

The Morphology, Phylogeny  
and Higher Classification of  
the Butterflies (Lepidoptera:  
Papilionoidea)

by Paul R. Ehrlich

*B. A., University of Pennsylvania, 1953*

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## PART I

# THE INTEGUMENTAL ANATOMY OF THE MONARCH BUTTERFLY, DANAUS PLEXIPPUS LINNAEUS (LEPIDOPTERA: NYMPHALIDAE)

### INTRODUCTION

This is the first section of a work on the integumental morphology, phylogeny and classification of the butterflies (Papilionoidea). Despite the great popular interest in this group of insects they have been the subject of relatively little modern systematic work above the level of the generic revision. The interrelationships of the major groups are poorly understood, and some recent workers (e.g., Clark, 1948) have given family rank to such obviously non-equivalent entities as the papilionids and the argynnids.

It seems apparent that a mere rearranging of the butterflies on the basis of well studied characters such as wing venation or color pattern, or the introduction of a new phyletic arrangement and classification on the basis of one or two previously unstudied characters, would be of little significance. Therefore, an attempt will be made to reconstruct the phylogeny of the group and arrive at a reasonable classification by utilizing as much published work as possible in conjunction with a study of the comparative integumental morphology. Unfortunately practical



considerations will not permit simultaneous study of the characters existing in the immature forms, the visceral anatomy, the fine details of the microscopic anatomy, etc., nor of all the species or even all genera. However, it is hoped that sufficient characters and an adequate diversity of species can be studied so that major errors will be avoided.

This first section forms the basis for the comparative morphological study which is to follow. As far as could be determined this is the first detailed integumental anatomy of a butterfly. Several features of the Monarch's anatomy, however, have been described and figured in varying detail by other authors (Burgess, 1880; Kellogg, 1893; Shepard, 1930).

The Monarch was chosen for this study because it is common, widespread, and large. Both dried specimens and individuals preserved in Kahle's fixative were used, and these specimens were sometimes treated with Chlorox or KOH. Brushes and fine forceps were used for the tedious job of removing the scales. Procedure adopted in preparation of the figures was as follows: every structure studied was examined in a minimum of two specimens, in one specimen when the drawing was prepared, and in a second when the description was written. The vast majority of the structures have been seen in four or more individuals.

The simpler illustrations were prepared from the first specimen and merely checked in the second, while others, although outlined from one specimen, have been altered and adjusted after examination of additional specimens whose preparation showed certain features more clearly. The drawings were all made with the aid of an eyepiece grid to give proportions correctly.

The terminology used in this paper will be employed throughout the comparative study to follow. Most of the terms used by Michener (1952) in his study of the saturniid moth, Eacles imperialis (Drury), have been retained; however, the nomenclature of the male and female genitalia is that of Klots (1956).

Thanks are due to Dr. C. D. Michener, Dr. K. C. Doering and Dr. Ryuichi Matsuda, all of the University of Kansas, for their aid on many facets of the work. Thanks go also to my wife, Anne H. Ehrlich, for aid in the inking of drawings and the preparation of the plates.

## MORPHOLOGY

### THE HEAD

#### Figures 1-7

The most prominent features of the hypognathous head are the compound eyes; they are approximately hemispherical and their combined width is almost one-half that of the entire head. The sclerites of the frontal portion of the

head between the eyes are termed here, collectively, the face. The homologies of these sclerites are uncertain, but it seems unlikely that the terminology used by Michener (1952), which is based on that of DuPorte (1946), reflects the true situation. The nomenclature employed here for the facial sclerites is based on DuPorte's more recent work (1956). The central area of the face is occupied by the large, protuberant, roughly circular frontoclypeal sclerite. This structure is bounded above by a sulcus connecting the inner margins of the antennal sockets, the transfrontal suture. This suture is only weakly in evidence externally, but is represented by a fairly strong ridge internally. Dorsolaterally the sclerite is bounded by the antennal sockets, at the edges of which it is infolded to form strong ridges along the lower parts of the sockets. These ridges connect with the ridge of the transfrontal suture and each bears on its lateral end a small dorsal projection, the antennifer, which is an articulation point for the scape of the antenna. Laterally the frontoclypeal sclerite is bounded by the curved laterofacial sutures, which contain the prominent anterior tentorial pits and run from the dorsolateral edges of the labrum up to the ventral margins of the antennal sockets. These sutures, although not extremely prominent externally (they lie at the base of the forward thrust plateau of the frontoclypeal sclerite), are represented internally by large ridges which



paraocular area, behind and slightly lateral to the pilifer, is a small protuberance, the mandibular rudiment.

The antennae, situated at the dorsolateral margins of the frontoclypeal sclerite, are long (each being more than three times as long as the head is wide) and clubbed. The basal segment, or scape, of each antenna is relatively large, ring-like, and wider anteriorly than posteriorly. It has on its anterodorsal edge a small articulatory process. The second segment, or pedicel, is a simple ring approximately one-half the size of the scape. The remainder of the antenna is the flagellum, which in the monarch is composed of 43 segments. The segments increase very gradually in length, and the diameter of the antenna gradually becomes slightly greater from the proximal end to the vicinity of segment 33. In this region the width of the segments (and, of course, of the whole antenna) rapidly increases, while the length of the segments is somewhat reduced. The greatest width is reached in the vicinity of segments 39 and 40, while segments 41, 42 and 43 become progressively narrower. The resultant club is somewhat more than one-sixth the length of the antenna.

The ventral surface of the head between the eyes is occupied by the proboscoidal fossa, which is very shallow in this species. The maxillae occupy most of the anterior section of the fossa. Most prominent are the galeae,

which are greatly elongated, concave mesally, and grooved together to form a tube through which liquid food is drawn by the sucking pump. Supporting the galeae, and extending laterocaudally from them, are the stipites, each bearing a small tubercle directly behind and slightly lateral to the galea, the maxillary palp. Each stipes is infolded and longitudinally divided into two sections by an area of light sclerotization (shown by heavy stippling in figure 3). The inner margins of the stipites are bilobed. Behind each stipes is a small, triangular sclerite, the cardo. The central and posterior parts of the fossa are occupied by the somewhat triangular labial sclerite, which bears caudally the large sockets of the labial palps. An invagination along the midline of the sclerite produces an internal ridge, the labial apodeme. The anterior rim of each palpal socket has two short articular processes. The anterior parts of the walls of the proboscidal fossa, lateral to the maxillae, are the hypostomal areas. Projecting forward from their sockets at the rear of the labial sclerite and up across the face are the large, three-segmented labial palps. The middle segment of each palp is the longest; the distal one is the shortest. All segments are essentially cylindrical, but the distal one is terminally produced into a point.

The posterior surface of the head is broken centrally

by a large opening, the foramen magnum, which is bisected by a transverse bar, the tentorial bridge. At the lateral ventral corners of the bridge are two depressions, the areas of articulation of the cervical sclerites. Along its dorsal and dorsolateral margins the foramen is bordered by the postocciput. This sclerite is well defined dorsally by the arched postoccipital suture, but the suture is indistinct laterally as it runs down to the posterior tentorial pits. The latter portions of the suture are shown as dotted lines in figure 4. The ventral border of the foramen is the main portion of the labial sclerite behind the sockets of the palps; the ventrolateral borders consist of thin upward growths of the posterior corners of the labial sclerite. The suture separating this portion of the labial sclerite from the occiput is called here the paralabial suture. Internally the dorsal portion of the postoccipital suture is represented by a strong ridge, while the lateral portions can be detected only as areas of heavy sclerotization. The paralabial suture is, however, represented by a rather strong ridge, at least in the ventral two-thirds of its length.

Lateral to the paralabial and postoccipital sutures, and covering the greater portion of the caudal surface of the head capsule, is the occiput. Approximately the inner one-third of the occiput on each side of the foramen is



separated from the remainder by two arcuate, heavily sclerotized streaks, the transoccipital bands.

In the center of the dorsal surface of the head is the vertex, an area delimited by the transfrontal suture anteriorly, the antennal sockets anterolaterally, and the temporal suture laterally and caudally. The temporal suture is represented internally by a rather strong ridge, but both the suture and the ridge are indistinct near the antennal sockets and in the center of the caudal portion. Lateral to the temporal suture, and running parallel to it from the antennal sockets to the postoccipital suture, is the paratemporal suture, represented internally by a ridge which is not as distinct as that of the temporal suture. On the dorsal surface of the head the area between the two sutures is here called the temporal area; on the caudal surface of the head there is a U-shaped depression between the temporal suture and the paratemporal and postoccipital sutures, called here the temporal fossa. Within the fossa are two reniform areas (outlined with dotted lines in figure 4) in which there are a great many setae. These areas, possibly sensory, may be the chaetosemata of Jordan (1923).

It should be noted here that the homologies of the various features of the dorsal and caudal surfaces of the head capsule are much confused by the presence of secondary

sclerotizations. The above interpretation has been necessarily arbitrary in an attempt to arrive at names which can be employed throughout the comparative work which will follow this paper.

The tentorium consists of the posterior tentorial bar already described and two simple anterior arms running between the anterior and posterior tentorial pits. The anterior arms are somewhat thicker anteriorly than posteriorly. Between the anterior arms in the front of the head and attached to the cranial wall near the lower edge of the labrum is the sclerotic ventral part of the sucking pump. The structure is roughly semicircular and is made up principally of the hypopharynx (see Schmitt, 1938). The dorsal portion of the pump is not sclerotized and does not concern us here.

The compound eyes are separated from the head capsule by thin ocular diaphragms. These are membranous disks perforated by large oval openings (long axis dorsoventral) through which pass the optic nerves. The diaphragms each have a small sclerotized area bordering the opening.

#### THORAX

#### Figures 8-21

Prothorax: the prothorax is much smaller than either of the segments of the pterothorax. The pronotum is

considered to be divided into three parts, a curved, roughly triangular dorsal plate, and two flat, dorsomedially fused lateral plates. The dorsal plate is pointed caudally, the beak-like point being curved ventrally and articulated with the prescutum of the mesothorax. The fused portions of the lateral plates form a Y-shaped structure which articulates with the dorsal plate at the tips of the arms of the Y; the crotch of the Y is membranous. Just above the lateral plates of the pronotum and forward of the cephalic margin of the dorsal plate are the large, roughly hemispherical patagia. These well sclerotized, paired structures are the most conspicuous features of the dorsum of the prothorax. The ventral ends of the lateral plates of the pronotum are fused to the dorsal ends of the propleura, which in turn are fused with one another midventrally, the fusion being indicated by a faint discrimen. Between the ring formed by the lateral plates of the pronotum and the propleura and the foramen magnum of the head is the membranous cervix. Bridging this cervical membrane lateroventrally on each side are the cervical sclerites. They are T-shaped, and each has a circular sclerotic pad bearing numerous setae on the stem of the T; the pads are called here cervical organs. The stem of the T articulates internally with the lateral extremity of the tentorial bridge and the upper arm of the T externally with the dorsal part of the cephalic



margin of the propleuron. Just forward of the line of fusion of the propleura, but not cut by the discrimen, is a narrow midventral sclerite projecting into the cervix, called here the presternum.

Internally the discrimen is represented anteriorly by a very weak inflection and caudally by a small intercoxal lamella. Laterocaudally on the rim of the coxal socket is the pointed pleural articulation of the coxa. Externally the discrimen may be traced between the bases of the coxae as the mid-line marking the base of the intercoxal lamella; it ends at the caudal margin of the coxal sockets at the oval furcasternum. In the center of the furcasternum can be seen a dark area representing the furcal pit. Internally the furcasternum is produced into a heavily sclerotized two-pronged furca, which is joined to the pleuron by a largely transparent plate, the furcal lamella.

Bridging the pro-mesothoracic intersegmental membrane midventrally is a narrow sclerite, the prothoracic spinasternum. The spinasternum tapers to a point anteriorly where it joins the furcasternum of the prothorax, and gradually widens posteriorly, so that where it meets the mesothoracic katepisternum it is nearly as wide as the furcasternum. The caudal end of the spinasternum is notched so that it joins the katepisternum at two points with a

membranous triangle between them. Near its middle the spinasternum is deeply invaginated along with the adjacent membrane, forming an internal projection, the spina.

Midlaterally in the pro-mesothoracic intersegmental membrane is the first spiracle. The upper half of the anterior border of the spiracular opening is occupied by the narrow anterior spiracular sclerite, which bears near its ventral end a long apodeme. The entire posterior border is occupied by the posterior spiracular sclerite, which has a small apodeme at its lower end.

Mesothorax: the mesonotum occupies the greater part of the dorsum of the pterothorax. It is divided into three sclerites, the prescutum, scutum and scutellum. The smallest of these, and the most anterior, is the prescutum. It is curved strongly ventrally in front where it articulates with the pronotum, and bears on its anteroventral margin the thin, bilobed first phragma. Arising from the lateral margins of the first phragma and hanging free in the body cavity are a pair of phragmal arms. Each lower lateral angle of the prescutum is produced into a long, slender process of prealare extending laterocaudoventrally to just in front of the tegular arm. The suture between the prescutum and scutum is represented internally by a weak ridge.

The mesoscutum is the largest sclerite of the thorax. The lateral edges of the anterior part of the scutum are produced into sloping plates, the suralares. Internally

each suralare is separated from the main part of the scutum by a strong ridge, the scutal ridge, which runs from the posterior margin of the prescutum to the posterior margin of the scutal incision. The scutal incision is a deep notch in the lateral edge of the scutum just behind the suralare. From the scutum just behind the incision a plate, the adnotale, projects forward forming a lateral border for the posterior part of the incision. The first axillary sclerite articulates with both the suralare and the adnotale, which together make up the anterior notal wing process. Separating the scutum from the smaller mesoscutellum is the inverted V-shaped scuto-scutellar suture. This suture is represented internally by a strong ridge. Projecting forward and laterally from the end of the scuto-scutellar suture is a horizontal shelf, the postalar plate, the posterior portion of which is membranous. The anterior mesal part of the plate is in the form of a sclerotic arch which is continuous with the caudal part of the adnotale. This arch is hidden by the scutum in figure 28. The antero-lateral corner of the postalar plate is produced as the posterior notal wing process, to which is fused the fourth axillary sclerite. Behind the membranous part of the plate is a thin sclerotic strip, and mesal to this strip is the base of the membranous axillary cord. Lateral to the plate and mesal to the axillary cord a rounded process of the

postalar portion of the epimeron projects through the membrane. This process is partially fused to the sclerotic part of the postalar plate.

A narrow membranous area separates the postnotum (the phragma bearing plate) from the mesoscutellum. The second phragma is very large and somewhat triangular in lateral view, with dorsal and ventral angles posteriorly and a mid-lateral angle forward. The anterior angles are paired, and each articulates with the mesoscutum in a socket in a protuberance of the ventral edge of the scutum immediately behind the caudal end of the adnotale, the phragmal articulation. Dorsally, at the rear of the phragma, are two prominent triangular projections, the phragmal processes, whose tips serve for muscle attachment. The surface of the phragma itself displays a fairly complex pattern of ridges and varying sclerotization. Some major features of this pattern are a lightly sclerotized anteriorly recurved area at the lower angle of the phragma, a heavily sclerotized bracing strut along the lower edge (sloping from the articulation almost to the lower angle), and two well sclerotized ridges running ventrally from the lower bases of the phragmal processes to the lower angle. When viewed from behind the lower angle of the phragma is not pointed but is fairly broad and bilobed, continuous with the top of the phragmal process on each side, and arching cephalo-

ventrally from it, is a ridge which joins the marginal strut and with it forms a small lateroventral protuberance. On this ridge is attached the meso-metathoracic intersegmental membrane. This line of membrane attachment separates the internal phragma from the external postnotum.

The more prominent features of the sternopleural region of the mesothorax are the episternum, epimeron and coxa. The mesepisternum consists of a large katepisternum with a tiny anepisternum nestled between the dorsocaudal corner of the katepisternum and the ventral side of the basalare. Approximately the lower third of the katepisternum is separated from the rest of the sclerite by the precoxal suture, which runs from the pleural suture to the anterior margin of the katepisternum at the point where it is joined by the prothoracic spinasternum. This part of the katepisternum is called here the sternopleurite. Immediately in front of the coxa the sternopleurite is traversed by the marginopleural suture, which runs from the pleural suture to the discrimen. The internal marginopleural ridge is strongest where it merges with the pleural ridge, becoming progressively weaker until it meets the base of the lamella of the discrimen. Internally the precoxal suture forms a strong ridge, the precoxal ridge, which is continuous with the thickened upper edge of the lamella of the discrimen. Above the precoxal suture the katepisternum

is separated by a vertical suture, the pre-episternal suture, from a narrow anterior sclerite, the pre-episternum. The pre-episternal suture is represented internally by the pre-episternal ridge. This ridge is rather small at its origin near the anterior part of the precoxal ridge, but becomes increasingly prominent as it curves dorsally and merges with the pleural ridge.

Midventrally the sternopleurites unite in a suture, the discrimen, whose inflection forms the very high, transparent, lamella of the discrimen. The base of this lamella, in the form of two narrow strips of the sternopleurites, extends backward between the bases of the coxae to the ventral articulations of the coxae. Posteriorly the lamella of the discrimen merges into the mesothoracic furca, which arises from the discrimen above the coxal articulations. The furca, when viewed in caudal aspect, is roughly Y-shaped, the arms of the Y (the secondary furcal arms) fusing with the ventrocaudal corners of the prealar portions of the epimera. Running from the pleural ridges to the anteromesal parts of the secondary arms are the tendon-like primary furcal arms. The furca is a complex structure exhibiting varying degrees of sclerotization in different areas. Major features are three thin, rounded lamellae projecting posteriorly from the main stem of the furca and from near the lateral borders of each of the



secondary arms.

The mesepimeron is divided into two parts, an anterior prealar portion and a posterior postalar portion. The dorsal edge of the prealar portion curves strongly downward near the middle, leaving a relatively large area between it and the ventral side of the subalare. Near the dorsal part of the anterior border of the epimeron a small plate is separated from it, the pre-epimeron. The postalar portion is separated from the dorsocaudal corner of the prealar section by a line. The anterior end of this portion is inflected and curved downward into the body cavity as an apodeme and upward as a process which penetrates the two membranes mesal to the axillary cord and emerges lateral to the postalar plate. Externally the postalar portion of the epimeron appears as a long strip which fuses caudally with the dorsal part of the postnotum.

Between the epimeron and the episternum is the deeply inflected pleural suture. The internal manifestation of this suture, the pleural ridge, is the most prominent feature of the mesal wall of the mesothorax. Near its dorsal limit, at the point of attachment of the primary furcal arms, the ridge is produced mesocaudally into a small plate. The inflection producing this plate is responsible for the formation of the pre-epimeron, although the deep inflection of the pleural suture in this area

makes the exact method of its formation difficult to determine. Narrow strips of the anepisternum and epimeron, carrying with them the pleural suture, project dorsally between the basalare and subalare as the pleural wing process. From this process just mesad of the caudoventral corner of the basalare a tubular internal process, the tegular arm, projects anteriorly behind the basalare. The arm terminates just in front of the basalare in two lobes, one mesal to the other, whose surfaces are external. Articulating with the lateral lobe of the arm is the large, bilobed, tegula. The smaller, lower lobe of the tegula curves beneath the leading edge of the wing.

In the region of the pleural coxal articulation the pleural ridge becomes a quite complex structure as it is joined by the precoxal ridge, the marginopleural ridge, and the ridges formed by the inflected dorsal and anterior margins of the meron. The coxa (which is discussed here because it is an integral part of the thoracic capsule) consists of two sclerites, a relatively narrow, anterior eucoxa (Madden, 1944) and a bulbous posterior meron. The suture between the two (the coxal suture) seems to be a line suture, with the internal ridge representing the inflection of the border of the meron alone. The dorsomesal border of the eucoxa is inflected and produced into the relatively large eucoxal apodeme. The caudoventromesal part

of the coxa is membranous, containing one round sclerotic island, the coxal sclerule. A small caudomesal lip of the upper part of the meron, the postcoxal sclerite, is separated from the rest of that structure by the postcoxal suture, which is represented internally by a weak ridge continuous with the inflected border of the meron. At the top of the coxal suture there is a tiny sclerite, a lip of the meron beyond its inflected edge, the basicoxite.

Above the episternum in front of the pleural wing process is a roughly diamond shaped plate, the basalare. Internally a triangular cavity occupies the central part of the sclerite. A large, mostly lightly sclerotized apodeme is attached by an almost transparent tendon to the anterior corner of the basalare. Above the epimeron, and separated from it by a considerable expanse of membrane, is the other epipleurite, the large, elongate subalare. Internally the subalare has a concavity anteroventrally, and bears a conspicuous wing-like apodeme projecting from its mid-section into the body cavity.

In the meso-metathoracic intersegmental membrane close to the upper part of the prealar portion of the epimeron, is the second spiracle. It is bordered in front and behind by fringed, lightly sclerotized plates, the anterior and posterior spiracular sclerites.

Metathorax: In the metanotum the metascutum is

divided into two lateral portions by the metascutellum. The scuto-scutellar ridge is very strong and wall-like, dividing the bulging upper part of the metanotum into three compartments. The anterior notal wing processes are merely small projections of the anterolateral walls of the scutum, while the posterior notal wing processes are long, slender projections from the posterior part of the scutum. The scutal ridge is present in the same position as in the mesoscutum, but is, of course, much shorter. There is no scutal incision. A thin membranous area separates the complex metapostnotum dorsally from the metascutellum. The salient features of the postnotum are a ventrally truncated heart shaped area at the mid-line of the dorsum, and the phragma which is divided into two arms, each tipped with a flat, oval plate, which project into the body cavity from near the lateral extremities of the postnotum. The whole postnotum is so well fused with the tergum and epimeron laterally that its limits are difficult to ascertain.

As can be seen from the figures, the positions of the various sclerites of the metathoracic pleural and sternal areas are very similar to the positions of the homologous sclerites of the mesothorax, although their shapes are quite different. Therefore only major differences will be discussed here. The anepisternum is a small but well defined

sclerite just above the shoulder of the katepisternum. It bears numerous bristles, and although it is closely associated with the basalare and pleural wing process it is separated from each by a distinct line suture. The pre-coxal suture is absent, leaving the katepisternum as an undivided sclerite. There is an insignificant pre-episternum, which does not continue ventrally to the level of the coxa. The meron is sharply reduced in favor of the epimeron.

Internally the metathorax presents quite a different aspect from the mesothorax. The lamella of the discrimen is arched, arising at the base of the pre-episternal ridge and terminating at the base of the furca. The top of the lamella is thickened as in the mesothorax, and there are two short, pointed thickenings in the base of the lamella. There is, of course, no pre-coxal ridge. The eucoxal apodeme has on its dorsum a small tubercle to which a muscle is attached. The metafurca is entirely different from the mesofurca. Its most prominent feature is a forward thrust body, shaped somewhat like an arrowhead when seen in dorsal aspect, which overhangs the lamella of the discrimen. The posteriorly projecting secondary arms are fused together ventrally forming a V-shaped trough which becomes progressively shallower caudally. The arms are quite thin and are broadly fused to the epimera which are curved mesally and form the caudal border of the thorax beneath the attachment

of the abdomen. The transparent, tendon-like primary furcal arms arise near the base of the furca and attach to a plate which seems to be an outgrowth of both the pleural ridge and the epimeron just posterior to it. There is, however, no obvious pre-epimeron. The tegular arm and tegula are absent.

The basalare is much smaller than that of the mesothorax, and bears on its inner surface a relatively large, blunt, basalare apodeme. The subalare is small and seems to be merely an external manifestation of a sclerotic cap to which the subalare muscle is attached.

## LEGS

### Figures 22-27

The prothoracic legs of Danaus, as in all other so-called "four-footed butterflies," are greatly reduced. The procoxa is long (approximately the same length as the profemur) and grooved on its lateral face. The male tarsus is simple (not divided into tarsomeres) while that of the female is club shaped and divided into four tarsomeres, a long proximal one, and three compressed distal ones. On the caudal side of the distal end of the first three tarsomeres are paired spines. These are complemented by lobes on the caudal side of the proximal end of the last three tarsomeres which bear bundles of setae which cup

around the bases of the spines.

The meso and metathoracic legs are similar in both sexes. In specimens which have the scales intact, however, there is a small brush of narrow seta-like scales somewhat more than halfway up the mesal side of the tibia of the mesothoracic leg. The tibiae of the mesothoracic and metathoracic legs in the females bear numerous spines, while there are only a few scattered spines in the males. The spines of the proximal tarsomere are also more prominent in the female.

In the pretarsus, the unguifer (the dorsal plate to which the tarsal claws or ungues are articulated) is only slightly sclerotized. The most prominent feature of the ventral side of the pretarsus is the large, flat, unguitractor plate. This plate is tapered internally into a long, thin apodeme, the unguitractor tendon. Just in front of the unguitractor plate, between the basal parts of the claws, is a small, membranous lobe, the empodium. Just dorsal to the empodium is a small, lightly sclerotized protuberance, the arolium. Lateral to the unguitractor plate are two membranous lobes, the pulvilli. The ungues are not notched, and are abruptly hooked terminally and thickened basally.



## WINGS AND WING BASES

Figures 28-31, 33

The areas of the wing articulations present an extremely complex picture. Each area consists of two membranes and associated sclerotic plates; an upper membrane connecting the dorsum of the wing with the tergum, and a lower membrane connecting the venter of the wing with the pleurites. These membranes are called the upper and lower alary membranes respectively.

In these membranes are found a series of plates which are among the most important structures of the wing articulation, the axillary sclerites. In the mesothorax there are four axillary sclerites. The first axillary is visible only from the upper side. It is roughly Y-shaped, with the base of the Y articulating with the adnotale, the anterior arm with the suralare mesally and the second axillary laterally, and the posterior arm with the second axillary. The second axillary is bilobed when viewed from above. The mesal lobe articulates with the first axillary mesally and the third axillary posterolaterally; the lateral lobe is narrowly fused to its anterolateral corner. Distally the lateral lobe is in contact with the complex basal sclerotizations of veins Sc, R, Cu and 2V. Beneath the upper alary membrane both lobes of the second axillary

send plates ventrally which fuse into a blunt process. This process articulates with the pleural wing process; a small portion is exposed ventrally.

The third axillary is V-shaped, with the distal arm of the V lying in the upper membrane and appearing from above as a slightly oblong, arcuate sclerite. The proximal arm projects ventromesally between the membranes from the caudal end of the distal arm. A small portion of it penetrates the lower membrane and can be seen as a narrow strip above the subalare. The muscle of the third axillary sclerite is attached to the crotch and proximal arm of the V. The fourth axillary lies in the upper membrane and is fused to the posterior notal wing process, from which it is differentiated by a constricted area. Its distal end lies under the flap of membrane enclosing the third axillary muscle and works against the proximal arm of the third axillary.

In front of the first and second axillary sclerites is the pointed basal process of the subcosta (Sc), which articulates with the suralare and the anterior arm of the first axillary. On the ventral side the base of the fused Sc+R is expanded into a bilobed sclerite, the radial plate.

In the metathorax there are only three axillaries, the fourth axillary being absent. The pattern of the sclerites

is similar to that of the mesothorax, although their shapes are quite different. The first axillary is long and thin, with the posterior arm of the Y reduced to a mere bulge. The second axillary is very irregular and is fused anteriorly with the basal process of the Sc. Near the lateral edge the second axillary bears a ventral process which penetrates the lower alary membrane, producing a rather large, ventrally exposed sclerite which articulates with the pleural wing process.

The third axillary is shorter than that of the mesothorax, and the muscle is smaller. It is more triangular than V-shaped. The portion visible from above is oblong, and the anterior and posterior ends of this portion are inflected ventrally and fused together to form a process which penetrates the lower membrane. The muscle is attached to the posterior apex of the rough triangle thus formed. The posterior notal wing process articulates with the caudomesal side of the lower apex of the triangle.

Just mesal to the base of  $Sc+R_1$  and projecting anteriorly is a large costal sclerite. On the underside a bilobed radial sclerite is present.

Figures of the wing venation are presented for completeness and for orientation in connection with the figures of the wing bases. The venation of the Monarch has been figured numerous times before, and nothing new is

added here. The system of naming the veins is adopted from Klots (1951) with the substitution of vannal veins for "anal veins."

#### ABDOMEN

#### Figures 32, 34-41

Pregenital segments: Because of the modification of the eighth sternum of the male into pseudovalves, it can be said that there are seven pregenital abdominal segments in both sexes of Danaus plexippus. The first abdominal segment is highly modified, as in most higher insects, for articulation with the metathorax. The anterior part of tergum 1 is membranous. The sclerotic portion of the tergum is dorsocaudally bulged, giving a pouch-like effect. Its caudal margin slightly overhangs the second abdominal tergum. On each side of the first tergum, near its margins, is a deep inflection, the tergal groove. The heavy internal ridge of this inflection is called the tergal brace. The anterolateral corners of the tergum are produced laterally into small protuberances, the tergal lobes. The first abdominal sternum (sternum 1) is almost completely membranous, only a small posterior sclerotic portion remaining which is fused to sternum 2. This portion of the sternum is also fused to a thin process of the posterolateral corner of the tergum, the postspiracular bar.

Just in front of this point of fusion another thin process is emitted by the sternum which crosses the pleural area below the first abdominal spiracle and terminates just below the tergal lobe (not fusing with it). This process is called the prespiracular bar. The abdominal spiracles are all similar to the first thoracic spiracle but the abdominal anterior spiracular sclerites resemble the thoracic posterior spiracular sclerites and vice versa. There are brushes of bristles extending externally and caudally from the anterior spiracular sclerites of the abdomen.

The first, second and third terga and sterna are fused together and lack intersegmental membranes. From the 3-4 intersegmental area onward there is an increase in the amount of intersegmental membrane and the resultant amount of possible overlap of segments. The size and shape of pregenital segments 2-7 can be seen in figure 32. None of them bear significant internal processes.

Male genital segments: The eighth tergum is somewhat reduced, the eighth sternum is fairly normal, though lightly sclerotized, for the first one-fourth of its length. Its caudal portion, however, is heavily sclerotized and inflected, forming a U-shaped structure below and around the genitalia proper. The extreme caudal portions of the sternum extend beyond the pleural membrane as hollow, bilobed protuberances. These eighth sternal

structures have the appearance of paired valvae, and are called here pseudovalves, following Viette (1948). It should be noted that Klots (1956) is in error in regarding Viette's term as applying to enlargements of the ninth sternum (probably a lapsus calami).

Between the eighth and ninth sterna there is on each side an invagination of the intersegmental membrane which contains a hair pencil. The ninth sternum is a narrow U-shaped sclerotic band, termed by taxonomists the vinculum. Midventrally it bears a blind tubular apodeme directed anteriorly, the saccus. Articulated to the lateral arms of the vinculum are the paired valvae, morphologically probably the gonocoxites of the ninth segment. Each valva bears a sharp, elongate, caudomesal process. The ninth tergum, which in most Lepidoptera makes up the major portion of the heavily sclerotized tegumen, is membranous. The region of the tenth tergum is occupied by two fairly lightly sclerotized lobes, termed collectively the uncus. There is no sign of a gnathos, or any other sclerotization of the tenth sternum. A membrane closes the rear end of the abdominal cavity, running from the bases of the valvae and the vinculum to the uncus and anus. This terminal membrane is referred to as the diaphragma. The anus is situated in the lobe of the membrane which separates the parts of the uncus. The diaphragma is pierced roughly in

its center by the long, slender, heavily sclerotized aedeagus. The eversible cone of membrane around the aedeagus is termed the anellus. The only sclerotization in the diaphragma proper is a roughly triangular juxta lying below the aedeagus and presumably helping to support it.

Female genital segments: Although it is not properly a genital segment, it should be mentioned that the seventh sternum is somewhat modified to extend up and around the anterior borders of the sinus vaginalis. The sinus vaginalis is a conspicuous cavity in the ventral side of the abdomen, just caudal to the seventh sternum. The sinus contains two sclerotic plates, a large anterior, deeply incurved lamella antevaginalis, and a smaller posterior lamella postvaginalis. The two lamellae are joined laterally and enclose a small membranous area in the center of which is the receptive opening, the ostium bursae. Internally the heavily sclerotized ductus bursae leads from the ostium to the large, membranous corpus bursae. In the wall of the corpus bursae are a pair of spined signa, joined by a yoke at the anterior end of the corpus. The corpus, ductus and ostium bursae together compromise the bursa copulatrix. The lamella antevaginalis is a structure of the 7-8 intersegmental membrane and can be differentiated from the seventh sternum, while the lamella



postvaginalis, also presumably intersegmental in origin, cannot be distinguished from the eighth sternum. The eighth tergum is divided into two lateral plates, its dorsum being membranous.

The only well sclerotized structures beyond the eighth segment are two lateral plates fused to the papillae anales, which bear the apophyses posteriores, strongly sclerotized, paired apodemes which project forward into the body cavity. These plates are considered to represent the ninth tergum. The papillae anales are lightly sclerotized, setose lobes on either side of the membranous bulge of the anal area. They are presumably derived from the ninth or tenth terga or both. Just below and anterior to the papillae is a small, lightly sclerotized area which may be a remnant of the ninth or tenth sterna or both. The anus and oviporus, the former above and behind the latter, lie between the papillae. The ninth and tenth segments can be retracted within the eighth so that only the tips of the papillae can be seen, or they may be completely extruded so that the bulging, lightly ridged membrane around the anus protrudes between the papillae.

#### VARIATION

In the descriptive section of this work no mention is made of individual variation between the specimens examined.

Disregarding sexual dimorphism two types of variation were observed: variation in size and variation in shape. However, the structures studied were invariably present.

Variation in size was not extreme. The length of a primary (mesothoracic) wing from the base of the subcosta to the apex has been studied in order to give an idea of the magnitude of this variation. Twenty-one male specimens from Lawrence, Douglas County, Kansas showed a range for this measurement of 48-55 mm., with a mean of  $51.2 \pm .48$  mm. Fourteen females from the same locality showed a range of 49-57 mm., with a mean of  $52.1 \pm .67$  mm.

Variation in shape was also relatively slight. Some of it can be attributed to the circumstances of the insect's death (whether it was pinched, placed in a cyanide jar, or placed directly in fixative); the outline of the thoracic terga or the amount of membrane exposed between the meso- and metathoraces or the katepisternum and eucoxa of the metathorax may be affected. Proportions of various structures may vary, such as the ratio of the length of the meso-scutellum to the mesoscutum. The courses of most of the sutures show variability, some (e.g., the mesothoracic scuto-scutellar) being rather variable, while others (e.g., the mesothoracic pleural) being relatively stable. Sclerites in which greater than average variation in shape has been observed are, among others, the epimera of the

pterothorax, the mesothoracic subalare, and the mesoscutellum. However, it should be emphasized that this variation is still relatively minor and that in no case is the characteristic shape of the sclerite lost.

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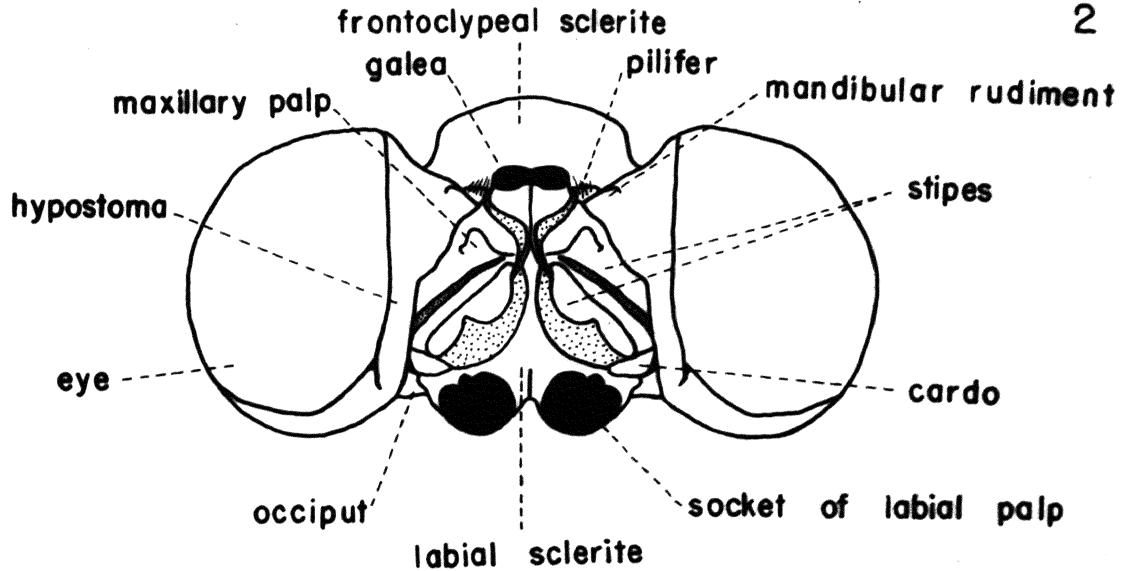
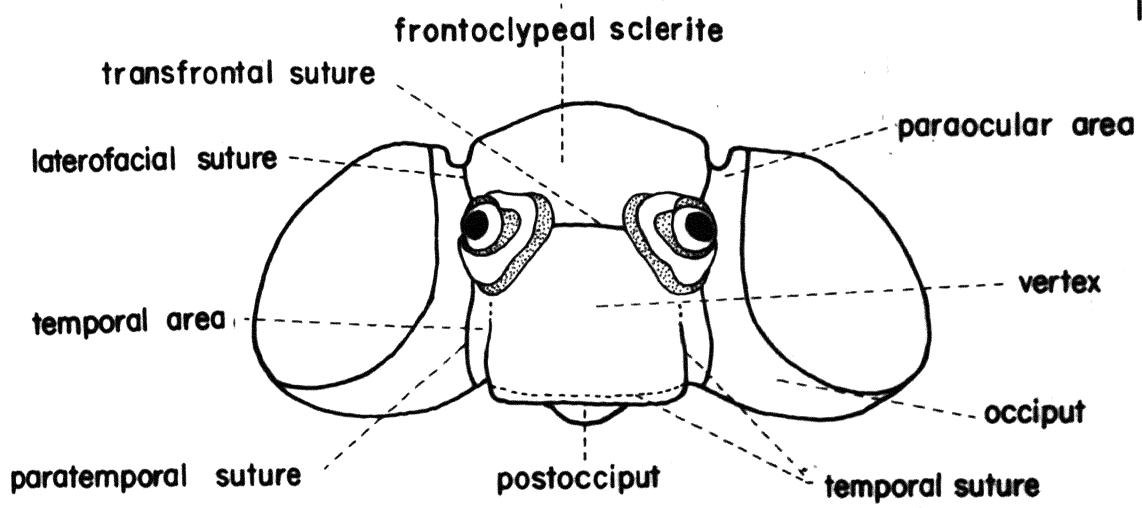
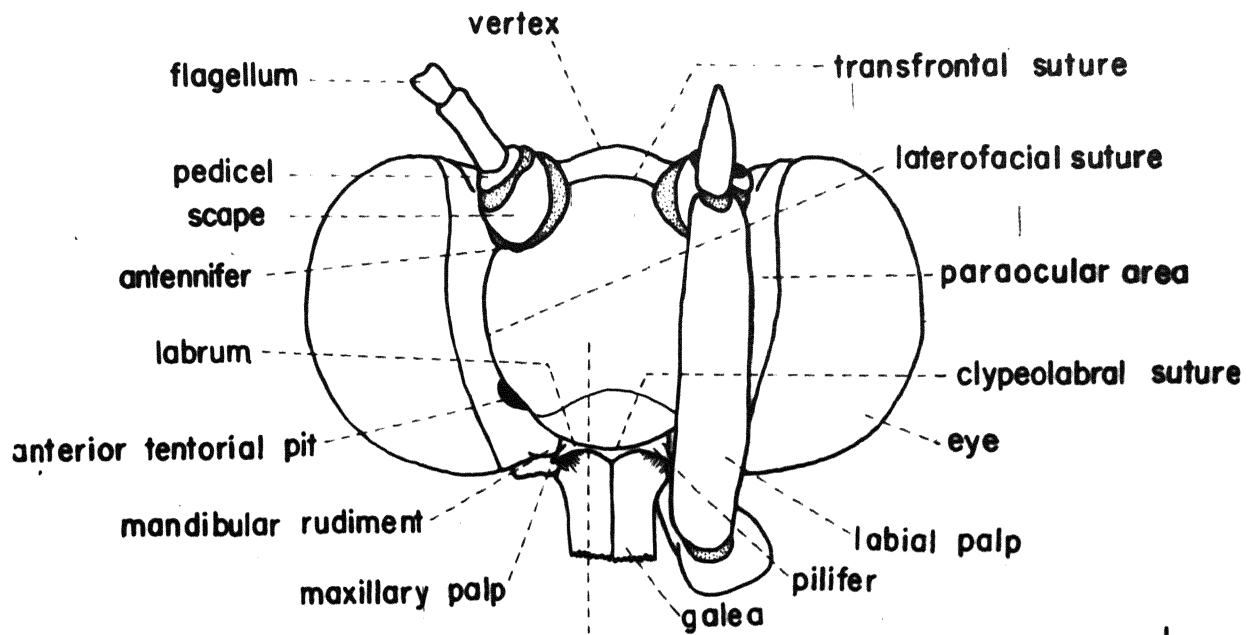
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Figures 1-3. 1. Front view of head. 2. Dorsal view  
of head. 3. Ventral view of head.



2mm

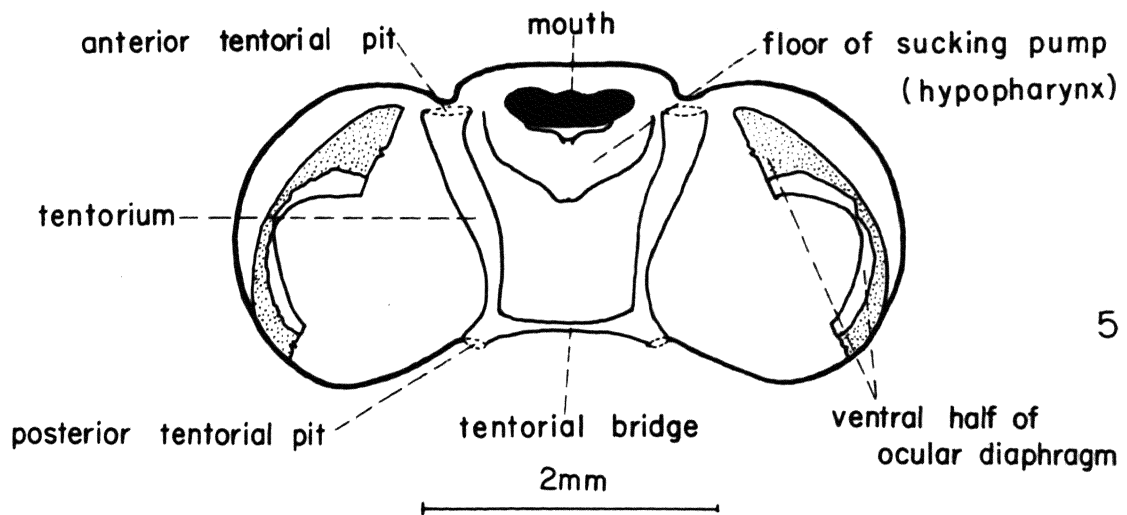
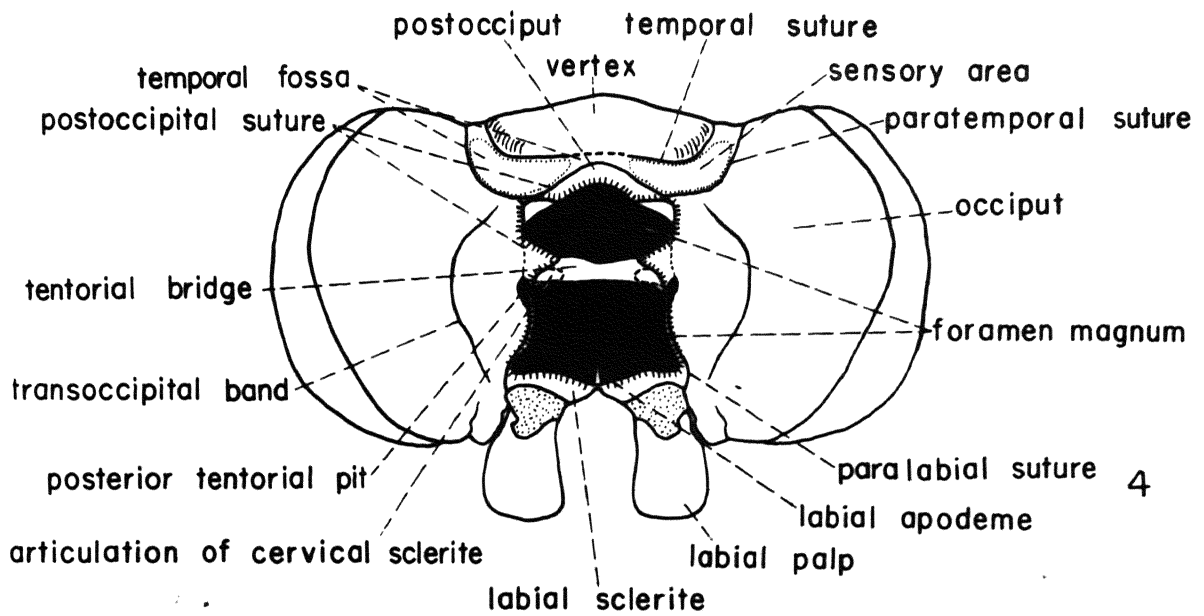
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Figures 4-5. 4. Posterior view of head (the line marked by short cross lines represents attachment of cervical membrane to head). 5. Dorsal view of dissection of head to show tentorium (diagramatic).



Figures 6-7. 6. Lateral view of head. 7. Antenna.

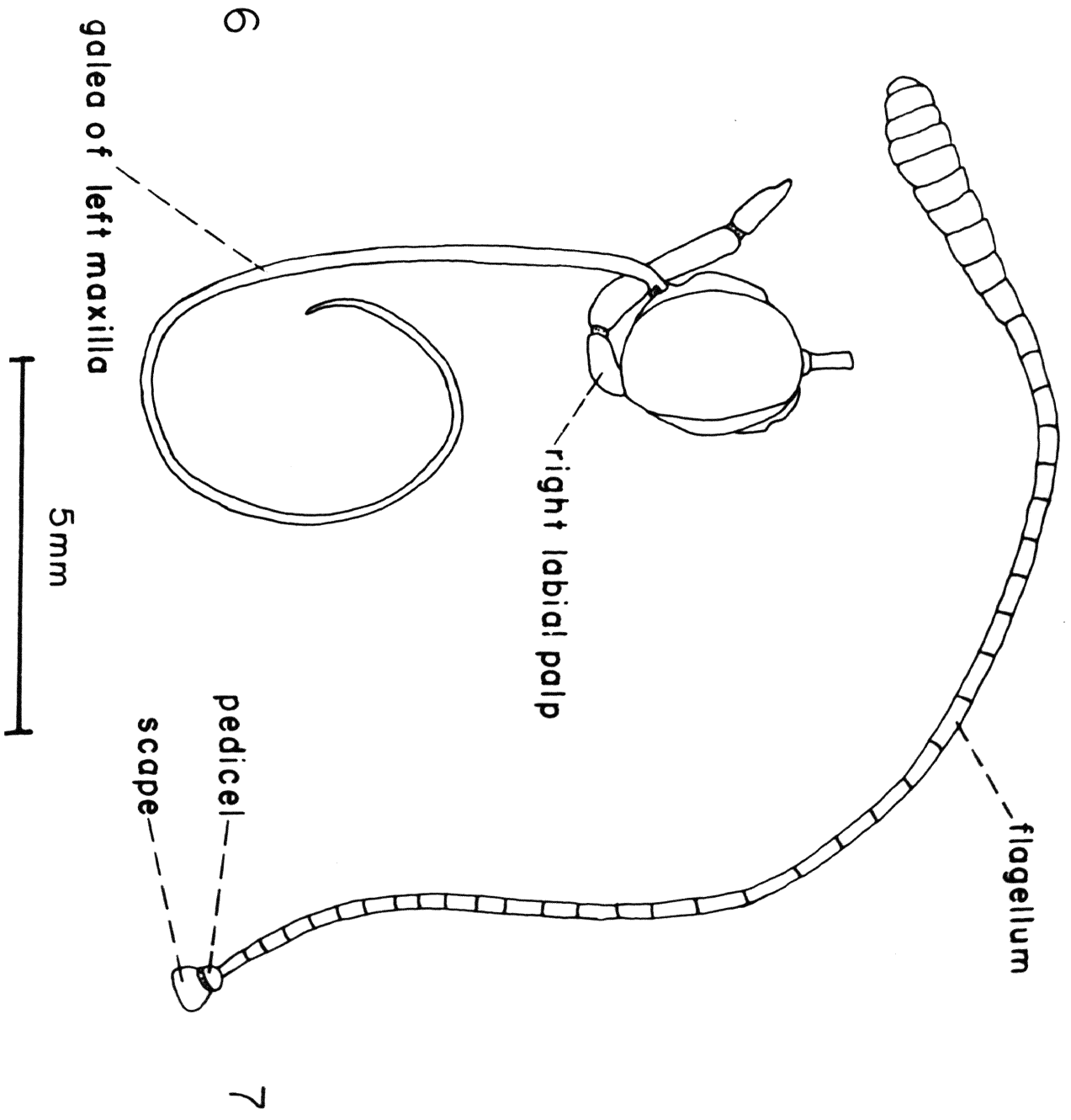


Figure 8. Posterior (internal) view of prothorax.

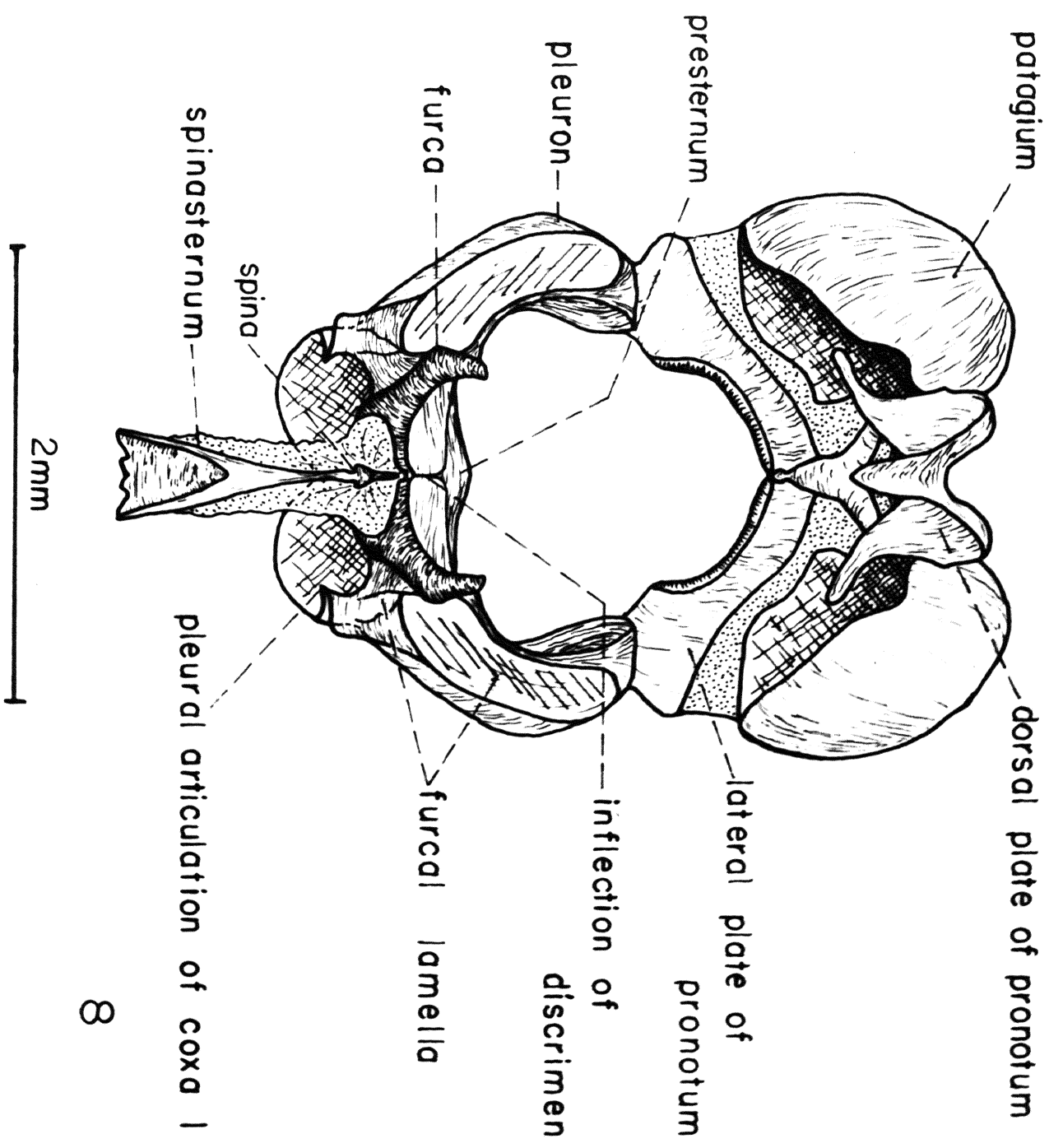


Figure 9. Lateral view of thorax. Broken line represents outline of tegula, removed to show structures beneath it.



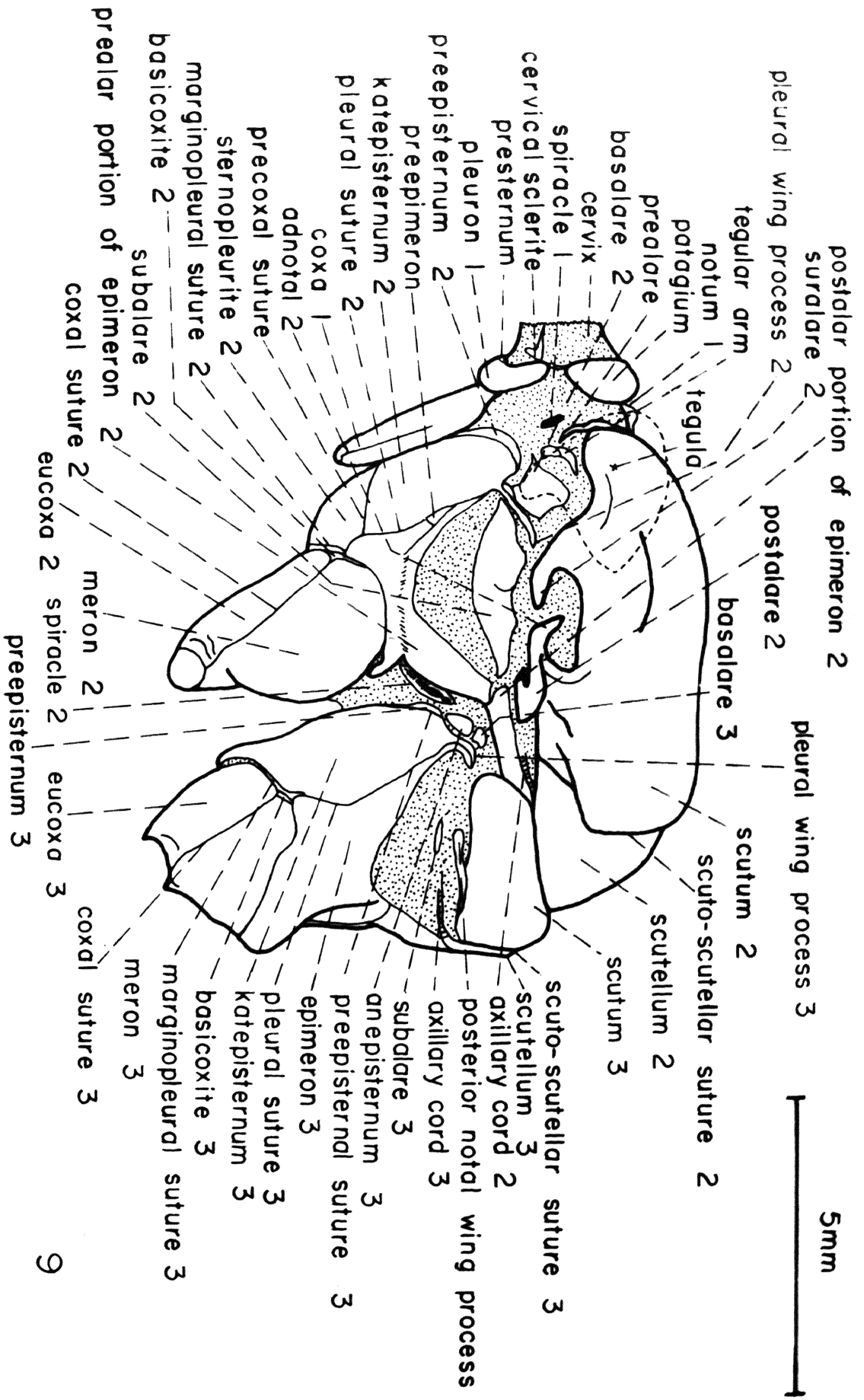
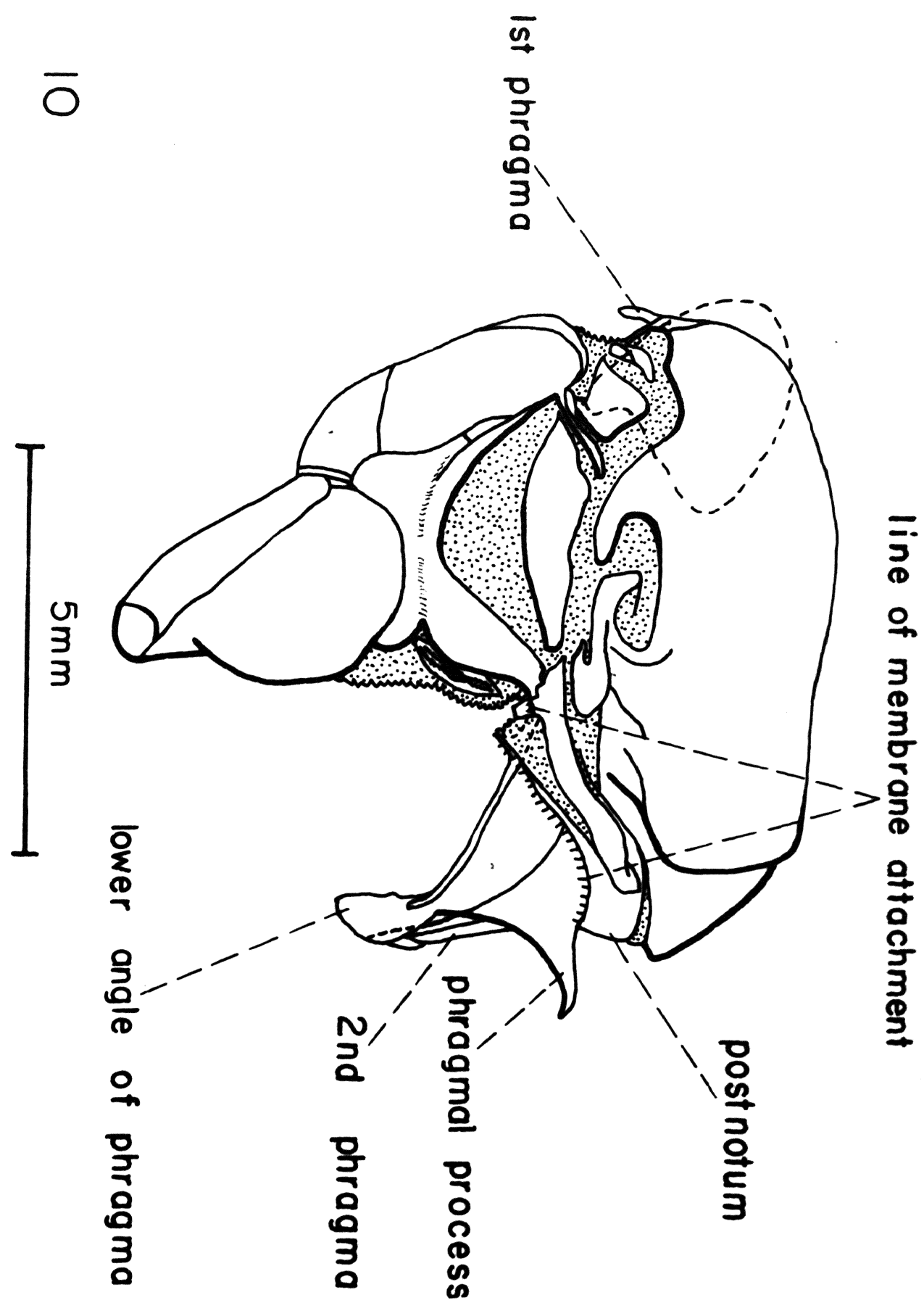


Figure 10. Lateral view of mesothorax, showing phragmata.



Figures 11-14. 11. Lateral view of cervical sclerite.  
12. Mesal view of first thoracic spiracle. 13. Mesal view of mesothoracic basalare. 14. Mesal view of mesothoracic subalare.

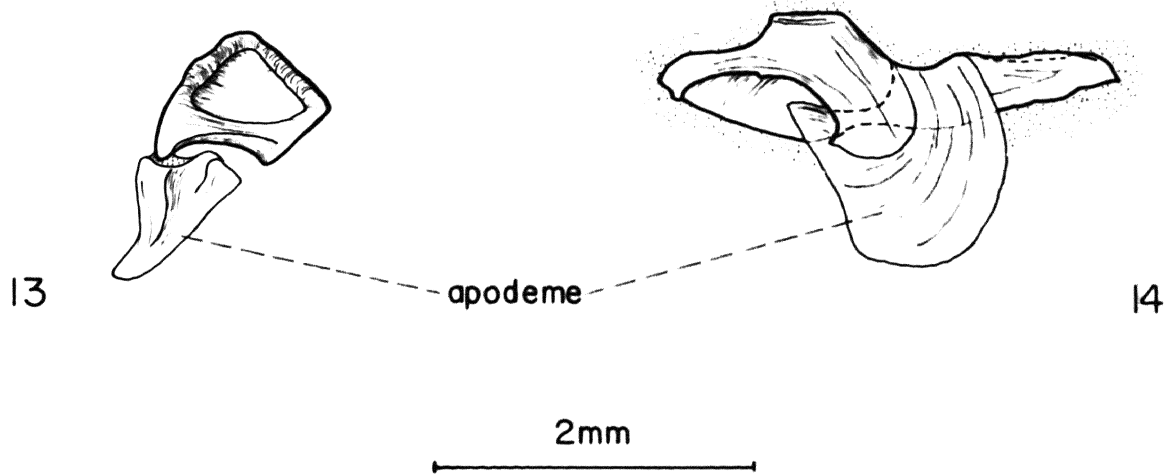
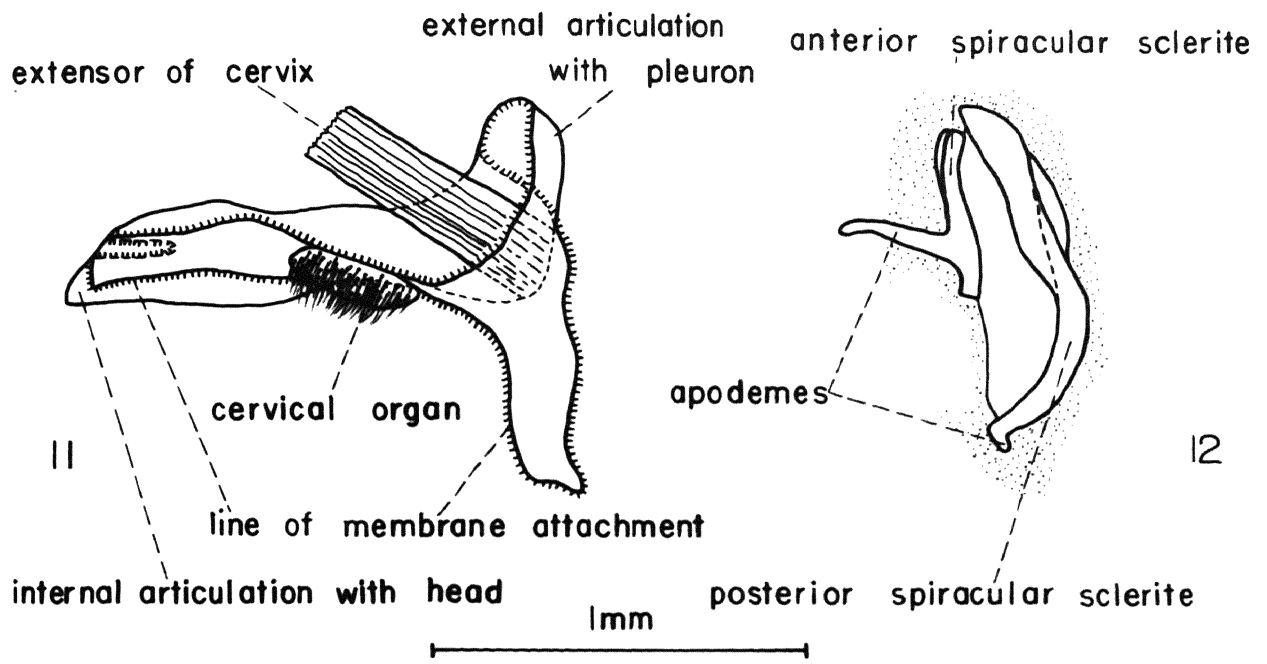


Figure 15. Dorsal view of thorax. Broken line represents outline of left tegula, removed to show structures beneath it.

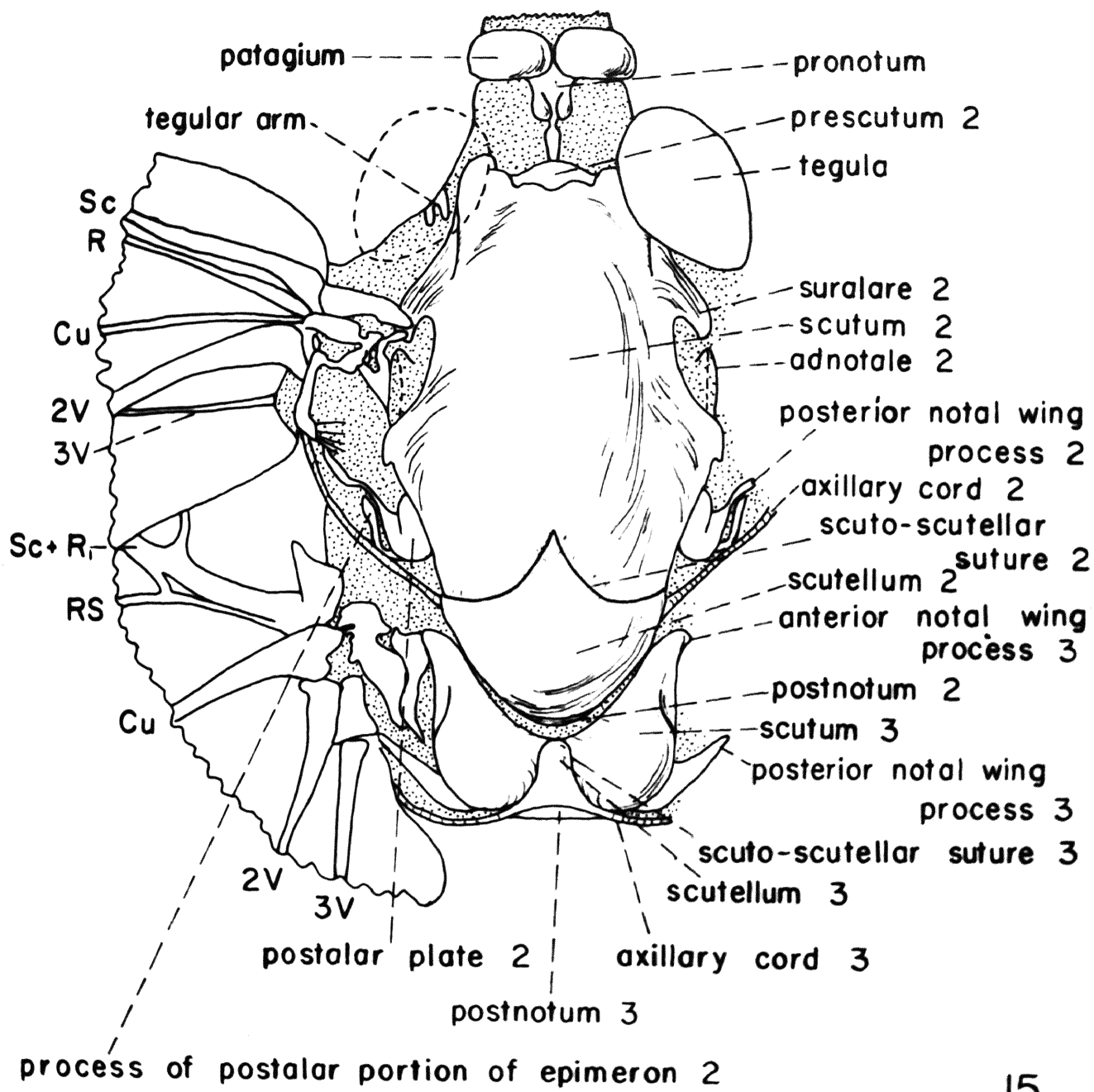


Figure 16. Mesal (internal) view of right half of meso and metathoracic terga. Metapostnotum and third phragma omitted.



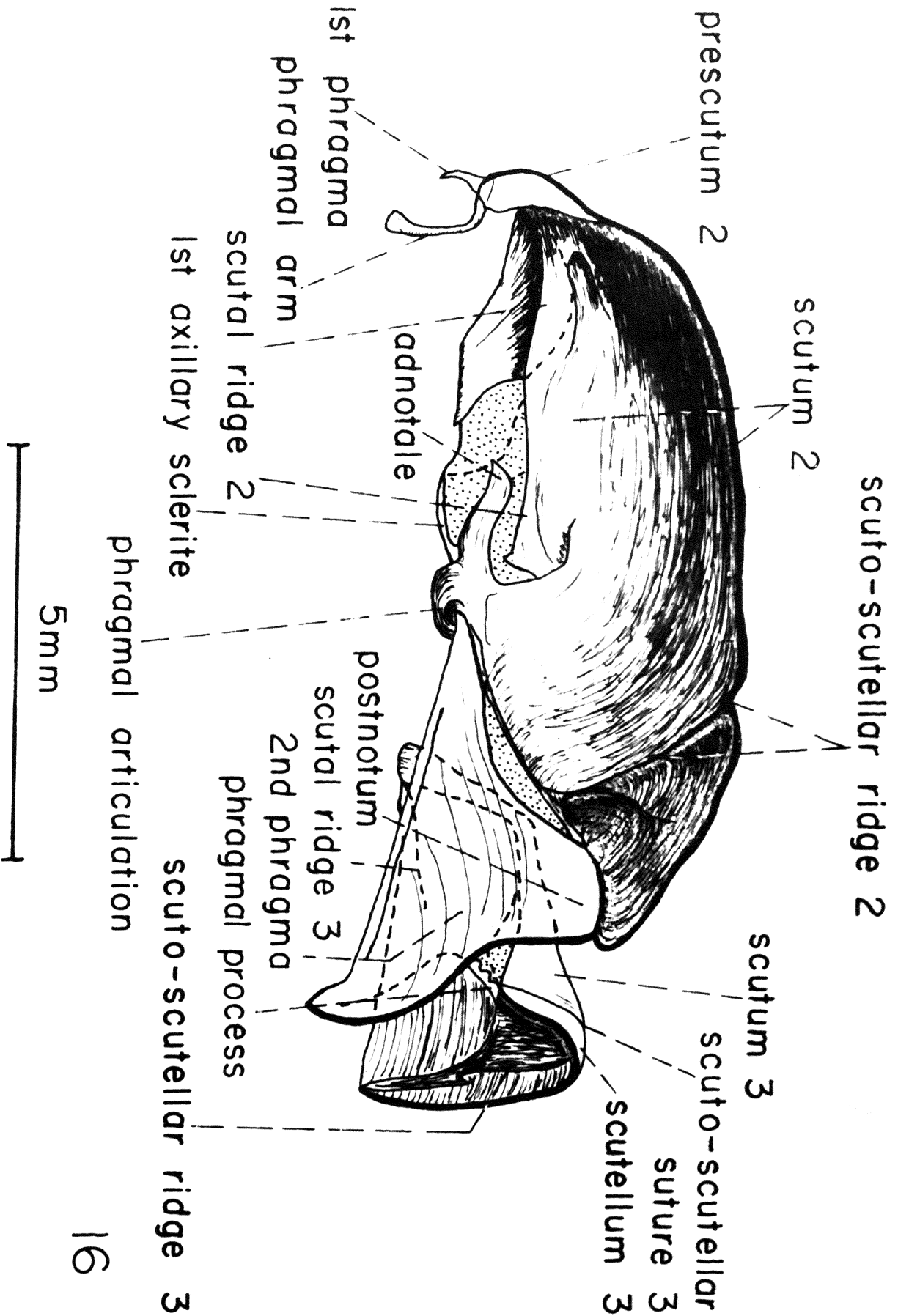
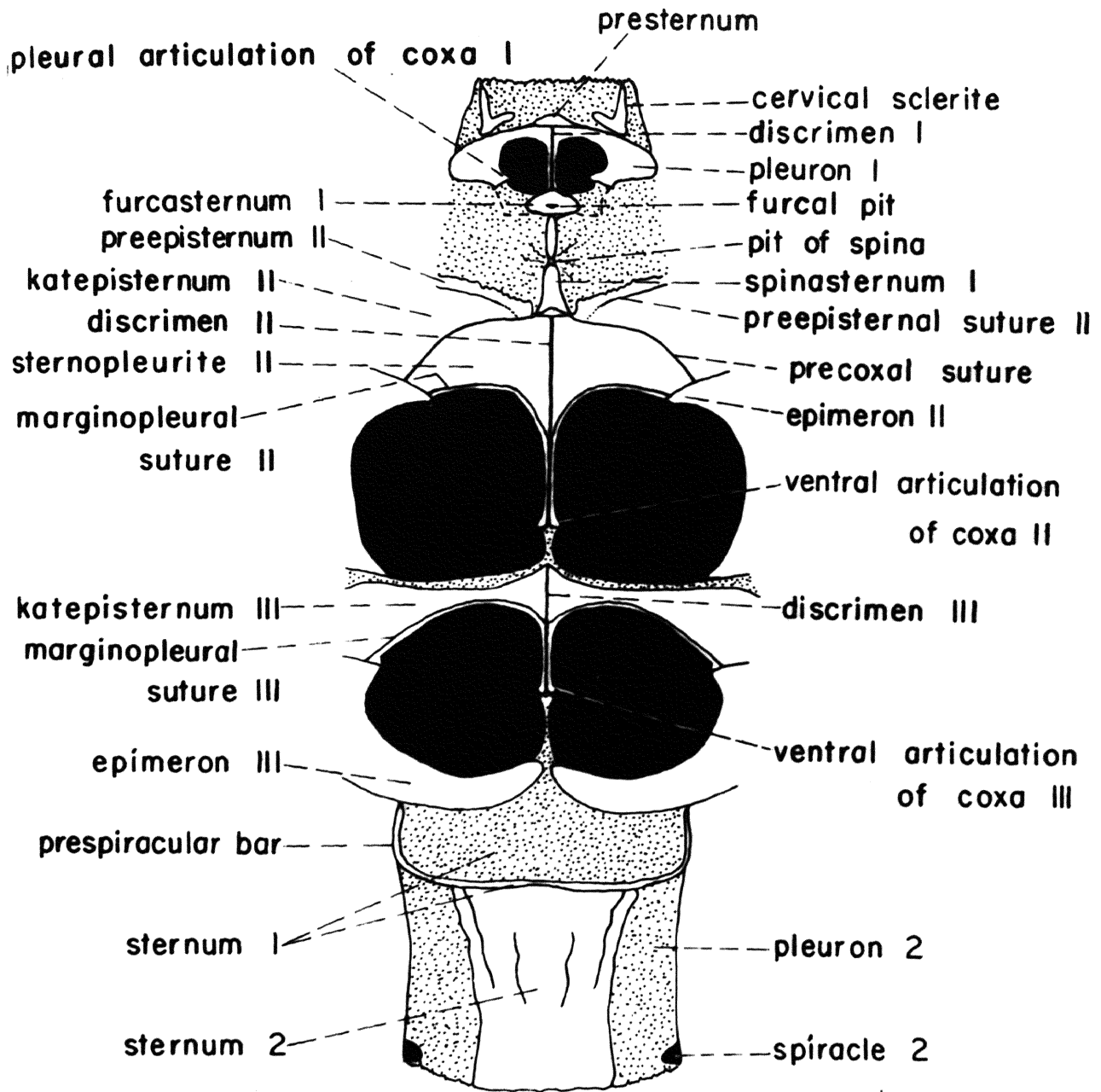


Figure 17. Ventral view of thorax and base of abdomen.



5mm

Figure 18. Mesal (internal) view of right half of mesopleuron and sternum and prothoracic spinasternum. Postalar portion of epimeron omitted.

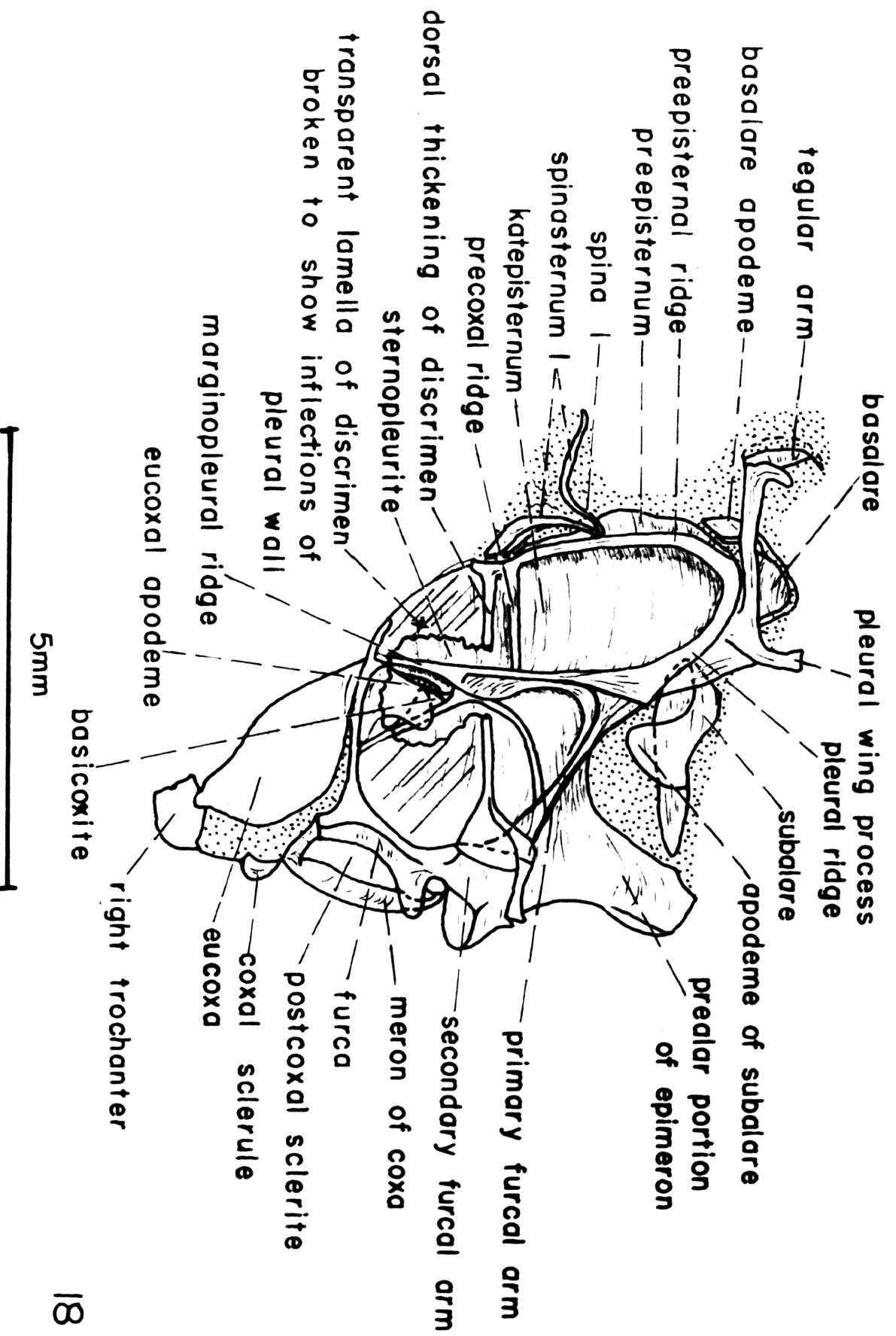
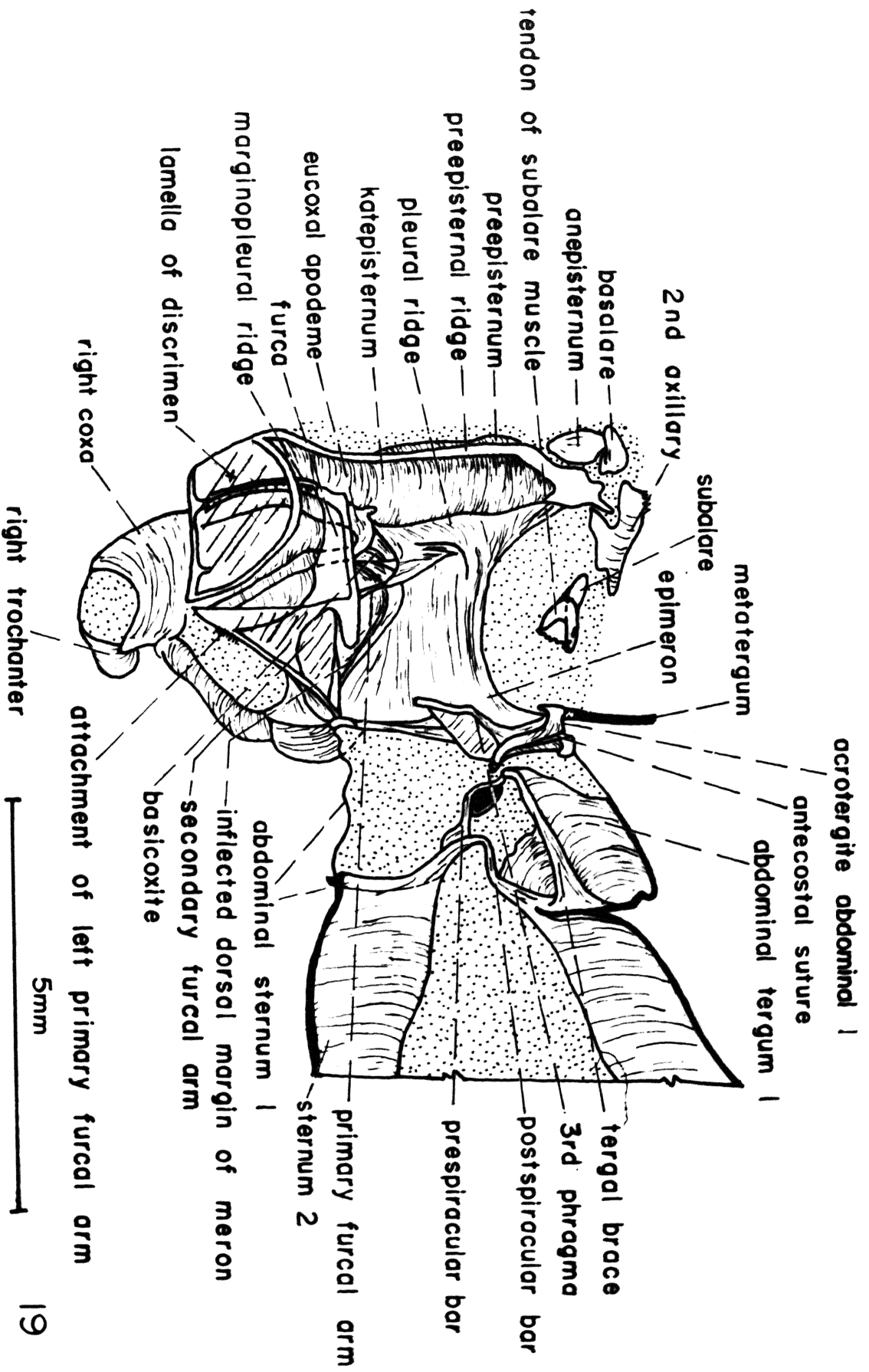
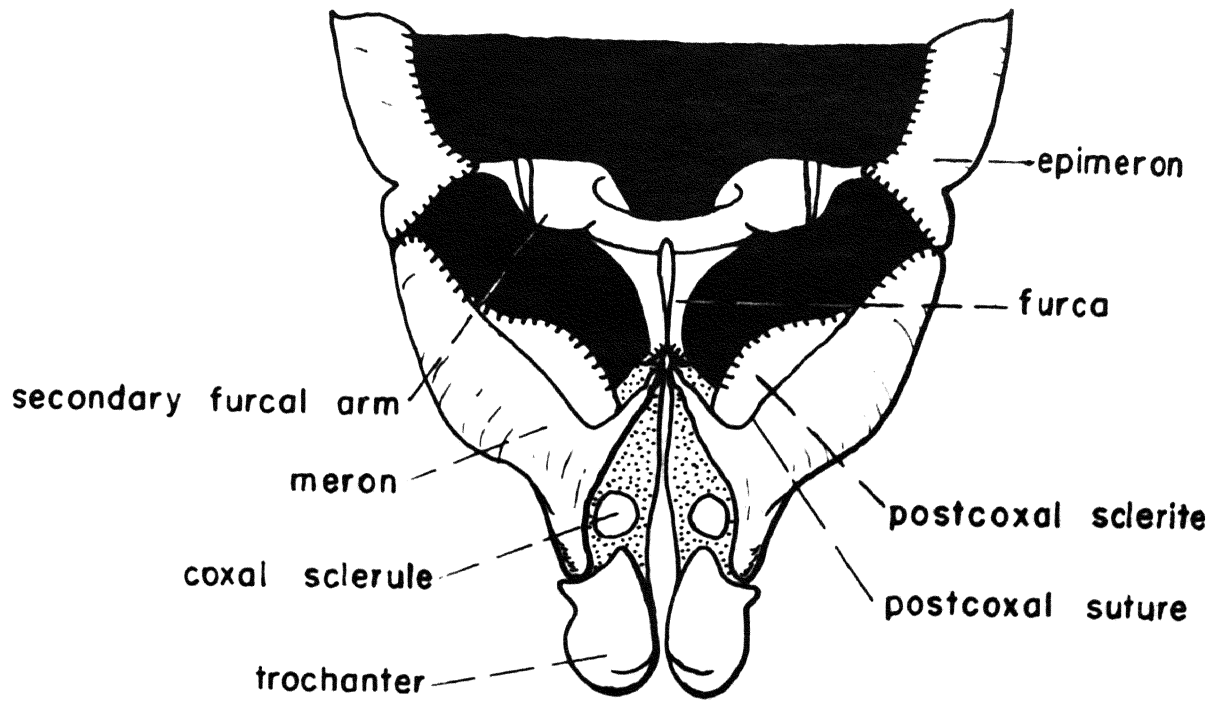


Figure 19. Mesal (internal) view of right half of metapleuron and sternum and base of abdomen.

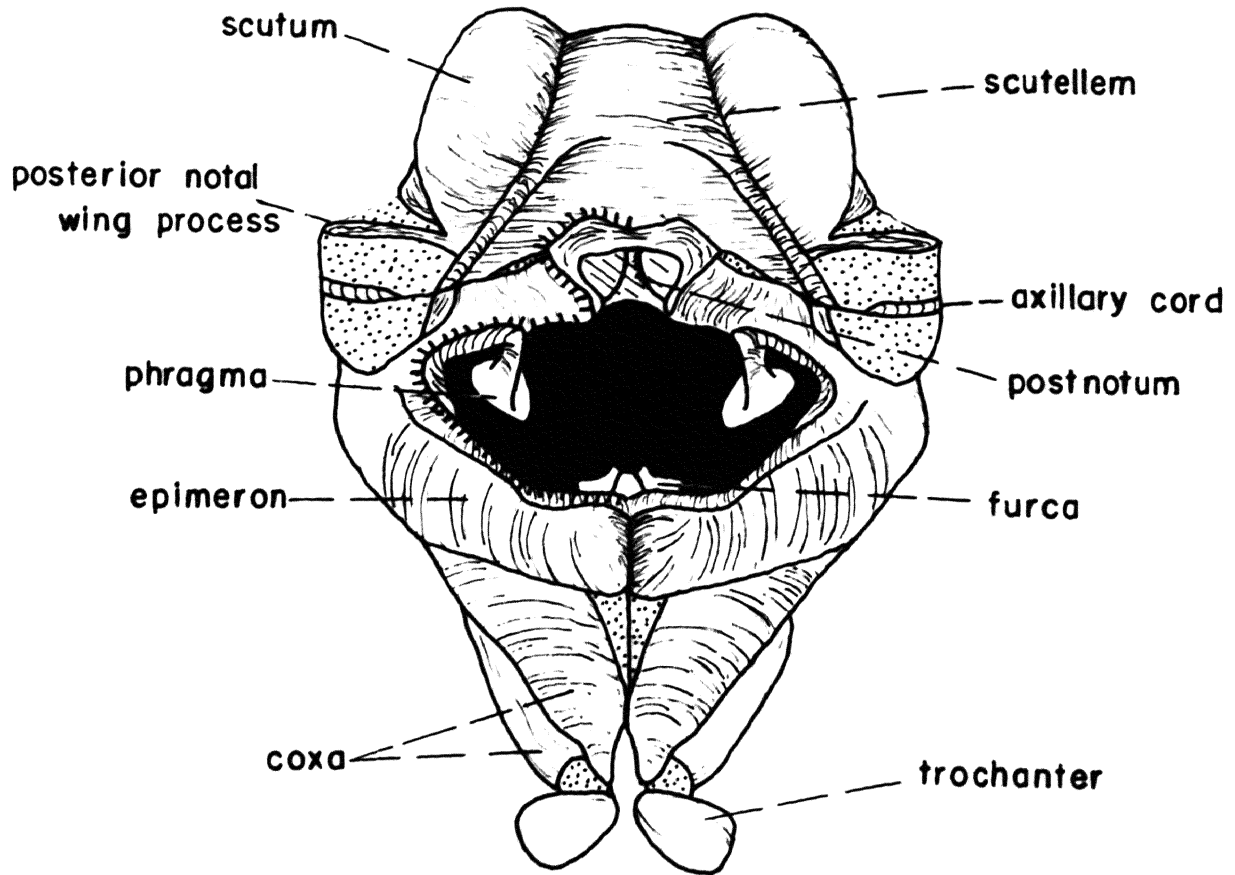


Figures 20-21. 20. Posterior view of mesothorax, tergum omitted (the line marked by short cross lines represents attachment of meso-metathoracic intersegmental membrane). 21. Posterior view of metathorax (line of metathorax-abdominal 1 intersegmental membrane indicated on left half of figure only).





20

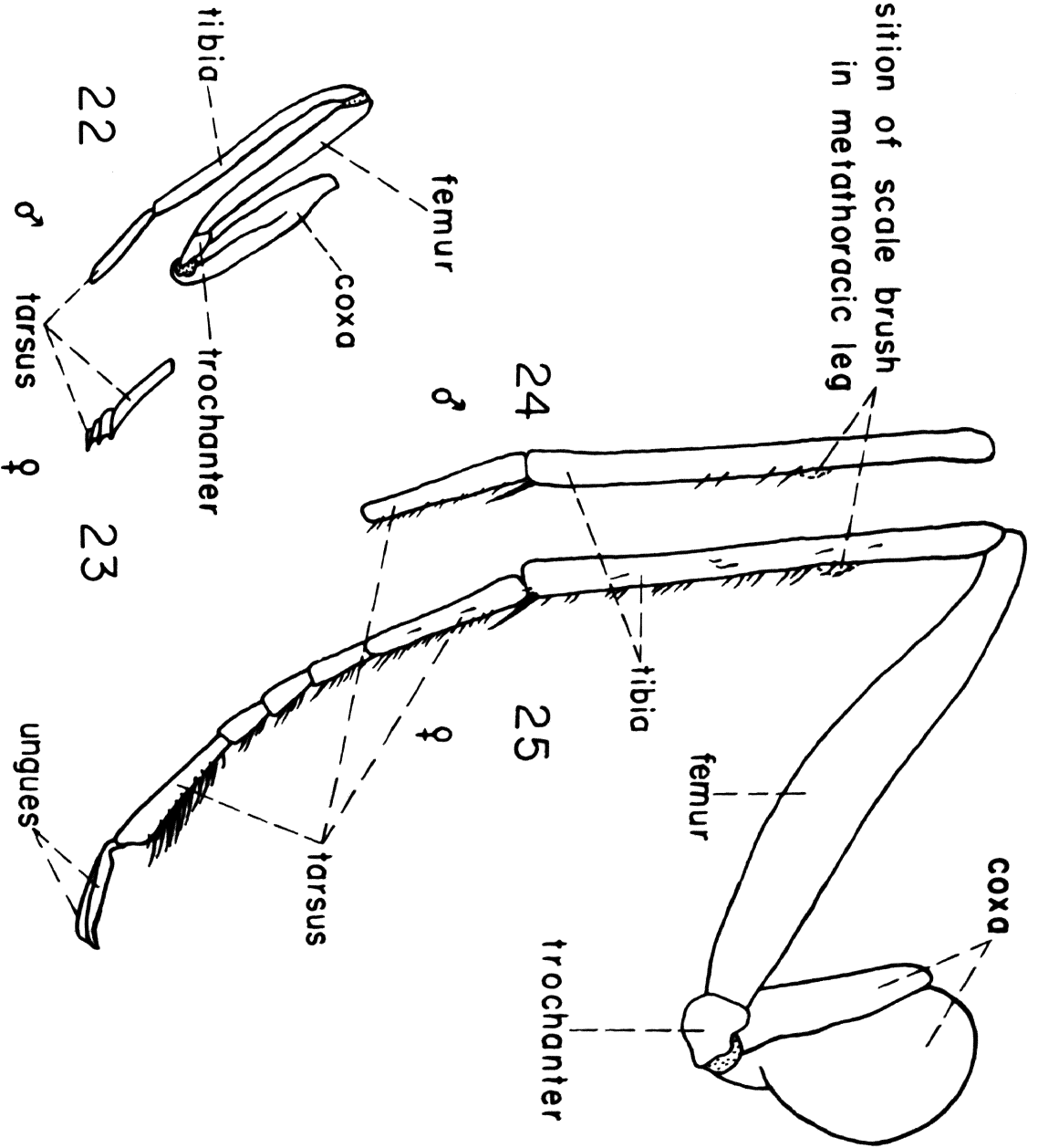


5mm

21

Figures 22-25. 22. Prothoracic leg of male. 23. Pro-  
tarsus of female. 24. Tibia and  
basal tarsomere of mesothoracic leg  
of male. 25. Mesothoracic leg of  
female.

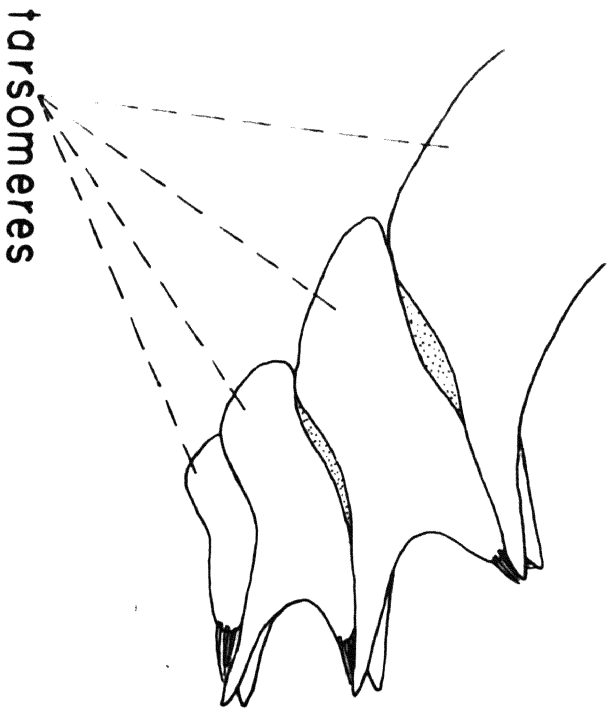
position of scale brush  
in metathoracic leg



5mm

Figures 26-27. 26. Detail of distitarsus of prothoracic leg of female. 27. Ventral view of pretarsus of pterothoracic leg.

26



unguitractor

plate

unguitractor tendon

distitarsus

empodium

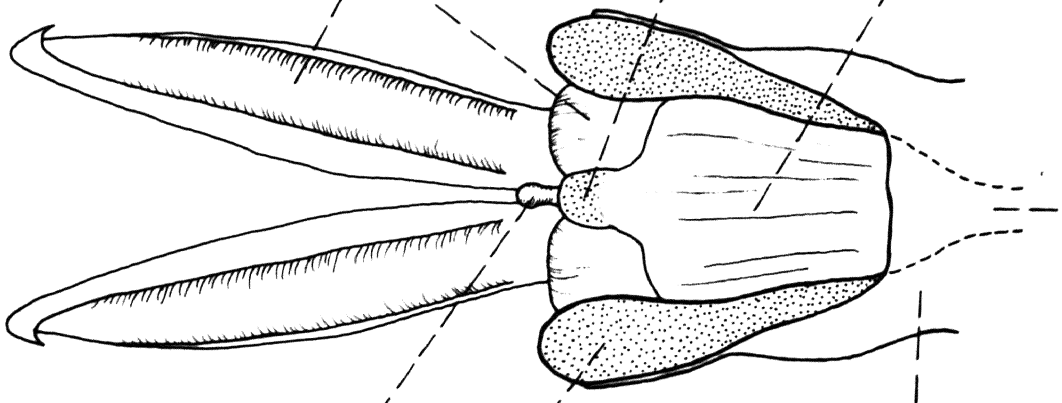
unguis

pulvillus

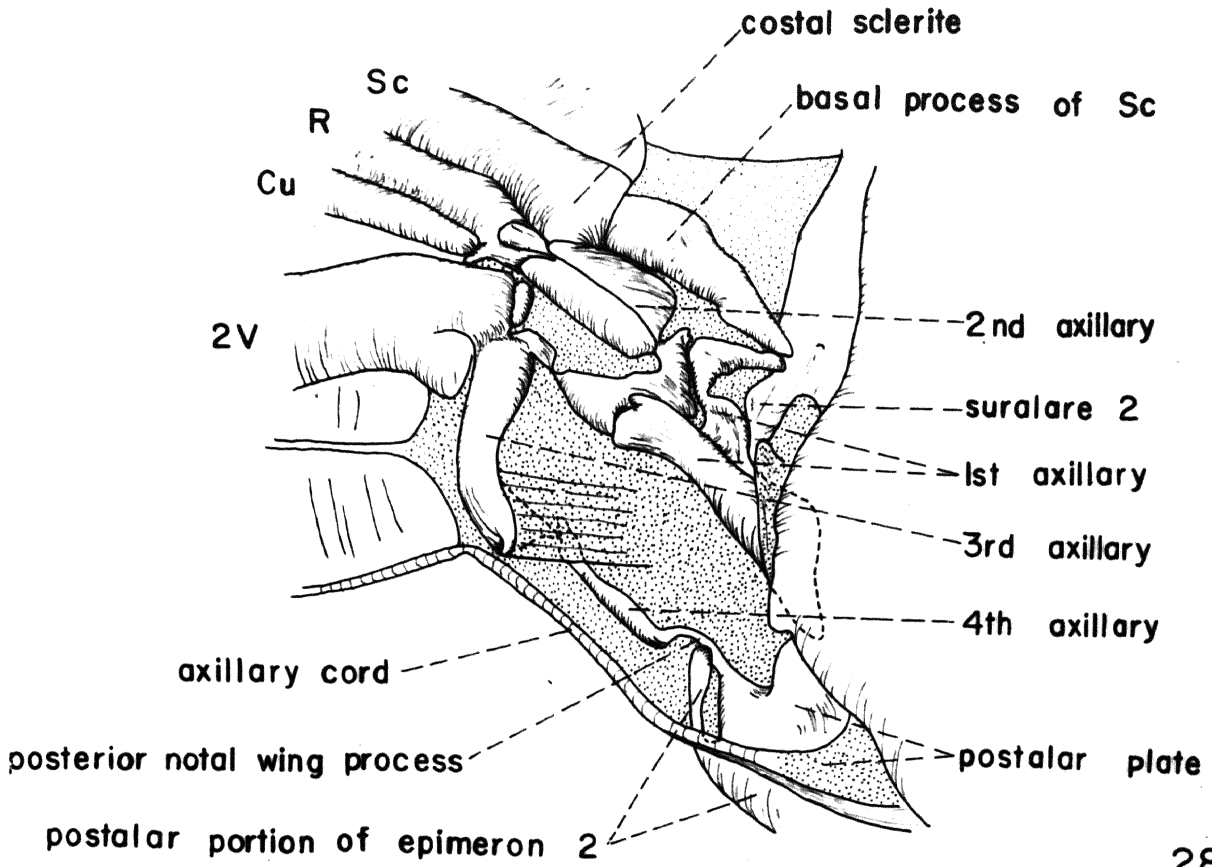
arollium

1mm

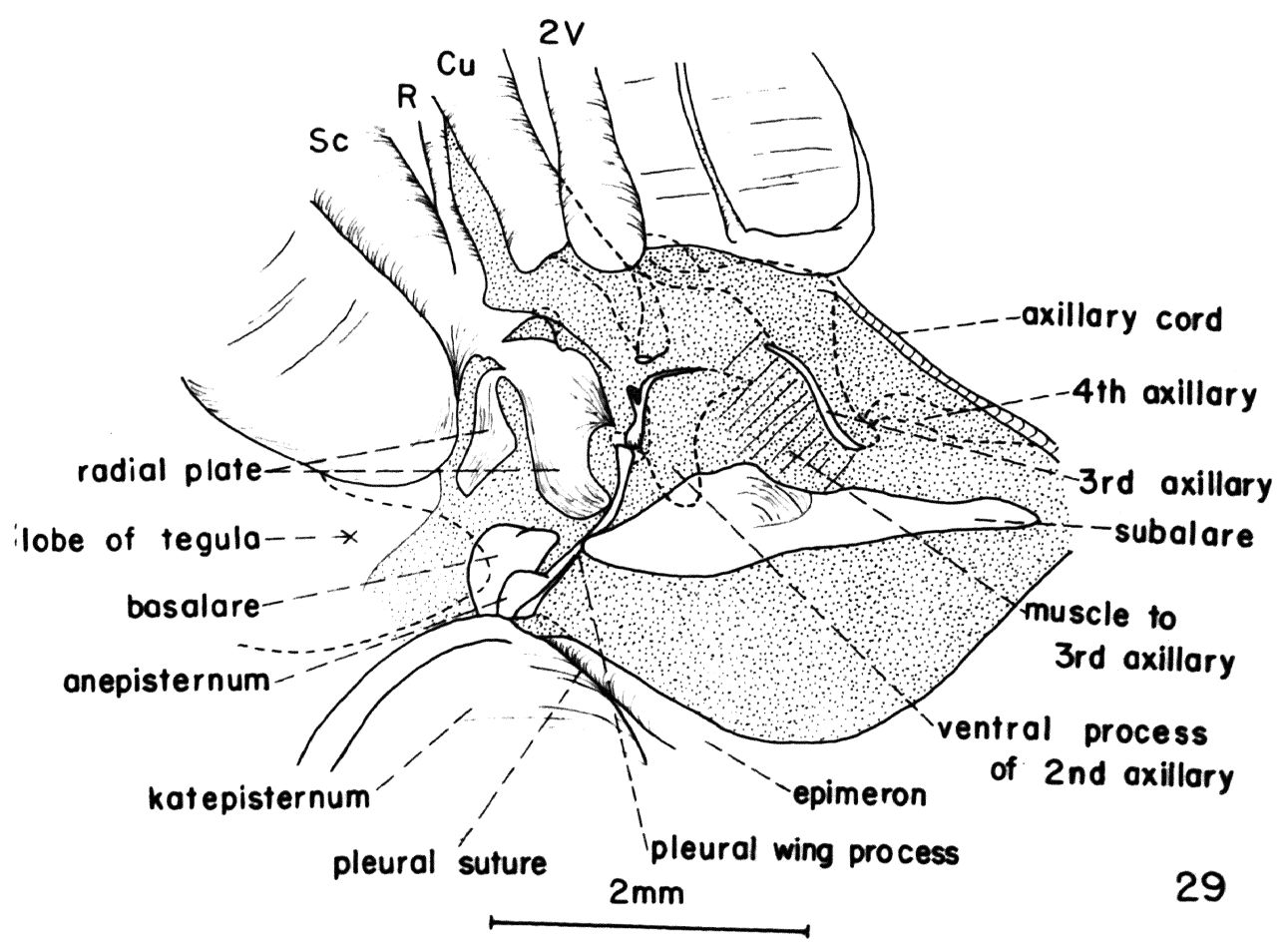
27



Figures 28-29. 28. Dorsal view of mesothoracic wing base, wing held horizontal.  
29. Lateral view of mesothoracic wing base, wing held vertical.



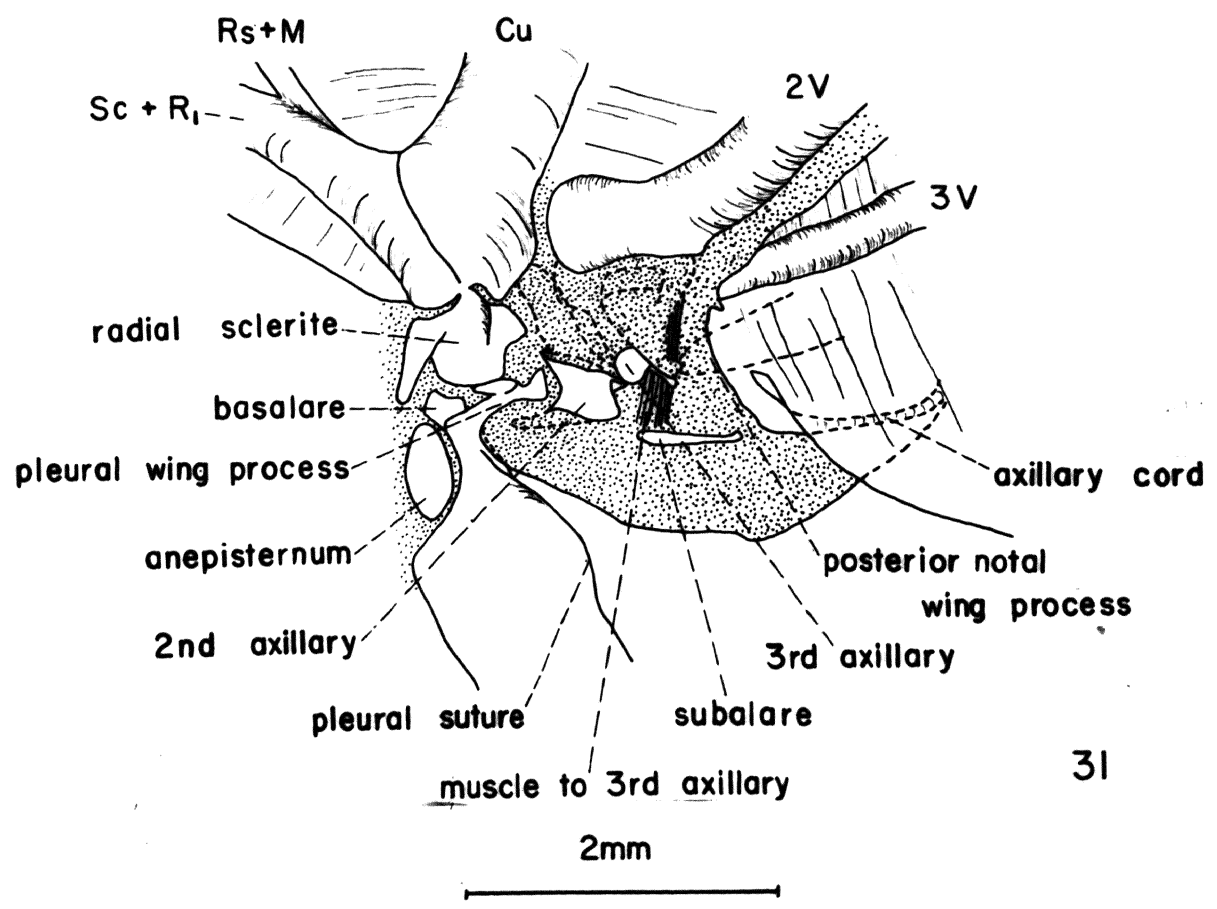
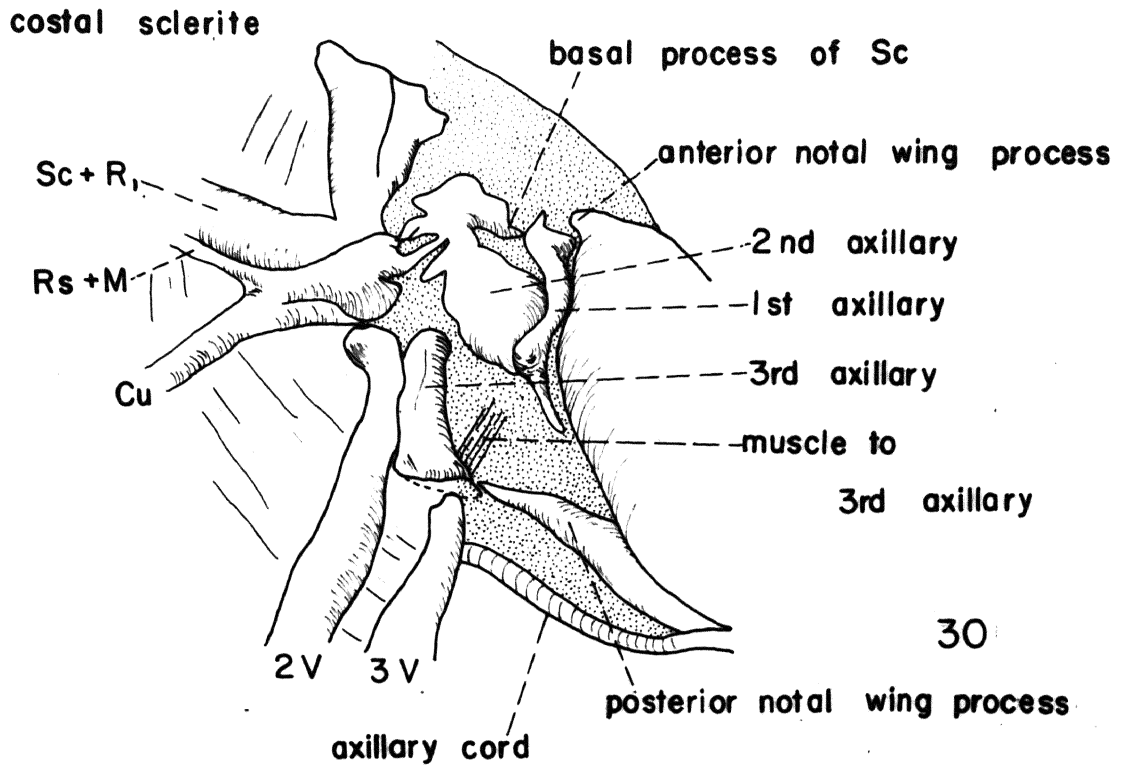
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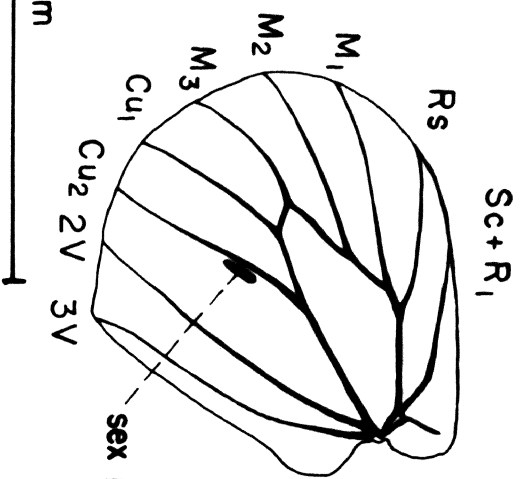
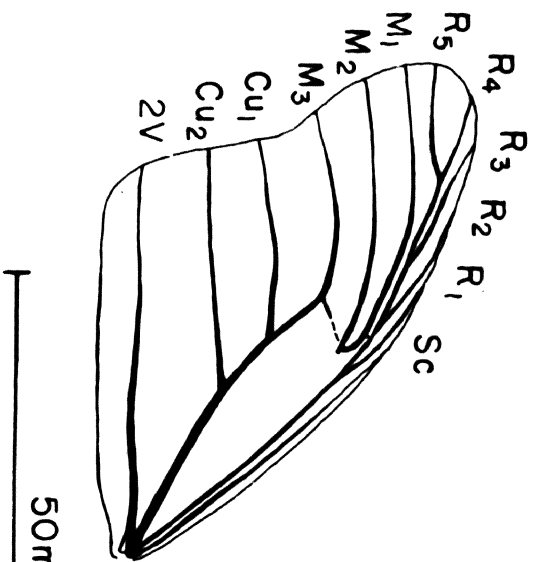
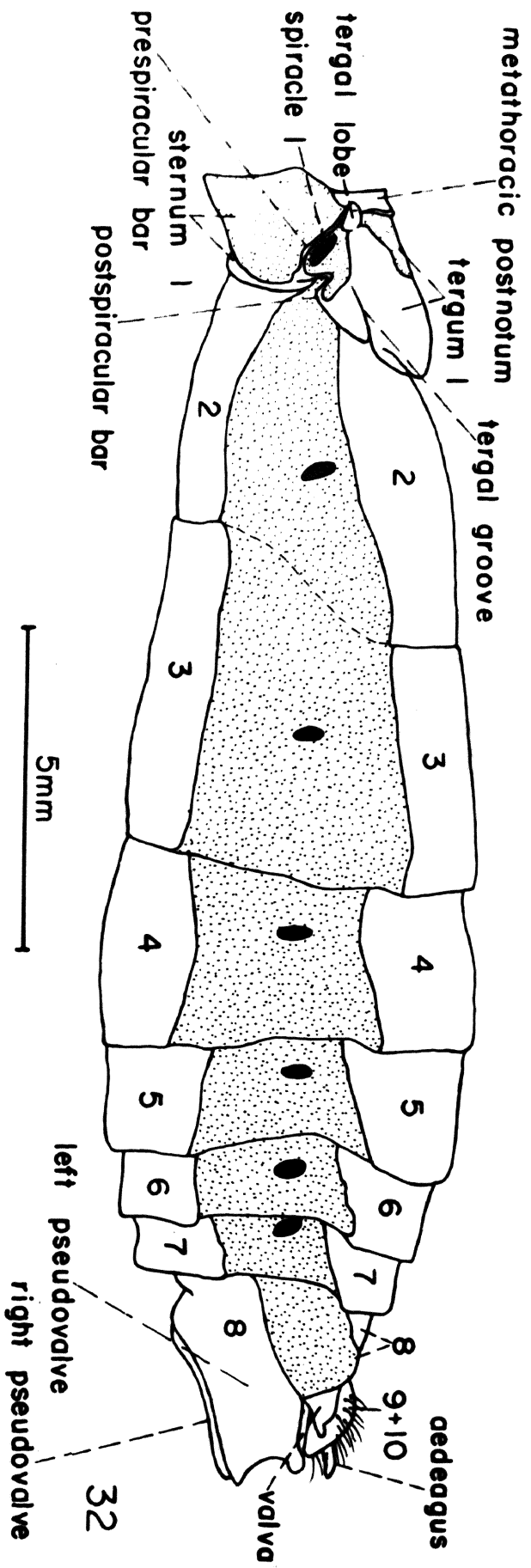
29

Figures 30-31. 30. Dorsal view of metathoracic  
wing base, wing held horizontal.  
31. Lateral view of metathoracic  
wing base, wing held vertical.





Figures 32-33. 32. Lateral view of male abdomen.  
33. Wing venation.



sex patch in male only

Figures 34-38. 34. Mesal view of fourth abdominal spiracle. 35. Ventral view of apex of male abdomen. 36. Lateral view of male genitalia proper (setae of valvae omitted). 37. Mesal view of right pseudovalve (setae omitted), hair pencil and sternum 9. 38. Posterior view of male genitalia proper (setae omitted).

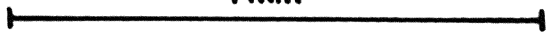
anterior spiracular sclerite

apodeme

34

posterior spiracular sclerite

1 mm



aedeagus

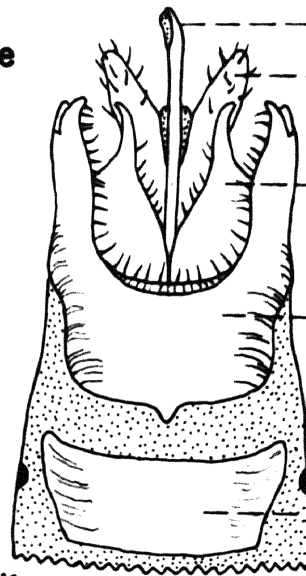
uncus

valva

sternum 8

sternum 7

35



tergum 9

uncus

aedeagus

hair pencil

valva

sternum 9

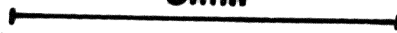
saccus

vinculum

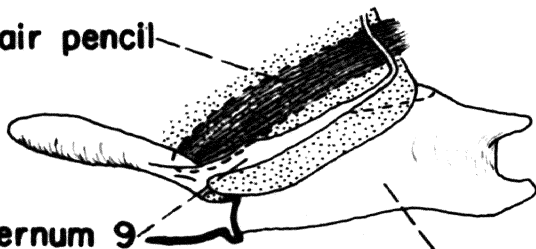
5 mm

sternum 8

36



37



anus

uncus

diaphragma

anellus

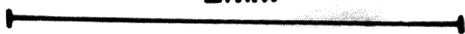
juxta

valva

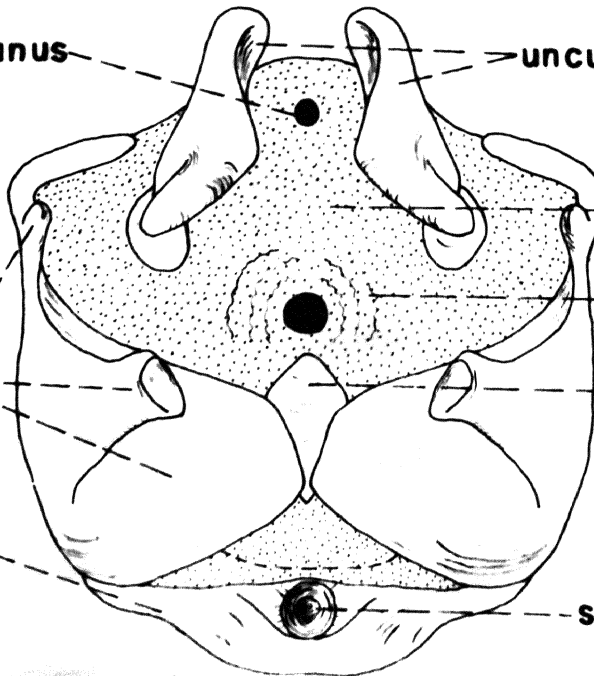
vinculum

saccus

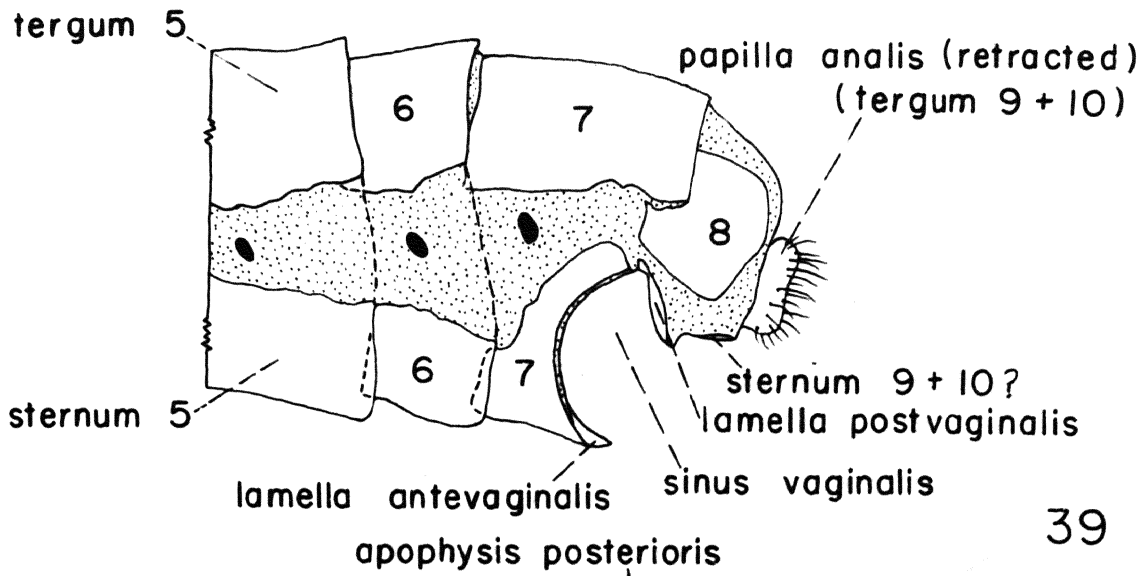
2 mm



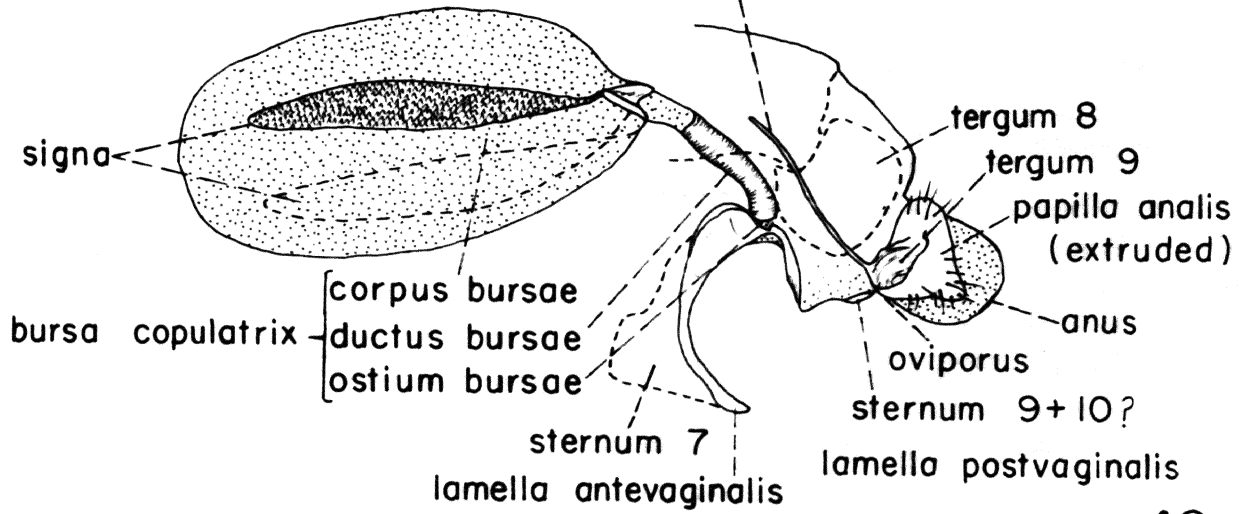
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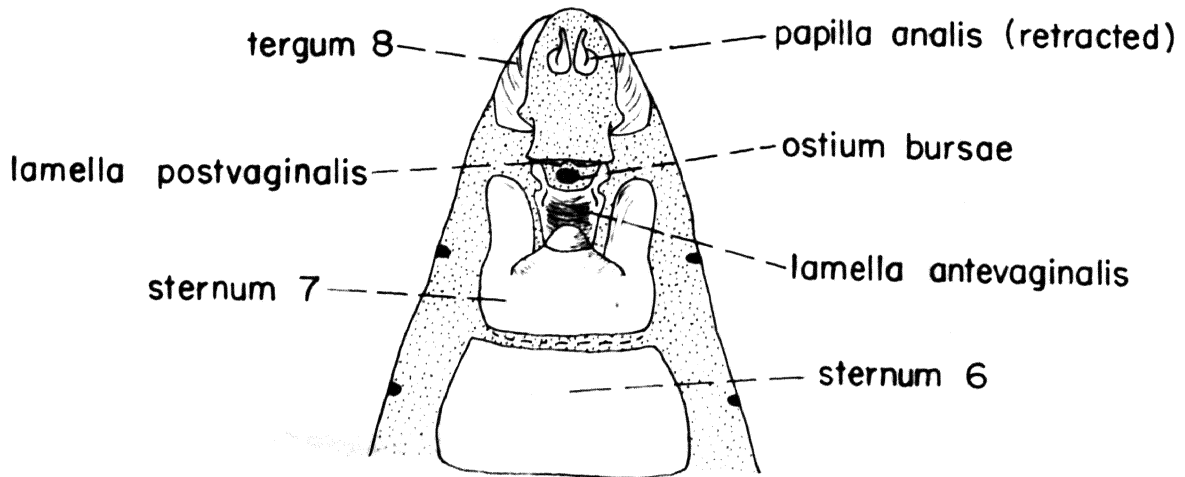
Figures 39-41. 39. Lateral view of apex of female abdomen. 40. Lateral view of apex of female abdomen showing internal structures. 41. Ventral view of apex of female abdomen.



39



40



5mm

41

## PART II

### THE COMPARATIVE MORPHOLOGY, PHYLOGENY AND HIGHER CLASSIFICATION OF THE BUTTERFLIES (LEPIDOPTERA: PAPILIONOIDEA)

#### INTRODUCTION

The first section dealing with the detailed integumental anatomy of the adult monarch butterfly (Danaus plexippus L.) laid the necessary foundation for the comparative morphological studies which are the central theme of the present work. An attempt has been made to integrate the new morphological data resulting from this study with pre-existing data (principally morphological) in order to provide the broadest possible base for the conclusions drawn<sup>1</sup>.

---

1. Characters of the larvae have been considered only rarely in this work. Unfortunately, there is a general lack of systematic information on these forms, especially of the homologies of their structures (e.g., tubercles on one larva are not necessarily homologous to tubercles on another). It should be noted that characters of the larvae are neither more nor less significant than those of the adult, and that properly conducted investigations of large numbers of larval characters would provide an interesting independent check of the conclusions arrived at here primarily on the characters of the imagines.



## SYSTEMATIC PRINCIPLES

Complete objectivity in arriving at classifications and phyletic relationships is at present a utopian concept, although advances are being made in this direction (see Michener and Sokal, 1957).

Some major sources of subjective error in taxonomic work are: 1) preconception (to some degree unavoidable when a worker is dealing with a group with which he has long been familiar); 2) unjustified character weighting (especially a tendency to give more weight to characters studied personally); 3) group favoritism (the tendency to consider one's favorite taxonomic group as higher in the hierarchy of classification than equivalent groups); and 4) frankly subjective decisions ("I feel that the Xidae are worthy of family rank" or "Yus is obviously more closely related to Zus than Xus"). Every attempt has been made to avoid these errors in the present work, but doubtless numbers 1 and 2 have not been completely eliminated. It is hoped that 3 and 4, abundantly represented in the literature, have been entirely excluded.

There are those (e.g., Warren, 1947) that claim that higher categories should be based on the distribution of one or two diagnostic characters. This is an unfortunate concept which may easily lead to polyphyletic

taxa and erroneous ideas of relationship. It should be pointed out that a character state found in all known members of a group (a diagnostic character) is probably of no greater significance from the viewpoint of phylogeny than one found in, say, 97% of the known members of a group. Whether the absence of a well developed third vannal vein (3V) in the hindwings was a diagnostic character of the Papilionidae hinged on the discovery of Baronia brevicornis, a rare papilionid unique in its family in possessing the vein. Many similar cases could be cited. The repeated failure of systems based on too few characters to stand the test of time is a matter of record and will not be discussed further here. In the present work the number of characters considered has been limited by time and practicality, but it is hoped that the sample has been sufficiently large to avoid major errors.

The question of the nomenclatorial status of the various taxa segregated has received considerable attention. Some previous classifications of butterflies, as exemplified by Clark (1948) have presented entomologists with a mass of largely undefined families, subfamilies, tribes and subtribes within the superfamily Papilionoidea. Fortunately this extreme splitting has been largely ignored.

In the present work it has been found that the

Papilionoidea divide primarily into five groups. In an attempt to align the classification of butterflies with that of other superfamilies of insects these five groups have been called families (Papilionidae, Pieridae, Nymphalidae, Libytheidae, Lycaenidae). The Apoidea (6 families) show much greater morphological and behavioral diversity than the butterflies. The Sphecoidea (3 to 18 families) show a variety of form and habits not even faintly approached in the Papilionoidea, as do the Fulgoroidea (which some authorities consider to represent a single family, the Fulgoridae). The same is true of the Chalcidoidea, Scaraboidea, Tipuloidea and others. Within these groups the major divisions are considered to be families. While it is difficult to compare and equate differences within major groups, it seems evident that the recognition of the primary divisions of the Papilionoidea with superfamilial designations such as "family group" would not be in keeping with accepted entomological practice.

As far as possible the morphological distinctness of the various taxa has been kept uniform within the next highest taxon. Thus, in order to have all the families in the superfamily more or less equivalent, the long standing "families" into which the nymphalids have been split previously must be considered to be subfamilies, since their

elevation to family rank would necessitate the raising to family rank of all the tribes of the Papilionidae, a move which has not been advocated even by the most extreme splitters. The degree of morphological distinctness of subgroups may vary greatly among higher taxa. By "morphological distinctness" is meant both the actual degree of morphological difference (e.g., presence or absence of a structure is ordinarily considered a greater difference than change of size or shape in a structure) and also the size of the gap between character states (i.e., whether the variation is essentially continuous or, if not, the degree of discontinuity). Thus, the subfamilies of the Nymphalidae have smaller gaps separating them and show less morphological diversity than those of the Papilionidae. This difficulty is inherent in the nomenclatorial system as usually interpreted. The only alternative that might help to give subfamilies in these two families equivalent rank would be to place all nymphalids in a single subfamily, more or less comparable to the papilionid subfamilies. This Nymphalinae could then be divided into tribes. In view of the size of the Nymphalidae, this heterodox system seems undesirable.

Much of the difficulty in butterfly (and other) nomenclature can be traced to workers who, starting at the specific level, have deemed it necessary to recognize nearly every branching of the phylogenetic tree with a

taxon. Using this system one is not far down the tree when the family level is reached, and the result is a large mass of family names with meaning only to specialists. For the benefit of other biologists it is suggested that conservatism (i.e., "lumping") be the rule at the ordinal, familial and generic levels. The complexities of phylogeny can be shown equally well with the aid of less important categories such as sub- and superfamily, tribe, subgenus, species group, etc.

The concept of the family Nymphalidae is a meaningful one to almost every entomologist and to many other biologists. It can be used without misgivings in ecological or experimental work, and is easily explained to beginning students. It is doubtful if the family Apaturidae is a meaningful entity to one in a thousand entomologists. Since convenience is the only excuse for nomenclature the conclusions seem obvious.

#### MATERIAL AND METHODS

Some 240 genera and 300 species of butterflies were dissected in the course of the present work as well as 41 representatives of 24 families of moths and skippers. Dried specimens were used exclusively. The wings were removed and preserved, along with locality labels (if any) in glassine envelopes. The body was then wetted with 80%

alcohol and heated in 10% KOH until the viscera were soft (semi-liquid). The specimens were then dissected under water, the scales being removed with brushes and the viscera with watchmakers forceps and pipettes. The dissected specimens were preserved in 80% alcohol.

Only determined specimens were used. It did not prove practical to verify all specific identifications, but all doubtful generic determinations were checked. The generic nomenclature employed has been made as up to date as possible; however, wherever a group has been commonly considered either a subgenus or a genus (e.g., Graphium, Zerene) it has been retained as a genus in order to accent the variety of the sampling. Since this paper is not primarily nomenclatorial, in no case does the use of such a name indicate endorsement of the usage employed.

The genera and species examined are listed below by families, alphabetically within the families. Except for the entities marked with an asterisk(\*) all were dissected as described above. Those marked with the asterisk were examined for superficial characters. Every character has not been examined in every species, since ordinarily only one sex of each species was dissected, and since sometimes parts were missing or damaged. It is hoped that this deficiency has been compensated at least in part by the large number of genera and species examined.

## NON-PAPILIONOIDS STUDIED

HEPIALIDAE: Hepialus humuli Linnaeus; MEGALOPYGIDAE: Megalopyge opercularis Smith; ZYGAENIDAE: Zygaena minos Fuessly; EUCLEIDAE: Sibine stimulea Clemens; TINEIDAE: Tinea pellionella Linnaeus; GELECHIIDAE: Gelechia serotina Busck; YPONOMEUTIDAE: Atteva aurea Fitch; AEGERIIDAE: Melittia satyriniformis Hübner; OLETHREUTIDAE: Carpocapsa pomonella Linnaeus, Exartema fasciatanum Clemens; COSSIDAE: Prionoxystus robiniae Peck; CASTNIIDAE: Castnia atymnius Dalman, Castnia licus Fabricius; THYRIDIDAE: Thyris lugubris Boisduval; PYRALIDAE: Crambus vulgivagellus Clemens, Desmia funeralis Hübner, Galleria mellonella Linnaeus, Loxostege similalis Guenée, Nymphula icciusalis Walker; PTEROPHORIDAE: Oidaematophorus monodactylus Linnaeus; URANIIDAE: Urania leilus Linnaeus, Urania madagascariensis Lesson; SATURNIIDAE: Actias luna Linnaeus, Eacles imperialis Drury; LASIOCAMPIDAE: Tolyte distincta French; GEOMETRIDAE: Haemotopsis grataria Fabricius; SPHINGIDAE: Celerio lineata Fabricius; NOTODONTIDAE: Datana ministra Drury; PHALAENIDAE (=NOCTUIDAE): Agrotis ypsilon Rottemburg, Catocala cerogama Guenée, Peridroma margaritosa Hübner, Polia adjuncta Boisduval; AMATIDAE: Ctenucha sp.; ARCTIIDAE: Haploe sp., Utethesia bella Linnaeus; HESPERIIDAE: Adopaea lineola Ochsenheimer, Calpodes ethlius Cramer, Erynnis juvenalis Fabricius, Megathymus neumogeni Edwards,

Poanes zabulon Boisduval and Leconte, Proteides clarus  
Cramer.

PAPILIONIDAE

Archon apollinus Herbst, Baronia brevicornis Salvin,  
Battus polydamus Linnaeus, Battus philenor Linnaeus,  
Battus devilliers Godart\*, Bhutanitis lidderdalei Atkinson,  
Cressida cressida Fabricius, Euryades duponcheli Lucas,  
Graphium agamemnon Linnaeus\*, Graphium agesilaus Guérin  
and Percheron\*, Graphium agates Westwood\*, Graphium anti-  
phates Cramer, Graphium bathycles Zinken\*, Graphium celadon  
Lucas\*, Graphium cloanthus Westwood, Graphium columbus  
Kollar\*, Graphium dolicaon Cramer\*, Graphium epidaus Double-  
day\*, Graphium eurypylus Linnaeus\*, Graphium evemon Boisduval\*,  
Graphium harmodius Doubleday\*, Graphium leonidas Fabricius,  
Graphium macareus Godart, Graphium marcellus Cramer,  
Graphium nomius Esper\*, Graphium pausanias Hewitson,  
Graphium philolaus Boisduval\*, Graphium policenes Cramer\*,  
Graphium protesilaus Linnaeus\*, Graphium sarpedon Linnaeus,  
Graphium thymbraeus Boisduval, Graphium xenocles Cramer\*,  
Hypermnestra helios Nickerel, Lamprotera (=Leptocircus)  
curius Fabricius, Lamprotera meges Zinken\*, Leuhdorfia  
puziloi Erschov, Ornithoptera priamus Linnaeus, Papilio  
ageius Donovan\*, Papilio alexiades Hopffer\*, Papilio  
anchisiades Esper\*, Papilio aristius Cramer\*, Papilio



aristodemus Esper\*, Papilio bianor Cramer\*, Papilio castor  
 Westwood\*, Papilio chaon Westwood\*, Papilio crespontes  
 Cramer, Papilio cynorta Fabricius, Papilio demetrius  
 Cramer, Papilio demolition Cramer\*, Papilio eurymedon Lucas\*,  
Papilio glaucus Linnaeus, Papilio hectorides Esper,  
Papilio indra Reakirt\*, Papilio machaon Linnaeus, Papilio  
memnon Linnaeus\*, Papilio montrouzieri Boisduval\*, Papilio  
multicaudatus Kirby\*, Papilio paeon Boisduval\*, Papilio  
palamedes Drury\*, Papilio paris Linnaeus\*, Papilio pilumnus  
 Boisduval\*, Papilio polyxenes Fabricius, Papilio proneus  
 Hübner\*, Papilio rutulus Lucas\*, Papilio thoas Linnaeus\*,  
Papilio torquatus Cramer\*, Papilio troilus Linnaeus, Papilio  
xuthus Linnaeus\*, Parides (=Atrophaneura) arcus Cramer\*,  
Parides aristolochiae Fabricius, Parides coon Fabricius\*,  
Parides latreilli Donovan\*, Parides montezuma Westwood\*,  
Parides mylotes Bates, Parides perrhebus Boisduval\*, Parides  
philoxenus Gray, Parides polydorus Linnaeus\*, Parides poly-  
zelus Felder, Parides rhodifer Butler\*, Parides sesostris  
 Cramer, Parides varuna White\*, Parnassius apollo Linnaeus\*,  
Parnassius clodius Ménétriés, Parnassius eversmanni Méné-  
 triés\*, Parnassius mnemosyne Linnaeus\*, Parnassius smintheus  
 Doubleday and Hewitson, Sericinus telamon Donovan, Teinopal-  
pus imperialis Hope, Trogonoptera brookiana Wallace\*,  
Troides helena Linnaeus, Troides rhadamantus Lucas\*,  
Zerynthia hypermnestra Scopoli, Zerynthia rumina Linnaeus.

## PIERIDAE

Anteos chlorinde Godart, Anthocharis midea Hübner,  
Aporia crataegi Linnaeus, Appias nephele Hewitson, Archonias  
tereas Hübner, Belenois mesentina Cramer, Cepora nadina  
 Lucas, Colias philodice Godart, Colotis achine Cramer,  
Colotis danaë Doubleday and Hewitson, Delias eucharis  
 Drury, Dismorphia nemesis Latreille, Dixeia cebron Ward,  
Euchloe belia Cramer, Eurema nicippe Cramer, Gonepteryx  
rhamni Linnaeus, Hebomoia glaucippe Linnaeus, Itaballia  
demophile Linnaeus, Ixias pyrene Linnaeus, Kricogonia  
lyside Godart, Leptidea sinapis Linnaeus, Leptophobia  
aripa Boisduval, Leptosia xiphia Fabricius, Leucidea brephos  
 Hübner, Melete isandra Boisduval, Nathalis iole Boisduval,  
Neophasia menapia Felder, Pereute callinira Staudinger,  
Perrhybris pyrrha Cramer, Phoebis sennae Linnaeus, Pieris  
protodice Boisduval and Leconte, Prioneris thestylis  
 Doubleday, Pseudopieris nehemia Boisduval, Pseudopontia  
paradoxa Felder, Zerene eurydice Boisduval, Zegris fausti  
 Cristopher.

## NYMPHALIDAE

Acraea encedon Linnaeus, Acraea esebria Hewitson,  
Acraea natalica Boisduval, Acraea sp., Actinote carycina  
 Jordan, Actinote neleus Latreille, Actinote ozomene Godart,

Ageronia amphinome Linnaeus, Agraulis vanillae Linnaeus,  
Amathusia phidippus Johansson, Amauris ochlea Boisduval,  
Amauris psyttaea Plötz, Anadebis himachala Moore, Anaea  
andria Scudder, Anaea appias Hübner, Antirrhaea miltiades  
Fabricius, Apatura iris Linnaeus, Aprotopus aedesia Double-  
day and Hewitson, Araschnia levana Linnaeus, Asterocampa  
celtis Boisduval and Leconte, Bia actorion Linnaeus, Boloria  
toddi Tolland, Brassolis astyra Godart, Brassolis sophorae  
Linnaeus, Byblia ilythea Drury, Caligo sp., Calinaga buddha  
Moore, Callerebia annada Moore, Callicore marchalii Guérin,  
Callitaera aurora Felder, Callithomia hezia Hewitson,  
Catagramma maimuna Hewitson, Catonephele numilia Cramer,  
Catuna crithea Drury, Ceratinia titutia Hewitson, Cera-  
tinia vallonis Hewitson, Cethosia chrysippe Felder, Charaxes  
brutus Cramer, Charaxes psaphon Westwood, Chlosyne janais  
Drury, Cirrochroa malaya Felder, Clothilda numida Hübner,  
Coenonympha hero Linnaeus, Coenophlebia archidona Hewitson,  
Corades inyo Hewitson, Cupha grymanthis Drury, Cynthia  
arsinoë Cramer, Cyrestis nivalis Felder, Danaus cleona  
Stoll, Danaus plexippus Linnaeus, Dichorragia nesimachus  
Boisduval, Didonis biblis Felder, Dione junio Cramer,  
Dircenna klugii Hübner, Discophora sondaica Boisduval,  
Doleschallia bisaltide Cramer, Doxocopa cyane Latreille,  
Doxocopa laurentia Godart, Dryadula phaetusa Linnaeus,  
Dyras iulia Hubner, Dynastor darius Felder, Elymnias

hypermnestra Linnaeus, Elymnias malelas Hewitson,  
Elymniopsis bammakoo Westwood, Enispe euthymius Doubleday,  
Epinephile jurtina Linnaeus, Erebia epipsodea Butler,  
Ergolis ariadne Linnaeus, Eryphanis aesacus Herrich-Schäffer,  
Eueides aliphera Godart, Eueides thales Cramer, Euphoedra  
eleus Drury, Euphoedra medon Linnaeus, Euphydryas chalcedona  
Doubleday and Hewitson, Euphydryas phaeton Drury, Euploea c  
core Cramer, Euploea diocletianus Fabricius, Euptoleta  
claudia Cramer, Euptychia hesione Sulzer, Euthalia garuda  
Moore, Faunis assamus Westwood, Faunis canens Hübner,  
Gynaecia dirce Linnaeus, Gyrocheilus patrobas Hewitson,  
Haematera thysbe Doubleday and Hewitson, Haetera piera  
Linnaeus, Heliconius charithonia Linnaeus, Heliconius  
chestertoni Hewitson, Heliconius hortense Guérin, Hetero-  
chroa bredowii Geyer, Hirsutis neitha Hopffer, Historia  
odius Fabricius, Hypna clytemnestra Cramer, Hypoleria  
andromica Hewitson, Hypolimnus bolina Linnaeus, Hypolimnus  
dubia Aurivillius, Idea idea Linnaeus, Ideopsis gaura  
Horsfield, Ithomia cleora Hewitson, Ituna phenareta Double-  
day, Kallima inachus Boisduval, Lethe eurydice Johannson,  
Lethe kansa Moore, Lethe sura, Hewitson, Limenitis bredowii  
Geyer, Limenitis populi Linnaeus, Lycorea cleobaea Godart,  
Marpesia petreus Bates, Mechanitis doryssus Bates, Megistanis  
baeotus Doubleday and Hewitson, Melanargia galathea Linnaeus,  
Melanitis leda Drury, Melinaea paraiya Reakirt, Melitaea  
artemis Schiffermuller, Melitaea dymas Edwards, Metamorpha

steneles Linnaeus, Minois pegala Fabricius, Morpheus  
ehrenbergi Hübner, Morpho achilles Linnaeus, Morpho aratos  
Fruhstorfer, Morpho hecuba Linnaeus, Morpho laertes Druce,  
Morpho sulkowskyi Kollar, Napeogenes thira Hewitson, Narope  
cyllabarus Westwood, Neope goschkevitschii Ménétriès,  
Neptis vikasi Horsfield, Nessaea obrinus Linnaeus,  
Nymphalis polychloros Linnaeus, Oeneis semidea Say,  
Opoptera sulcius Staudinger, Opsiphanes invirae Hübner,  
Panacea prola Doubleday and Hewitson, Pandita sinoria  
Felder, Pantoporia opalina Kollar, Pararge megera Linnaeus,  
Pardopsis punctatissima Boisduval, Parthenos gambrisius  
Fabricius, Perisama bonplandii Guérin, Philaethria dido  
Clerck, Phycoides tharos Drury, Pierella lamia Sulzer,  
Planema aganice Hewitson, Precis sp., Prepona chromus  
Guérin, Pronophila thelebe Doubleday and Hewitson,  
Pseudergolis wedah Kollar, Pyrrhogyra typhoeus Felder,  
Ragadia crisilda Hewitson, Sais rosacia Cramer, Salamis  
cytora Doubleday and Hewitson, Satyrus circe Fabricius,  
Satyrus semele Linnaeus, Scada theaphia Bates, Smyrna  
blomfieldia Fabricius, Speyeria cybele Fabricius,  
Stobochiona nicea Gray, Stichophthalma camadeva Westwood,  
Taenaris phorcas Westwood, Taygetis ypthima Hübner,  
Tellervo zoilus Fabricius, Temenis laothoe Cramer, Thyridia  
confusa Butler, Tithorea harmonia Cramer, Yoma sabina  
Cramer.

## LIBYTHEIDAE

Libythea celtis Fuessly, Libythea geoffroy Godart,  
Libythea laias Trimen, Libythea myrrha Godart, Libytheana  
bachmanni Kirtland.

## LYCAENIDAE

Abisara neophron Hewitson, Amblypodia micale Blanchard,  
Anatole zygia Hübner, Ancyluris inca Saunders, Anteros  
carusius Westwood, Apodemia mormo Felder, Apodemia nais  
 Edwards, Atlides halesus Cramer, Baeotis bacaenis Hewitson,  
Calephelis iris Staudinger, Callictita cyora Bethune-  
 Baker, Callophrys rubi Linnaeus, Candalides dimorphus  
 Röber, Candalides meeki Bethune-Baker, Caria lampeto Godman  
 and Salvin, Cupido minima Fuessly, Curetis bulis Doubleday  
 and Hewitson, Duedoryx epijarbas Moore, Dodona durga Kollar,  
Durbania amakosa Trimen, Echenais aristus Stoll, Elaphrotis  
telephus Cramer, Euselasia aurantiaca Godman and Salvin,  
Euselasia eulione Hewitson, Euselasia mys Herrich-Schäffer,  
Fenesica tarquinius Fabricius, Helicopsis cupido Linnaeus,  
Hemiargus hanno Stoll, Hypochrysops rex Boisduval,  
Hypolycaena philippus Felder, Ialmenus evagoras Hübner,  
Incisalia augustinus Westwood, Lasaia sessilis Schaus,  
Leucochimona lagora Herrich-Schäffer, Lycaena helloides  
 Boisduval, Lycaenopsis pseudargiolus Boisduval and Leconte,

Lymnas iarbas Fabricius, Lysandra coridon Poda, Mampava nigronotata Bethune-Baker, Megalopalpus zymia Doubleday and Hewitson, Mesosemia telegone Boisduval, Metacharis lucius Fabricius, Mimacraea dohertyi Rothschild, Mitoura gryneus Hübner, Nemeobius lucina Linnaeus, Niphanda fusca Bremer and Grey, Nymphidium cachrus, Fabricius, Ogyris oroestes Hewitson, Philiris innotatas Miskin, Plebejus icaroides Boisduval, Poretia hewitsoni Moore, Pseuderesia libertina Hewitson, Rhetus dysonii Saunders, Riodina lysippus Linnaeus, Satyrium fuliginosa Edwards, Siseme alectro Westwood, Siseme aristoteles Latreille, Stalachtis euterpe Linnaeus, Stalachtis phlegia Cramer, Stiboges sp., Styx infernalis Staudinger, Syrmatia dorilas Cramer, Taraka hamada Druce, Telipna bimacula Plötz, Teriomima hildegarda Kirby, Tharsalia arota Boisduval, Theope mania Godman and Salvin, Thestor ballus Fabricius, Thisbe irenea Stoll, Thysonotis danis Cramer, Thysonotis hymetus Felder, Zeltus antifaunus Doubleday and Hewitson, Zemeros flegyas Cramer.

To facilitate comparisons all characters in the family diagnoses have been given numbers and all characters in the subfamily diagnoses have been given letters. Thus, in all the families character number one is the shape of the eye, and throughout the subfamilies of the Nymphalidae character "a" is the amount of scaling on the antennae.



All illustrations for the comparative section of this work have been drawn so that the same structures of different genera are the same size. In many cases figure citations refer to illustrations of genera other than those under discussion which show the characteristics alluded to. Citations of figures followed by "- Pt. I" refer to the illustrations of the monarch butterfly in the first section of this work (Ehrlich, 1957).

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#### COMPARATIVE MORPHOLOGY

This section gives a brief summary, arranged by structures rather than by systematic categories, of the morphological variation found within the butterflies. It emphasizes variation which was found to have taxonomic significance, and variation which was relatively easy to describe. Since many characters which were later found to be of little systematic significance were recorded for about the first 40 genera dissected, these genera appear as a disproportionately high number of the examples cited.

Time has not permitted detailed studies of any organs as have been done by Jordan (1898) on the antennae and Reuter (1897) on the labial palpi. A number of major areas

(area of head around and above foramen magnum, axillary sclerites, female genitalia) have been largely ignored because of difficulties in dissecting, describing or comparing them. It is hoped that future studies will fill in these gaps.

The terminology used here is that of the first section of this work (Ehrlich, 1957).

#### HEAD

With the exception of the majority of the Lycaenidae, the eyes of butterflies are entire. In most lycaenids the eyes are emarginate (i.e., notched opposite the bases of the antennae - see fig. 5), and do not extend caudally as far as those in the other families (figs. 6, 7). Many genera of the Lycaenidae and Nymphalidae have the eyes hairy to a greater or lesser degree, while they are bare in the remainder of the butterflies.

The structure of the antennae of the butterflies has been the subject of an exhaustive study by Jordan (1898). Of most systematic interest is the variation in the amount of scaling (ranging from completely unscalded to completely scaled) and the arrangement of the antennal sulci and carinae<sup>2</sup>. A sulcus is a depressed line on the ventral

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2. Terminology after Clench, 1955.

surface of the antenna formed by a groove or series of pits (one to a segment). The carinae are ridges between and flanking the sulci. No original work on the antennal structure has been done in connection with this paper. The carinae are present only in the Nymphalidae and Libytheidae, in which they are almost universal. The presence of the sulci is variable in the Papilionidae and they are usually absent in the Lycaenidae. The antennae of the Pieridae always have one or three sulci.

The distance between the bases of the antennae is very variable, ranging from much less than one-half the width of the scape to more than the width of the scape. The area between the antennae may be concave if the antennae are very close together, and there may be a strengthening inflection between the bases of the antennae (the transfrontal suture of DuPorte, 1956). The presence of this inflection is at least to some degree a function of the interantennal distance, it is almost never present when the antennae are close together.

The position of the laterofacial sutures and the concomitant size of the paraocular areas are quite variable. In general the lycaenids have the laterofacial sutures contiguous or nearly contiguous with the eye margins, with the paraocular areas extremely reduced or absent (fig. 5). In the other families the laterofacial sutures may be rather

close to the eye margins and largely parallel to them (many genera, Amathusia, Calinaga, Leptidea, Papilio, Teinopalpus, etc., see fig. 1) or they may be some distance from the eye margins and curved inward dorsally and ventrally (various nymphalids including Danaus, fig. 1 - Pt. I). A complicating factor is that in some genera (e.g., Calinaga, fig. 1) the anterior tentorial pits do not lie at the juncture of the laterofacial and clypeolabral sutures as they do in Danaus, but rather at the free ends of the clypeolabral suture. In these genera the laterofacials pass laterad of the pits. Detailed studies of a great many different Lepidoptera as well as members of related orders will be necessary before we can hope to have a reasonable understanding of the structures of the face of the Lepidoptera.

In many Papilionidae and Lycaenidae the face is essentially flat (fig. 7) while in the other families it is at least somewhat protuberant. Teinopalpus imperialis (figs. 2, 3) has the entire frontoclypeal sclerite expanded into a balloon-like structure which accounts for about one-half the total length of the head. Certain pierid genera (Anthocharis, Leptidea, Pseudopontia, etc.) also have very protuberant frontoclypeal sclerites. In most non-lycaenid genera the face is at least somewhat indented near the eye margins lateral to the frontoclypeal protuberance (fig. 2 - Pt. I).

In most of the lycaenids the anterior tentorial pits are low on the face, usually about one-seventh of the total height of the face from the lower margin of the labrum. In the other families the pits are somewhat higher.

The labrum of the butterflies is often difficult to define because of the obscurity of the clypeolabral suture. The labrum is greatly reduced in many genera (especially in the Lycaenidae - fig. 5). The pilifers are well developed in most groups, but are reduced or absent in some, including the Lycaenidae, Baronia, Dismorphia, Lamproptera, Metamorpha, Pseudopontia, and Zerynthia. The size and shape of the mandibular rudiment was also very variable, but it was difficult to describe the variation because of the indefinite boundaries of the rudiment. There is some variation in the depth of the proboscis fossa (it is usually deeper in the Lycaenidae and Pieridae than in the other families), but it has not been systematically studied.

The maxillary palpi showed surprising development in some genera (including Baronia, Caligo, Calinaga, Metamorpha and Pseudopontia), being distinctly two-segmented in Baronia. The galeae of the maxillae are fringed with papillae at the distal end in Actinote, Anaea, Apodemia, Atlides, Caligo, Calinaga, Heliconius, Libytheana, Lycaena, Lycaenopsis, Metamorpha, Morpho, Oeneis, Telipna and many others. Numerous genera, principally papilionids, pierids and (to

a lesser extent) nymphalids do not show this fringing or at least have the papillae greatly reduced. A detailed study of these structures would probably reveal taxonomic characters.

The labial palpi have been studied in great detail by Reuter (1897). The palps vary in length from as long as the thorax (some libytheids) to less than the length of the head (some papilionids and lycaenids). There is much variation in the proportions of the three segments and in the pattern of scaling and setation.

In the Nymphalidae, Libytheidae and Lycaenidae (except Styx) the labial sclerite is completely sclerotized, both in front of and behind the palpal sockets (figs. 3, 4 - Pt. I). However, in most papilionids there is a loss of sclerotization in front of the sockets and in many pierids there is a loss of sclerotization behind the sockets.

On the vertex of the head there is a setiferous patch (presumably sensory) called the chaetosema. The variation in this organ is described and figured by Jordan (1923).

The anterior tentorial arms show a great deal of diversity. In some genera (Apatura, Danaus, Heliconius, Historis, Ithomia, Leptidea, etc.) they are relatively straight and simple (fig. 15), not greatly enlarged or downcurved anteriorly and not bearing crests. At the opposite extreme are genera such as Lamproptera and

Graphium which bear extremely high dorsal crests (figs. 18, 19). In many genera, especially in the Lycaenidae, the arms are bent strongly downward anteriorly (fig. 17) and/or are more than twice as thick anteriorly as posteriorly.

#### CERVIX

In all of the Papilionidae studied (and in none of the other butterflies) the cervical sclerites were found to be joined beneath the neck by a narrow sclerotic band (fig. 24) which may be faint or slightly interrupted in middle. Variation was observed in the shape of the cervical sclerites and in the position and shape of the cervical organ, but no study of this variation was made.

In Lamproptera curius, Papilio machaon, Parnassius smintheus, Teinopalpus imperialis and other papilionids as well as in Apatura cyane and Historis odia a small ventral sclerite was observed in the cervix close to the head (fig. 24). Among others it was absent from the following genera: Actinote, Anaea, Apodemia, Atlides, Baronia, Caligo, Dismorphia, Fenesica, Ithomia, Leptidea, Libytheana, Lycaena, Lycaenopsis, Metamorpha, Pieris, and Phoebis.

#### THORAX

Prothorax: In all the butterflies except the Pieridae the lateral plates of the pronotum fuse together to form

a triangular or Y-shaped structure (fig. 8 - Pt. I) which articulates with the dorsal plate. No such structure is found in the pierids (fig. 28). The dorsal plate itself may be roughly triangular, T-shaped, Y-shaped or sagittate.

Sclerotized patagia of varying size are found in all the Nymphalidae (fig. 37), the Coliadinae of the Pieridae (fig. 25), various groups of the Papilionidae and the Libytheidae (fig. 26). In the libytheids and certain groups of the Papilionidae (Cressidini in particular) the sclerotized area is very small. All of the lycaenids, most of the pierids and a great many papilionids have the patagia unsclerotized. In some of these groups, particularly in certain lycaenids, the membranous patagia are rather prominent and protuberant, in others they are essentially indistinguishable from the rest of the membrane connecting the lateral plates of the pronotum with the mesothorax.

The Charaxinae of the Nymphalidae are the only butterflies in which sclerotized parapatagia have been found (fig. 37).

The presternum is generally present in the Nymphalidae, Libytheidae and Lycaenidae, although it is sometimes indistinctly separated from the ventrally fused propleura. It is absent in the Papilionidae and Pieridae.



The profurcal arms are simple (figs. 32, 33) in the Lycaenidae, Nymphalidae and Libytheidae. They usually have a secondary anterior lamella or prong in the Papilionidae and Pieridae (figs. 28, 29, 30, 31).

The intercoxal lamella is quite prominent (fig. 29) in the Pieridae and some Lycaenidae (Atlides, Euselasia, Lycaena, Lycaenopsis, Megalopalpus, Telipna, etc.). It is not prominent but present (fig. 33) in most of the Nymphalidae, the Libytheidae, and some Lycaenidae (Apodemia, Fenesica, etc.). In the Papilionidae the intercoxal lamella has migrated caudally, where it usually forms a prominent semicircular lamella almost between the furcal arms (fig. 30). In many of the papilionids (Lamproptera, Papilio, Troides, etc. but not Parnassius, Teinopalpus, etc.) and virtually all the pierids the discrimen is represented internally by a small anterior spine or lamella (figs. 29, 30).

In all the Papilionidae except Baronia the spinasternum is produced laterally at the spina (figs. 34, 35, 36). The process may be long (laterally visible, fig. 24) as in Lamproptera, Papilio, Parnassius and Zerynthia or short (not laterally visible) as in Teinopalpus and Ornithoptera. In most genera the processes are narrow; in Zerynthia they are broadened at the ends. In Papilio (at least some species) and Lamproptera there are areas of light sclero-

tization in the membrane around the processes, especially between the processes and the mesothoracic pre-episternum (fig. 34). Lateral processes of the spinasternum have not been found elsewhere in the butterflies.

In the vast majority of the Papilionoidea the spina is essentially an invaginated sclerotized strip with membranous sides (figs. 8, 18 - Pt. I). However, in a number of papilionids (e.g., Ornithoptera priamus), the spina is a tubular apodeme (completely sclerotized).

In the Nymphalidae, Libytheidae, and Lycaenidae the spinasternum is generally a narrow strip, invaginated at the spina, and gradually broadening caudally until it joins the thorax at two points with a membranous triangle between them (fig. 17 - Pt. I). However, in the Pieridae the spinasternum is widened into a small oval or diamond-shaped plate between the furcasternum and spina (fig. 31). This is faintly reminiscent of the lateral expansion of the papilionids.

In the Cressidini and Ornithoptera of the Papilionidae the spinasternum caudal to the spina is usually broad and plate-like (figs. 35, 36).

Mesothorax: The prescutum of the Libytheidae is vertical to the main axis of the body or has its upper end slightly anterior to its lower end, giving the mesonotum a truncated appearance (fig. 26). This effect is also noticeable in a number of genera of lycaenids (Apodemia, Euselasia,

Fenesica, Lycaena, Lycaenopsis, Megalopalpus, etc.). The remainder of the butterflies have the lower end of the pre-scutum anterior to the upper end and lack the truncated aspect (fig. 25).

In Baronia the scuto-scutellar suture is obsolescent, and in other genera such as Leptidea, Lycaenopsis and Zerynthia it is incomplete centrally.

The shape of the scuto-scutellar suture, especially the depth and angle of the inverted "V" is very variable but did not appear to have useful characters at the higher taxonomic levels.

The adnotale is sagittate in the Libytheidae (fig. 26); it is variable in shape but not sagittate in the other butterflies.

In general the processes of the second phragma are well developed. However, in many genera of the Lycaenidae (Atlides, Euselasia, Lycaena, Lycaenopsis, Megalopalpus, etc.) they are reduced to a greater or lesser degree.

In the sternopleural region of the butterflies there is a great amount of variation in the sutures and in the anepisternum<sup>3</sup>. The latter sclerite is present as a separate

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3. The nomenclature of the sternopleural region employed throughout this work has, as far as possible, been brought into line with the ideas of Matsuda (con't on next page)

unit (figs. 37, 38, 39) in many papilionids (including Baronia); the Satyrinae, Morphinae, Calinaginae and Charaxinae of the Nymphalidae; the Styginae, Riodininae and a few Lycaeninae of the Lycaenidae. It is not present as a separate unit in the remainder of the butterflies (fig. 9 - Pt. I).

There is a great deal of variation in the size and extent of the pre-episternum and the strength of the pre-episternal suture. The pre-episternum is about as wide as the katepisternum in Anaea, Apodemia, Heliconius, Lycaenopsis, Megalopalpus, Speyeria and many others. It is about one-half as wide as the katepisternum in a large number of genera (Amathusia, Anthocharis, Caligo, Calinaga, Dismorphia,

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(1956). Since the katapleuro-coxal muscle is absent from Danaus (and presumably from all butterflies due to the great degree of fusion of the coxae with the thorax proper) it has been impossible to identify with certainty the pleural costa. The choice of position of the pleural costa seems to lie between the pre-episternal and precoxal sutures (if indeed the pleural costa has not disappeared without a trace in the specialized lepidopterous thorax), and Matsuda agrees (personal communication) that considering the pre-episternal suture to be equivalent to the pleural costa gives the most satisfactory interpretation.

Morpho, Styx, Teinopalpus - fig. 38) and is merely a narrow lip in a great many others such as Actinote, Baronia, Danaus, Lamproptera, Papilio, Parnassius, Pieris, Phoebis, Pseudopontia, etc., fig. 24).

The greatest reduction of the pre-episternum is found in the nymphalid subfamilies Ithomiinae and Satyrinae, where it is sometimes essentially absent (fig. 39).

The pre-episternal suture varies from being absent in the Libytheidae (fig. 26) to being well developed with a strong internal ridge in a great many genera (Actinote, Leptidea, Papilio, Parnassius, Pieris, Telipna, etc.).

The precoxal suture is absent in the Papilioninae and Baroniinae of the Papilionidae and in the Pieridae. It is obsolescent or absent in the Libytheidae and in numerous genera of the Nymphalidae and Lycaenidae (Actinote, Amathusia, Anaea, Apodemia, Atlides, Caligo, Fenesica, Lycaenopsis, Megalopalpus, Telipna, etc.).

In some pierids the epimeron is fused to the meron, the suture which normally separates the two being absent anteriorly. The most extreme example of this is found in Pseudopontia.

In some genera, especially lycaenids, the marginopleurite (region between the marginopleural suture and eucoxa) is relatively wide (fig. 27). Some butterflies, especially Pieridae, have the discrimen forked (often

broadly) at its anterior end.

The postcoxal sclerite is very variable in width and length. It is one-half or more the width of the visible meron in caudal view (fig. 20 - Pt. I) in Actinote, Euselasia, Heliconius, Caligo, Danaus, Fenesica, Lamproptera, Libytheana, Lycaena, Metamorpha, Morpho, Oeneis, Speyeria and many others. In Dismorphia, Euselasia, Heliconius, Megalopalpus, Ornithoptera, Papilio, Parnassius, and others it is much less than one-half the width of the visible meron.

In most genera the postcoxal sclerite ends well below the top of the meron (fig. 20 - Pt. I); however, in many nymphalids (some Ithomiinae, some Satyrinae, some Nymphalinae, and all Morphinae, Calinaginae and Charaxinae) it is long (fig. 53), reaching the top of the meron.

Coxal sclerules were found only in the Danainae, Historis and Ithomia. They were absent in Actinote, Anaea (a trace present), Apodemia, Caligo, Calinaga, Dismorphia, Euselasia, Fenesica, Lamproptera, Leptidea, Libytheana, Lycaenopsis, Megalopalpus, Metamorpha, Ornithoptera, Papilio, Phoebis, Pieris, Telipna, and many others.

The epimeron was found to be very variable, both in the presence of the pre-epimeron and various secondary sutures and ridges, but also in its height below the subalare in comparison with the epimeron-subalare distance.

A systematic study of these features has not been made.

Another very variable character is the shape of the subalare. However, since the exact angle at which it is viewed is greatly responsible for its apparent shape, and since its position differs greatly from specimen to specimen this character was not used taxonomically.

Internally the principal variation studied was in the form of the lamella of the discrimen. The lamella is continuous with the furca (the dorsum of the lamella being essentially a straight line, fig. 40) in all the butterflies except the Lycaenidae and Baronia of the Papilionidae. In the Lycaenidae the lamella does not reach the furca, but instead curves downward to the base of the furca (fig. 42). The condition of the lamella in Baronia is intermediate (fig. 41).

A variable internal feature that was not studied in detail is the ventral process of the postalar portion of the epimeron. It varies both in length and in the shape of the end (conspicuously spatulate or more or less pointed).

Metathorax: In the Libytheidae the metanotum is almost completely covered by the mesoscutellum (fig. 26), being below it in position. In the other butterflies the metanotum is below and behind the mesoscutellum and is not completely covered by it (fig. 24).

The third phragma of most of the Papilionidae is in the form of paired simple lobes (fig. 55). In Apatura, Caligo, Danaus, Morpho, Pieris and others the phragma consists of paired stalked lobes (fig. 21 - Pt. I). Most genera appear to be intermediate between the above conditions, having stalks but no lobes on their tips.

In the Libytheidae (fig. 26), Fenesica, Zerynthia and a few other forms of anepisternum is pointed ventrally to a greater or lesser degree. In the remainder of the butterflies it is rounded ventrally.

The relative size and position of the meron and eucoxa are subject to a great deal of variation. In Dismorphia, Leptidea, Phoebis and other pierids the meron is much larger than the eucoxa and arches high above it. In Actinote, Caligo, Calinaga, Danaus, Historis, Libythea, Geneis, Pieris, Pseudopontia and many others the meron and eucoxa are of approximately equal size, but the former may arch above the latter to a variable extent. In general in the Lycaenidae the meron is somewhat larger than the eucoxa but does not arch high above it.

In the Papilionidae there is a transverse suture, represented internally by a lamella (the meral suture and meral lamella) crossing the meron (fig. 24). This suture is absent or indistinct in the rest of the butterflies.



The caudal part of the epimeron (beneath the base of the abdomen) varies from very thin (fig. 54) to very broad (fig. 55). Because it was a difficult character to quantify it was used very little in the taxonomic portion of this work.

In the vast majority of the butterflies the lamella of the metadiscimen curves downward to the base of the furca. In certain Papilioninae, however, the lamella joins the furca above its base, and in Pseudopontia it runs straight into the furca as in the mesothorax.

#### LEGS

The various stages of reduction in size and fusion of segments in the prothoracic legs of butterflies are well known. It will suffice to say that the foreleg varies from a completely developed, full sized, functional appendage bearing tarsal claws and a tibial epiphysis (in the Papilionidae) to a vestigial appendage lacking both the tarsal claws and the epiphysis, in which the entire tibia and tarsus are reduced to a small ball at the end of the femur (certain Ithomiinae).

A rarely noted unique condition of the prothoracic leg of the Riodininae should be emphasized here. In this subfamily the coxa extends below the joint of the trochanter as a cylindroconical protuberance (fig. 57).

The pterothoracic tarsal claws of many butterflies are simple and symmetrical. However, they are strongly bifid in all the Pieridae<sup>4</sup>, in Lamproptera curius (but not L. meges) and the payeni group of Graphium in the Papilionidae, in some Acraeinae, and in some Lycaenidae. The tarsal claws also tend to be asymmetrical in the Parnassiinae and Acraeinae.

Although most butterflies possess well developed aroliar pads and pulvilli (the latter often bifid) on the pterothoracic legs, one or both of these are reduced or absent in the Papilionidae, Baltia, Colias, Gonepteryx, Nathalis and Phulia of the Pieridae, and certain Nymphalidae (Acraea, Actinote, Agraulis, Euptoieta, etc.).

## WINGS

Most of the information in this work on wing venation has been taken from Schatz and Röber (1892), who illustrate the venation of some 480 genera of Papilionoidea.

The terminology "cubitus apparently trifid (or quadri-

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4. In the Pieridae and Papilionidae the prothoracic legs share the characters of the pterothoracic legs, as do the prothoracic legs of the females of the Libytheidae and Lycaenidae.

fid)" has been adopted from Clench (1955). When  $M_2$  of the forewing arises distinctly closer to  $M_3$  than to  $M_1$  and/or the vein connecting  $M_2$  and  $M_3$  appears to be a continuation of the vein connecting  $M_3$  and  $Cu_1$ , then the cubitus is said to appear "quadrifid" - the four branches being actually  $M_2$ ,  $M_3$ ,  $Cu_1$  and  $Cu_2$ . When  $M_2$  arises midway between  $M_1$  and  $M_3$  or closer to the former, and/or the vein connecting  $M_2$  and  $M_3$  runs at a distinct angle to the vein connecting  $M_3$  and  $Cu_1$ , then the cubitus is said to appear "trifid" - the three branches being  $M_3$ ,  $Cu_1$  and  $Cu_2$ .

It should be noted that the vein called cu-v in the Papilioninae is said to be a basal vestige of the first vannal vein.

#### ABDOMEN

Pregenital segments: The tergum of the first abdominal segment is strongly pouched in most butterflies. However, in some papilionids the amount of pouching is reduced. In a few groups (Anaea, Caligo, etc.) the first abdominal tergum is largely membranous.

The prespiracular bar is present in all groups except the Pieridae (fig. 25). The postspiracular bar is reduced (does not completely bridge membrane between tergum and sternum) or absent in the Papilionidae (fig. 24), Lycaenidae, and most Nymphalidae. Both bars are complete in some

nymphalid genera (Danaus, Ithomia, Metamorpha, etc.) and in the Libytheidae (where the postspiracular bar is especially broad, fig. 26).

There is considerable variation in the size and degree of sclerotization of the pregenital terga and sterna, but it has not been studied systematically.

There are occasionally special organs on the pregenital segments, such as pads bearing specialized scales on segments 4, 5, and 6 in Caligo and a deep pouch in the tergum of the second segment of Faunis.

Male genital segments: A number of species were found to have pseudovalves derived from the eighth tergum (e.g., Parnassius smintheus) or the eighth sternum (e.g., Danaus plexippus).

Variation of significance in the higher classification of the butterflies was found in the relative length of the tegumen and uncus; the presence or absence of a superuncus (fig. 62); the form of the uncus (simple or bifid); the form of the gnathos (complete, incomplete, absent), the form of the valvae (size as compared to the genitalia as a whole, thin or thick, dentate or smooth, etc.) and in the presence or absence of terminal hair brushes. The majority of the Lycaenidae possess genitalia with a more or less characteristic form (uncus not a pointed process, gnathos in the form of curved crossed arms, valvae reduced,

etc.) but there was too much variation to merit employing these characters to differentiate the family.

Female genital segments: Although much variation is known to occur in these segments, especially in the lamella anti- and postvaginalis and the bursa copulatrix, no study of this variation has been undertaken.

### PHYLOGENY

#### PRIMITIVE AND SPECIALIZED CHARACTERS

In order to make reasonable estimates of whether characters in a group studied are primitive or specialized it is usually necessary to have some knowledge of the state of the characters in the taxa presumed to be ancestral to the group under consideration. Since almost certainly the "Protopapilionoidea" have become extinct, leaving no known fossil record, it is necessary to determine the primitive state of butterfly characters by inference from their states in various groups considered to be related to the butterflies. In order to do this a brief survey of the Lepidoptera has been carried out (see "Material and Methods" for list of non-papilionoids studied) with emphasis on groups which have been thought by various authors to be relatively closely allied to the butterflies (Hesperioidea; Castniidae; Cossidae, Tortricoidea, etc.). The information obtained in this survey in combination with that

gleaned from the literature (particularly Shepard, 1930, on the pterothorax; Schultz, 1914, on the pronotum and patagia; Weber, 1924, on the thorax; and Forbes, 1923, on venation, early stages, etc.) and from trends in the characters within the butterflies themselves has been used to arrive at the judgements presented in Table I. In general any character state which was found to be widely distributed in the moths was considered to be primitive among the butterflies.

The development of some of the structures can be traced with ease and clarity from the primitive to the specialized state. The form of the lamella of the meso-discrimen is such a character. In the neuropteroid insects (including Lepidoptera) there is probably no anterior sternal center of sclerotization in the thoracic segments, the anterior ventral sclerotizations in these segments consisting presumably of downgrowths from the pleural (coxal) regions. The line of fusion of these downgrowths is called the discrimen (Ferris, 1940). In the mesothorax (and to a lesser degree in the prothorax and metathorax) of the Lepidoptera this downgrowth seems to have continued, causing an invagination at the line of the discrimen and forming a thin internal "lamella of the discrimen." The lamella probably serves as a longitudinal strengthening device in the pterothoracic segments.

TABLE I  
 PRIMITIVE AND SPECIALIZED CHARACTERS  
 IN THE PAPILIONOIDEA

<u>Primitive</u>	<u>Specialized</u>
Eyes bare	Eyes hairy
Eyes entire	Eyes emarginate
Face at most moderately protuberant	Face extremely protuberant
Laterofacial sutures fairly close to eye margins	Laterofacial sutures far from eye margins or contiguous with them
Anterior tentorial arms simple, straight	Anterior tentorial arms crested, curved, etc.
Antennae approximately one-half to one scape width apart	Antennae much less than one-half or much more than one scape width apart
Antennae moderately long	Antennae very short or very long
Antennae scaled	Antennae unscaled
Pilifers conspicuous	Pilifers reduced or absent
Mandibular rudiments large*	Mandibular rudiments small
Maxillary palpi prominent, moveable, segmented	Maxillary palpi not prominent, immovable, unsegmented

\*Judgement open to some doubt.

Labial sclerite sclerotized all around palpal sockets*	Labial sclerite membranous either in front or behind sockets
Labial palps approximately twice length of head	Labial palps much longer or shorter than twice length of head
Cervical sclerites not joined	Cervical sclerites joined by a ventral sclerotic strip
No sclerotizations in cervix aside from cervical sclerites	A small anteroventral sclerite in cervix
Patagia well sclerotized and large	Patagia not well sclerotized or small
Parapatagia well sclerotized and large	Parapatagia not well sclerotized or small
Lateral plates of pronotum fused dorsally into Y- shaped or triangular struc- ture	Lateral plates of pronotum not fused dorsally into a Y-shaped or triangular structure
Presternum absent	Presternum present
Spine of prodiscrimen absent	Spine of prodiscrimen present
Profurcal arms simple	Profurcal arms with second anterior prong or lamella

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\*Judgement open to some doubt.



Spinasternum not laterally produced	Spinasternum laterally produced
Spinasternum essentially an invaginated strip	Spinasternum a tubular apodeme
Pre-episternum of mesothorax broad	Pre-episternum of mesothorax narrow
Anepisternum of mesothorax a large, separate sclerite	Anepisternum of mesothorax reduced in size or not a separate sclerite
Precoxal suture present	Precoxal suture absent
Scuto-scutellar suture complete	Scuto-scutellar suture obsolete centrally
Metatergum not completely covered by mesotergum	Metatergum completely covered by mesotergum
Lamella of mesodiscrimen curved downward before furca	Lamella of mesodiscrimen complete to furca
Processes of second phragma small	Processes of second phragma large
Lamella of metadiscrimen curving downward to base of furca	Lamella of metadiscrimen not curving downward to base of furca
Third phragma in the form of lobes	Third phragma in the form of stalks or stalked lobes

Dorsum of first abdominal  
tergum not pouched or  
weakly pouched

Prespiracular bar present

Postspiracular bar absent

Abdominal sclerites rela-  
tively large

Abdominal sclerites well  
sclerotized

Pseudovalves absent

Tegumen well sclerotized

Uncus a single, well  
sclerotized projection

Arms of gnathos fused  
ventrally

Valvae large, broad, complex

Sphragis absent

Prothoracic legs normal  
size and functional

Procoxae not extended to  
form a spinelike process  
below articulation with  
trochanter

Dorsum of first abdominal  
tergum strongly pouched

Prespiracular bar absent

Postspiracular bar present

Abdominal sclerites rela-  
tively small

Abdominal sclerites weakly  
sclerotized

Pseudovalves present

Tegumen membranous

Uncus bifid or weakly  
sclerotized

Arms of gnathos not fused  
ventrally

Valvae reduced, narrow,  
simple

Sphragis present

Prothoracic legs reduced in  
size, atrophied or not  
functional

Procoxae with spinelike  
cylindroconical projec-  
tion below articulation  
with trochanter

Protibial epiphyses present	Protibial epiphyses absent
Tarsal claws symmetrical	Tarsal claws asymmetrical
Tarsal claws simple	Tarsal claws bifid
Aroliar pad present	Aroliar pad absent
Pulvilli present	Pulvilli absent
Tibial spurs present	Tibial spurs absent
Radius 5-branched	Radius 3- or 4-branched
Forewing with 2V and 3V free and running to margin	Forewing with 3V absent or fused after a short dis- tance with 2V
Hindwing with 2V and 3V present	Hindwing with 3V lost
Wings with cell closed	Wings with cell open
Wings evenly rounded	Wings tailed, scalloped, angulate, falcate, etc.
Size moderate	Size extreme (very small or very large)
Body stout	Body slender
Flight powerful and rapid	Flight weak, fluttery
Dull colored	Brightly colored
Colors pigmentary only	Colors in part structural
Non-mimetic	Mimetic
Pupa with partial cocoon or girdle	Pupa without partial cocoon or girdle
Larvae herbivorous	Larvae carnivorous

In the Hepialidae (which show a great many primitive characters - i.e., characters shared by other orders of insects) the mesothoracic discriminial lamella is quite small. It is fairly strongly developed in the Cossidae and Castniidae and variable but usually rather weak in the Tortricidae, Yponomeutidae, Pyralididae and Thyrididae examined. In most of the higher moths, the skippers, and the lycaenids the lamella has reached the penultimate stage - high and strong but dipping completely to the base of the furca. In the remaining Papilionoids and in Urania (leilus but not madagascariensis) it has reached the highest stage of development, being complete to and fused with the furca. Weber (1924, fig. 3, a, b, & c) shows the progressive development of the lamella in Hepialus, Zygaena and Papilio.

In the above case the decision as to what is the primitive and what is the specialized case is relatively easy because of the morphologically logical sequence. In other cases the evidence is only slightly less conclusive. Sclerotized patagia are almost universal in their occurrence in the Lepidoptera; thus their absence in some members of an advanced group such as the papilionoids would seem almost certainly to represent a specialized loss rather than a primitive state.

The prespiracular bar of the butterflies was thought at first to be homologous with anterolateral apodemes found

on the second abdominal sternite of many moths (including the Cossidae and Castiniidae). The bar (presumably the homologue of the apodeme lying in the membrane) was found in the butterflies (except the Pierids where it is presumably lost), skippers and a number of moths (Thyris, Desmia, Peridroma, etc.). Catocala cerogama shows a condition apparently transitional between apodeme and bar. However, in Zygaena, Peridroma and Archips, among others, both the bars and the apodemes are clearly present, making it certain that the two structures are not homologous. A trace of the apodeme can also be seen in Thyris. Interestingly in Hepialus there is no sign of either the apodeme or the prespiracular bar, but there is an extension of the first abdominal tergum which is very similar to the postspiracular bar. The question of which is primitive, bar or apodeme, will not be answered with real assurance until an exhaustive study of the moths is completed. In this work absence of the prespiracular bar is considered primitive in the Lepidoptera as a whole, but advanced within the Papilionoidea where it is lost in the Pieridae.

Similar problems have arisen in connection with other characters. Is the joining of the cervical sclerites of the Papilionidae by a ventral sclerotic band an adaptation from the primitive condition of the sclerites meeting at the center of the prothoracic "sternum" (see Weber, 1924,

fig. 1, c [Hepialus] and f [Zygaena]), or is it a secondary advanced condition, developed after the sclerites had become free? The latter alternative is chosen here since both sclerites are free in the Cossidae, Castniidae, Hesperiidae, and the majority of the moths.

In most cases, however, the decision as to what state of a character was primitive and what state specialized was relatively simple.

#### THE PAPILIONOIDEA AS A TAXON

There is little doubt that Papilionoidea is a monophyletic taxon. With the Hesperioidea (except for Euschemon) they may be separated from the rest of the Lepidoptera by the combined loss of the frenulum and retinaculum and the possession of clubbed or distally swollen antennae. They may be separated from the hesperioids by the form of the head (discussed later). However, these distinctions could be considered somewhat superficial if they were not accompanied by certain trends, which help to characterize the Papilionoidea. It should be noted that these trends are not necessarily universal within the Papilionoidea or absent from all other Lepidoptera. Among the trends are: loss of ocelli; extreme atrophy of maxillary palps; loss of sclerotization of labial sclerite; loss of sclerotized patagia; loss of sclerotized parapatagia; de-

velopment of a presternum; reduction in the size of the prothoracic legs; fusion of segments in the prothoracic legs; loss of protibial epiphyses; loss of tibial spurs; simplification of the mesothoracic sternopleural region with loss of the precoxal suture and reduction of the anepisternum; development of a pair of prominent processes on the second phragma; extreme development of the lamella of the discrimen in the mesothorax and metathorax; development of stalks alone without lobes or stalked lobes instead of simple lobes of the third phragma; reduction, through fusion (including "stalking") and loss, of the number of wing veins; modification of wing shape (tails, scalloping, etc.); development of pre- and postspiracular bars; pouching of the first abdominal tergum; reduction and simplification of the valvae; development of relatively narrow thorax and long slender abdomen; reduction of scales and hairs (on thorax and antennae especially); upright egg; loss of use of silk at pupation; development of diurnal habits; development of brilliant pigmentary and structural colors.

It should be emphasized once again that the above, with very few exceptions, are only trends developed in the Papilionoidea, not diagnostic characters of the group.

#### RELATIONSHIPS OF THE PAPILIONOIDEA

Although any definitive statements on the relation-

ships of the Papilionoidea with the remainder of the Lepidoptera will have to await a comprehensive study of the entire order, a few provisional observations are presented here.

Not surprisingly the Hesperioidea appear to be the closest living relatives of the papilionoids. With the exception of the male of Euschemon, which has a frenulum, the skippers all share the papilionoid diagnostic characters of the loss of the frenulum and the clubbed antennae. They are most readily separated from the papilionoids by the shape of the head, which is extremely wide in proportion to its height, and by the concomitant extreme separation of the bases of the antennae (the interantennal distance being at least twice the width of the scape). With rare exceptions the twelve veins of the primary wing of Hesperiidae (3V is vestigial or fused with 2V) all arise from the cell or wing base (i.e., are "unstalked").

The best generalized morphological description of the hesperioids is that they appear to be papilionoids which possess a great many primitive characters. Aside from the above-mentioned distinctions they differ from the papilionoids mainly in this concentration of primitive characters<sup>5</sup>

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5. According to Yagi (1953) they are separated from the butterflies by having eyes of the (con't on next page)



in each species, not in the characters themselves. For instance, all hesperioids examined retain the protibial epiphyses (in the papilionoids retained only in the Papilionidae); both sclerotized patagia and parapatagia (among papilionoids found in certain nymphalids only); lamella of discrimen curved downward before furca (lycaenids only); reduced but still relatively prominent mesothoracic anepisternum (retained in various butterfly groups) and stout body (retained in relatively few butterflies).

Not surprisingly the hesperioids have acquired some rather advanced characters, such as the extreme shape of the head, the trend towards stalks on the third phragma, the overhanging of the metanotum by the mesonotum, (Calpodes, Proteides), and the "neck" of the larva.

It seems advisable at present to retain a separate  

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superposition type. This is a most interesting character, if substantiated, since this type of eye is characteristic of nocturnal insects and is designed for maximum utilization of available light. The skippers are fully as diurnal as the butterflies. However, Yagi further states that the eye is functionally of the apposition type, because the shape of the crystalline cone causes the light passing through it to be concentrated on the end of the rhabdome, rather than allowing it to pass on to other ommatidia.

superfamily for the skippers despite their obvious affinities with the papilionoids. It would be unwise to discard this well accepted nomenclatorial practice without further study of the hesperioids.

The relationships of the butterflies with the various groups of moths is less clear, partially because of the difficulty of recognizing convergence without a more thorough knowledge of the moths. However, it seems evident that the direct ancestors of the Papilionoidea are no longer in existence. Aside from the Hesperioidea which are quite similar and closely related to the Papilionoidea, there are no groups showing clear evidence of intimate relationships to butterflies. There are, however, some groups which show a hint of papilionoid affinities, perhaps because of distant phyletic relationship.

The Castniidae are often mentioned as a possible papilionoid ancestor. It seems likely that these moths are a primitive offshoot of the line of Lepidoptera which leads eventually to the papilionoids. They possess clubbed antennae; a reasonable start (for so primitive a group) toward a lycaenid-type lamella of the mesodiscrimen; a strong, but low and unarched, lamella of the metadiscrimen; an upright egg; bright colors; and butterfly-like habits. Most of the other characters of the group are primitive and not particularly associated with the papilionoid line

(e.g., ocelli usually present; tentorial bridge "inside" of head rather than at the foramen magnum; large mesothoracic anepisternum; venation complex, etc.).

The cossid studied showed a slight reduction in the size of the mesothoracic anepisternum. Aside from this and the possession by the members of the subfamily Cossinae of an upright egg, there is little to connect the Cossidae with the papilionids.

None of the tortricoids, pyraloids, yponomeutoids, uranioids, etc. studied showed any combination of characters to suggest that they are crucial to the matter at hand. They are doubtless more closely related to the butterflies than some of the more specialized moths such as the saturnoids, but beyond this little can be said.

In summary, the evidence seems to indicate that the butterflies and skippers are highly evolved representatives of a line which is well isolated from all other living Lepidoptera.

#### INTERRELATIONSHIPS OF THE FAMILIES OF THE PAPILIONOIDEA

Of the five families of butterflies only two pairs can be associated with any degree of certainty as being more closely related to each other than to the other families. These are the Papilionidae and Pieridae and the Nymphalidae and Libytheidae.

The classical character which associates the papilionids and pierids is the complete development of the prothoracic legs. Accompanying this is the similar trend in the development of the patagia, the absence of the presternum, the loss of the precoxal suture, the similarities in the profurca and prodiscrimen, the general similarity of the head structure (including a tendency towards loss of sclerotization in the labial sclerite) and the general tendency towards broadening of the spinasternum<sup>6</sup>. The quadrifid cubitus which is characteristic of the Papilionidae is found also in the Dismorphiinae of the Pieridae (and nowhere else in the butterflies). The bifid tarsal claws which are universal in the Pieridae are found also in a few papilionids as well as in certain nymphalids and lycaenids. Hypermestra helios is a papilionid which has facies very similar to those of certain pierids (Euchloe sp.)<sup>7</sup>. Some workers have

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6. The above characters are discussed in detail in the section on comparative morphology and in the family diagnoses.

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7. The investigations of Homma (1954) on the alimentary canals of butterflies, although relatively incomplete, tend to support the systematic relationships put forth in the present work. Homma states, "The externals of the canal of Papilionidae are somewhat similar to those of Pieridae, and those of Nymphalidae closely resemble those of Satyridae."

associated the Pieridae with the Lycaenidae rather than the Papilionidae, but the great mass of evidence is against this. The Pieridae differ from the Lycaenidae in almost every character of the head, in the development of the prothoracic legs, in almost every character of the prothorax, in most of the characters of the mesothorax (including the form of the lamella of the discrimen) and in the development of the prospiracular and postspiracular bars and male genitalia.

The Libytheidae share so many characters with the Nymphalidae that very serious consideration was given to including them in the Nymphalidae as a subfamily.

The libytheids differ from the nymphalids in having almost completely developed prothoracic legs in the females, only small sclerotic areas on the patagia, and the metanotum almost completely beneath the mesoscutellum. The long labial palpi usually associated with the Libytheidae are short enough in some species to cause overlap with the length of the palpi of some nymphalid genera. A number of other characters which are typical of the Libytheidae also can be found within the nymphalids so that they cannot be considered diagnostic.

One other entity, the Baroniinae, was considered to be of possible family rank. Baronia differs from the rest of the papilionids in (among other characters) not having the spinasternum laterally produced (some other papilionids

have it only slightly produced), in having a well-developed second vannal vein in the hindwing (absent or rudimentary in the other papilionids), and in having the lamella of the mesodiscrimen curved downward before it joins the furca (a condition unique in the butterflies). In this case it was decided to retain the Baroniinae as a subfamily, since these differences did not seem as great as those separating the Nymphalidae and Libytheidae<sup>8</sup>.

As stated earlier it does not seem wise to place labels of "primitive" or "specialized" on groups as closely related as the families of butterflies. However, as a matter of interest, the distribution among families of 36 characters for which the primitive and specialized states had been hypothesized was studied. Each character was rated for each family on a scale from 0 to 5, 0 indicating that the character was found throughout the family in its most primitive state and 5 indicating that it was found throughout the family in its most specialized state. Both intermediate states of the characters and their distributions within the families were considered in estimating the intermediate values. A family possessing all the characters in their most specialized state in all its members would then score 180 points. The sums of the figures were determined

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8. Necessarily a partly subjective decision.

for each family and then divided by 180 and multiplied by 100 so that they were expressed as a percentage of the maximum score. The results were: Papilionidae - 53%; Pieridae - 42%; Nymphalidae - 42%; Libytheidae - 37%; Lycaenidae - 43%. Considering the crudity of the method the only conclusion which is drawn from these data is that there is certainly no indication that the Papilionidae are "primitive" as has been claimed (largely because of the completely developed prothoracic legs and presence of the epiphyses). Indeed this method showed them to have the highest percent of specialized characters of any family.

Figure 64 is a dendrogram giving the author's ideas on the phyletic relationships of the families and sub-families of the Papilionidae. The reasons for the arrangement of the various branches are discussed in this section, and under the various families in the following section. The vertical scale is my judgement of what might be called evolutionary distance, being evolutionary rate multiplied by time. It is, of course, impossible to distinguish these two quantities on the basis of neozoological evidence. The horizontal positions of the taxa and spacing of the lines are determined by convenience.

CLASSIFICATIONKEY TO THE FAMILIES OF THE PAPILIONOIDEA<sup>9</sup>

1. Lamella of mesodiscrimen continuous with furca,  
 dorsum of the lamella essentially straight  
 (somewhat downcurved in Baronia); eyes  
 not emarginate; patagia either sclerotized  
 or unsclerotized. . . . . 2
- Lamella of mesodiscrimen not continuous with  
 furca, curving downward to base of furca;  
 eyes usually emarginate; patagia un-  
 sclerotized . . . . . Lycaenidae
2. Cervical sclerites not joined beneath cervix;  
 epiphyses absent; hindwing with two distinct  
 vannal veins. . . . . 3

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9. Since butterfly specimens have always been, and will continue to be identified by comparison of facies and genitalia with illustrations, no attempt has been made to construct superficial keys. This key and those that follow are based on what appear to be the most dependable characters, regardless of accessibility. Wherever possible they have been designed to be used with adults of either sex. They will probably prove most useful in placing new or little known forms.



- Cervical sclerites joined or nearly joined by a sclerotic band beneath cervix; epiphyses present; hindwing with only one distinct vannal vein (two in Baronia). . . . .Papilionidae
3. Prespiracular bar well developed; prothoracic legs atrophied (smaller than the pterothoracic legs) to some degree (only slightly in females of Libytheidae); tarsal claws very rarely strongly bifid . . . . . 4
- Prespiracular bar reduced or absent, prothoracic legs fully developed (as large as pterothoracic legs); tarsal claws always strongly bifid. .Pieridae
4. Patagia prominent, rounded, sclerotized structures; metanotum not entirely below mesoscutellum, only partially covered by it . . . . .Nymphalidae
- Patagia not prominent or rounded, bearing only small lateral sclerotizations; metanotum essentially entirely below mesoscutellum, covered by it . . . . . Libytheidae

#### FAMILY PAPILIONIDAE

- 1) Eyes entire; 2) eyes bare; 3) face at least somewhat protuberant; 4) laterofacial sutures separated from eye margins; 5) paraocular areas relatively small (fig. 1);

6) antennae close together to widely separated; 7) anterior tentorial pits high on face; 8) proboscoidal fossa shallow; 9) labial palps much shorter than thorax; 10) labial sclerite well sclerotized only behind palpal sockets, not extended lip-like beneath cervix; 11) anterior tentorial arms greatly enlarged anteriorly but not strongly down-curved (fig. 23), sometimes bearing crests (figs. 18, 19, 20, 21) which may be very high; 12) antennae not carinate; 13) cervical sclerites united beneath neck by a narrow sclerotic band (which is sometimes weak or broken at center); 14) dorsal plate of pronotum sagittate; 15) spina-sternum laterally produced to a greater or lesser degree at the spina (except in Baronia); 16) profurcal arms with secondary anterior prong or lamella (fig. 30) except in Baronia; 17) intercoxal lamella and lamella of prodiscrimen variable; 18) lateral plates of pronotum fused dorsally into a Y-shaped or triangular structure; 19) patagia membranous or with relatively small, elongate sclerotic areas; 20) parapatagia membranous; 21) presternum absent; 22) adnotale not sagittate; 23) lamella of mesodiscrimen complete to furca (curved downward somewhat in Baronia); 24) processes of second phragma prominent; 25) precoxal suture absent except in Parnassiinae); 26) pre-episternum of mesothorax narrow (except in Teinopalpus); 27) mesothoracic anepisternum variable in character, often a

separate sclerite; 28) prescutum not vertical; 29) meral suture and lamella present and prominent (except in Parnassius and Baronia); 30) third phragma consisting of simple lobes (fig. 55); 31) metatergum not completely overhung by mesotergum; 32) caudal part of metathoracic epimeron variable in width; 33) prespiracular bar fully developed; 34) postspiracular bar reduced or absent; 35) cubitus of forewing apparently quadrifid; 36) 3V of forewing present and running to inner margin; 37) hindwing with only one well developed vannal vein (two in Baronia); 38) prothoracic legs fully developed in both sexes; 39) protibiae bearing epiphyses (fig. 56); 40) tarsal claws simple (except in Lamproptera curius and the payeni group of Graphium); 41) aroliar pad and pulvilli absent or reduced; 42) pupa with girdle (except in Parnassius, modified in Zerynthia); 43) larva with osmateria.

The most recent work on the classification and evolution of the Papilionidae is that of Ford (1944). Unfortunately so many of the conclusions arrived at in the present work are diametrically opposed to those of Ford that a detailed discussion of the problems involved and the points of difference seems necessary.

Perhaps the greatest differences center around the concepts of primitive and specialized species and characters. As stated in the introduction it would appear to be

dangerous to label entities as "primitive" or "specialized" unless one is dealing with considerable systematic distance, and even in this case the terms should be used with reservation. In a group as uniform as the Papilionidae assigning these labels to species, genera, or subfamilies is in all likelihood biologically meaningless. However, there is nothing wrong for attempting to label character states in the family as primitive or specialized as long as one is willing to admit ignorance when the data will not permit a decision to be made.

Ford states (p. 210) that "the presence of a tail, supported by vein 4 of the hind-wings, must be regarded as an ancestral characteristic of the family." There is little doubt that tails have been lost secondarily in many of the species of Papilio (s.l.). However, if Ford is correct, then the ancestral papilionid must have developed a tail, which has then been independently lost in Baronia and the Parnassiini as well as in Zerynthia. The alternative hypothesis is that the possession of tails is an advanced character which has not been developed in Baronia or the Parnassiini, and is being developed in Zerynthia. For want of evidence to settle the question we are bound by the rule of parsimony to consider seriously the latter hypothesis.

Again, Ford concludes that short palpi are "doubtless" primitive in the Papilionidae "for they are long only in

the somewhat specialized Zerynthiinae and in the highly specialized Teinopalpus, in which latter they are produced to an extravagant degree." Considering the shape of the head, the palps of Teinopalpus are not at all extravagant. The palps are also not extremely short in the Parnassiini. Once again parsimony would have us select palps of "normal" length as primitive in the family, rather than the extremely reduced palps of Baronia and most Papilioninae.

The sphragis or "female pouch" is of such sporadic occurrence in the family that it would seem wise to exclude it from phylogenetic discussion except to say that the tendency to possess it is an advanced character of the family as a whole. Ford considers the sphragis to be primitive in the family and vestigial in Parides (= Atrophaneura) proneus Hübner (and in certain other neotropical species of Parides where it also occurs).

Ford's very interesting pigment characters have been employed by him with proper restraint (differences in the presence of anthoxanthins have been used by at least one other worker as proof of specific distinctness) but once again his reasoning about their primitive and specialized states is inconclusive if not incorrect.

## KEY TO THE SUBFAMILIES AND TRIBES OF THE PAPILIONIDAE

1. Forewing with vein cu-v absent or (rarely)  
 vestigial, if vestigial face not extremely  
 protuberant; male with tarsal claws usually  
 asymmetrical, females with tarsal claws  
 sometimes asymmetrical. . . . . 2
- Forewing with vein cu-v complete or (rarely)  
 vestigial, if vestigial face extremely  
 protuberant; tarsal claws symmetrical . . . . .  
 . . . . .Papilioninae 4
2. Hindwing with two distinct vannal veins;  
 spinasternum not produced laterally at  
 spina; tarsal claws symmetrical . . . . .Baroniinae
- Hindwing with only one distinct vannal  
 vein; spinasternum produced laterally at  
 least to some extent; tarsal claws  
 usually asymmetrical in males, some-  
 times in females. . . . . Parnassiinae 3
3. Antennae unscaled; labial palps more than  
 twice length of head; margin of hind-  
 wing scalloped or with tails; radius  
 5-branched. . . . . Zerynthiini
- Antennae scaled; labial palps less than  
 twice length of head; margin of hind-

- wing smooth; radius 4-branched (except  
in Archon). . . . . Parnassiini
4. Face extremely protuberant; cu-v cross vein  
of forewing vestigial . . . . . Teinopalpini
- Face not extremely protuberant; cu-v cross  
vein of forewing not vestigial. . . . . 5
5. Patagia membranous. . . . . Papilionini
- Patagia each with at least a small  
sclerotic area. . . . . 6
6. Patagia with strong, fairly large  
sclerotizations; anterior tentorial arms  
with very high crests (figs. 18, 19). . . Graphiini
- Patagia with weak, small sclerotizations;  
anterior tentorial arms with medium  
sized crests (figs. 20, 21) . . . . . Cressidini

#### PAPILIONINAE

a) Antennae close together to far apart; b) labial  
palps very short, approximately as long as head (somewhat  
longer in Teinopalpus); c) tentorial arms with or without  
prominent crests; d) patagia membranous or sclerotized;  
e) spinasternum laterally produced at spina; f) profurcal  
arms with second anterior prong or lamella; g) intercoxal  
lamella prominent and caudad of its usual position in the  
butterflies; h) prodiscrimen often represented by a promi-

nent anterior spine; i) lamella of mesodiscrimen not curved downward before furca; j) precoxal suture absent; k) meral suture and lamella prominent; l) lamella of metadiscrimen curved downward to base of furca or complete to furca; m) forewing with vein cu-v complete (except in Teinopalpus), radius 5-branched; n) hindwing with one well-developed vannal vein; o) tarsal claws symmetrical, simple in all except Lamproptera curius and the payeni group of Graphium in which they are bifid; p) pupa without a cocoon.

Worldwide in distribution but mainly tropical. Greatest morphological diversity found in Old World tropics.

Genera examined: Battus, Cressida, Euryades, Graphium, Lamproptera (= Leptocircus), Ornithoptera, Papilio, Parides (= Atrophaneura), Teinopalpus, Trogonoptera\*, Troides.

In order to save the reader the trouble of referring constantly to Table I, a (P) or an (S) will be placed after each character state mentioned in the following discussion to show whether it is considered to be primitive or specialized.

The Papilioninae are provisionally divided into four tribes, three of which contain fragments of the old polyphyletic genus Papilio. The tribe Graphiini contains at present two genera, Graphium and Lamproptera (= Leptocircus).

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\*Not dissected.



Aside from the more classical characters which relate these two genera, they both possess highly crested anterior tentorial arms (S) (figs. 18, 19), a narrow spinasternum (P), well sclerotized patagia (for the Papilionidae) (P), a lamella of the metadiscrimen which is curved downward to the base of the furca (P), and a tendency towards bifid tarsal claws (S). They both lack the spine of the prodiscrimen (P). Ford's statement that the Graphiini "must have been derived from some ancestral stock within the Troidini" is probably incorrect. Of course, the two share at some point a common ancestor, but all the genera placed by Ford in the "Troidini" (Battus, Troides, Parides) either have patagia which are membranous or at most possess very small sclerotizations. In order for the Graphiini to be derived from one of these genera the sclerotizations would have to have been reduced or lost, and then regained.

The tribe Cressidini contains three genera, the small, very closely related Cressida (1 species) and Euryades (2 species), and the large, widespread Parides (= Atrophaneura). In these genera the tentorial arms have medium sized crests (S), the spinasternum is usually quite broad posteriorly, often with parallel sides (S) (figs. 35, 36), the patagia have very reduced sclerotizations (S), the lamella of the metadiscrimen is not curved downward to the base of the furca (S) and the tarsal claws are simple

(P). These genera all possess the spine of the prodiscrimen (S) (fig. 30).

The tribe Papilionini contains the various ornithopteran genera as well as Papilio and Battus. In these genera the tentorial arms either have medius sized (S) or very reduced crests (P), the spinasternum is either narrow (P) (fig. 34) or widened (S) (fig. 35), the patagia are completely membranous (S), the lamella of the metadiscrimen may (P) or may not (S) curve downward to the base of the furca. The tarsal claws are simple and the spine of the prodiscrimen may (S) or may not (P) be present. This heterogeneous tribe needs considerable additional study. It is quite possibly polyphyletic. Ornithoptera and Troides share the broadened spinasternum with the genera of the Cressidini and may actually be more closely related with them than with Papilio.

The final tribe of the Papilioninae is the Teinopalpini, with one genus, Teinopalpus (1 or 2 species). The tribe is characterized by the unique expansion of the frontal area of the head (S) (figs. 2, 3) and a correlated elongation of the palpi (S), by highly crested tentorial arms (S), membranous patagia (S), loss of the spine of the prodiscrimen (P), a narrow spinasternum (P), a lamella of the metadiscrimen which curves downward to the base of the furca (P), and simple tarsal claws (P).

## PARNASSIINAE

a) Antennae close together (separated by less than one-half width of scape); b) labial palps longer than head; c) tentorial arms crested; d) patagia membranous or sclerotized; e) spinasternum laterally produced at spina; f) profurcal arms with second anterior prong or lamella; g) intercoxal lamella prominent, and somewhat caudad of its usual position in the butterflies; h) prodiscrimen not represented anteriorly by a spine; i) lamella of mesodiscrimen not curved downward before furca; j) at least a trace of precoxal suture present; k) meral suture and lamella varying in prominence; l) lamella of metadiscrimen curved downward to base of furca; m) forewing lacking vein cu-v, radius 4- or 5-branched; n) hindwing with one well-developed vannal vein; o) tarsal claws usually asymmetrical, always simple; p) pupa with or without cocoon.

Holarctic and oriental with greatest diversity in Asia.

Genera examined: Archon, Bhutanitis, Hypermnestra, Leudorfia, Parnassius, Sericinus, Zerynthia.

The Parnassiinae are divided into two tribes, Parnassiini and Zerynthiini. These entities are considered to be of subfamily rank by Ford, and there is some justification for this view. Parnassius, Archon and Hypermnestra

form a very closely knit group, sharing among other things an unusual type of pupa (S), scaled antennae (P), and relatively well-developed patagia (P). Archon differs from the other two genera in having a 5-branched radius (P), and Hypermnestra differs from the others in having nearly symmetrical tarsal claws, in both sexes (there are reports of Parnassius species in which the males have nearly symmetrical claws, but Schatz and Röber (1892) are in error when they illustrate this condition for P. apollo L.). All three genera of the Parnassiini lack any hint of tails on the hindwing (P).

The Zerynthiini differ from the Parnassiini in possessing bare antennae (S), and hindwings which are either scalloped or tailed (S). The pupa is not formed in a cocoon as in the Parnassiini and (except in Leudorfia) the patagia are not very well sclerotized (S). The radius is universally 5-branched (P), differing in this respect from all the Parnassiini except Archon. In both tribes the labial palpi are much longer (P) than in the Papilioninae or Baroniinae, but they are shorter in the Parnassiini than in the Zerynthiini.

As can be seen from the above the Parnassiinae divides rather clearly into two tribes which could be raised to the rank of subfamily. However, considering the types of differences found between the tribes of the Papilioninae,

it would appear that the level of difference between the Parnassiini and Zerynthiini, within the nomenclatorial structure used in this paper, is tribal rather than subfamilial. No reason can be found for placing these two tribes at opposite sides of a diagram of relationships as has been done by Ford (1944). Indeed, even after accepting without question all of the assumptions which he has employed as a basis for the diagram, it is difficult to find justification for this. For the characters shared by the Parnassiini and Zerynthiini the reader is referred to the subfamily diagnosis<sup>10</sup>.

#### BARONIINAE

a) Antennae close together (separated by less than one-half width of scape); b) labial palps very short, approximately as long as head; c) tentorial arms somewhat crested (fig. 22); d) patagia with relatively small, elongate sclerotizations; e) spinasternum not laterally produced at spina; f) profurcal arms simple; g) intercoxal lamella prominent, not caudad of its usual position in the butterflies; h) prodiscrimen not represented an-

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10. Homma's (1954) work on the alimentary canal places Leudorfia (the only zerynthiine which he studied) very close to Parnassius.

teriorly by a spine; i) lamella of mesodiscrimen curved downward somewhat at furca (not to base); j) precoxal suture absent; k) meral suture and lamella ventral and not prominent; l) lamella of metadiscrimen curved downward to base of furca; m) forewing lacking vein cu-v, radius 4-branched; n) hindwing with two well-developed vannal veins; o) tarsal claws symmetrical, simple; p) pupa unknown.

Represented by a single monobasic genus from southwestern Mexico.

Genus examined: Baronia.

#### FAMILY PIERIDAE

1) Eyes entire; 2) eyes bare; 3) fact at least somewhat protuberant; 4) laterofacial sutures not contiguous with eye margins; 5) paraocular areas small (fig. 1); 6) antennae widely separated (more than one-half scape width apart); 7) anterior tentorial pits high on face; 8) proboscoidal fossa shallow or deep; 9) labial palps much shorter than thorax; 10) labial sclerite usually well-sclerotized only in front of palpal sockets, rarely extended lip-like below cervix; 11) form of anterior tentorial arms variable (not highly crested); 12) antennae not carinate; 13) cervical sclerites not united beneath neck; 14) shape of dorsal plate of pronotum variable; 15) spinasternum not laterally produced at spina but

slightly enlarged in front of spina into an oval or diamond-shaped plate; 16) profurcal arms with secondary anterior prong (figs. 28, 29, 31) (except in Pseudopontia); 17) intercoxal lamella prominent, prodiscrimen represented anteriorly by a second small lamella or spine (fig. 29); 18) lateral plates of pronotum fused dorsally but not forming a Y-shaped or triangular structure (fig. 28); 19) patagia membranous or sclerotized; 20) parapatagia membranous; 21) presternum absent; 22) adnotale not sagittate; 23) lamella of mesodiscrimen complete to furca; 24) processes of second phragma prominent; 25) precoxal suture absent; 26) pre-episternum of mesothorax narrow to one-half size of katepisternum; 27) mesothoracic anepisternum not present as a separate sclerite; 28) prescutum not vertical; 29) meral suture and lamella absent or not prominent; 30) third phragma variable in character; 31) metatergum not completely overhung by mesotergum; 32) caudal part of metathoracic epimeron thin (fig. 54); 33) prespiracular bar greatly reduced or absent (fig. 25); 34) postspiracular bar normal; 35) cubitus of forewing appears either quadrifid or trifid; 36) 3V or forewing when present fusing with 2V, not running to inner margin; 37) hindwing with two well-developed vannal veins; 38) prothoracic legs fully developed in both sexes; 39) protibial epiphyses absent; 40) tarsal claws strongly bifid;

41) aroliar pad and pulvilli usually present; 42) pupa with girdle; 43) larvae lacking osmateria.

KEY TO THE SUBFAMILIES OF THE PIERIDAE

1. Forewing with  $M_2$  arising from end of cell; hindwing with  $Sc+R_1$  not secondarily fused with  $R_5$ ; hindwing with  $M_2$  arising from cell. . . . . 2
 

Forewing with  $M_2$  stalked with  $R_{3+4+5}$ ; hindwing with  $Sc+R_1$  secondarily fused with  $R_5$  before middle of wing; hindwing with  $M_2$  stalked with  $M_1$  . . . . . Pseudopontiinae
2. Forewing with 3 to 5 radials present, at least one arising from the cell; forewing with cubitus appearing trifid. . . . . 3
 

Forewing with 5 radials present, all stalked; forewing with cubitus appearing quadrifid . . . . . Dismorphiinae
3. Patagia unsclerotized; humeral vein usually long; tegumen longer than uncus . . . . . Pierinae
 

Patagia sclerotized; humeral vein usually greatly reduced or absent; tegumen usually considerably shorter than uncus . . . . . Coliadinae



## PSEUDOPONTIINAE

a) Patagia unsclerotized; b) forewing with three radial veins; c) forewing with all radial veins arising from cell; d) forewing with  $M_2$  stalked with  $R_{3+4+5}$ ; e) forewing with cubitus apparently trifid; f) hindwing with humeral vein well developed; g) hindwing with  $Sc+R_1$  secondarily fused with  $R_5$  about one-third of wing radius from wing base; h) hindwing with  $M_2$  stalked with  $M_1$ ; i) tegumen extremely reduced, much shorter than uncus; j) uncus reduced to two small lobes, one on either side of anus; k) valvae fused together along ventral and lower distal margins.

Represented by a single monobasic genus from West Equatorial Africa.

Genus examined: Pseudopontia.

## DISMORPHIINAE

a) Patagia unsclerotized; b) forewing with five radial veins; c) forewing with all radial veins stalked; d) forewing with  $M_2$  arising from cell; e) forewing with cubitus apparently quadrifid; f) hindwing with humeral vein well developed; g) hindwing with  $Sc+R_1$  not secondarily fused with  $R_5$ ; h) hindwing with  $M_2$  arising from cell; i) tegumen reduced, much shorter than uncus; j) uncus well developed,

bilobed; k) valvae fused together along ventral and lower distal margins.

Primarily neotropical but with one small palearctic genus (Leptidia).

Genera examined: Dismorphia, Leptidia, Pseudopieris.

#### PIERINAE

a) Patagia unsclerotized; b) forewing with three to five radial veins; c) forewing with at least one radial vein arising from cell; d) forewing with  $M_2$  arising from cell; e) forewing with cubitus apparently trifid; f) hindwing with humeral vein usually well developed; g) hindwing with  $Sc+R_1$  not secondarily fused with  $R_5$ ; h) hindwing with  $M_2$  arising from cell; i) tegumen not reduced, longer than uncus; j) uncus well developed, simple; k) valvae not fused together.

Cosmopolitan, reaching greatest variety in the tropics.

Genera examined: Anthocharis, Aporia, Appias, Archonias, Belenois, Cepora, Colotis, Delias, Dixeia, Euchloe, Hebomoia, Itaballia, Ixias, Leptophobia, Leptosia, Melete, Neophasia, Pereute, Perrhybris, Pieris, Prioneris, Zegris.

#### COLIADINAE

a) Patagia sclerotized; b) forewing with three to five radial veins; c) forewing with at least one radial

vein arising from cell; d) forewing with  $M_2$  arising from cell; e) forewing with cubitus appearing trifid; f) hindwing with humeral vein usually reduced or absent; g) hindwing with  $Sc+R_1$  not secondarily fused with  $R_3$ ; h) hindwing with  $M_2$  arising from cell; i) tegumen not extremely reduced, but usually considerably shorter than uncus; j) uncus well developed, simple; k) valvae not fused together.

Cosmopolitan, reaching greatest variety in the tropics.

Genera examined: Anteos, Colias, Eurema, Gonepteryx, Kricogonia, Leucidea, Nathalis, Phoebis, Zerene.

The subfamilial classification of the Pieridae adopted in this work is based principally on Klots' (1933) generic revision of the family. The only major change is the elevation of Klots' tribe "Rhodocerini" to subfamily status (Coliadinae), a move which has been made previously by other authors (e.g., Ford, 1945). The discovery of the consistent differences in the patagia (involving even such atypical appearing "yellows" as Leucidia) seemed to favor giving the group subfamily status.

#### FAMILY NYMPHALIDAE

1) Eyes entire; 2) eyes bare or hairy; 3) fact at least somewhat protuberant; 4) laterofacial sutures not contiguous with eye margins; 5) paraocular areas small (fig. 1) to large (fig. 1 - Pt. I); 6) antennae close to-

gether to widely separated; 7) anterior tentorial pits high on face; 8) proboscoidal fossa usually shallow; 9) labial palps much shorter than thorax; 10) labial sclerite well-sclerotized all around palpal sockets, rarely extended lip-like below cervix; 11) form of anterior tentorial arms variable; 12) antennae almost always tricarinate; 13) cervical sclerites not united beneath neck; 14) shape of dorsal plate of pronotum variable; 15) spinasternum not laterally produced at spina; 16) profurcal arms simple; 17) intercoxal lamella not prominent, or absent; 18) lateral plates of pronotum fused dorsally forming a Y-shaped or triangular structure (fig. 8 - Pt. I); 19) patagia prominent, well sclerotized (fig. 37); 20) parapatagia membranous or sclerotized; 21) presternum present; 22) adnotale not sagittate; 23) lamella of mesodiscrimen complete to furca; 24) processes of second phragma prominent; 25) precoxal suture usually present, with varying inflection; 26) pre-episternum of mesothorax narrow or essentially absent to one-half magnitude of katepisternum; 27) mesothoracic anepisternum often present as a separate sclerite; 28) prescutum usually not vertical; 29) meral suture and lamella absent or not prominent; 30) third phragma very variable in form but not consisting of simple lobes; 31) metatergum not completely overhung by mesotergum; 32) caudal part of metathoracic epimeron intermediate between thin and broad in width to broad (never

thin); 33) prespiracular bar fully developed; 34) postspiracular bar variable in development; 35) cubitus of forewing appears trifid; 36) 3V of forewing, when present, fusing with 2V, not running to inner margin; 37) hindwing with two well-developed vannal veins; 38) prothoracic legs atrophied in both sexes, clawless (except in Calinaga and some ithomiines in which there are small claws in the females); 39) protibial epiphyses absent; 40) tarsal claws usually simple (bifid in some acraeines); 41) aroliar pad usually well-developed, pulvilli usually large and bifid; 42) pupa without girdle; 43) larva without osmateria.

Because of the tremendous diversity of appearance found in the vast assemblage of the nymphalids, the Nymphalidae (s.l.) have been previously broken up into a large number of families and subfamilies. Clark (1948) recognized eight families and twenty-three subfamilies in the group "Nymphalides" (excluding Libytheidae which he erroneously placed with the lycaenids).

Morphologically the Nymphalidae are a comparatively uniform group in spite of the large number of genera and species included. In general, the differences between the subfamilies outlined below are equivalent (insofar as it is possible to equate them) to those found between tribes or genera of the Papilionidae. The variation which does exist is in many cases continuous, leaving few obvious gaps at which to set up subfamilial limits. Likewise discon-

tinuities in the variation of one character often do not coincide with discontinuities in the variation of others. In spite of these difficulties, several distinct lines of evolution may be detected within the group (see diagram of relationships - fig. 64).

One line includes the Ithomiinae and Danainae. Both of these subfamilies have lost the separate mesothoracic anepisternum (S)<sup>11</sup>, have a pronounced caudal bulge of the mesomeron (found only in these two subfamilies) (S), have the base of vein 3V free in the forewing (P), and have the forewing and hindwing discal cells closed by tubular veins (P). Also certain ithomiines show reduction of the female protarsus to the four segmented condition (S) found universally in the danaines.

Four subfamilies of the Nymphalidae (Satyrinae, Morphinae, Calinaginae, Charaxinae) have retained the mesothoracic anepisternum as a separate sclerite. Two of these, Satyrinae and Morphinae appear to be quite closely related. Both groups have rather simplified dentate valvae (S) (a few exceptions in the Morphinae), the discal cell of the forewing closed (P), a tendency towards closure of the discal cell of the hindwing (P) (all satyrines and most morphines), larvae with bifid tails (S) and monocotyledonous

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11. (S) signifies a character believed to be specialized, (P) primitive.

foodplants (all except Morpho)(S?). The Satyrinae and Morphinae both usually have prominent eye-spots in the pattern.

The monobasic subfamily Calinaginae is apparently allied to the satyrines and morphines, having the cells of both wings closed by relatively thick veins. Unfortunately its early stages are unknown.

The subfamily Charaxinae is somewhat anomalous. In almost all characters except the condition of the anepisternum and parapatagia it appears to belong with the Nymphalinae<sup>12</sup>.

The Nymphalinae and Acraeinae are connected by a series of nymphaline genera sometimes segregated as the subfamily "Heliconiinae" (Heliconius, Eueides, Dryas, Dryadula, Dione, Agraulis, Philaethria). Both subfamilies lack the separate anepisternum, and with minor exceptions have no trace of vein 3V at the base of the forewing. The aroliar pads of the pterothoracic tarsi are lost in some genera of each subfamily (S).

KEY TO THE SUBFAMILIES OF THE NYMPHALIDAE

- 1. Mesothoracic anepisternum absent as a distinct sclerite (fig. 9 - Pt. I) . . . . . 2

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12. The genus Stibochiona of the Nymphalinae also has sclerotized parapatagia.

- Mesothoracic anepisternum present as a distinct sclerite (fig. 37). . . . . 5
2. Forewing with vein 3V free at base (2V apparently bifid at base); mesothoracic pre-episternum at its widest much less than one-half width of katepisternum (fig. 9 - Pt. I); mesomeron with prominent caudal bulge (fig. 9 - Pt. I). . . 3
- Forewing with vein 3V not free at base (2V not bifid at base)(except in Kallima<sup>13</sup>); mesothoracic pre-episternum at its widest at least one-half width of katepisternum (except in Pardopsis); mesomeron with or without (fig. 25) prominent caudal bulge. . . . . 4
3. Antennae naked; male with a pair of hair pencils at end of abdomen; female protarsus 4-segmented, strongly clubbed (fig. 26 - Pt. I) . . . . .Danainae
- Antennae scaled; male without a pair of hair pencils at end of abdomen; female protarsus 4- or 5-segmented, not strongly clubbed . . . . .Ithomiinae
4. Hindwing with cell closed by a well developed tubular vein (3rd discocellular); tarsal

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13. The base of 3V is present also in Apaturina and Dryas as a spur which does not anastomose with 2V.



claws usually toothed or asymmetrical,  
especially in males (normal in Pardopsis);  
gnathos absent or at most vestigial

(Pardopsis) . . . . . Acraeinae

Hindwing cell not closed by tubular vein

(3rd discocellular absent or vestigial)

(except in Heliconius, Euides); tarsal

claws simple, symmetrical; gnathos

usually well developed. . . . . Nymphalinae

- 5. Forewing with veins not swollen; mesothoracic pre-episternum well developed, varying in size, pre-episternal suture usually well developed; hindwing cell often not closed by a tubular vein (see couplet 4) . . . . . 6

Forewing usually with at least one vein swollen at base; mesothoracic pre-episternum usually greatly reduced or separated from katepisternum by a very weak pre-episternal suture; hindwing cell always closed by a tubular vein. . . . . Satyrinae

- 6. Parapatagia with at least a trace of sclerotization; hindwing cell not closed by a tubular vein. . . . . Charaxinae

Parapatagia without a trace of sclerotization; hindwing cell sometimes

closed by a tubular vein. . . . . 7

7. Forewing with vein 3V free at base; male  
with superuncus (fig. 62); female  
protarsus with small but perfect tarsal  
claws; hindwing cell closed by a weak  
tubular vein; humeral cell absent . . . Calinaginae

Forewing with vein 3V not free at base; male  
without superuncus; female protarsus with-  
out claws; hindwing cell open or closed by  
a tubular vein, species with closed cell  
also have humeral cell present. . . . . Morphinae

#### DANAINAE

- a) Antennae naked; b) interantennal distance variable;  
c) anterior tentorial arms usually not enlarged anteriorly,  
no trace of crests (fig. 15); d) parapatagia membranous;  
e) mesothoracic pre-episternum narrow, sometimes almost  
absent; f) mesothoracic anepisternum not a separate  
sclerite; g) tegulae with distal end relatively blunt  
(fig. 45); h) mesomeron with a pronounced caudal bulge  
and sharp caudoventral constriction (fig. 9 - Pt. I);  
i) postcoxal sclerite short (fig. 20 - Pt. I); j) arms of  
gnathos variable, may be absent; k) valvae broad and com-  
plex (fig. 36 - Pt. I); l) males with hair pencils at the  
end of the abdomen (fig. 37 - Pt. I); m) protarsus of fe-  
male 4-segmented, clubbed (fig. 26 - Pt. I), without well

developed tarsal claws; n) pterothoracic legs with tarsal claws simple, symmetrical; o) pterothoracic legs with aroliar pad and pulvilli variable in presence and development; p) forewing without any veins thickened at the bases; q) forewing with base of vein 3V free; r) forewing cell closed by tubular vein; s) hindwing cell closed by tubular vein; t) larvae without bifid tail.

Cosmopolitan but with greatest development in the tropics, especially in the Old World.

Genera examined: Amauris, Clothilda, Danaus, Euploea, Idea, Ideopsis, Ituna, Lycorea.

Nothing has been found in the present work which would seem to justify dividing the danaines into tribes. The most obvious variation observed was in the habitus and venation, Lycorea and Ituna differing from each other and from the rest of the danaines in the facies and the arrangement of the discocellulars of the hindwing. Euploea has a lobe-like extension of the inner margin of the forewing not found elsewhere in the family. There is some indication that the venation is quite variable within genera or even within species (e.g., most Lycorea cleobaea males have much more sharply angled 2nd and 3rd discocellulars than do L. cleobaea females).

Considering the structural uniformity of the group and the relatively small number of genera it contains, it would seem best to consider the above-mentioned differences as

merely generic.

A great many species of this family are reputed to be distasteful to predators. Butterflies of other groups very often mimic danaines.

#### ITHOMIINAE

a) Antennae scaled; b) antennae slightly less than one-half the width of the scape apart; c) anterior tentorial arms not enlarged anteriorly, no trace of crests; d) parapattalia membranous; e) mesothoracic pre-episternum completely absent or narrow and set off by distinct pre-episternal suture; f) mesothoracic anepisternum not a separate sclerite; g) tegulae with distal end relatively blunt (fig. 44); h) mesomeron with a pronounced caudal bulge and sharp caudoventral constriction (fig. 9 - Pt. I); i) postcoxal sclerite long (fig. 53) or short (fig. 29 - Pt. I); j) arms of gnathos variable, may be absent; k) valvae variable; l) males without hair pencils at the end of abdomen; m) protarsus of female 4- or 5-segmented, unclubbed, without well-developed tarsal claws; n) pterothoracic legs with tarsal claws simple, symmetrical; o) pterothoracic legs with aroliar pad and pulvilli present and well developed; p) forewing without one or more veins thickened at base; q) forewing with base of vein 3V free; r) forewing cell closed by a tubular vein; s) hindwing cell closed by a

a tubular vein; t) larvae without bifid tail.

Neotropical except for the monobasic genus Tellervo which is papuan.

Genera examined: Aprotopus, Callithomia, Ceratina, Dircenna, Hirsutis, Hypoleria, Ithomia, Mechanitis, Melinaea, Napeogenes, Sais, Scada, Tellervo, Thyridia, Tithorea.

Fox is at present working on the Ithomiinae and has published the first section of his revision (1956). For reasons discussed earlier in this work the ithomiines are considered here to be of subfamilial rank. By nomenclatorially downgrading Fox's system we arrive at two tribes under the Ithomiinae, Tellervini (Tellervo only)(male without hair pencil on hindwing, proximal segment of labial palp much more than one-half length of second segment), and Ithomiini (all other genera)(male with hair pencil on hindwing, proximal segment of labial palp much less than one-half length of second segment). The other tribes recognized by Fox would then become subtribes or genera under the Ithomiini.

#### SATYRINAE

a) Antennae scaled (only on proximal joints of Pierella and allies); b) antennae less than one-half the width of the scape apart; c) anterior tentorial arms at

least somewhat enlarged anteriorly (at least a trace of a crest) (fig. 14); d) parapatagia membranous; e) mesothoracic pre-episternum very reduced in width (fig. 39) or if not very reduced, pre-episternal suture essentially absent; f) mesothoracic anepisternum (fig. 39) a small but separate sclerite (very small in some genera such as Erebia, Callerebia); g) tegulae variable in shape, some with distal end relatively blunt, others with quite pronounced points; h) mesomeron without pronounced caudal bulge or sharp caudoventral constriction (fig. 25); i) postcoxal sclerite long (fig. 53) or short (fig. 20 - Pt. I); j) arms of gnathos free (fig. 60); k) valvae usually slender (fig. 60) and often dentate; l) males without hair pencils at end of abdomen; m) protarsus of female usually 5-segmented, unclubbed (sometimes extremely reduced as in Melanargia); n) pterothoracic legs with tarsal claws simple, symmetrical; o) pterothoracic legs with aroliar pad and pulvilli present and well developed; p) forewing usually with one or more veins thickened at the base; q) forewing with base of vein 3V usually not free (free only in Pierella, Haetera and Cithaeris); r) forewing cell closed by tubular vein; s) hindwing cell closed by tubular vein; t) larvae with bifid tail.

Cosmopolitan, well represented in temperate regions and arctic.

Genera examined: Anadebis, Antirrhaea, Bia,

Callerebia, Callitaera, Coenonympha, Corades, Elymniopsis,  
Elymnius, Epinephile, Erebia, Euptychia, Gyrocheilus,  
Haetera, Lethe, Melanargia, Melanitis, Minois, Neope,  
Oeneis, Pararge, Pierella, Pronophila, Ragadia, Satyrus,  
Taygetis.

No attempt is made in this work to divide the Satyrinae into tribes. A number of groups have been previously separated, principally on differences in the venation (condition of base of Sc+R<sub>1</sub> and position of 3rd discocellular in hindwing among others). However, variation in other structures shows some discordance with these venational characters and a thorough generic revision of the subfamily should be completed before final decisions are made concerning its partitioning.

Some of the characters which merit investigation are the form of the genitalia, especially of the gnathos (stubby or absent in Haetera, Callitaera, Antirrhaea, Pierella, Melanitis, etc.; well formed in many genera); the shape of the tegulae, the hairiness of the eyes (very hairy in Lethe and allies, Pronophila, moderately hairy or naked in many others); development of precoxal suture; development of mesothoracic pre-episternum; and length of postcoxal sclerite (reaching to dorsum of meron in Bia, Neope, Minois, Elymnius, Haetera, Pierella, Melanitis, etc., much shorter in Oeneis, Gyrocheilus, Taygetis,

Hipparchia, etc.).

A detailed study of these as well as many other characters of the satyrines may well show that although there is considerable variation within the subfamily, the genera do not segregate well into tribal groups.

It should be noted that Bia, which is placed by some authors (e.g., Clark, 1948) in the "Brassolidae" appears to be a typical satyrine.

The classical character of greatly swollen bases of the wing veins is absent from many satyrine genera (e.g., Anadebis, Antirrhaea, Lethe, Melanitis, Oeneis) and is present in many nymphaline genera (e.g., Bulboneura, Callicore, Custineura, Pyrrhogyra, Vila).

#### MORPHINAE

a) Antennae scaled or naked; b) antennae less than one-half the width of the scape apart; c) anterior tentorial arms at least somewhat enlarged anteriorly (at least a trace of a crest); d) parapatagia membranous; e) mesothoracic pre-episternum well developed, narrow to broad, pre-episternal suture usually well developed; f) mesothoracic anepisternum a relatively large, separate sclerite (fig. 37); g) tegulae variable in shape, some with relatively blunt points distally, others with quite pronounced points; h) mesomeron without pronounced caudal bulge or sharp caudo-ventral constriction (fig. 25); i) postcoxal sclerite long



(fig. 53); j) arms of gnathos free; k) valvae usually slender and dentate (broad in Morpho); l) males without hair pencils at end of abdomen; m) protarsus of female 5-segmented, unclubbed or weakly clubbed without well developed tarsal claws; n) pterothoracic legs with tarsal claws simple, symmetrical; o) pterothoracic legs with aroliar pad and pulvilli present and well-developed; p) forewing veins never thickened at base; q) forewing with base of vein 3V usually not free (free only in some Taenaris); r) forewing cell closed by tubular vein; s) hindwing cell open or closed by tubular vein; t) larvae with bifid tail (reduced in Morpho).

Indomalayan and neotropical in distribution.

Genera examined: Amathusia, Brassolis, Caligo.

Discophora, Dynastor, Enispe, Eryphanis, Faunis, Morpho, Narope, Opoptera, Opsiphanes, Stichophthalma, Taenaris.

Considering the present level of knowledge it seems unwise to divide the morphines into tribal groups. The subfamily as a whole seems quite uniform structurally, and most of the characters (venation, foodplant, genitalia, etc.) which have been employed to separate the group into two "families" would doubtless have been considered at most subfamilial had the size and popularity of the insects been smaller. Unfortunately the above mentioned characters show some discordance (Morpho differs from most of the others on larval characters, foodplant, genitalia and coloration,

etc., while the whole subfamily divides well elsewhere on the basis of several characters of the venation of the hindwing). As in the rest of the butterflies, detailed generic revisions including studies of the immature forms will be needed before a definitive classification can be set up.

#### CALINAGINAE

a) Antennae scaled; b) antennae less than one-half the width of the scape apart; c) anterior tentorial arms with anterior crest (fig. 9); d) parapatagia membranous; e) mesothoracic pre-episternum more than one-half width of katepisternum, pre-episternal suture strong dorsally, obsolescent ventrally; f) mesothoracic anepisternum a large, separate sclerite; g) tegulae produced distally into a fairly long point (fig. 47); h) mesomeron without pronounced caudal bulge or sharp caudoventral constriction (fig. 25); i) postcoxal sclerite long; j) arms of gnathos absent; k) valvae broad, not dentate (fig. 62); l) males without hair pencils at end of abdomen; m) protarsus of female 5-segmented, unclubbed, with well developed tarsal claws; n) pterothoracic legs with tarsal claws simple, symmetrical; o) pterothoracic legs with aroliar pad and pulvilli present and well developed; p) forewing without one or more veins thickened at the base; q) forewing with base of vein 3V free; r) forewing cell closed by a weak tubular vein; s) hindwing cell closed by a weak tubular

vein; t) larvae unknown.

Represented by a single monobasic genus from the Himalayas.

Genus examined: Calinaga.

#### CHARAXINAE

a) Antennae scaled; b) antennae usually about one-half the width of the scape apart; c) anterior tentorial arms enlarged anteriorly, usually crested (fig. 10); d) parapagia with at least a trace of sclerotization (fig. 37); e) mesothoracic pre-episternum well-developed, usually more than one-half width of katepisternum, pre-episternal suture variable in development; f) mesothoracic anepisternum a large separate sclerite (fig. 37); g) tegulae produced distally into a long, relatively fine point; h) mesomeron without pronounced caudal bulge or sharp caudoventral constriction (fig. 25); i) postcoxal sclerite long (fig. 53); j) arms of gnathos well developed, free or fused; k) valvae fairly broad, rather simple (fig. 61); l) males without hair pencils at end of abdomen; m) protarsus of female 5-segmented, may be slightly clubbed; n) pterothoracic legs with tarsal claws simple, symmetrical; o) pterothoracic legs with aroliar pad and pulvilli present and well developed; p) forewing without one or more veins thickened at the base; q) forewing with base of vein 3V not free; r) forewing cell not closed by a tubular vein; s) hindwing cell not closed

by a tubular vein; t) larvae with or without bifid tail.

Tropicopolitan in distribution, sparsely entering temperate regions.

Genera examined: Anaea, Charaxes, Coenophlebia, Hypna, Prepona.

No tribal division of the Charaxinae is suggested at this time.

#### NYMPHALINAE

a) Antennae scaled (scaling rarely restricted to most basal joints); b) interantennal distance very variable; c) anterior tentorial arms may or may not be enlarged anteriorly; d) parapatagia membranous (except in Stibochiona); e) mesothoracic pre-episternum about one-half width of katepisternum, often very short and ventral, pre-episternal suture usually well developed; f) mesothoracic anepisternum not a separate sclerite; g) tegulae variable in shape; h) mesomeron without pronounced caudal bulge or sharp caudoventral constriction (fig. 25); i) postcoxal sclerite variable in length; j) gnathos usually present, often complete; k) valvae variable; l) males without hair pencils at the end of abdomen; m) protarsus of female 5-segmented, unclubbed or slightly clubbed; n) pterothoracic legs with tarsal claws simple, symmetrical; o) pterothoracic legs usually with aroliar pad and pulvilli present and well

developed; p) forewing sometimes with one or more veins thickened at base; q) forewing with base of vein 3V not free (except in Kallima, Apaturina and Dryas); r) forewing cell usually not closed by tubular vein; s) hindwing cell not closed by tubular vein; t) larvae with bifid tail.

Cosmopolitan in distribution.

Genera studied: Ageronia, Agraulis, Apatura, Araschnia, Asterocampa, Boloria, Byblia, Callicore, Catagramma, Catonephele, Catuna, Cethosia, Chlosyne, Cirrochroa, Cupha, Cynthia, Cyrestis, Dichorragia, Didonis, Dione, Doleschallia, Doxocopa, Dryadula, Dryas, Ergolis, Eusides, Euphoedra, Euphydryas, Euptoieta, Euthalia, Gynaecia, Haematera, Heliconius, Historis, Hypolimnus, Kallima, Limenitis, Marpesia, Megistanis, Melitaea, Metamorpha, Morpheis, Neptis, Nessaea, Nymphalis, Panacea, Pandita, Pantoporia, Parthenos, Perisama, Philaethria, Phyciodes, Precis, Pseudergolis, Pyrrhogyra, Salamis, Smyrna, Speyeria, Stibochiona, Temenis, Yoma.

This large subfamily is more in need of thorough generic work than any other subfamily of the Nymphalidae. This subfamily includes the following subfamilies of Clark (1948): Apaturinae, Marpesiinae, Nymphalinae, Ergolinae, Limenitinae, Argynninae, Heliconiinae. It is possible that some or all of these should be retained as tribes, but additional work is needed before the decisions

can be made. Of the above "subfamilies" the Heliconiinae appear to be closest to actual subfamily rank. However, they appear to fall in a continuum between the acraeines and Argynnis and allies, with the largest gap coming between the Acraeinae and the heliconians.

#### ACRAEINAE

a) Antennae scaled (scales may be sparse); b) antennae about one-half the width of the scape apart; c) anterior tentorial arms not prominently enlarged anteriorly, lacking crest (fig. 11); d) parapatagia membranous; e) mesothoracic pre-episternum usually about one-half width of katepisternum (except in Pardopsis where it is extremely narrow), pre-episternal suture well developed; f) mesothoracic anepisternum not a separate sclerite; g) tegulae very small, blunt distally (fig. 50); h) shape of mesomeron variable; i) postcoxal sclerite short; j) gnathos usually absent (fig. 58), rarely vestigial (Pardopsis, fig. 59); k) valvae usually slender, non-dentate, simple (except in Pardopsis, fig. 59); l) males without hair pencils at end of abdomen; m) female protarsus 5-segmented, unclubbed, without well-developed tarsal claws; n) pterothoracic legs with tarsal claws bifid (toothed) or asymmetrical except in Pardopsis; o) pterothoracic legs with aroliar pad and pulvilli reduced (essentially absent) except in Pardopsis; p) forewing

without one or more veins thickened at the base; q) forewing with base of vein 3V not free; r) forewing cell closed by a tubular vein; s) hindwing cell closed by a tubular vein; t) larvae without bifid tail.

Indomalayan, Ethiopian and neotropical in distribution with the greatest diversity in Africa.

Genera examined: Acraea, Actinote, Pardopsis, Planema.

The Acraeinae seem to fall into two tribal groups:

Acraeini with a relatively wide mesothoracic pre-episternum, tarsal claws toothed or asymmetrical, reduced aroliar pads and pulvilli, and completely reduced gnathos (Acraea, Actinote, Planema); and Pardopsini with a very narrow mesothoracic pre-episternum, tarsal claws simple and symmetrical, well developed aroliar pads and pulvilli, and a vestigial gnathos (Pardopsis).

#### FAMILY LIBYTHEIDAE

1) Eyes entire; 2) eyes bare; 3) face somewhat to quite protuberant; 4) laterofacial sutures not contiguous with eye margins; 5) paraocular areas small to large; 6) antennae more than one-half width of scape apart; 7) anterior tentorial pits high on face; 8) proboscidial fossa variable in depth; 9) labial palps variable in length, often almost as long as, or as long as the thorax; 10) labial sclerite well sclerotized all around palpal

sockets, extended lip-like below cervix; 11) anterior tentorial arms enlarged anteriorly but not downcurved (fig. 13); 12) antennae tricarinate; 13) cervical sclerites not united beneath neck; 14) dorsal plate of pronotum Y-shaped; 15) spinasternum not laterally produced at spina; 16) profurcal arms simple; 17) intercoxal lamella present but not prominent; 18) lateral plates of pronotum fused dorsally forming a triangular structure; 19) patagia membranous except for a small lateral sclerotic area on each (fig. 26); 20) parapatagia membranous; 21) presternum present; 22) adnotale sagittate (fig. 26); 23) lamella of mesodiscrimen complete to furca; 24) processes of second phragma prominent; 25) precoxal suture present with reduced inflection; 26) pre-episternum of the mesothorax wide (same magnitude as the katepisternum) but pre-episternal suture essentially absent, the presence of the pre-episternum indicated by a notch (fig. 26); 27) mesothoracic anepisternum not a separate sclerite; 28) prescutum vertical or with dorsum anterior to venter (fig. 26); 29) meral suture and lamella absent or not prominent; 30) third phragma consisting of a pair of pointed processes; 31) metatergum essentially overhung by mesotergum (fig. 26); 32) caudal part of metathoracic epimeron intermediate in width; 33) prespiracular bar fully developed; 34) postspiracular bar fully developed, broad (fig. 26); 35) cubitus of forewing appears



trifid; 36) 3V of forewing fusing with 2V, not running to inner margin; 37) hindwing with two vannal veins; 38) prothoracic legs atrophied in male, fully developed except for a slight reduction in size in female; 39) protibial epiphyses absent; 40) tarsal claws simple; 41) aroliar pad present, pulvilli present and bifid; 42) pupa without girdle; 43) larva without osmateria.

Cosmopolitan in distribution.

Genera examined: Libythea, Libytheana.

In spite of its clearly nymphaloid relationships, this family has been often associated with the riodinines because of the lyncaenoid form of the prothoracic legs.

#### FAMILY LYCAENIDAE

1) Eyes emarginate (fig. 5) (or at least with eye and edge of antennal socket contiguous); 2) eyes bare or hairy; 3) face flat or at most slightly protuberant (fig. 7); 4) laterofacial sutures contiguous or nearly contiguous with eye margins (fig. 5); 5) paraocular areas absent or extremely narrow; 6) antennae close together to very widely separated; 7) anterior tentorial pits usually low on face; 8) proboscidial fossa usually deep; 9) labial palps much shorter than thorax; 10) labial sclerite well sclerotized all around palpal sockets (except in Styx), rarely extended lip-like below cervix; 11) anterior tentorial arms en-

larged and downcurved anteriorly (fig. 17); 12) antennae not carinate; 13) cervical sclerites not united beneath neck; 14) shape of dorsal plate of pronotum variable; 15) spinasternum not laterally produced at spina; 16) profurcal arms simple; 17) intercoxal lamella present, variable in prominence; 18) lateral plates of pronotum fused dorsally to form a V-shaped or triangular structure; 19) patagia membranous (fig. 27); 20) parapatagia membranous; 21) presternum present; 22) adnotale not sagittate; 23) lamella of mesodiscrimen curves downward to base of furca (fig. 42); 24) processes of second phragma prominent or essentially absent; 25) at least a trace of precoxal suture present; 26) pre-episternum usually about same magnitude as katepisternum (fig. 27); 27) mesothoracic anepisternum sometimes present as a separate sclerite; 28) prescutum vertical or nearly vertical; 29) meral suture and lamella absent or not prominent; 30) third phragma variable, but not consisting of simple lobes; 31) metatergum not completely overhung by mesotergum; 32) caudal part of metathoracic epimeron intermediate to thin, not broad; 33) prespiracular bar fully developed; 34) postspiracular bar reduced (may be almost complete) or absent; 35) cubitus of forewing appears trifid; 36) 3V of forewing when present fusing with 2V, not running to inner margin; 37) hindwing usually with two vannal veins, rarely with only one; 38) prothoracic

legs of males moderately to strongly atrophied, almost always clawless, of females slightly reduced in size but with claws; 39) protibial epiphyses absent; 40) tarsal claws simple or weakly bifid; 41) aroliar pad well developed, pulvilli present but not bifid; 42) pupa usually with girdle; 43) larva without osmateria.

#### KEY TO THE SUBFAMILIES OF THE LYCAENIDAE

1. Mesothoracic anepisternum either absent or, if present, not strongly convex; labial sclerite completely sclerotized; male prothoracic tarsi neither segmented nor bearing claws (except in some species of Thestor) . . . . . 2
- Mesothoracic anepisternum a prominent, strongly convex, separate sclerite (fig. 38); labial sclerite sclerotized principally behind (strongly) and between (lightly) the palpal sockets; male prothoracic tarsi segmented and bearing a claw each<sup>14</sup> . . . . . Styginae

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14. The single complete male prothoracic leg which it was possible to examine bore only a single tarsal claw. It is quite possible that there was also a second claw which had been broken off.

2. Male prothoracic coxae not extending spinelike below articulation of trochanter (slightly extended in Curetis); male prothoracic legs more than one-half length of pterothoracic legs; hindwing without vein along basal part of costal margin; hindwing with humeral vein usually absent; mesothoracic anepisternum usually not a distinct, separate sclerite. . . . .Lycaeninae

Male prothoracic coxae extending spine-like below articulation of trochanter (fig. 57); male prothoracic legs less than one-half length of pterothoracic legs; hindwing often with vein along basal part of costal margin; hindwing with humeral vein usually present (when absent vein on costal margin present); mesothoracic anepisternum always a distinct, separate sclerite. . . . .Riodininae

#### STYGINAE

a) Eyes hairy; b) palps very short, approximately same length as head; c) labial sclerite sclerotized principally behind (strongly) and between (lightly) the palpal

sockets; d) male prothoracic leg doubtfully functional, less than one-half length of pterothoracic legs; e) male prothoracic coxae not extending spinelike below articulation of trochanter; f) male prothoracic tarsus segmented, bearing a tarsal claw (see footnote to key); g) mesothoracic anepisternum a strong, convex, separate sclerite (fig. 38); h) tegulae small and blunt (fig. 51); i) forewing with two short recurrent veins at end of cell; j) hindwing with a humeral vein; k) hindwing without a vein along the costal margin.

Represented by a single monobasic genus from the Peruvian Andes.

Genus examined: Styx.

#### LYCAENINAE

a) Eyes hairy or naked; b) palps only rarely as short as head is long; c) labial sclerite completely sclerotized (figs. 3, 4 - Pt. I); d) male prothoracic leg functional, more than one-half length of pterothoracic legs; e) male prothoracic coxae not extending spinelike below articulation of trochanter (slightly in Curetis); f) male prothoracic coxae not segmented or bearing tarsal claws (except in Thestor); g) mesothoracic anepisternum usually not present as a separated sclerite, when present not prominent or strongly convex; h) tegulae usually fairly long (fig. 52);

- i) forewing rarely with one, never with two recurrent veins at end of cell; j) hindwing usually lacking humeral vein (present in Pentila, Liptena, Durbania, etc.); k) hindwing without a vein along the base of the costal margin.

Cosmopolitan in distribution.

Genera examined: Amblypodia, Atlides, Callictita, Callophrys, Candalides, Cupido, Curetis, Deudoryx, Durbania, Fenesica, Hemiargus, Hypochrysops, Hypolyceana, Ialmenus, Incisalia, Lycaena, Lycaenopsis, Lysandra, Mampava, Megalopalpus, Mimacraea, Mitoura, Niphanda, Ogyris, Philiris, Plebejus, Poretia, Pseuderesia, Satyrium, Taraka, Thestor, Telipna, Teriomima, Tharsalia, Thysonotas, Zeltus.

#### RIODININAE

- a) Eyes hairy or naked; b) palps only rarely as short as head is long; c) labial sclerite completely sclerotized (figs. 3, 4 - Pt. I); d) male prothoracic leg not functional, less than one-half length of pterothoracic legs; e) male prothoracic coxae extend spinelike below articulation of trochanter (fig. 57); f) male prothoracic coxae not segmented or bearing tarsal claws; g) mesothoracic anepisternum always present as a separate sclerite, but not prominently or strongly convex; h) tegulae usually fairly long (fig. 52); i) forewing rarely with one, never with two recurrent

veins at end of cell; j) hindwing with humeral vein usually present; k) hindwing with a vein along the base of the costal margin (always present when humeral vein absent).

Tropicopolitan in distribution, a few nearctic and palearctic. By far most diversly and abundantly represented in the neotropical region.

Genera examined: Abisara, Anatole, Ancyluris, Anteros, Apodemia, Baeotis, Caria, Diorrhina, Dodona, Echenais, Elaphrotis, Euselasia, Helicopsis, Lasaia, Leucochimona, Lymnas, Mesosemia, Metacharis, Nemeobius, Nymphidium, Riodina, Sisime, Stalachtis, Stiboges, Sumachia, Syrmatia, Theope, Thisbe, Zimeros.

Of all the butterflies the Lycaenidae seem to be most badly in need of detailed work at all levels. Clench (1955) has begun such work with very detailed studies of the male protarsus and other organs. Although the morphological survey and nomenclatorial criteria adopted in the present work have indicated a more conservative treatment than that of Clench, his work seems to be a step in the right direction and the detailed revision which will follow his preliminary work should do much to correct the present situation.

The great mass of the lycaenids seem to divide neatly into the two classical categories "blues" (Lycaenidae auct.)

and "metal marks" (Riodinidae auct.) on the basis of correlated characters in the male prothoracic tarsi and the venation. As discussed earlier these two entities do not seem worthy of more than subfamily rank within the nomenclatorial framework of this work. Time and available material have not permitted an investigation of supra-generic categories within these subfamilies; doubtless many of Clench's groupings will have value there.

A third subfamily, Styginae, is recognized in the present work for the anomalous Styx infernalis Staudinger. The lycaenoid character of this insect (which has been placed both in the Pieridae and the "Riodinidae") seems almost beyond question (see diagnoses)<sup>15</sup>. The species is unique but close to the riodinines in the form of the mesothoracic anepisternum; close to the lycaenine Thestor in the structure of the male prothoracic leg<sup>16</sup>; unique in the form of the labial sclerite; unique in the occurrence of two recurrent veins in the cell of the forewing; and

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15. The male genitalia of Styx (fig. 63) are quite lycaenid-like.

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16. Clench (1955) reports fully developed (clawed) prothoracic legs in males of his subfamily Thestorinae. This is based on a detailed examination of (con't on next page)



perhaps unique in its tendency towards great variation and asymmetry in the anterior veins of the hindwing.

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\*Not seen.

Figures 1-8. Head. 1. Calinaga buddha Moore, front view; 2. Teinopalpus imperialis Hope, lateral view; 3. Same, dorsal view; 4. Papilio machaon Linnaeus, dorsal view; 5. Lycaena helloides Boisduval, front view; 6. Same, caudal view; 7. Same, dorsal view; 8. Phoebis sennae Linnaeus, dorsal view.

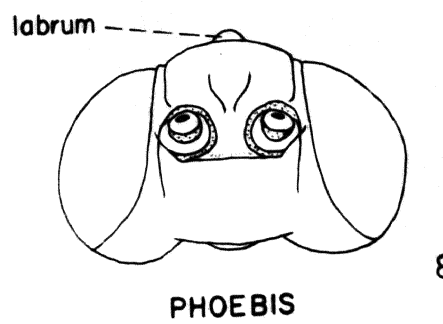
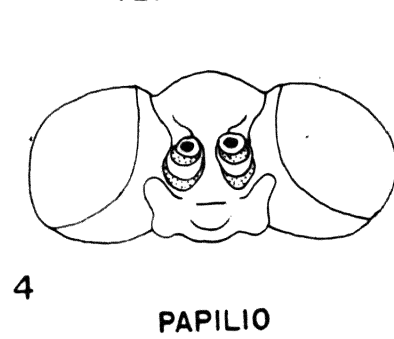
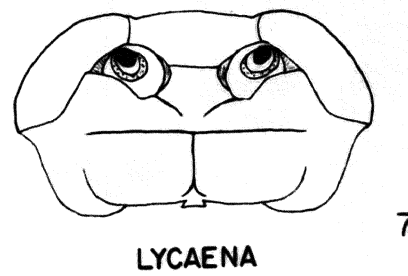
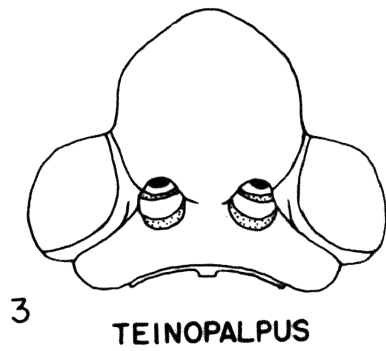
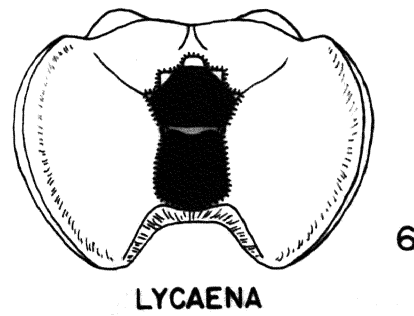
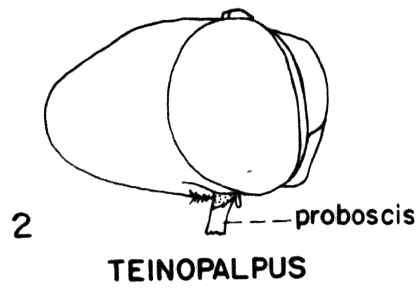
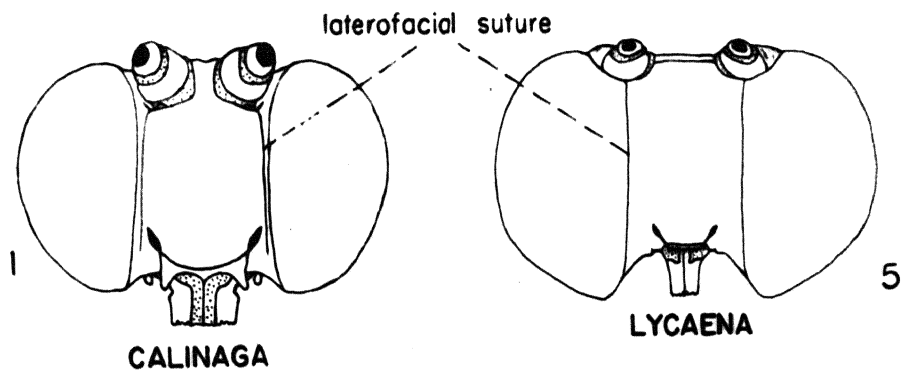
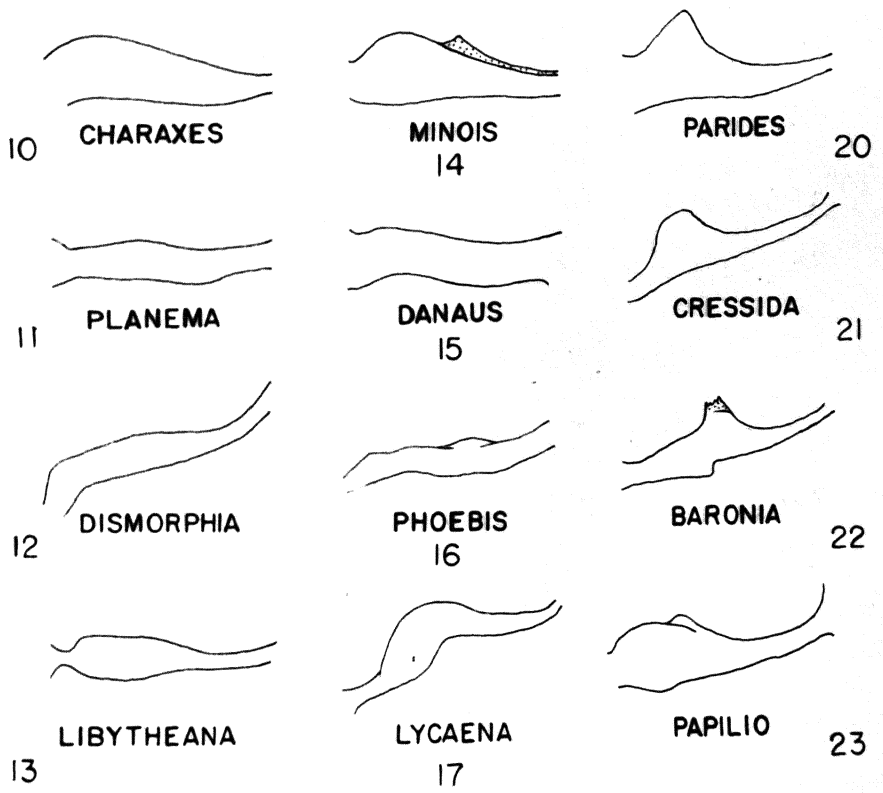
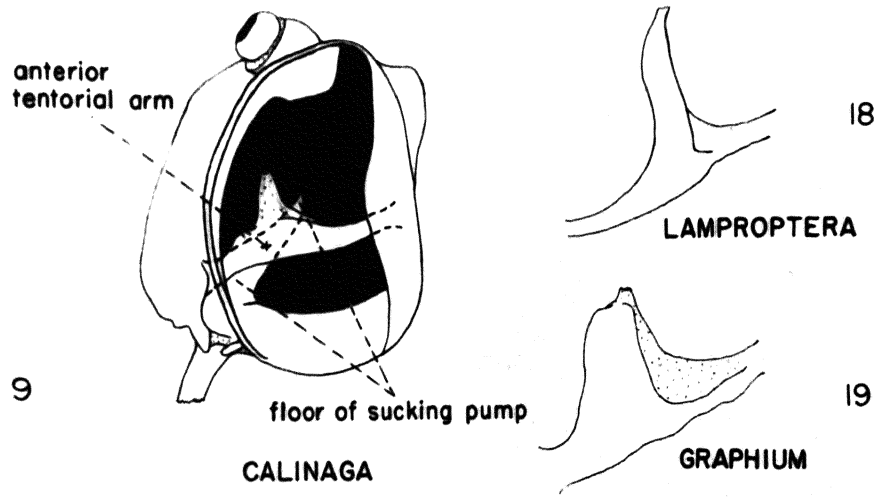


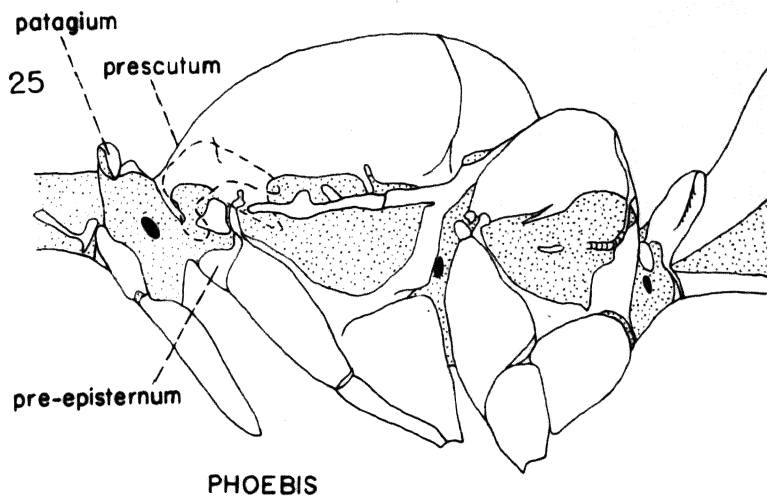
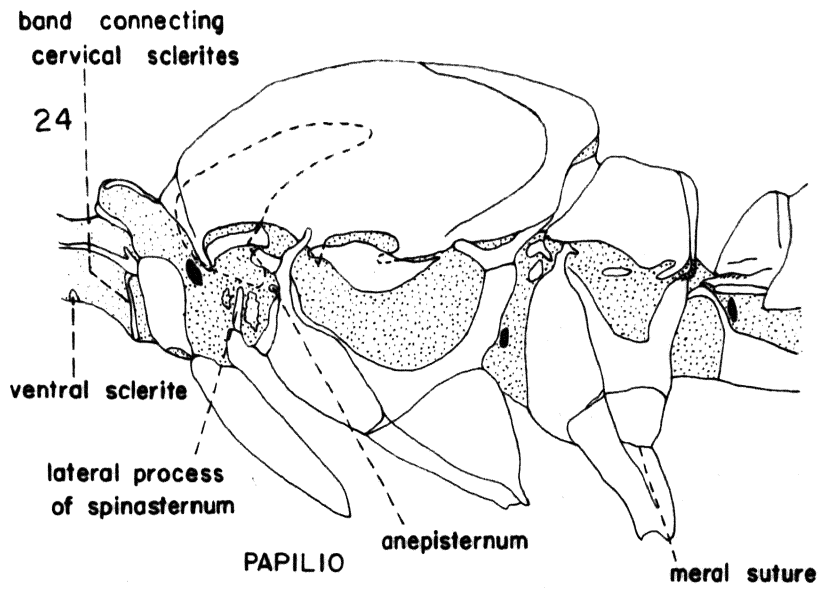
Figure 9. Calinaga buddha Moore, lateral view of head with eye removed to show position of anterior tentorial arm and floor of sucking pump. Figures 10-23. Lateral views of anterior tentorial arms, anterior end to left.

10. Charaxes brutus Cramer; 11. Planema aganice Hewitson; 12. Dismorphia nemesis Latreille; 13. Libytheana bachmanni Kirtland; 14. Minois pegala Fabricius; 15. Danaus plexippus Linnaeus; 16. Phoebis sennae Linnaeus; 17. Lycaena helloides Boisduval; 18. Lamproptera curius Fabricius; 19. Graphium sarpedon Linnaeus; 20. Parides polyzelus Felder; 21. Cressida cressida Fabricius; 22. Baronia brevicornis Salvin; 23. Papilio machaon Linnaeus.

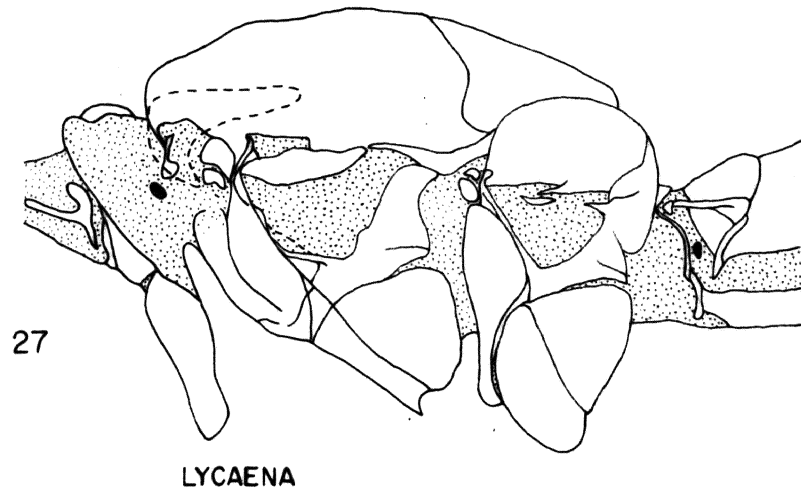
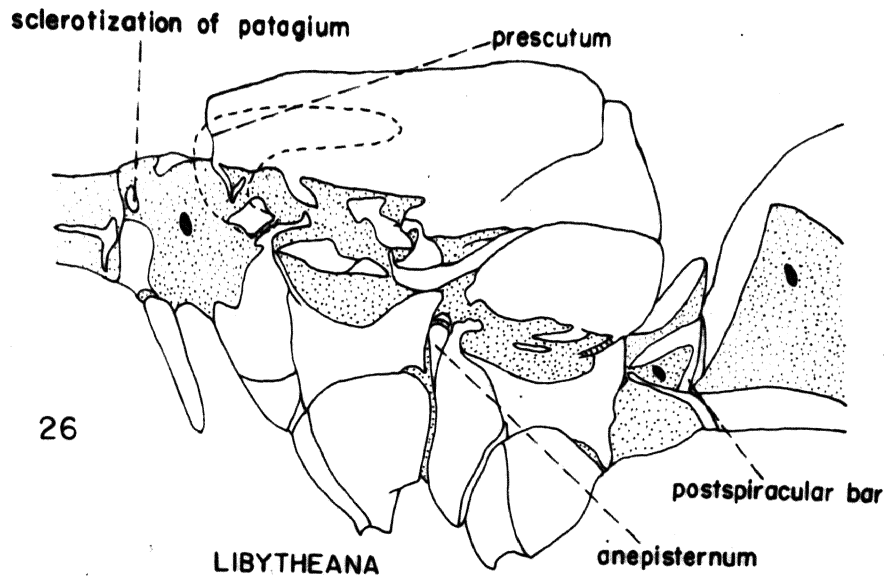




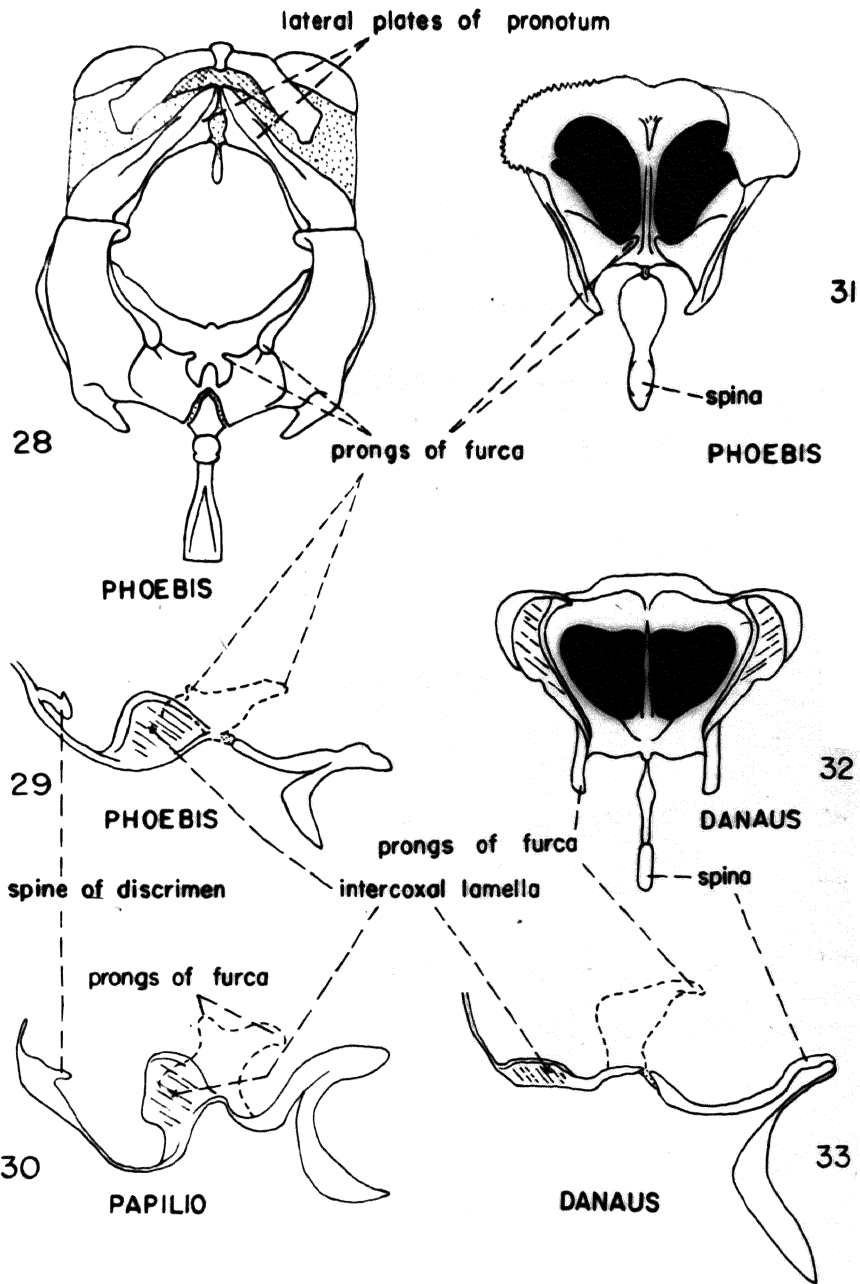
Figures 24, 25. Lateral views of cervix, thorax and base of abdomen. Tegulae shown by broken lines. 24. Papilio machaon Linnaeus; 25. Phoebis sennae Linnaeus.



Figures 26, 27. Lateral views of cervix, thorax,  
and base of abdomen. Tegulae shown by  
broken lines. 26. Libytheana bachmanni  
Kirtland; 27. Lycaena helloides.  
Boisduval

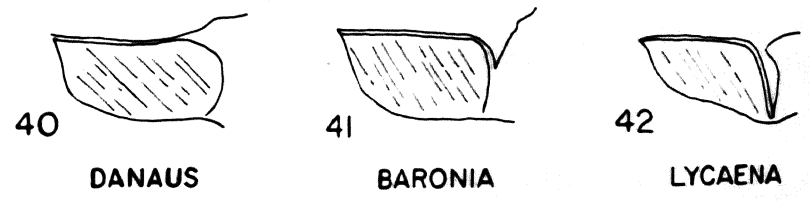
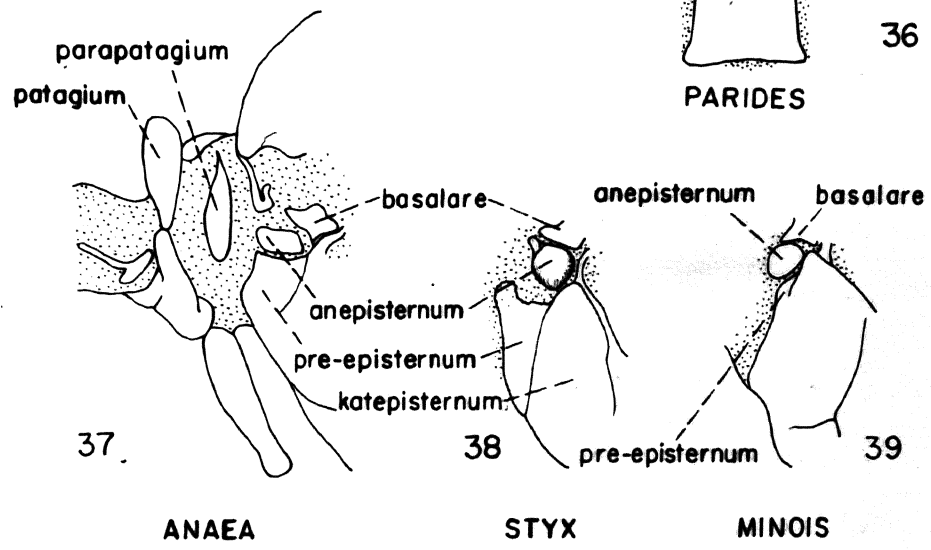
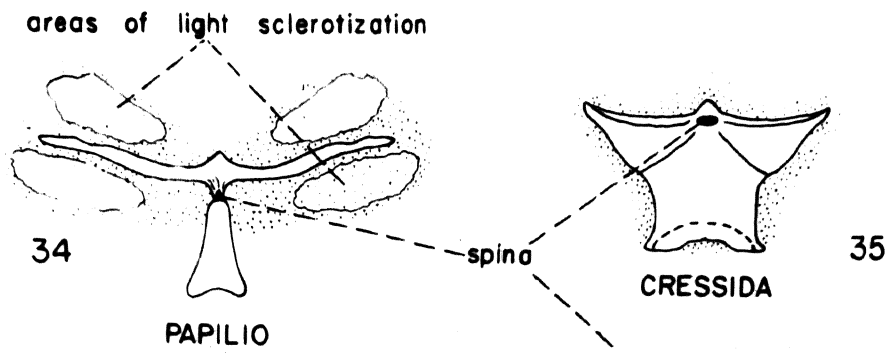


Figures 28-33. Prothorax. 28. Phoebis sennae Linnaeus, caudal (internal) view;  
29. Same, lateral view of structures of midline of pleurosternal area, position of furca shown by broken lines; 30. Papilio machaon Linnaeus, same view as fig. 29;  
31. Phoebis sennae Linnaeus, dorsal (internal) view of pleurosternal area, dorsal part of left pleuron removed, spinasternum caudal to spina not shown; 32. Danaus plexippus Linnaeus, dorsal (internal) view of pleurosternal area, spinasternum caudal to spina not shown; 33. Same, same view as fig. 29.



Figures 34-36. Ventral views of spinasterna.

34. Papilio machaon Linnaeus; 35. Cressida cressida Fabricius; 36. Parides polyzelus Felder. 37. Anaea andria Scudder, lateral aspect of cervix, prothorax and cephalic portion of mesothorax. Figures 38, 39. Lateral views of front portion of mesopleural area. 38. Styx infernalis Staudinger; 39. Minois pegala Fabricius. Figures 40-42. Lateral views of lamella of mesodiscrimen (semi-diagrammatic). 40. Danaus plexippus Linnaeus; 41. Baronia brevicornis Salvin; 42. Lycaena helloides Boisduval.





Figures 43-52. Outline of tegulae, anterior end upward, ventral side to the left. 43. Papilio machaon Linnaeus; 44. Ithomia cleora Hewitson; 45. Danaus plexippus Linnaeus; 46. Caligo sp.; 47. Calinaga buddha Moore; 48. Charaxes brutus Cramer; 49. Speyeria cybele Fabricius; 50. Planema aganice Hewitson; 51. Styx infernalis Staudinger; 52. Lycaena helloides Boisduval. Figure 53. Morpho achilles Linnaeus, caudal view of right mesomeron and postcoxal sclerite. Figure 54. Phoebis sennae Linnaeus, caudal view of metathoracic pleurosternal region. Figure 55. Ornithoptera priamus Linnaeus, caudal view of metathorax (line with short cross lines indicates attachment of intersegmental membrane). Figures 56, 57. Prothoracic legs. 56. Papilio machaon Linnaeus; 57. Apodemia nais Edwards.



43  
PAPILIO



44  
ITHOMIA



45  
DANAUS



46  
CALIGO



47  
CALINAGA



48  
CHARAXES



49  
SPEYERIA



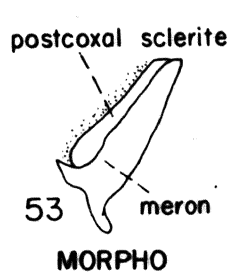
50  
PLANEMA



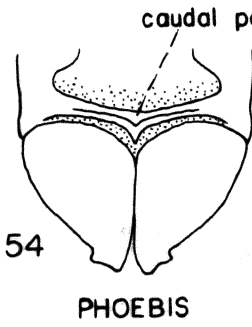
51  
STYX



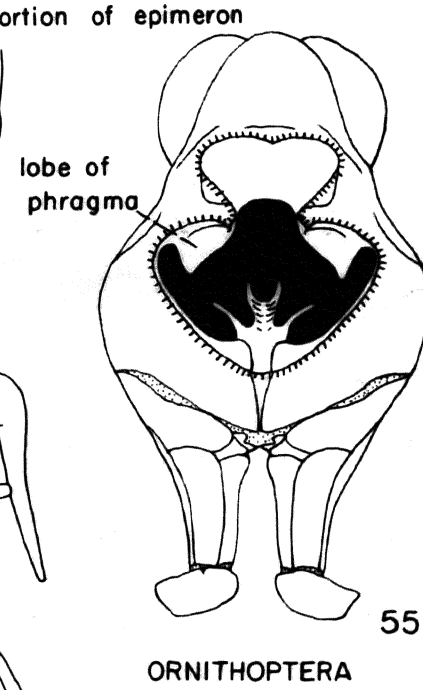
52  
LYCAENA



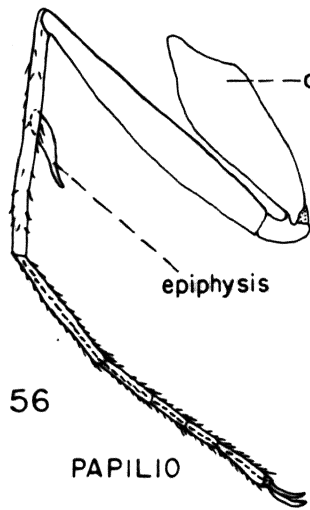
53  
MORPHO



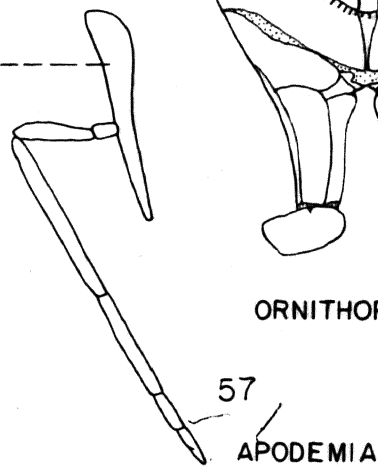
54  
PHOEBIS



55  
ORNITHOPTERA

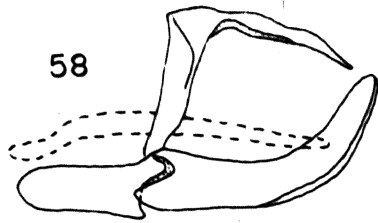


56  
PAPILIO



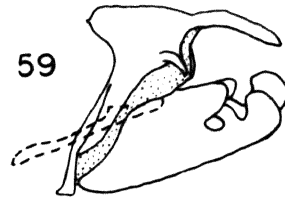
57  
APODEMIA

Figures 58-63. Lateral views of male genitalia,  
aedeagus shown by broken lines. 58. Acraea  
protea Doubleday and Hewitson; 59. Pardopsis  
punctatissima Boisduval; 60. Minois pegala  
Fabricius; 61. Charaxes brutus Cramer;  
62. Calinaga buddha Moore; 63. Styx infer-  
nalis Staudinger.



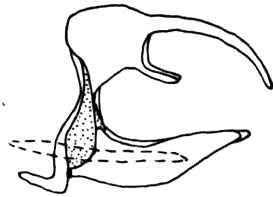
58

ACRAEA



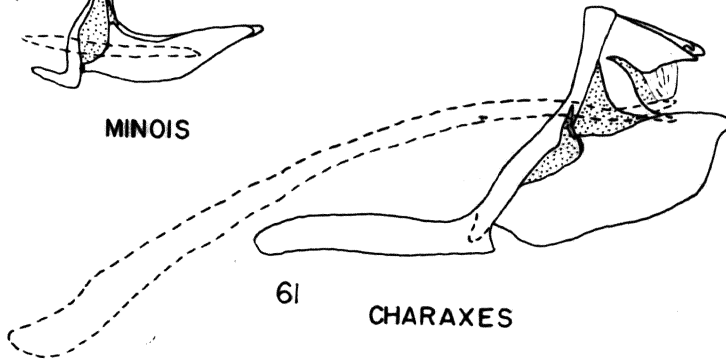
59

PARDOPSIS



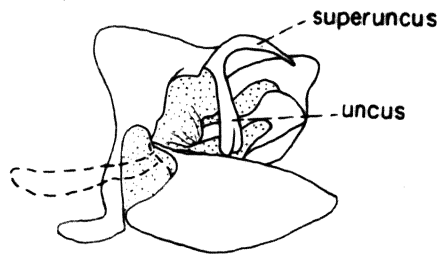
60

MINOIS



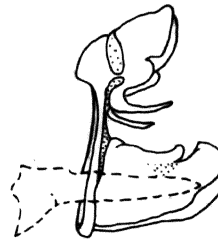
61

CHARAXES



62

CALINAGA



63

STYX

Figure 64. Relationships of the families and sub-families of the butterflies.

