets of the genital ducts, and which, therefore, do not have the distinctive feature of a pair of primitive penes. The single outlet duct of the phallus is formed as a median invagination of the body wall *between* the bases of the primary component lobes of the definitive organ. Anatomically the phallus appears usually to be situated between the ninth and tenth abdominal segments, but in most insects its rudiments arise on the

ninth segment, and its adult musculature pertains to this segment. Where the embryonic history of the vasa deferentia has been followed in connection with the development of the phallus, it is observed that the terminal ampullae of the ducts leave their primary points of attachment on the ventral ectoderm of the tenth abdominal segment, or in

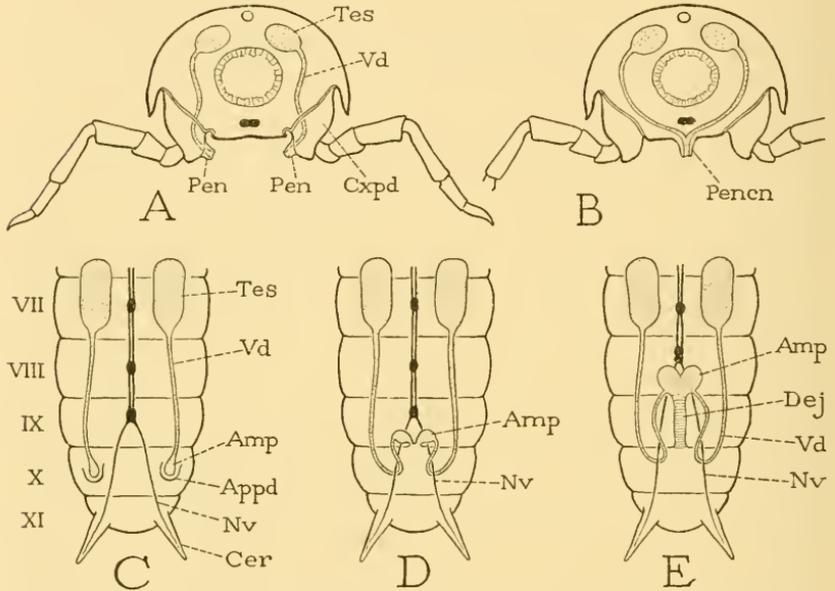


FIG. 1.—Evolution of the male genital ducts and outlets, diagrammatic.

A, theoretical primitive position of arthropod genital apertures on mesal surfaces of coxopodites of a pair of segmental appendages, the male ducts opening through a pair of penes (*Pen*); the actual condition in many Crustacea and Diplopoda. B, derived condition in which the male ducts discharge through a single median penis. C, early embryonic condition in certain Orthoptera in which the ampullae of vasa deferentia lie within appendage rudiments of tenth abdominal segment. D, later embryonic stage in which ampullae have migrated mesally and forward beneath nerves of cerci (*Nv*) to base of tenth segment. E, adult condition, with ampullae united on anterior end of median ectodermal ductus ejaculatorius (*Dej*), and vasa deferentia looped beneath cercal nerves.

Amp, terminal ampulla of vas deferens; *Appd*, vestigial appendage of tenth abdominal segment; *Cer*, cercus; *Cxp*, coxopodite; *Dej*, ductus ejaculatorius; *Nv*, cercal nerve of eleventh abdominal segment; *Pen*, penis; *Penen*, median penis, probably formed by conjunction of a pair of lateral penes; *Tes*, testis; *Vd*, vas deferens; *VII-XI*, seventh to eleventh abdominal segments.

the appendage rudiments of this segment, and migrate mesally and forward to the base of the tenth segment or into the posterior part of the ninth (fig. 1 D). Here a median ectodermal ingrowth is formed that unites with the ampullae and becomes the definitive ductus ejaculatorius (E, *Dej*). The vasa deferentia, through having their pos-

terior ends carried mesally and forward, come to be looped ventrally around the cercal nerves (*Nv*) of the eleventh abdominal segment. This phase of embryonic development may be interpreted literally as phylogenetic recapitulation.

The phallic rudiments usually first appear in nymphal or larval stages as a pair of minute papillae formed as outgrowths of the body wall immediately laterad of the site where the ductus ejaculatorius will be formed by invagination between their bases (fig. 2 A, *Phm*). In orthopteroid insects the exact segmental relation of the primary phallic lobes is difficult to determine; the lobes originate behind the sternum or "coxal plates" of the ninth abdominal segment, but the inflected poststernal membrane usually belongs to the segment preceding it. Qadri (1940) says the genitalia rudiments of Orthoptera probably represent appendicular outgrowths of the tenth segment, and he asserts that the ductus ejaculatorius belongs to this segment. In Homoptera it is generally stated (Pruthi, 1924a; George, 1928; Metcalfe, 1932a) that the phallic rudiments pertain to the ninth abdominal segment. In holometabolous larvae the genital papillae unquestionably first appear on the posterior part of the venter of the ninth segment, where usually they become sunken in a "peripodal" pocket of the epidermis beneath the cuticle.

The primitive nature of the primary phallic lobes has been the subject of much discussion and of various theories. Two opinions are current: one, that the lobes are merely outgrowths of the integument at the sides of the gonopore developed specifically to subserve the intromittent function; the other, that they are derivatives of segmental appendages secondarily adapted to the functions they assume. At the ontogenetic stage when the ampullae of the vasa deferentia lie between the bases of the phallic lobes, where presumably at some corresponding early phylogenetic stage they opened to the exterior (fig. 2 A), the relation of the associated structures suggests a pair of primary genital ducts opening at the bases of a pair of segmental appendages (fig. 1 A). It has been claimed, in fact, by Else (1934) that the phallic lobes of the grasshopper *Melanoplus* are the appendage rudiments of the tenth abdominal somite, which in the embryo follow the genital ducts in their migration to the base of the tenth segment, where they unite and develop into the phallic organ of the adult. According to Roonwal (1937) the phallic rudiments are formed in *Locusta* by the union of the ninth and tenth abdominal appendages.

The concept that the phallic lobes are the appendages of the tenth abdominal segment encounters no difficulty in apterygote or exopterygote insects, in which the tenth segment otherwise is without

appendages; but it cannot be carried over to holometabolous insects, since in many of these there are on the tenth abdominal segment of the larva well-developed appendages that take no part in the formation of the genital organ, the rudiments of which are present at the same time in the same species as a pair of small disks on the venter of the ninth segment (fig. 3 A). There is no evidence, either embryological or anatomical, that the numerical tenth abdominal segment of these insects is not the true tenth somite, though the terminal appendage-bearing segment of holometabolous larvae might logically seem to be the homolog of the cercus-bearing eleventh somite of more generalized insects.

On the other hand, it is also impossible to see in postembryonic stages of insects any relation of the phallic rudiments to the appendages of the ninth abdominal segment, since the latter form the "coxal plates" of the definitive ninth sternum. These plates are shown by Sharif (1937) in the larva of the rat flea (fig. 2 H, *cxpl*) to be developed entirely independent of the phallic lobes, which are sunken in a pocket of the venter of the ninth segment. In *Lepisma*, according to Lindsay (1940), the genital rudiments of the male that eventually form the penis appear first in the eighth instar as two small lobes on the intersegmental membrane at the base of the cleft in the ninth sternum. The cleft "ninth sternum" of *Thysanura*, however, becomes the completely separated stylus-bearing "coxal plates" of the ninth segment, which have no direct connection with the definitive genital organ. Also in *Machilis* it is shown by Qadri (1940) that the primary phallic lobes develop independently of the ninth-segment appendages.

The embryonic abdominal appendages of insects can represent at most only the bases of former limbs, since it is to be presumed that the abdominal telopodites were all lost before the phallus was evolved. There remain of the abdominal limbs, therefore, only the bases and their appurtenances, such as styli, eversible vesicles, and gonapophyses. The phallic lobes are not styli or gonapophyses, since in some species of the thysanuran *Machilis* both these structures are present on the genital segment in addition to the phallic organ, nor can they be eversible vesicles because they are never borne on the plates representing the limb bases. It is true that the phallic rudiments in early stages of development much resemble the parts of the ovipositor developed on the ninth abdominal segment of the female, but the rudiments of the ovipositor clearly are derivatives of abdominal limbs, as is evident in *Thysanura* and in nymphal Blattidae in which the ninth-segment elements of the ovipositor bear a pair of styli. In conclusion,

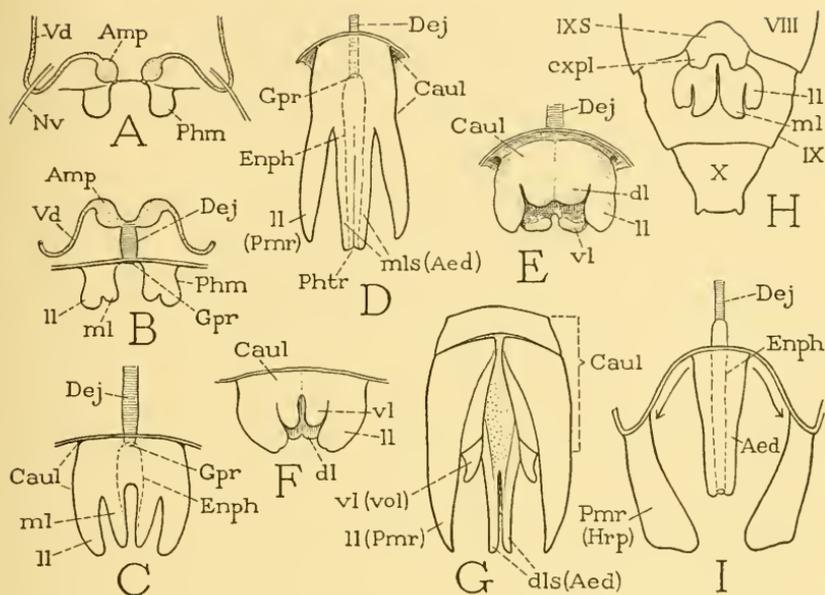


FIG. 2.—Development of the phallus, diagrammatic.

A, primary phallic lobes, or phallomeres (*Phm*), with ampullae of vasa deferentia at their bases, where presumably they opened at a corresponding phylogenetic stage. B, ductus ejaculatorius (*Dej*) formed by ingrowth of body wall between bases of phallic rudiments, the latter divided distally into secondary lateral and median lobes (*ll*, *ml*). C, later stage of phallic development: distal lobes elongated, bases of primary lobes united to form a common phallobase, or caulis (*Caul*), enclosing an endophallic chamber (*Enph*), into which opens the ductus ejaculatorius. D, coleopterous type of mature phallus with common base supporting a pair of free lateral lobes (parameres, *Pmr*) and united median lobes forming an aedeagus (*Aed*) on which the endophallus opens through a phallostreme (*Phtr*). E, orthopterous type of phallus with a common base and three pairs of secondary terminal lobes (dorsal, lateral, and ventral). F, hymenopterous type of phallus in pupal stage, resembling the orthopterous type (E) in having three pairs of terminal lobes. G, mature hymenopterous phallus with common base (*Caul*) bearing free lateral parameral lobes (*Pmr*), free ventral volsellar lobes (*vol*), and united dorsal aedeagal lobes (*Aed*). H, terminal abdominal segments of male prepupa of a flea (simplified from Shariif, 1937), showing four-lobed phallus of ninth segment, and independent coxal plates (*cxpl*) of ninth sternum. I, phallic structure of most Rhynchota and holometabolous insects, in which the movable claspers (harpagones, *Hrp*) appear to be the parameres entirely separated from the aedeagus.

Aed, aedeagus; *Amp*, ampulla of vas deferens; *Caul*, phallobase, or caulis; *cxpl*, coxal plates of ninth abdominal sternum (*IXS*); *Dej*, ductus ejaculatorius; *dl*, dorsal lobe of immature phallus; *dls*, united dorsal lobes of mature phallus; *Enph*, endophallus; *Gpr*, gonopore; *Hrp*, harpago; *ll*, lateral lobe of immature phallus; *ml*, median lobe of immature phallus; *mls*, united median lobes of mature phallus; *Nv*, cercal nerve of eleventh segment; *Phm*, phallomere, or primary phallic lobe; *Phtr*, phallostreme; *Pmr*, paramere; *Vd*, vas deferens; *vl*, ventral lobe of immature phallus; *vol*, volsellar lobe of mature phallus.

therefore, concerning the origin of the insect phallus, we can say only that the facts at present known about the development of the organ are not sufficient to warrant any definite statement, but that they appear to favor the view that the phallus is an independent genital structure. The male genital organ of insects has no homolog with a genital function in any other arthropod group.

The ontogenetic origin of the phallus from a single pair of primary phallic lobes has been observed in nearly all the larger orders of insects from Thysanura to Hymenoptera, with the exception of Mecoptera and Diptera. In the Blattidae and Mantidae the lobes develop individually into variously modified genital structures. In most of the other orders each primary lobe, or *phallomere* (fig. 2 A, *Phm*), first branches distally into two or three secondary lobes (B), and then the undivided proximal parts unite (C) to form a common basal stalk, the *phallobase*, or *caulis* (*Caul*). When, as in the majority of insects, each primary lobe forms only two secondary lobes (B), the immature phallus (C) has a pair of lateral distal lobes (*ll*) and a pair of median lobes (*ml*); if each primary lobe gives rise to three secondary lobes, the composite organ (E, F) bears distally a pair of lateral lobes (*ll*), a pair of dorsal lobes (*dl*) corresponding with the median lobes in the first case, and a pair of ventral lobes (*vl*). In Rhynchota and all holometabolous insects in which the phallic development is known, the median lobes (C, *ml*), or the corresponding dorsal lobes in six-lobed forms (F, *dl*) unite and produce a single median structure, which is the *aedeagus* of the adult (D, G, I, *Aed*). The lateral lobes of Homoptera, Coleoptera, and Hymenoptera become the *parameres* (*Pmr*). The ventral lobes, present in Orthoptera (E, *vl*) and Hymenoptera (F), are transformed in Hymenoptera into the movable volsellar lobes of the mature phallus (G, *vol*). The six-lobed type of phallic structure appears to be fundamental in Orthoptera, as it is in Hymenoptera, but in the Orthoptera (E) there is little uniformity in the development of the lobes, and only in Acrididae do the lobes of the dorsal pair unite partially to form an aedeagus (see Snodgrass, 1937).

The basal union of the primary phallic lobes takes place dorsally and ventrally, thus leaving within the caulis an open space, the walls of which constitute an inner phallic sac, or *endophallus* (fig. 2 C, *Enph*), into which the ductus ejaculatorius (*Dej*) discharges proximally through the original gonopore (B, C, *Gpr*). In most Orthoptera the endophallus remains widely open distally between the terminal phallic lobes (E); but in insects in which the median or dorsal lobes

unite to form an aedeagus, the endophallus is extended into the latter (D, *Enph*), and its distal aperture, the *phallostreme* (*Phtr*), is carried out upon the aedeagus, which becomes specifically the intromittent element of the phallus.

The mature external male genital apparatus of Rhynchota and the holometabolous orders presents two types of structure. In Coleoptera and Hymenoptera, as shown by Pruthi (1924), Metcalfe (1932), and Zander (1900), the primary phallic lobes are not completely divided into secondary parameral and aedeagal lobes (fig. 2 C, F), so that the adult phallus in these orders (D, G) is a compact organ with a common basal stalk, the *caulis*, supporting the aedeagus and the parameres. On the other hand, in Rhynchota, according to Pruthi (1924a, 1925), George (1928), Metcalfe (1932a), and Rawat (1939, 1939a), and in Trichoptera and Lepidoptera, according to Zander (1901, 1903), the parameral lobes are entirely split off from the aedeagus, and are transposed laterally to the annulus of the ninth abdominal segment (fig. 2 I), where they are said to become the variously developed, independently muscled, appendicular genital organs commonly known as the *claspers*, *valvae*, *harpes*, or *harpagones*.

The evidence of phallic derivation of the claspers appears to be conclusive in Homoptera, and in this group the claspers (parameres) are associated with the base of the aedeagus. On the other hand, in most Heteroptera, Mecoptera, most Trichoptera, Lepidoptera, and Diptera they are independently articulated on the lateral walls or the "coxal plates" of the ninth abdominal segment. It is claimed by Mehta (1933), in opposition to Zander (1901), that the "valvae" (harpes) of Lepidoptera arise independently from the lobes that form the aedeagus, and are therefore not phallic structures. The observed fact, of course, may be interpreted as an ontogenetic elision. However, it should be noted that Zander's (1903) contention that the "valvae" of Trichoptera are offsets from the primary phallic lobes is based on studies of limnophilid species alone, particularly *Limnophilus bipunctata*, and according to Zander's own statement the "valvae" of the Limnophilidae have an entirely different structure from the movable muscled claspers of other Trichoptera, since they are immovable lobes of the lateral walls of the "penis pouch" and are devoid of muscles. It must be admitted, therefore, that we still have no conclusive evidence as to the nature of the movable muscled claspers borne on the lateral walls or on the "coxal plates" of the ninth abdominal segment, such as occur in Heteroptera, Mecoptera, Trichoptera other than Limnophilidae, Lepidoptera, and Diptera. These

organs have been regarded by some students of comparative anatomy as representing the ninth-segment styli of Ephemeroptera and Orthoptera (see Snodgrass, 1935a).

II. THE TERMINAL BODY SEGMENTS AND THE PHALLUS OF HYMENOPTERA

The abdomen of Hymenoptera contains at least 10 segments, here designated segments *I* to *X* regardless of whether the first segment is retained in the abdominal region (Chalastogastra), or becomes an integral part of the definitive thorax (Clistogastra).

THE TERMINAL BODY SEGMENTS

Ten abdominal segments are distinct and well developed in most hymenopterous larvae (figs. 3 A, 4 A), the last segment bearing the anus (*An*) and, in Chalastogastra, the last pair of abdominal larval legs, or pygopods (fig. 3 A, D, *Pgp*). It is reasonable to assume, however, that the numerical tenth segment may include somites *X* and *XI*. The larva gives little positive evidence as to the composition of this segment, though the latter is without doubt mostly somite *X*. In chalastogastrous larvae (fig. 3 D) it contains the muscles of the pygopods, the last segmental set of ventral longitudinal muscles, and the dilator muscles of the narrow exit channel of the rectum, while on its base are attached the evacuator muscles of the rectal sac. The posterior surface of the terminal segment is deeply cleft transversely by the wide anal aperture (*An*) between a rounded supra-anal lobe (*a*) and a similar subanal lobe (*b*).

With the transformation of the larva to the pupa (fig. 3 B) the upper part of the ninth abdominal segment is greatly shortened, though the tergum (*IXT*) is expanded laterally in the female, and the terminal segment is much reduced in size. The anal lobes (*a*, *b*), however, are still prominent and enclose between them the transverse anal cleft (*An*); but proximal to the anal lobes there is differentiated a narrow area (*c*) within which will be formed the tergites of the tenth segment of the adult (*C*, *XT*), and at the lower ends of this area in the pupa (*B*) at the base of the subanal lobe there is on each side a small but distinct lobe (*d*). The larval legs of the tenth segment, on the other hand, have completely disappeared, unless they are represented by the small lobes (*d*) just noted.

By removing the loosened cuticula in a late pupal stage the immature imaginal structure is revealed (fig. 3 C). The ninth tergum (*IXT*) has the same shape as in the pupa. Immediately behind its

narrow dorsal part are the small lateral tergites of the tenth segment (*XT*) formed in the region of the pupa (*B, c*) differentiated proximal to the bases of the persisting anal lobes. Each tergal plate of the imaginal tenth segment bears ventrally on its posterior margin a minute pygostyle (*C, Pgs*), which normally lies exactly within the small lobe of the pupal skin (*B, d*) at the base of the subanal lobe,

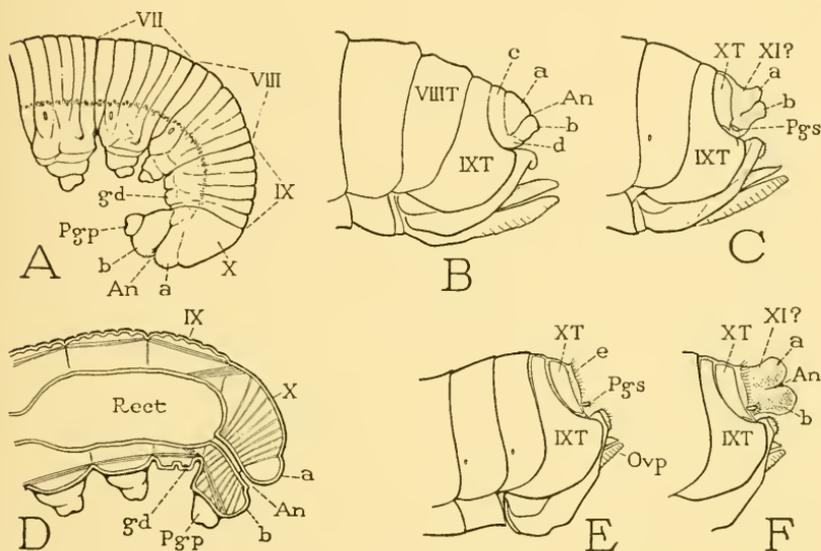


FIG. 3.—Postembryonic transformations of the terminal abdominal segments of a female sawfly, *Gilpinia polytoma* (Htg.).

A, posterior segments of mature larva. B, same segments of pupa. C, corresponding segments of immature imago within pupal cuticle. D, diagrammatic section of posterior larval segments. E, end of abdomen of mature imago, usual condition. F, terminal segments with "anal vesicle" (apparent eleventh segment) everted.

a, supra-anal lobe; *An*, anus; *b*, subanal lobe; *c*, dorsum of tenth segment; *d*, pupal lobe of tenth segment covering imaginal pygostyle; *e*, posterior marginal membrane of tenth tergum; *gd*, genital disk of ninth segment; *Ovp*, ovipositor; *PgpP*, pygopod; *Pgs*, pygostyle; *Rect*, rectum; *VII-XI*, seventh to eleventh abdominal segments.

and is therefore evidently represented by this lobe (*d*) in the pupa. The anal lobes now appear to belong to a distinct region lying posterior to that of the tenth tergal plates (*C*). In the fully matured imago (*E*) the anal lobes are ordinarily not in evidence; the dorsum of the abdomen ends with a short membranous fold (*e*) fringed with hairs bordering the tenth tergal sclerites, beneath which is a vertical membranous area containing a transverse exit aperture of the alimentary tract. However, an occasional specimen may be found in

which there has been everted from this opening a large vesicle on which the rectum opens through a transverse cleft between bulging dorsal and ventral lobes (F). This everted structure is the region of the anal lobes of the immature imago and the pupa, which ordinarily in the adult is concealed by invagination. The functional anal opening of the adult, therefore, is the aperture of the invagination cavity formed by the retraction of the anal lobes, but the true anus is the opening of the rectum into the anterior end of this cavity. In the male of the ichneumonid *Megarhyssa lunator* the everted anal vesicle is seen to bear a pair of small setigerous appendages similar to the pygostyles of the tenth segment (pl. 4 O, P, *Cer?*).

A consideration of the facts above described leads to the conclusion that the pygostyles of adult Hymenoptera belong to the tenth abdominal segment, and that they are possibly derived from the pygopods (tenth-segment appendages) of the larva. It is suggested, moreover, that the eversible anal vesicle of the adult (fig. 3 F), or the region of the external anal lobes of the pupa (B) and the larva (A), represents the eleventh abdominal segment combined with the tenth. The setigerous appendages of the anal vesicle in the male of *Megarhyssa lunator* (pl. 4 O, P, *Cer?*), therefore, might be regarded as true cerci of the eleventh segment. Though these appendages have not been observed in any other hymenopterous species, and are not present in the female of *Megarhyssa*, the rectum of all adult Hymenoptera opens into a terminal invagination chamber, within which the lips of the anus may form a pair of distinct anal lobes.

THE PHALLUS AND PHALLIC NOMENCLATURE

The male genital organ of Hymenoptera is usually of relatively large size, and can be easily extracted from the genital chamber at the end of the body, either in a fresh insect or in a dry specimen after relaxing or boiling in water. The general structure of the phallus is remarkably consistent throughout the order, and in a comparative study little difficulty is encountered in identifying corresponding parts. Special types of modification, however, are in many cases characteristic of superfamily groups, and details of structure undoubtedly will be found to be diagnostic of species among the Hymenoptera as in most other insect orders.

The development of the hymenopterous phallus from a pair of primary phallic rudiments on the posterior part of the venter of the ninth abdominal segment in the larva has been described by Seurat (1899) in the braconid *Dorcycles*, by Michaëlis (1900) in *Apis*, by

Zander (1900) in *Vespa*, *Bombus*, and *Apis*, and by Boulangé (1924) in *Sirex*.

The first rudiments of the male genital organ of *Vespa maculata* appear in a late larval stage, probably the last larval instar, as a pair of slight thickenings in a small oval disk of the integument near the posterior margin of the venter of the ninth abdominal segment (fig. 4 A, B, C, *gd*). By removing the cuticula containing the genital disk

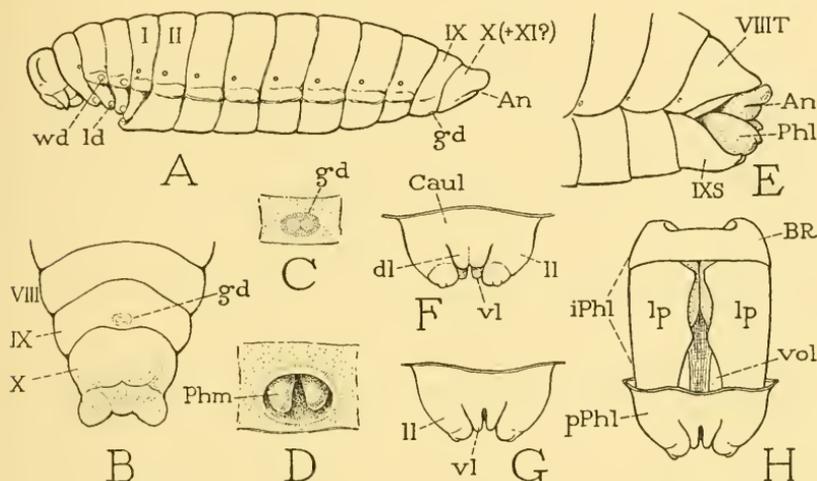


FIG. 4.—Postembryonic development of the phallus of *Vespa maculata* (L.).

A, mature larva. B, posterior end of same, ventral view, showing genital disk on ninth segment. C, piece of cuticula from same containing genital disk. D, body wall beneath genital disk, exposed by removal of cuticula, showing pocket containing the phallic rudiments (*Phm.*). E, end of abdomen of pupa, showing large external phallus (*Phl*). F, pupal phallus, dorsal. G, same, ventral. H, phallus of immature imago (*iPhl*) exposed by removal of pupal cuticula, with terminal lobes still in corresponding parts of pupal phallus (*pPhl*).

An, anus; *BR*, basal ring; *Caul*, phallobase, or caulis; *dl*, dorsal lobe of immature phallus; *gd*, genital disk; *iPhl*, imaginal phallus; *ld*, leg disk; *ll*, lateral lobe of immature phallus; *lp*, parameral plate; *Phl*, phallus; *Phm*, primary phallic lobe, phallomere; *pPhl*, pupal phallus; *vl*, ventral lobe of immature phallus; *vol*, volsellar lobe of mature phallus; *wd*, wing disk.

(C), there is exposed beneath the latter an oval pit of the epidermis with a pair of minute papillae emerging from its inner wall (D). The papillae are the primary phallic lobes, or phallomeres (*Phm*), sunken into a "peripodal" pocket of the epidermis. The early development of the phallic lobes of *Vespa germanica* is described by Zander (1900) as follows: Each rudiment becomes first divided distally by a vertical cleft, and thus differentiated into a basal part and two secondary terminal lobes, one lobe being lateral and the other mesal, but soon there is found a third dorsomesal lobe, giving the appendage

finally a tripartite structure. Before pupation the undivided proximal parts of the two appendages coalesce, and the dorsomesal lobes unite in a thick median structure. The newly formed phallus, thus derived from two entirely separate rudiments, now consists of a thick basal stalk, of a pair of lateral parameral lobes ("valvae externae"), a median aedeagal lobe, and a pair of mesoventral volsellar lobes ("valvae internae"). Meanwhile, the mouth of the "peripodal" cavity has enlarged, and, with the pupal ecdysis, the phallus is extruded and assumes an external position on the body of the pupa.

The pupal phallus of *Vespa maculata* appears as a large organ partially exposed at the end of the body projecting between the proctiger above and the ninth sternum below (fig. 4 E, *Phl*). It consists of a broad base (*F*, *Caul*), a pair of thick lateral lobes (*ll*), a short median dorsal lobe (*dl*) still showing evidence of its dual composition, and a pair of slender ventral lobes (*vl*). The form and size of the pupal phallus are retained without change in the pupal cuticula throughout the life of the pupa, but at an early stage of the imaginal development within the pupal skin the imaginal phallus increases greatly in size and soon takes on its final form. In an old pupa the imaginal organ (*H*, *iPhl*) has extended far forward from the base of the pupal organ (*pPhl*), so that only its terminal lobes lie within the latter, but the relationships show clearly that the lateral lobes of the pupal phallus become the parameres of the adult, the composite median dorsal lobe the aedeagus, and the ventral lobes the volsellar lobes. From the base of the imaginal organ there is set off a distinct basal ring (*BR*), which is said by Zander to be differentiated from the proximal part of the pupal phallus by a secondary growth of the epidermis in this region.

The development of the phallus in *Sirex* and in *Bombus*, as described respectively by Boulangé (1924) and by Zander (1900), differs in no essential respect from that of *Vespa*, except for such differences as exist in the adult structure of the organ in these species. The volsellae are greatly reduced in *Bombus*; and in most of the Apoidea, including *Bombus*, the aedeagus takes on a tripartite form, as will be shown later.

The mature hymenopterous phallus is typically a strongly sclerotized, elongate structure (fig. 5 A, B) having a cylindrical base, the *caulis* (*Caul*), from which arise distally the median *aedeagus* (*Aed*) and the lateral *parameres* (*Pnr*). Between the bases of the parameres and the aedeagus there is usually on each side one or two pairs of volsellar lobes (*B*, *cus*, *dig*), collectively the *copulatory ossicles* of

Crampton (1919). In the base of the caulis is an annular sclerite, the *basal ring* (*BR*), by which the phallus is attached to the wall of the genital chamber. The parameres are usually continuous from a pair of lateral *parameral* plates of the caulis (*lp*), though in many species they are movably articulated on the latter. The volsellar lobes are supported on a pair of ventral *volsellar plates* (*B, lv*), which either lie horizontally adjoining the ventral edges of the parameral plates (*C, lv*), or are inflected dorsally on the latter in a deep concavity on the ventral side of the caulis (*D*). The aedeagus contains a pair of lateral *aedeagal sclerites*, or *penis valves* (*A, B, pv*), which are extended proximally into the lumen of the caulis as a pair of *aedeagal apodemes* (*G, apa*). The phallotreme is either ventral or terminal on the aedeagus (*B, G, H, I, Phtr*). The terms "dorsal" and "ventral" as used above must be understood to be reversed in their application to Tenthredinoidea and certain species of Xyelidae, in which the entire phallus is normally inverted.

The phallic nomenclature adopted in this paper is partly taken from other sources, but a number of new terms are introduced in order to give designations better adapted to specific description. The history of the genital nomenclature in Hymenoptera has been so fully reviewed by Boulangé (1924) and by Beck (1933) that it need not be repeated here. The principal synonymy of the terms used in this paper, however, is given in the following general descriptions of the parts of the phallic organ.

THE PHALLOBASE, OR CAULIS (*Caul*).—The caulis is the basal stalk of the phallus bearing the free terminal lobes (fig. 5 A, B). On its base are inserted the muscles that move the phallus as a whole, and its lumen contains the intrinsic phallic muscles, including muscles of the aedeagus, of the volsellae, and of the parameres when the last have muscles. The caulis is often regarded as consisting of two segments, the basal ring, or "gonocardo," and a distal segment, or "gonostipites" (cupule and spathe of Audouin, 1821), but its five sclerites, namely, the basal ring (*BR*), the two parameral plates (*lp*), and the two volsellar plates (*B, lv*), constitute the anatomical units most useful for descriptive purposes. The dorsal surface of the caulis (*A*) between the parameral plates is usually membranous and continuous with the dorsal wall of the aedeagus. The ventral surface (*B*) likewise is generally membranous between the volsellar plates and continuous with the ventral wall of the aedeagus, but it is flat or concave according as the volsellar plates are horizontal (*C*) or inflected upward against the mesal surfaces of the parameral plates

(D, E). The caulis is variable in length and sometimes it is greatly reduced by a proximal extension of the clefts between the aedeagus and the parameres. Its lateral parts may be produced at the sides of the aedeagus into basiparameral lobes bearing the parameres. The caulis and the parameres together are analogous to the "tegmen" of the coleopterous phallus as defined by Sharp and Muir (1912).

THE BASAL RING, OR LAMINA ANNULARIS (*BR*).—*Cupule* Audouin (1821); *pièce basilaire* Dufour (1841); *cardo* Thomson (1872), Schmiedeknecht (1882-'84), Zander (1900); *lamina annularis* Verhoeff (1893a); *plaque basilaire* Seurat (1899); *gonocardo* Crampton (1919), Peck (1937); *sclérite accessoire*, or *cardo* Boulangé (1924); *basal ring* Beck (1933), Snodgrass (1935).

The basal ring is typically an annular sclerite in the base of the caulis surrounding the foramen by which the lumen of the phallus communicates with the general body cavity. The foramen may be directed anteriorly, anterodorsally, or anteroventrally, and sometimes it lies almost in the dorsal or ventral plane of the phallus. The basal ring is correspondingly of greater width above or below, and it may be incomplete; sometimes it is reduced to a narrow band, but only rarely is it completely suppressed. The ventral anterior margin of the ring often bears a small median process or knob, the *gonocondyle* of Crampton (1919), on which muscles are attached (fig. 6 A, *gc*). According to Zander (1900) the basal ring of *Vespa germanica* is differentiated relatively late in development as a thickening of the epidermis at the base of the phallus. As contended by Verhoeff (1893a) the annular sclerite is evidently a special feature of the hymenopterous phallus, and has no homolog in other insects.

The extrinsic phallic muscles all arise on the sternal plate of the ninth abdominal segment and are inserted on the basal ring of the phallus. Boulangé (1924) has shown that there are generally present three pairs of these muscles (fig. 6 A, 1, 2, 3), two of which insert on the gonocondyle, and one on the ventrolateral margins of the basal ring. In species in which the phallus permanently assumes an inverted position these muscles are twisted upon one another to the right or the left according to the direction of the phallic revolution.

THE LAMINAE PARAMERALES, OR BASIPARAMERES (*lp*).—Basal parts of *forceps* Dufour (1841); *stipites* Thomson (1872), Zander (1900); *gonostipites* Crampton (1919), Peck (1937); *pièces principales* or *stipites* Boulangé (1924); *coxopodites* Beck (1933).

The parameral plates (fig. 5 A, B, *lp*) are usually regarded as the basal parts of the parameres (*Pmr*), since they are generally con-

tinuous with the outer walls of the latter. It should not be overlooked, however, that anatomically these plates are sclerotizations of the walls of the caulis, and that their continuity with the parameres is incidental to the fact that the parameres are outgrowths of the caulis.

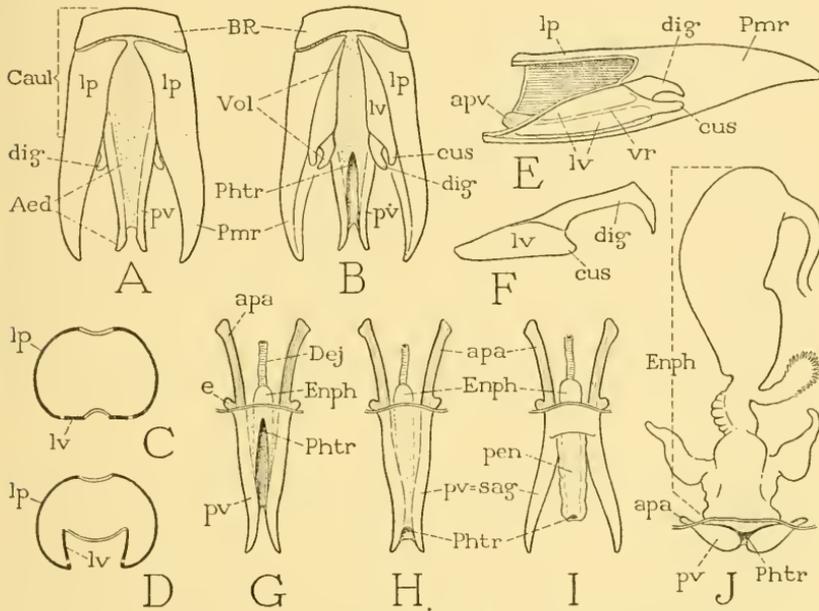


FIG. 5.—Structure of the hymenopterous phallus, diagrammatic.

A, B, typical form and structure of the ectophallus in dorsal and ventral view. C, transverse section of caulis with horizontal volsellar plates (B, *lv*). D, section of caulis with volsellar plates inflected dorsally on lower edges of parameral plates (E). E, mesal view of right parameral plate (*lp*) and paramere, with volsellar plate (*lv*) inflected dorsally on lower edge of parameral plate. F, volsella with reduced cuspis and large digitus. G, usual structure of the aedeagus, ventral view, with phallotreme at base of ventral channel. H, same, with subapical phallotreme. I, phallic structure characteristic of most bees, in which the penis valves (*pv*), known as sagittae (*sag*), are separated from a median penis (*pen*) bearing the phallotreme. J, phallus of the honey bees (*Apis*), in which the ectophallus is reduced and the endophallus (*Enph*) greatly enlarged.

Aed, aedeagus; *apa*, aedeagal apodeme; *apv*, basal apodeme of volsella; *BR*, basal ring of caulis; *Caul*, phallobase, or caulis; *cus*, cuspis of volsella; *Dej*, ductus ejaculatorius; *dig*, digitus of volsella; *e*, basal process of aedeagal apodeme; *Enph*, endophallus; *lp*, lamina parameralis of caulis; *lv*, lamina volsellaris of caulis; *pen*, median lobe, or penis, of aedeagus of bees; *Phtr*, phallotreme; *Pmr*, paramere; *pv*, lamina aedeagalalis, or penis valve; *sag*, sagitta, lateral process of aedeagus of bees (free penis valve); *Vol*, volsella.

Moreover, in most of the Chalastogastra and many of the Clistogastra the parameres are demarked from the parameral plates of the caulis by distinct lines of flexibility or articulation. Dorsally (A) the parameral plates are usually separated from each other by a median

membranous area of the caulis wall, though often the basal angles are united by a sclerotic bridge, and sometimes the entire dorsal margins are contiguous, or even confluent. Ventrally (B) the parameral plates are either closely connected by membrane with the volsellar plates or are directly united with them. In various unrelated chalastogastrous and clistogastrous species the posteromesal areas of the dorsal parts of the parameral plates are produced into lobes (fig. 6 A, *pa*) termed *parapenes* by Crampton (1919). In strophandrious forms the parapenial lobes are secondarily on the under side of the phallus.

Four pairs of intrinsic phallic muscles extend between the basal ring and the parameral plates, which are shown by Boulangé (1924) to be of general occurrence in the Hymenoptera. The muscles of one pair arise on the gonocondyle or median ventral part of the basal ring (fig. 6 A, 4) and are inserted ventrally on the bases of the parameral plates; those of a second pair (5) arise laterally on the basal ring and are inserted mesally on the ventral ends of the parameral plates; those of the third and fourth pairs (6, 7) cross each other on each side, going from the dorsal wall of the basal ring to the dorsal basal margins of the parameral plates.

THE PARAMERES (*Pmr.*).—*Harpides* Audouin (1821); *cochlearia* Hartig (1837); *forceps*, *truelles*, or *spatules* Dufour (1841); *squamac* Thomson (1872), Schmiedeknecht (1882-'84); *valvae externae* Zander (1900); *styli* Beck (1933); *harpcs* Crampton (1919); *palettes* Boulangé (1924); *parameres* Verhoeff (1893), Snodgrass (1935); *gonosquamac* Peck (1937).

The parameres of Hymenoptera, as in other insects, are the lateral branches of the primary phallic lobes. In the adult, therefore, they are hollow extensions of the distal lateral angles of the caulis (fig. 5 A, B, *Pmr.*). Because the sclerotization of their outer surfaces is usually continuous with the parameral plates of the caulis, the parameres generally appear to be merely prolongations of the parameral plates, and when they are not anatomically separated from the latter the division between plate and paramere must be taken to be the base of the free lobe that constitutes the paramere. In many families throughout the Hymenoptera, however, the parameres are specifically demarcated from the parameral plates by lines of flexibility or by true articular sutures, so that the parameres become flexible or freely movable appendages of the supporting plates. In such cases the joint is not always at the base of what might otherwise be called the paramere, but may be at some point distal to the latter, with the result that the caulis is produced into a pair of lateral basiparameral lobes

bearing the movable parameres (pl. 1 A, R; pl. 29 P). The articulation of the parameres on the parameral plates is a feature particularly characteristic of the chalastogastrous families other than Orussidae and Cephioidea (pl. 1 A, H, R; pl. 2 C, M; pl. 3 H, J), and is here accompanied by the presence of a pair of specific parameral muscles, a flexor and an extensor, arising on the parameral plates (pl. 2 E, 15, 16). The parameres, however, are flexible or articulated also in various clistogastrous forms, as in some Formicoidea (pl. 11 F, M; pl. 12 E), Chrysidoidea (pl. 13 M, R), Bethyloidea (pl. 15 E), Sphecoidea (pl. 20 Q), and particularly in Apoidea (pl. 26 Q, S; pl. 27 C, H, M, T; pl. 28 J, K; pl. 30 A, B), but in these groups the writer has only rarely found specific parameral muscles (pl. 15 O, pl. 28 B), though in some cases a muscle of the aedeagus or of the volsella may encroach on the base of the paramere or arise even within the paramere. In form and relative size the parameres are highly variable, being spatulate, forcipate, branched, hooked, broad or slender, sometimes reduced to small lobes, and occasionally they are absent.

A special feature of the parameres in certain chalastogastrous families in which these lobes are movable is the presence on the end of each paramere of an eversible membranous area (pl. 1 I, v) that is retractile by a muscle arising in the base of the paramere (M, 17). Crampton (1919) refers to these membranes as "gonomaculae," or "sensory areas"; but as appears from the study of Boulangé (1924) each organ is evidently an adhesive "vacuum cup" (*ventouse*) exerting suction against an opposing surface by the contraction of its muscle. The structures are here termed *cupping disks*.

THE AEDEAGUS (*Aed.*)—*Paramèsc* Audouin (1821); *fourreau de la verge* Dufour (1841); *penis* Hartig (1837), Zander (1900), Crampton (1919); *gaine du penis* Boulangé (1924); *aedeagus* Beck (1933), Snodgrass (1935), Peck (1937).

The aedeagus is specifically the intromittent part of the phallic apparatus since it contains the terminus of the genital exit tract. The primary mesodorsal lobes of the phallus, in uniting to form the aedeagus, coalesce first by their dorsal margins, producing an inverted trough open below by a long median slit, and this primitive condition (fig. 5 B, G) is retained in the adult of many Hymenoptera, particularly in Chalastogastra and Ichneumonoidea. In others, however, the ventral edges of the aedeagal lobes also unite for a varying distance from their bases, thus converting the aedeagus into a tube opening by a distal slit on its ventral surface or by a terminal orifice (H, *Phtr.*).

The lateral walls of the aedeagus contain a pair of elongate sclerites (fig. 5 G, *pv*), the *laminae aedeagales*, or *penis valves* (*thyrses* Audouin, 1821; *baguettes du fourreau* Dufour, 1841; *crochets* Seurat, 1899; *penisvalvae* Crampton, 1919; *valves du pénis* Boulangé, 1924). The distal ends of the aedeagal sclerites usually project more or less as a pair of free apical points or lobes, and are sometimes deeply separated by a long median cleft. Proximally the aedeagal sclerites are directly continued into the lumen of the caulis as two strong, usually divergent arms (*apa*), the *aedeagal apodemes* ("parameres" of Peck, 1937), on which are inserted most of the aedeagal muscles (fig. 6 B). At the bases of the apodemes, however, are two small lateral processes (*e*), the *ergots* of Boulangé, which also give attachment to muscles, and in some cases serve as a pair of trunnions, or points by which the aedeagus articulates on the adjoining margins of the parameral plates. The dorsal wall of the aedeagus is generally membranous and distensible, but it is sometimes weakly sclerotized, and it may contain a median rod or plate prolonged proximally into the dorsal wall of the caulis. Some of the various shapes assumed by the aedeagus will be shown in following sections of this paper. In strophandrious species the primarily ventral groove or phallosome of the aedeagus becomes secondarily dorsal.

The usual musculature of the aedeagus, as shown by Boulangé (1924), includes five pairs of muscles (fig. 6 B). Two pairs arise ventrally on the proximal ends of the parameral plates, one (*δ*) going to the apices of the aedeagal apodemes, the other (*ρ*) to the basal processes (ergots, *e*) of the latter. A third pair (*10*) arises dorsally on the posterior mesal parts of the parameral plates, or on the parapenial lobes of the latter when such lobes are present, and goes anteriorly to the apices of the aedeagal apodemes. Another pair (*11*) arises on the mesal dorsal margins of the parameral plates or their parapenial lobes and is inserted distally on the inner faces of the penis valves of the aedeagus. The fifth pair (*12*) arises laterally on the parameral plates and is inserted mesally on the basal processes of the aedeagal apodemes. In addition to these usual muscles of the aedeagus Boulangé reports the occurrence of a strong muscle uniting the apodemes observed in the tenthredinid *Abia* and in the bee *Anthidium*. Finally, in the Cephoidea a double series of fine transverse muscle fibers goes from the aedeagal apodemes to a median rod in the dorsal wall of the aedeagus and caulis (pl. 3 R, *14*), and in *Sphécus speciosus* among the Sphecoidea there are similar fibers inserted on the endophallus (pl. 18 O, *14a*).

The aedeagus of the Apoidea must be given special attention because in most of the bees the lateral aedeagal plates are deeply separated from the median part of the organ, so that the apoid aedeagus has typically a tripartite structure (fig. 5 I). The median lobe ("spatha" of Thomson, 1872, "uncus" of Franklin, 1912, 1913) retains the genital exit passage and the phallotreme (*Phtr*), and may therefore be termed the *penis* (*pen*); the lateral processes (*sag*) are commonly called the *sagittae* (Thomson, 1872), but there can be no question that the sagittae of the bees are the usual penis valves (H, *pv*) of other Hymenoptera. They always maintain a connection with the base of the penis, and their bases are produced into the aedeagal apodemes (*apa*) giving attachment to the same muscles that in other groups are attached on these processes. According to Zander (1900) the sagittae of *Bombus* are shown by their development to be the true aedeagal lobes of the phallus, which have united only at their bases; the penis is a median outgrowth between them containing the opening of the endophallus ("ductus ejaculatorius" of Zander). There is no possible excuse for mistaking the sagittae for volsellar lobes. Though volsellae are entirely absent in many of the bees, they are present as reduced structures in various species. The median aedeagal lobe, or penis, may be entirely membranous, and is evidently extensible by eversion of the endophallus, but it sometimes contains a dorsal sclerotization. Though the aedeagus thus becomes a relatively complex organ in most of the Apoidea, it retains the simple generalized structure in some families, and in *Apis* it is reduced to a pair of valvelike lobes (fig. 5 J, *pv*), from between which is everted the huge endophallus (*Enph*).

THE ENDOPHALLUS (*Enph*).—The endophallus is the internal, more or less eversible sac of the phallus, receiving the ductus ejaculatorius at its anterior end, and opening distally through the phallotreme of the aedeagus (fig. 5 G, *Enph*). It is the terminal part of the definitive genital exit tract formed between the united phallic rudiments, by most writers generally regarded as a continuation of the ductus ejaculatorius. In the Hymenoptera the endophallus is variable in size; it may be a mere pocket receiving the ductus ejaculatorius, and it does not usually extend much beyond the base of the aedeagus (G, H, I). Probably it is always eversible, but it is not often found everted in museum specimens. In the genus *Apis* the endophallus attains an extraordinary size and development (J, *Enph*), accompanied by a reduction of the ectophallus, and when everted at the time of mating constitutes the functional "penis" of the bee.

THE VOLSELLAE (*Vol*).—It is difficult to give the synonymy of the volsellae because most writers have applied the term "volsella"

to one of the free volsellar lobes, or have named the lobes and the supporting plates as if they had no relation to each other. As already shown, each volsella (fig. 5 E) consists typically of a basal *lamina volsellaris* (*lv*), or *basivolsella* (Peck, 1937), and of two free distal lobes. One of the lobes is a direct continuation of the volsellar plate, and is here named the *cuspis volsellaris* (*cus*); the other is movable on the end of the volsellar plate, and is named the *digitus volsellaris* (*dig*). The volsellar plate is anatomically a ventral sclerite of the caulis ("pièce complémentaire" of Boulangé, 1924). The digitus and cuspis are the *copulatory ossicles* of Crampton (1919). Ontogenetically the volsellar digiti represent a pair of mesoventral lobes of the caulis ("valvae internae" of Zander, 1900). Unfortunately the development of the phallus has been studied only in species in which the cuspides are very small or absent, but the cuspidal lobes would appear to be merely secondary outgrowths of the volsellar plates. It is probable that the term "volsella" (volselle or tennette of Dufour, 1841), meaning "a pair of tweezers," was first given to the copulatory ossicles to distinguish these small inner pincerlike structures from the large "outer forceps" formed by the parameres. However, inasmuch as each pair of ossicles and the supporting plate, together with their muscles, constitute a definite mechanical unit in the phallic apparatus, the writer follows Peck (1937) in applying the term *volsella* to the entire structure. The *cuspis* is the "distivolsella" of Peck; other writers have not recognized its individuality. The *digitus* is the "lacinia" of Thomson (1872), the "valva interna" of Zander (1900) in *Vespa*, the "pièce en trébuchet" of Boulangé (1924), the "gonolacinia" of Peck (1937), the "sagitta" of Pratt (1940). In the Apoidea the term "volsella" has usually been misapplied to a lobe of the paramere, and in the Vespoidea the digitus has been mistaken for the sagitta of the aedeagus in the bees.

The volsellar plates lie in the ventral wall of the caulis along the mesal margins of the parameral plates (fig. 5 B, *lv*), from which they are usually separated by narrow lines of membrane, though sometimes the volsellar plates are united with the corresponding parameral plates or completely merged into the latter. Generally a median membranous area of the caulis wall intervenes between the volsellar plates, but in some cases the plates are joined by a basal bridge, or may even be fully united with each other. Typically each volsellar plate is strengthened by an internal longitudinal ridge (E, *vr*), the external groove of which divides the plate into a lateral and a mesal area. If one area is desclerotized the ridge becomes marginal on the other, and the ridge persists when both areas are membranous. The anterior end

of each plate usually forms an apodemal inflection (*apv*) for the attachment of muscles. The volsellar plates either lie horizontally between the parameral plates (fig. 5 C), or they are inflected dorsally against the inner surfaces of the latter (D, E) and thus form the lateral walls of a concavity on the ventral side of the caulis. In the horizontal position the cuspis is lateral and the digitus is mesal on the end of the volsellar plate, but with the dorsal inflection of the plate (E) the digitus assumes a dorsal position relative to the cuspis. When

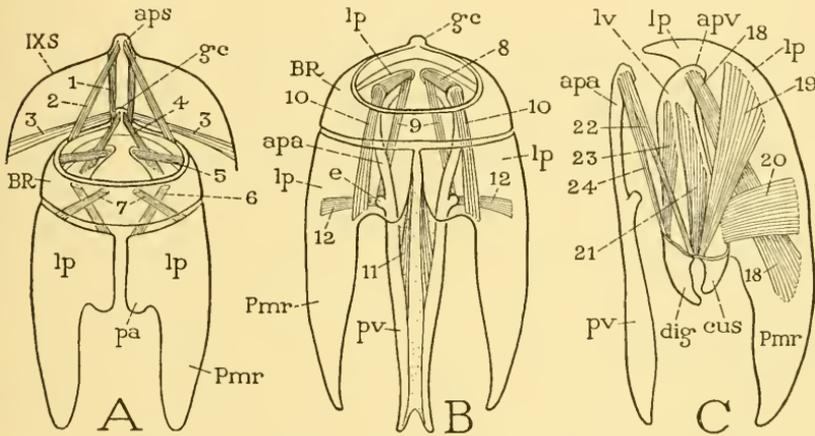


FIG. 6.—The phallic musculature, diagrammatic (based partly on Boulangé, 1924).

A, extrinsic muscles of the phallus arising on ninth abdominal sternum, and intrinsic muscles between basal ring and parameral plates of phallus, dorsal view. B, muscles of the aedeagus, dorsal view. C, complete musculature of a volsella, dorsal view of right organ, but all muscles shown not present in any one species.

aps, basal apodeme of ninth abdominal sternum; *apv*, basal apodeme of volsellar plate; *BR*, basal ring of caulis; *cus*, cuspis of volsella; *dig*, digitus of volsella; *gc*, gonocondyle of basal ring; *lp*, lamina parameralis; *lv*, lamina volsellaris; *pa*, parapenial lobe of parameral plate; *Pmr*, paramere; *pv*, penis valve; figure 1-24, phallic muscles (see text, pages 16 to 24, for explanation).

both cuspis and digitus are present the two ossicles of each pair usually form a pair of small pincers (E, *cus*, *dig*), but sometimes one is much longer than the other, or one may be absent. When one lobe alone is present, or greatly exceeds the other in size, the functional lobe is generally the movable digitus (F). In strophandrious species of the *Chalastogastra* the volsellae are secondarily dorsal.

The volsellar musculature includes muscles that move the volsella as a whole, and muscles that move the terminal lobes—eight muscles in all, though they do not all occur in the same species. Seven of these muscles, shown diagrammatically at C of figure 6, are as follows: 18, protractor of the volsella, arising posteriorly on the side of the para-

meral plate or in the base of the paramere, inserted anteriorly on the basal apodeme (*apv*) of the volsellar plate; 19, retractor of the volsella, arising anteriorly on the parameral plate, inserted posteriorly on the base of the cuspis; 20, rotator of the volsella, present in Vespoidea, arising dorsally on the side of the parameral plate, inserted ventrally on the lateral margin of the volsellar plate; 21, intrinsic muscle of the volsella, arising anteriorly on the volsellar plate, inserted posteriorly on the base of the cuspis or between cuspis and digitus, probably closing the ossicles against each other; 22, aedeagal flexor of the digitus, from the apex of the aedeagal apodeme (*apa*) to the outer or ventral angle of the base of the digitus (muscle *m* of Boulangé, observed only in Siricidae); 23, volsellar extensor of the digitus, arising on the volsellar plate, inserted on the mesal or dorsal angle of the base of the digitus (muscle *s* of Boulangé, present in Tenthredinoidea, Siricidae, Cephidae, and Ichneumonidae, variable in other groups, usually absent); 24, aedeagal extensor of the digitus, arising on the aedeagal apodeme, inserted on the mesal or dorsal angle of the base of the digitus (muscle *n* of Boulangé, present in Pamphiliidae, Siricidae, and Ichneumonidae, generally absent in other groups). An exceptional muscle, observed only in the sphecoid *Sphecius speciosus* (pl. 18 M, 25), arising on the base of the parameral plate and inserted on the apodeme of the volsellar plate, evidently serves as a direct antagonist to the protractor of the volsella (18). The volsellar muscles most commonly present are 18, 19, and 21. Though the digitus is always the movable unit of the volsellar pincers, it is curious that in most species there are no muscles inserted directly upon it, but it can be demonstrated in many cases that pressure on the base of the cuspis closes the two ossicles upon each other.

The strong and elaborate musculature of the volsellae indicates that these organs are important elements of the male copulatory apparatus. According to Peck (1937) specimens of the ichneumonid *Angitia fenestralis* taken *in copula* show that the pincers of the volsellae grasp the conjunctival membrane of the female in the neighborhood of the vulva, evidently keeping the membrane taut while the aedeagus is inserted. The volsellae are characteristic genital features of the Hymenoptera having in other insects no counterparts, except possibly the undifferentiated ventral lobes of the phallus in Orthoptera.

III. CHALASTOGASTRA

The comprehensive work of Boulangé (1924) on the male genitalia of the Chalastogastra not only is an exhaustive study of the genital apparatus within this group, but also it establishes a foundation for a

comparative study of the male organ in all other Hymenoptera. The general application of Boulangé's results has been discussed in the introductory parts of this paper, and nothing has been found to discredit any of his descriptions or interpretations in the Chalastogastra.

There is no feature of the male genital organ that would separate all members of the Chalastogastra from clistogastrous Hymenoptera, but the chalastogastrous families can be divided concisely into two major groups according as the parameres of the phallus are articulated on the parameral plates, or are directly continuous with the latter. The second group includes the Cephoidea and the family Orussidae; the first comprises all the other families. The articulation of the parameres in Chalastogastra is accompanied by the presence of specific parameral muscles, an extensor and a flexor for each appendage, arising on the parameral plates. These muscles are absent in Cephoidea and Orussidae, and only rarely among clistogastrous species having articulated parameres has the writer observed the occurrence of parameral muscles, as in the bethylid *Pristocera armifera*, the vespid *Cryptocheilus unifasciatus* (pl. 15 O), and the apoïd *Crocisa crucifera* (pl. 28 B).

A second feature known only among the Chalastogastra is the presence of cupping disks on the ends of the parameres. The cupping disks, however, are limited to a certain group of families among those that have articulated parameres, including the Xyelidae, Megalodontidae, Pamphiliidae, Syntectidae, Xiphidriidae, and Siricidae. They are absent in the families usually included in the Tenthredinoidea, which also have articulated parameres.

A third feature of the genital apparatus, again occurring only within the Chalastogastra, is the inversion of the phallus. The strophandrious (inverted) condition is characteristic of the Tenthredinoidea, but it is not entirely distinctive of this superfamily because it occurs also in at least two species of Xyelidae (*Xyela minor* and *Pleroneura koebeleri*). Since the Xyelidae would appear in many respects to be generalized Chalastogastra, it is interesting to note that both the orthandrious and the strophandrious condition occurs among them. That the Xyelidae are not closely related to the other strophandrious families having articulated parameres is shown by their lack of a hypostomal bridge closing the back of the head.

The aedeagus of most of the Chalastogastra has the form of an inverted trough (secondarily open above in strophandrious forms) with the phallotreme at its base; in Cephoidea, however, the aedeagus is tubular and the phallotreme is apical or subapical.

The possible grouping of the chalastogastrous families on a basis of characters in the male genitalia shown above may be tabulated as follows:

- I. Parameres articulated on the parameral plates and movable by special muscles, aedeagus troughlike.
 - A. Cupping disks present.
 1. Head without hypostomal bridge—Xyelidae.
 2. Head with hypostomal bridge—Megalodontidae, Pamphiliidae, Syn-tectidae, Xiphydriidae, Siricidae.
 - B. Cupping disks absent—Tenthredinoidea.
- II. Parameres continuous from the parameral plates, devoid of muscles, cupping disks absent.
 1. No constriction at base of abdomen, cenchri present, aedeagus troughlike—Orussidae.
 2. Abdomen constricted between first and second segments, cenchri absent, aedeagus tubular—Cephoidea.

XYELIDAE.—*Macroxyela ferruginea* (Say) (pl. 1 A-E), *Xylecia nearctica* Ross, *Megaxyela langstoni* Ross, *Xyela minor* Norton (pl. 1 F-M), *Pleroneura koebelei* Roh.

The abdomen of the Xyelidae has the typical tenthredinoid structure. In *Xyela minor* (pl. 1 F, G) the first abdominal tergum is divided medially and the venter of the first segment is unsclerotized. The ninth sternum forms a large, exposed subgenital plate (G, IXS), but the dorsum of the ninth segment is membranous except for two lateral sclerotic tergal remnants on the anterior margin (L, IXT), as also in *Macroxyela ferruginea* (C). The tenth segment is membranous and bears the pygostyles laterally (C, F, L, X).

The Xyelidae are classed by Ross (1937) with the Pamphiliidae and Megalodontidae in the superfamily Megalodontoidea, of which all the members are presumed to be orthandrious, since the Tenthredinoidea are said by Ross to be "unique in having the male genitalia inverted." The strophandrious condition, however, occurs in two of the five nearctic genera of Xyelidae given by Ross, namely *Xyela* and *Pleroneura*. The orthandrious type of phallic structure is illustrated by Crampton (1919, figs. 27, 28) in *Megaxyela aenca*, and by Ross (1937, fig. 167) in *Macroxyela ferruginea*. The phallus of these species is of simple form (pl. 1 A, B), the basal ring opens anterodorsally, the parameral plates (*lp*) form long basiparameral lobes supporting the movable parameres (*Pmr*), the aedeagus is deeply cleft between its lateral plates, and is open below (A, B, *Aed*, D). The volsellae are ventral, but are not seen unless the parameral plates are spread apart. The volsellar plates lie against the mesal faces of the

basiparameral lobes (E, *lv*); each plate ends in a simple cuspidal process (*cus*) and bears a movable digitus (*dig*).

The strophandrious type of phallic structure is well shown in *Xyela minor* (pl. 1 H, I). The basal ring here opens directly forward, and the usual dorsal surface of the phallus is turned downward (H). The volsellar surface (I) is therefore secondarily dorsal, and the phallotreme (*Phtr*) lies on the upper surface of the aedeagus (*Aed*). The volsellae have the usual structure (K), except that the inversion of the phallus gives the digiti a ventral position relative to the cuspides (I). Because of the anterior position of the foramen of the basal ring the phallus is easily revolved, but of many specimens examined none was found to have the phallus in other than the inverted position. The phallus of *Pteroneura koebele* appears at first sight to be orthandrious because the parameres are turned downward, instead of upward as in *Xyela minor*, but a closer inspection shows that the aedeagus is open dorsally, and that the volsellar plates are connected with the upper edges of the parameral plates. Only one specimen of this species was available for examination.

The presence of well-developed cupping disks on the ends of the parameres in the Xyelidae (pl. 1 M, *v*) separates the members of this family from the Tenthredinoidea, and might seem to relate them to the Xiphydriidae and Siricoidea, but the Xyelidae are in many respects more generalized than the latter groups, and are readily distinguished from them by the absence of a hypostomal bridge between the foramen magnum and the base of the labium.

TENTHREDINOIDEA.—*Gilpinia polytoma* (Htg.) (pl. 1 N, P, R, S), *Neodiprion sertifer* (Geoff.) (pl. 1 O, Q), *Pteronidea ribesii* (Scop.) (pl. 2 A-I).

The general form and structure of the abdomen of *Gilpinia polytoma* is shown at N of plate 1, that of *Pteronidea ribesii* at A of plate 2. The first abdominal tergum in each species is divided medially by a triangular membranous area; its acrotergite (*atg*) is distinct, but is not united with any part of the thorax. The dorsum of the ninth segment contains a pair of lateral tergites (pl. 1 O, P; pl. 2 B, *IXT*), but is mostly or entirely concealed beneath the eighth tergum (pls. 1 N, 2 A). The ninth sternum forms the large subgenital plate (*IXS*). The tenth segment bears laterally the pygostyles, and its dorsal surface contains a pair of weakly sclerotized tergal sclerites separated medially (pl. 1 O, P, X).

The male genital organ of the Tenthredinoidea is characterized by the articulation of the parameres on the parameral plates, the absence of cupping disks on the parameres, and the inversion of the phallus.

Crampton (1919) gives illustrations of the phallic structure in 12 species of the group, and Boulangé (1924) describes and figures species representing 22 genera. The three species here included will sufficiently show the general features of the tenthredinoid phallus.

Because of the inversion of the phallus the lower side (pl. 1 R; pl. 2 C) is the true dorsal surface, and the upper side (pls. 1 S, 2 D) the primary ventral surface. As a consequence, the foramen of the basal ring is turned anteroventrally, the volsellae appear on the upper surface, and the groove of the aedeagus containing the phallotreme (*Phtr*) at its base is exposed dorsally. The parameral plates (*lp*) are produced into thick basiparameral lobes that support the movable parameres on their distal ends. On the upper (true ventral) surface of the phallus the parameral plates are widely divergent (pl. 1 S; pl. 2 D, *lp*); on the lower surface their bases are produced mesally into a pair of parapenial lobes extending beneath the base of the aedeagus (pl. 1 R, *pa*). In *Pteronidea ribesii* the parapenial lobes (pl. 2 C, H, *pa*) project upward and are therefore seen from above (D) overlapping the mesal angles of the parameres. The parapenial lobes are morphologically dorsal, and always have this position where they occur in orthandrious species. The aedeagus is simple; its lateral plates, or penis valves (pl. 1 S; pl. 2 D, *pv*), are separate distally, membranously united proximally by their lower edges, and produced basally into a pair of slender apodemes (pl. 2 G, *apa*). The upper surface of the aedeagus presents a deep open channel, with the phallotreme (*Phtr*) in its anterior end. The volsellae are of typical structure (pl. 1 Q; pl. 2 I), though reversed in position by the inversion of the phallus. The elongate volsellar plates lie along the mesal margins of the parameral plates on the upper surface of the phallus (pl. 1 S, *lv*); in *Pteronidea ribesii* they are united with the parameral plates (pl. 2 D, *lv*). Owing to the phallic inversion, the digiti are dorsal and the cuspides ventral (pl. 2 H).

PAMPHILIIDAE.—*Acantholyda erythrocephala* (L.) (pl. 2 J-O, S).

The pamphiliids are included by Ross (1937) with the Xyelidae and Megalodontidae in a superfamily Megalodontoidea, but though they have in common with the Xyelidae (and Siricoidea) the cupping disks of the parameres, they differ from the xyelids in that the head is closed behind by a hypostomal bridge between the lower angles of the postgenae, as in the siricids. Judging from the male genitalia alone, the Pamphiliidae would appear to be more closely related to the Siricoidea than to any other superfamily of the Chalastogastra.

The dorsum of the ninth abdominal segment of *Acantholyda erythrocephala*, ordinarily concealed by retraction beneath the eighth tergum

(pl. 2 J), contains two lateral tergites (L, *IXT*). The tenth segment has a well-developed tergal plate (J, L, *XT*) with only a small membranous median area. The subgenital sternum is relatively small and simple (K, *IXS*). The phallus is not inverted (M, N). The basal ring (*BR*) is narrow above and below, the parameral plates (*lp*) lack parapenial lobes; the parameres (*Pmr*) are articulated on the parameral plates and provided distally with cupping disks (N, *v*); the aedeagus (*Aed*) is small, bifid terminally, presents a deep open groove below (N, O) with the phallosome (*Phtr*) at its base, and has long basal apodemes (O, *apa*) continuous from its lateral plates (*pv*). The volsellae are conspicuous on the ventral side of the phallus (N), where the volsellar plates (*lv*) adjoin the mesal margins of the parameral plates (*lp*). The cuspides (*cus*) are much reduced, the digits (*dig*) are long and curved laterally (S). The general structure of the phallus in *Acantholyda erythrocephala* shows no essential difference from that in *Pamphilius persicus* (MacG.), *Cephaleia fascipennis* (Cress.), and *Cephaleia frontalis* (Westw.) as figured by Crampton (1919), or in *Neurotoma (Pamphilius) flaviventris* Retz. as described by Boulangé (1924).

XIPHYDRIIDAE.—*Xiphydria maculata* (Say) (pl. 2 P, Q, R; pl. 3 F, J, K).

The tergal plates of the first abdominal segment are separated by a narrow median line; the ninth sternum is a fairly large subgenital plate, but the distal parts of the phallus project beyond it (pl. 2 P); the ninth and tenth terga (Q) are so nearly confluent that it is difficult to detect a separating line, but the anterior margin of tergum IX is definite and unbroken, as shown also by Crampton (1919) in *Xiphydria mellipes* (Say).

The phallus of *Xiphydria maculata* (pl. 3 J, K) is of generalized form and structure; the basal ring (*BR*) is narrow above and below, and opens anterodorsally; the parameral plates (*lp*) are produced into long basiparameral lobes bearing at their ends the relatively short parameres (*Pmr*), which are articulated, muscled, and provided with subapical cupping disks (*v*); the aedeagus (*Aed*) is laterally compressed, bifid distally, and presents ventrally (K) a deep open groove with the phallosome (*Phtr*) at its base between the broad lateral plates (F, *pv*); the long volsellar plates lie against the elongate ventral margins of the parameral plates (K, *lv*), and bear each a small cuspis (*cus*) and digitus (*dig*), the latter provided with a large extensor muscle arising on the corresponding volsellar plate (pl. 2 R, 23). The genital organ of *Xiphydria maculata* is illustrated also by Ross (1937), and closely resembles that of *X. mellipes* (Say) as

figured by Crampton (1919), and of *X. dromedarius* F. as described and illustrated by Boulangé (1924).

SIRICIDAE.—*Sirex abbottii* Kirby (pl. 3 A-E, H, I).

Boulangé (1924) in his treatment of the Siricidae includes the segmentation and musculature of the distal abdominal segments of *Sirex juvencus* L., and a full account of the structure and musculature of the copulatory organ of *Sirex juvencus* and *Xeris spectrum* L. The phallus of *Tremex columba* (L.) and of *Sirex edwardsii* Brullé is figured by Crampton (1919), and that of *Urocerus flavicornis* Fab. by Ross (1937).

In *Sirex abbottii* the ninth abdominal tergum, which is mostly concealed beneath the eighth (pl. 3 A, *IXT*), consists of two large triangular lateral plates united by a narrow sclerotic median bridge (C). The tenth tergum (A, C, *XT*), bearing the small pygostyles laterally, projects beyond the eighth, and overlaps the base of the freely protruding phallus (A, *Phl*), which is supported below on the large triangular subgenital plate formed by the elongate ninth sternum (A, B, C, *IXS*).

The phallus of *Sirex abbottii* (pl. 3 H, I) resembles that of *S. edwardsii* and *S. juvencus* described respectively by Crampton and by Boulangé. The parameral plates are contiguous dorsally (H, *lp*) beyond the broad dorsal surface of the basal ring (*BR*), but ventrally (I) they are widely separated and prolonged anteriorly into a deep emargination of the ventral surface of the basal ring. The broad articulated parameres (*Pmr*) are strongly muscled, and each bears distally a large oval cupping disk (I, *v*) provided with a wide retractor muscle arising in the base of the paramere. The aedeagus is short, deeply grooved below to the base of the free part between its lateral plates, proximal to which a slender median rod continues anteriorly in the ventral wall (E, *d*), as described by Boulangé for *Sirex juvencus*. The lateral sclerites of the aedeagus (E, *pv*) are produced proximally each into a short aedeagal apodeme (*apa*). The large volsellar plates are freely exposed on the ventral surface of the phallus (I, *lv*) between the widely separated ventral edges of the parameral plates. Each volsellar plate, as shown by Boulangé in *Sirex juvencus*, is divided by a longitudinal ridge (*vr*) into a median and a lateral part. The median part bears distally a large, freely movable, strongly toothed digitus (I, D, *dig*), the lateral part a very small cuspis (*cus*). The phallus of *Xeris spectrum* described by Boulangé would appear to be much like that of *Sirex*, but the phallus of *Tremex columba* as shown by Crampton is more elongate, and the parameral plates are divergent dorsally.

ORUSSIDAE.—*Orussus sayi* Westw. (*terminalis* Newm.) (pl. 4 D-J).

The orussids were given the status of a suborder (Idiogastra) of Hymenoptera by Rohwer and Cushman (1917) because of certain peculiar features they possess, such as characters of the wing venation and the ventral position of the antennae. The orussids, these authors say, are more nearly allied by adult characters to the siricoid families of the Chalastogastra, while on larval characters they would appear to be related to the Clistogastra. Ross (1937) places the Orussidae under the Siricoidea. On a basis of the male genitalia the orussids fall in with the Cephoidea by reason of the continuity of the parameres with the parameral plates (pl. 4 I, J); but, on the other hand, the crussid aedeagus is widely open below (J, *Aed*) and the phallotreme (*Phtr*) is basal, as in noncephoid Chalastogastra, while, furthermore, the orussids possess cenchri, which are absent in the cephoids, and they have no constriction between the first and second segments of the abdomen (F). Finally, the orussids differ from all other Chalastogastra in the lack of a median division of the first abdominal tergum, and in the separation of the metapleuron (F, *Pl*₃) into anterior and posterior sclerites as in Clistogastra.

The abdomen of *Orussus sayi* presents eight distinct tergal plates in the dorsum; the venter ends with the ninth sternum (pl. 4 F). The tergum of the first segment is undivided by a median suture or membranous area, and the antecostal suture behind the acrotergal area (*atg*) is scarcely perceptible, though it is marked internally by a strong transverse ridge. The metapleuron (*Pl*₃) is divided into a slender anterior epipleurite, and a large triangular hypopleurite, and the pleural suture is almost suppressed. The tergum of the ninth abdominal segment consists of a pair of triangular lateral tergites (G, *IXT*), between which is a single median tergal plate (*XT*) of the tenth segment, which latter bears the pygostyles (*Pgs*).

The phallus has a generalized structure, and a simplified appearance because of the shortness of the parameres (pl. 4 I, J). The basal ring (*BR*) is wide above, narrow below, and opens anterodorsally. The parameral plates (*lp*) are partly contiguous on the dorsal surface (I) and are prolonged anteriorly on the ventral surface (J). They are directly continued into the short parameres (*Pmr*). The volsellar plates (D, J, *lv*) are long, narrow, and widely separated; each is produced into a long cuspidal process (*cus*) and bears a smaller digitus (*dig*), both of which, however, project far beyond the short parameres and aedeagus. The digitus is strongly toothed at its apex (E). The aedeagal valves are widely open below (H, *pv*), separated distally by

a deep notch, and prolonged proximally into short aedeagal apodemes (*apa*) with prominent basal apophyses (*c*). The phallotreme (*Phtr*) lies at the base of the aedeagus, where it opens into the ventral groove of the latter.

CEPHOIDEA.—*Cephus cinctus* Nort. (pl. 3 G, L-P, T), *Cephus pygmaeus* (L.), *Janus integer* (Nort.), *Trachelus tabidus* (F.) (pl. 3 Q-S), *Hartigia trimaculata* (Say) (pl. 4 A-C). The phallus of *Cephus cinctus* is illustrated also by Crampton (1919), that of *Janus integer* by Ross (1937), and that of *Cephus pygmaeus* and of *C. pallipes* Kl. by Boulangé (1924).

The Cephoidea are set off from all other Chalastogastra by the tubular form of the aedeagus (pl. 3 T), and from all but the Orussidae by the continuity of the parameres with the parameral plates, with which feature is associated the absence of specific parameral muscles. Though Boulangé (1924) in his figures of *Cephus pygmaeus* and *C. pallipes* appears to represent the parameres ("palettes") as articulated on the parameral plates, he says (p. 214), "il faut remarquer que si la palette nous a semblé devoir être considéré comme une pièce distincte nous croyons qu'elle est plutôt flexible que réellement articulée." He notes that the "palettes" are devoid of muscles. An examination of *Cephus pygmaeus* shows that the parameral lobes are conspicuously differentiated from the basiparameral regions by their bright yellow color, that they are flexible at their bases, but not truly articulated, and have no muscles. Both Crampton (1919) and Ross (1937) show the parameres of *Cephus cinctus* and of *Janus integer* continuous with the parameral plates. The parameres have no cupping disks. Another distinctive feature of the Cephoidea is the separation of the lateral tergites of the first abdominal segment by a wide, triangular, membranous dorsal area, and the constriction between the first and second segments (pl. 3 L). Cenchri are absent on the metanotum. The dorsal areas of the ninth and tenth abdominal segments are well differentiated in *Cephus cinctus* (pl. 3 M, N) and *Trachelus tabidus* (S), and each dorsum contains an undivided tergal plate. The pygostyles (N, S, *Pgs*) are borne laterally on the tenth segment.

The cepheid phallus (pl. 3 O-R; pl. 4 A, B) has a distinctive appearance because of the large size of the basal ring (*BR*), which is widely open anterodorsally. The parameral plates (*lp*), which are directly continuous with the parameres (*Pnr*), are short on the upper surface of the phallus, but greatly extended proximally on the ventral surface. The volsellar plates (*lv*) are slender and closely associated with the ventral margins of the parameral plates, from

which they may not be completely separated anteriorly. The cuspis and digitus (*cus, dig*) of each volsella are of approximately equal length, and the digitus has an extensor muscle arising on the volsellar plate (pl. 4 C, 23). The tubular form of the cephaloid aedeagus, as contrasted with the troughlike structure of the organ in other Chalcidogastra, results from a membranous union of the ventral edges of its lateral plates (pl. 3 P, R, T; pl. 4 B, *Acd*). The phallosome is therefore terminal or subterminal (pl. 3 T, *Phtr*) instead of basal. The membranous ventral wall of the aedeagus is strengthened by a long slender median rod (pl. 3 R, T, *d*), on which, as shown by Boulangé (1924, fig. 119), are inserted a double series of transverse intra-aedeagal muscle fibers (R, 14).

IV. ICHNEUMONOIDEA

Only three families of Ichneumonoidea are here discussed, namely, the Ichneumonidae, the Evanidae, the Braconidae, and of these, principal attention is given to the last because the genital structures of the ichneumonids have been well described by Peck (1937), and their taxonomic value discussed by Pratt (1939).

ICHNEUMONIDAE.—*Megarhyssa lunator* (F.) (pl. 4 K, L, N-U), *Ichneumon irritator* F. (pl. 4 M), *Protichneumon grandis* (Brullé) (pl. 5 A-I), *Therion morio* (F.) (pl. 5 J-P), *Trogus vulpinus* (Grav.) (pl. 5 Q-W), *Megaplectes monticola* (Grav.) (pl. 5 X-Z'), *Paniscus* spp. (pl. 6 A, B), *Arotes amoenus* Cress.

The last fully exposed dorsal plate of the ichneumonid abdomen is tergum VIII; the tergal plates of segments IX and X are either partly exposed behind tergum VIII, or are entirely retracted beneath it, though the pygostyles are not completely covered (pl. 4 N; pl. 5 A, B, L, Q, X). On the venter, however, sternum IX is always a free subgenital plate. The tergum of segment IX in the ichneumonids, as shown by Peck (1937), is usually divided medially into a pair of lateral tergites (pl. 4 M, *IXT*). The ninth-segment tergites, however, are generally more or less united with the tenth tergum, the three plates, when tergum X is entire, forming a composite *syntergum*; but more commonly tergum X itself is divided into a pair of lateral tergites (M, P), in which case the combined tergites of segments IX and X form a pair of lateral *syntergites*. The division between the segmental components of the tergal plates may be partly retained, or entirely obliterated. According to Pratt (1939) in the Acoenitini and Xoridini the tenth tergum is entire, and is distinct from the lateral tergites of segment IX. The pygostyles are always closely associated with the

posterior margin of the tenth tergum or tergites, but they are directly attached to a post-tergal membrane (pl. 4 M, P, *Pgs*) that forms a small supra-anal fold. Between the supra-anal fold and a corresponding subanal fold of the tenth segment is an invaginated pocket, into which the rectum opens anteriorly. In the male of *Megarhyssa lunator*, as already shown (p. 12), the walls of the anal pocket bear a pair of small setigerous, cercuslike appendages, which are fully exposed when the pocket is everted (pl. 4 O, P, *Cer?*). The presence of these cercuslike appendages on the eversible anal pocket suggests that the latter represents the eleventh segment, and that the appendages are the true cerci.

The phallus of the ichneumonids needs little discussion; it has a generalized structure in which the parts are easily identified. Typical examples of the phallus are seen in *Megarhyssa lunator* (pl. 4 K, L), *Protichneumon grandis* (pl. 5 D, E), *Therion morio* (pl. 5 M, N), *Trogus vulpinus* (pl. 5 U, V), and *Megaplectes monticola* (pl. 5, Z, Z'). The parameres are simple prolongations of the parameral plates; in *Paniscus* they have an armature on their mesal surfaces (pl. 6 A, B, *p*, *b*), described by Townes (1938). The aedeagus is relatively small and of simple structure (pl. 4 U; pl. 5 F, I, J, W); its lateral sclerites (*pv*) are united dorsally, widely open below, more or less separated at their apices, and produced basally into a pair of long apodemes (*apa*). The phallotreme is at the proximal end of the ventral aedeagal groove (pl. 4 U; pl. 5 W, *Phtr*). The ichneumonid volsellae are well developed and show good examples of the typical volsellar structure and musculature (pl. 4 S, T; pl. 5 H). The volsellar plates are turned dorsally on the lower edges of the parameral plates, and thus lie against the mesal surfaces of the latter (pl. 4 R; pl. 5 G; pl. 6 A, *lv*). The freely articulated digitus of each volsella, therefore, arises dorsally from the distal end of the volsellar plate (pl. 4 R, S, T; pl. 5 G, H, P, Y, *dig*); it usually curves downward against or past the immovable cuspis (*cus*). In *Paniscus* (pl. 6 A), however, the cuspis (*cus*) is reflected anteriorly on the outer side of the volsellar plate, and the digitus (*dig*) turns forward to meet it. In the genera *Arotēs* and *Colcocentrus* it is shown by Pratt (1939) that the cuspides ("distivolsellae") are absent, which feature, Pratt says, is characteristic of the tribe Acoenitini. The absence of the cuspides gives a suggestion of the volsellar structure of the Braconidae, but the volsellar plates of *Arotēs* are turned dorsally on the lower edges of the parameral plates in typical ichneumonid fashion. The volsellar musculature is strongly developed in the Ichneumonidae (pl. 4 T; pl. 5 H), a special feature

being the presence of the digital extensor muscle (24) arising on the apodeme of the aedeagus.

EVANIIDAE.—*Evania punctata* Brullé (pl. 6 C-F).

The stalked abdomen of *Evania* (pl. 6 C) contains eight distinct segments (II-IX). A pair of large spiracles is present on the sides of tergum VIII, but no spiracles are to be found on the other segments. The ninth tergum consists of two lateral plates separated by a deep median notch and only narrowly united before the latter. Whether this plate is tergum IX alone or terga IX and X united is not evident. Beyond it is a small anal papilla, but no pygostyles. The phallus (D, E) has a complete basal ring, large simple parameres continuous from the parameral plates, a slender aedeagus, and well-developed volsellae. The elongate volsellar plates (E, *lv*) lie horizontally on the ventral side of the phallus between the parameral plates (*lp*). Each plate bears a large expanded lateral cuspidal lobe (E, F, *cus*), and a slender mesal articulated digitus (*dig*). The aedeagus (D, E, *Aed*) is slender, simple and grooved below.

BRACONIDAE.—*Helcon pedalis* Cress. (pl. 6 G-J), *Rogas terminalis* (Cress.) (pl. 6 K, L), *Spathius canadensis* (Ashm.) (pl. 6 M-O), *Atanycolus rugosiventris* (Ashm.) (pl. 6 P; pl. 7 A, B, E), *Microgaster gelechiae* Riley (pl. 6 Q; pl. 7 C, D, K), *Macrocentrus cerasivoranae* Vier. (pl. 7 F-J), *Spinaria* sp. (pl. 7 L, M, N, Q), *Phanerotoma tibialis* (Hald.) (pl. 7 O, P, R), *Chelonus sericeus* (Say) (pl. 8 A-E), *Trachypetus clavatus* Guer.

The abdomen of the Braconidae shows a tendency toward an irregularity of segmentation, accompanied by a partial or complete union of some of the anterior segmental terga and a reduction in size of the posterior terga. Thus, among the species named above, the segmentation is fairly regular in *Helcon pedalis* (pl. 6 H), *Spathius canadensis* (M), *Atanycolus rugosiventris* (P), *Microgaster gelechiae* (Q), and *Macrocentrus cerasivoranae* (pl. 7 F), but in *Spinaria* sp. (pl. 7 L) the posterior three tergal plates are much reduced and concealed beneath tergum VI, and in *Phanerotoma tibialis* (O, R) terga II, III, and IV are united in a long carapace, behind and below which are crowded the small tergal plates of the following segments, while in *Chelonus sericeus* (pl. 8 A, B) the completely fused terga of segments II, III, and IV almost encapsulate the rest of the abdomen. The tergum of the genital segment, designated "IXT" on the figures, is perhaps, by comparison with the Ichneumonidae, to be regarded as the united tergal plates of segments IX and X, but no evidence of such a composition was observed specifically in the Braconidae. Otherwise, the tenth segment consists of the anal region, which bears laterally a

pair of small pygostyles (pl. 7 G; pl. 8 C, X). The exposed subgenital plate is usually sternum IX.

The braconid phallus, as illustrated in the species here studied, has a distinctive feature in the character of the volsellae. The volsellar plates, instead of being folded dorsally against the mesal surfaces of the parameral plates, as in Ichneumonidae, lie in a horizontal plane between the parameral plates, with their edges approximated beneath the base of the aedeagus (pl. 6 J, L, O; pl. 7 D, P, Q; pl. 8 E, *lv*). In some cases each volsellar plate is marked by a strong median ridge (pl. 6 O; pl. 7 D; pl. 8 E, *vr*), and if the plate becomes membranous the ridge alone remains (pl. 7 B, *lv*), giving support to the digitus, and attachment to the volsellar muscles. The volsellar cuspides are either suppressed or are represented by small lateral extensions of the volsellar plates (pl. 6 L, N, *cus*). The digits, on the other hand, are strongly developed, freely articulated lobes, usually toothed or hooked at their apices, and turn laterally and dorsally on the ends of the volsellar plates (pl. 6 J, L, N, O; pl. 7 A, B, D, J, N, P, Q; pl. 8 D, E, *dig*). The function of the volsellae in the Braconidae thus depends on the action of the digital lobes alone. It is interesting to note that a similar condition recurs in the Chalcidoidea and Cynipoidea. The braconid aedeagus is of simple structure, broad or slender, notched at the apex, grooved below (pl. 6 I-L, N, O; pl. 7 A-D, H-J, N, P, Q; pl. 8 D, E, *Aed*).

V. CHALCIDOIDEA

Berecynthus bakeri How. (pl. 8 F-H), *Callimome* sp. (pl. 8 I-K), *Callimome sackeni* (Ashm.) (pl. 8 L), *Tetrasticus bruchophagi* Gah. (pl. 8 M, P), *Pteromalus puparum* (L.) (pl. 8 N, O), *Leucospis affinis* (Say), (pl. 8 Q-T), *Ormyrus* sp. (pl. 9 A, B, D), *Brachymeria ovata* (Say) (pl. 9 C, E), *Cheiropachus colon* (L.) (pl. 9 F, G).

The chalcidoid abdomen is variable in form and in the relative size of its segments, as shown in *Berecynthus bakeri* (pl. 8 G), *Callimome* sp. (I), *Pteromalus puparum* (N), *Tetrasticus bruchophagi* (P), *Leucospis affinis* (Q, R), *Ormyrus* sp. (pl. 9 A), and *Brachymeria ovata* (C). In *Leucospis affinis* (pl. 8 Q, R) terga V-VIII are united. There are only two pairs of abdominal spiracles, the first on the propodium (pl. 8 F, *ISp*), the other on segment VIII of the "post-abdomen" (I, Q, *VIII Sp*). The petiole segment (II) is always small, and may be reduced to a narrow ring (F, II) concealed between the propodium (I) and segment III. Posteriorly the abdomen usually ends with the tergal and sternal plates of segment IX (pl. 8 I, Q;

pl. 9 C), though the ninth sternum is sometimes concealed (pl. 8 G). Since the small setigerous pygostyles are borne on the apparent ninth tergum (pl. 8 I, J, *Pgs*), it is to be presumed that this tergal plate represents terga IX and X united.

The phallus of the chalcidoids has a characteristic elongate, compact form owing to the close union of all its parts and the reduction of the parameres (pl. 8 H, K, L, M, O, S, T; pl. 9 B, E, F, G). The wider basal part of the organ, or caulis, is composed of the elongate parameral plates and the volsellar plates though the latter are seldom distinct sclerites; a basal ring is usually not evident, though it is present in some species (pl. 8 L, T, *BR*). The narrower distal lobe of the phallus is the aedeagus (*Aed*), and from its base there extends proximally into the caulis a pair of long slender aedeagal apodemes (pl. 8 H, K, M; pl. 9 B, E, F, *apa*). At the distal end of the caulis the parameres usually are evident as a pair of small lateral lobes (pl. 8 K, L, M, T; pl. 9 B, E, F, G, *Pmr*), but they may be so reduced as to be practically absent (pl. 8 G, H). Between the parameres, below the base of the aedeagus, is a pair of conspicuous volsellar lobes, which, being movable, are probably the *digiti* (pl. 8 H, K, L, M, O; pl. 9 B, E, G, *dig*). They are very similar to the digital lobes of Braconidae, being characteristically turned outward from the ends of the volsellar plates, and are armed distally with strong spines. The phallus in some species is relatively large and projects far from the end of the abdomen (pl. 8 G, I), but ordinarily it is either entirely concealed, or only its distal part is exposed. In *Berecynthus bakeri* the aedeagus is armed ventrally with a pair of small hooks (pl. 8 G, H, *h*).

VI. CYNIPOIDEA

Ibalia maculipennis Hald. (pl. 9 H-L), *Diplolepis multispinosus* Gill (pl. 9 M, N, O), *Figites quinquelincata* Say (pl. 9 P, Q, R). These three species represent the families Ibalidae, Cynipidae, and Figitidae, respectively.

The exposed abdominal segments are of approximately equal length in *Ibalia* (pl. 9 H), except the peduncular segment (*II*), which is a short, slender stalk supporting the rest of the abdomen. The eighth segment forms the rounded end of the body, and bears laterally the only pair of spiracles present on the "postabdomen" in the cynipids, as in the chalcids. The ninth tergum is small (*I, IXT*), and only its apex is exposed beyond the eighth (*H*). Pygostyles are absent. The slender ninth sternum (*I, IXS*) is entirely concealed above sternum *VIII*. In *Diplolepis multispinosus* (*O*) segment *III*, or particularly

its tergal plate, is greatly enlarged and constitutes nearly one-half of the ovate abdomen. The peduncular segment (*II*) is short, the eighth tergum (*VIIIT*) bears the spiracles, the ninth tergum (*IXT*) is partly exposed beyond the eighth. In *Figites quinquelineata* (R) segment *II* forms the greater part of the abdomen, and the extended ventrolateral parts of its tergal plate overlap each other beneath the sternum. The peduncular segment (*II*) is very small in this species and is completely concealed normally within the projecting anterior margin of segment *III*, but it is a complete segmental annulus connecting the "postabdomen" with the propodeum, and must be included in the enumeration of the segments.

The cynipoid phallus is characterized by the union of the volsellar plates with the parameral plates, and by the presence of only one pair of volsellar lobes, which resemble those of the Chalcidoidea, and are evidently the digiti. The phallic structure is comparatively generalized in *Ibalia maculipennis* (pl. 9 K, L), in which species the parameres (*Pmr*) are of usual form, and the volsellar plates (L, *lv*) are partially demarked from the parameral plates (*lp*). In *Diplolepis multispinosus* and *Figites quinquelineata* the parameral and volsellar plates are entirely confluent on each side (M); the parameres are slender in both species, short in the second (Q). The aedeagus is simple in form, variable in length according to the length of the parameres, but in the three species illustrated it is somewhat longer than the parameres (K, L, M, *Aed*). The volsellar digiti are small, flattened; movable lobes arising from the ends of the volsellar plate areas (K, M, Q, *dig*), and are turned upward from the latter (J, N, P) at the base of the aedeagus (K). Each digitus is toothed on its dorsal margin, and is provided with a flexor muscle (J, P, *mcl*) arising anteriorly on the region of the united parameral and volsellar plates.

VII. SERPHOIDEA

Loboscelidia defecta Kief. (pl. 10 A, B), *Serphus florissantensis* Roh. (pl. 10 C-G), *Pelecinus polyturator* (Dru.) (pl. 10 H-L), *Ashmeadopria* sp. (pl. 10 M), *Trichopria cubensis* Fouts (pl. 10 N), *Galesus manilae* Ashm. (pl. 10 O, P), *Scelio calopteni* Riley (pl. 10 Q, R), *Sparasion pilosum* Ashm. (pl. 10 S).

The serphoid abdomen is highly variable in shape and segmentation. A relatively simple type of structure is seen in *Pelecinus polyturator* (pl. 10 H), in which the segments are distinct and not unusually different in size. The last exposed segmental plates are tergum *VIII* above and sternum *IX* below, but tergum *IX* is a well-developed plate

(I, *IXT*) concealed beneath tergum *VIII*, and beyond it is a small anal segment (*X*), without pygostyles. Sternum *IX* is closely connected with sternum *VIII*, and bears a long median apodeme (I, *aps*). In *Serphus florissantensis* (C) the abdomen has a large anterior dorsal plate evidently composed of three united terga (*II*, *III*, *IV*); behind this are four free tergal plates, of which the last is clearly tergum *VIII*, since there is concealed beneath it the usual complex of tergum *IX* and segment *X*, the latter bearing a pair of small setigerous pygostyles. The long anterior ventral plate appears to include sterna *II*, *III*, *IV*, and *V*; the subgenital plate is sternum *VIII*. In the pear-shaped abdomen of *Galesus manilae* (O) segment *II* forms the peduncle, the tergum of segment *III* covers the rest of the dorsum; on the venter, sternum *III* is the principal plate, but is followed by a series of narrow sclerites representing sterna *IV* to *IX*. The abdomen of *Scelio calopteni* (Q) has a regular segmentation, ending at the apex with tergum *IX* above and sternum *VIII* below, sternum *IX* being a small plate concealed above sternum *VIII*.

The phallus of the serphoids attains the highest degree of modification and specialization to be found in all the Hymenoptera. A progressive union takes place between the aedeagus and the volsellae, which, accompanied finally by an elimination of the parameres, converts the phallus into a single, two-segmented shaft composed of the basal ring of the caulis, and of the united aedeagus and volsellae. A simple generalized phallic structure occurs in *Lobosclidia defecta* (pl. 10 A). Here the volsellar plates (*lv*) lie between the parameral plates (*lp*), and each is produced into two free lobes (B). It is difficult to identify the volsellar lobes, but the short median one (*dig*) may be regarded as the digitus, and the longer, lateral one (*cus*) as the cuspis. The aedeagus is entirely free from the volsellae, and its lateral sclerites end in two free points (A, *Aed*). In *Serphus florissantensis* the phallus is elongate and slender (F, G); on its ventral surface (G) are plainly exposed the long median volsellar plates (*lv*), each bearing a single terminal lobe (*dig*), which, being freely articulated on the supporting plate, is probably the digitus. The slender aedeagus projects from between the volsellar plates (G, *Aed*), but dissection reveals that the distal ends of the latter are united with it (E). The small, upturned digiti (*dig*), therefore, closely embrace the free distal part of the aedeagus. Proximally the aedeagus has a pair of large divergent lateral apodemes (E, *apa*), and its dorsal wall contains a slender median rod (*c*).

The association of the volsellae with the aedeagus is carried much farther in *Pelecinius polyturator*, in which the volsellar plates (pl. 10 L,

lv) are united with the entire ventral surface of the aedeagus, though they retain narrow basal connections with the parameral plates (*lp*). As a result, the aedeagus and the volsellae together form a thick median shaft of the phallus, on the dorsal surface of which are the long, slender aedeagal sclerites (*J, K, pv*) terminating proximally in the aedeagal apodemes (*J, apa*), and on the ventral surface the volsellar plates (*J, L, lv*) bearing distally the toothed digiti (*dig*) turned upward at the base of the free terminal part of the aedeagus.

In the family Diapriidae the aedeagal and volsellar elements of the phallus have become so thoroughly unified, as shown in *Ashmeadopria* sp. (pl. 10 M) and in *Trichopria cubensis* (N), that they have almost lost their identities in the median aedeago-volsellar shaft (*A-V*) of the genital organ. The aedeagal apodemes (*apa*), however, project from the base of the shaft, the free part of the aedeagus forms a terminal median lobe (*Aed*), and at the base of the latter are attached ventrally the volsellar digiti (*dig*). The individuality of the aedeago-volsellar shaft is still further accentuated by the deep separation of the parameres (*Pmr*), which are split off from the median parts almost to the basal ring. An extreme condition of the phallic modification in the Diapriidae is found in the genus *Galesus*, here illustrated in *G. manilae* (pl. 10 P). The phallus, which is retracted far into the abdomen, consists of three long, slender, curved rods arising from a small common base. The median rod (*Aed*) must be the aedeagus at least, no volsellar elements being evident in its composition; the lateral rods are the parameres (*Pmrs*).

Finally, in the family Scelionidae, the last stage in the evolution of the serphoid phallus is reached, in which the genital organ is further simplified by the elimination of the parameres (pl. 10 R, S). The phallus thus comes to consist of a proximal segment formed of the long basal ring (*BR*), and of a distal segment, which is the aedeago-volsellar shaft (*A-V*). The latter bears the volsellar digiti (*dig*) on its ventral surface, and ends with the free apical lobe of the aedeagus (*Aed*). Other genera having this same type of phallic structure, including *Microphanurus*, *Telenomus*, and *Nardo*, are illustrated by Nixon (1936, 1937, 1938).

VIII. FORMICOIDEA

DORYLIDAE—*Eciton coccum* (Latr.) (pl. 12 A-G); PONERIDAE—*Paraponera clavata* (F.) (pl. 12 H-O); PSEUDOMYRMIDAE—*Pseudomyrma gracilis* (F.) (pl. 13 D-I); MYRMICIDAE—*Pogonomyrma barbatus* (F. Sm.) (pl. 12 P-S; pl. 13 A-C); DOLICHODERIDAE—

Liometopum sp. (pl. 11 H-O); FORMICIDAE—*Formica* sp. (*fusca* group) (pl. 11 A-G).

The last exposed segmental plates of the abdomen of male ants are tergum *VIII* and sternum *IX* (pl. 11 A, I; pl. 12 A, I, P; pl. 13 D), but the membranous tenth segment may project beyond the eighth tergum. Tergum *IX* is always concealed. It may be a transverse plate in the dorsum at the base of the tenth segment (pl. 12 H), but generally it is much constricted medially (pl. 12 Q), or separated into a pair of lateral sclerites (pl. 11 D, J; pl. 13 F). The tenth segment is always membranous, and usually bears a pair of pygostyles at the sides of the anus (pl. 11 D, J; pl. 12 H, Q; pl. 13 F), but in *Eciton* (pl. 12 B) pygostyles are absent. The functional anal aperture (*An*) leads into a small anal vestibule (pl. 11 D, *anv*), within which the rectum (*Rect*) opens anteriorly. Sternum *VIII* is never entirely concealed, and it undergoes relatively little modification in form (pl. 12 C, J, R; pl. 13 E); sternum *IX* is more variable in shape, though usually conservative (pl. 11 E, K; pl. 12 G, K, S; pl. 13 E).

The phallus of Formicoidea is relatively large and protrudes at the end of the abdomen between the eighth tergum and the ninth sternum. In the Dolichoderidae it attains an extraordinary size (pl. 11 I, *Phl*); structurally its greatest modifications occur in the Dorylidae (pl. 12 D). A generalized condition of the organ is shown in *Formica* (pl. 11 F, G), in which all the usual phallic parts are present in relatively simple form. The aedeagus (*Aed*) appears to be slender in dorsal or ventral view; from the side (C) it is seen that its lateral plates (*pv*) are broad dorsoventrally, and serrated on their lower margins. Each volsella (B) has large digital and cuspidal lobes, the cuspis (*cus*) being a direct continuation of the volsellar plate (*lv*), while the long base of the digitus (*dig*) is hinged to the dorsal margin of the plate.

The huge phallus of *Liometopum* sp. (pl. 11 I, *Phl*) shows no unusual feature other than that of size, its form being simple when seen from above or below (M, N). The aedeagus (*Aed*) is relatively short, but exceptionally deep in a vertical plane (H). The volsellae are mostly concealed from below by ventral lobes of the parameral plates (N, *o*), but they have the usual position against the inner faces of the basiparameral lobes (L). The slender basal plate of each organ (O, *lv*), terminating in a small cuspis (*cus*), lies horizontally and only its inner edge is visible in a direct mesal view (L); the large dorsal plate seen in this figure (L) is the base of the digitus (*dig*).

The unusual appearance of the phallus in *Eciton coecum* (pl. 12 D) results from the large size of the cup-shaped basal ring (*BR*), the

partial invagination of the parameral plates (*lp*) into the basal ring, and the form of the broadly expanded, petiolate parameres (*Pmr*). Both the aedeagus (*F*) and the volsellar digiti (*E, dig*), however, are also exceptional in shape. The volsellar plates are small and have no cuspidal lobes (*E, lv*), but the digiti are long, slender arms (*D, E, dig*), each with a large dorsal branch near its distal end.

In *Paraponera clavata* (pl. 12 L, M), *Pogonomyrmex barbatus* (pl. 13 A), and *Pseudomyrma gracilis* (pl. 13 H, I), the phallus presents no striking features, though the parameres, the aedeagus, and the volsellae have distinctive characters. The volsellae of the first species are of typical structure (pl. 12 N), and are freely exposed between the aedeagus and the parameres (L, M). In the second species volsellar cuspides appear to be absent (pl. 13 B), each volsellar plate (*lv*) bearing only a large hooked digitus (*dig*) lying against the inner face of the corresponding paramere (*Pmr*). In *Pseudomyrma gracilis* the volsellae are greatly reduced (pl. 13 G), the basal plate of each organ being a slender sclerite (*lv*) attached to the lower margin of the corresponding parameral plate (*lp*), bearing only a single, small, setigerous lobe, the digitus (*dig*).

IX. CHRYSIDOIDEA

Chrysis kansensis Vier. (pl. 13 J-N), *Chrysis conica* Brullé (pl. 13 O), *Parnopes edwardsii* (Cress.) (pl. 13 P, R), *Holopyga ventralis* (Say) (pl. 13 Q).

The abdomen of the chrysidoids consists of an anterior visceral region composed of three, four, or sometimes five segments (pl. 13 J, L), and of a concealed genital cone including the other segments and containing the phallus. The exposed tergal plates have ventral flaps, or laterotergites (*L, ltg*), which, except the first, bear the spiracles. The first sternal plate (*L, IIS*) is divided transversely, but the two parts do not represent two segments. The genital cone contains five or six segments, according as there are four or three exposed segments in the visceral region. The tenth segment is much reduced and lacks pygostyles.

The phallus of the chrysidoid species above listed has a simple form, but presents the unusual feature of having the parameral plates completely united on the dorsal surface of the caulis (pl. 13 M, R, *lp, lp*). The slender parameres (*Pmr*), therefore, are articulated on the lateral angles of a common parameral plate. The aedeagus of *Chrysis kansensis* (M, *Aed*), *C. conica* (O), and *Holopyga ventralis* is elongate, deeply cleft distally, and bears proximally a pair of short apodemes

(O, *apa*) and prominent basal processes (*e*). In *Parnopes edwardsii*, on the other hand, the aedeagus is short and broad (P, R). The volsellae of *Chrysis* and *Holopyga* consist principally of two pairs of elongate lobes lying at the sides of the aedeagus (M). The larger lobe of each pair (N, Q, *cus*), being continuous from the small volsellar plate (*lv*), is evidently the cuspis; the slenderer, articulated lobe (*dig*) is hence the digitus, but in *Holopyga* (Q) it overlaps the base of the cuspidal lobe and has a lateral position. In *Parnopes edwardsii* the volsellae are reduced to a single pair of small weak lobes projecting beneath the base of the broad aedeagus.

X. MUTILLOIDEA

Dasymutilla sp. (pl. 14 A-F), *Scolia nobilitata* F. (pl. 14 G-L), *Myzine quinquecincta* (F.) (pl. 14 M-S). These three species, representing the families Mutillidae, Scoliidae, and Typhiidae, respectively, are described separately because they have in common no genital features that are characteristic of the superfamily.

Dasymutilla sp.—The abdomen (pl. 14 A) is strongly constricted between segments II and III, and terminates with tergum VIII above and sternum IX below. Sternum IX (B) is of simple form and bears a long median anterior apodeme (*aps*). The concealed dorsum of segment IX contains two lateral tergal plates (B, *IXT*) separated on the back by a membranous area, which is continuous posteriorly with the small membranous anal cone of the tenth segment (X). At the sides of the anal cone, behind the lateral parts of the ninth tergal plates, are two small sclerites bearing a pair of long, densely setose appendages (*Pgs*). The appendages are evidently the pygostyles since their supporting sclerites are attached to the sides of the anal cone and are prolonged anteriorly in the dorsal wall of the genital chamber. The phallus of *Dasymutilla* (D, E) is slender; the basal ring (*BR*) is elongate, the parameres (*Pmr*) long and tapering, and the parameral plates (*lp*) have dorsal parapenial lobes (D, *pa*) and shorter ventral lobes (E, *o*) concealing the base of the aedeagus (*Acd*). The short aedeagus has deep lateral plates (C) ending in decurved points, between which is a median lobe bearing the phallotreme. The volsellae consist principally of the slender digital and cuspidal lobes seen projecting between the parameres beyond the end of the short aedeagus (D, E, *dig*, *cus*). The basal plate of each organ (F, *lv*) is little more than the base of the cuspis (*cus*) attached distally to the lower margin of the corresponding parameral plate (*lv*), and giving insertion to a large muscle (*19*) arising proximally on the parameral plate. The rodlike digitus (*dig*) is attached mesally on the volsellar plate.

Scolia nobilitata F.—In this species the apex of the abdomen (pl. 14 G) is formed by tergum *VIII* above and sternum *VIII* below, the small three-pronged ninth sternum (G, H, *IXS*) being almost entirely concealed by retraction above the eighth. The tergum of segment *IX* is a transverse dorsal plate (H, *IXT*) at the base of the small anal tube of segment *X*. Pygostyles are absent. The phallus (*Phl*) is protractile on an ample basal membrane. The form of the phallus (J, K) is quite different from that in *Dasymutilla*, the parameres (*Pmr*) being relatively short and broad, parapenial lobes absent, and the aedeagus longer. The lateral plates of the aedeagus are strongly serrate below (I, *pv*) and enclose between them a deep ventral groove, at the base of which is the phallotreme (*Phtr*). The volsellae are of particular interest. Each volsella consists of a single large, strongly muscled lobe (L, *cus*), the base of which clearly represents the volsellar plate (*lv*) because it contains a small intrinsic muscle (*21*). The free part of the lobe is therefore the cuspis, and the digitus is absent. Except for the absence of the digitus, the volsella of *Scolia* thus has the same character as that of *Dasymutilla* (F).

Mysine quinquecincta (F.).—The ninth abdominal sternum of this species (pl. 14 M, *IXS*) is mostly exposed, since its distal part, proceeding from a small, concealed basal plate (O), consists of a long tapering spine curving upward behind the apex of the abdomen formed by tergum *VIII*. The concealed ninth tergum (N) is a small triangular plate with a pair of basal arms. Projecting from beneath its posterior margin are seen the small pygostyles of the tenth segment. The form and structure of the phallus are shown at P, Q, and S. The parameral plates (P, Q, *lp*) are so deeply separated from the long slender aedeagus (*Acd*) that their distal parts form a pair of independent basiparameral lobes. The elongate parameres (*Pmr*) are produced distally from the ventral angles of the parameral plates (Q, S), and the broad cuspidal lobes of the volsellae (S, *cus*) project at the sides of the aedeagus above the parameres. The volsellae are of more typical structure in *Mysine* than in either *Dasymutilla* or *Scolia*. Each has a broad basal plate (R, *lv*) produced distally into a large cuspidal lobe (*cus*), and armed on its mesal surface with a close series of strongly sclerotized, fine-toothed ridges. The digitus (*dig*) is articulated dorsally on the volsellar plate, and bears on its ventral margin a row of strong spines.

XI. BETHYLOIDEA

Pristocera armifera (Say) (pl. 15 A-D), *Goniozus hortorum* Brues (pl. 15 E, F), an unidentified gonotopodine male (pl. 15 G). These

species show the principal types of phallic structure found in the superfamily, but the genitalia of a much larger series of species are illustrated by Richards (1939).

The exposed part of the bethylid abdomen usually ends with the tergal and sternal plates of segment *VIII*, the ninth sternum being generally small, concealed above the eighth, and closely associated with the under side of the phallus. In *Pristocera armifera* (pl. 15 A), however, sternum *IX* is well exposed behind sternum *VIII*. Pygostyles are absent in the species examined.

The phallus of *Pristocera armifera* (pl. 15 B, C) is not in all respects typical of the phallic organ of other bethylid species. The basal ring (*BR*) is extremely narrow, the parameral plates are much reduced on the dorsal surface (*B, lp*), and the apparent volsellar plates are united with their ventral mesal margins (*C, lv*). The parameres are movable lobes (*Pmr*), each provided with a muscle from the corresponding parameral plate inserted on the mesal angle of its base. The broad aedeagus (*Acd*) is set deeply into the emargination between the parameral plates. The volsellar lobes are of particular interest because the immovable lobe, continuous from the volsellar plate, is mesal in position (*B, C, cus*), and the movable lobe (*dig*) is lateral. The insertion of the volsellar muscles on the mesal lobe (*D, cus*), however, leaves little doubt that this lobe is the cuspis, and that the movable lateral lobe (*dig*) is the digitus, since this is the usual insertion of the volsellar muscles, but the reversed position of the two lobes is difficult to explain.

Most bethylid species have a well-developed basal ring in the phallus (pl. 15 E, F, G, *BR*), and large volsellar plates (*F, G, lv*) overlapped by the ventral edges of the parameral plates (*lp*), and usually divided each by a prominent volsellar ridge (*G, vr*) into lateral and mesal areas. In *Goniozus hortorum* (*E, F*) each volsellar plate bears two terminal lobes (*cus, dig*), of which, by comparison with *Pristocera armifera* (*D*), the inner would appear to be the cuspis, and the outer the digitus. Several species of bethylids illustrated by Richards (1939, figs. 32, 37, 84) are shown to have two distinct volsellar lobes on each side, and in such cases it is the lateral lobe that is articulated on the volsellar plate.

The most common type of volsellar structure in the Bethyloidea is here illustrated in an unidentified gonotopodine male (pl. 15 G). The large volsellar plates (*lv*) are entirely free from the parameral plates (*lp*), which normally are closer together and overlap a greater area of the volsellar plates than shown in the figure. Each volsellar plate has a strong, obliquely longitudinal volsellar ridge (*vr*), and bears a

single terminal lobe (*dig*), which is freely movable on the plate, and is hence identified as the digitus, though in species having also an immovable lobe the latter projects from the mesal part of the volsellar plate. Further examples of this type of phallic structure are shown by Richards (1939, figs. 41, 47, 53, 57, 60, 66, 72, 75, 82, 90).

XII. VESPOIDEA

Cryptocheilus unifasciatus (Say) (pl. 15 H-Q), *Monobia quadridens* (L.) (pl. 16 A-D), *Odynerus* sp. (pl. 16 E-H), *Polistes canadensis annularis* (L.) (pl. 16 I-P), *Vespula maculata* (L.) (pl. 17 A-H), *Vespa crabro* L. (pl. 17 I-Q; pl. 18 A-D).

The exposed part of the male abdomen in Vespoidea ends with tergum *VIII* above and sternum *IX* below (pl. 15 H; pl. 16 E, I; pl. 17 A), but sternum *VIII* is never visible externally, so the venter of the "postabdomen" appears to have only seven sternal plates corresponding (deceptively) with the seven exposed tergal plates of the dorsum. Sternum *VIII* is much reduced in size and is concealed above sternum *VII* (pl. 15 J) at the base of sternum *IX*, with which it is either closely connected by membrane (pl. 16 P) or firmly united (pl. 16 C, F; pl. 17 B, C, I, L). Sternum *IX* is variable in shape, but it always has a prominent median basal apodeme (pl. 15 K, *aps*), which projects forward above sternum *VIII* regardless of the connection of the latter with sternum *IX* (pl. 16 C, F, P; pl. 17 B, C, I, L). The intimate association of the reduced and concealed eighth abdominal sternum with the base of the ninth sternum is a characteristic feature of the Vespoidea, but it occurs also in the genus *Apis* of the Apoidea (pl. 33 C, D), though in *Apis* the ninth sternum has no basal apodeme. Tergum *IX* of the vespooid abdomen is represented only by a pair of lateral sclerites in the dorsal wall of the genito-anal chamber (pl. 17 B, I, J, K, *IXT*), which connect proximally with the basal angles of sternum *IX* (B, I), and may extend distally into the dorsal wall of the proctiger at the base of the free anal lobe (B, J, *IXT*). A pair of small pygostyles is present in *Cryptocheilus unifasciatus* at the sides of the anus.

The phallus of the Vespoidea is highly variable in structure, but appears to have no feature distinctive of the group, though in the Vespidae the volsellae attain a type of structure characteristic of this family. The following examples will illustrate the structural variations and specializations of the vespooid phallus.

Cryptocheilus unifasciatus (Say).—The phallus seen from above (pl. 15 I) presents a long basal ring (*BR*), a pair of parameral plates

(*lp*) extended distally into long parapenial lobes (*pa*), lateral parameres (*Pmr*) articulated on the parameral plates, a median bilobed aedeagus (*Aed*), and two mostly concealed volsellar lobes (*dig*). These same parts are shown laterally at N, and are more clearly seen when spread out in ventral view as at L (basal ring omitted). The parameres are not only movably articulated on the parameral plates, but each is provided with a muscle (O). The long slender aedeagus (M) has a pair of divergent basal apodemes (*apa*), and its lateral plates (*pv*) project distally as two long, free spatulate arms. The volsellae are strongly developed (P, Q); each consists of an irregular basal plate (*lv*) attached to the mesal ventral margin of the corresponding parameral plate (L), and of a large quadrangle digital lobe (*dig*). The volsellar digiti project between the aedeagus and the parameres (L, *dig*), though they are mostly concealed from above (I) by the long parapenial lobes (*pa*) of the parameral plates.

Monobia quadridens (L.).—The phallus is elongate and cylindrical (pl. 16 A, B). The lengthened parameral plates (*lp*) are continued into short parameral lobes (*Pmr*), but each bears mesad of the paramere on the dorsal side a long, tapering, spinelike process (*f*), which might be regarded as a modified parapenial lobe, more typically represented in *Cryptocheilus* (pl. 15 I, *pa*), though it can hardly be taken for the paramere. This same parameral spine recurs in *Odynerus*, *Polistes*, and *Vespa*. The slender aedeagus of *Monobia* (pl. 16 A, D, *Aed*) has the usual basal apodemes (D, *apa*), but from its dorsal surface a long, tapering arm (*c*) extends proximally in the membrane uniting the upper parts of the parameral plates. The phallotreme is at the base of a long groove on the ventral side of the aedeagus (D, *Phtr*). The volsellae are well developed; the volsellar plates appear as mesoventral lobes of the parameral plates (B, *lv*), the cuspides are small, scalelike processes (A, *cus*), but the digiti are long lobes (*dig*) loosely articulated on the volsellar plates, diverging distally, and bearing each a broad fringe of bristles on its mesal margin.

Odynerus sp.—The phallus of *Odynerus* (pl. 16 H) more closely resembles the phallus of *Monobia* (A, B) than that of typical vespoids such as *Polistes* and *Vespa*. The parameres (*Pmr*) are relatively short prolongations of the parameral plates, and the parameral spines (*f*), arising mesad of the parameral bases, are long and slender. The volsellar plates are prominent ventral sclerites of the caulis (*lv*) flanking the base of the aedeagus; the cuspides are inconspicuous, the digiti (*dig*) are large, pincerlike lobes crossed above the aedeagus. The aedeagus (G) is narrowly spatulate, and has a median, tapering, basal

arm (*c*) prolonged from the dorsal surface between the lateral apodemes (*apa*).

Polistes canadensis annularis (L.).—The phallus of the Vespidae is a thick and strongly sclerotized organ having a truncate appearance because of the shortness of the parameres (pl. 17 D, E). It is characterized by a special development of the volsellae, particularly of the digital lobes, which latter various writers have mistaken for homologs of the aedeagal sagittae of the bees.

The phallus of *Polistes* (pl. 16 K) is in some respects more generalized than that of *Vespa*, but it has the vespid characteristics. The parameres (*Pmr*) are relatively broad lobes directly continuous from the parameral plates (*lp*), and the parameral spines (*f*) arise dorsally from the mesal margins of the parameral plates (J, L) at the bases of the parameres. The slender aedeagus (M) has the usual basal apodemes (*apa*) and a long median dorsal arm (*c*). The volsellae lie against the inner surfaces of the parameres, the volsellar plates (L, *lv*) forming the mesal walls of the basiparameral lobes. Each volsellar plate is triangular in form (O) with a long ventral base separated by a narrow membranous area from the lower edge of the corresponding parameral plate (L). The distal angle of the volsellar plate represents the cuspis (L, O, *cus*); the anterior angle forms the usual volsellar apodeme (*apv*). A special feature of the volsellar plate, however, is the presence on the dorsal angle of a short, thick apodemal process (J, O, *g*) directed mesally and downward. The digitus is a large, flat, elongate lobe (J, L, *dig*) attached to the dorsal part of the volsellar plate by two basal rami (J, N), one ramus mesal (*mr*), the other lateral (*lr*). The mesal ramus articulates on the upper margin of the volsellar plate (N, O, indicated by arrows); the lateral ramus lies above the dorsal apodeme (*g*) of the volsellar plate (J, *lr*). The volsellar musculature includes four distinct muscles (J, L), three of which are extrinsic, and one intrinsic. Of the former, one is the usual retractor of the volsella (*19*) inserted on the dorsal apodeme (*g*) of the volsellar plate, another is the protractor (*18*) inserted on the anterior apodeme (*apv*), the third (J, *20*) is a muscle observed by the writer only in the vespids, which arises dorsolaterally on the parameral plate and is inserted ventrally on the lower margin of the volsellar plate. The single intrinsic muscle (J, *21*) extends from the anterior apodeme (*apv*) to the dorsal apodeme (*g*) of the volsellar plate.

The volsellar structure described above in *Polistes* is the same in *Vespula* and *Vespa*. There is no possible reason for doubting that the free lobe identified as the digitus pertains to the volsella. It is difficult to understand, therefore, why Boulangé (1924) terms this lobe the

“sagitta” in *Vespa*, and hesitates to identify it with the “pièce en trébuchet” (digitus) of *Chalastogastra*.

Vespula maculata (L.).—The phallus of *Vespula* (pl. 17 D, E) is deeply cleft between the large lateral basiparameral lobes and the broad, median aedeagus. Each basiparameral lobe ends in two small processes, of which the tapering dorsal one (*f*) corresponds with the parameral spine, and the shorter ventral one (*Pmr*) with the paramere of other species. The basiparameral lobes, the outer walls of which are continuous with the parameral plates (*lp*), cannot themselves be the parameres because their mesal walls are formed by the volsellar plates (F, *lv*). The aedeagus (D, E, *Aed*, H) terminates in a pair of falcate processes, proximal to which is the slitlike phallotreme on the ventral surface (H, *Phtr*); its lateral sclerites (*pv*) are prolonged into a pair of basal apodemes (*apa*), and the dorsal wall is produced into a tapering median arm (*c*) extended to the bases of the parameral plates (D, *c*). The volsellae have the same structure and musculature as in *Polistes* (F, G). The basal plate of each organ (*lv*) lies against the inner face of the corresponding basiparameral lobe, and has well-developed anterior and dorsal apodemes (G, *apv*, *g*). The digitus (F, G, *dig*) is of irregular shape, with relatively long basal rami (F, *mr*, *lr*) having the same relations to the volsellar plate (G) as in *Polistes*. The volsellar musculature is strongly developed (G).

Vespa crabro L.—The phallus of *Vespa* (pl. 18 A, B) resembles that of *Vespula*, but the parameres (*Pmr*) and the parameral spines (*f*) are relatively larger, and the aedeagus (*Aed*) is more nearly cylindrical. The elongate aedeagus (C, D) bears distally a pair of spatulate lobes, between the bases of which is the ventral phallotreme (D, *Phtr*); proximally the dorsal aedeagal wall is extended beyond the bases of the apodemes (*apa*) as a broad median plate (A, D, *c*), which abruptly tapers between the approximated basal ends of the parameral plates (A, *lp*) and gives off here two lateral processes (C, *k*) that articulate with the latter. The volsellae differ in no essential respect from those of *Vespula maculata*. The basal plate of each organ (pl. 17 M, O, Q, *lv*) lies against the mesal surface of the corresponding basiparameral lobe, and has the same musculature as in *Vespula* and *Polistes* (Q, muscle 20 shown in N). The free digital lobe is relatively small (O, *dig*), but it is attached to the volsellar plate by long basal rami (O, P, *lr*, *mr*) as in the other two species described.

The specialized structure and strong musculature of the vespid volsellae suggest that these organs play some particularly important part in the copulatory act. The volsellar mechanism, however, is not clear

from an anatomical study, since all the muscles of each organ are inserted on the volsellar plate, and the free digital lobe has no evident means of independent movement. Even the powerful muscles of the volsellar plate can give only slight movements to the volsella as a whole, considering the close membranous connections of the volsellar plate with the basiparameral lobe, but it is perhaps possible that the digitus has a rotary motion on the long hinge line of its mesal ramus (pl. 17 O, *mr*), produced by contraction of the muscles inserted on the dorsal apodeme (Q, *g*), with which the lateral ramus (O, *lr*) is closely associated.

XIII. SPHECOIDEA

Sphécus speciosus (Drury) (pl. 18 E-O), *Megastizus brevipennis* (Walsh) (pl. 19 A-G), *Microbembex monodonta* (Say) (pl. 19 H, Q, R; pl. 20 A, B), *Bicyrtes ventralis* (Say) (pl. 19 I-L), *Bembix spinolae* Lep. (pl. 19 M-P), *Philanthus gibbosus* (F.) (pl. 20 C-E), *Alysson oppositus* Say (pl. 20 F-H), *Zanysson texanus* (Cress.) (pl. 20 I-K), *Astata unicolor* Say (pl. 20 L, M), *Larra analis* F. (pl. 20 N, P, Q), *Crabro interruptus* (Lep.) (pl. 20 O, R), *Cerceris fumipennis* Say (pl. 21 A-E), *Dolichurus stantoni* (Ashm.) (pl. 21 F, G), *Gorytes phaleratus* Say (pl. 21 H-K), *Trypoxylon politum* Say (pl. 21 L, Q, R), *Trypoxylon frigidum* F. Sm. (pl. 21 M-P), *Rhinopsis canaliculata* (Say) (pl. 22 A-D), *Psen kohli* Fox (pl. 22 E-J), *Ammobia ichneumonca* (L.) (pl. 22 K-N, Q, R), *Podalonia luctuosa* (F. Sm.) (pl. 22 O, P, S, T), *Sceliphron caementarium* (Drury) (pl. 23 A-F), *Podium naematogastrum* Spin. (pl. 23 G, I), *Chalybion cyaneus* (F.) (pl. 23 H, J, L), *Sphex* sp. (pl. 23 K, M-R).

The abdomen of the Sphecoidea varies in shape and size largely in correlation with the length of the petiole (pl. 18 E; pl. 19 Q; pl. 21 A, F, H, L; pl. 22 A, E, K; pl. 23 A, H, M). The petiole, regardless of its length, is always the anterior part of segment *II* (first segment of the "postabdomen"), this segment being never given over entirely to the formation of the petiole. Posteriorly the exposed part of the abdomen ends with tergum *VIII* above, and sternum *VII*, *VIII*, or *IX* below according to the retraction of the terminal sternal plates, but sternum *VIII* is never reduced and united with sternum *IX* as in the Vespoidea, nor are sterna *VIII* and *IX* so curiously modified and closely associated with each other as in the Apoidea. Sternum *IX*, however, is sufficiently variable in shape to suggest that it should furnish characters of taxonomic value (pl. 18 I; pl. 19 C, G, H, J, M; pl. 20 D, G, I, M; pl. 21 B, K, M, P; pl. 22 B, I, L, M, O; pl. 23

B, G). The ninth tergum of the Sphecoidea is in some cases a well-developed plate continuous across the dorsum above the base of the tenth segment (pl. 18 H; pl. 19 C; pl. 20 I; pl. 22 M); in others it is incomplete dorsally and divided into two lateral sclerites (pl. 23 C, G, N). The tenth segment is a small membranous lobe beyond the dorsum of segment IX (pl. 19 I, N; pl. 23 C, G, N, X). In some species it bears a pair of slender pygostyles (pl. 22 M; pl. 23 G, *Pgs*); in *Bembix spinolae* these appendages appear to be represented by a pair of thick hairy lobes (pl. 19 N, *Pgs?*). The functional anus (*An*) at the end of segment X is the aperture of a short invagination cavity into which opens the rectum (pl. 19 I).

The phallus of the Sphecoidea is so variable in shape and in the relative size of its parts that no characteristic of form can be ascribed to it (pl. 18 J, K, L; pl. 19 E, F, K, R; pl. 20 E, H, J, L, P, Q, R; pl. 21 C, G, J, N, O, Q, R; pl. 22 D, J, Q, R, T; pl. 23 D, L, O, P). The basal ring opens either anteroventrally, or so directly downward that its ventral margin underlaps the bases of the parameral and volsellar plates (pl. 21 J, R). The parameres (*Pmr*) are usually continuous with the parameral plates, but exceptionally (pl. 20 P, Q), they are partially separated from the latter. In *Trypoxylon politum* (pl. 21 N, O) each parameral plate (*lp*) bears two free parameral lobes (*Pmr*) of equal size. The aedeagus is generally long and cylindrical (pl. 18 O; pl. 19 E, K; pl. 20 E, H, K; pl. 21 D, Q, R; pl. 22 S; pl. 23 E, K), and has well-developed lateral plates, or penis valves (*pv*), which usually project distally as a pair of apical lobes, though they may be deeply separated by a median cleft (pl. 20 E; pl. 22 D, Q). In some species, however, the aedeagus is relatively short (pl. 20 R), and it may consist principally of the terminal lobes (pl. 18 J, K).

The volsellae present perhaps the most characteristic features of the sphecoid phallic complex. The volsellar plates are usually large sclerites entirely free from the parameral plates (pl. 19 F, O; pl. 21 G, J; pl. 22 D, T; pl. 23 P, *lv*), but they are commonly united with each other at their bases by a sclerotic bridge (pl. 18 M, N; pl. 19 L; pl. 23 I, J, Q, *j*), and sometimes there is present between them an intervening basal sclerite (pl. 22 N, P; pl. 23 J, *i*). Each volsellar plate generally bears a well-developed cuspis and digitus, the digitus particularly being variable in size and shape (pl. 18 M, N; pl. 19 L, P; pl. 20 B, C; pl. 22 C, H, N, P; pl. 23 F, I, J, Q). In *Bembix spinolae* (pl. 19 O, P) the cuspis (*cus*) is longer than the digitus (*dig*), but usually the cuspis is relatively small, and may be absent (pl. 20 R;

pl. 21 E). In *Trypoxylon* there is only one pair of volsellar lobes (pl. 21 O, Q, R, *vol*), and it is not clear what part of the volsellae they represent since there are no distinct volsellar plates.

XIV. APOIDEA

The pregenital part of the abdomen of male bees (except in Apidae) ends with the eighth tergum above and the seventh sternum below, and, with species in which the genito-anal chamber is ordinarily closed, it is always sternum *VII* that shuts against the lower margin of tergum *VIII*. Sterna *VIII* and *IX*, tergum *IX*, and the proctiger, or segment *X*, are then concealed within the genito-anal chamber. Tergum *VIII*, however, may be almost completely covered by tergum *VII*, and sternum *VII* may be underlapped by sternum *VI*, or sometimes sternum *V* conceals all the succeeding sternal plates. On the other hand, the genito-anal chamber is not always a closed cavity; when it is open the phallus may be either visible within it, or partly protruding, and the margin of the seventh sternum does not correspond in shape with the lower edge of the eighth tergum. The ninth tergum is represented only by a pair of lateral sclerites in the dorsal wall of the genito-anal chamber. These marginal remnants of tergum *IX* usually extend posteriorly to the sides of the anus, but they have no dorsal connection with each other. The proctiger, or segment *X*, forms the posterior part of the roof of the genito-anal chamber in which usually there is a subanal plate, but only the anal lips of the tenth segment project as a free lobe. Pygostyles are absent. The functional anal opening leads into a secondary invagination cavity having the true rectal opening in its anterior wall. The sternal plates of the genital region are highly variable in form and relative size, but the eighth and the ninth particularly have a tendency to assume unusual and often fantastic shapes. Sternum *IX* is generally retracted above sternum *VIII*, and is closely associated with the ventral side of the phallus, which it supports. Only in Apidae are these two sterna consecutive and united with each other.

The phallus of the Apoidea has the usual hymenopterous structure except in the Apidae, in which family the ectophallus is more or less reduced and the endophallus highly developed. The parameres are either continuous from the parameral plates or articulated on them. The volsellae are always small or vestigial when present, and may be entirely absent. The principal distinctive feature of the apoid phallus pertains to the aedeagus, in which the usual lateral plates, or penis valves, are generally more or less separated from a median penial

lobe to form a pair of free lateral arms commonly known as the *sagittae*. Because of the reduction or absence of the true volsellae, the *sagittae* have sometimes been supposed to be the volsellar lobes, but their aedeagal origin is clearly shown by the fact that they are continuous basally with the aedeagal apodemes on which the usual aedeagal muscles are attached. Moreover, the degree of separation of the *sagittae* from the penis is variable, and the *sagittae* are always attached at least to the base of the latter. It is shown by Zander (1900) in *Bombus* that the *sagittae* are the penis lobes of the phallic rudiments, but that, instead of uniting in the usual way to form an aedeagus, they grow out as two independent processes, which finally unite only at their bases, forming here a median structure around the aperture of the ductus ejaculatorius, which later grows out as the penis. Among the Apoidea all gradations may be found from a condition in which the aedeagus has the usual single structure, to others in which the penis valves project as free processes at the end of the organ, and finally become independent lateral arms, or *sagittae*, but the last condition is that most prevalent in the group.

The order in which the families are given in the following descriptions is approximately that usually followed by taxonomists, but, in the structure of the phallus, the Andrenidae, the Megachilidae, and the Apidae stand apart from the others, because in these three families the penis valves are not separated from the membranous middle part of the aedeagus. It is not here claimed that this feature relates these families to one another, or gives them a generalized status among the Apoidea; the fact mentioned, however, is worthy of attention, since it is not clear how these three groups could separately revert to a generalized condition.

ANDRENIDAE.—*Andrena crataegi* Robt. (pl. 24 A-C, L-P),
Andrena fragilis F. Sm. (pl. 24 D-K).

The sternal plates of segments VIII and IX are retracted in the usual manner and are covered by sternum VII (pl. 24 A). Sterna VII, VIII, and IX of *Andrena crataegi* and of *A. fragilis* are shown at A-C and D-F, respectively. The phallus is of simple form (G, H, L, M); in *A. fragilis* (G) the parameral plates (*lp*) bear dorsally a pair of long parapenial lobes (*pa*) projecting above the aedeagus (*Aed*). Volsellae are present, but much reduced (H, *Vol*); each consists of a small, strongly muscled basal plate (I, J, P, *lv*) and of two free lobes that are evidently the cuspis and the digitus (*cus*, *dig*). The aedeagus is a short, thick structure (K, N, O) with strong basal apodemes (*apa*) and a pair of tapering distal processes, but otherwise the lateral plates, or penis valves, are incorporated in the

body of the organ, so that there are no free sagittal arms of the aedeagus.

PANURGIDAE.—*Perdita octomaculata* (Say) (pl. 24 Q-U), *Halictoides calochorti* Ckll. (pl. 24 V-Y).

The forms of the retracted eighth and ninth sterna of *Perdita octomaculata* are shown at R and S of plate 24, those of *Halictoides calochorti* at V and W. The phallus of these species (Q, Y) is typically apoid in that the aedeagus consists of a median penis and lateral sagittal arms. In *P. octomaculata* the aedeagus (T) has a long undivided basal part, from which the apodemes (*apa*) arise proximally and the sagittae (*sag*) distally, and the bilobed membranous penis (*pen*) projects from beneath the bases of the sagittae; in *H. calochorti* (Y) the penis (*pen*) is short and lies between the bases of the sagittae (*sag*). The small volsellae arise ventrally at the sides of the aedeagus (Q, *Vol*); each organ is two-lobed in *P. octomaculata* (U), but consists of a single lobe in *H. calochorti* (X, *Vol*).

HYLAEIDAE.—*Hylaeus basalis* (F. Sm.) (pl. 25 A-C, G-K), *Hylaeus cressoni* (Ckll.) (pl. 25 D-F, L, M), *Colletes inaequalis* Say (pl. 25 N, O, T-V), *Colletes armatus* Patt. (pl. 25 P-S).

The sternal plates of segments VIII and IX attain highly diversified forms in this family. Those of *Hylaeus basalis* are illustrated at B and C of plate 25, those of *H. cressoni* at D and E, the latter being shown also in their natural superposed position as seen from below at F. The corresponding plates of *Colletes inaequalis* and *C. armatus* are given at N and O, and at P and Q, respectively. The ninth tergum is represented by a pair of lateral sclerites (G, *IXT*) in the membranous dorsal wall of the genito-anal chamber beneath tergum VIII, and between their posterior ends is a median subanal plate (*l*) of the proctiger. The phallus is variable in the size and shape of the parameres and in the form of the sagittae. The parameres are broad, spatulate extensions of the parameral plates in *Hylaeus basalis* (H, I, *Pmr*), tapering lobes in *H. cressoni* (L, M), elongate in *Colletes armatus* (R), oval with apical points in *C. inaequalis* (T). The sagittae are large, free, distal prolongations of the penis valves, generally undivided (L, M, R, T, U, *sag*), but in *Hylaeus basalis* each sagitta is itself bifurcate (I, K, *sag*). The penis is a short median membranous lobe between the bases of the sagittae (U, *pen*). The volsellae are small; in *Hylaeus basalis* each volsella consists of a single lobe resting against the ventral margin of the parameral plate (I, M, *Vol*), but in the two species of *Colletes* there is a distinct basal volsellar plate (*S, lv*) ending with a cuspis (*S, V, cus*) and bearing an articulated digitus (*dig*).

CTENOPLECTRIDAE.—*Macropis ciliata* Patt. (pl. 26 A-G).

Figures A, B, and C of plate 26 give the shapes and relative sizes of the sternal plates of segments VII, VIII, and IX in the single representative studied in this family. The phallus (D) is characterized by the small size of the basal ring (BR), the three-branched form of the parameres (D, E, *Pmr*), the strong development of the sagittae (D, G, *sag*), and the great reduction of the penis (G, *pen*). The inconspicuous volsellae are borne on the ventral margins of the parameral plates beneath the base of the aedeagus (E, *Vol*). Each organ consists of a small basal plate (F, *lv*) set into an emargination of the corresponding parameral plate (*lp*) and invaginated above the latter. The plate is produced into a thick cuspis (*cus*), and bears mesally opposed to the cuspis a short, toothed digitus (*dig*).

ANTHOPHORIDAE.—*Anthophora abrupta* Say (pl. 26 H-N), *Anthophora pallipes*, *Diadasia australis* (Cress.) (pl. 26 O-R), *Tetralonia atriventris* (F. Sm.) (pl. 26 S-V), *Melissodes* sp. (pl. 27 A-E).

The sternal plates of the genital region are variable in the degree of their modifications from relatively simple to complex forms, as seen in *Anthophora abrupta* (pl. 26 H, I, J), *Diadasia australis* (O, P), *Tetralonia atriventris* (U, V), and *Melissodes* sp. (pl. 27 A, B). The phallus (pl. 26 K, L, Q, S; pl. 27 C, D) is characterized by the articulation of the parameres on the parameral plates. In the two species of *Anthophora* (pl. 26 K, L) and in *Melissodes* sp. (pl. 27 C, D) the parameral plates (*lp*) are produced into large basiparameral lobes at the sides of the aedeagus, and the parameres (*Pmr*) are relatively small; in *Anthophora* they appear as mere appendicular processes of the basiparameral lobes (pl. 26 K). The basiparameral lobes themselves, as in *Anthophora pallipes* (not illustrated), may be irregular and branched. A more usual structure is seen in *Diadasia australis* (pl. 26 Q) and in *Tetralonia atriventris* (S). The aedeagus has strongly developed, often irregular sagittae (pl. 26 M, N, R, T; pl. 27 E, *sag*) continuous proximally with the aedeagal apodemes (*apa*). The median penis (*pen*) is a short membranous tube, but at its base is a strong dorsal plate (pl. 26 M, Q, R, S; pl. 27 C, *m*), which supports the bases of the sagittae, and may articulate by lateral extensions with the parameral plates (pl. 26 S; pl. 27 C). Volsellae were not observed in the anthophorid species studied.

NOMADIDAE.—*Nomada bella* Cress. (pl. 27 F-J).

The sternal plates of the genital region in *Nomada bella* are relatively simple (pl. 27 F, G), though sternum IX bears a long, median, distal arm. The phallus, shown in dorsal view at H, presents the usual parts. The parameres (*Pmr*), which are divided each into a larger

dorsal lobe and a smaller ventral lobe (J, *Pmr*), are flexibly articulated on the parameral plates but appear to have no muscles to move them. The volsellae are reduced to a pair of small, simple plates (J, *Vol*) visible from below as two small lobes between the approximated lower edges of the parameral plates. The aedeagus (I) consists of lateral sagittae (*sag*) and a median, tubular, membranous penis (*pen*). The sagittae articulate on the parameral plates by their widely divergent bases (H), which are narrowly bridged through the base of the penis.

MELECTIDAE.—*Melecta armata* (Panz.) (pl. 27 K-Q), *Crocisa crucifera* Ckll. (pl. 27 R-V; pl. 28 A, B), *Triepeolus concavus* (Cress.) (pl. 28 C-N).

Examples of the forms assumed by the genital sterna in this family are shown at K, L, R, and S on plate 27, and at D, F, and G on plate 28. A progressive dissection of the parts of the genital segments is illustrated at C-I on plate 28. In the usual condition (C) the genito-anal chamber at the end of the abdomen is closed by the approximation of sternum *VII* against tergum *VIII*. The seventh sternum itself (D) is largely concealed, but when removed there is exposed above it (E) the entire ventral margin of tergum *VIII*, together with sterna *VIII* and *IX* superposed on each other. Above the sternal plates is the cavity containing the phallus and the proctiger, which cavity is more fully exposed on removal of sternum *VIII* (H), leaving sternum *IX* in its natural position. The phallus being omitted in these figures, there are seen on the roof of the genito-anal chamber two lateral sclerites (H, *IXT*), which are the remnants of tergum *IX*. Finally, on taking away the enclosing eighth tergum (I) it is seen that the dorsal wall of the chamber is prolonged distally beyond the ninth tergal plates (*IXT*) as the ventral wall of a short flattened median tube (*X*), which is the tenth abdominal segment, or proctiger, having the anus at its extremity.

The phallus of the Melectidae resembles that of Anthophoridae and Nomadidae in that the parameres are flexible on the parameral plates, and the sagittae are strongly developed lateral lobes of the aedeagus (pl. 27 M, T; pl. 28 J). In *Crocisa crucifera*, at least, each paramere is provided with a muscle (pl. 28 B) arising on the parameral plate. Volsellae are present but are inconspicuous. In *Melecta armata* and *Crocisa crucifera* each volsella consists of a small basal plate and of two free lobes turned upward (pl. 27 O; pl. 28 A, *Vol*), but the identity of the lobes is not clear. In a ventral view (pl. 27 N, U) the volsellae are seen lying mesad of the bases of the parameres. The sagittae of the aedeagus are variable in form and size (pl. 27

M, Q, T, V; pl. 28 J, M, N, *sag*), as is also the penis (*pen*), which lies between them. In *Triepcolus concavus* the entire aedeagus is particularly large and strongly developed (pl. 28 J, M, N), and is supported from below on a pair of large ventral lobes projecting mesally from the parameral plates (K, L, *o*). The sagittae exceed the parameres in size (J) and the penis (*pen*) extends beyond the sagittae. The lateral walls of the penis are strengthened by a pair of elongate sclerites (J, M, *x*), and the base of the organ contains a transverse dorsal sclerite (*m*) supporting the sagittae laterally. That the lateral sclerites of the penis are not the primary penis valves is evident from the fact that they are not produced into the aedeagal apodemes, which are basal arms of the sagittae (N, *apa*). The phallosome is a large subterminal opening on the ventral side of the penis (N, *Phtr*).

MEGACHILIDAE.—*Megachile* sp. (pl. 28 O-T), *Ashmeadiella bucconis* (Say), *Hoplites albifrons* (Kirby), *Heriades variolosa* (Cress.), *Osmia lignaria* Say, *Prochelostoma philadelphia* (Robts.), *Coelioxys* sp. (pl. 29 A-F), *Coelioxys texana* Cress., *Anthidium porterae* Ckll.

The abdomen ends with tergum *VII*, which is strongly deflexed or produced posteriorly, and generally armed with several spinous processes (pl. 28 O, P; pl. 29 A); but the apex of tergum *VIII* is usually exposed beneath the seventh tergum (pl. 28 O, P) and its lateral parts extend forward to the sides of sternum *VIII* (P, Q). The exposed part of the abdominal venter may end with sternum *V*, but generally sternum *VI* is the last visible sternal plate (pl. 28 O; pl. 29 A). Sternum *VII* may be entirely hidden above *VI*, but it always fits into the concave lower margin of tergum *VIII* and thus closes the genito-anal cavity when the phallus is fully retracted. Sterna *VIII* and *IX* are relatively small and always mostly concealed; sternum *VIII* may be reduced to a narrow plate or transverse bar (pl. 28 Q; pl. 29 C), but sternum *IX* is a triangular or elongate plate (pl. 28 R; pl. 29 C) closely associated with the ventral side of the phallus.

The phallus is usually of simple form with slender parameres and a relatively large aedeagus (pl. 28 S, T; pl. 29 E, F). The ventral surfaces of the parameral plates are characteristically produced into a pair of oval lobes (*o*). These lobes have been regarded as the volsella (see Sandhouse, 1939), but they have none of the features of a volsella, being entirely continuous with the parameral plates and not provided with muscles. They are analogous to the similar ventral lobes of the parameral plates that recur in various hymenopterous

groups, already noted among the bees in the melectid *Tricpeolus concavus* (pl. 28 K, L, o), and which in the megachilid *Anthidium porterae* (not illustrated) attain a length almost equal to that of the parameres themselves. True volsellae are absent in Megachilidae.

The aedeagus of the Megachilidae, as in Andrenidae and Apidae, retains the generalized hymenopterous structure in that its lateral sclerites, or penis valves, are not sufficiently separated from the median part of the organ to form a pair of "sagittae," though their terminal parts may project as free apical processes of the aedeagus (pl. 28 S, T; pl. 29 D). The middle membranous part of the aedeagus is sometimes omitted in taxonomic illustrations (as by Sandhouse, 1939, in *Osmia*) in order to show more clearly the outlines of the lateral sclerites, but this practice is misleading anatomically, and fails to record a characteristic feature of the Megachilidae. Within the aedeagus is an ample endophallic sac opening at the distal end of the median membranous part of the organ.

XYLOCOPIDAE.—*Xylocopa virginica* (L.) (pl. 29 G-M).

The abdomen of the male in *Xylocopa*, as in the other bees, terminates with tergum *VIII* above and sternum *VII* below. When the seventh sternum is removed, therefore, the genito-anal chamber containing the phallus and the proctiger is exposed beneath the eighth tergum (pl. 29 G), and lying anterior to it are seen the eighth and ninth sterna (*VIII*S, *IX*S). These sternal plates, however, instead of having the curious shapes characteristic of most other apoid families, are simple transverse arcs (G, H, I, *VIII*S, *IX*S) except that sternum *IX* has a strong median apodeme (*aps*). Sternum *VIII* lies transversely between the anterior ventral angles of tergum *VIII* (G), but the ends of sternum *IX* curve upward into the dorsal wall of the genito-anal chamber where they meet the anterior ends of a pair of sclerotic bars lying laterally in the dorsal wall of the chamber. These bars (G, *I*X T) are remnants of the ninth abdominal tergum. Each bar (I, *I*X T) is enlarged anteriorly as a small plate (*t*) and is produced posteriorly in a slender arm reaching the side of the anus, but has no dorsal connection with the bar of the opposite side. The region of the tenth segment (G, *X*), or proctiger, is a broad membranous area between the posterior arms of the ninth tergal sclerites, bearing the functional anus (*An*), but only the anal lips project as free lobes. The wide functional anal opening (*An*) leads into an invaginated pocket having the true anus in its anterior wall.

The phallus of *Xylocopa virginica* is short, broad, and strongly sclerotized (pl. 29 J, K). The basal ring (*BR*) is narrow above and below, and is widely open anteroventrally (K); the wide parameral

plates (*lp*) are produced into thick basiparameral lobes, of which the terminal parts may be regarded as the parameres (*Pmr*), though it is questionable if they are properly so designated. Volsellae are absent. The aedeagus (J, *Acd*) is broad and almost rectangular in shape. The strong lateral sagittae (J, K, L, *sag*) are sharply decurved distally (M), produced proximally into the aedeagal apodemes (L, M, *apa*), and bear laterally a pair of basal articular knobs (*e*). The median penis (L, *pen*) is a wide membranous tube, supported basally on a transverse dorsal plate of the aedeagus (*m*), which is united laterally with the bases of the sagittae.

BOMBIDAE.—*Bombus americanorum* (F.) (pl. 29 N, O; pl. 30 A-G), *Bombus lapidarius* (L.) (pl. 29 P).

The rounded end of the male abdomen in *Bombus* is formed by the eighth tergum, against which the seventh sternum closes from below and shuts in the genito-anal chamber, concealing thus within the latter not only the phallus and the proctiger, but also the eighth and the ninth sternal plates. In *Bombus americanorum* sternum *VIII* is a thin, crescent-shaped plate (pl. 29 N) having its lateral angles prolonged to meet the basal angles of tergum *VIII*. Sternum *IX*, which is retracted above sternum *VIII*, is a relatively small, median plate (O, *IXS*) with long basal arms extending laterally and dorsally into the roof of the genital chamber, where they meet the outer branches of the Y-shaped tergal sclerites of the ninth segment (*IXT*). The latter, as in *Xylocopa* (G), have posterior arms extending to the sides of the anus, but are not connected dorsad of the latter.

The phallus of *Bombus* is large and strongly constructed (pl. 29 P; pl. 30 A, B). It consists of a basal ring (*BR*) with a wide ventral foramen, a pair of elongate parameral plates (*lp*) bearing each two small apical parameral lobes (*Pmr*), and an aedeagus with well-developed sagittae (*sag*) flanking the median penis (*pen*). The parameral plates are firmly united dorsally by a strong basal bridge (pl. 30 C).

The two pairs of terminal lobes borne by the parameral plates in the Bombidae have often been regarded as the parameres ("squamae") and the volsellae. A close examination, however, shows that the two lobes of each pair are connected both laterally (pl. 30 F) and mesally (G) by membranes, which leave only the distal parts of the lobes free from each other. This connection suggests that the two lobes are merely subdivisions of the paramere (*Pmr*). The relatively short dorsal lobe (*q*) is articulated to the distal end of the parameral plate (*lp*); the outer wall of the ventral lobe (*r*) is extended proximally as a long sclerite articulated basally on the ventral margin of the

parameral plate (B, G), and is thus comparable in position with a volsellar plate. The fact, however, that the sclerite in question (*r*) is partially united by membrane with the dorsal parameral lobe (*q*), and has no muscles, while the volsellae are always strongly muscled, would contradict the more superficial evidence of its volsellar nature. Finally, it has been shown by Zander (1900, fig. 5) that the two lobes on each side (*q*, *r*) are formed ontogenetically as secondary subdivisions of the primary "valva externa" (paramere), and that the volsella of *Bombus* is developed at the median ventral angle of the parameral plate, and never becomes more than a minute scale. The true volsellae of *Bombus americanorum*, therefore, are probably the small lobes borne directly on the lower angles of the parameral plates (G, *Vol*). It is scarcely to be supposed that volsellae would be well developed in Bombidae, while in other higher families of Apoidea they are vestigial or absent.

The aedeagus of *Bombus americanorum* has the typical apoid structure (pl. 30 D, E). The penis valves are strong sagittal processes (*sag*) arising laterally at the base of the median penis (*pen*) and continuous proximally with the aedeagal apodemes (*apa*). The thick membranous penis has a dorsal plate (D, *m*) in its base, prolonged distally as a median sclerite (*n*) known as the "spatha" (the "uncus" of Franklin, 1912, 1913), the tip of which projects as a free point over the end of the penis. The phallosome is a large sub-terminal aperture on the ventral side of the penis (E, *Phtr*) and leads into a spacious endophallic sac (Enph). In *B. lapidarius* (pl. 29 P) the aedeagus is of similar structure, though the penis is more slender and the sagittae are longer.

MELIPONIDAE.—*Trigona testacea cupira* (F. Sm.) (pl. 30 H-M), *Trigona compressa* (Latr.) (pl. 30 N, O), *Melipona favosa* (F.) (pl. 31 A-F).

The last exposed segmental plates of the abdomen are tergum *VIII* above and sternum *VII* below (pl. 30 H), but the two plates are not applied to each other, and the terminal parts of the phallus freely protrude from the open genito-anal chamber. Tergum *VIII*, moreover, is small and mostly covered by tergum *VII*; its lateral parts are extended forward as tapering arms in the dorsal wall of the genito-anal chamber (pl. 30 J; pl. 31 D, *VIIIT*). The concealed eighth and ninth sterna (pl. 30 I; pl. 31 A, *VIIIS*, *IXS*) are closely associated with each other in the ventral part of the genital chamber; the elongate ninth sternum is retracted above the eighth and supports the base of the phallus. The tergum of segment *IX*, as in *Xylocopa* and *Bombus*, is represented by a pair of slender lateral sclerites in

the dorsal wall of the genital chamber (pl. 30 J; pl. 31 D, *IXT*) extending posteriorly to the sides of the proctiger (*X*).

The phallus of *Trigona testacea cupira* (pl. 30 K, L), of *Trigona compressa* (pl. 30 N, O), and of *Melipona favosa* (pl. 31 E, F) is simple in form, but the long slender parameres (*Pmr*) arise laterally from the parameral plates (*lp*) and at points near the bases of the latter. Volsellae are absent. The aedeagus consists of a pair of tapering sagittal arms (*sag*) arising from thick bases, and of a median membranous penis (*pen*), the variable size of which suggests that it is partly the everted endophallus. The base of the penis contains a large dorsal plate (pl. 30 K, N; pl. 31 E, *m*) supporting laterally the bases of the sagittae. From the enlarged basal part of each sagitta there extends anteriorly a flat, free dorsal lobe (*s*), either membranous or sclerotic, that partially overlaps the parameral plate (*lp*) of the same side. The opening into the sagitta from the interior of the aedeagus is reduced to a small foramen (pl. 30 M) just behind the basal lobe (*s*), mesad of which arises the short aedeagal apodeme (*apa*). The proximal origin of the parameres on the parameral plates and the presence of the basal lobes of the sagittae constitute two unusual features of the phallus that would appear to be distinctive of the Meliponidae.

APIDAE.—*Apis florea* F. (pl. 31 I, J, L), *Apis indica* F. (pl. 31 H, M, N), *Apis mellifera* L. (pl. 31, G, K, O; pl. 32 A-O; pl. 33 A-D).

The male abdomen of the Apidae ends with the deflected eighth tergum above (pl. 31 G, H, O, *VIIIT*) as in other bees, but the ninth sternum (*IXS*) may be well exposed, though the eighth is always concealed above the seventh. The ninth tergum is reduced to a pair of small sclerites lying laterally in the dorsal wall of the genital chamber (pl. 31 O, *IXT*) anterior to the base of the proctiger (*X*), and each tergite bears internally an apodemal process (K, *apt*) on which muscles are attached. The ninth sternum is well developed in *Apis mellifera* (G, O, *IXS*) and *A. indica* (H, N), though its lateral extremities in these two species are widely separated from the ninth tergal sclerites in the dorsal wall of the genital chamber (N, O, *IXT*). In *A. florea*, on the other hand, the ninth sternum is reduced to a narrow transverse bar (L, *IXS*), but it connects laterally with the ninth tergal sclerites (*IXT*). The concealed eighth sternum is a narrow transverse plate in *A. florea* (*VIIIS*) with tapering lateral apodemes (*ap*); in *indica* and *mellifera* (O) it is attenuated medially and expanded laterally, where it meets the eighth tergum (*VIIIT*), and gives off anteriorly a pair of slender apodemal arms (*ap*).

The male genital organ of the Apidae is characterized by a reduction of the ectophallus and a great elaboration of the endophallus to form a large eversible structure, which becomes the functional intromittent organ usually termed the penis. The ectophallus is so greatly reduced in *Apis indica* and *A. mellifera* that it is difficult to identify its remnants. In *A. florea*, however, the ectophallic parts are retained in almost typical hymenopterous form (pl. 31 I, J), except for the reduction of the parameres and the absence of a differentiated basal ring. The large base of the phallus contains dorsally (I) a pair of parameral plates (*lp*), each of which ends distally in a small lobe (*Pmr*), evidently the reduced paramere, bearing a brush of long setae. The aedeagus is a thick, obtuse median lobe of the phallus with large lateral sclerites, or penis valves (*pv*), provided with the usual basal apodemes (J, *apa*), and embracing distally a wide aperture, the phallotreme (I, *Phtr*), leading into an extensive endophallic sac. Ventrally (J) the base of the phallus is almost entirely occupied by the basal foramen.

Closely associated ventrally with the base of the phallus in *Apis florea* is the narrow, transverse sternal bar of the ninth segment (pl. 31 J, *IXS*). The somewhat expanded lateral parts of the bar present three short branches, one of which on each side adjoins the corresponding lateral sclerite of the ninth tergum (L, *IXT*), while another (*u*), it should be noted particularly (J), abuts against the anterior margin of the ventral part of the parameral plate (*lp*) close to the parameral lobe (*Pmr*). The primitive relations of the ninth sternum to the ninth tergal sclerites and to the base of the phallus that are preserved in *Apis florea* will help to explain certain modifications that have taken place in the other species of *Apis*.

The phallus of *Apis indica* (pl. 31 M) and of *A. mellifera* (pl. 32 A, B) differs from that of *A. florea* principally in the reduction of the parameral plates to small lateral sclerites (*lp*) overlapping the basal angles of the penis valves (*pv*), and the separation of the penis valves by a broad, soft, median dorsal lobe of the phallic integument (*w*) overhanging the phallotreme (*Phtr*), which last is fully exposed when the penis valves are pressed apart (pl. 32 B). Each parameral plate bears a small setigerous parameral lobe (*Pmr*) as in *florea*. Basally each penis valve is produced into a small apodemal arm (pl. 32 N; pl. 33 C, *apa*) on which are inserted a pair of muscles (pl. 33 D, *12*, *13*) arising on the corresponding parameral plate (*lp*). There can thus be little question as to the identity of the genital lobes in these species of *Apis*, which sometimes have been termed "claspers" (Snodgrass, 1925).

The ninth sternal plate of *Apis indica* and *A. mellifera*, though well developed ventrally (pl. 31 G, H, O, *IXS*), does not, as in *florea* (L), extend laterally to the tergal sclerites of its segment, because the parameral plates of the phallus intervene laterally between the sternum and the tergites (N, O, *lp*). It was observed in *florea*, however, that an arm of the sternum on each side (L, *u*) abuts against the base of the parameral plate. In *mellifera* and *indica* a marginal ridge of the parameral plate (M, N, *u*) has the relation of a link between the sternum (N, *IXS*) and the tergite (*IXT*). It would appear, therefore, that the parameral plates of *mellifera* and *indica* have incorporated into their basal parts the primitive lateral arms of the ninth sternum, and this inference is substantiated by the fact that there is attached on the upper end of the basal ridge of each parameral plate a muscle from the eighth sternum (pl. 33 D, *II*), which corresponds with the lateral intersternal muscles (*II*) of the preceding segments (pl. 33 B).

The endophallus is a large and complex organ in each of the three species of *Apis* here studied. Its form in *A. mellifera* and its size relative to that of the ectophallus are shown at D of plate 32. The phallic structure of the Apidae gives no suggestion of derivation from that of any other family of the Apoidea. The apid phallus, as developed in *Apis florea*, would appear to be of a generalized type of structure, since the penis valves are integral parts of the aedeagus. The disparity between the apid phallus and the phallic structure of other bees is nowhere more evident than between the Apidae and the Meliponidae.

The development of the ectophallus of *Apis mellifera* has been followed in detail by Michaëlis (1900) and by Zander (1900). The principal stages in the growth of the organ are readily seen in whole specimens. A late larval instar shows on the ventral side of the ninth abdominal segment a small oval genital disk with two slight thickenings (pl. 32 F, G, *gd*). Beneath the disk, however, in the integument of the succeeding instar developing within the external skin, there is a small oval pit (H) containing a pair of rounded lobes, which are the phallic rudiments. With later development these primary phallic lobes unite basally, and divide distally into four secondary lobes. At the transformation to the pupa the immature phallus is exerted and appears now as a thick body with a broad base and four terminal lobes projecting from the end of the pupal abdomen between the proctiger and the ninth sternum (M). Viewed from above (I) or below (J) the pupal phallus is seen to be roughly triangular. The thick median terminal lobes are the penis valves (*pv*) with the slitlike

phallotreme between them; the smaller lateral lobes are evidently the parameres (*Pmr*), while the lateral parts of the broad base of the organ represent the areas of the parameral plates (*lp*). The latter are surrounded at this stage by lateral extensions of the ninth sternum (J, M, *IXS*). In a horizontal section of the pupal phallus (K), Zander shows the rudiments of a pair of aedeagal apodemes (*apa*) arising from the bases of the penis lobes and projecting proximally within the parameral plates ("valvae externae"). The large internal tube of the phallus, termed by Zander the "ductus ejaculatorius," is clearly the endophallus. The pupal organ shows no change externally during the pupal period, but within the pupal cuticula the imaginal organ completes its development and attains the final structure before the pupal skin is shed (L, O). In the mature stage the endophallus has acquired the highly complex form and structure of the eversible "penis" of the drone bee (D, *Enph*).

The general abdominal musculature of *Apis mellifera* is much more strongly developed in the drone than in either the queen or the worker, but in segments *I* to *VI*, inclusive, the same muscles are present in each sex. The entire musculature of the "postabdomen" of the drone, which has been described by Morison (1927), is shown at B of plate 33. In segments *IV*, *V*, and *VI* there are present in each segment *II* muscles, including a pair of spiracular muscles (not shown), but not the fibers of the dorsal and ventral diaphragms. The somatic muscles in any one of these segments comprise three intertergal dorsal muscles (*1, 2, 3*), three tergo-sternal lateral muscles (*6, 7, 8*), and three intersternal ventral muscles (*9, 10, 11*). In segment *VII* there is only one lateral muscle (*7*), and only one ventral muscle, which is the lateral internal ventral (*11*) attached posteriorly on a long apodemal arm (C, D) of sternum *VIII*. Segment *VIII* has but one dorsal muscle (B, *2*), one lateral muscle (*7*), and one ventral muscle (*11*). The last arises laterally on the eighth sternum (B, D) but is inserted posteriorly on the dorsal apodeme of the small parameral plate of the phallus (D, *lp*). This muscle, however, so clearly falls in line with the lateral internal ventral muscles (*11*) of the preceding segments that its identity as one of this series can scarcely be questioned. The muscle relations, therefore, conform with the evidence already given which suggests that the anterior marginal ridge of the parameral plate in *Apis indica* and *A. mellifera* (C, *u*) is derived from the lateral part of the ninth sternum.

The intraphallic musculature of *Apis mellifera* includes on each side only the two small muscles (pl. 33 D, *12, 13*) converging from the parameral plate (*lp*) to their insertions on the apex of the basal

apodeme of the penis valve (*pv*). Their size and position might suggest, as observed by Morison (1927, p. 456), that these muscles represent the external intersternal protractors (B, 9) of the pregenital segments; there can be little doubt, however, that they are remnants of the usual aedeagal musculature of other species. The only other phallic muscle of the honey bee is a slender muscle (D, 17) extending from the apex of the aedeagal apodeme to the mucous gland of the same side, on which it is attached just laterad of the end of the vas deferens.

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ABBREVIATIONS AND LETTERING ON THE PLATE FIGURES

- a*, subapical tooth of penis valve in *Pteronidea*.
Aed, aedeagus.
An, functional anus, probably secondary opening of invaginated eleventh abdominal segment.
av, anal vestibule.
ap, apodeme.
apa, apodema aedeagalis, basal apodeme of aedeagus.
aps, apodema sternalis, median apodeme of ninth abdominal sternum.
apt, apodema tergalis, apodeme of ninth tergum.
apv, apodema volsellaris, anterior apodeme of volsellar plate.
atg, acrotergite.
A-V, aedeago-volsellar shaft.
- b*, "brace" of parameral armature in *Paniscus*.
BR, basal ring, lamina annularis.
- c*, dorsal rod or plate of aedeagus.
Caul, caulis, or phallobase.
Cer, cercus.
cus, cuspis volsellaris, cuspis (distivolsella).
Cx, coxa.
- d*, ventral rod of aedeagus.
Dcj, ductus ejaculatorius.
dig, digitus volsellaris, digitus.
- e*, basal process of aedeagal apodeme (ergot).
Enph, endophallus.
Epm, epimeron.
Eps, episternum.
- f*, parameral spine.
- g*, dorsal apodeme of volsellar plate in Vespidae.
gc, gonocondyle.
GC, genital chamber.
- h*, aedeagal hook in *Berecynthus bakevi*.
- i*, plate between bases of volsellae.
- j*, sclerotic bridge uniting bases of volsellae.
- k*, basal hinge of aedeagus on parameral plate in *Vcspa*.
- l*, subanal plate of segment X.
lp, lamina parameralis, parameral plate of caulis (basiparamere).

lr, lateral basal ramus of digitus.

ltg, laterotergite, or laterotergal area.

lv, lamina volsellaris, volsellar plate of caulis (basivolsella).

m, dorsal plate at base of penis in Apoidea uniting with bases of sagittae.

mcl, muscle.

mr, mesal basal ramus of digitus.

n, plate in dorsal wall of penis ("spatha") in Apoidea.

N₂, mesonotum.

N₃, metanotum.

o, ventral lobe of parameral plate.

p, "pad" of parameral armature in *Paniscus*.

pa, parapenial lobe (dorsal) of parameral plate.

pen, penis, median lobe of aedeagus in Apoidea.

Pgs, pygostyle.

Phl, phallus.

Phtr, phallotreme (aperture of endophallus).

Pl, pleuron.

PLS, pleural suture.

Pmr, paramere.

PN₂, postnotum of mesothorax.

Ptgr, proctiger.

pv, penis valve, lamina aedeagalis.

q, dorsal lamella of paramere in Bombidae.

r, ventral lamella of paramere in Bombidae.

Rect, rectum.

s, basal lobe of sagitta in Meliponidae.

S, sternum.

sag, sagitta, lateral lobe of aedeagus in Apoidea (penis valve).

Sp, spiracle.

t, expanded anterior end of ninth-segment tergite.

T, tergum.

u, process of ninth abdominal sternum in *Apis* adjoining parameral plate, or united with the latter.

v, retractile vesicle, or cupping disk (ventouse), of paramere.

Vd, vas deferens.

vol, volsellar lobe.

Vol, volsella.

vr, volsellar ridge, carina volsellaris.

w, membranous dorsal lip of phallotreme in *Apis*.

x, lateral sclerite of penis in Apoidea.

I-X, abdominal segments, including propodeum.

EXPLANATION OF PLATES

PLATE I

CHALASTOGASTRA

- A, *Macroxyela ferruginca* (Say) (Xyelidae), phallus, dorsal.
- B, same, phallus, ventral.
- C, same, terminal segments, dorsal.
- D, same, aedeagus, dorsal.
- E, same, right parameral plate, paramere, and volsella, mesal.
- F, *Xyela minor* Norton (Xyelidae), abdomen, dorsal.
- G, same, abdomen, ventral.
- H, same, phallus, lower side (dorsal).
- I, same, phallus, upper side (ventral).
- J, same, aedeagus, lateral.
- K, same, right volsella, dorsal.
- L, same, terminal segments, dorsal.
- M, same, paramere, showing muscle (17) of cupping disk (v).
- N, *Gilpinia polytoma* (Htg.) (Tenthredinoidea), abdomen and base of thorax.
- O, *Neodiprion sertifer* (Geoff.) (Tenthredinoidea), terminal segments, dorsal.
- P, *Gilpinia polytoma* (Htg.), terminal segments, dorsal.
- Q, *Neodiprion sertifer* (Geoff.), volsella.
- R, *Gilpinia polytoma* (Htg.), phallus, lower side (dorsal).
- S, same, phallus, upper side (ventral).

PLATE 2

CHALASTOGASTRA

- A, *Pteronidea ribesii* (Scop.) (Tenthredinoidea), abdomen and base of thorax, lateral.
- B, same, terminal segments, lateral.
- C, same, phallus, under side (dorsal).
- D, same, phallus, upper side (ventral).
- E, same, phallus, lateral.
- F, same, right penis valve and muscles, mesal.
- G, same, left penis valve, lateral.
- H, same, right parameral plate, paramere, and volsella, mesal.
- I, same, left volsella, lateral.
- J, *Acantholyda erythrocephala* (L.) (Pamphiliidae), end of abdomen, dorsal.
- K, same, end of abdomen, ventral.
- L, same, terminal segments, dorsal.
- M, same, phallus, dorsal.
- N, same, phallus, ventral.
- O, same, aedeagus, ventral.
- P, *Xiphydria maculata* (Say) (Xiphydriidae), end of abdomen, ventral.
- Q, same, terminal segments, dorsal.

R, same, left volsella, dorsal.

S, *Acantholyda erythrocephala* (L.) (Pamphiliidae), terminal lobes of left volsella, dorsal.

PLATE 3

CHALASTOGASTRA

A, *Sirex abbottii* Kirby (Siricidae), end of abdomen, dorsal.

B, same, end of abdomen, ventral.

C, same, terminal segments, dorsal.

D, same, terminal lobes of left volsella, dorsal.

E, same, aedeagus, lateral.

F, *Xiphydria maculata* (Say) (Xiphydriidae), aedeagus, lateral.

G, *Cephus cinctus* Nort. (Cephoidea), terminal lobes of right volsella, ventral.

H, *Sirex abbottii* Kirby (Siricidae), phallus, dorsal.

I, same, phallus, ventral.

J, *Xiphydria maculata* (Say) (Xiphydriidae), phallus, dorsal.

K, same, phallus, ventral.

L, *Cephus cinctus* Nort. (Cephoidea), posterior part of thorax and base of abdomen, lateral.

M, same, terminal segments, lateral.

N, same, terminal segments, dorsal.

O, same, phallus, dorsal.

P, same, phallus, ventral.

Q, *Trachclius tabidus* (F.) (Cephoidea), phallus, dorsal.

R, same, phallus, ventral.

S, same, end of abdomen, lateral.

T, *Cephus cinctus* Nort., aedeagus, ventral.

PLATE 4

CHALASTOGASTRA

A, *Hartigia trimaculata* (Say) (Cephoidea), phallus, dorsal.

B, same, phallus, ventral.

C, same, left volsella, dorsal.

D, *Orussus sayi* Westw. (Orussidae), left volsella, ventral.

E, same, left volsella, laterodorsal.

F, same, abdomen and base of thorax, lateral.

G, same, terminal segments, dorsal.

H, same, aedeagus, ventral.

I, same, phallus, dorsal.

J, same, phallus, ventral.

ICHNEUMONOIDEA

K, *Megarhyssa lunator* (F.) (Ichneumonidae), phallus, dorsal.

L, same, phallus, ventral.

M, *Ichneumon irritator* F. (Ichneumonidae), terminal segments, dorsal.

N, *Megarhyssa lunator* (F.), end of abdomen, lateral, anal vesicle everted.

O, same, terminal segments, lateral.

- P, same, terminal segments, dorsal.
 Q, same, ninth abdominal sternum.
 R, same, right parameral plate, paramere, and volsella, mesal.
 S, same, right volsella, mesal.
 T, same, left volsella, lateral.
 U, same, aedeagus, ventral.

PLATE 5

ICHNEUMONOIDEA

- A, *Protichneumon grandis* (Brullé) (Ichneumonidae), abdomen, lateral.
 B, same, end of abdomen, ventral.
 C, same, terminal segments, ventral.
 D, same, phallus, dorsal.
 E, same, phallus, ventral.
 F, same, aedeagus, lateral.
 G, same, right parameral plate, paramere, and volsella, mesal.
 H, same, right volsella and muscles, mesal.
 I, same, aedeagus, ventral.
 J, *Therion morio* (F.) (Ichneumonidae), aedeagus, lateral.
 K, same, ninth abdominal sternum.
 L, same, abdomen, lateral.
 M, same, phallus, dorsal.
 N, same, phallus, ventral.
 O, same, ninth abdominal segment and phallus, lateral.
 P, same, right volsella, mesal.
 Q, *Trogus vulpinus* (Grav.) (Ichneumonidae), end of abdomen, lateral.
 R, same, terminal segments and phallus, lateral.
 S, same, ninth abdominal sternum.
 T, same, terminal segments, ventral.
 U, same, phallus, dorsal.
 V, same, phallus, ventral.
 W, same, aedeagus, ventral.
 X, *Megaplectes monticola* (Grav.) (Ichneumonidae), end of abdomen, lateral.
 Y, same, right volsella, mesal.
 Z, same, phallus, dorsal.
 Z', same, phallus, ventral.

PLATE 6

ICHNEUMONOIDEA

- A, *Paniscus* sp. 1 (Ichneumonidae), right parameral plate, paramere, and volsella, mesal.
 B, *Paniscus* sp. 2, mesal surface of right paramere.
 C, *Evania punctata* Brullé (Evaniiidae), abdomen, lateral.
 D, same, phallus, dorsal.
 E, same, phallus, ventral.
 F, same, right volsella, ventral.
 G, *Helcon pedalis* Cress. (Braconidae), left volsella, ventral.
 H, same, abdomen, lateral.

- I, same, phallus, dorsal.
 J, same, phallus, ventral.
 K, *Rogas terminalis* (Cress.) (Braconidae), phallus, dorsal.
 L, same, phallus, ventral.
 M, *Spathius canadensis* (Ashm.) (Braconidae), abdomen, lateral.
 N, same, phallus, dorsal.
 O, same, phallus, ventral.
 P, *Atanycolus rugosiventris* (Ashm.) (Braconidae), abdomen, lateral.
 Q, *Microgaster gelechia* Riley (Braconidae), abdomen, lateral.

PLATE 7

ICHNEUMONOIDEA

- A, *Atanycolus rugosiventris* (Ashm.) (Braconidae), phallus, dorsal.
 B, same, phallus, ventral.
 C, *Microgaster gelechia* Riley (Braconidae), phallus, dorsal.
 D, same, phallus, ventral.
 E, *Atanycolus rugosiventris* (Ashm.), terminal segments, ventral.
 F, *Macrocentrus cerasivoranae* Vier. (Braconidae), abdomen, lateral.
 G, same, ninth abdominal tergum and tenth segment, ventral.
 H, same, phallus, dorsal.
 I, same, phallus, ventral.
 J, same, aedeagus and volsellae, ventral.
 K, *Microgaster gelechia* Riley, terminal segments, ventral.
 L, *Spinaria* sp. (Braconidae), abdomen, lateral.
 M, same, abdomen, ventral.
 N, same, phallus, dorsal.
 O, *Phanerotoma tibialis* (Hald.) (Braconidae), abdomen, lateral.
 P, same, phallus, ventral.
 Q, *Spinaria* sp., phallus, ventral.
 R, *Phanerotoma tibialis* (Hald.), abdomen, ventral.

PLATE 8

ICHNEUMONOIDEA

- A, *Chelonus scriccus* (Say) (Braconidae), abdomen, lateral.
 B, same, abdomen, ventral.
 C, same, terminal segments, ventral.
 D, same, phallus, dorsal.
 E, same, phallus, ventral.

CHALCIDOIDEA

- F, *Berecynthus bakeri* How., propodeum and second segment of abdomen, posterior.
 G, same, abdomen and phallus, ventral.
 H, same, phallus, ventral.
 I, *Callimome* sp., abdomen, lateral.
 J, same, last tergal plate of abdomen and pygostyles.
 K, same, phallus, ventral.

- L, *Callimome sackeni* (Ashm.), phallus, ventral.
 M, *Tetrasticus bruchophagi* Gah., phallus, ventral.
 N, *Pteromalus puparum* (L.), abdomen, dorsal.
 O, same, phallus, ventral.
 P, *Tetrasticus bruchophagi* Gah., abdomen, dorsal.
 Q, *Leucospis affinis* (Say), abdomen, lateral.
 R, same, abdomen, ventral.
 S, same, phallus, dorsal.
 T, same, phallus, ventral.

PLATE 9

CHALCIDOIDEA

- A, *Ormyrus* sp., abdomen, ventral.
 B, same, phallus, ventral.
 C, *Brachymeria ovata* (Say), abdomen, lateral.
 D, *Ormyrus* sp., last tergal plate of abdomen and pygostyles.
 E, *Brachymeria ovata* (Say), phallus, ventral.
 F, *Cheiropachus colon* (L.), phallus, dorsal.
 G, same, phallus, ventral.

CYNIPOIDEA

- H, *Ibalia maculipennis* Hald. (Ibaliidae), abdomen, lateral.
 I, same, ninth abdominal segment, ventral.
 J, same, right half of phallus, mesal.
 K, same, phallus, dorsal.
 L, same, phallus, ventral.
 M, *Diplolepis multispinosus* Gill. (Cynipidae), phallus, ventral.
 N, same, volsellar digitus and supporting ridge.
 O, same, abdomen, lateral.
 P, *Figités quinquelineata* Say (Figitidae), right parameral plate, paramere, and volsella, mesal.
 Q, same, phallus, dorsal.
 R, same, abdomen, lateral.

PLATE 10

SERPHOIDEA

- A, *Loboscelidia defecta* Kief., phallus, ventral.
 B, same, right parameral plate, paramere, and volsella, mesal.
 C, *Serphus florissantensis* Roh., abdomen, lateral.
 D, same, phallus, lateral.
 E, same, aedeagus and left volsella, lateral.
 F, same, phallus, dorsal.
 G, same, phallus, ventral.
 H, *Pelecinus polyturator* (Dru.), abdomen, lateral.
 I, same, terminal segments, lateral.
 J, same, aedeagus and left volsella, lateral.
 K, same, phallus, dorsal.

- L, same, phallus, ventral.
 M, *Ashmeadopria* sp., phallus, ventral.
 N, *Trichopria cubensis* Fouts, phallus, ventral.
 O, *Galesus manilac* Ashm., abdomen, ventral.
 P, same, phallus, lateral.
 Q, *Scelio calopteni* Riley, abdomen, lateral.
 R, same, phallus, ventral.
 S, *Sparasion pilosum* Ashm., phallus, ventral.

PLATE II

FORMICOIDEA

- A, *Formica* sp. (*fusca* group) (Formicidae), abdomen, lateral.
 B, same, right parameral plate, paramere, and volsella, mesal.
 C, same, aedeagus, lateral.
 D, same, terminal segments, dorsal.
 E, same, ninth abdominal sternum.
 F, same, phallus, dorsal.
 G, same, phallus, ventral.
 H, *Lionetopum* sp. (Dolichoderidae), aedeagus, lateral.
 I, same, abdomen, lateral.
 J, same, terminal segments, dorsal.
 K, same, ninth abdominal sternum.
 L, same, right parameral plate, paramere, and volsella, mesal.
 M, same, phallus, dorsal.
 N, same, phallus, ventral.
 O, same, right volsella (flattened), ventral.

PLATE I2

FORMICOIDEA

- A, *Eciton coccum* (Latr.) (Dorylidae), abdomen, lateral.
 B, same, terminal segments, dorsal.
 C, same, eighth abdominal sternum.
 D, same, phallus, ventral.
 E, same, right parameral plate, paramere, and volsella, mesal.
 F, same, aedeagus, lateral.
 G, same, ninth abdominal sternum.
 H, *Paraponera clavata* (F.) (Poneridae), terminal segments, dorsal.
 I, same, abdomen, lateral.
 J, same, eighth abdominal sternum.
 K, same, ninth abdominal sternum.
 L, same, phallus, dorsal.
 M, same, phallus, ventral.
 N, same, right volsella, ventral.
 O, same, aedeagus, dorsal.
 P, *Pogonomyrmex barbatulus* (F. Sm.) (Myrmicidae), abdomen, lateral.
 Q, same, terminal segments, dorsal.
 R, same, eighth abdominal sternum.
 S, same, ninth abdominal sternum.

PLATE 13

FORMICOIDEA

- A, *Pogonomyrmex barbatus* (F. Sm.) (Myrmicidae), phallus, dorsal.
 B, same, right parameral plate, paramere, and volsella, mesal.
 C, same, aedeagus, lateral.
 D, *Pseudomyrma gracilis* (F.) (Pseudomyrmidae), abdomen, lateral.
 E, same, end of abdomen, ventral.
 F, same, terminal segments, dorsal.
 G, same, right parameral plate, paramere, and volsella, mesal.
 H, same, phallus, dorsal.
 I, same, phallus, ventral.

CHRYSIDOIDEA

- J, *Chrysis kansensis* Vier., abdomen, lateral.
 K, same, ninth abdominal sternum.
 L, same, abdomen, ventral.
 M, same, phallus, dorsal.
 N, same, right volsella, mesal.
 O, *Chrysis conica* Brullé, aedeagus, dorsal.
 P, *Parnopes edwardsii* (Cress.), aedeagus, ventral.
 Q, *Holopyga ventralis* (Say), left parameral plate, paramere, and volsella, latero-ventral.
 R, *Parnopes edwardsii* (Cress.), phallus, ventral.

PLATE 14

MUTILLOIDEA

- A, *Dasymutilla* sp. (Mutillidae), abdomen, lateral.
 B, same, terminal segments, lateral.
 C, same, aedeagus, lateral.
 D, same, phallus, dorsal.
 E, same, phallus, ventral.
 F, same, right parameral plate, paramere, and volsella, mesal.
 G, *Scolia nobilitata* F. (Scoliidae), abdomen, lateral.
 H, same, terminal segments and phallus, lateral.
 I, same, aedeagus, ventral.
 J, same, phallus, dorsal.
 K, same, phallus, ventral.
 L, same, right parameral plate, paramere, and volsella, mesal.
 M, *Myzine quinquicincta* (F.) (Typhiidae), end of abdomen, lateral.
 N, same, ninth abdominal tergum, with pygostyles projecting from beneath it.
 O, same, ninth abdominal sternum.
 P, same, phallus (without basal ring), dorsal.
 Q, same, phallus (without basal ring), ventral.
 R, same, right volsella, mesal.
 S, same, phallus, lateral.

PLATE 15

BETHYLOIDEA

- A, *Pristocera armifera* (Say), abdomen, ventral.
 B, same, phallus, dorsal.
 C, same, phallus, ventral.
 D, same, right volsellar lobes, dorsal.
 E, *Goniozus hortorum* Brues, phallus, dorsal.
 F, same, phallus, ventral (parameres spread).
 G, Gonotopodine male of unidentified species, phallus, ventral (parameres spread).

VESPOIDEA

- H, *Cryptocheilus unifasciatus* (Say) (Psamocharidae), abdomen, lateral.
 I, same, phallus, dorsal.
 J, same, seventh and eighth abdominal sterna, dorsal.
 K, same, ninth abdominal sternum.
 L, same, phallus, ventral (basal ring removed, parameres spread).
 M, same, aedeagus, ventral.
 N, same, phallus, lateral.
 O, same, right paramere, mesal.
 P, same, right volsella, mesal.
 Q, same, left volsella, lateral.

PLATE 16

VESPOIDEA

- A, *Monobia quadridens* (L.) (Eumenidae), phallus, dorsal.
 B, same, phallus, ventral.
 C, same, eighth and ninth abdominal sterna, ventral.
 D, same, aedeagus, ventral.
 E, *Odynerus* sp. (Eumenidae), abdomen, lateral.
 F, same, eighth and ninth abdominal sterna, ventral.
 G, same, aedeagus, dorsal.
 H, same, phallus, ventral.
 I, *Polistes canadensis annularis* (L.) (Vespidae), abdomen, lateral.
 J, same, right parameral plate, paramere, and volsella, dorsal (semidiagrammatic).
 K, same, phallus, lateral.
 L, same, right parameral plate, paramere, and volsella, mesal.
 M, same, aedeagus, lateral.
 N, same, digitus of right volsella, removed from volsellar plate (O) as indicated by arrows.
 O, same, right volsellar plate, mesal.
 P, same, eighth and ninth abdominal sterna, ventral.

PLATE 17

VESPOIDEA

- A, *Vespa maculata* (L.) (Vespidae), end of abdomen, lateral.
 B, same, terminal segments, lateral.
 C, same, eighth and ninth abdominal sterna, ventral.
 D, same, phallus, dorsal.
 E, same, phallus, ventral.
 F, same, right volsella and supporting part of parameral plate, mesal.
 G, same, right volsella and muscles, mesal.
 H, same, aedeagus, ventral.
 I, *Vespa crabro* L. (Vespidae), terminal segments, lateral.
 J, same, tenth abdominal segment and ninth tergites, dorsal.
 K, same, tenth abdominal segment and ninth tergites, ventral.
 L, same, eighth and ninth abdominal sterna, ventral.
 M, same, right half of phallus with entire aedeagus, mesal.
 N, same, right half of phallus with aedeagus removed (except right apodeme), showing muscles, mesal.
 O, same, right volsella, mesal.
 P, same, digitus of right volsella, mesal.
 Q, same, right parameral plate, parameral spine (*f*), paramere (*Pmr*), and volsella with volsellar muscles (except *zo* shown at N), mesal.

PLATE 18

VESPOIDEA

- A, *Vespa crabro* L. (Vespidae), phallus, dorsal.
 B, same, phallus, ventral.
 C, same, aedeagus, dorsal.
 D, same, aedeagus, ventral.

SPHECOIDEA

- E, *Sphecius speciosus* (Drury), abdomen, lateral.
 F, same, genital segments, lateral.
 G, same, eighth abdominal segment and exposed apex of ninth sternum, lateral.
 H, same, ninth abdominal segment and phallus, lateral.
 I, same, ninth abdominal segment and phallus, ventral.
 J, same, phallus, dorsal.
 K, same, phallus, ventral.
 L, same, phallus, lateral.
 M, same, volsellae and muscles, dorsal.
 N, same, volsellae, ventral.
 O, same, aedeagus, ventral.

PLATE 19

SPHECOIDEA

- A, *Megastizus brevipennis* (Walsh), end of abdomen, ventral.
 B, same, eighth abdominal segment, lateral.

- C, same, ninth abdominal segment, lateral.
 D, same, aedeagus, right parameral plate, paramere, and volsella, mesal.
 E, same, phallus, dorsal.
 F, same, phallus, ventral.
 G, same, ninth abdominal sternum.
 H, *Microbembex monodonta* (Say), ninth abdominal sternum.
 I, *Bicyrtes ventralis* (Say), tenth abdominal segment, ventral.
 J, same, ninth abdominal sternum.
 K, same, phallus, dorsal.
 L, same, volsellae, ventral.
 M, *Bembix spinolae* Lep., ninth abdominal sternum.
 N, same, tenth abdominal segment, ventral.
 O, same, phallus, ventral.
 P, same, volsellae, ventral.
 Q, *Microbembex monodonta* (Say), abdomen, lateral.
 R, same, phallus, lateral.

PLATE 20

SPHECOIDEA

- A, *Microbembex monodonta* (Say), aedeagus, dorsal.
 B, same, right volsella, mesal.
 C, *Philanthus gibbosus* (F.), right volsella, mesal.
 D, same, ninth abdominal sternum.
 E, same, phallus, dorsal.
 F, *Alysson oppositus* Say, eighth abdominal sternum.
 G, same, ninth abdominal sternum.
 H, same, phallus, dorsal.
 I, *Zanysson texanus* (Cress.), ninth abdominal segment, ventral.
 J, same, phallus, ventral.
 K, same, aedeagus, dorsal.
 L, *Astata unicolor* Say, phallus, ventral.
 M, same, ninth abdominal sternum.
 N, *Larra analis* F., end of abdomen, ventral.
 O, *Crabro interruptus* (Lep.), end of abdomen, ventral.
 P, *Larra analis* F., phallus, lateral.
 Q, same, phallus, ventral.
 R, *Crabro interruptus* (Lep.), phallus, ventral.

PLATE 21

SPHECOIDEA

- A, *Cerceris fumipennis* Say, abdomen, ventral.
 B, same, ninth abdominal sternum.
 C, same, phallus, lateral.
 D, same, aedeagus, lateral.
 E, same, volsellae, ventral.
 F, *Dolichurus stantoni* (Ashm.), abdomen, lateral.
 G, same, phallus, ventral.

- H, *Gorytes phaleratus* Say, abdomen, lateral.
 I, same, eighth abdominal sternum.
 J, same, phallus, ventral.
 K, same, ninth abdominal sternum.
 L, *Trypoxylon politum* Say, abdomen, lateral.
 M, *Trypoxylon frigidum* F. Sm., ninth abdominal sternum.
 N, same, phallus, dorsal.
 O, same, phallus, ventral.
 P, same, ninth abdominal sternum.
 Q, *Trypoxylon politum* Say, phallus, ventral.
 R, same, phallus, lateral.

PLATE 22

SPHECOIDEA

- A, *Rhinopsis canaliculata* (Say), abdomen, lateral.
 B, same, ninth abdominal sternum.
 C, same, penis valve and volsellar lobes.
 D, same, phallus, ventral.
 E, *Psen kohli* Fox, abdomen, lateral.
 F, same, eighth abdominal sternum.
 G, same, aedeagus, lateral.
 H, same, right parameral plate, paramere, and volsella, mesal.
 I, same, ninth abdominal sternum.
 J, same, phallus, ventral.
 K, *Ammobia ichneumonea* (L.), abdomen, ventral.
 L, same, ninth abdominal sternum.
 M, same, ninth abdominal tergum with pygostyles of tenth segment projecting from beneath it.
 N, same, volsellae, ventral.
 O, *Podalonia luctuosa* (F. Sm.), ninth abdominal sternum.
 P, same, volsellae, ventral.
 Q, *Ammobia ichneumonea* (L.), phallus, dorsal.
 R, same, phallus, ventral.
 S, *Podalonia luctuosa* (F. Sm.), aedeagus, dorsal.
 T, same, phallus, ventral.

PLATE 23

SPHECOIDEA

- A, *Sceliphron caementarium* (Drury), abdomen, lateral.
 B, same, ninth abdominal sternum.
 C, same, tenth abdominal segment and ninth-segment tergites, dorsal.
 D, same, phallus, ventral.
 E, same, aedeagus, dorsal.
 F, same, volsellae, ventral.
 G, *Podium naematogastrum* Spin., ninth and tenth abdominal segments, dorsal.
 H, *Chalybion cyaneus* (F.), abdomen, lateral.
 I, *Podium naematogastrum* Spin., volsellae, ventral.

- J, *Chalybion cyaneus* (F.), volsellae, ventral.
 K, *Sphex* sp. aedeagus, dorsal.
 L, *Chalybion cyaneus* (F.), phallus, dorsal.
 M, *Sphex* sp., abdomen, lateral.
 N, same, ninth and tenth abdominal segments, posterior.
 O, same, phallus, dorsal.
 P, same, phallus, ventral.
 Q, same, volsellae, ventral.
 R, same, volsellae and muscles, dorsal.

PLATE 24

APOIDEA

- A, *Andrena crataegi* Robt. (Andrenidae), terminal segments, ventral.
 B, same, eighth abdominal sternum.
 C, same, ninth abdominal sternum.
 D, *Andrena fragilis* F. Sm. (Andrenidae), seventh abdominal sternum.
 E, same, eighth abdominal sternum.
 F, same, ninth abdominal sternum.
 G, same, phallus, dorsal.
 H, same, phallus, ventral.
 I, same, right parameral plate, paramere, and volsella, mesal.
 J, same, volsella.
 K, same, aedeagus, lateral.
 L, *Andrena crataegi* Robt. (Andrenidae), phallus, dorsal.
 M, same, phallus, ventral.
 N, same, aedeagus, ventral.
 O, same, aedeagus, lateral.
 P, same, right volsella, mesal.
 Q, *Perdita octomaculata* (Say) (Panurgidae), phallus (basal ring removed), ventral.
 R, same, eighth abdominal sternum.
 S, same, ninth abdominal sternum.
 T, same, aedeagus, dorsal.
 U, same, left volsella, lateral.
 V, *Halictoides calochorti* Ckll. (Panurgidae), eighth abdominal sternum.
 W, same, ninth abdominal sternum.
 X, same, right parameral plate, paramere, and volsella, ventral.
 Y, same, phallus, dorsal.

PLATE 25

APOIDEA

- A, *Hylaeus basalis* (F. Sm.) (Hylaeidae), seventh abdominal sternum.
 B, same, eighth abdominal sternum.
 C, same, ninth abdominal sternum.
 D, *Hylaeus cressoni* (Ckll.) (Hylaeidae), eighth abdominal sternum.
 E, same, ninth abdominal sternum.
 F, same, eighth and ninth abdominal sterna in relative positions, ventral.

- G, *Hylaeus basalis* (F. Sm.), eighth abdominal tergum, ventral, and dorsal wall of genital chamber with ninth tergites and subanal plate.
 H, same, phallus, dorsal.
 I, same, phallus, ventral.
 J, same, right parameral plate and volsella, mesal.
 K, same, aedeagus, ventral.
 L, *Hylaeus cressoni* (Ckll.), phallus, dorsal.
 M, same, phallus, ventral.
 N, *Colletes inaequalis* Say (Hylaeidae), eighth abdominal sternum.
 O, same, ninth abdominal sternum.
 P, *Colletes armatus* Patt. (Hylaeidae), eighth abdominal sternum.
 Q, same, ninth abdominal sternum.
 R, same, phallus, dorsal.
 S, same, right volsella, ventral.
 T, *Colletes inaequalis* Say, phallus, dorsal.
 U, same, aedeagus, ventral.
 V, same, right volsellar lobes, ventral.

PLATE 26

APOIDEA

- A, *Macropis ciliata* Patt. (Ctenoplectridae), seventh abdominal sternum.
 B, same, eighth abdominal sternum.
 C, same, ninth abdominal sternum.
 D, same, phallus, dorsal.
 E, same, right parameral plate, paramere, and volsella, mesal.
 F, same, left volsella with muscles and part of supporting parameral plate, ventral.
 G, same, aedeagus, ventral.
 H, *Anthophora abrupta* Say (Anthophoridae), seventh abdominal sternum.
 I, same, eighth abdominal sternum.
 J, same, ninth abdominal sternum.
 K, same, phallus, dorsal.
 L, same, phallus, ventral.
 M, same, aedeagus, dorsal.
 N, same, aedeagus, ventral.
 O, *Diadasia australis* (Cress.) (Anthophoridae), eighth abdominal sternum.
 P, same, ninth abdominal sternum.
 Q, same, phallus, dorsal.
 R, same, aedeagus, dorsal.
 S, *Tetralonia atriventris* (F. Sm.) (Anthophoridae), phallus, dorsal.
 T, same, aedeagus, ventral.
 U, same, eighth abdominal sternum.
 V, same, ninth abdominal sternum.

PLATE 27

APOIDEA

- A, *Melissodes* sp. (Anthophoridae), eighth and ninth abdominal sterna in natural relative positions, ventral.
 B, same, ninth abdominal sternum.

- C, same, phallus, dorsal.
 D, same, phallus, ventral.
 E, same, aedeagus, ventral.
 F, *Nomada bella* Cress. (Nomadidae), eighth abdominal sternum.
 G, same, ninth abdominal sternum.
 H, same, phallus, dorsal.
 I, same, aedeagus, ventral.
 J, same, right parameral plate, paramere, and volsella, mesal.
 K, *Melecta armata* (Panz.) (Melectidae), eighth abdominal sternum.
 L, same, ninth abdominal sternum.
 M, same, phallus, dorsal.
 N, same, phallus (aedeagus removed), ventral.
 O, same, right parameral plate, paramere, and volsella, mesal.
 P, same, penis, lateral.
 Q, same, aedeagus, lateral.
 R, *Crocisa crucifera* Ckll. (Melectidae), eighth abdominal sternum.
 S, same, ninth abdominal sternum.
 T, same, phallus, dorsal.
 U, same, phallus (aedeagus removed), ventral.
 V, same, aedeagus, lateral.

PLATE 28

APOIDEA

- A, *Crocisa crucifera* Ckll. (Melectidae), right half of caulis with paramere and volsella (aedeagus removed), mesal.
 B, same, right paramere and muscle, mesal.
 C, *Tricpeolus concavus* (Cress.) (Melectidae), end of abdomen, ventral.
 D, same, seventh abdominal sternum.
 E, same, eighth abdominal segment and enclosed ninth sternum, ventral.
 F, same, eighth abdominal sternum.
 G, same, ninth abdominal sternum.
 H, same, eighth abdominal tergum and ninth sternum exposed in place by removal of eighth sternum, ventral (compare with E).
 I, same, ninth and tenth abdominal segments (phallus removed), ventral.
 J, same, phallus, dorsal.
 K, same, caulis and parameres (aedeagus removed), dorsal.
 L, same, caulis and parameres, ventral.
 M, same, aedeagus, dorsal.
 N, same, aedeagus, ventral.
 O, *Megachile* sp. (Megachilidae), end of abdomen, ventral.
 P, same, seventh and eighth abdominal segments, ventral.
 Q, same, eighth abdominal segment, ventral.
 R, same, ninth abdominal sternum.
 S, same, phallus, dorsal.
 T, same, phallus, ventral.

PLATE 29

APOIDEA

- A, *Cochlioxys* sp. (Megachilidae), end of abdomen, ventral.
 B, same, seventh abdominal sternum.

- C, same, eighth and ninth abdominal segments, with projecting parameres of phallus, ventral.
 D, same, aedeagus, ventral.
 E, same, phallus, dorsal.
 F, same, phallus, ventral.
 G, *Xylocopa virginica* (L.) (Xylocopidae), eighth, ninth, and tenth abdominal segments, with phallus exposed in genital chamber, ventral.
 H, same, eighth abdominal sternum.
 I, same, ninth abdominal sternum, and dorsal wall of genital chamber containing tergites of ninth segment and ending with tenth segment.
 J, same, phallus, dorsal.
 K, same, phallus, ventral.
 L, same, aedeagus, dorsal.
 M, same, aedeagus, lateral.
 N, *Bombus americanorum* (F.) (Bombidae), eighth abdominal sternum.
 O, same, ninth and tenth abdominal segments (phallus removed), with margin of eighth tergum, ventral.
 P, *Bombus lapidarius* (L.) (Bombidae), phallus, dorsal.

PLATE 30

APOIDEA

- A, *Bombus americanorum* (F.) (Bombidae), phallus, dorsal.
 B, same, phallus, ventral.
 C, same, dorsal bridge uniting basal angles of parameral plates.
 D, same, aedeagus, dorsal.
 E, same, aedeagus, ventral.
 F, same, right parameral plate and paramere, lateral.
 G, same, right parameral plate and paramere, mesal.
 H, *Trigona testacea cupira* (F. Sm.) (Meliponidae), abdomen, lateral.
 I, same, eighth and ninth abdominal sterna, ventral.
 J, same, seventh and eighth abdominal terga, with dorsal wall of genital chamber containing ninth tergites, ventral.
 K, same, phallus, dorsal.
 L, same, phallus, ventral.
 M, same, right sagitta of aedeagus, mesal.
 N, *Trigona compressa* (Latr.) (Meliponidae), phallus, dorsal.
 O, same, phallus, ventral.

PLATE 31

APOIDEA

- A, *Melipona favosa* (F.) (Meliponidae), terminal segments exposed by removal of seventh abdominal sternum, showing eighth and ninth sterna in natural relative positions, ventral.
 B, same, eighth abdominal sternum.
 C, same, ninth abdominal sternum.
 D, same, terga of seventh and eighth abdominal segments, and tergites of ninth segment in exposed dorsal wall of genital chamber, ventral.

- E, same, phallus, dorsal.
 F, same, phallus, ventral.
 G, *Apis mellifera* L. (Apidae), end of abdomen, ventral.
 H, *Apis indica* F. (Apidae), abdomen, ventral.
 I, *Apis florea* F. (Apidae), phallus, dorsal.
 J, same, phallus, ventral.
 K, *Apis mellifera* L., left tergite and apodeme of ninth abdominal segment.
 L, *Apis florea* F., eighth and ninth abdominal sterna, and ninth-segment tergites, ventral.
 M, *Apis indica* F., phallus, dorsal.
 N, same, sternum and tergites of ninth abdominal segment, with intervening parameral plates of phallus, posterior.
 O, *Apis mellifera* L., end of abdomen, posterior, showing phallic plates and phallotreme exposed between tenth segment and ninth sternum.

PLATE 32

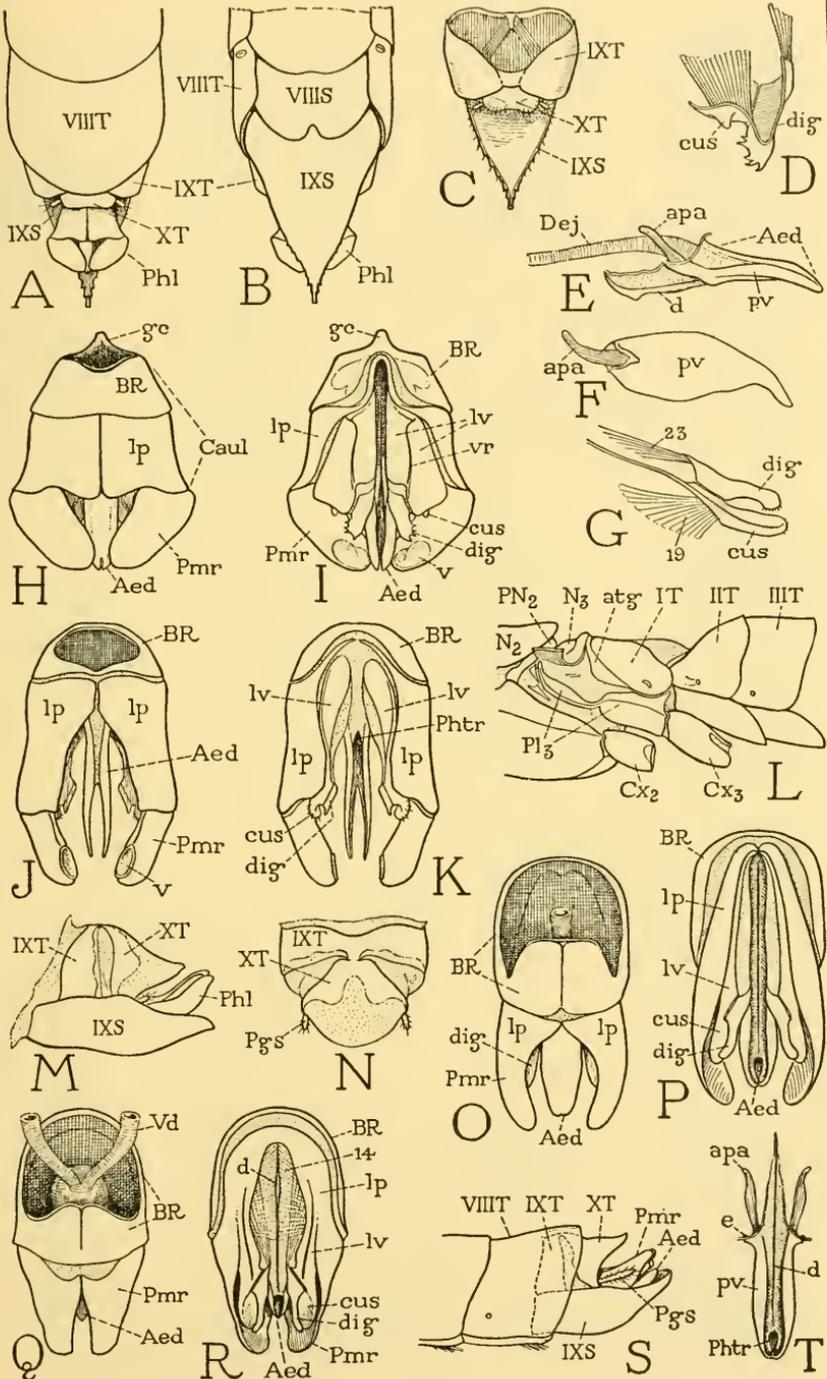
APOIDEA

- A, *Apis mellifera* L. (Apidae), phallus, dorsal.
 B, same, phallus, valve plates (*pv*) separated, dorsal.
 C, same, right parameral plate and parameral lobe.
 D, same, ectophallus and endophallus, dorsal.
 E, same, plates in wall of endophallic bulb.
 F, same, end of abdomen of male larva, 18 mm. long, lateral.
 G, same, end of abdomen of same larva, ventral.
 H, same, primary phallic lobes of larva in "peripodal" pit exposed by removal of outer cuticula.
 I, same, phallus of pupa, dorsal.
 J, same, phallus of pupa, ventral.
 K, same, ventral half of pupal phallus cut horizontally (from Zander, 1900).
 L, same, end of abdomen of immature male imago removed from pupal cuticula, lateral.
 M, same, end of abdomen of male pupa, posterior.
 N, same, right phallic plates of fully matured imago, mesal.
 O, same, end of abdomen of immature imago, posterior.

PLATE 33

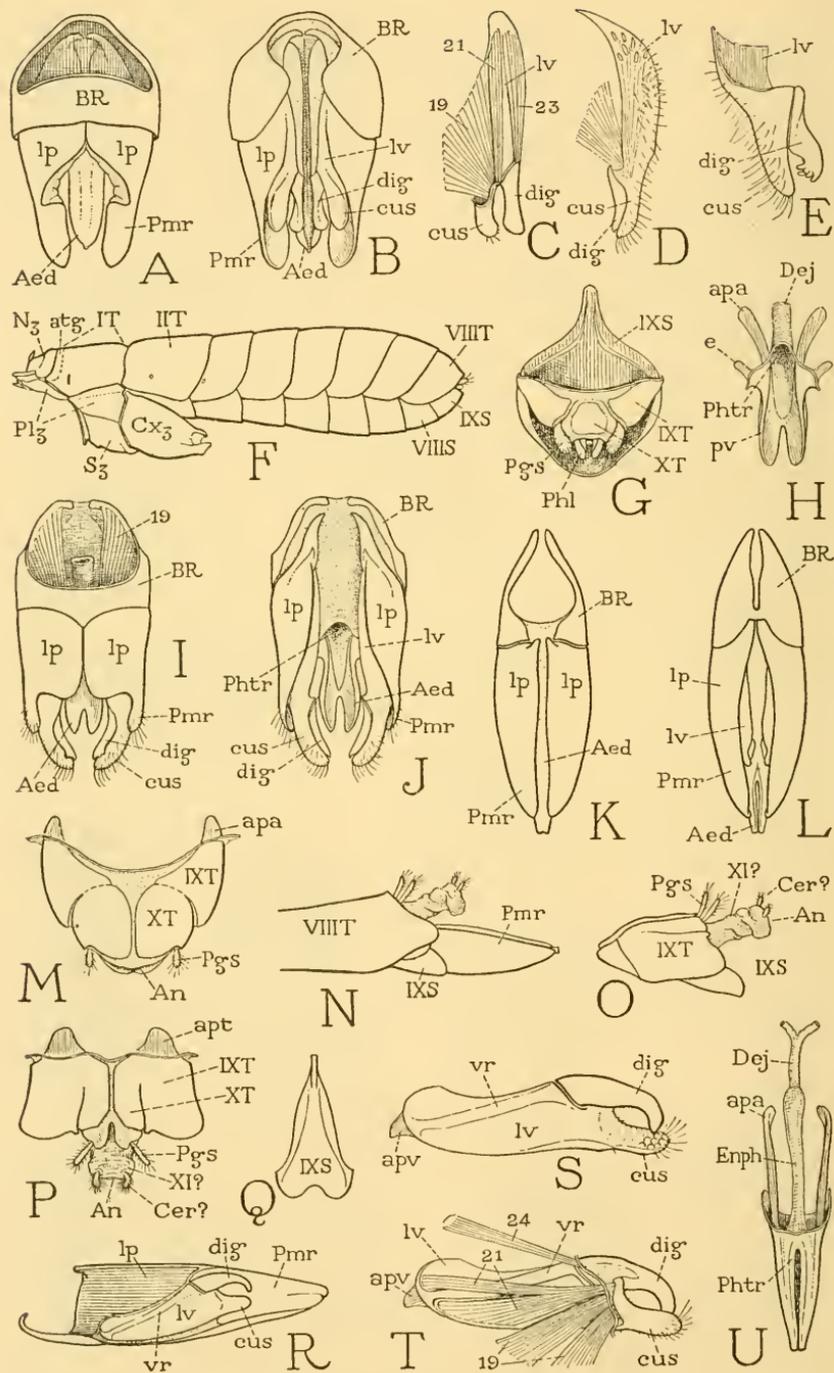
APOIDEA

- A, *Apis mellifera* L., right half of abdominal wall of male, mesal.
 B, same, muscles of right half of male abdomen, mesal.
 C, same, right halves of eighth and ninth abdominal sterna, and phallic plates of same side, mesal.
 D, same, sclerites shown at C, with muscles, mesal.



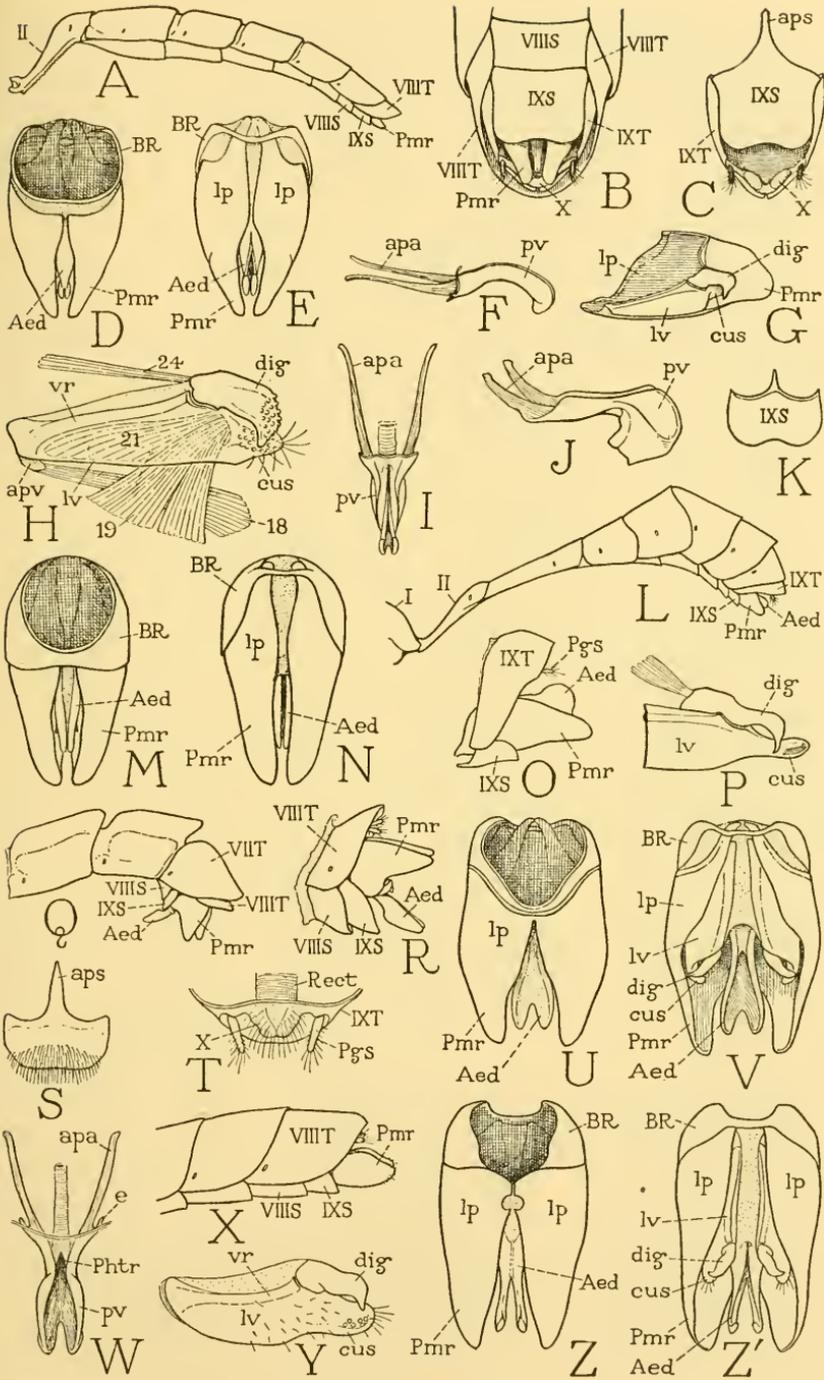
CHALASTOGASTRA

(For explanation, see page 72.)



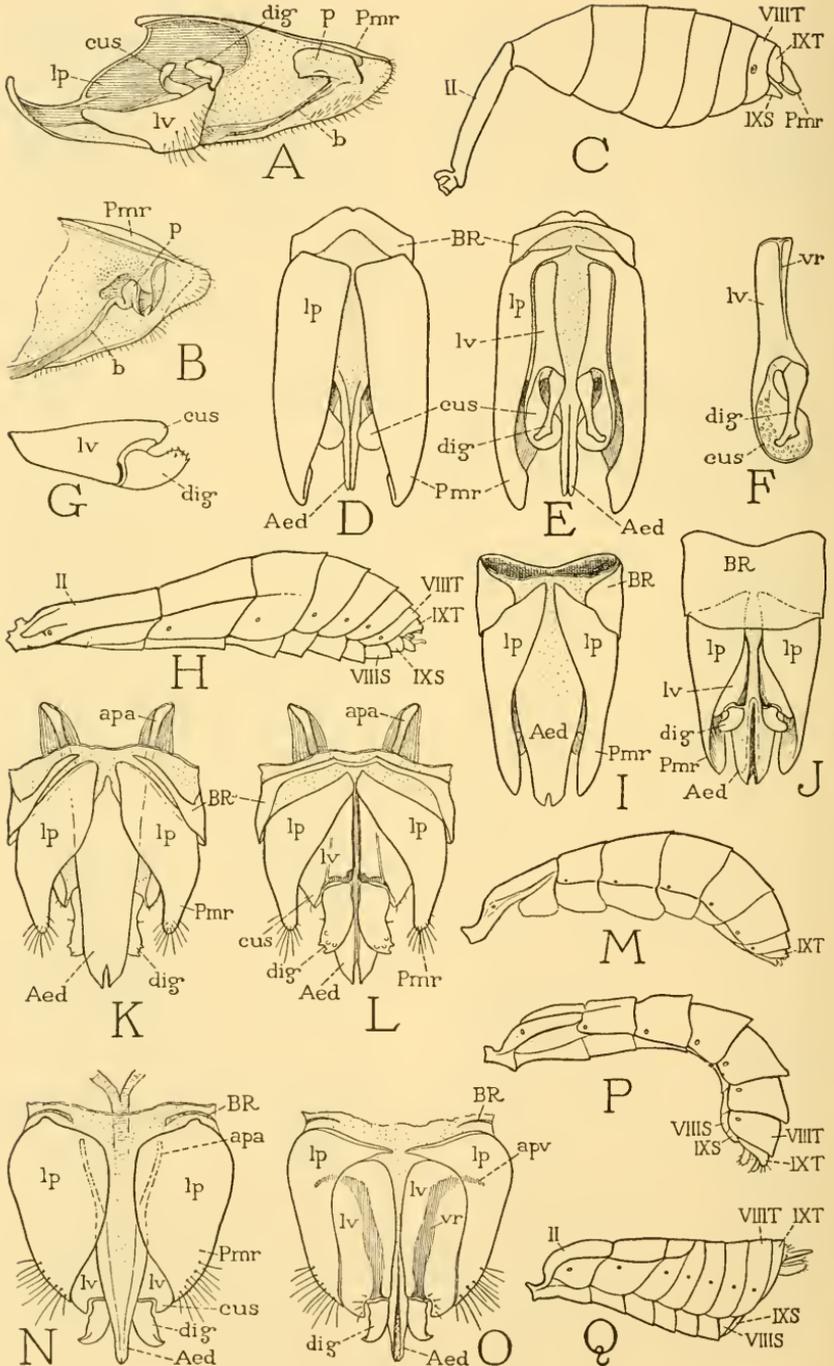
CHALASTOGASTRA. ICHNEUMONOIDEA

(For explanation, see page 72.)



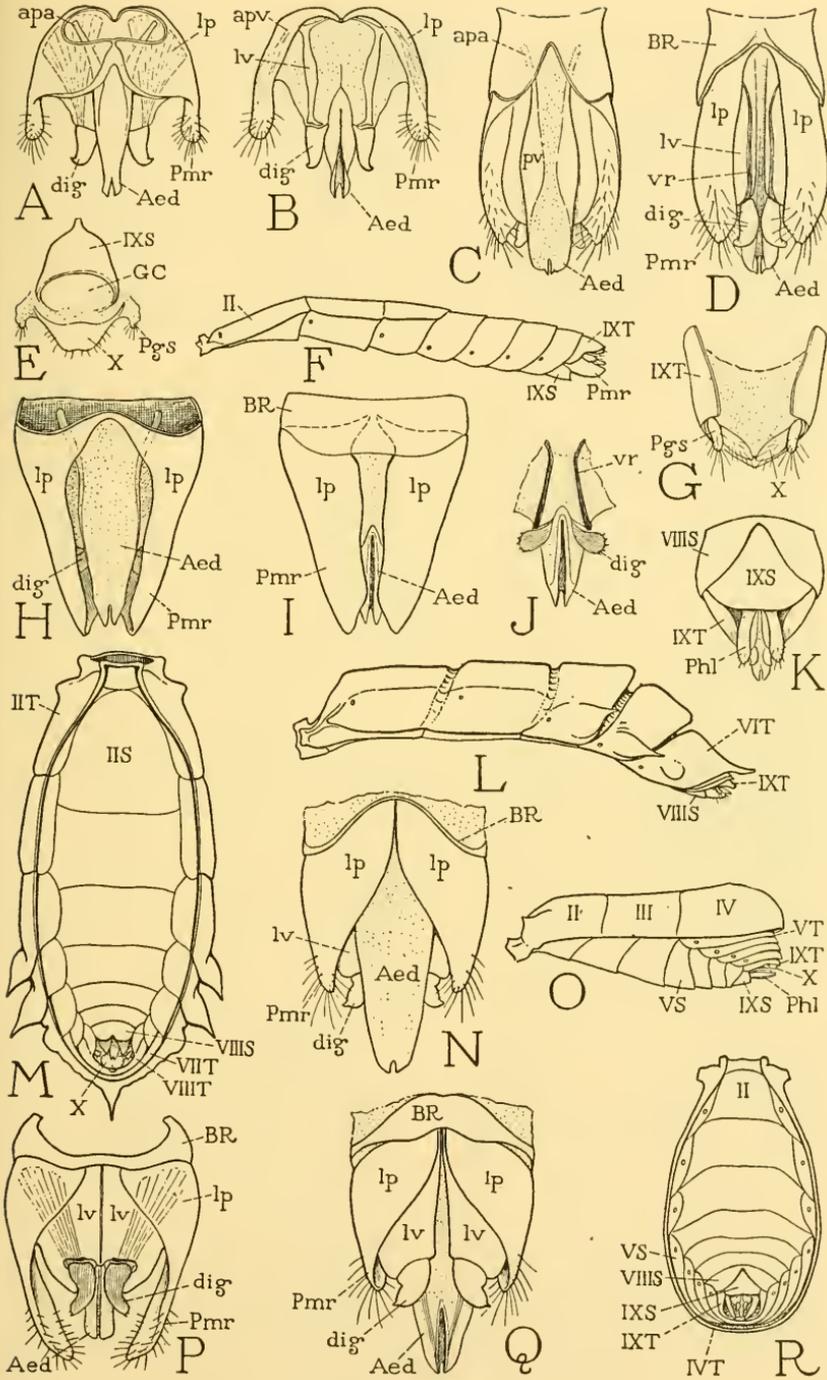
ICHNEUMONOIDEA

(For explanation, see page 73.)



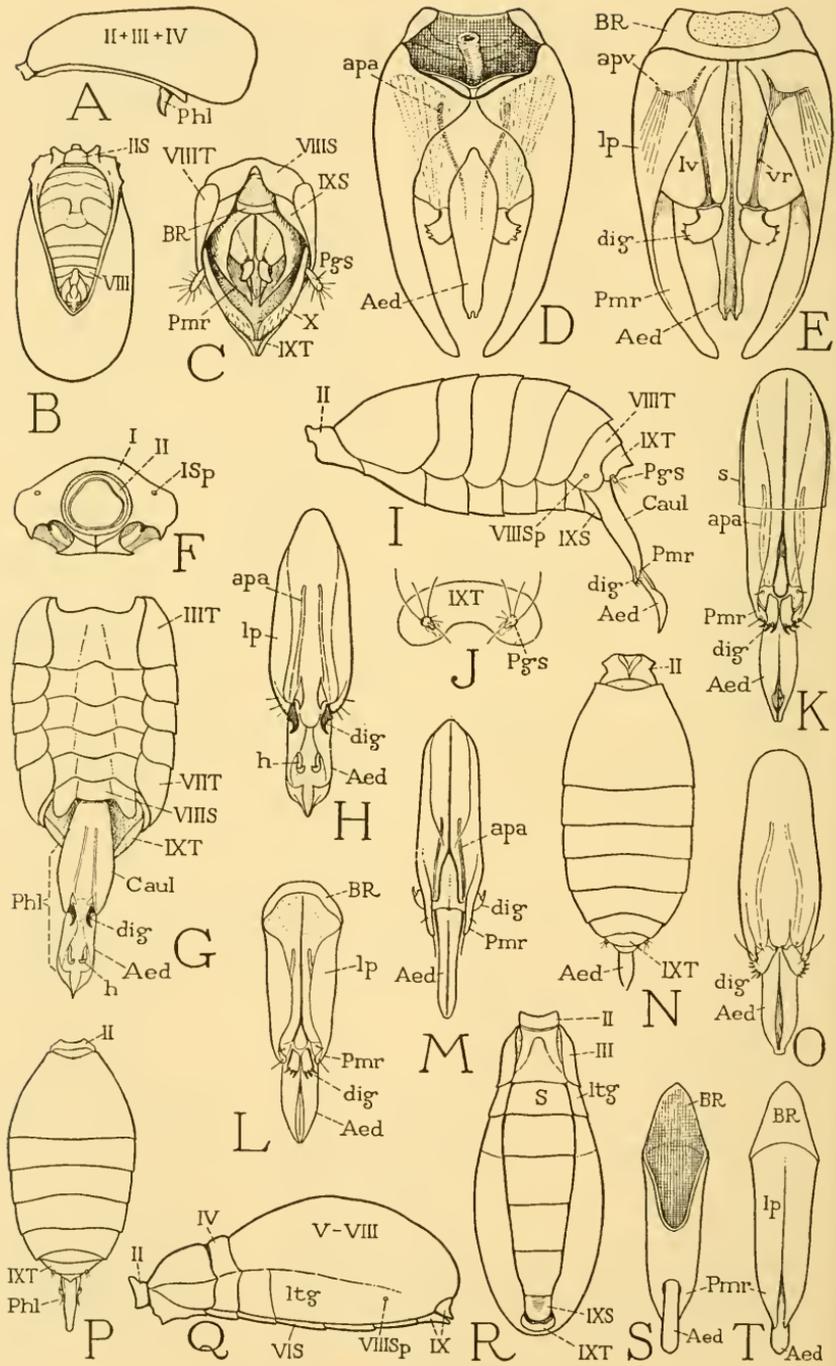
ICHNEUMONOIDEA

(For explanation, see page 73.)



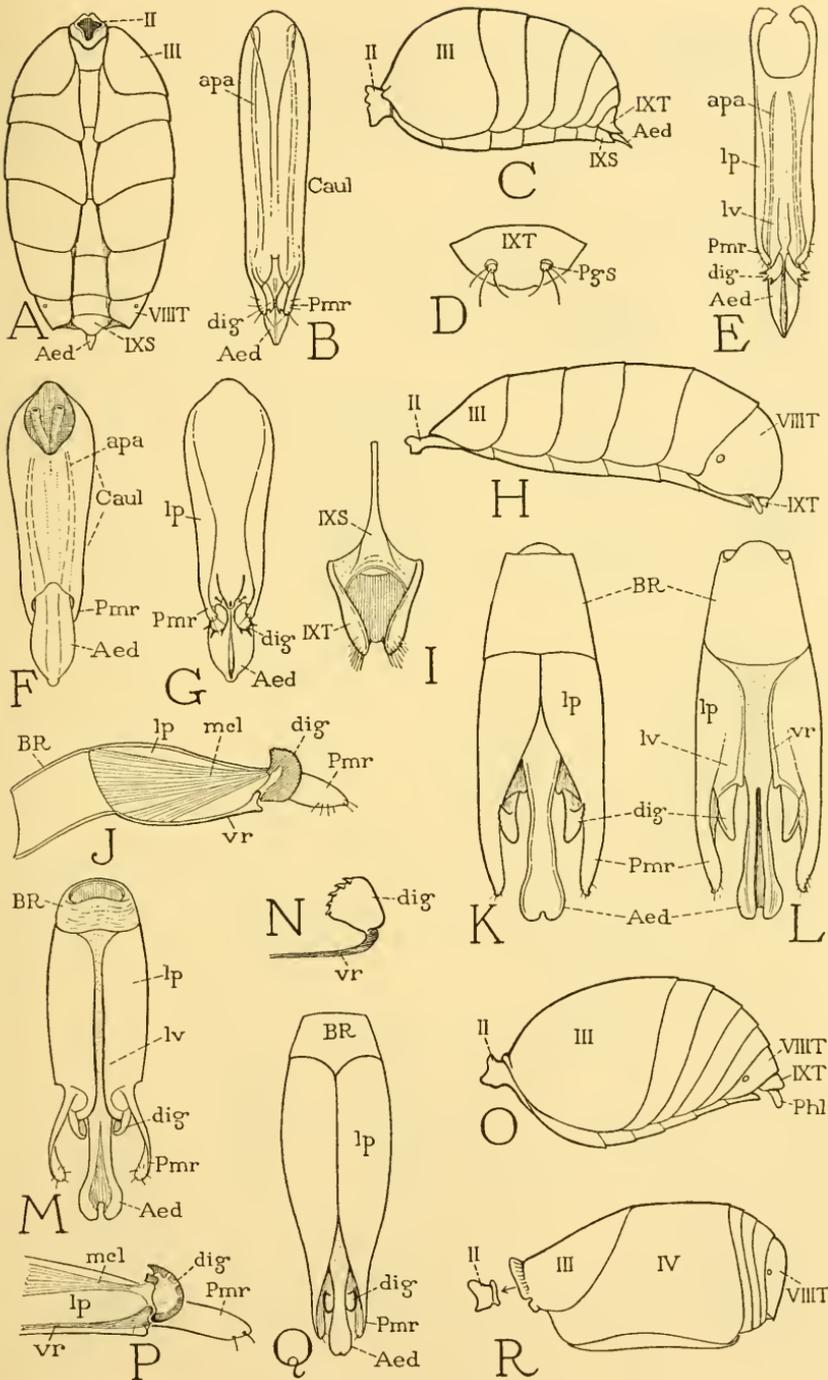
ICHNEUMONOIDEA

(For explanation, see page 74.)



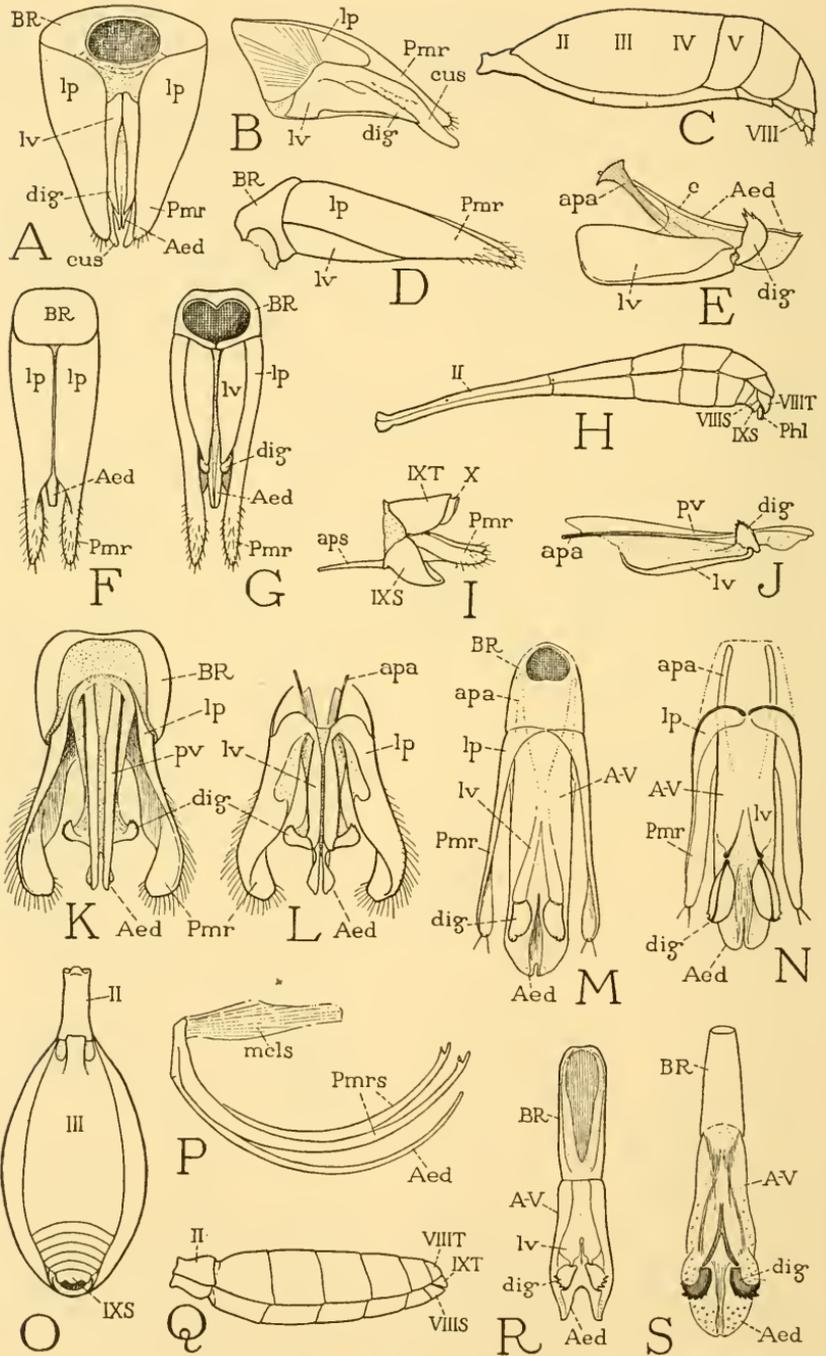
ICHNEUMONOIDEA. CHALCIDOIDEA

(For explanation, see page 74.)



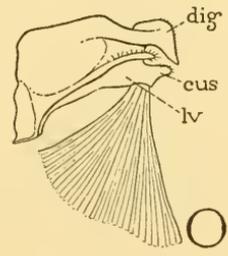
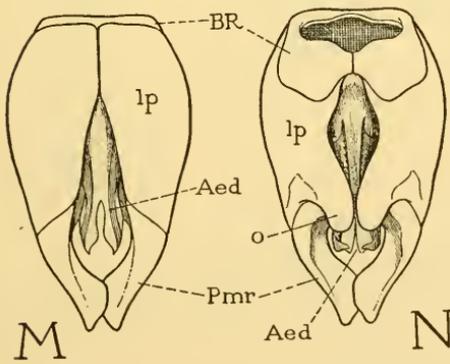
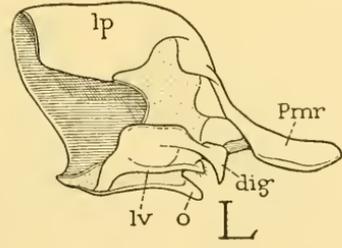
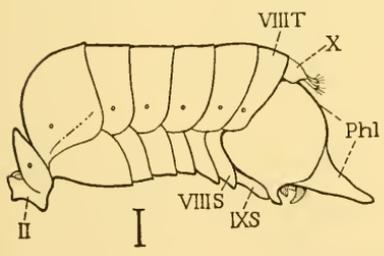
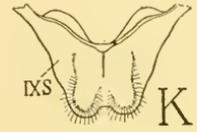
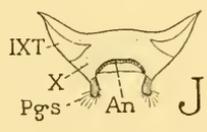
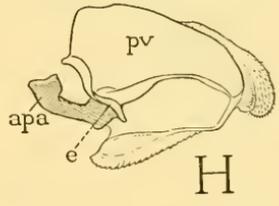
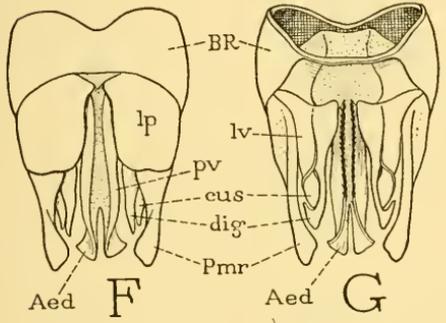
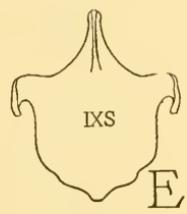
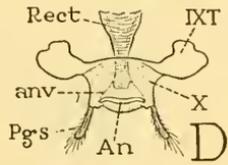
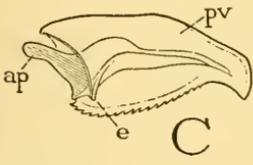
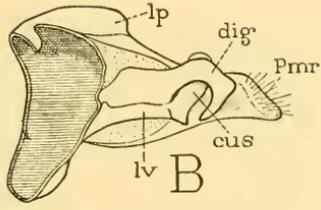
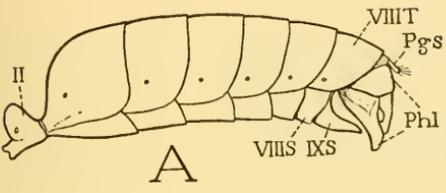
CHALCIDOIDEA. CYNIPOIDEA

(For explanation, see page 75.)



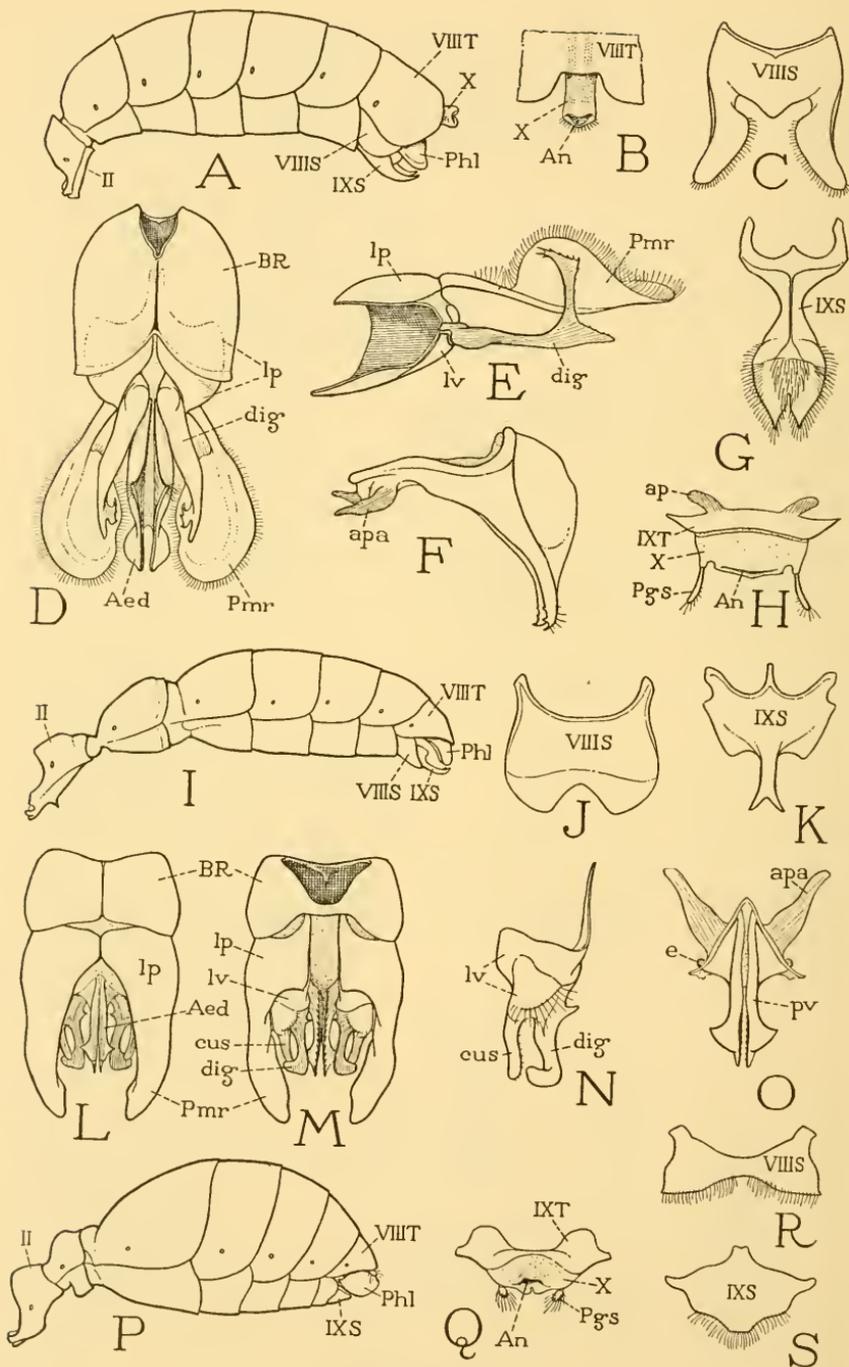
SERPHOIDEA

(For explanation, see page 75.)



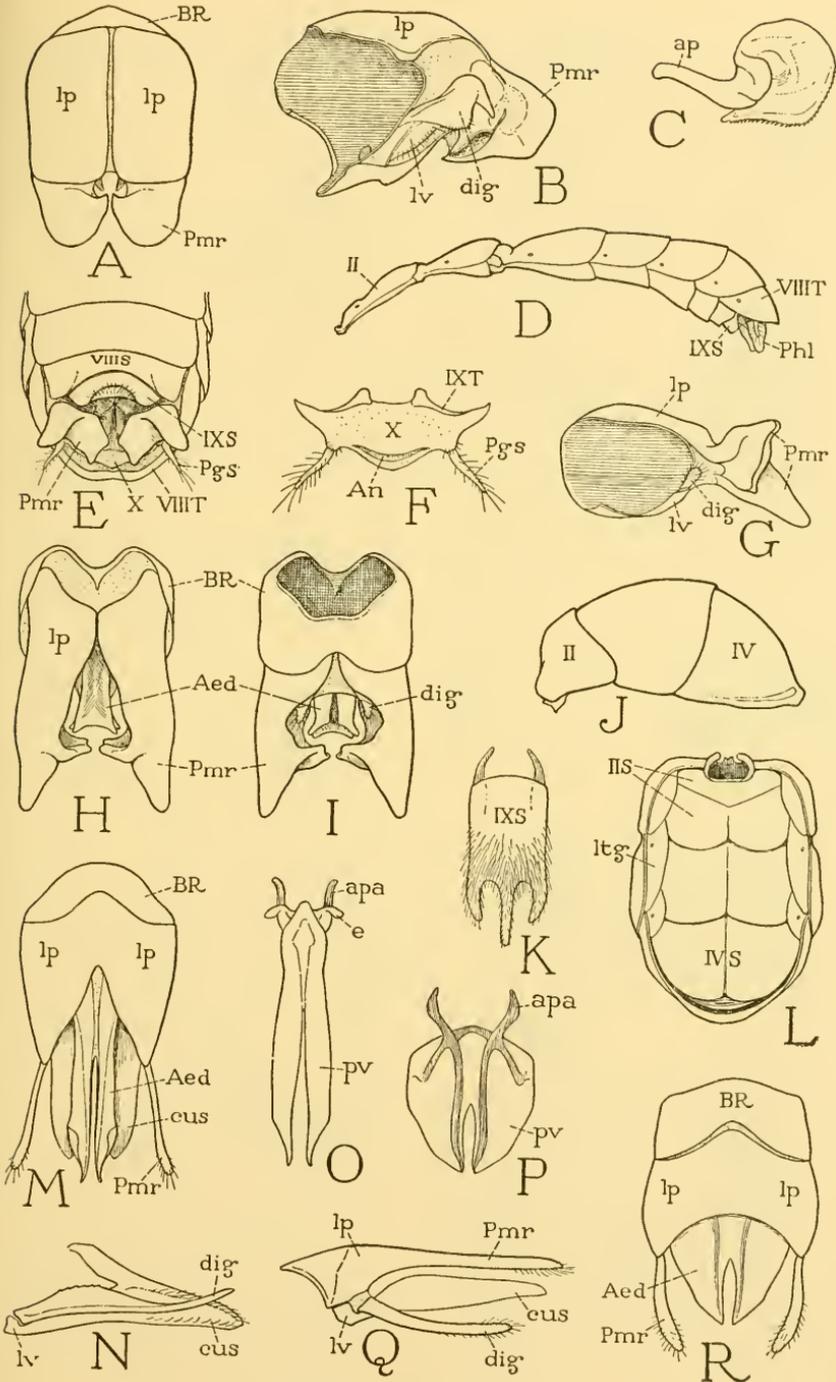
FORMICOIDEA

(For explanation, see page 76.)



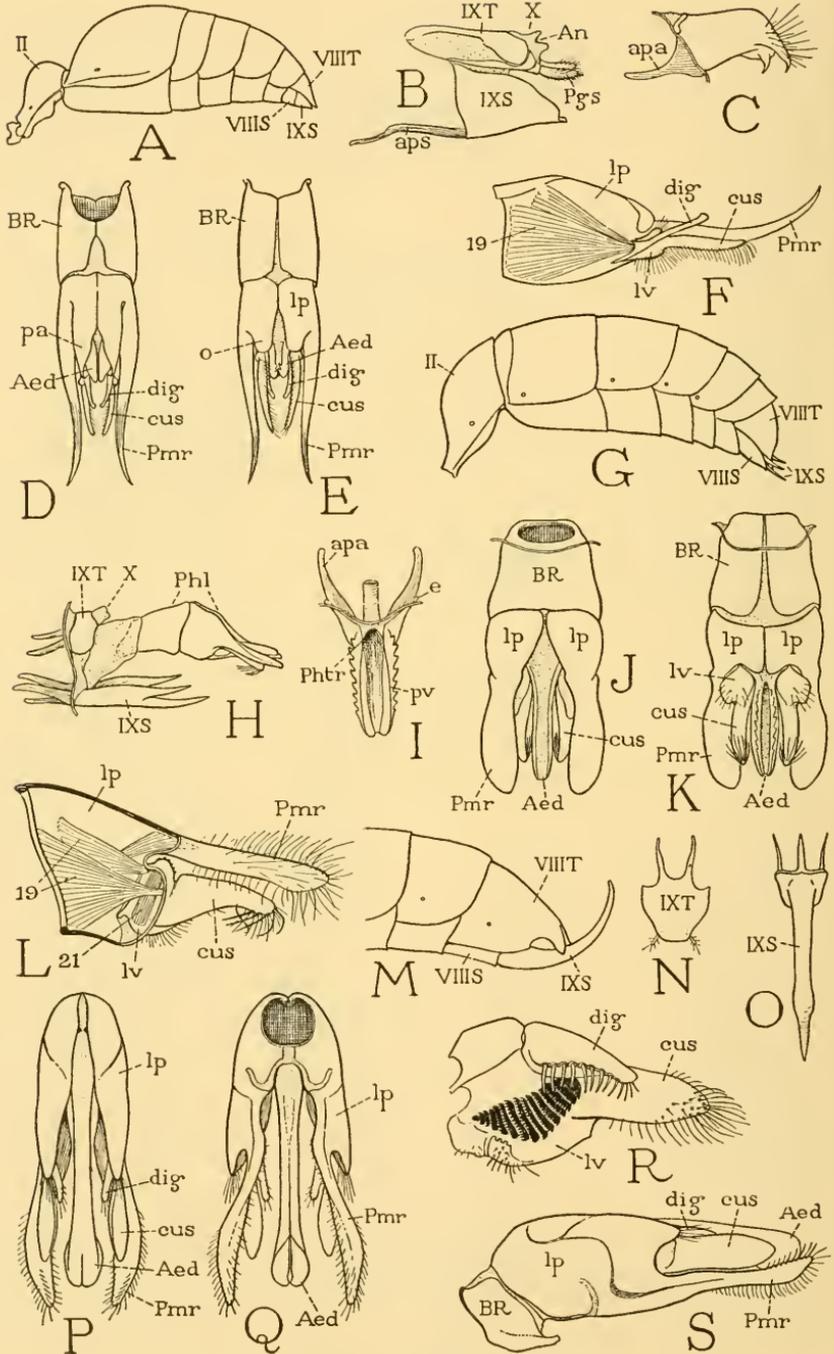
FORMICOIDEA

(For explanation, see page 76.)



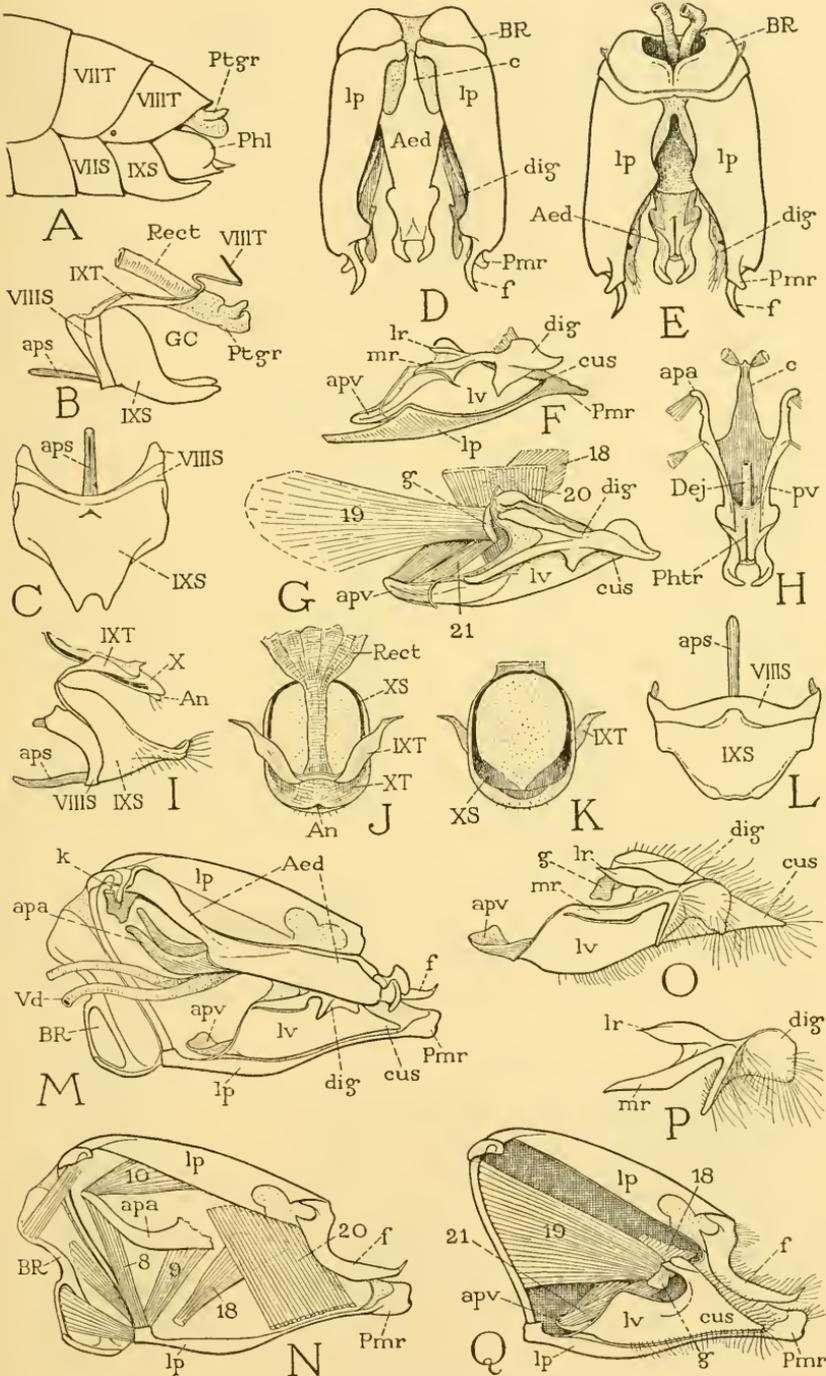
FORMICOIDEA. CHRYSIDOIDEA

(For explanation, see page 77.)



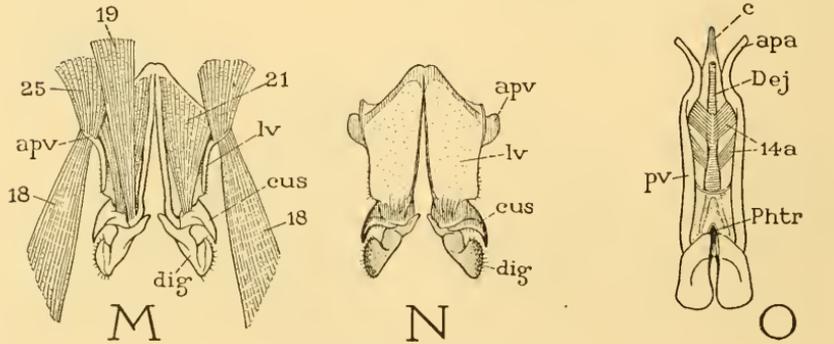
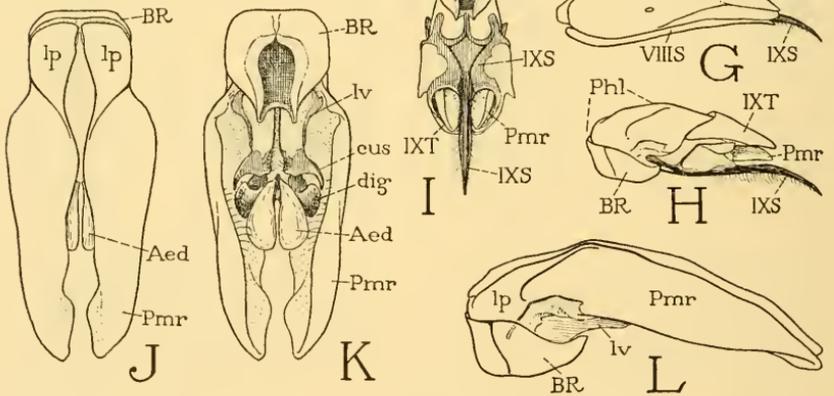
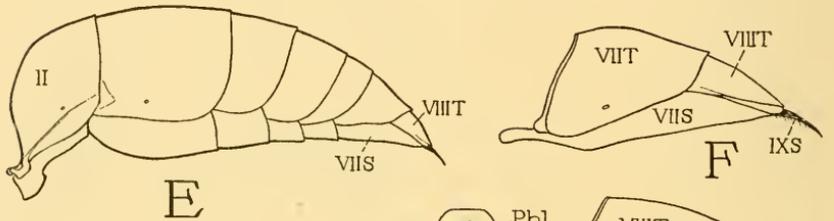
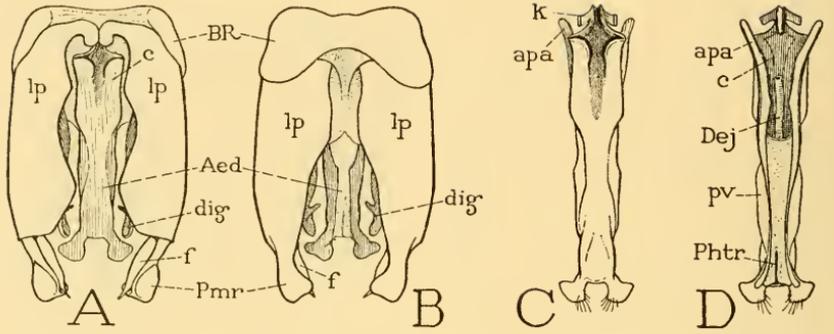
MUTILLOIDEA

(For explanation, see page 77.)

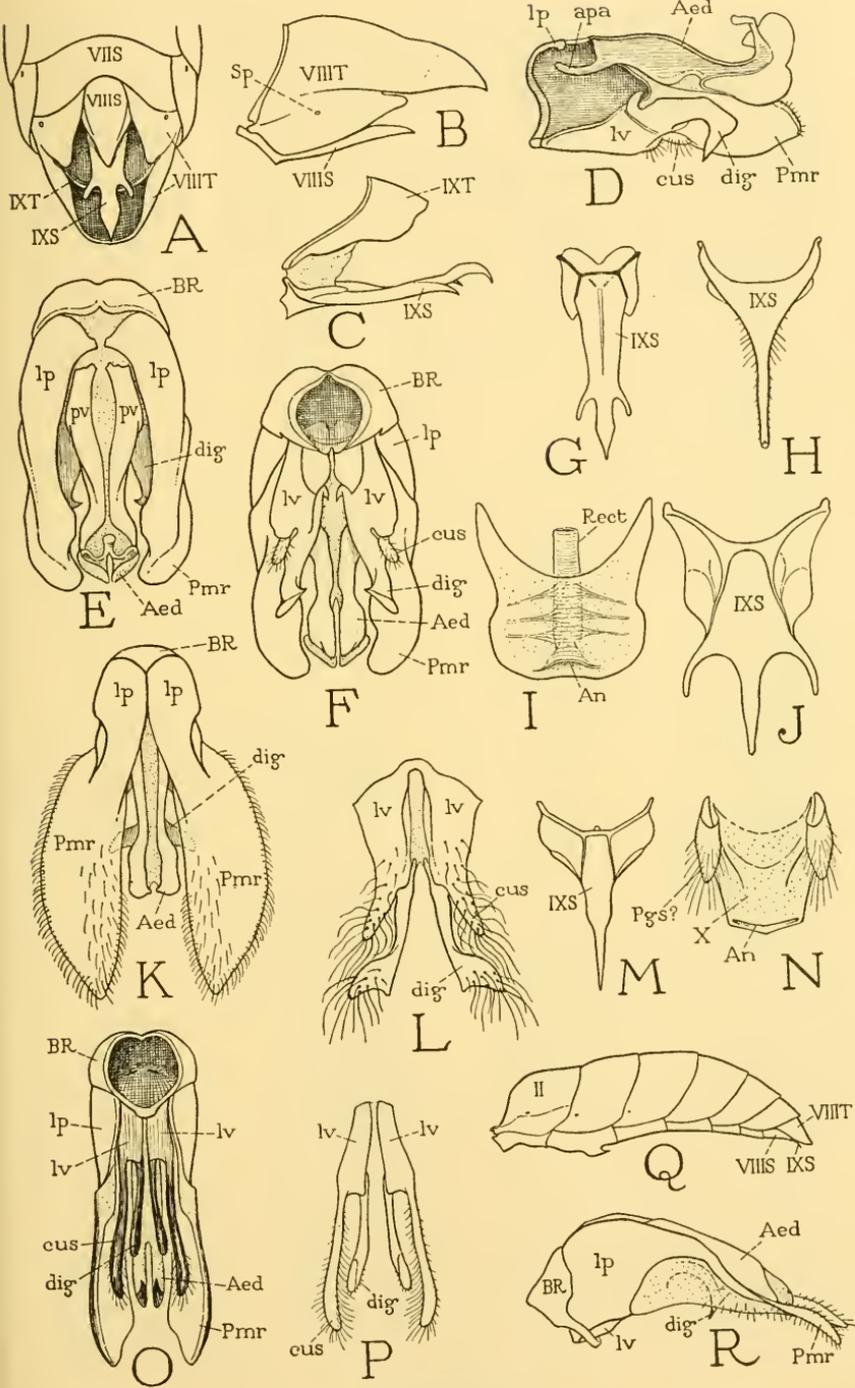


VESPOIDEA

(For explanation, see page 79.)

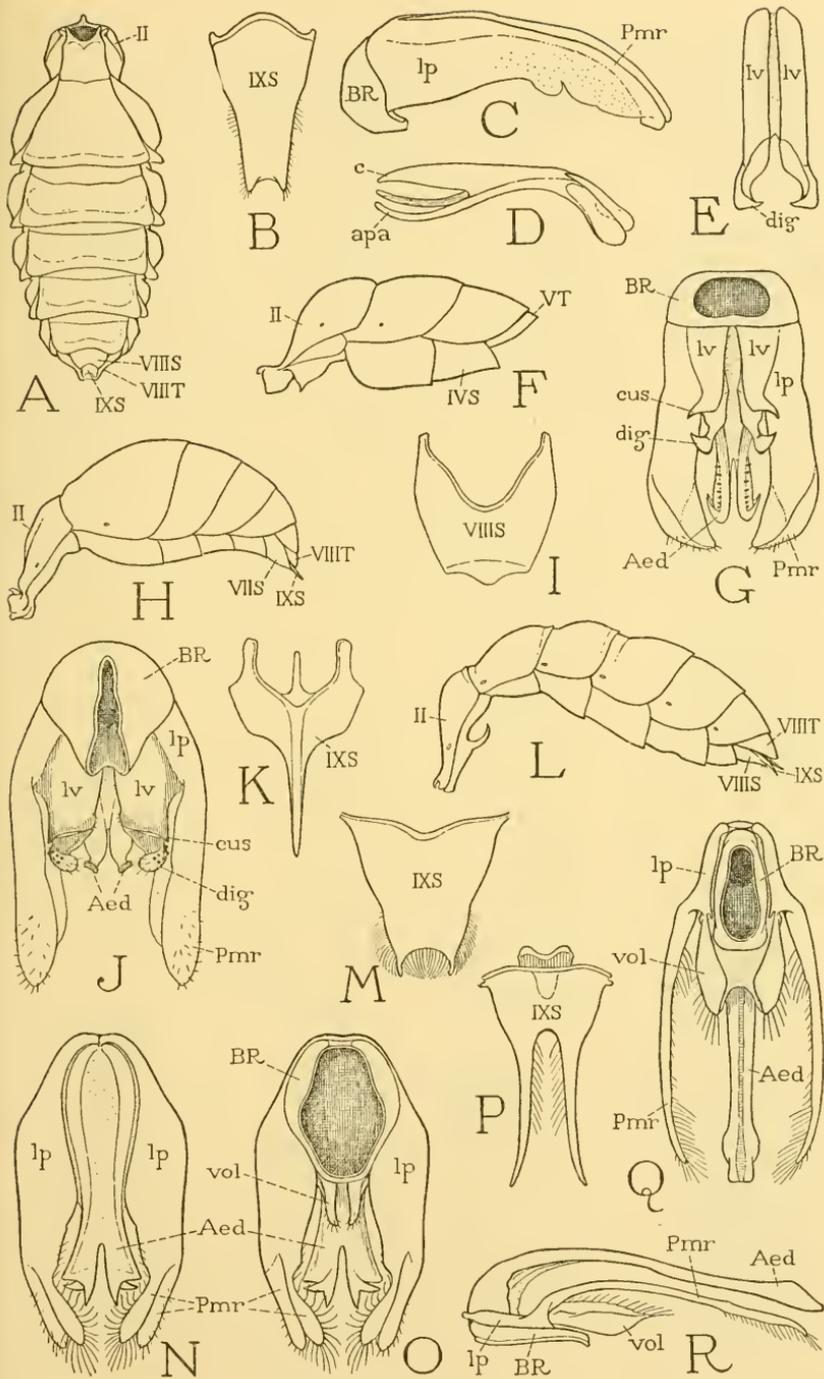


VESPOIDEA. SPHECOIDEA
(For explanation, see page 79.)



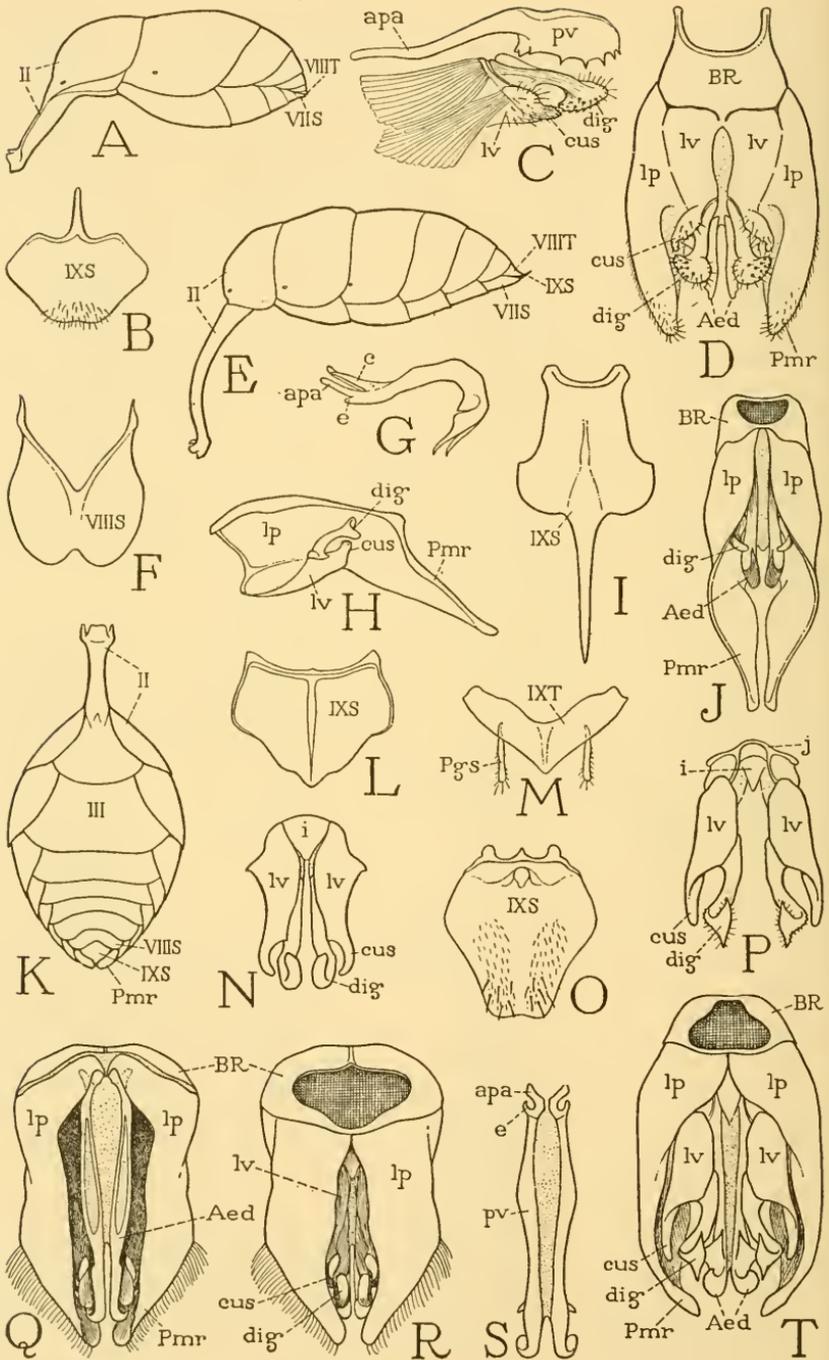
SPHECOIDEA

(For explanation, see page 79.)



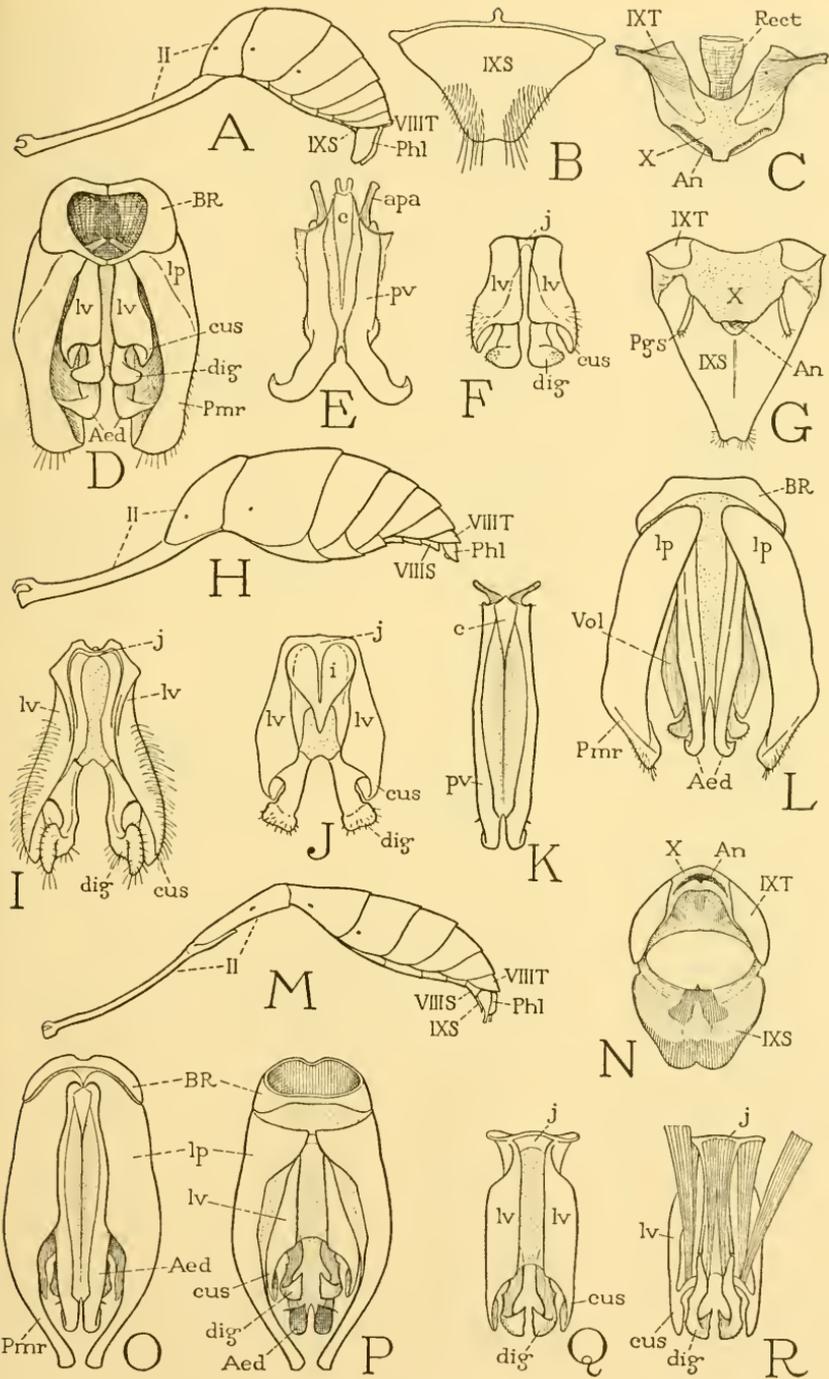
SPHECOIDEA

(For explanation, see page 80.)



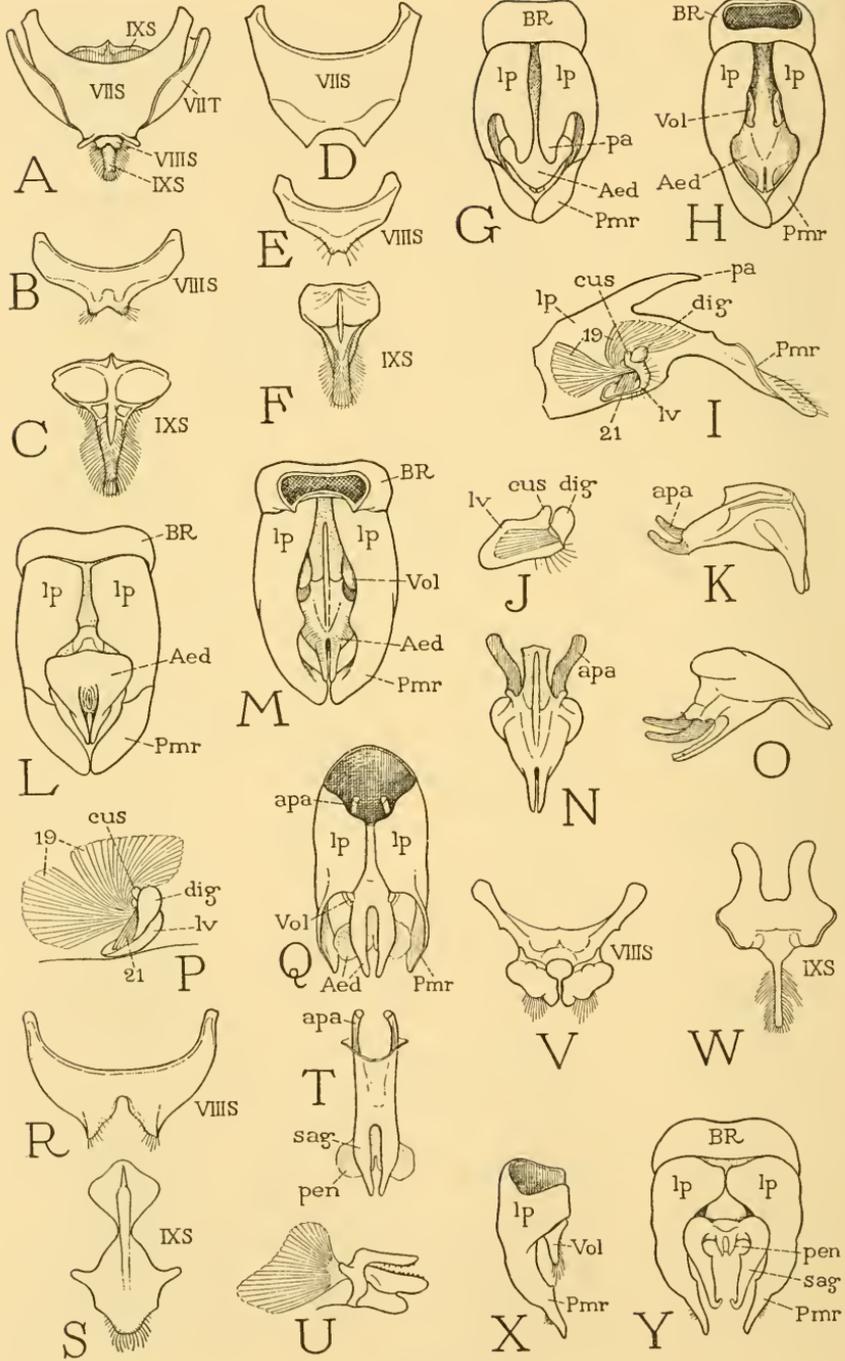
SPHECOIDEA

(For explanation, see page 81.)



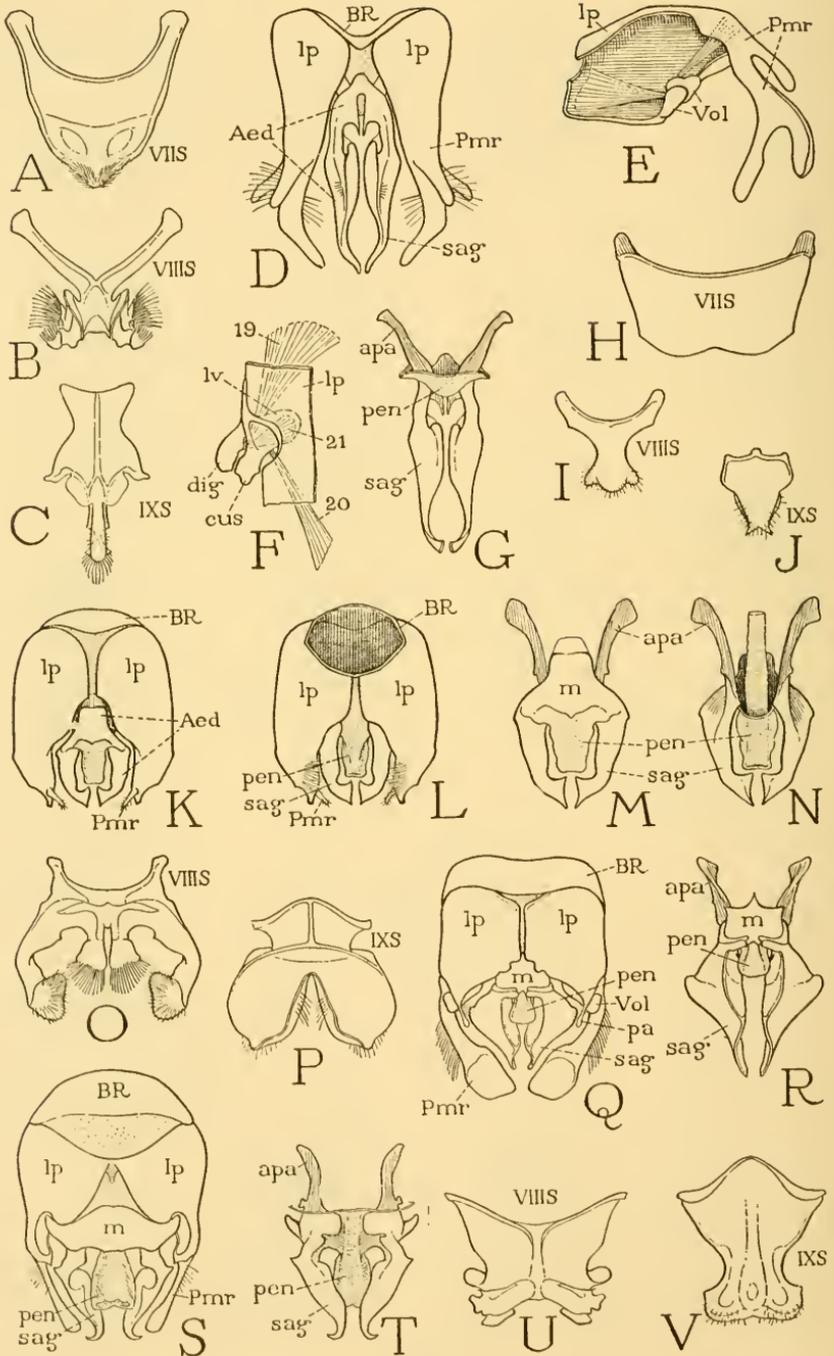
SPHECOIDEA

(For explanation, see page 81.)



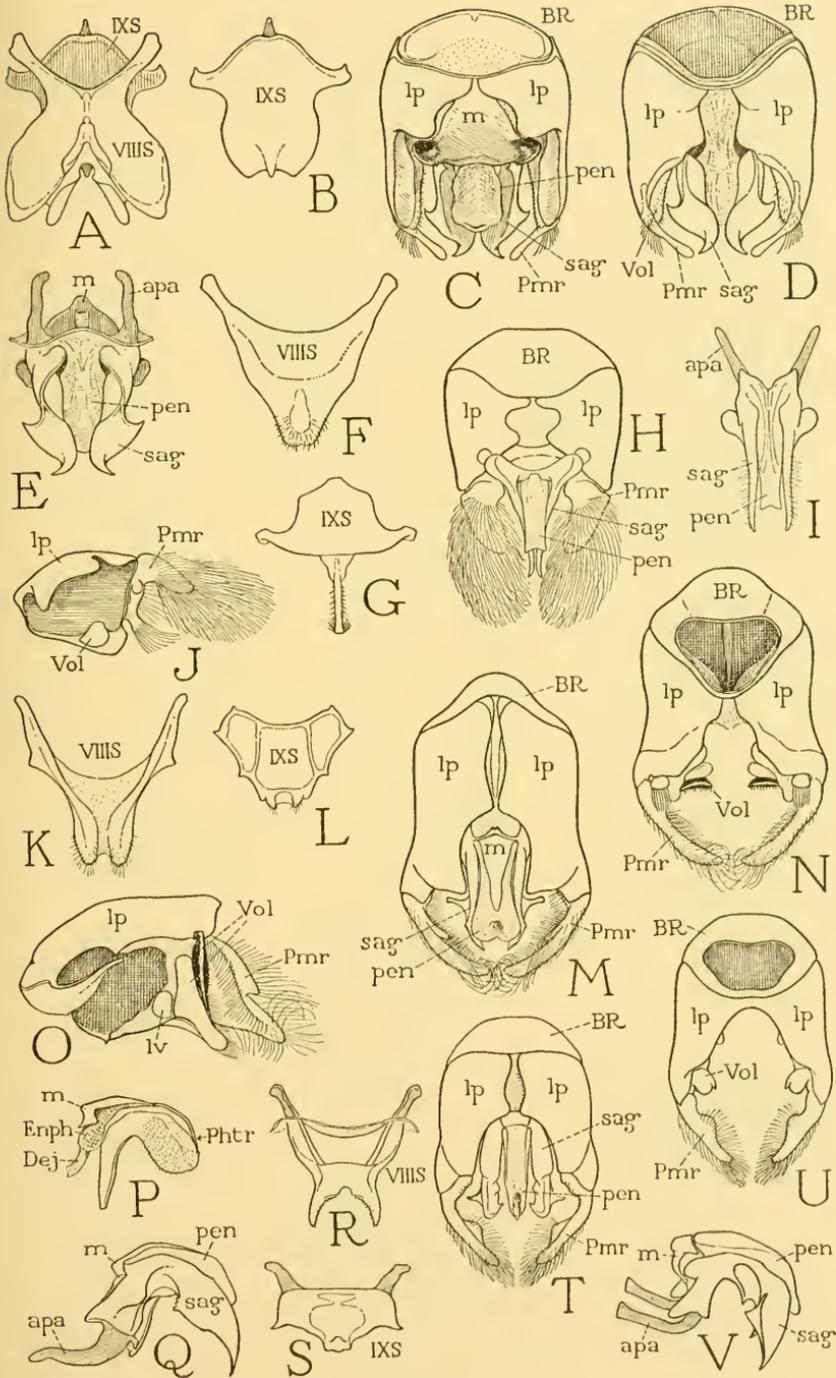
APOIDEA

(For explanation, see page 82.)



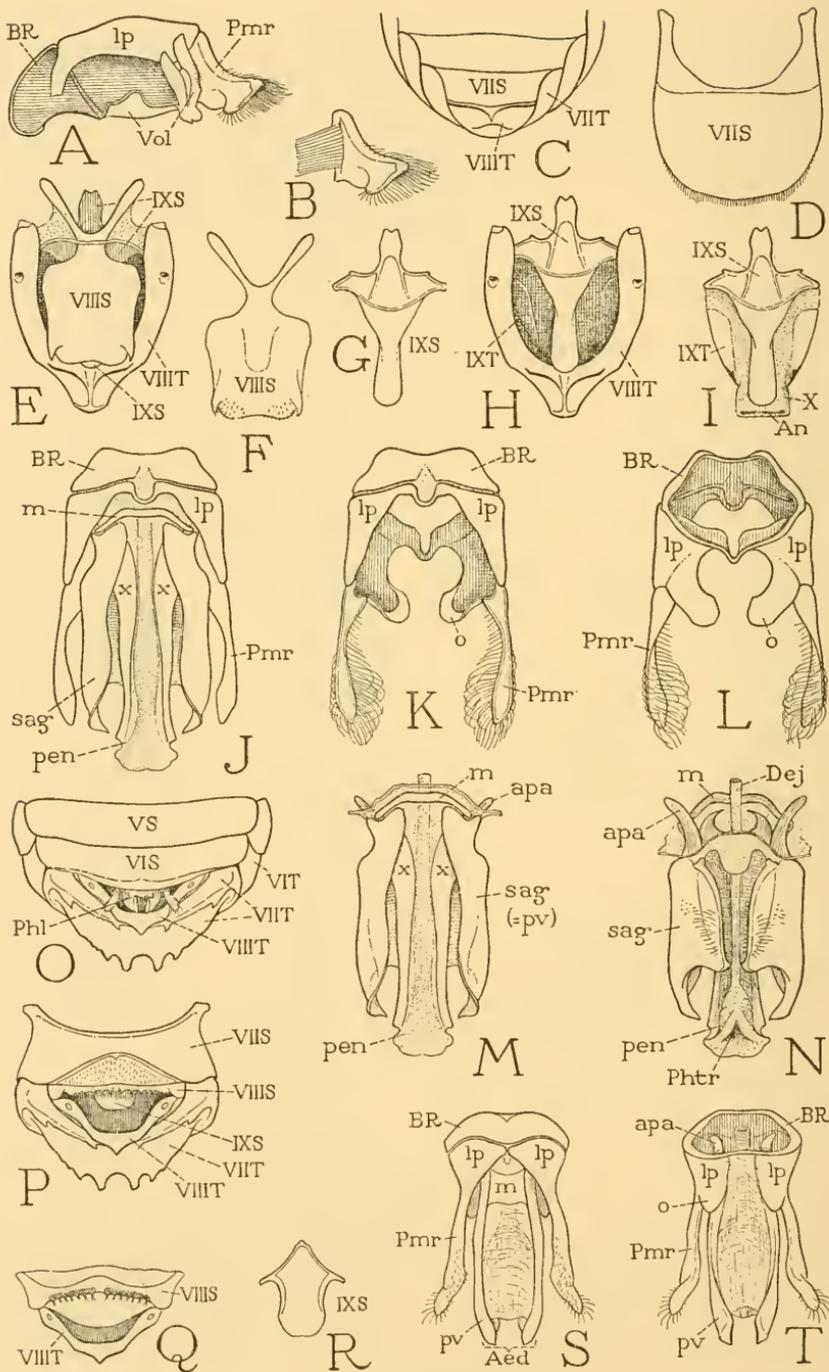
APOIDEA

(For explanation, see page 83.)



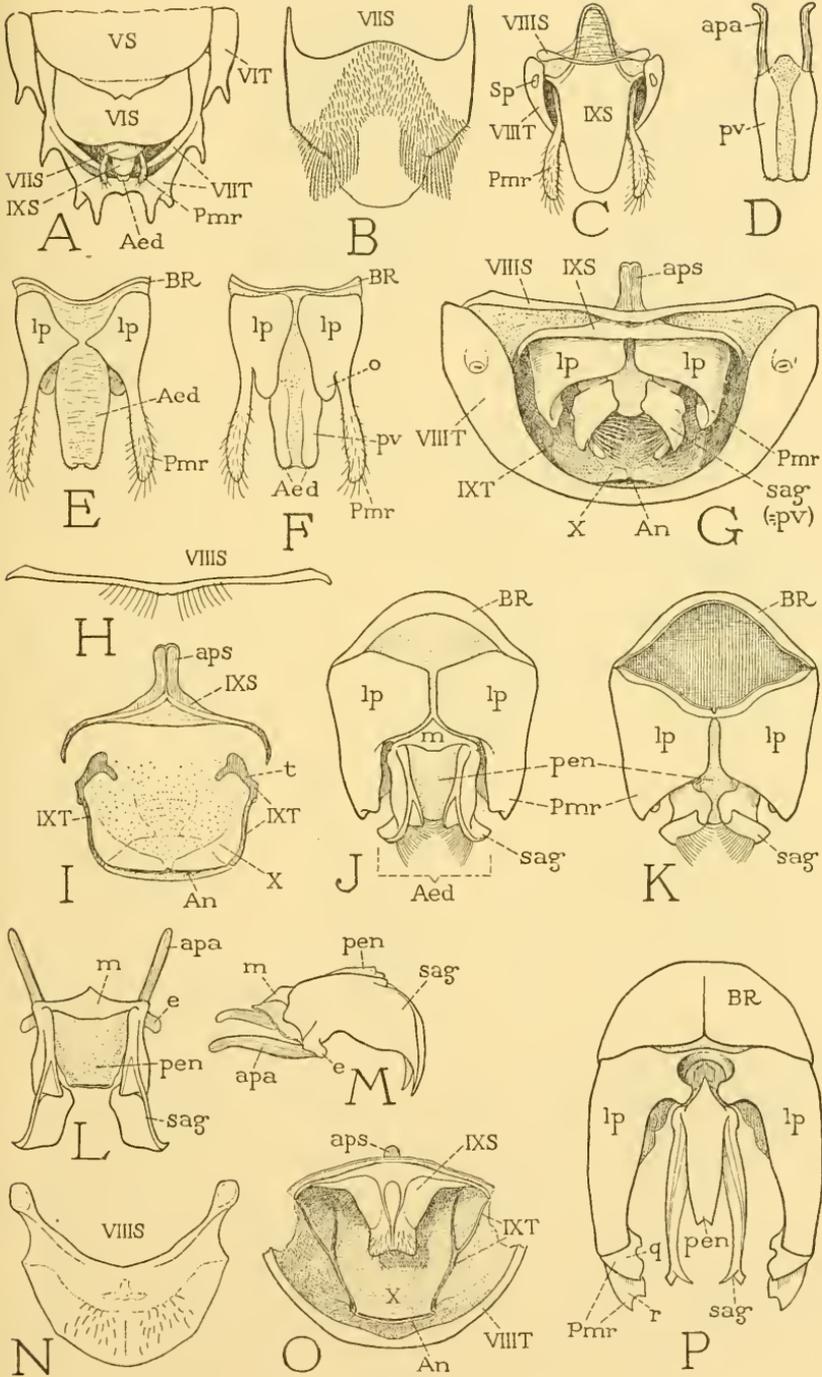
APOIDEA

(For explanation, see page 83.)



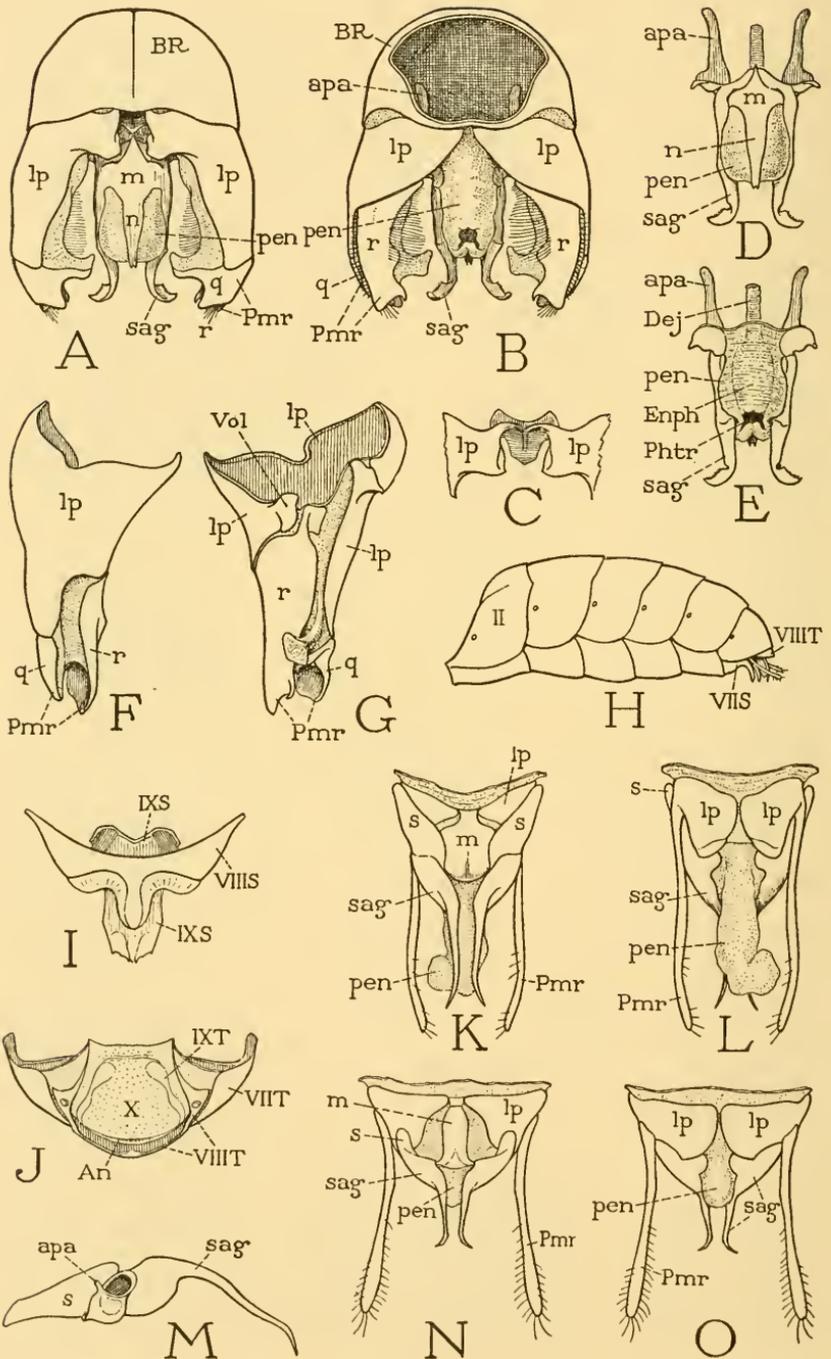
APOIDEA

(For explanation, see page 84.)



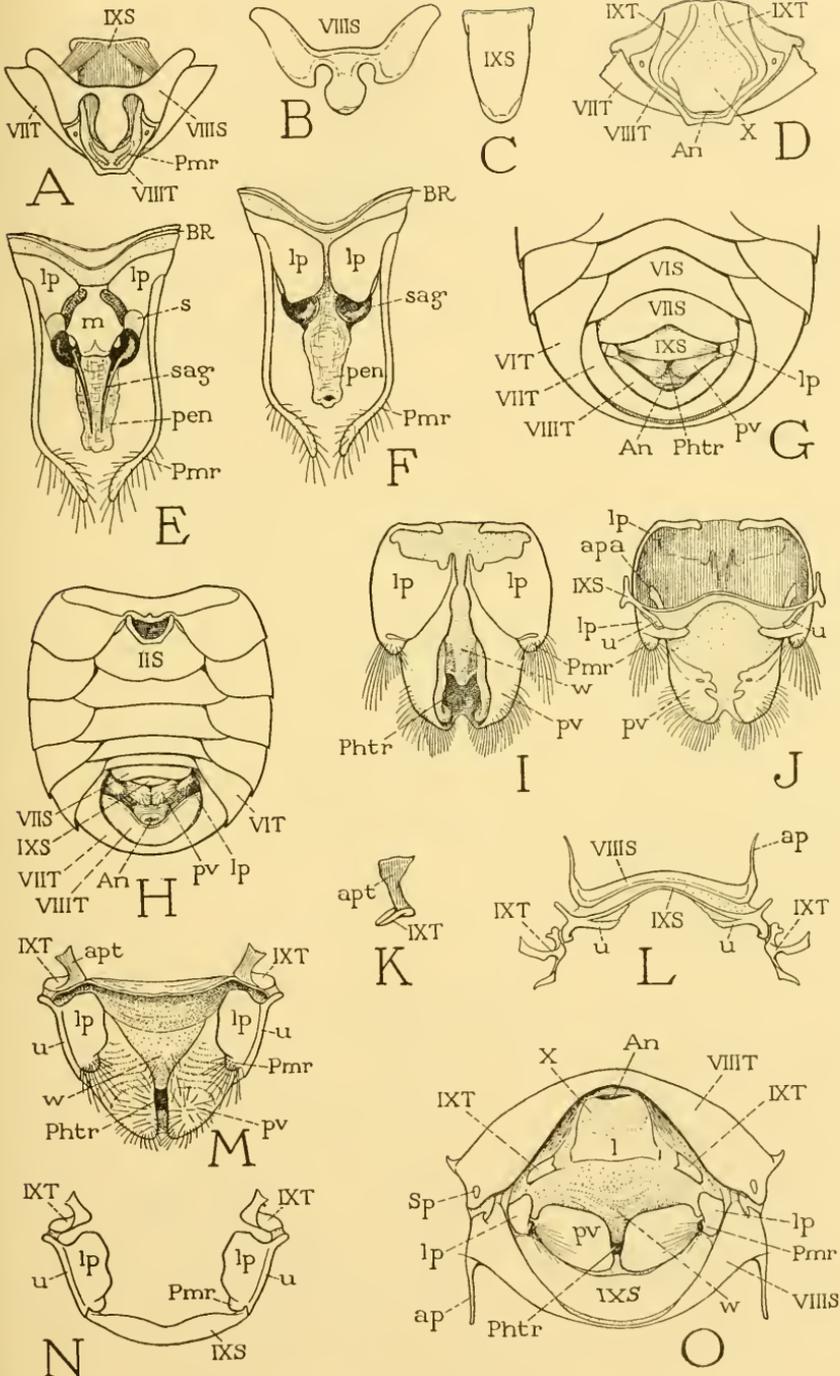
APOIDEA

(For explanation, see page 84.)

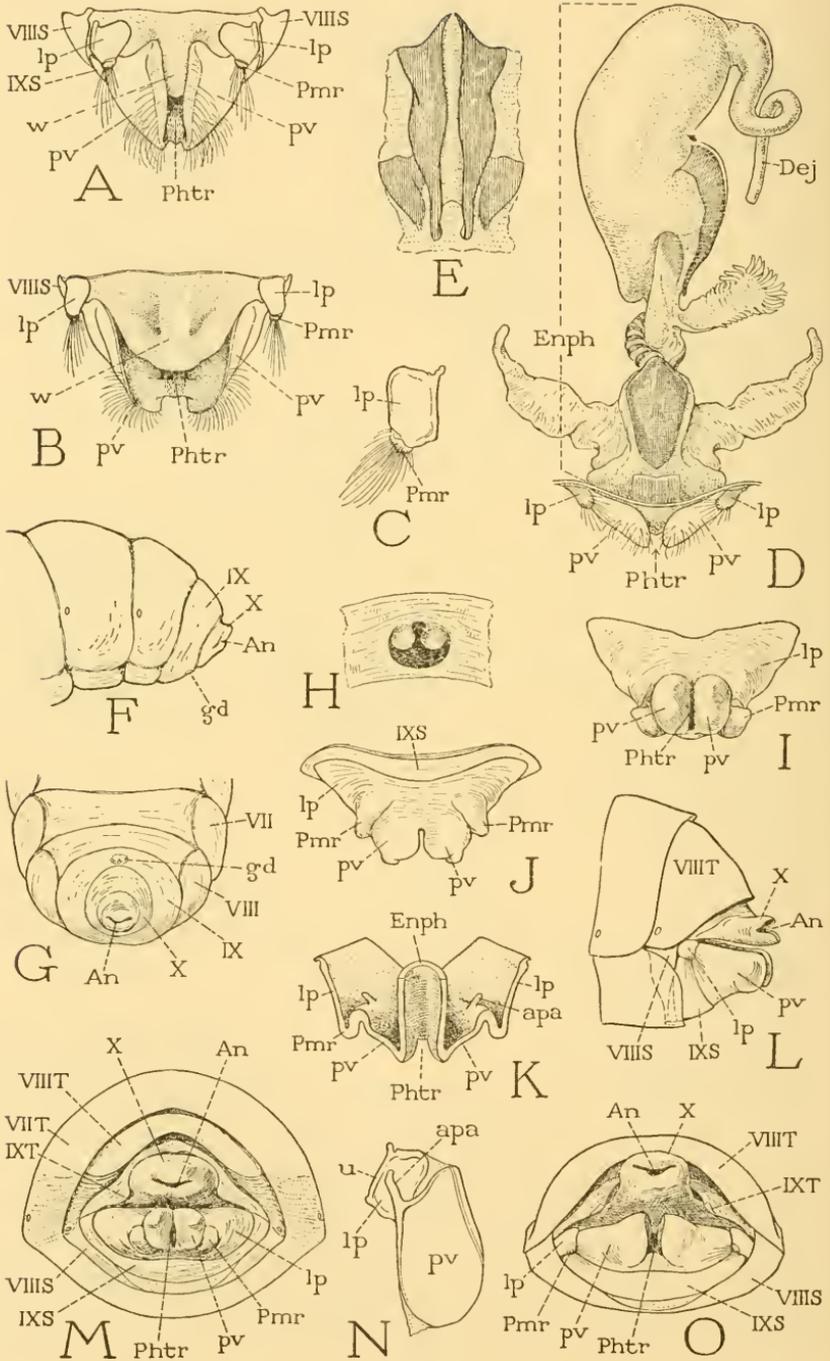


APOIDEA

(For explanation, see page 85.)

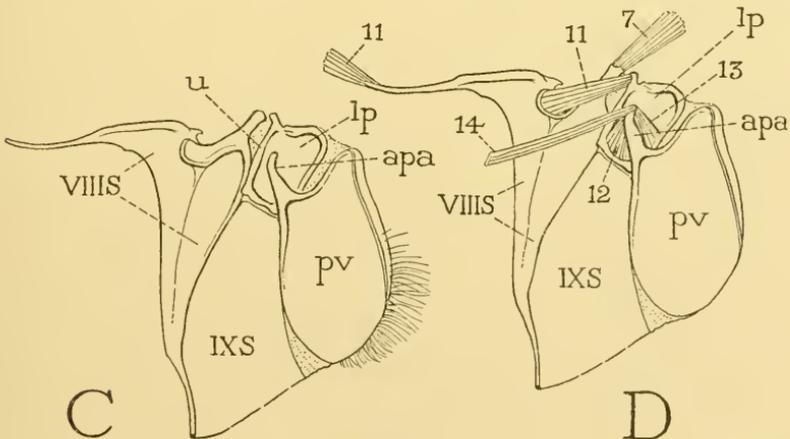
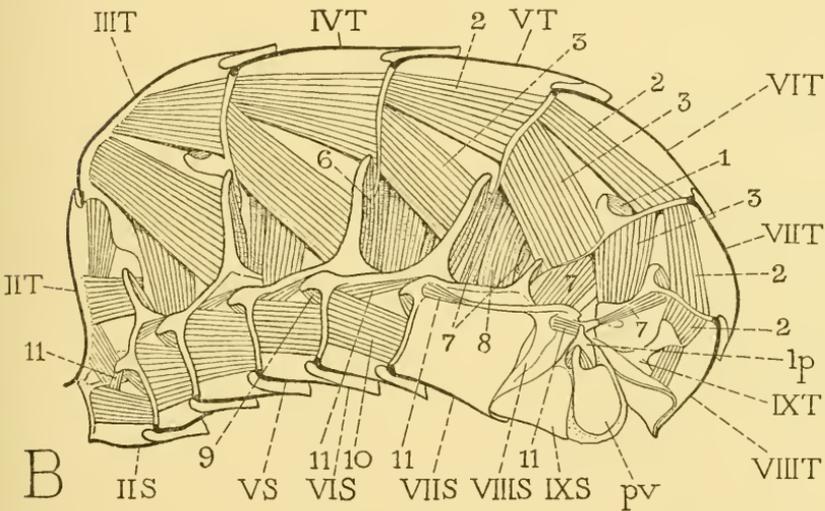
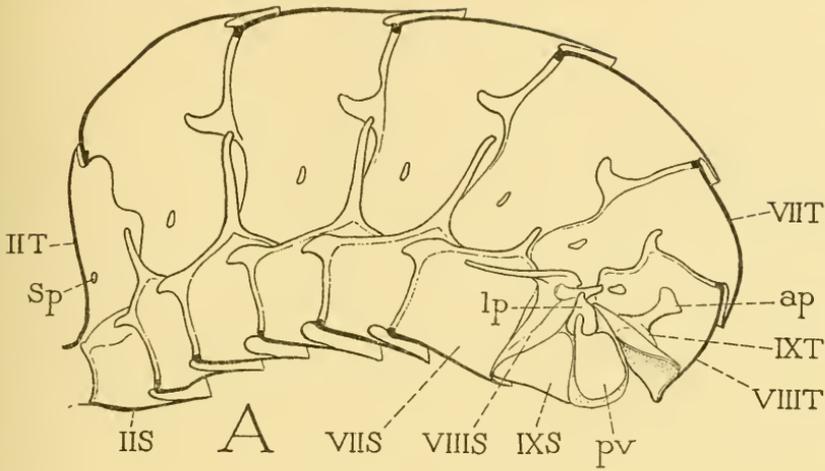


APOIDEA
(For explanation, see page 85.)



APOIDEA

(For explanation, see page 86.)



APOIDEA

(For explanation, see page 86.)