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THE MORPHOLOGY OF ESTHIOPTERUM DIOMEDEAE (FABRICIUS) (MALLOPHAGA)

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This paper is the seventh of a series in which it is proposed to consider the morphology of representatives of various insect groups. It is, in addition, merely the first part of a larger study which is now in progress on the morphology of the Order Mallophaga. The diversity of form in this highly specialized Order is such that no one species can be selected which will afford a complete picture of all the developments that are to be found within the group and the best that can be done as a beginning is to find some species that will be advantageous as a starting point. For this purpose the species here considered, *Esthiopterum diomedeae* (Fabricius), has been selected, not necessarily because it represents one of the most generalized Mallophaga, but more because of the availability of material, its suitability of size, its definiteness of sclerotization and the absence of the more extreme modifications of structure which appear in some representatives of the Order. The family to which the species should be referred is doubtful. Depending upon which of the equally unsatisfactory systems of classifications is used, it may be referred either to the Lipeuridae or the Philopteridae.

It has proven to be a quite satisfactory species. Adopting the point of view which has been developed in earlier papers of this series, and with the aid afforded by the earlier paper on the morphology of a species of the Order Psocoptera, which the author prepared as a preliminary to the present work, this Mallophagan seems to offer no insuperable problems in comparative morphology.

A word may here be said in regard to earlier morphological work on representatives of this Order. Kellogg (1896), in a paper based mostly on work by Snodgrass, discussed and figured the mouthparts of several species. Snodgrass (1899) presented a paper in which he figured and described in detail much more than had been done by any earlier worker. This was followed by a paper in 1906, in which he somewhat revised his earlier opinions. Cummings (1913) and Harrison (1915) are the only other workers who have contributed materially to our knowledge of the morphology of the Order, although there have been references to bits of Mallophagan structure in various papers by other authors.

It should here be noted that throughout the present paper the author has based his conclusions primarily upon the female, departures from this practice being made only in those cases where the sexual dimorphism is important and where something is to be gained by study of nymphal structures.

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THE HEAD (FIGURES 54-57)

As in all Mallophaga, the head of this species is prognathous and is greatly modified by the dorso-ventral flattening that is characteristic of the Order. In this particular species, as in practically all of the suborder Ischnocera, to which it is ordinarily referred, there is an extreme production of the anterior portion of the head and in the region thus produced it is evident, as one glances over a series of species, that numerous secondary developments are present. So much is this true that it becomes difficult to determine the extent to which these secondary developments have obscured, or replaced, or perhaps even simulated, the original primary structures. In addition the interpretation of the head structures is complicated by the development of areas, bands and points of thickening and sclerotization of the wall of the head capsule. It is possible that in some cases these sclerotizations obscure sutures that are present, or they may at times lead to other misinterpretations. They are apparently not—or certainly not entirely—indices to the morphological composition of the head capsule.

In the face of these circumstances, it is necessary in attempting to arrive at any understanding of the Mallophagan head to focus attention closely upon those "landmarks" which experience has shown to be of special stability and of special significance. These primary landmarks are the anterior tentorial pits, the anterior and posterior mandibular articulations and the posterior tentorial pits. It is desirable also to have at hand and to keep in mind some obviously generalized heads such as those of *Machilis* and of a cockroach, these being especially helpful in revealing the primary relations of the anterior tentorial pits, the anterior mandibular articulation, the antennal foramina and the eyes.

The Head Capsule (Figures 54-55)

In using the "landmarks" for the determination of areas of the head capsule of this species the most helpful morphological point is the anterior articulation of the mandible. In all the pterygote insects in which the situation is at all clear, this articulation of the mandible is upon a short, lateral extension of the postclypeus. Consequently, in such a form as this Mallophagan, we are justified in assuming that the point at which this articulation occurs defines a point on the clypeus. This is here especially important, for the anterior tentorial pits, which would ordinarily be sought for first, are somewhat obscure and might even be regarded as doubtfully present. However, at each side of the head, just laterad of the anterior mandibular articulation and just anterior to the base of the antenna is a fold in the lateral margin which is ordinarily tightly closed but which can be opened in prepared specimens. This fold has back of it, internally, a sclerotized process which buttresses the mandibular articulation. Without much doubt this fold represents the anterior tentorial pit and the buttress is all that is present to be called the anterior tentorial arm.

It is evident, therefore, that the entire prolongation of the head, anterior to the anterior mandibular articulation and the tentorial pits, both dorsally and ventrally, is of clypeal and labral origin. Since there is no clypeo-frontal suture, the posterior limits of the clypeus are not defined and can be determined only roughly by the arrangement of muscles, which indicates a posterior limit somewhat as shown on the accompanying figures.

The antennae are set at the extreme side of the head slightly posterior to the anterior tentorial pits. The space between them and the pits forms a

narrow, sclerotized band about the anterior margin of the antennal foramen, this band apparently being derived from a portion of the gena or from the fused gena and lateral region of the frons. Because of the slit formed by the tentorial pits, this band assumes a somewhat lobe-like form. It is of special significance, since it forms a basis for the interpretation of the peculiar, movable lobes or flaps that occur at the base of the antennae in some other Mallophaga and that are commonly called the "trabeculae."

The eyes are formed of a single facet and are set at the extreme margin of the head, just behind the antennal foramina. From their position it seems clear that these single facets represent the compound eyes.

On the ventral side of the head, there is a broad, membranous region posterior to the mouthparts. The minute posterior tentorial pits are set far posteriorly, at the margins of this membranous area. In the membranous area between the tentorial pits is a broad plate which does not quite conform to the definition of a gular plate, since it is partially anterior to the pits, but which may be regarded as actually gular. The membranous area anterior to the gular plate may be assumed to belong to the labium.

Dorsally, extending posteriorly from the eyes to the posterior border of the head are lines marking the borders of sclerotized bands. At present it is not possible to regard these as anything more than merely secondary strengthening elements, although the occurrence of actual sutures or folds along similar lines in other insects indicates that there is a possibility of some more fundamental significance. The epicranial suture and its branches are entirely lacking, not only in the adult but in the last nymphal instar.

The cranium, therefore, is practically a solid box in which all evidence of the primary sutures has been lost and it is possible to identify the various regions only in general terms as indicated on the accompanying figures. Even the "occipital suture," which is usually to be seen, is here suppressed.

The Clypeus and Labrum (Figures 54, 57A)

Correlated with the prolongation of the clypeus and the flattening of the head are some peculiar developments. As has been stated, we accept the area between the bases of the antennae as representing the postclypeus. Toward the apex of the head is a conspicuous, curving suture which cuts off an apical sclerite and by a short lateral branch on each side also defines a small, lateral lobe. We have sought diligently to trace the ending of the posterior lateral branch, but as nearly as it has been possible to determine it ends blindly at the side of the head. The anterior branch continues to the ventral side of the head and passes posteriorly as the mesal margin of a sclerotized, lateral area which bears the anterior articulation of the mandible.

The identity of this suture is open to question. There are three possible interpretations. It may be the clypeo-frontal suture. It may be the clypeal suture between postclypeus and anteclypeus. It may be the clypeo-labral suture. Upon the interpretation adopted depends the interpretation of the apical sclerite.

A longitudinal section of this area reveals sets of muscles which are very similar to those found typically within the clypeus, as shown by Snodgrass (Principles of Insect Morphology, figure 155). If the suture is the clypeo-frontal, we must assume that the dorsal (= anterior) origins of all the intraclypeal muscles have shifted posteriorly to the frons. If it could be shown that the posterior lateral branch of this suture continues posteriorly to the tentorial pit we might be forced to accept such an interpretation. But, as has been pointed out, we have been unable to determine that this happens. With this possibil-

ity eliminated, the transverse dorsal suture becomes either the clypeal or clypeo-labral and the plate anterior to it becomes either the anteclypeus or the labrum.

With either of the two last possibilities, the little lateral lobes—which in some Mallophaga become extremely prominent features, but in others are entirely lacking—must be interpreted merely as secondary lobes of the postclypeus.

Before the question of the identity of the terminal plate may be decided it is necessary to discuss the features of the ventral side of the anterior prolongation of the head.

It has been noted that on each side the dorsal transverse suture passes to the ventral side and posteriorly as the mesal margin of a sclerotized lateral area which bears the anterior articulation of the mandibles. Bearing in mind the normal articulation of the mandible anteriorly to the postclypeus it seems that this lateral area on each side is undoubtedly a portion of the postclypeus.

The median region, between the arms of the postclypeus, presents some peculiar developments. Anteriorly, beneath the apical plate it is slightly sclerotized. Posterior to this is a prominent pad-like lobe, which has no lumen and which is not sclerotized (Figure 57A). This lobe occurs in many of the Ischnocera, but it apparently has no name and consequently we here designate it as the *pulvinus*. Caudad of this and crowded between it and the mandibles is a narrow band of sclerotization which bears a few setae and which laterally is prolonged posteriorly into a little sclerotized arm (Figures 54B, 55C).

It would appear at first glance that the little sclerotized band in front of the mandibles represents the labrum. If such an interpretation is adopted the apical plate of the head becomes the anteclypeus. But if it is adopted we encounter certain difficulties. We must first of all assume that the labrum has become separated by an extensive membranous area from the anteclypeus and has migrated to the oral face of the postclypeus to which it has become attached laterally by membranous connections. We must regard the pulvinus as a development from the membrane that morphologically belongs to the clypeo-labral suture. And we must admit an extraordinary bending and distortion of the anteclypeus.

If we interpret the apical plate of the head as the labrum, we must then adopt the opinion that the anteclypeus is lacking and that all the developments in the median region of the ventral aspect are epipharyngeal in origin. The only disturbing questions have to do with the appearance of setae on the little plates anterior to the mandible, which are morphologically almost within the mouth and in the fact that a structure similar to these plates appears throughout the suborder Amblycera in a position such as to indicate that it is the labrum. However, it is quite evident that the cephalic structures of the Amblycera have developed along lines which are very different from those found in the Ischnocera and they remain still to be explained.

In the light of all the facts known to us and of the considerations that have been presented the opinion here adopted is that the anteclypeus is lacking as a separate plate, that the suture in question is the clypeo-labral suture, that the apical plate is the labrum and that the pulvinus and the sclerotizations anterior to the mandibles on the ventral side are developments from the epipharynx.

The Tentorium (Figures 54, 55)

The tentorium is very much reduced. As has been pointed out, all the tentorial pits are present, the anterior pits forming a marginal slit-like fold just anterior to the antennal base and the posterior pits being situated at the

margin of the gular region on the ventral side of the head. The anterior arms are represented only by short, heavily sclerotized, buttress-like structures which strengthen the body wall laterad of the mandibular bases, while the posterior arms are slender, almost thread-like processes which extend forward into the head lumen and are not connected with each other or the anterior pits.

The Antennae (Figures 54, 55)

The position of the antennal foramina at the extreme lateral margin of the head conforms to what seems to be characteristic of generalized insects. It is essentially the same position as is found in the cockroach, for example. An extreme sexual dimorphism is exhibited by the antennae of the species here considered and in many other members of its suborder. In this species the antennae of the female are of the simple, filiform type, with five segments. The antennae of the male have the same number of segments, but the first segment is enormously enlarged and elongated and bears a spine-like lobe on the anterior margin near the base; the second segment is smaller but is curved; the last three segments are quite small. The whole structure is curved forward and upward, and the antennae function as grasping organs to hold the female during copulation.

The Eyes

The eyes consist each of a single facet, which is set just posterior to the antennal base. From their position, which corresponds closely to that of the eyes in such forms as the cockroaches, it may confidently be assumed that they represent the compound eyes. No trace of ocelli appears.

The Mandibles (Figures 55C, 57B)

The structure and mechanics of the mandibles are fairly well known, Kellogg (1896) and Snodgrass (1899, 1905) having described and figured them in various species. The mandibles of the species here considered are large and heavy and each is excavated along its posterior side, the excavation receiving and partially enclosing the apex of the corresponding maxilla. The articulations are so arranged that the movement of the mandibles is in a dorsoventral plane and through an arc of almost 90 degrees.

The Maxillae (Figure 57D)

The maxillae are greatly reduced, each consisting merely of a short, basally somewhat constricted cylinder which is strengthened by sclerotization of parts of its walls and which terminates distally in a slightly bulbous enlargement that is mostly membranous and which bears two small lobes. An apodeme is present which inserts about halfway up the maxilla and is probably that of what is ordinarily the cranial flexor muscle of the maxilla. Further homologies are undeterminable.

The Labium (Figures 54B, 57C)

The labium likewise is very much reduced. The portions which may be assumed to represent the mentum and submentum are entirely membranous. Apically there are present a pair of structures which seem to represent one-segmented palpi. Between the bases of these is a pair of very low apical lobes, which are strengthened by small, sclerotized plates and which represent either the glossae

or paraglossae. The opinion is here tentatively adopted that they are paraglossae, since in most insects the glossae tend to disappear sooner than do the paraglossae. On both oral and aboral aspects of the prelabium there are present small areas of sclerotization which presumably represent vestiges of the normal sclerites but which can hardly be designated by names.

The Hypopharyngeal Region (Figure 56)

The structures of the hypopharynx and associated organs appear to be directly homologous with those found in the Psocoptera. Cope (1940), working with *Psocus confraternus*, developed the view that the large lobe anterior to the labium in members of that Order is not the hypopharynx, as had previously been held by other authors, but is merely a secondary lobe of the oral face of the labium. Such a lobe is present in *Esthiopterum* and some other Mallophagans, but in a much reduced form. The so-called "oesophageal sclerite" is considered to be a development of the salivarium, since the salivary duct empties directly into it. No basal sclerites are present in *Esthiopterum*, so the only truly hypopharyngeal element is the membranous region between the orifice of the salivary duct and the stomodeum. The sclerotized sacs lying in the head cavity, partly in the labium and partly in the lobe anterior to the labium are considered here, as in the Psocoptera, to be salivary reservoirs, and the tubes leading from them and joining medially are the salivary ducts. The structure called the "brush" on the anterior lobe of the labium in the Psocoptera is not present in *Esthiopterum*.

THE CERVIX (FIGURES 58-61)

The head and prothoracic elements being rather closely approximated, the cervical region is much reduced. The usual two pairs of cervical sclerites are present, the more anterior pair articulating with the back of the head and being situated dorsally. The second pair articulates anteriorly with the first pair and posteriorly with the episternum of the prothorax.

The gular plate (Figure 54B) has encroached to some degree upon the cervical region, but is evidently not a cervical structure.

THE PROTHORAX (FIGURES 58-62)

The prothorax, as in apparently all other Mallophaga, is definitely separated from the pterothorax. Its dorsum is formed from a single large notal plate which is but little produced downward at the sides and which is in no degree fused with the pleural (= subcoxal) elements.

The dorsal arc of the subcoxa, constituting what are commonly called the pleural sclerites, is extremely well developed. Above the coxal condyle is the usual pleural fold, dividing the pleurite into an anterior episternum and a posterior epimeron. The episternum shows no division into anepisternum or katepisternum and is not continued ventrally into a precoxal arc. Anteriorly it articulates with the posterior cervical sclerite. The epimeron is unusually enlarged and extends in an arc down behind the coxa to the ventral side of the body. Here it terminates just short of the meson, where it bears the ventral articulation of the coxa. Slightly posterior to and laterad of this articulation is the sternal apophyseal pit, which here is definitely involved in the subcoxa. From the termination of the postcoxal arc to the beginning of the episternum the

derm is membranous and there are no suggestions of the presence of any sclerotized element that can be called the sternite.

The metathoracic spiracle, in addition to migrating forward to the prothorax, as occurs in many insects, is here involved within the posterior limits of the epimeron.

THE PTEROTHORAX (FIGURES 58-62)

The segments of the pterothorax show a high degree of modification which is associated chiefly with the close union of the two segments and with shifts in proportions of the various parts, in the angle of the metathoracic pleural elements and in the position of the sternal apophyseal pits. The fusion of the segments has been carried to such a degree that it is difficult, if not impossible, to indicate definitely all of the line of segmental division.

The dorsal areas (Figure 58)

The notal elements of the two pterothoracic segments are completely fused, so much so that there is no external evidence as to how much of the single notal plate originates from either segment. However, it seems evident that both segments are represented on the dorsum, since muscles from meso- and metathoracic legs originate on the notum. Associated presumably with the absence of the wings, the elaborate structures of winged insects are entirely lacking, no divisions into the parts commonly found can be recognized and there is no development of postnotal elements or of phragmata. The dorsal plate can be indicated only as the notum, although presumably it is composed principally of the scuta.

The pleural areas (Figure 59)

The pleural (= subcoxal) elements of the two pterothoracic segments exhibit a marked diversity of development and arrangement. The mesothorax bears a very small episternal plate which carries the dorsal coxal articulation, with the pleural fold not evident, the epimeron lacking and a reduced pleural apophysis present. Ventrad of the coxal foramen is a small, somewhat rectangular plate which articulates by a definite condyle at its extreme anterior margin to the coxa, is somewhat produced posteriorly and bears the sternal apophysis at its mesal border. If we assume this ventral coxal articulation to be identical with that seen in the Neuropteroid series of Orders, this plate is evidently a fragment of the ventral arc of the subcoxa, and since most of it is posterior to the point of articulation it must belong to the postcoxal portion of this arc.

The metathorax, on the other hand, has the subcoxal elements very strongly developed, but their vertical axis has turned forward until it is nearly or quite parallel to the longitudinal axis of the body. From the dorsal coxal condyle the pleural fold extends anteriorly, dividing the "pleurum" into an exceedingly narrow, morphologically posterior, band which is evidently the epimeron and a very broad, morphologically anterior, piece which is evidently the episternum, that extends downward to the ventral side of the body. There is no apparent division into anepisternum and katepisternum, the pleural cleft being entirely obliterated. The pleural apophysis is exceedingly small (Figure 59B) and invaginates just above the coxal condyle. The metathoracic spiracle is present, although it is lacking in most of the Mallophaga. It occupies a most peculiar position. It should be remembered that typically this spiracle lies at the

anterior border of its segment. But here it is involved in what morphologically —after making allowance for the forward tilting of the vertical axis of the subcoxa—is the posterior border of the segment, an extraordinary shift of position. This situation, coupled with the fact that in apparently the majority of the Mallophaga, if not in all of them other than the family to which the species here considered belongs, the metathoracic spiracle is lacking, requires examination.

One explanation which immediately comes to hand is the assumption that this spiracle is actually that of the first abdominal segment, which has migrated forward and become involved with the metathorax, much as the mesothoracic spiracle has migrated to the prothorax. Unfortunately, in contradiction of any such assumption stands the fact that no first abdominal spiracle is present even in forms in which this spiracle is lacking on the metathorax.

The piece which must be called the episternum is much elongated and extends forward to a point just posterior to the mesothoracic coxal foramen and downward to the ventral side where it occupies the lateral third of the ventral aspect. It bears a definite articulation with the anterior, ventral margin of the coxa, which from its position suggests that it may be the trochantinal articulation, although no trochantin is present as a separate piece. By analogy with the mesothorax, however, this is here considered to be the ventral articulation. Close to the ventral margin of the episternum and some distance forward from the ventral articulation is the very minute metathoracic sternal apophyseal pit. There is no trace of any portion of the postcoxal part of the ventral subcoxal arc.

The Sternal Areas (Figures 60, 61)

It is here considered that a true sternum exists on the pterothorax, this being a single large, elongate plate which occupies the median third of the ventral aspect and is separated from the subcoxal elements by distinct, membranous areas. It is quite evident that an extreme modification of the generalized condition of the pterygote insects has developed. In earlier papers in this series it has been maintained that the sternal apophyses of pterygote insects are primitively invaginations between the ventral arcs of the members of each pair of subcoxae and that consequently their primitive position was close together on the midline of the body. It has also been maintained that when the members of the pairs of apophyses are separated from each other this separation has occurred by reason of their migration laterally and that it is under such conditions that a median plate forms which can be regarded as genuinely sternal. These conditions are here completely fulfilled and the median plate may be regarded as definitely and genuinely the sternite. We have here, however, one peculiar development, in that the apophyses of all three of the thoracic segments have remained during their migration attached each to the mesal border of its corresponding subcoxa, rather than becoming involved in the margin of the sternite. Such a development seems to be characteristic of the Mallophaga as a group.

It will be noted that there is but a single sternal plate on the pterothorax. It could not be determined from the material at hand whether or not this plate represents the fused sterna of the two pterothoracic segments or whether it belongs only to the metathorax and the mesothoracic sternite is suppressed. The evidence derived from the muscles, however, suggests that a mesothoracic element remains in this plate, for muscles from both pairs of legs arise upon it. Furthermore, in some related species the mesothoracic sternal apophyses arise from the sternal plate, this also indicating the presence in it of a mesothoracic element. It is in all probability a compound structure.

The Legs (Figures 62C, D)

The prothoracic legs are short and stout, lying with the distal ends carried up under the head. Coxa, trochanter, femur, and tibia are quite normal, but the tarsus is reduced to a single segment. The ungues are attached to the tarsus without unguitractor plate, pulvilli, or empodia. Setae and spines accompany the ungues on the tarsus. (Figure 62C.)

The mesothoracic and metathoracic legs are essentially alike, but differ from those of the prothorax in being considerably longer and in being carried in a more lateral position. The same elements are present here as in the prothorax, with larger spines on the mesothoracic and metathoracic legs.

All legs possess thickenings in their walls which appear as double contours of various shapes.

No particularly large trochantinal apodemes are present, and no trochantinal signum is evident.

THE ABDOMEN (FIGURES 63-64)

Some confusion as to the actual size and position of the sclerites of the abdomen may arise because of the presence of areas of pigmentation which do not correspond with and do not indicate the limits of actual sclerotization. An attempt has been made (Figures 63, 64) to indicate the relation of the pigmented areas to the actual sclerites. The pigmented areas have been indicated by shading one or more areas and enclosing others of the same type within broken lines.

Nine apparent segments are present in the abdomen of both male and female. From the position of the spiracles and the vulva of the female, it is evident that in the adult of this sex spiracles are present on the third to eighth segments and that the first abdominal segment is entirely suppressed. In each sex two apparent segments occur posterior to the gonopore, but it is clear from what takes place during development that these two segments are not exactly the same in the two sexes. It is desirable at this point to revert to the nymph for a better understanding of the morphology of this region.

Wilson (1936), in a paper on the life history of *Lipeurus heterographus* (Nitzsch), has concluded that at the third molt the ninth and tenth segments fuse, thus reducing the number of apparent segments. This observation is in part substantiated by the present author's observations. A last instar nymph, which seems to be that of a female, bears three segments posterior to that which, because of the arrangement of the spiracles, is evidently the eighth. The adult female, however, shows but two apparent segments in a similar position. It seems certain either that there has been a fusion of the ninth and tenth segments or that one segment has been suppressed. In the light of Wilson's work on chaetotaxy and the fact that the apparent ninth segment of the adult is relatively larger than the true ninth and tenth in the nymph, it is here believed that fusion has occurred.

However, the segmentation of the male presents a problem which can not be solved on the basis of the material and information now available. No male nymph is available in the material at hand, but if such a nymph bears the same number of abdominal segments as does that of the female and if the ninth and tenth segments fuse to form the apparent ninth segment in the adult, the question arises as to the fate of the gonopore, which belongs morphologically to the area between the ninth and tenth segments, and appears in its apparently normal position in the adult male of this species. In the adult male there is but one

segment posterior to the gonopore, which is evidently either the tenth and eleventh fused—instead of the ninth and tenth as in the female—or is the tenth segment with the eleventh reduced to a membranous condition. It is possible that the nymph of the male has one less segment than does that of the female, but until this point is settled some uncertainty as to the exact situation in the terminal segments of the adults remains.

In any case, whatever the exact disposition of the terminal segments, it seems clear that the first segment is entirely suppressed in both sexes, no trace of either its tergite or sternite remaining. In the succeeding segments the tergite extends around the margin of the body to the ventral side, where it is separated from the corresponding sternite by an area of membrane. Distinct sternal plates are present on segments 2-9 in both sexes.

A feature of the abdomen which appears in many Mallophaga and is extremely well represented in the species at hand is the occurrence of thickenings of the body wall, generally at the extreme lateral margin. These thickenings project into the body cavity in the angle formed by the sharp bending of the tergite around the lateral margin of the body and are usually so deeply pigmented as to be clearly visible externally. As far as the author knows no name has been suggested for these structures in the past and they are here called *buttresses*.

It should be noted that extreme diversity of form is shown by the buttresses from segment to segment of the same sex and between corresponding segments of the opposite sexes. In some cases buttresses are present on the sternites, as is strikingly shown on the second abdominal sternite of the species here considered, where they resemble a pair of apophyses that extend upward to lie adjacent to the buttresses of the tergite of the same segment (Figures 59-61).

Terminalia of the Female (Figures 65A, B, C)

Reduction and simplification of parts has gone far in the case of the terminal segments and genitalia of the female of this species, modification beginning with the seventh segment. Here the sternite is deeply emarginate posteriorly. On the eighth segment the sternite is divided medially into two parts, each of which bears a lobe that may be regarded as representing a gonopod, the two gonopods fused to each other distally and bearing apically a brush of stiff setae. Internally, invaginating from the vulva, which is between the eighth and ninth segments is a bulbous genital chamber the walls of which show a peculiar pattern of sclerotized lines.

The 9th + 10th segment has the sternite, which must belong actually to the ninth segment, divided longitudinally into two very small plates. The terminal segment, which seems to be the eleventh bears a pair of small plates which are here regarded as the paraprocts.

Terminalia of the Male (Figures 65D, 66)

In the male, modification of the segments begins with the ninth sternite, which is much reduced in size and forms a small, posteriorly pointed median genital plate, the opening of the phallocrypt being just posterior to its apex. The tenth segment, as is normal, bears no sternite, but the tergite is produced ventrad in the form of narrow points and dorsally is narrowed and produced posteriorly. The anus lies immediately beneath the apex of this point and there is no evidence of paraprocts.

The genitalic apparatus (Figure 66) is quite simple, apparently more so than in most of the Mallophaga. There is no evidence whatsoever of coxopodites

or styles, or even of the disputed structures commonly called parameres. The phallus is retracted into the body, a phallocrypt being formed, the walls of which form the endotheca and are membranous. These walls then fold posteriorly again, closely enveloping the endophallus to which they fuse at the apex of the latter. The endophallus is formed primarily by another infolding, the walls of which are partially sclerotic, this infolding forming a sac which extends into the body until it merges with the ejaculatory duct. The sclerotization of its wall extends proximally for about half the length of this sac, then splits into two parts which become free from the sac, pass around it on each side and reunite again ventrad of the sac to form a long basal apodeme upon which muscles insert that serve to withdraw the phallus into the body after it has been exserted by blood pressure in copulation.

Unfortunately, this species throws no light upon certain genitalic structures of the male which occur in many other Mallophaga and the examination of other more suitable species will be necessary to permit any complete understanding.

THE RESPIRATORY SYSTEM (FIGURES 62, 64)

Harrison (1915), in a rather comprehensive investigation of the respiratory system of the Mallophaga, presented certain conclusions which are partially untenable in the light of the facts here presented. Harrison voiced the general statement that "In all Mallophaga except *Gliricola* and *Trimenopon* there are seven pairs of stigmata, one prothoracic and six abdominal."

The so-called prothoracic spiracles are, in the light of generally accepted evidence, morphologically of mesothoracic origin. As herein pointed out, a pair of spiracles is certainly present on the metathorax at least of the family to which the species here considered belongs, although these spiracles occupy a peculiar position. Furthermore, there are more than six pairs of abdominal spiracles present in the nymph of the species here considered, a pair of reduced spiracles occurring on the tergite of the morphologically second segment (Figure 64B) making the total number of pairs for the body of the nymph nine and for the adult eight.

The complete tracheal system has not been worked out in connection with the present paper, but the general features of the tracheal trunks in the thoracic region are shown in Figure 62. In general there is agreement in this portion with the conditions considered by Harrison to represent the generalized situation in Mallophaga, other than in the factors involving the presence of the metathoracic spiracle.

The Spiracles (Figure 62B)

The thoracic spiracles, in the main, follow the general form of homologous structures in other insects, consisting of a modified slit-like orifice. The mesothoracic spiracle bears an elongated slit which is beset with spines extending inward from the lips of the slit, giving the impression of a filtering apparatus of some sort. The metathoracic spiracle contains a bulbous sclerotized sac which lies beneath the body wall.

The abdominal spiracles are essentially all of the same form, being merely a pit-like depression with an orifice in the bottom. An arm-like extension is seen below the surface of the adjacent body wall which appears to be part of the occluding apparatus of the spiracle. This occluding apparatus has not here been considered in detail.

GENERAL OBSERVATIONS

Aside from the loss of the wings, the principal modifications of structure involving anything more than the loss or fusion of parts are to be found the head and thorax.

The extreme flattening of the head, the reduction of the eyes, the great duction of all the mouthparts except the mandibles, the prolongation of the ypeal region anteriorly and the development of peculiar structures in the ipharyngeal membrane, are striking features but have actually involved but ttle digression from the normal pattern of the generalized insect head as seen such forms as the cockroaches. The landmarks, with the exception of the occipital suture and a few other sutures, are all in place.

The thorax presents most extreme modifications but yet is clearly comrable with that of such insects as the Neuropteroids that have been considered earlier papers of this series. In fact, on the basis of a comparison with ese Neuropteroids there is little in the thorax of this Mallophagan that reins difficult to interpret, the only doubts, in fact, involving the exact mits of the segments in the fused notal and sternal parts. The most peculiar ature is the separation of the members of the pairs of sternal apophyseal pits d the retention of these pits within the ventral arcs of the subcoxae, a feare that seems to be in some degree developed in and characteristic of all the llophaga. The single large sternal plate of the pterothorax, involving probly a fusion of the secondarily developed sternites of both segments is a riking peculiarity.

The retention of the ventral coxal articulation on the prothorax is an tremely peculiar feature which, as far as is at present known, is confined to e Mallophaga and the Psocoptera.

Although there is nothing to be seen in this Mallophagan which tends to ny the assumption of some relationship between this Order and the Psocoptera, ere are but few facts which definitely support the belief in such a relationip. The common possession of what is commonly called the "pharyngeal sclete," which is here considered to be a development from the salivarium, and e common retention of the ventral coxal articulation on the prothorax are all at appear in this species and the winged Psocopteran previously considered in is series.

However, these particular species do not by any means tell the complete story of the morphology of either the Psocoptera or the Mallophaga. cursory examination of such a Psocopteran as a species of the wingless genus *-octes* shows developments which are very different from anything that is to be en in the winged forms and other Mallophaga show features, such as the presce of the "maxillary pick," which are not indicated in the single species here nsidered. Several more species of each Order must be treated in detail before shall have any understanding of their morphology which will be sufficient to rmit any broad generalizations.

The morphology of the Mallophagan here considered is offered merely as an troduction to the morphology of the Order, but this species affords a favorle port of entry into the work that still remains to be done.

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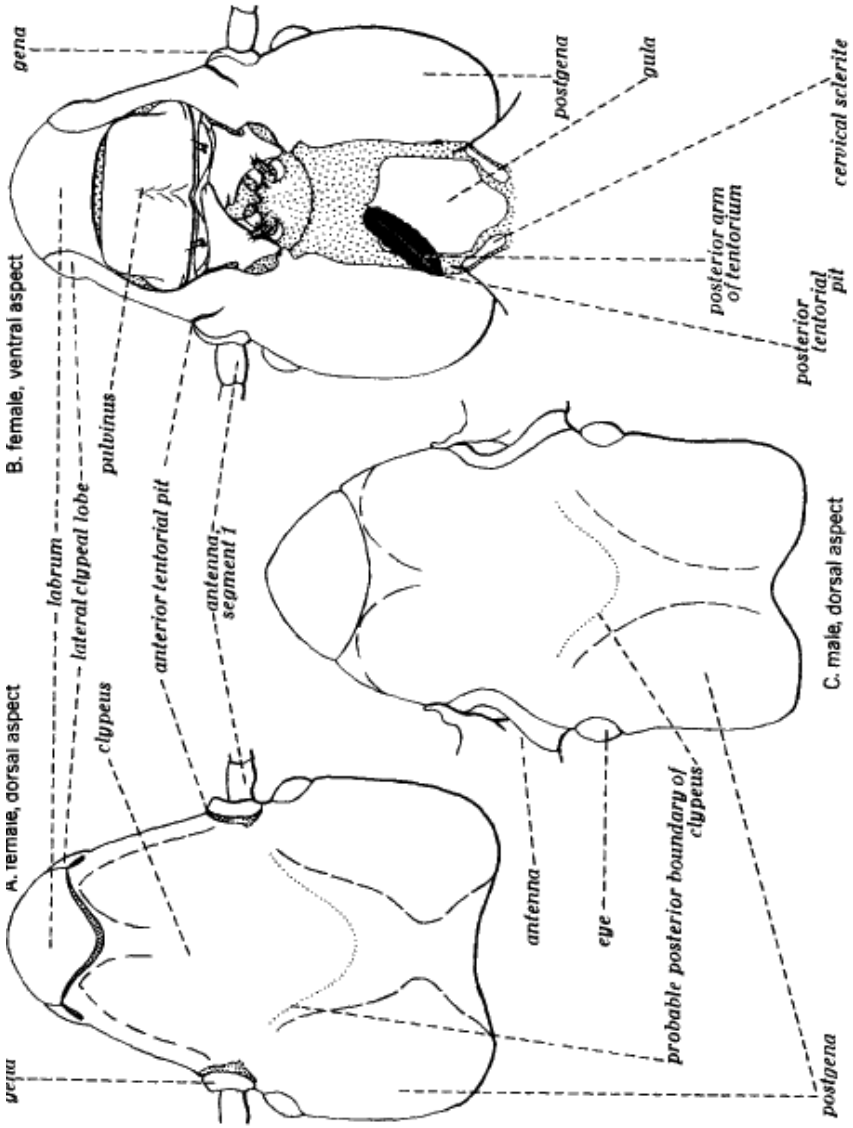
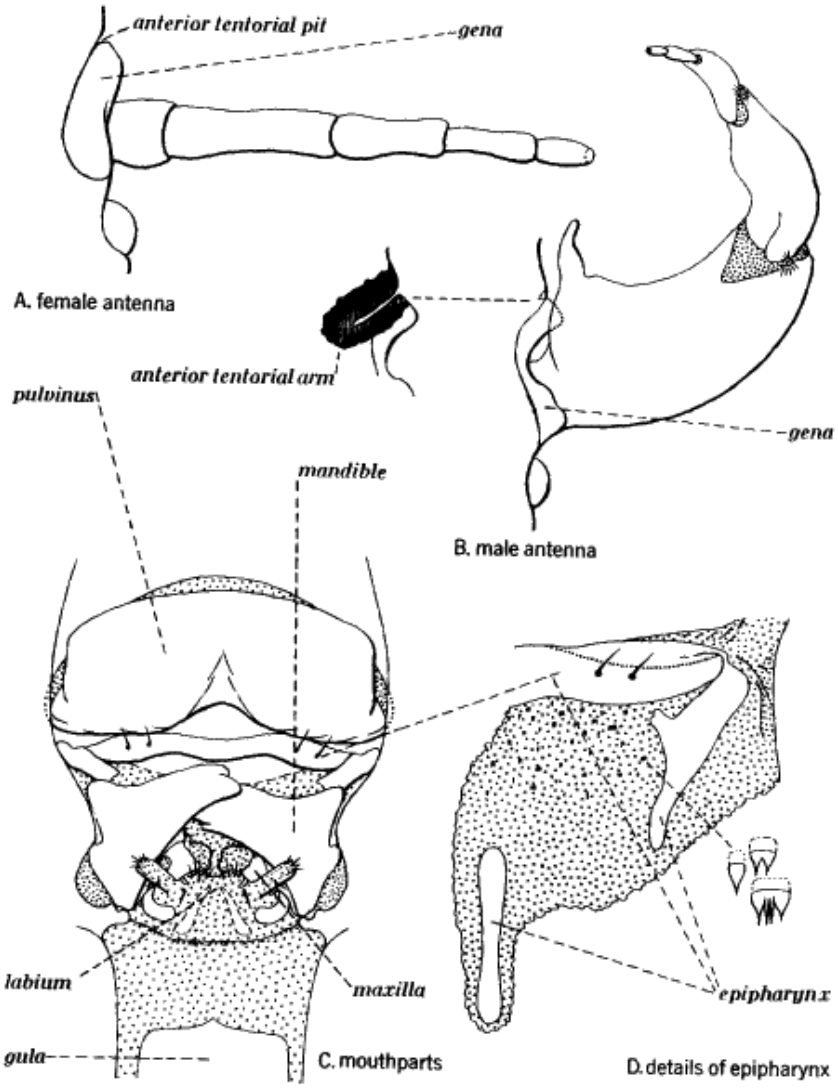


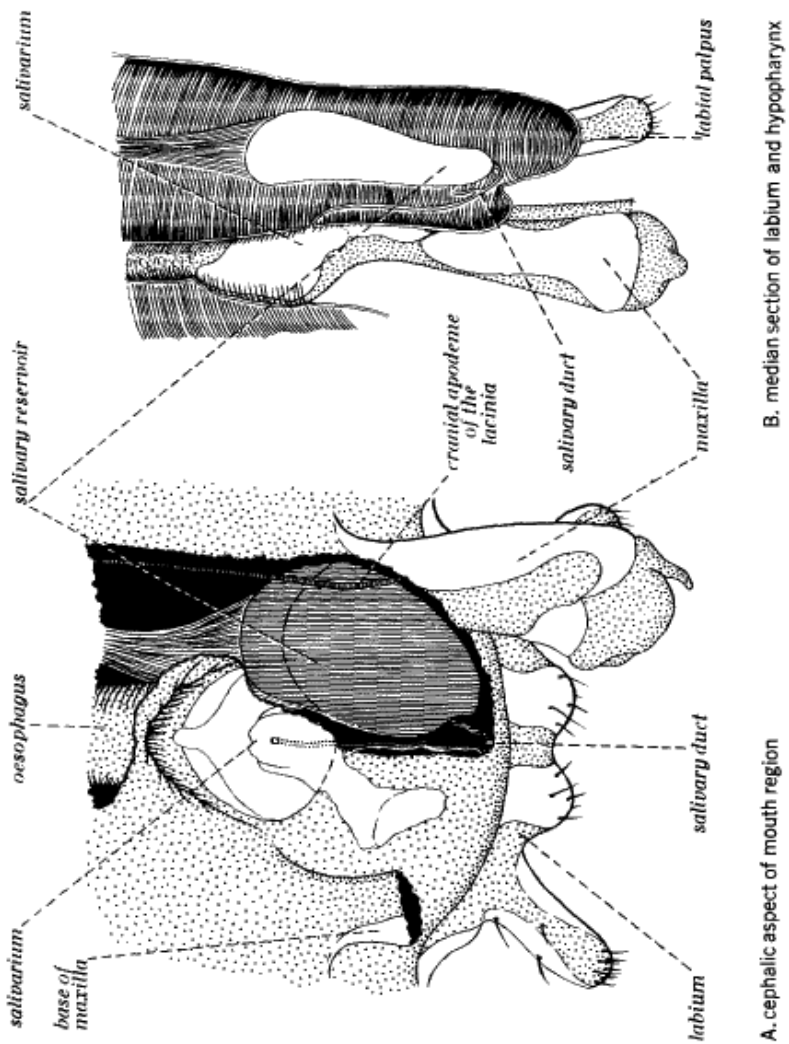
Esthiopterum diomedeae, head

Figure 54



Esthiopterum diomedeae, details of head structures

Figure 55

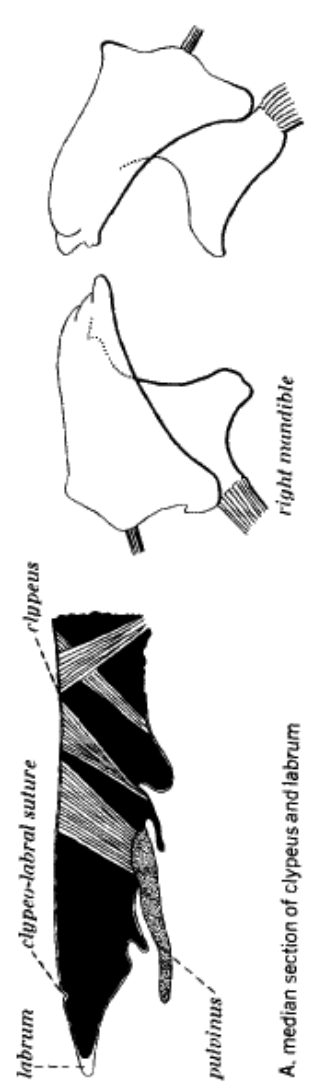


B. median section of labium and hypopharynx

A. cephalic aspect of mouth region

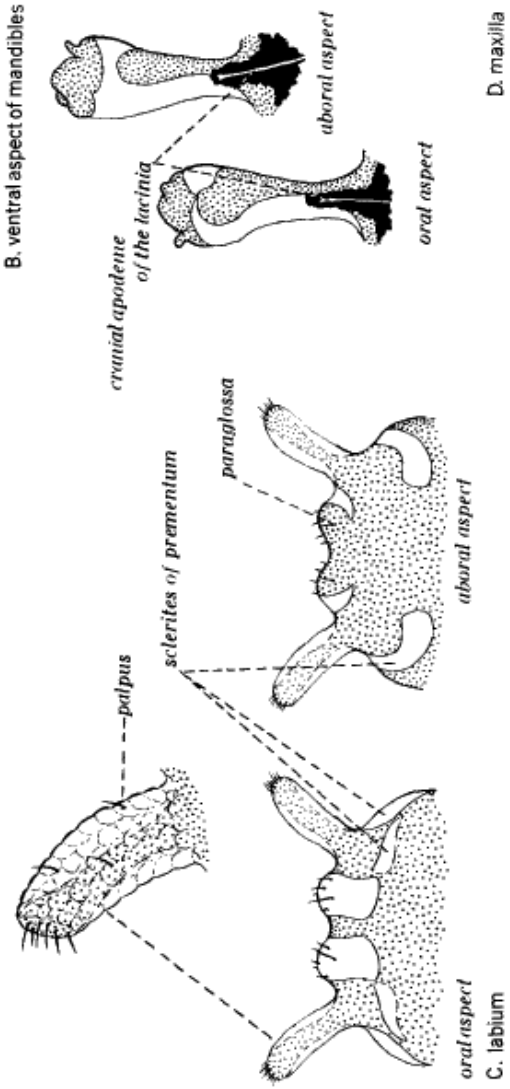
Esthiopterum diomedeae, details of mouthparts

Figure 56



B. ventral aspect of mandibles

A. median section of clypeus and labrum

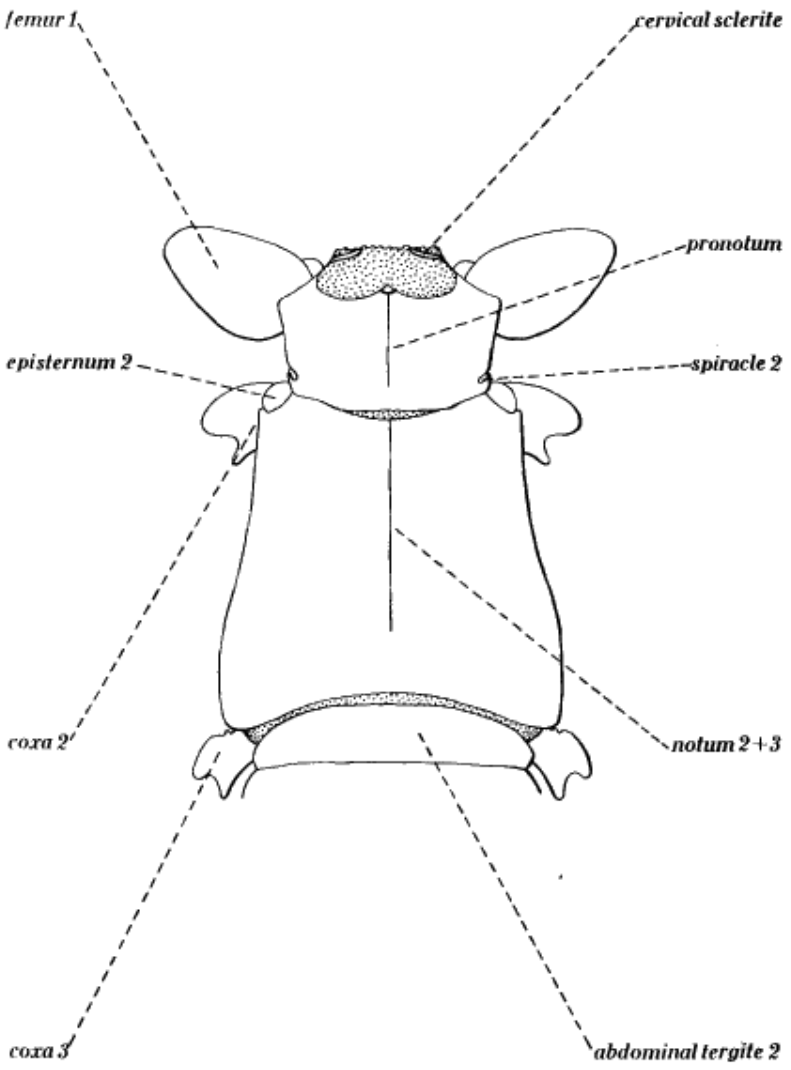


D. maxilla

C. labium

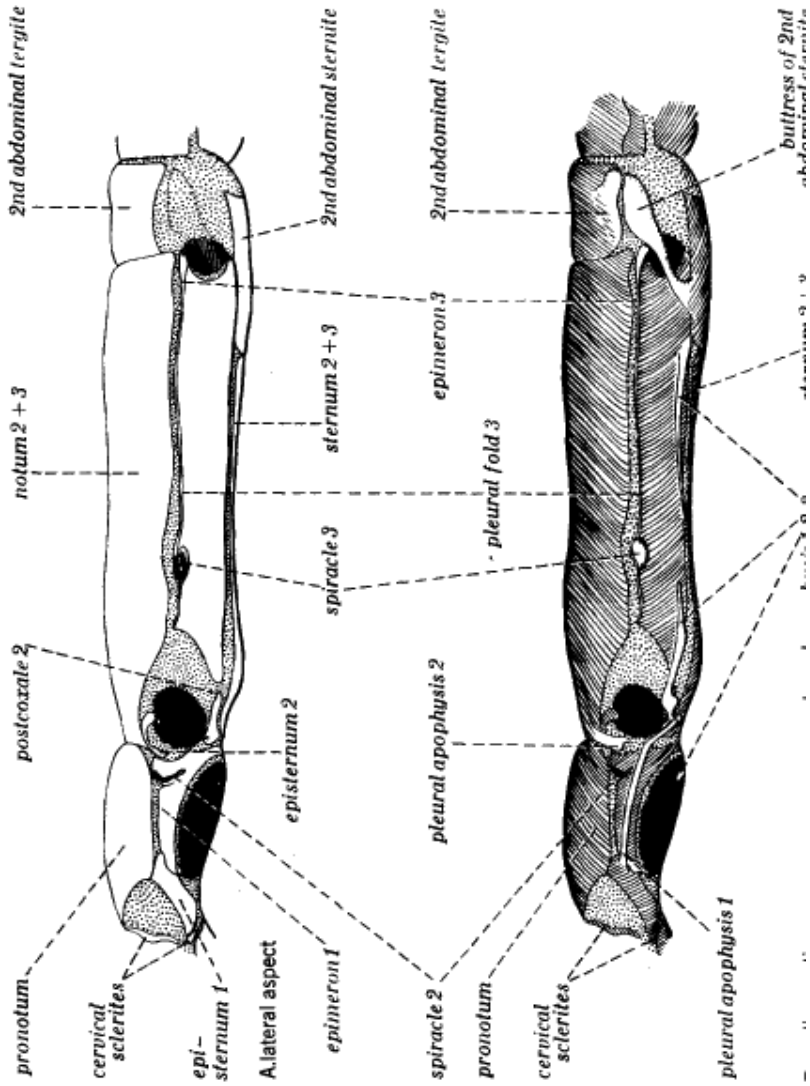
Esthiopterum diomedeae, details of mouthparts

Figure 57



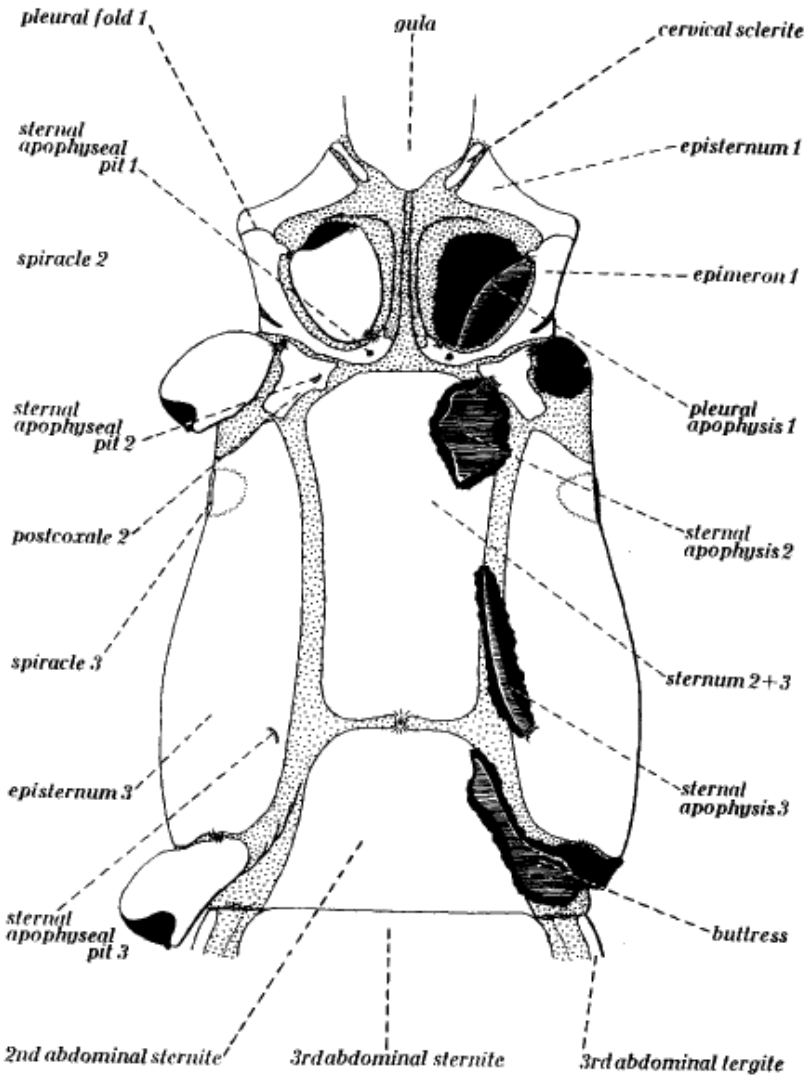
Esthiopterum diomedeae, dorsal aspect of thorax

Figure 58



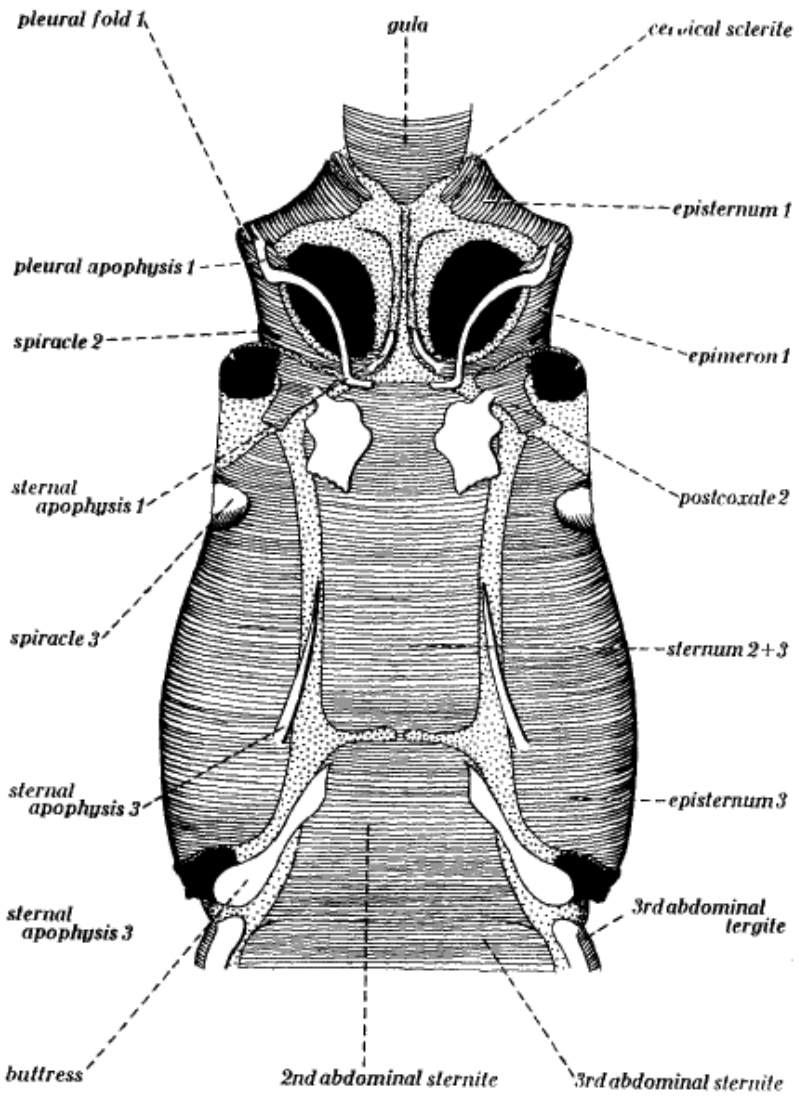
Esthiopterum diomedeae, lateral aspect of thorax

Figure



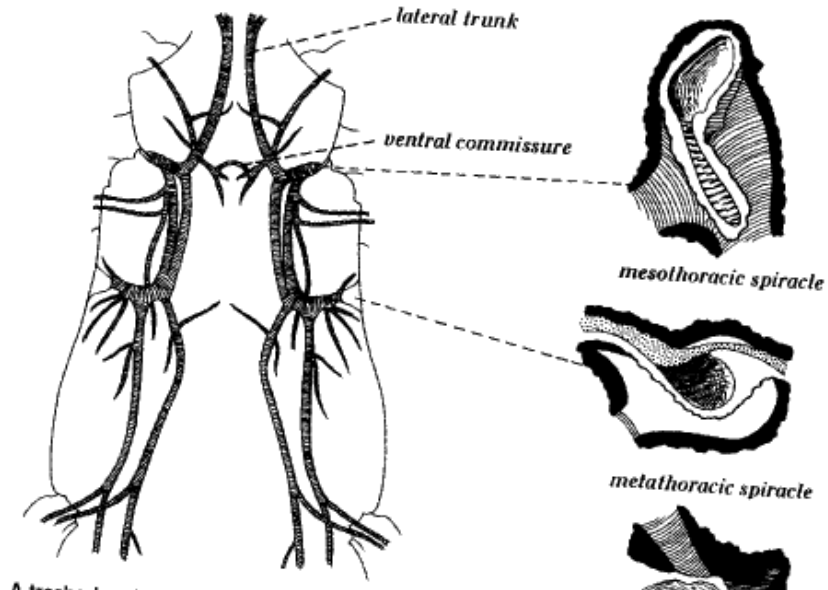
Esthiopterum diomedeae, ventral aspect of thorax

Figure 60



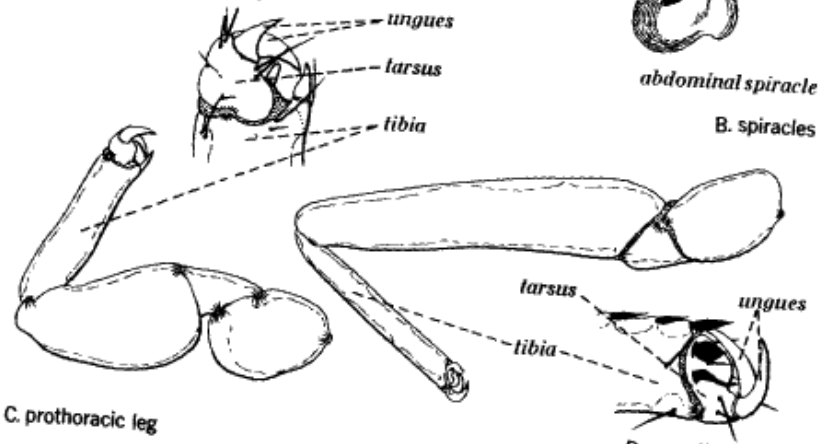
Esthiopterum diomedeae, skeleton of thorax, dorsum removed

Figure 61



A. tracheal system of thorax

B. spiracles

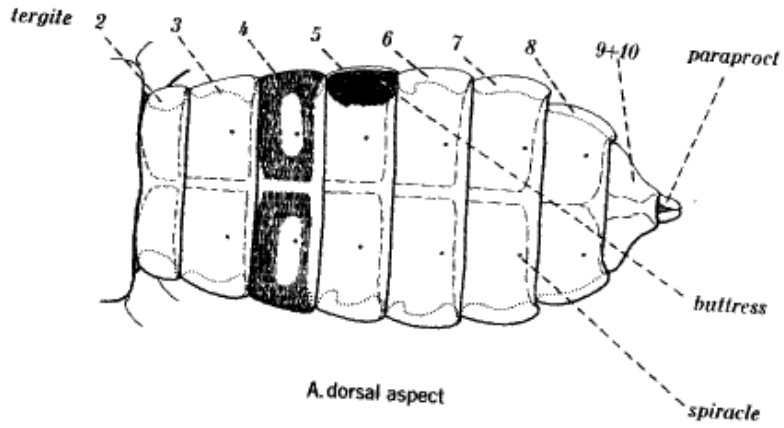


C. prothoracic leg

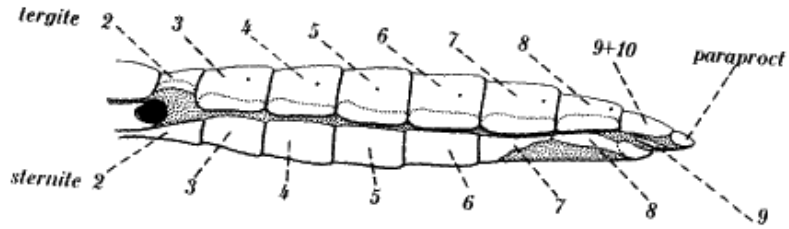
D. mesothoracic leg

Esthiopterum diomedeae, tracheal system and legs

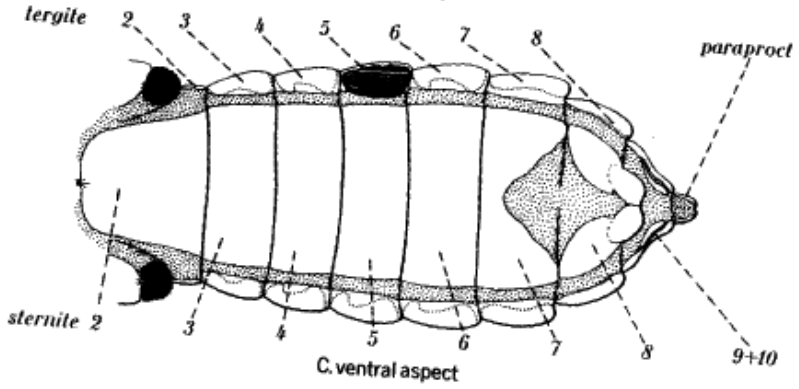
Figure 62



A. dorsal aspect



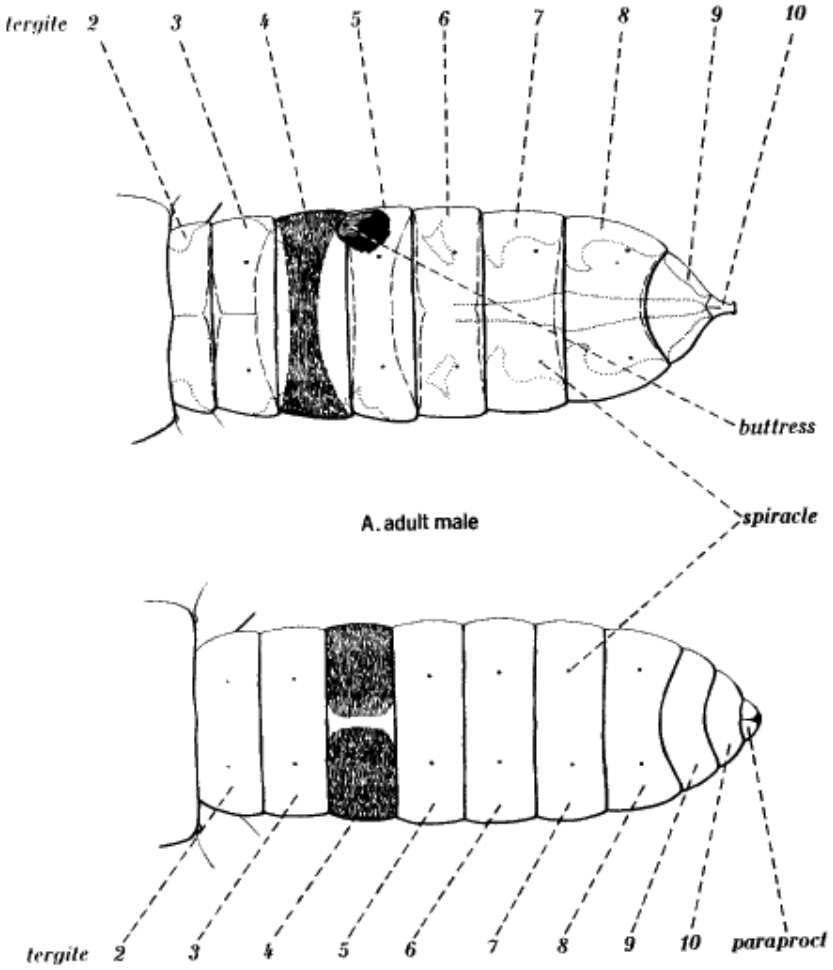
B. lateral aspect



C. ventral aspect

Esthiopterum diomedeae, segmentation of female abdomen

Figure 63

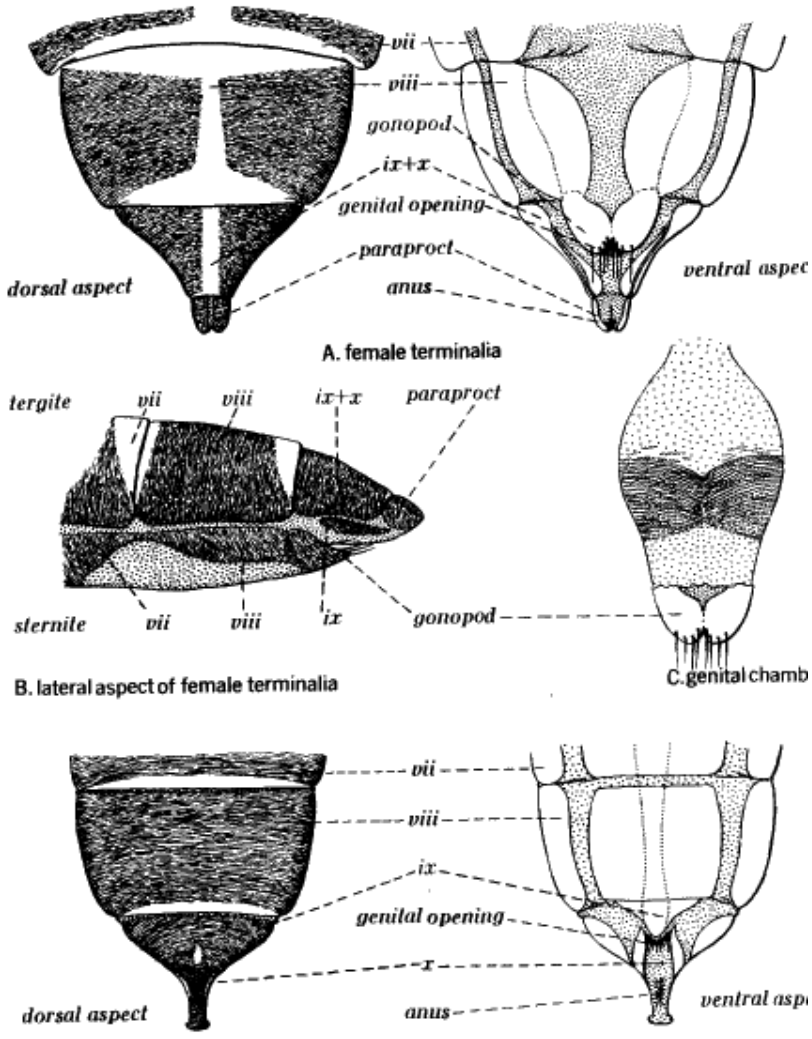


A. adult male

B. female nymph

Esthiopterum diomedeae, segmentation of abdomen

Figure 64



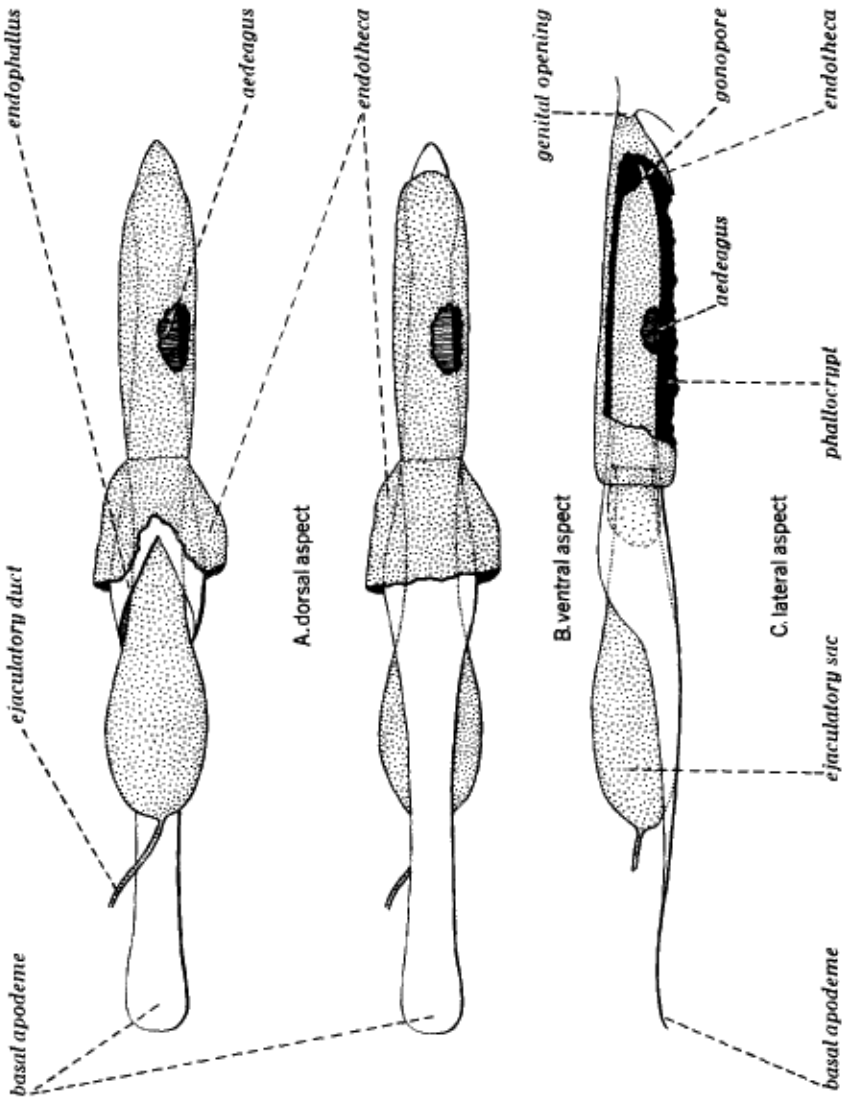
A. female terminalia

B. lateral aspect of female terminalia

D. male terminalia

Esthiopterum diomedeae, terminalia of male and female

Figu



Esthiopterum diomedeae, male genitalia

Figure 66