CHAPTER - IV.

DISCUSSION

In the light of the observational data and comparative tables of various muscles presented in the previous chapter, an attempt is hereby made to find out resemblances and differences between the muscular systems of the representatives of main insectan orders already alluded to in the chapter II. It is hoped that the salient features obtained in the process will help in determination of the major evolutionary trends of the insectan muscular patterns. Incidentally, this may also serve to illuminate, at least in some instances, the phylogenetic relationships of the insectan orders.

PART I: THE HEAD MUSCULATURE AND ITS BEARING ON THE OPERATION OF THE CEPHALIC APPENDAGES:

The salient features regarding muscular patterns of the cephalic appendages of the presently-investigated insectan types as obtained by their comparison, are discussed below:-
(A) **THE ANTENNARY MUSCLES**

a) The extrinsic antennary musculature in the thysanuran type (Vide Plate No. 1, Fig. No. I; Chart No. 1, Col. 1.) is represented by two pairs of depressors and a single pair of levators. Very similar observations are also made by Imms (1939), Chaudonneret (1950) and Woo wi Chun (1950) in the cases of *Lepisma saccharina*, *Ctenolepisma urbana*, and *Thermobia domestica*, respectively.

The well-developed depressor muscles originate on the rigid fulcrum, the highly sclerotized anterior tentorial arm and insert on either side of the antennal pivot that always remains, ventrolateral in the Thysanura-Pterygota complex (Imms 1939, Snodgrass 1952, '60; Schmitt 1964; Matsuda 1965). Consequently, the antenna in the thysanuran type has extensive horizontal mobility at a lower plane.

In contrast to this, the levator muscles are short and originate on the flexible fulcrum, the rudimentary dorsal tentorial arm (Snodgrass 1952, '60; Matsuda, 1965). As a result the dorsal and vertical movements of the antenna are much restricted. This degenerated condition, however, is indirectly compensated to some extent by the intrinsic antennary musculature comprising a levator and a depressor, which provide vertical mobility to the flagellum.
All these above features of the antenna and its musculature are in compliance with the floor-bound life of the Thysanura in concealed narrow habitats like in-between books, under stones or in the forest humus.

(b) As compared to the condition in the thysanuran type, the antennary musculature in the ephemerid type is an extremely degenerated one. Its extrinsic complement consists of only very short slender and unpaired levator and depressor muscles, originating on the dorsal and anterior tentorial arms respectively (Plate No. 6, Fig. No.1, Chart No. 1, Col.2). This degeneration is further emphasized by the reduction in size of the intrinsic complements - a levator and a depressor of the flagellum.

Strenger (1953), Brown (1961) and Noars (1961) have described similar conditions in different ephemerid species.

All these features are obviously correlated with the genetically predominant aquatic nymphal stage in the life-cycle of the Ephemeroptera, followed by a very short-lived aerial imaginal stage.

(c) As in the case of the ephemerid type, the extrinsic components of the antennary musculature in the zygoptera- and anisoptera representatives of the Odonata dealt with, are unpaired levator and depressor muscles arising
on the dorsal and anterior tentorial arms respectively, Asahina (1954), Snodgrass (1954), Mathur (1956), Mathur and Mathur (1961), Hakim (1964) and Srivastava and Mehta (1965), have noted very similar features in the other odonatan species.

The occurrence of an unpaired levator and depressor has led to the functional inconvenience, which is reduced partly by the relative elongation and oblique disposition of these existing muscles (Plate Nos. 10, 14; Fig. No. 1, Chart No. 2, Cols. 3,4) to provide more leverage and more amplitude to the vertical outwardly slanting movements of the antenna. Furthermore, it is also compensated indirectly to a certain extent by the intrinsic antennary muscles peculiarly acting in a horizontal plane, since the intrinsic levator inserts mesad, while the depressor inserts lateral at the base of the pedicel so as to impart horizontal mobility to the flagellum. This state of affairs, found in the odonatan types, has no parallel in any other insectan representative investigated.

Thus, on the whole, inspite of its above-mentioned degenerated musculature, the antenna in the odonatan types has greater mobility, far greater than that in the ephemered type.
All these features in the odonatan types are in correlation with the reduced cranial cavity due to occurrence of huge compound eyes, which in turn are entailed by the genetically aerial predatory nature in the adults of the Odonata.

The presence of such unique feature in the odonatan types supports the belief that the Odonata had a very early and independent divergence from the main protohexapodan stock - even earlier to the origin of the ephemerids.

(d) In the case of the dictyopteran representative, the extrinsic antennary depressors are the paired muscles arising on the rigid fulcrum - the highly sclerotized anterior tentorial arm, whereas the extrinsic levators are represented by a single muscle originating on the flexible fulcrum - the tendonous dorsal tentorial arm (Hudson 1945, Imms 1961). Snodgrass (1952) has described similar conditions. Thus, in effect the antenna in the dictyopteran type has an extensive horizontal play at its ventral side, while its dorsal and vertical mobility is restricted considerably. This feature, obviously goes with the floor-bound life of the Dictyoptera. However, the above-alluded functional inconvenience caused due to the occurrence of only a single levator is attenuated by the intrinsic antennary musculature comprising a levator and a depressor which act in a vertical plane, (Plate No.18, Fig.No.1, Chart No.1, Col.5).
In the case of the alate swarming isopteran type, the extrinsic antennary muscles are the reduced levator and depressor pairs. The levator pair arises on the tentorial body, whereas the depressor pair originates on the anterior tentorial arm; the tentorium in the Isoptera is devoid of the dorsal arm (Hudson 1947, Snodgrass, 1960), Imms (1961). The features noted here corroborate those of Vishnoi (1962) in the various castes of _Odontotermes obesus_ (Plate No. 22, Fig. No. I, Chart No. 1, Col. 6).

In keeping with the above-mentioned degeneration, the intrinsic levator and the intrinsic depressor muscles also show general reduction in size.

Understandably, therefore, the antennary movements in the alate swarming isopteran type are slow and meagre, which can be correlated with genetically predominant subterranean life of the Isoptera. It may also be pointed out further, that in the termite royal forms the antennary musculature undergoes pronounced reduction in size as compared to the condition in the alate swarming form. This feature, probably, may be due to their sedentary life in the royal chamber.

(f) In the case of the orthopteran type, the antennary musculature is well-developed. Its extrinsic complements are the levator and depressor pairs arising on the dorsal
tentorial arm. All these muscles are equally well-developed. (Plate No. 32, Fig. No. I, Chart No. 1, Col. 7). As such, the concomitantly well-developed antenna in the orthopteran type is provided with agile play in all the planes and directions. This, however, is further emphasized by the hyper-development of its intrinsic complements - the levator and the depressor of the flagellum. Imms (1939), Rakshpal (1946), Albrecht (1953) and Richards (1954) also have noted similar features in the different orthopteran species.

Conceivably, the various characters of the antenna and its musculature mentioned above are correlated with the active aerial and terrestrial mode of life in the Orthoptera.

(g) The antennary muscular pattern in the gymnocerate heteropteran type is only a modified version of the situation found in the case of the dictyopteran representative, for in both the cases the extrinsic complements are the paired depressors and an unpaired levator, whereas the intrinsic ones are a levator and a depressor (Plate No. 36, Fig. No. I, Chart No. 1, Col. 8). Thus, in both the cases the degeneration is parallel and is most conspicuous in the absence of one of the extrinsic levator muscles.

Yet, the antennary muscular pattern in the gymnocerate-heteropteran type is peculiar and characteristic in that all its extrinsic complements originate on the inner facet
of the anteclypeus. This feature appears to have been offset by the overgrowth of the clypeus in the Heteroptera to form the entire dorsal cephalic wall leading subsequently to the secondary absence or extreme reduction of the tentorium in the group (Quadri, 1959, Imms, 1961, Parsons, 1962, Matsuda, 1965).

In accordance with all these modifications, the mobility of the antenna in the gymnocerate-heteropteran type is less precise, and slow. Further, it is very much restricted in the vertical plane and at the dorsal side.

All the foregoing degenerated features of the antenna and its musculature in the gymnocerate-heteropteran type are correlated with the sluggish epiphytic (or epizoic) life of the Heteroptera - Gymnocerata consequent upon the piercing and sucking mode of feeding.

In the cryptocerate-heteropteran representative, the degeneration of the antenna and its muscles is more highly pronounced. For, here the entire complement of the antennary musculature is made of a single extremely reduced antennary depressor. (Plate No. 40 Fig. No.I, Chart No.1, Col.9). Thus the concomitantly degenerated antenna in this case has very less play. This can be correlated with the aquatic habitat of the species. Hufner (1939), Benwitz (1936) and Parsons (1960) have noted similar features in the aquatic and littoral heteropterans.
The anatomical make-up of the antennary muscular pattern in the neuropteran and mectopteran types is similar to that found in the orthopteran representative. For in these cases also, the extrinsic component muscles are the levator and depressor pairs, whereas the intrinsic complement is made up of a levator and a depressor. All these muscles are well-developed. (Plate Nos. 44, 56, Fig. No. I, Chart No. 1, Cols. 10, 12).

Notwithstanding this underlying similarity, the antennary muscular pattern in the cases of the neuropteran and mectopteran types exhibits a dispositional variation in that its extrinsic depressors arise on the anterior tentorial arm, while the extrinsic levators originate on the dorsal tentorial arm. Thus in the neuropteran and mectopteran representatives all the extrinsic antennary muscles have a spread-out disposition. Consequently, the antennae in these cases have more leverage and more play in all directions and planes. This is quite unlike the situation in the orthopteran type, wherein all the antennary muscles are found to originate on the dorsal tentorial arm exhibiting closer disposition. It may be mentioned here in passing, that similar observations are made by Heddergot (1938), Korn (1943), Kelsey (1954) and Matsuda, (1956), in the various species of Mecoptera and Neuroptera.
All the above alluded modifications, which have led to advanced features in the cases of the neuropteran and mecopteran types are strictly correlated with their genetically predominant aerial imaginal stages. It appears that these features are perhaps entailed by the shifting of the antennae to the anteromesal portions of the frons during the evolutionary changes of the cephalic capsules in the Neuroptera and Mecoptera (Duporte, 1946, Snodgrass 1947, Hinton 1958, and Imms 1944, 61).

(i) In the case of the coleopteran type dealt with in this work, both the extrinsic and intrinsic complements of the antennary muscular pattern are degenerated, since they are made up of unpaired levator and depressor muscles (Plate No. 48, Fig. No.1, Chart No. 1, Col. 11).

Further, these muscles in this coleopteran type have their own speciality, for they are oriented and hence operate in a horizontal plane. This peculiarity in the case of the coleopteran type appears to have been offset by the shifting of the antennae to the anterolateral portion of the head capsule due to the overgrowth of the frons to form a horn (Imms 1961).

In effect, therefore, the concomitantly reduced antenna in the coleopteran type has a meagre field of play limited to the horizontal plane.
All these above modifications of the antenna and its musculature are perhaps correlated with the endophytic mode of life in this coleopteran type.

(5) Much similar to that described in the neuropteran and mecopteran types, the antennary muscular pattern in the hymenopteran and lepidopteran representatives is also made up of the extrinsic paired levator and depressor complements and the intrinsic unpaired levator and depressor composites. (Plate Nos. 52, 60, Fig. No.1, Chart No.1, Cols. 13,14).

Perhaps as a further modification of that in the neuropteran and mecopteran types, the antennary muscular pattern in the hymenopteran and lepidopteran representatives, shows a dispositional variation. This variation is most conspicuous in that all its extrinsic complements arise on the anterior tentorial arm, whereas in the neuropteran and mecopteran types, the levators arise on the dorsal tentorial arm and depressors originate on the anterior tentorial arm. Schmitt (1938), Snodgrass (1942, '56), Alam (1951), Eassa (1953, '63b) Eastham and Eassa (1955), Matsuda (1957) and Srivastava (1957) and Vasudeva (1957) have noted similar features in the various species of Lepidoptera and Hymenoptera.

Mention may be made here that the above-mentioned modification, in the cases of the hymenopteran and lepidopteran types, is strictly due to the absence or rudimentary nature
of the dorsal tentorial arm in the groups (Easthan & Eassa 1955, Snodgrass 1956). However, it has no effect on the functional efficiency of the well-developed antennae, in these groups.

(k) In contrast to the state of affairs described in all the holometabolous types, in the case of the brachycerous dipteran type, the antennary musculature exhibits degeneration in number as well as in size. Its extrinsic components are the minute paired levators and an unpaired depressor; one of the levators and the depressor arise on the dorsal tentorial arm. Strangely, the other levator component originates on the frons. It may be pointed out here that this situation has no parallel in any of the insectan types investigated presently, and this anomaly is difficult to account for especially in the presence of a well-developed tentorium in the Diptera.

In keeping with general degeneration mentioned above, the intrinsic unpaired levator and depressor in this type are also reduced. (Plate No. 64, Fig. No. 1, Chart No. 1, Col. 15). As a result the concomitantly degenerated antennae in the dipteran type move only in the vertically oblique plane slanting outwardly. This feature of the brachycerous dipteran type appears to be entailed by its highly enlarged compound eyes and accompanying reduction of the cranial cavity. (Snodgrass 1935,"44, '53, '60, Hoyt 1952, Richards and Davies 1964).
Mention may be made in passing that similar observations are made by Bonhag (1951) and Bletchley (1954) in different species of the brachycerous Diptera.

(B) THE LABRAL MUSCLES:

(a) As a symplesiomorphic condition, the labral muscular pattern in the thysanuran, ephemerid, odonatan, dictyopteran, alate swarming isopteran, orthopteran and neuropteran representatives is identical. In all these cases, it is made up of two pairs of extrinsic muscles and a pair of intrinsic muscles (Plate Nos. 2, 6, 10, 14, 18, 22, 32, 44, Figs. No. I & II, Chart No. 1, Cols. 1, 2, 3, 4, 5, 6, 7, 10).

The extrinsic complements are the paired levators and depressors. The former originate mesally on the frons and insert medially on the dorsal proximal margin of the labrum, whereas the latter arise on the lateral frontal area and insert on the labral torma or on the corresponding portion.

The intrinsic complement is made up of a pair of labral compressors. These muscles arising from the labral wall are inserted on the epipharyngeal wall.
All these labral muscles are well-developed in the cases of various insectan representatives mentioned above and they provide an efficient mobility to the appendage for prehension and ingestion.

However, in the royal forms these muscles exhibit reduction unlike the worker caste which goes out foraging.


Thus, without invoking further discussion it may be inferred here that the above described labral muscular pattern is a generalized one in the Insecta, inasmuch as it occurs in the representatives of all the primitive and generalized orders.

(b) As compared to its generalized condition described above in the representatives of the primitive and generalized orders, the labral musculature in the case of
the heteropteran types shows extreme degeneration and an unparalleled modification.

The degeneration is most conspicuous in that, its entire complement is made up of only one pair of muscles - the labral depressors; all other component muscles are absent. (Plate Nos. 36, 40, Fig. Nos. I & II, Chart No. 1, Cols. 8, 9).

Further, these persisting labral depressors in the heteropteran types are believed to have become modified into the protractors of the mandibular stylet, since according to Matsuda (1965), the labral depressor muscle in the Thysanoptera functions as a muscle of the left mandible. The evidences from developmental investigations (Newcomer 1948) and from studies on the innervation pattern (Pesson 1944) serve to support this concept.

All the foregoing degenerated features and modifications in the labral musculature of the heteropteran types can be relegated to the degeneration of the appendage itself consequent upon the evolution of the sucking apparatus and advanced entognathy in the Heteroptera.

(c) In its anatomical make up, the labral muscular pattern in the mecopteran type is very much similar to the generalized condition described in the representatives of
the primitive and generalized orders. However, it differs from the latter in only one respect that its extrinsic complements, the levator and depressor pairs occur as elongated slender muscle bundles, which have shifted their points of origin to the clypeus. Consequently, more leverage and resulting agility is imparted to the appendage. (Plate No. 56, Fig No. 1, Chart No. 1, Col. 12). This feature, obviously, is offset by the formation of rostrum and carcass-feeding habit in the Mecoptera. Heddergot (1938), Bierbrodt (1942) and Imms (1944) have noted similar features in the various species of the Mecoptera.

(d) The labral musculature in the coleopteran type exhibits degeneration, when compared with the generalized pattern described in the representatives of the primitive and generalized orders. Its complement consists of only the extrinsic depressor pair and the intrinsic compressor pair; the extrinsic levator pair being absent. Inasmuch as similar features are reported in the representatives of almost all coleopteran groups (Dorsey 1943, Butt 1951, Saxena 1953, Evans 1961), it appears that the absence of extrinsic labral levators is the usual condition in the Coleoptera.

This degeneration of the labral musculature in the Coleoptera is correlated with the concomitantly reduced
labrum due to anterior outgrowth of the frons and the clypeus. It is also probably correlated with the high degree of sclerotization of the head capsule.

(e) The labral musculature in the hymenopteran type, again exhibits an extreme degeneration when compared with the typical condition described in the representatives of the primitive and generalized orders. This degeneration is most impressive in the absence of its extrinsic levator pair and intrinsic compressor pair. (Plate No. 52, Fig. No.1, Chart No. 1, Col. 13).

In effect, the concomitantly reduced labrum in the hymenopteran type is imparted with less precise and slow mobility by the extrinsic depressor pair alone. These features noted here are in conformity with those observations of Snodgrass (1942). It appears that Morison (1927), perhaps made an observational error, when he termed the extrinsic depressor muscles in Apis mellifera as the levators of the labrum.

All the foregoing features of the labrum and its musculature in the hymenopteran type can be correlated with the occurrence of the maxillolabial proboscis as a necessary adaptation for the lapping and sucking mode of feeding.
(e) Unlike in all the other insectan types investigated here, in the lepidopteran representative the labrum is devoid of all labral muscles. Conceivably, this feature is in conformity with the extreme atrophy of the labrum and its subsequent fusion with the clypeus, in the Lepidoptera, to occur as a minute immovable lobe between the pilifers (Snodgrass 1935; Schmitt 1938; Eassa 1953, '63; Eastham and Eassa 1955; Richards and Davies 1964; Eaton 1970, '73).

These modifications obviously appear to have been entailed by the presence of a galeal proboscis as an adaptive prerequisite for the siphoning mode of feeding in the Lepidoptera.

(f) In the case of the brachycerous dipteran type, the labral muscular pattern is again a degenerated and modified one, but altogether in a different plane, for its entire complement is made up of only the extrinsic median unpaired levator and the intrinsic paired compressors. Thus, the degeneration in this pattern is most evident in the absence of the extrinsic depressor complements. This is in contrast to the situation aforementioned in the cases of the hymenopteran and coleopteran types, wherein the degeneration has been most conspicuous in the loss of the extrinsic levator pair. (Plate No. 64, Fig. No. I, Chart No. 1, Col. 15).
Further, the persisting extrinsic levator muscles of the labrum, in the case of the brachycerous dipteran type, exhibit a curious modification in that instead of their usual paired condition, they are represented as a median unpaired muscle which has shifted its origin from the frons to the clypeus, to become the clypeo-labral muscle. Similar features are also noted by Snodgrass (1935, '44, '53) Gouin (1949) Bonhag (1951), Hoyt (1952), Bletchley (1953, '54, '55), Schiemenz (1957) and Detheir (1959) in the various species of the Diptera. Thus, as Snodgrass (1935) expressively says, "the presence of a clypeo-labral muscle is a special feature of the Diptera and constitutes an exception to the general rule that the labral muscles take their origin on the frons."

On contraction, this muscle retracts the labrum and thereby, keeps it in close contract with the mandibles and hypopharynx. Supposedly this action helps in the formation of the food meatus and keeping it open while the insect is feeding (Snodgrass 1935, Bonhag 1951, Bletchley 1955).

Mention may be made here in passing that the clypeo-labral muscle in the Diptera is believed to be the fusion product of the labral levator pair, mainly on the basis of comparative studies. (Snodgrass, 1944; '53; Bletchley 1955, Schiemenz 1957; Matsuda 1965). However, correlative evidences from embryological studies are needed.
The various afore-said modifications of the labrum and
its musculature in the dipteran type are evidently correlated
with extreme reduction of the frons due to overgrowth of the
compound eyes and genae in the Diptera during the evolution
of their piercing and sucking type of trophic appendages
(DuPorte 1946; Snodgrass 1947, 53; Bonhag 1951; Richards
and Davies 1964).

(C) THE MANDIBULAR MUSCLES:

As a symplesiomorphic feature, the mandible that
occurs in the thysanuran and ephemerid types is of a
'thysanuroid' type (Borner 1909, vide Matsuda 1965; Hennig
1953; Tuxen 1959). This type of mandible is elongate and
its inner margin is deeply excavated for accommodation of
muscles. The whole mandible is homologous with the apical
lacinial lobe and with at least a large part of the cardjo-
stipital area of the mytiapodan mandible (Snodgrass, 1928,
'32, '35, '50 and '58; Chaudonneret 1950; Hennig 1953; Tuxen
1959; Bitsch 1963b). According to Matsuda, (1965), the
'thysanuroid' type of mandible is also homologous with the
apical lacinial lobe and with at least a large part of the
cardio-stipital area of the maxilla.
(a) In thysanuran representative, this type of mandible is moved by two sets of muscles—the dorsal and ventral. The dorsal complements of the mandibular muscular pattern are the four muscles, the main and second cranial adductors and the main and second cranial abductors. All these muscles arise on the various parts of the cranial wall. The adductors insert on the apodeme arising from the mandibular base, whereas the abductors insert on the apodeme at the posterior articulation of the mandible. (Plate No. 2, Fig. No. II; Chart No. 1, Col. 1).

The ventral complements of the mandibular musculature are the main and second ventral muscles. The main ventral muscles comprise two groups—the posterior or proximal group functions as the abductor, while the anterior or distal group acts as the adductor. Both the groups originate on the anterior tentorial arm and insert on the basal part of the lateral mandibular wall. The second ventral muscle arises on the loral arm of the hypopharyngeal suspensorium and inserts near the adductor apodeme and thus functions as the adductor of the mandible.

All these muscles in the thysanuran type are well-developed and provide an efficient horizontal mobility to the appendage which has a double articulation (Chaudonneret 1950; Matsuda, 1965).
Very similar features as regards the muscular pattern are noted by Chaudonneret (1950), Francois (1959), Tuxen (1959), Wolter (1963) and Bitsch (1963b) in the representatives of the various primitive apterygote groups. Further, it may also be pointed out that the above described mandibular musculature in the thysanuran type is suggestive of the myriapodan pattern though no intrinsic muscles are found in it (Snodgrass 1935,'51,'52; Francois 1959; Tuxen 1959).

Thus, on the strength of the aforesaid account it may be concluded here that the mandibular muscular pattern described in the thysanuran type is quite a generalized and primitive one.

(b) As compared to the situation in the thysanuran type, the mandibular muscular pattern in the ephemerid representative exhibits reduction in the number of complementary muscles, which is quite evident in the absence of two of the dorsal muscles - the second cranial adductor and abductor muscles. The resultant functional inefficiency, however, is fully and directly compensated by the better development of the main cranial adductor and abductor muscles. (Plate No.6, Fig. No. II, Chart No. 1, Col2).

The ventral complement of the mandibular musculature is well retained in the ephemerid type— both the main and
second ventral mandibular muscles being present. Further, in the main ventral muscle, both the functional groups, the adductor and the abductor can be recognized, as is the condition in the thysanuran representative.

On the whole therefore, the aforesaid reduction of the complement number in the mandibular muscular pattern has very little effect on the functional efficiency of the appendage.

The various features discussed above corroborate the findings of Strenger (1953), Brøn (1961) and Noars (1961) in the various species of Ephemeroptera.

(c) The mandibular muscular pattern in the odonatan, dictyopteran and isopteran types is a reduced version of the one described in the ephemerid representative. For in these cases, as a further degeneration of the pattern described in the ephemerid type, the main ventral mandibular muscle is represented by only one functional group the adductors; the abductor group being absent. The consequent functional inefficiency is, however, directly compensated by the better development of the main cranial abductor complement. (Plate, Nos. 10, 14, 18, 22, Figs. Nos. II, Chart No. 1, Cols. 3, 4, 5, 6).
The aforementioned synapomorphic degeneration of the mandibular muscular pattern is strictly correlated with the loss of basal portions of the mandibles to become an 'orthopteroid' type of the mandible in the Odonata, Dictyoptera and Isoptera, during the course of the evolution of their cephalic capsules (Matsuda, 1965).

Snodgrass (1935, '44, '52, '54), Dorsey (1943), Asahina (1954), Short (1955), Mathur (1956), Vishnoi (1956, 62), Mathur and Mathur (1961), Hakim (1964), Srivastava and Mehta (1965), have noted similar features in the different species of the Odonata, Dictyoptera and Isoptera.

(d) The mandibular muscular pattern in the cases of the orthopteran neuropteran and dipteran types in its turn is a further reduced version of the one described in the cases of the odonatan, dictyopteran and isopteran representatives. For its entire complement is made up of the reduced main ventral mandibular muscle alone; the second ventral mandibular muscle present in the cases of the odonatan dictyopteran and isopteran types is absent. The eventual functional inefficiency, however, is directly compensated by the more pronounced development of the dorsal complements - the main muscles which provide efficient horizontal mobility to the appendage. (Plate, Nos. 32, 44, 64, Fig. No. II, Chart No. 1, Cols. 7, 10, 15).
In the case of the dipteran type the mandibles do not exhibit the protraction and retraction. The thrust of the piercing mandibles is made by a forceful action of the head and body of the fly and the initial puncturing on the hosts' skin is probably done by this action. (Snodgrass 1935, Bonhag 1951, Wenk 1962).

All the afore-mentioned synapomorphic modifications of the mandibular muscular patterns in the orthopteran, neuropteran and dipteran types are evidently correlated with the further loss of the basal portions of the mandibles, during the evolutionary processes of their cephalic capsules. (Matsuda, 1965).

Snodgrass (1935), Korn (1943), Bonhag (1951), Hoyt (1952), Albrecht (1953), Hetchley (1954), Kelsey (1954), Rakshpal (1954), Richards (1955), and Matsuda (1956), have described similar situations in the different orthopteran, neuropteran and dipteran types.

(e) As compared to the conditions described above in the insectan representatives, the mandibular muscular pattern in the case of the heteropteran types exhibits extreme degeneration and unique modifications. (Plate Nos. 36, 40, Fig. No. 1, Chart No. 1, Cols. 8, 9).
The degeneration is quite evident in that its entire complement is made up of only two muscles - the protractors and retractors of the mandibular stylet, all the other component muscles being absent.

Of the persisting muscles, the retractors of the mandibular stylet are believed to be the highly modified homologues of the main ventral muscles of the mandible, on the bases of comparative studies, Kremer (1950), Billing (1960), Matsuda, (1965). Pesson (1944) proposed the same interpretation based on the innervation pattern studies. Developmental studies by Newcomer (1948) also corroborate the above supposition.

The shift in the origin of this muscle to the cranial wall, is possibly due to the absence of the tentorial structures in the Heteroptera. The antagonistic mandibular muscle, the protractors of the mandibular stylet in the Heteroptera are, however, the modified labral depressors, as already discussed earlier.

The various aforesaid degenerated features and modifications of the mandibular musculature in the Heteroptera, can be correlated with the modifications in the appendage itself, which in turn are entailed by the evolution of sucking apparatus and entognathy in the group.
(f) The mandibular muscular pattern in the coleopteran, mecopteran and hymenopteran types in its turn is a reduced version of the one described in the orthopteran, neuropteran and dipteran representatives, for its entire complement is made up of the dorsal mandibular muscles alone, whereas the ventral mandibular muscles, present in the latter, are lacking in it. The functional inefficiency caused by this absence of the ventral muscles is, however, directly compensated by the persisting highly developed dorsal components - the main cranial adductor and abductor muscles (Plate Nos. 48, 56, 52, Fig. No. II; Chart No. 1, Cols. 11, 12, 13).

The absence of the ventral mandibular muscles in the coleopteran, mecopteran and hymenopteran types appears to be correlated with the further loss of the basal mandibular portions which are homologous with the cardo and stipes of the myriapodan mandible (Snodgrass 1935, '52; Matsuda 1965).

It may also be pointed out here that the persisting main cranial adductor and abductor muscles in the mecopteran type exhibit a developmental variation in that they occur as the elongated muscles inserted on the elongated apodemes from the mandibular base. Thus, they provide more leverage and more precise manipulatory movements to the appendage. This feature appears to be correlated with the elongation of the head capsule and carcass-feeding habit in the
Mecoptera (Heddergott, 1938).

Heddergot (1938), Pradhan (1938), Duncan (1939), Beirbrodt (1942), Snodgrass (1942), Imms (1944), Alam (1951), Butt (1951), Saxena (1953), Matsuda (1959), Barth (1960), and Evans (1961b), have noted similar features in the various representatives of the Coleoptera, Mecoptera and Hymenoptera.

(g) In the case of the lepidopteran type the mandibular musculature is completely absent, since the mandible is genetically greatly reduced or is sometimes completely lost (Mosher 1915 vide Matsuda 1965, Vasudeva 1957) during the evolution of galeal proboscis.

(D) THE MAXILLARY MUSCLES:

(a) As a symplesiomorphic feature, the maxilla found in the representatives of the Thysanura, Ephemeroptera, Odonata, Dictyoptera, Isoptera, Orthoptera, Neuroptera and Coleoptera is a generalized one and is least evolved of all the gnathal appendages in the Insecta. For such maxilla is also prevalent in the entognathous Apterygota, Symphyla and even in Anaspedes (Crustacea). (Teigs 1940, Snodgrass 1951, '52, Manton 1964, Matsuda 1965). (Plate Nos. 2, 6, 10, 14, 18, 22, 32, 44, 48, Fig. No. III, Chart Nos. 1, Cos. 1, 2, 3, 4, 5, 6, 7, 10, 11).
As is expected from the above, the muscular pattern associated with such maxilla is also a generalized one in the representatives of the Thysanura, Ephemeroptera, Odonata, Dictyoptera, Isoptera, Orthoptera, Neuroptera and Coleoptera. Further, it is remarkably similar in all these cases and comprises of the following muscles - the dorsal retractor of the cardo, the ventral adductor of the stipes, the cranial flexor of the lacinia, the stipital flexor of the lacinia, the stipital flexor of the galea, the extrinsic levator and depressor of the palp. All these muscles are well-developed, and provide an efficient mobility to the appendage during prehension and ingestion.

Apparently, however, minor variations have prevailed in these cases as mentioned below, without involving any fundamental differences in the pattern-

1) In the thysanuran type, the intrinsic levators occur in the segments 1-3 only instead of in 1-4, whereas the intrinsic depressors of the palp occur in segments 1-4. The exclusive presence of a minute accessory stipitopalpal muscle is also a peculiarity of this type.

2) In the ephemerid type, the intrinsic levator and depressor are present only in the first palpal segment instead of in segments 1-4.
3) In the odonatan types, the flexors of the lacinia and galea are fused to form a single flexor of the 'dentate mala', the fusion product of the galea and lacinia. This concept derives its support from the embryological studies of Ando (1962). No intrinsic palpal muscles occur in these types, since the palp occurs as a unisegmented solid spine (Snodgrass 1954; Mathur and Mathur 1961; Richards and Davies 1964). These features in the odonatan types are apparently correlated with their aerial predatory habit.

4) In the dictyopteran and isopteran types, the intrinsic palpal levators are restricted to the first palpal segment, while the depressors are present in the segments 1-4.

5) In the orthopteran, neuropteran and coleopteran types the intrinsic palpal levators are present in the segments No. 1 and 2 only whereas the depressors occur in the segments 1-4. It appears that these variations in the distribution of the intrinsic palpal muscles mentioned with reference to the five groups are correlated with the different types of manipulatory movements performed by the maxillary palp. Similar features regarding the maxillary musculature are also noted by Dorsey (1943), Snodgrass (1944, '52), Chaudonneret (1950), Hyot (1952), Kelsey (1954), Albrecht, Rakhspal (1954), Richards (1955), Mathur (1956), Matsuda (1956), Vishnoi (1956, '62), Brown (1961), Mathur and
Mathur (1961), Hoars (1961), Popham (1961), Srivastava and Mehta (1965) for the various species of Thysanura, Ephemeroptera, Odonata, Dictyoptera, Isoptera, Orthoptera, Neuroptera and Coleoptera.

(b) As compared to the generalized maxillary muscular pattern described earlier in the representatives of the generalized orders, the one that is present in the heteropteran types is extremely degenerated and highly modified. (Plate Nos. 36, 40, Fig. No. II; Chart No. 1, Cols. 8, 9).

The degeneration is reflected in the fact that its entire complement is made up of only two muscles - the retractors and protractors of the maxilla which are really the modified cranial and stipital flexors of the lacinia.

These conclusions are made on the basis of direct comparison of these muscles with the maxillary muscles in Psocoptera and Thysanoptera (Matsuda, 1965). However, correlative evidences from developmental investigations are lacking. Similar observations regarding the maxillary muscles are also noted by Snodgrass (1928, '35, '38); Pesson (1944), Newcomer (1948), Quadri (1949, '51, '59), Aziz and Quadri (1950), Benwitz (1959), Akabar (1957), Saxena, (1953), Parsons (1959, '62) in other hemipteran types.
The various aforesaid degenerated features and modifications of the maxillary musculature in the Heteroptera, can be correlated with the modifications in the appendage itself, which in turn are entailed by the evolution of sucking apparatus and entognathy in the group.

(c) When compared with the typical conditions found in the representatives of the generalized orders, the maxillary musculature in the mecopteran type exhibits degeneration. This degeneration reaches its climax in the disappearance of the dorsal retractor of the cardo, the stipital flexors of the lacinia and galea and the extrinsic depressor of the palp. Curiously, the functional inefficiency entailed by the aforesaid degeneration is fully compensated in various ways by unusual modifications of the persisting muscles. (Plate No. 56, Fig. No. III; Chart No. 1, Col. 12).

In the first instance, the ventral adductor of the cardo has shifted its point of origin to the clypeus. This, however, has no functional significance.

Secondly, the ventral adductor of the stipes is represented by two well-developed fasciculi, both arising on the clypeus; one is horizontally oriented and abducts the whole maxilla, thereby acting as the functional replacement for the missing dorsal retractor of the cardo,
the other component of this muscle is obliquely disposed and has the normal function of adducting the stipes.

Thirdly, the cranial flexor of the lacinia is also represented by two massive fasciculi: one arises on the clypeus, while the other originates on the postocciput. Both insert on the elongated forked apodeme arising from the bases of the galea and lacinia to get modified as the abductors of the terminal lobes. This directly compensates for the absence of the stipital flexors of the galea and lacinia.

Finally the intrinsic levators present in the first two palpal segments and the depressors present in the first four segments help in the more precise manipulatory movements of the palp during prehension and ingestion.

The aforesaid ensemble of modifications in the case of the mecopteran type are in correlation with the elongation of the clypeus to form the characteristic rostrum and the carcass-feeding habit of the group.

This entire situation described above generally resembles the observations of Grell (1938), Heddergott (1938), Imms (1940) and Hinton (1958) in the different species of Mecoptera.
(d) When compared to the condition in the representatives of generalized orders the maxillary muscular pattern in the case of the hymenopteran type again is a degenerated one, since its complement very conspicuously lacks the ventral adductor of the cardo, the cranial flexor of the lacinia, the extrinsic and the intrinsic palpal levators, and the depressors. (Plate No. 52, Fig. No. III; Chart No. 1, Col. 13).

The eventual functional inefficiency, however, is attenuated to a great extent by the following modifications in the persisting muscles. Firstly, the dorsal retractor of the cardo has shifted its point of origin to the postgena to function as the retractor of the entire maxillo-labial complex. Secondly, the ventral adductors of the stipes has undergone hyper-development and is represented by three fasciculi, arising on the clypeus. As a result, these muscles act as adductors of the stipes and also as retractors and protractors of the whole maxillo-labial complex. Finally, the well-developed stipital flexor of the galea, folds the galeal blade on contraction.

The rudimentary lacinia and maxillary palp are, however, operated by the stipital flexor of lacinia and the intrinsic palpal depressor respectively.
All the peculiarities afore-mentioned are obviously in correlation with the presence of the maxillolabial complex, a prerequisite in the formation of lapping and sucking type of trophic appendages in the Hymenoptera.

Similar conditions regarding the maxillary musculature are also noted by Morison (1927), Duncan (1939), Snodgrass (1942, '56) and Alam (1951) in the other hymenopteran species.

(e) Compared to the different patterns of the maxillary musculature described above, that in the lepidopteran representative is extremely degenerated and curiously modified: its entire extrinsic complement is made up of only three muscles - the protractors, retractors and the extensors of the galeal proboscis, unlike the several ones met with in the generalized orders (Plate No. 60, Fig. Nos, I, II & III; Chart No. 1, Col. 14).

The protractor complement is made up of a single muscle bundle which arising on the anterior tentorial arm inserts on the rudiments of the cardo. From its attachments, this muscle appears to be the homologue of the ventral adductor of the cardo.

The retractor complement also consists of a single muscle bundle which arises on the anterior tentorial arm...
and inserts on the 'galea cuticle' situated at the junction of the galea and the stipes. From its attachment with the galea, this muscle appears to be the modified stipital flexor of the galea.

In contrast to the above two, the extensor complement, however, is represented by three fasciculi - one arises on the clypeus, whereas the other two originate on the anterior tentorial arm. All these fasciculi insert on the stipital apodeme and hence appear to be the modified ventral adductor of the stipes found in the other types. It may be recalled here that similar shift in the origin of the muscle has also taken place in the cases of the mecopteran and hymenopteran types.

The maxilla in the lepidopteran type is also provided with the unique intrinsic muscles. These muscles are the proximal and distal elevators, and the secondary oblique muscles in the galea. Since these muscles do not occur in any other insectan types the determination of their homology is elusive.

The proximal and distal elevators of the galea serve to compress the galeal cylinder and in the process, they raise the basal region of the proboscis throughout the coilable length. Thus, in conjunction with the hydrostatic
pressure produced by the haemocele fluid, these muscles serve to uncoil and extend the proboscis. The recalling of the proboscis takes place automatically due to the elasticity of galeal wall, when these muscles relax.

The secondary oblique muscles occur only in the 'knee-bend' region of the proboscis. Since these muscles have exact opposite orientation as compared to the proximal and distal levators of the galea, they only control the action of the latter two. The combined actions of these intrinsic muscles help in probing the nectaries with the minimum of the body movements.

All the above modifications in lepidopteran type are in conformity with the formation of galeal proboscis and consequent evolutionary changes in the cephalic capsule of the group.

Mention may be made here that the views expressed here regarding the homology of the various muscles are identical to the interpretations made by Schmitt (1938), Eastham and Bassa (1955), Bassa (1953, '63b, '67), on the bases of embryology and mode of innervation. Comparative studies by Srivastava (1957) and studies by Vasudeva (1957), Mitchell and Seabrook (1971) and Macfarlane and Eaton (1973) in the various lepidopteran types also are in agreement with all the afore-mentioned peculiarities.
(f) The maxillary muscular pattern in the case of the brachycerous dipteran type also is a degenerated and a modified one, but in a very different plane, when compared to the others investigated here.

The degeneration is very conspicuous in the absence of the dorsal retractor of the cardo, the stipital flexor of the lacinia, the stipital flexor of the galea, the extrinsic levator of the palp and the intrinsic palpal levators and depressors. (Plate No. 64, Fig. No. III; Chart No. 1, Col. 15).

Further, the persistent muscles show functional modifications as follows: the ventral adductors of the cardo and stipes function as the retractors of the maxillary stylet, whereas the cranial flexor of the lacinia acts as the protractor of the stylet; the small extrinsic depressor of the palp, however, operates the concomitantly reduced maxillary palp.

The various foregoing features of the maxillary and its musculature are in correlation with the piercing and sucking type of feeding entailed by the ectoparasitic life in the brachycerous Diptera.

Very similar features are also noted by Bonhag (1951), Bletchley (1954), Krystoph (1961), and Wenk (1962), in the various species of brachycerous Diptera.
(a) The definitive labium in Thysanura and lower Pterygota is composed of the proximal postmentum and the distal prementum, the latter bearing the paired glossae and paraglossae internally and the palp externally. The prementum is homologous with the maxillary stipes, the glossa with the lacinia and the paraglossa with the galea of the maxilla. The palp is the teolpodite and is three-segmented in Thysanura and lower Pterygota. (Snodgrass 1935, Das 1937, Dorsey 1943, Matsuda, 1965).

Such a generalized labium in the case of the thysanuran type is operated by the following muscles - the cranial depressor of the glossa, the cranial levator of the paraglossa, the cranial retractor of the prementum, the retractor of the prementum, the intrinsic flexors of the glossa and paraglossa, the extrinsic levator and depressor of the palp and the intrinsic levator and depressors of the palp in the first two palpal segments. (Plate No.2, Fig. No. IV; Chart No.1, Col. 1).

All these muscles are very well-developed in the thysanuran type and provide an efficient movement to the appendage during prehension and ingestion.
Chaudonneret (1948, '50) has noted the identical features in the case of *Thermobia domestica*, (Lepismatidae). He has further shown convincingly that the condition met with in *Thermobia* is more generalized than that in *machiilla*.

 Obviously, it may be inferred here, without entering into further discussions that the labial muscular pattern described above in the thysanuran type is a generalized and a primitive one.

 (b) When compared to that in the thysanuran type, the labial muscular pattern in the case of the ephemend type is a degenerated one, since it conspicuously lacks the cranial depressor of the glossa, the cranial levator of the glossa, the tentorial retractor of the prementum, the extrinsic flexor of the paraglossa, the median retractor of the prementum, the retractor of the mentum, the intrinsic levators and depressors of the labial palp. (Plate No. 6, fig. No. IV; Chart No. 1, Col. 2).

 The absence of such a large number of muscles obviously has led to the inefficiency in the working of the appendage which is attenuated to a certain extent by the following modifications in the persisting muscles. Of these, the cranial retractor of the prementum acts as the retractor of the entire labium. The cranial depressor of
the paraglossa has shifted its insertion to the apical area of the prementum and thus acts as the flexor of the whole labium. The intrinsic flexors of the glossa and paraglossa are well-developed to operate the terminal parts. The extrinsic palpal depressor and levators insert at the base of the second palpal segment to provide more leverage and efficiency to the palp. Further, the ventral dilator muscle of the salivarium the homology of which obscure, has shifted its attachment to the hypopharynx in the absence of the salivary apparatus. Thus, it acts as the retractor of the prementum.

Very similar features are also noted by Strenger (1953), Brown (1961) and Hoars (1961) in the various species of the Ephemeroptera.

It may be pointed out that the above-mentioned degeneration and modifications in the labial muscular pattern presumably are correlated with the pronounced sclerotization of the head capsule and appendages and also with the cuticular attachment of the labium to the head by the fusion of the postmental arms with the sides of the occipital foramen. (Strenger 1953).

(c) When compared with the situation in the thysanuran and ephemeralid types, the labial muscular pattern in the case of the odonatan types is extremely degenerated and exhibits certain unique features.
The degeneration is very conspicuous in that its entire complement is made up of only two muscles - the abductor of the lateral lobe and the hypopharyngeo-premental retractor muscle. Of these, the first one is a modified intrinsic flexor of the glossa or a modified intrinsic flexor of the paraglossa or it may be a fusion product of the both, since on the bases of embryological and comparative studies, the labial lateral lobe in the Odonata is proved to be a fusion product of the glossa, paraglossa and the palp (Munscheid 1933; Snodgrass 1954; Asahina 1954; Ando 1962; Matsuda 1965). The second muscle, however, is a modified ventral dilator of the salivarium, which has shifted its attachment to the hypopharynx in the absence of the salivarium in this group. (Plate Nos. 10, 14, Fig. No. IV; Chart No.1, Cols. 3, 4).

Thus with such a degeneration, the labium merely holds the prey which is usually caught in the basket of the grasp of the prehensile legs (Snodgrass 1954, Matsuda, 1965).

The functional inefficiency of the labium is, however, attenuated, although to a very less extent by the occurrence of two exclusive and special muscles - the elbow muscles in the junctional area of the pre-and post-mentum. According to Munscheid (1933), Snodgrass (1954)
Ando (1962), these 'elbow-muscles' are coenogenetically acquired in the nymphal stages, persist during metamorphosis, and are retained in the adult Odonata also. Since these muscles are unique and do not occur in the other insectan types, the homology of these muscles is impossible to determine.

Very similar features as regards the labial musculature are also noted by Asahina (1954); Mathur (1956); Mathur and Mathur (1961); Srivastava and Mehta (1965) in various species of the Odonata.

The various aforesaid degenerated features and modifications are evidently correlated with the aerial predatory habit in the Odonata.

(d) When compared to the situation described in the thysanuran type, the labial muscular pattern in the dictyopteran, isopteran and orthopteran types again is a degenerated one, for it conspicuously lacks the cranial depressor of the glossa, the cranial levator of the glossa, the cranial levator of the paraglossa and the retractor of the prementum. This degeneration in the case of the orthopteran type, however, is further emphasized by the absence of another muscle - the median retractor of the prementum. (Plate Nos. 18, 22, 32, Fig. No. IV; Chart No. 1, Cols. 5, 6, 7).
It appears that the aforesaid reduction in the number of labial muscles is perhaps offset by the high degree of sclerotization of the cephalic capsule and the appendages in the Dictyoptera, Isoptera and the Orthoptera.

The eventual limitation of mobility and the consequent functional inefficiency in these cases, however, is compensated indirectly by the better development of the persisting muscles, which coupled with the more sclerotization of the head and its appendages in these groups, can impart more precise and articulate movements to the labium.

Mention may be made here that notwithstanding the above alluded fundamental similarity in their anatomical makeup, apparent variations occur in these three cases with regard to their intrinsic palpal muscles. In the dictyopteran and isopteran types, the intrinsic levators and depressors occur in the first two palpal segments, whereas in the orthopteran representative the intrinsic levators occur only in the first segment and intrinsic depressors occur only in the second segment.

The aforesaid variation in the distribution of the intrinsic palpal muscles is correlated with different manoeuvring movements performed by the palp.
The various foregoing features of labial musculature conform with those noted by Dorsey (1943), Snodgrass (1944, 52), Albrecht (1953), Rakshpal (1954), Richards (1955), Vishnoi (1956, '62), and Popham (1961) in the various species of the Dictyoptera, Isoptera and Orthoptera.

(e) As compared to the situations described in the cases of other insectan types, the labial muscular pattern in the heteropteran representatives also shows degeneration and unique modifications but altogether in a different plane. The degeneration is most conspicuous in that its entire complement is made up of only three muscles - the retractor of the rostrum, the protractor of the rostrum and the proximal adductor of the rostrum. Of these, the retractor of the rostrum is believed to be the homologue of the cranial or tentorial retractor of the proventrum on the bases of comparative studies (Butt 1943; Kramer 1943; Matsuda 1965). The correlative evidences from embryology and innervation patterns are, however, needed.

The protractor of the rostrum is supposed to be a modified hypopharyngeo-premental protractor muscle, since the first definitive segment of the rostrum is a modified prementum. (Matsuda, 1965). This view derives support also from the embryological studies of Newcomer (1948).
Further, the proximal adductors of the rostrum are regarded as the derivatives of the extrinsic palpal levator or depressor muscle, since the rostral segments distal to the prementum are believed to be the modified palpi. (Matsuda, 1965). This view derives its support from the circumstantial evidence that similar beaks in Siphonoptera and Diptera are palpal in origin. However, there is no direct developmental evidence supporting the palpal origin of the rostrum in the Hemiptera. If the palpal origin of the rostrum in the Heteroptera is valid, the intrinsic distal retractors and protractors of the rostrum are to be considered as the derivatives of the intrinsic levator and depressor of the labial palp.

Snodgrass (1928, '35, '38), Pesson (1944), Newcomer (1948), Quadri (1949, '51, '59), Aziz and Quadri (1950), Barth (1953), Akbar (1957), Benwitz (1959), Parsons (1959, '62), and Saxena (1963), have noted similar features in the various species of Heteroptera.

The above-mentioned ensemble of modifications in the labium and its musculature is obviously correlated with the formation of the rostrum and the occurrence of entognathy in the Heteroptera.

(f) The labial muscular pattern in the neuropteran type is a reduced and modified version of the one described
in the cases of the dictyopteran and isopteran representatives, for it conspicuously lacks the median retractor of the prementum and the intrinsic flexors of the glossa and paraglossa. The absence of the median retractor of the prementum is both anatomically and functionally compensated by the occurrence of another muscle - the retractor of the mentum. The occurrence of the retractor of the mentum is characteristic of the neuropteran type alone and is perhaps entailed by the division of the postmentum into the submentum and mentum in this group. (Snodgrass 1935, Korn 1943, Hoyt 1952, Matsuda, 1956, 65).

The absence of the intrinsic flexors of the glossa and paraglossa are, however, obviously correlated with the fact that in the Neuroptera the paraglossae are absent and the glossae form a circular ligula by median fusion. (Kelsey 1954). Thus, the mobility and consequent functional efficiency of the distal part of the labium is much reduced in this group. (Plate No. 44, Fig. No. IV; Chart No.1, Col.10).

Very similar features regarding the labial musculature are also observed by Korn (1943), Hoyt (1952), Kelsey (1954) and Matsuda (1956), in different species of Neuroptera.
(g) The labial muscular pattern in the coleopteran type in its turn is only a highly degenerated variant of the one described in the dictyopteran and isopteran types.

Its degeneration is evidently seen in the absence of the intrinsic flexors of the glossa and paraglossa and the extrinsic depressor of the palp. In conformity with this, the intrinsic depressor and levators are also lacking in the first and second segment of the labial palp. These degenerated features in the coleopteran type are correlated with the heavy sclerotization of the head and its appendages and consequent functional debility in the genetically-reduced terminal labial parts in the Coleoptera (Dorsey 1943, Richards and Davies 1964). According to Evans (1961b), the reduction in the labial musculature is also due to the absence of the muscles associated with the salivary opening. (Plate No. 48, Fig. IV; Chart No. 1, Col. 11).

Mention may be made here that similar degeneration in the labial musculature is also observed by Pradhan (1938), Dorsey (1943), Butt (1951), Saxena (1953) and Evans (1961) in the different species of Coleoptera.

(h) When compared to the situations in the other insectan types, the labial muscular pattern in the case of the hymenopteran type again exhibits degeneration and unique modifications. (Plate No. 52, Fig. No. IV; Chart No. 1, Col. 13).
Its degeneration is quite conspicuous in the absence of the median retractor of the prementum, the retractor of the mentum and the extrinsic levator of the palp. Moreover, in compliance with this degeneration, the intrinsic depressor is lacking in the first palpal segment, whereas the intrinsic levator is absent in the second palpal segment. The consequent functional inefficiency, however, is fully compensated by the following modifications of the persisting muscles. Firstly, the cranial retractor of the prementum has shifted its origin to the anterior tentorial arm and its insertion to the tendon from the median proximal part of the prementum. Thus, it acts as the posterior adductor of the labium. Secondly, the tentorial retractor of the prementum has shifted its origin to the cranial wall and is inserted on the distal end of the ligular arm of the prementum. Hence, this muscle acts as the anterior adductor of the labium.

Thirdly, the intrinsic flexors of the paraglossae act as the retractor of the entire ligula, whereas the intrinsic flexors of the glossa bring about the retraction and rotation of the tongue. Finally, the extrinsic depressor of the palp and the intrinsic levator and depressor of the palp serve to flex the palp.
These features mentioned conform with those noted by Morrison (1927), Snodgrass (1942, '56) and Alam (1951) in various species of the Hymenoptera.

The aforesaid degeneration and ensemble of modifications are obviously entailed by the presence of maxillo-labial proboscis as a necessary adaptation for the lapping and sucking mode of feeding in the Hymenoptera.

(1) The labial muscular pattern in the mecopteran type is a reduced variant of the one described in the case of the neuropteran type. Its degeneration is evidently seen in the absence of the retractor of the mentum, the cranial retractor of the prementum and the tentorial retractor of the prementum. In conformity with this, the intrinsic palpal musculature is entirely lacking. (Plate No. 56, Fig. No. IV; Chart No.1, Col. 12).

The eventual functional deficiency is attenuated to a certain extent by the presence of the median retractor of the prementum, which acts as a direct replacement for the missing retractor of this part of the appendage. Further, it is also compensated to some extent by the occurrence of two extrinsic depressors of the palp, one of which inserts at the base of the second palpal segment to replace functionally the missing intrinsic palpal muscles. With
such a reduced musculature, the labium only functions as a prop against the food during feeding.

All these degenerated features of the labial musculature, noted here, concur with those observed by Heddergot (1938), Imms (1944) and Hinton (1958) in different mecopteran types. They are obviously correlated with the elongation and lateral compression of the labium that is devoid of the glossa and the paraglossa, thus forming the ventral portion of the characteristic rostrum in this group.

(j) The labial musculature in the case of the lepidopteran type is extremely degenerated, unlike the condition in the other insectan types, for it is represented by only one muscle - the levator of the palpus arising from the hypostomal bridge. Similar observations are also made by Bassa (1953, '63b), Eastham and Bassa (1955), Srivastava (1957), Vasudeva (1957), Mitchell and Seabrook (1971) Macfarlaine and Eaton (1973), in the various species of Lepidoptera. According to Schmitt (1938), the labial musculature in some species of Lepidoptera is represented both by the levator and depressor of the palp, whereas in others the labial musculature may be completely absent. This degeneration of the labial musculature is correlated with reduction of the appendage and its fusion with the hypostomal bridge, which in turn is entailed by the formation
of the galeal proboscis for siphoning the food. In this group (Matsuda 1965) (Plate No. 60, Fig. No. II; Chart No. 1, Col. 14).

(k) When compared to the situations in the other insectan types, in the dipteran type the labial muscular pattern is highly degenerated and curiously modified. These features are reflected in that its entire complement is made up of only three modified muscles - the retractor of the proboscis, the extensor-rotator and the retractor-flexor of the labellum. The retractor of the proboscis is inserted on the proximal ridge of the prementum and thus functions as the retractor of the prementum and hence of the proboscis. On the basis of its attachments, this muscle appears to be the homologue of the cranial retractor of the prementum. (Plate No. 64, Fig. No. IV, V; Chart No. 1, Col. 15).

The extensor rotator of the labellum arises on the dorsal wall of the premental theca and inserts on the dorsal proximal part i.e. on the hypoglossal paraphysis of the labellum. Since the labellum is a modified palpus, (Imms 1944) this muscle can be regarded as the derivative of the extrinsic levator of the labial palp.
The retractor (thf: flexor) of the labellum is represented by two fasciculi - both of which arise on the ventral wall of the premental theca. One of these inserts on the furcal sclerite at the proximal part of the labellum whereas the other inserts on the epifurcal sclerite at the distal part of the labellum. Inasmuch as the labellum is a modified palpus and the furcal and epifurcal sclerites in the labellum mark the basal parts of the first and second palpal segments, (Graham-Smith 1930; Imms 1944; Schiemann 1957; Wenk 1962), these muscles here, appear to be the homologues of the extrinsic depressors of the labial palp inserting on the modified basal parts of the first and second palpal segments.

It may be recalled here that in the mecopteran type also, the depressor of the second palpal segment is found to originate on the prementum. This perhaps is a sympleisiomorphic feature indicating the closer relationship between the Mecoptera and the Diptera.

Besides all these above-discussed muscles, the labial musculature in the dipteran type has also special complementary muscles - the compressors of the labial haustellum which serve to control the depth of the labial gutter. Since these muscles do not occur in any other insectan types, their homology remains obscure. Perhaps they are neogenetic.
Mention may be made here that the views expressed here regarding the homologies and other features of the various muscles, are in agreement with those of Imms (1944), Goin (1949), Bonhag (1951), Hoyt (1952), Bletchley (1954), Schiemenz (1957), Snodgrass (1959), Krystoph (1961), Wenk (1962) and Matsuda (1965) on the bases of comparative and functional studies. Dethier's (1959) studies on the modes of innervation also conform with the aforementioned homologies and peculiarities of the labial muscles. However, correlative embryological evidences regarding their homologies are necessary.
II. THORACIC MUSCULARITY AND ITS ROLE IN LOCOMOTION.

The salient features of the thoracic muscular patterns of the presently-investigated insectan types, as obtained from their comparative studies, are discussed in the succeeding pages.

A) PECULIARITIES OF THE THORACIC MUSCULAR PATTERN IN THE THYSAANURAN TYPE. (Vide Plate Nos. 3, 4, 5; Chart No. 2, Col. 1).

(a) The occurrence of the lateral transegmental dorsal longitudinal muscles is a remarkable archaic feature in the thysanuran type, since such muscles, which cross the segmental borders are reported to occur characteristically in the primitive Apterygota and Myriapoda (Barlet, 1953, 1954, 1967; Barlet et Carpentier 1962; Gruner 1953; Manton 1952b, 1954). Contraction of these muscles lifts the body and thus assists the weak thoracic legs in locomotion.

Amongst the Pterygota, similar muscles occur only in the odonates as will be discussed later.

It may be pointed out here that the presence of such transegmental dorsal longitudinal muscles, in the Odonata, is in striking contrast to the condition assumed
and depicted by Snodgrass (1927, '35, '58) in his hypothesis of the insectan intersegmental relationship, wherein dorsal longitudinals are typically shown attached between the successive antecostae (endonota). Such a condition, in fact, is an advanced one, since it is only in most Pterygota, with already well-developed phragma, that the distribution of dorsal and other muscles is largely confined within each segment.

Thus, Snodgrass' hypothesis does not explain the significance of the transegmental dorsal longitudinal muscles. And, therefore, his interpretation of insectan intersegmental relationship, perhaps, is not correct. As Matsuda (1970) states "Clearly, Snodgrass" theory was based on the preconception that the phragma arises only from the antecosta (endonotum)..........................and that postnotum is an enlarged acrotergiten".

Indeed, as Matsuda (1970) has interpreted it convincingly, the endonotum is only an inconspicuous rudimentary adjunct in the definitive pterygote phragma and not its lone precursor. Since such definitive phragmata are not yet formed in the Thysanura, the segmental borders in its representative are marked only by the inconspicuous rudimentary endonota which occur in their primary condition and allow the free crossing of the longitudinal muscles beyond the segmental borders.
(b) The dorsal and ventral intersegmental longitudinal muscles in the thorax of the thysanuran type, are well developed and in conjunction with each other produce traction and lateral undulations in the flexible and less sclerotized thorax. This is of immense value in the locomotion of the thysanuran type, since the legs are very weak and do not lift the thorax above the ground level. Manton (1952b, 1953, 1954) has fully described this feature in the Myriapoda also.

Thus, this characteristic appears to be simplesiomorphic in the two groups. It, perhaps, is an inheritance from the annelidan type of ancestor, (Snodgrass 1935, '38, '58; Manton 1952b, '53, '54; Barlet 1953, '54, '67), in which phylum the phragmata do not occur and transsegmental muscles are present.

(c) Muscles strictly occurring within the pleuron in the pterygotes i.e. muscles 12-27 (t-p4 to t-p26 of Matsuda, 1970) and muscles 39-42 (p-1 to p-5 of Matsuda)- are absent in the thysanuran type. This primitive feature, obviously, is correlated with the membranous and undifferentiated pleuron in the thysanuran type (Barlet 1951, '53, '54, '67; Snodgrass 1958; Matsuda 1970).
(d) As is pointed out by Barlet (1951,'53,'54), the tergoanapleural and the tergoketapleural muscles are numerous in the thysanuran type, since the anapleuron and the ketapleuron occur as undifferentiated sclerotized areas.

(e) The lateral tergo-sternal muscles occur abundantly, unlike the condition in the pterygote types to be described later. Maki (1938), Barlet (1951,'53, '54, '67) and Bretfeld (1963), have pointed out similar features in the other apterygotes also.

These lateral tergosternals act antagonistic to the longitudinal muscles in the thorax and help in effecting the lateral undulations in the body essential in this traction movement.

(f) The muscles operating the legs - the tergotrochantinals, tergocoxals, sternocoxals, pleurocoxals and the trochanteral muscles are numerous and well-developed. Likewise in other apterygotes also Maki (1938), Barlet (1951,'53,'54,'67) and Bretfeld (1963) Matsuda (1963a,b) have noted very similar features.

Thus, as Snodgrass (1958) says - "It is clear that the thoracic musculature of the apterygotes is adapted to the needs of these insects and could hardly serve as the
basis for the wing musculature of the pterygotes. No apterygote could fly even if it had wings.

(B) **PECULIARITIES OF THE THORACIC MUSCULAR PATTERN IN THE EPHEMEROPTERA.** (Vide Plate Nos. 7, 8, 9; Chart No. 2, Col. 2).

(a) The tergo-anapleural and ketapleural muscles which are present in all the thoracic segments of the thysanuran type are found to persist only in the prothorax in the case of the ephemerid representative. Obviously, this can be correlated with the lesser sclerotization and differentiation of the prothoracic pleuron in the Ephemeroptera (Snodgrass 1958). It appears that the presence of these muscles in the representatives of both the Thysanura and Ephemeroptera is a primitive synapomorphic feature in the two groups.

Conversely, the absence of these muscles in the meso- and metathorax of the ephemerid type can be assigned to the occurrence of the wings and better sclerotization of the wing-fulcrum, basalar and subalar and the 'pseudo-pteralia' of Grandi (1947b) or the usual wing sclerites. (Snodgrass 1958; Matsuda 1956, 1970; Brodsky 1970).

(b) The presence of a large number of tergo-ternal muscles (Muscles Nos. 28, 30, 32 and 34) is
decidedly a primitive feature in the ephemerid type, since such muscles occur abundantly in the thysanuran type alone.

The foregoing features 'a' and 'b' are essentially similar to those noted by Knox (1935), Maki (1938), Grandi (1947) and Matsuda (1956b, '70) in the different species of Ephemeroptera.

(c) The usual important indirect flight muscles in the other pterygote types excepting the Odonates - the median dorsal longitudinal muscles, the fourth tergopleural muscles, and the tergal depressor of the trochanter are well developed and function as the principal wing motors in the ephemerid type also. The wing mechanism of the mayfly is thus clearly of the indirect type, in striking contrast to the direct wing mechanism of the Odonates to be described later. The Ephemeroptera and Odonata, therefore, are not related insects; they perhaps represent two early lines of pterygote evolution wherein the mechanism of flight was differentiated by two different methods adopted for moving the wings. (Snodgrass 1958).

Brodsky (1970) has corroborated this view in his investigation on the E. vulgata.

(d) The special characteristic of the flight mechanism in mayfly, however, lies in the presence of a
greater number of direct flight muscles too, in addition to
the afore-mentioned indirect ones. As is explained by
Grandi (1947b) and Brodsky (1970), these indirect flight
muscles are found to function as follows -

(i) The contraction of the fifth pleurosternal
muscle (Muscle No. 49, p-s12 of Matsuda 1970) causes the
extension of the wing, since the basalare to which this
muscle is attached is connected to the tegula and the
humeral plate.

(ii) The tergal promotor of the coxa (Muscle
36; t-cx4 of Matsuda) and the trochanteral muscle of the
third axillary sclerite (Muscle 64; t-tr2 of Matsuda) are
inserted dorsally on the first axillary sclerite. These
muscles are responsible for holding the wings vertically
along the axillary inflection, when at rest.

The tergal promotor of the coxa, (t-cx4 of Matsuda)
is elsewhere found only in the odonatan types in the
pterygotes.

The occurrence of the trochanteral muscle of the
third axillary sclerite (t-tr2 of Matsuda) is an exclusive
feature of the ephemerid type, since this muscle is not
found in any other insectan type investigated.
(iii) The furcal muscle of the third axillary sclerite (Muscle 34; t-s3 of Matsuda) has shifted its attachment to the junction of the second and third axillary sclerites. The contraction of this muscle, therefore, causes slight wing-flexion.

(iv) The muscle of the fourth axillary sclerite (Muscle 19; t-p15 of Matsuda) also helps for holding of the wings vertically along the axillary inflection, when at rest.

(e) Brodsky (1970) asserts that the vertical position of wings at rest in ephemerids is not primary, but a secondary adaptive feature in the evolution of the Insecta. The ephemerids possess all features required for wing folding and - flexing-viz. the four wing-sclerites (pseudopteralia of Grandi 1947b), a wing flexor muscle - the muscle of third and fourth axillary sclerites (Pleuroalar muscle of Brodsky 1970) and jugal fold, but these muscles serve other purposes in the order.

(f) The second tergo-basalar muscle (Muscle 15; t-p8 of Matsuda) connects the episternum and the lateral scutal margin above the basalare. Because of this shift in its insertion, the second tergobasalar muscle plays completely a minor role in the wing movements.
(vi) The furco-subalar muscles (Muscles 30 t-s4 and 5 of Matsuda) and subalar coxal muscles (Muscle 38 t-cx8 of Matsuda 1970) cause active change in the stroke-plane in controlling of the power output (via amplitude stroke) and in controlling of the elasticity of the thoracic capsule. Bekker (1954) also emphasized the importance of the subalar muscles in lowering of the wings.

(vii) As is described by Bocharova and Messner (1965), the fourth pleural muscle (muscle 42, p5 of Matsuda) or the pleuro-basalar muscle, the muscle of the first axillary sclerite (Muscle 16, t-p10, 11 of Matsuda) and the pleural promotor of the coxa (Muscle 59, p-cx4, 5) also act as the direct wing muscles.

The fourth pleural muscle (the pleuro-basalar) pronates and depresses the wing and thus acts as a functional replacement for the missing third pleural muscle.

The muscle of the first axillary sclerite helps in holding the wing vertically along the axillary inflection.

The pleural promotor of coxa acts as the pronator-extensor of the wing.

(g) To overcome the interaction between the pterothoracic segments and to reduce the effect of the
phase-difference between the wing pairs during flight, the metathorax, its wings and its muscles in the ephemeral type are reduced. Main power for motivation is derived from the mesothoracic muscles (Pringle 1957). This reflects, in a less pronounced manner, the condition in the higher insects like Diptera and Hymenoptera. This feature supports the proper placing of the Ephemeroptera in the neopteran groups.

(h) It is noteworthy that inspite of all the above-mentioned advanced features, the flight in the ephemeralds is weak. According to Edmunds and Traver (1954) some of the concave veins in the ephemeral wings have weakened spots called 'bullae', which allow the concave veins to bend; consequently during the upstroke these concave veins fail to support the distal half of the wing. On the upstroke, the distal half of the wing then bends downward under the presence of the opposing air. The opposing air slips away in such a manner that it offers lessened resistance to the upstroke of the wing. According to Matsuda (1970), in such a flight the fifth pleurosternal muscles, (Muscle 49; ps12 of Matsuda), help keep the anterior margin of the wing somewhat rigid.

(i) Curiously, the pleuro-trochantinal muscles and the third pleural muscle are lacking in the ephemeral
type too, as is the situation in the thysanuran representative. This perhaps, appears to be a primitive synapomorphic feature in the two groups indicating their closer relationships.

(i) The appendicular muscles - the coxal and trochanteral muscles are all well-developed and profusely differentiated, much like the condition in the thysanuran type. Obviously, this is correlated with the genetically predominant aquatic nymphal life in the Ephemeroptera, involving the more use of legs. The tergotrochantinals have shifted their insertion to the anterior coxal margin, since the trochantin is lacking in Ephemeroptera.

(C) **PECULIARITIES OF THE THORACIC MUSCULAR PATTERN IN THE ODONATAN TYPES.** (Vide Plate Nos. 11, 12, 13, 15, 16, 17; Chart No. 2, Cols. 3, 4).

(a) The presence of the median transegmental dorsal longitudinal muscles forms an archaic feature, in the odonatan representatives, since the homologues of these muscles are reported to occur in Oncojapyx (Diplura) and *Lepismachilis* (Thysanura) (Barlet and Carpentier 1962; Barlet 1967; Matsuda 1970). Furthermore, muscles similar to these - the lateral transegmental dorsal longitudinals -
are found only in *Lepisma* and not in any of the pterygote types investigated. Ballets' (1947, '51, '54) observations in this regard are essentially similar.

Thus, as Matsuda (1970) has said, "the tran-segmental distribution of the dorsal longitudinal muscles in Odonata is apparently a reduced version of the dorsal thoracic musculature in Apterygota".

The presence of this character in these groups is probably symplesiomorphic and it corroborates the view that the Odonata had a very early divergence from the main protaehexapod stock even earlier to the origin of the *Ephemeroptera*. (Lemche 1940, Snodgrass 1958, Matsuda 1970).

(b) Characteristically, the distribution of the median transegmental dorsal longitudinal muscles, the fifth to tenth tergopleural muscles, the third tergosternal muscle and the thoracico-abdominal ventral longitudinal muscle is confined to odonatan types only.

The presence of the tergal promotor of the coxa (t-cx4 of Matsuda) is shared by the odonatan and ephemerid types.

Asahina (1954), Tannert (1958), Hakim (1963, '64), Hatch (1966), have also noted similar features in the
different odonatan species. The occurrence of such a large number of unique muscles, obviously is in conformity with concomitant modifications in the thoracic skeleton (Matsuda 1970).

(c) The common indirect flight muscles found in the other pterygote types - the median dorsal longitudinal muscles, the fourth tergopleural muscle and the third pleural muscle - are very conspicuously lacking in the odonatan types. This again is strictly correlated with the concomitant modifications in the thoracic exoskeleton. (Asahina 1954, Tannert 1958; Hakim 1963, '64; Hatch 1963, '64).

Eventually, the power for wing motivation is derived from the direct wing muscles in striking contrast to the other pterygotes including mayflies. This feature clearly indicates that the Odonata represents an early and separate line of pterygote evolution differentiated by the direct type of wing mechanism. (Lamche 1940; Snodgrass 1958, Matsuda 1970).

(d) As is pointed out by Tannert (1958) and Neville (1960), the direct wing muscles in the Odonatan types can be well defined by their action into two categories - those concerned with elevation and depression and those responsible for supination and pronation.
(i) Among the levators, the second tergosternal (Muscle 32; t-sl10 of Matsuda 1970) is attached dorsally to the tergal apophysis, whereas the third tergosternal (Muscle 33; t-x11 of Matsuda) is attached to the ventral process of the scutum. Among the depressors the seventh tergopleural is attached dorsally to the anterior captendon, which in turn is connected with the median area of humeral plate. The eighth tergo-pleural (Muscle 25; t-p24 of Matsuda) is attached to the articular process of the R+M veins through the posterior captendon; and the ninth tergopleural (Muscle 26; t-p25 of Matsuda) is inserted on the posterior margin of the axillary plate. The contraction of these muscles directly causes wing depression because of their more lateral positions.

(ii) The wing supination is caused by the tergal promotor of coxa (Muscle 36; t-cx4 of Matsuda) and the fifth tergopleural muscle (Muscle 22; t-p21 of Matsuda) during the last phase of downstroke and during upstroke. The pronation is caused by the sixth and seventh tergopleural muscles (Muscles 23 and 24; t-p22 and t-p23 of Matsuda) during the last phase of upstroke and the downstroke. The supination control of the pronation is done by the ninth tergo-pleural muscle (Muscle 26; t-p25 of Matsuda), which thus brings about the pronation-supination balance.
(e) In both the pterothoracic segments of the zygopteran type and in the metathorax of the anisopteron type, the muscle of the first axillary sclerite (Muscle 16; Muscle t-p11 of Matsuda) has shifted its attachments - it connects the pleural wing process and the tergal apophysis.

In the mesothorax of the anisopteron type, however, this muscle has retained its normal attachments. Here it connects the flexible plate lateral to the scutum (First axillary sclerite of Asahina 1954) and the lower portion of the pleural wing process.

Tannert (1958), therefore, supported Magnon's (1934) hypothesis that in the Zygoptera the fore- and hindwings both function similarly maintaining comparatively more of the phase-difference between their beats. This feature when coupled with the petiolate type of wings accounts for the slow flight in Zygoptera, since the 'thrust' and 'lift' produced by one pair of wings are opposed by those of the other.

In contrast to this, according to Magnon (1934) and Tannert (1958) the above-mentioned features of the first axillary muscle, in Anisoptera, cause the forewings and hindwings function differently with comparatively reduced phase-difference between their beats. Neville (1960) also, proved experimentally that comparatively less
phase-difference exists constantly between the wing-beats. This feature when coupled with the well-developed wings with broad base and narrow tips as well as to the stiff veins accounts for the efficient flight in the Anisoptera. For in this case 'lift' and 'thrust' produced by one pair of wings are enhanced by those of the other. Thus Tannert (1958) pointed out "Odonata are indeed remarkable in that they have developed such an efficient flight mechanism without sacrificing the function of one of the two pairs of wings (usually the hindwing) by reduction". It should be mentioned here that the highly efficient flight in Diptera to be discussed later, for instance, is by the nearly total reduction of the hind-wing.

(f) The tergotrochantinal muscles in odonatan types insert on the anterior coxal margin, since the trochantin is absent in Odonata.

(g) The only sternocoxal muscle present in the odonatan types is the second sternal promotor of the coxa (Muscle 56; s-cx3 of Matsuda).

(h) Characteristically, the various muscles operating the legs are exclusively meant for the purpose. The only leg muscle that is involved in the flight is the tergal promotor of the coxa (Muscle 36; t-cx4 of Matsuda).
Observations of Magnon (1934), Clark (1940), Asahina (1954) and Tannert (1958), are essentially similar as regards the above features of the leg-muscles.

Thus, the legs in the Odonatan types are freely movable even during flight, which is a unique adaptation for aerial predation.

(D) PECULIARITIES OF THE THORACIC MUSCULAR PATTERN IN THE DICTYOPTERAN TYPE. (Vide Plate Nos. 19, 20, 21; Chart No. 2, Col. 8).

(a) The thoracic musculature in the dictyopteran type is characteristic in the absence of the indirect wing levators like the posterior fourth tergo-pleural muscle (Muscle 13, t-p6 of Matsuda) and the third pleural muscle (Muscle 41; p3 of Matsuda), which are strongly developed in the other pterygotes; their absence again is correlated with the considerable reduction of the preepisternum in the Dictyoptera. Likewise, it is also characterized by the poor development of the indirect wing depressor - the median dorsal longitudinal muscles. In effect, therefore, the cockroaches are weak fliers and only occasionally take to flight.
(b) Very peculiarly, the fourth tergopleural muscle (Muscle 13; t-p5 of Matsuda 1970) in the dictyopteran type occurs only in the mesothorax. The metathoracic homologue of this muscle is absent, probably in correlation with the high degree of reduction in the metathoracic preepisternum unlike the mesothoracic one. This feature naturally contributes to the comparative degeneration of the faculty of flight in the dictyopteran type, since it normally acts as the main indirect wing elevator in other pterygotes. Observations of Carbonell (1947), Ewer & Naylor (1967), are also similar in this matter.

(c) Perhaps, the most unique feature of the thoracic musculature of the dictyopteran type is the neogenetic presence of the pleurotrochantinal muscle, (Muscle 58; p-ti 23 of Matsuda). Since this muscle is found to be absent in the cases of the thysanuran, ephemerid and odonatan types, it appears that this muscle has arisen secondarily as a flight muscle in the neopterous insects, as is proposed by Teigs (1955) and Matsuda (1970).

(d) During such occasional flights of the dictyopteran type, the wing levation is caused by the contraction of the relatively large number of the tergocoxals (Muscles 36 and 37; t-cx4 to t-cx7 of Matsuda), tergotrochantinals (Muscle 35; t-til to t-ti3) and the
tergotrochanteral muscles (Muscles 63 and 64; t-trl and 2 of Matsuda).

On the other hand, the leg muscles inserted dorsally on the subalare (Muscle 38; t-cx8 of Matsuda), the basalare muscle 67 & 59; muscles p-tr3 and P-cx4 and 5 of Matsuda), and the anepisternum (Muscle 58; P-ti 2, 3 of Matsuda) directly lower the wings. These above-alluded findings corroborate inferences of Chadwick (1953) regarding flight mechanism in insects which lack well developed dorsal longitudinal muscles. According to Ewer and Naylor (1967), the pleurotrochantinal muscles (Muscle 58; P-ti 2, 3 of Matsuda) depress the wing and cause its extension. Thus, the well-developed leg-muscles in the dictyopteran type are bifunctional, since occasionally they serve to operate the wings also.

(e) The aforesaid bifunctional muscles are equally well-developed in both the pterothoracic segments of the dictypteran type, since these thoracic segments and their wings are also equally well-developed. Eventually, there is a maximum interaction between the two segments of the thorax leading to maximum of phase difference in the contraction of their muscles, which in turn produces maximum phase difference in the fore-and hind wing beats. Thus, the occasional flights in the dictyopteran type are of
the flapping type. (Sotavaara, 1952, '54; Pringle 1957 and Snodgrass 1958).

(f) In the dictyopteran type, only one direct flight muscle - the second muscle of the third axillary sclerite (Muscle 18; t-p14 of Matsuda) is directly responsible for opening and folding of the wing. A highly complex connection of the third axillary sclerite with the neighbouring sclerites accounts for this action. Similar observations were also made by Carbonell (1947). In this respect the dictyopterans have advanced beyond the ephemerids and odonates.

(g) As is pointed out by Matsuda (1970) in the presence of comparatively large number of muscles arising form and within the pleuron (Muscles 8, 13, 14, 16, 18, 19, 35, 44 to 48, 51, 58, 59, 61, 67), the thoracic muscular pattern found in the dictyopteran type is more specialized than that in the ephemerid representative.

(h) All the sternocoxal muscles are very well-developed, in correlation with the floor-bound life of the Dictyoptera.

All the aforementioned features serve to testify Snodgrass' views (1958) that - "the members of the blattopteroid group have made little progress, if any,
toward the development of an indirect type of wing mechanism; rather, they seem to have not a very efficient type of mechanism of their own based somewhat on the dragonfly scheme of direct wing movement. There is no evidence that the dorsal musculature has been secondarily reduced, since structural features of the thorax that are essential to the indirect type of wing mechanism, such as postnotal plates between the wing-bearing plates and intersegmental phragmata, are entirely undeveloped. The cockroaches and the mantids very probably never flew better than they do today. The Blattopteroidae, on the basis of their wing musculature and thoracic structure, are appropriately separated in classification from the rest of the orthopteroid insects.

(E) PECULIARITIES OF THORACIC MUSCULAR PATTERN IN THE ISOPTERAN TYPE. (Vide Plate Nos. 23, 24, 25, 26, 27, 28, 29, 30, 31; Chart No. 2, Col. 6).

(a) In recognition of Matsudas' interpretation (1970), the thoracic muscular pattern in the alate swarming isopteran type has been found to be only a reduced version of that in the dictyopteran representative. In the former, fewer muscles of each category are present than in the latter. This similarity appears to be correlated with the
general resemblance in the thoracic structure of the
Dictyoptera and Isoptera (Fuller 1924; Crampton 1926a;

(b) Evidently, the median dorsal longitudinal
muscles (Muscle 1; t-t of Matsuda), and the pleurotro-
chantinal muscles (Muscle 58; p-ti 1 to 3) are too much
reduced in size and number to have any indirect action on
the wings.

According to Fuller (1924), however, these muscles
are completely absent in the representatives of Isoptera,
he dissected.

(c) During the nuptial flights, therefore, the
coco-subalar muscle (Muscle 38; t-cx of Matsuda), the
pleural depressor of the trochanter (Muscle 67; P-tr3 of
Matsuda) and the pleural levator of the coxa (Muscle 59;
P-cx of Matsuda) depress the wings.

The wing levation is caused by the tergocoxals
(Muscles 35; 37; t-cx of Matsuda) the tergotrochantinals
(Muscles 35; t-ti of Matsuda) and the tergotrochanterals
(Muscles 63 and 64; t-tr of Matsuda) as in the case of
the dictyopteran type. Thus, in the alate swarming
isopteran type also, the leg-muscles are bifunctional.
Since the pterothoracic segments and their wings are equal in size, the above alluded flight muscles in them are also similar in development. This has led to the maximum interaction between these thoracic segments causing ultimately maximum phase-difference in the contraction of their wings and in the eventual fore- and hind-wing beats. This, in turn, is the cause of flapping type of flight in the alate swarming isopteran representative. (Pringle 1957).

(d) In the royal forms of Isoptera, the thoracic muscles conspicuously exhibit still higher degree of reduction in size. This feature is very different from the muscle resorption in Heteroptera (Larsen 1949b) or from the degeneration of flight muscles known to occur in Coleoptera (Jackson 1952, Tietze 1963). This secondary reduction in the size of thoracic muscles in the termite royal forms seems to be correlated with their genetically predominant sedentary life in the royal chamber.

(F) PECULIARITIES OF THE THORACIC MUSCULAR PATTERN IN THE ORTHOPTERAN TYPE. (Vide Plate Nos. 33, 34, 35; Chart No. 2, Col. 7).

(a) In the othopteran type, the third pleural muscle and the pleurotrochantinal muscle (Muscles 41 and 58; muscles p3 and p-ti2 of Matsuda) function as the pronator-extensors of the wings. As pointed out by
La Greca (1947b), these muscles act on the costa-subcostal region of the wing through a ligamentous connection on the basicoxales. Since C-Sc vein acts as a pivot, the contraction of these muscles extends the wing. This peculiar feature has been also observed by Albrecht (1953), Ewer (1953, 1955, 1958, '64), Cambell (1961), Wilson (1962), Yu and Luh (1964) and Blackith and Blackith (1967).

(b) All the sterno-coxal muscles are well-developed. The second sternal promotor of the coxa (Muscles 53, 54, 56; S-cx 4 and 5 of Matsuda) originate on the secondary ridge formed in the area posterolateral to the furcal base, which is in contrast to the situation in other pterygotes, wherein these sternal leg muscles, arise on the furca of the basisternum and on the spina. This feature in the orthopteran type is consequent upon the shift forward of the mesosternum and metasternum (Snodgrass 1929; Misra 1946, '47; La Greca 1947, Albrecht 1953).

However, the above muscles still maintain their primitive points of insertion on the coxal margin and the above alluded shift in the points of their origin has seemingly no effect on their functional efficiency. Misra, 1946, '47; Albrecht 1953, Ewer 1955, '58, '64; Wilson 1962, and Yu and Luh 1964, have also noted essentially a similar feature in the different orthopteran types.
Unlike the situation in the ephemerid and dictyopteran types, in the orthopteran representatives, the tergosternal and the tergopleural muscles have undergone considerable reduction in the number. The only muscles of these categories occurring are the intersegmental tergosternal muscle (Muscle 28; t-sl of Matsuda), the tergo-interpleural muscle (Muscle 7 t-pl and 2 of Matsuda), the fourth tergopleural muscle (Muscle 13; t-p5 and 6 of Matsuda) and the second muscle of the third axillary sclerite (Muscle 18 t-p14 of Matsuda). These aforementioned persisting muscles, however are well-developed and functionally compensate the missing complements. (Some of the tergo-sternals and the tergopleurals). It appears that the reduction in the number of these muscles, perhaps, is associated with the higher degree of sclerotization of the thoracic capsule in the Orthoptera. These features confirm those noted by La Greca (1947b), Misra (1946, '47), Thomas (1953), Ewer (1953, '54a, '54b, '54c, '58, '64), Wilson (1962), Yu and Luh (1964) and Blackith and Blackith (1967).

The well-developed dorsal longitudinal muscle (Muscle 1; t 11 and 14 of Matsuda) acts as the indirect wing depressor. Its action is further supported by the neogenetic third pleural muscle (Muscle 41; p3 of Matsuda). The new muscle in the orthopteran type is decisively an advancement over the thoracic musculature of the ephemerid.
and dictyopteran representatives. It is obviously a forward step in the evolution of indirect wing mechanism in the Insecta. Thus, Teigs (1955) says of Orthoptera that they are of primary importance in the evolution of the wing mechanism for the light they "can still throw on the initial adaptation of the thoracic musculature to flight". In keeping with this, the fourth tergopleurals (Muscle 13; t-p5 & 6 of Matsuda) are also well developed to act as the indirect wing levators. The second muscle of the third axillary sclerite (Muscle 18, t-p14 of Matsuda) is directly responsible for wing flexion as in other pterygotes.

(e) Yet, the thoracic musculature of the orthopteran type is primitive, since many of the lateral and pleural complements are bifunctional, similar to the condition in the ephemeroptera and dictyopteran types. As is experimentally proved by Wilson (1962), the following muscles are found to function both as leg and flight muscles—

(i) The tergotrochantinals (muscles 35; t-ti 1-3 of Matsuda)—elevator of the wing and promotor of the coxa.

(ii) The tergal remotors of the coxa (Muscle 37; t-cx6, 7 of Matsuda)—elevator of the wing and remotor of the coxa.

(iii) The pleurotrochantinal muscle (Muscle 58; p-ti 1-3 of Matsuda)—Pronator—depressor of the wing and
promotor of the coxa.

(iv) The subalar-coxal muscle (Muscle 38; t-cx 8 of Matsuda) - Supinator - depressor of the wing and remotor of the coxa.

(v) The tergal depressor of the trochanter (Muscle 63; t-tri of Matsuda) - elevator of the wing and depressor of the trochanter.

(f) The thoracic muscular pattern in the orthopteran type is again primitive in one more respect. For, in this case also the pterothoracic segments and their wings are equal in size. Concomitantly the flight muscles in them are also equally well-developed. This has led to the maximum interaction between these thoracic segments causing the maximum phase difference in the contraction of their muscles, and in the eventual fore- and hind-wing beats. Thus, the flight in the orthopteran type also is of a 'flapping type', which is a reflection of the primitive condition found in the dictyopteran representative. (Sotavalta 1952, '54; Weis-Fogh and Jensen 1956, Pringle 1957).
(G) PECULIARITIES OF THE THORACIC MUSCULAR PATTERN IN THE HETEROPTERAN TYPES. (Vide Plate Nos. 37, 38, 39, 41, 42, 43; Chart No. 2, Cols. 8, 9).

(a) In the case of the heteropteran types, the wingbase, hidden beneath the posterior lobe of the pronotum is to be exposed before the wings can spread. This is accomplished by the contraction of one of the prothoracic dorsal longitudinals (M. pronoti-teritus of Larsen 1945b; op-t 3 of Matsuda), which raises the posterior pronotal lobe to expose the wing base.

Malouf (1933), Larsen (1945b; 1949a), Akbar (1957), Lauck (1959), Khanna (1963), Parsons (1963, '68, '69), and Goel (1967) also have made such observations in different heteropteran species.

(b) After this is accomplished as is experimentally proved by Pringle and Barber (1966) the disengaging of the fore wings from the locking devices is achieved by the contraction of the oblique dorsal longitudinal muscles (Muscle 2; t12, 13 of Matsuda). Further, the forewings unfold and click into action by the contraction of the median dorsal longitudinal muscles (Muscle 1; t-14 of Matsuda) and the fourth tergopleural muscles (Muscle 13; t-p5 and 6 of Matsuda).
The hindwings also spread passively, since they are fastened to the forewings by special wing coupling devices (Larsen 1949a, Guamont and Moreau 1961; Ewald 1963). Thus the fore and hindwings function simultaneously and the movement of the hindwing is affected to a large extent by the action of the mesothoracic muscles.

(c) The first muscle of the third axillary sclerite (Muscle 17; t-p13 of Matsuda), on contraction flips the third axillary sclerite and flexes the wing. When the wings are brought back to the resting position, contraction of another prothoracic muscle (M. pronotii quartus of Larsen 1945b; cv(d)-ti of Matsuda) brings pronotal lobe down against the wing base.

In general, this conforms with the explanations of Maloef (1953), Larsen (1945c, d, 1949a), Akbar (1957), Lauck (1959), Parsons (1963, 68, 69), Khanna (1963b) and Goel (1967).

(d) Peculiarly, the metathoracic median dorsal longitudinal muscles (Muscle 1; t-14 of Matsuda) in the heteropteran type are inserted on the anterolaterally or laterally isolated metanotal plate. (Larsen 1945c, d; Parsons 1960a, 63). This isolated part is connected with the wing base in such a way that the pull of this muscle causes sideward spread of the wing and its anterior margin.
In cryptocerate heteropteran type, in spite of the well-developed anterolateral metanotal plate the median dorsal longitudinal muscle is poorly developed and functions as the levator of the abdomen, as pointed out by Larsen (1949a). In such cases the tergotrochantinal muscle (muscle 35; t-cx2 of Matsuda) and the tergal depressor of the trochanter (Muscle 63; t-tri of Matsuda) replace the function of the median dorsal longitudinals.

Thus as pointed out by Larsen (1949a), some of the leg muscles in Heteroptera are bifunctional. Obviously, this is a reflection of the primitive feature found in cases of the dictyopteran and orthopteran representatives.

These bifunctional muscles are fewer in number, and when compared to the dictyopteran/orthopteran types. These are:—

(1) the tergal depressor of the trochanter (muscle 63; t-tri of Matsuda); the tergotrochantinal. (Muscle 35; t-cx2 of Matsuda); the subalar coxal muscle (Muscle 38; tocx8 of Matsuda)—all of which act as the wing depressors in the absence of the median dorsal longitudinal muscles.

(ii) the tergal remotors of coxa (Muscle 37; t-cx6, 7 of Matsuda) act as the wing levators.
(e) Perhaps to reduce the interaction between the thoracic segments and to minimize the effect of consequent phase-difference between the wing beats, the metathorax and its muscles are reduced, compared to the mesothorax and its muscles. This is a reflection of the advanced feature found in the Diptera and Hymenoptera.

(f) Strangely, all the flight muscles in the heteropteran types exhibit general reduction in size, even in the presence of well-developed flight apparatus. Their reduction is more pronounced in the cryptocerate heteropteran type perhaps in correlation with their aquatic habitat. This is in striking contrast to the situation in the other insectan types described earlier. Poisson (1924), Larsen and Young (1961, '65a) have made similar observations in this regard.

The reduction of flight muscles in macropterous Heteroptera, according to Young (1965a), is a result due to the arresting of their further development after eclosion rather than from degeneration of normally developed muscles.

As is thought by Teitze (1963) in the case of Coleoptera, such reduction in the flight muscles, perhaps, is a first step towards the evolution of micropterous forms and wing rudimentation.
(g) It is observed here that in spite of the presence of the flight apparatus and flight muscles, the heteropteran type dealt with here, *Cyclopelte siccifolia* is incapable of flying. Such feature is also noted by Larsen (1950) and Parsons (1960a) in some other heteropteran species. This perhaps may be due to the atypical, nonstriated and nonfunctional nature of flight muscles as is observed by Larsen (1945c) in some of the nymphal heteropterans. Larsen (1950) also proposed that, alternatively, this may also be due to the absence of the nervous elements involved with flight. A detailed investigation in this regard is called for.

(h) The muscles operating the legs — the tergocoxals (Muscles 35, 37, 38 - t-tl 1, 2, 3; t-cx 5, 6, 7; t-cx, 1 of Matsuda), the sternocoxals (Muscles 54, 56 - S-cx 6, 7; S-cs, 4, 4 of Matsuda) the pleurocoxals (Muscles 58, 59 - P-cx 1, 2, 3; P-cx 4, 5), the trochanteral muscles (Muscles 63, 65, 66, 68 - t-trl; P-tr 3, 4; P-tr 2; S-tr 1 of Matsuda) are well-developed and operate the legs efficiently, in correlation with the epiphytic habits of the gymnocerate heteropteran type.

It may be added that in the case of this crypto­cerate heteropteran type the development of the leg muscles
is still more pronounced than in other species which probably is correlated with its rowing type of locomotion in the water. (Taylor 1952).

(H). PECULIARITIES OF THORACIC MUSCULAR PATTERN IN THE NEUROPTERAN TYPE. (Vide Plate Nos, 45, 46, 47; Chart No. 2, Col. 10).

(a) The presence of the prothoracic tergo-anapleural and tergoketapleural muscles (Muscles 10 & 11; t-p and t-p of Matsuda) is decidedly a primitive feature in the thoracic muscular pattern of the neuropteran type, because it is shared only by the primitive thysanuran and ephemerid types as described earlier. Such a feature is also reported by Maki (1936), Korn (1943), Czihak (1956) and Kelsey (1954, '57) in the other neuropteran insects.

(b) Characteristically, the muscles attached to the pleuron (Muscles No. 7-13; 17-19; 39-41 and 44-46 i.e. muscles of t-p, p and p-s category of Matsuda) are present in abundance, although some of them are neogenetic. This again is suggestive of the primitive feature found in the thysanuran and ephemerid types. Corroborating evidences in this regard can be obtained in the works of Korn (1943), Czihak (1956) and Kelsey (1954, '57).
(c) Remarkably, relatively rare muscles like the second and third remotors of the coxa (Muscles 61, 62; p-cx 7, 8, 9 of Matsuda) and the sternal adductors of the coxa (S-cx 9) are present in the neuropteran representative, as observed by Korn (1943) Czihak (1956) and Kelsey (1954, '57).

(d) In striking contrast to the situations described earlier in the representatives of the hymenopterous orders, the thoracic muscular pattern in the neuropteran type is unique in the presence of two muscles of the third axillary sclerite (Muscles 17 and 18; t-p 13 and 14 of Matsuda). Studies of Korn (1943), Kelsey (1954, '57) and Czihak (1956) on the other neuropteran insects corroborate this finding.

Perhaps as a synapomorphic character, this feature is found to occur persistently in all the cases of the holometabolous representatives to be described later.

(e) In the neuropteran type, besides all the well-developed direct and indirect flight muscles, some of the leg muscles also serve to operate the wings. These bifunctional muscles are -

1) the tergotrochantinals (muscles 35; t-ti, 1-3 of Matsuda) - elevator of the wing and promotor of the coxa.
ii) the tergal remotors of the coxa (Muscles 37; t-cx 5-7 of Matsuda) - elevator of the wing and remotor of the coxa.

iii) the pleurotrochanteral muscle - (Muscle 58; p-ti 1-3 of Matsuda) - Promotor - depressor of the wing and promotor of the coxa.

iv) the subalar coxal muscle - (Muscle 38; t-cx 8 of Matsuda) - the supinator-depressor of the wing and the remotor of the coxa.

v) the tergal depressor of the trochanter (Muscle 63; t-tr 1 of Matsuda) - the elevator of the wing and depressor of the trochanter.

Thus, in the presence of such bifunctional muscles, the thoracic muscular pattern in the neuropteran type is primitive resembling closely that in the orthopteran type.

(f) Inspite of the well-developed flight muscles, the flight in the neuropteran type is weak, probably due to the presence of equally well-developed flight muscles in the two almost equal-sized pterothoracic segments. This has ultimately led to the production of maximum phase difference between the strokes of the equal-sized wings, leading to the 'flapping' mode of flight in the neuropteran type also, which is similar to that described in detail in
the case of the orthopteran representative. (Sotavalta 1952; Weis. Fogh & Jensen 1956).

(g) All the leg muscles are well-developed in the neuropteran type, very similar to those in the case of the orthopteran representative, to provide considerable mobility to the legs.

Thus, when surveyed resumptively, all the various aforesaid features lead to the conclusion that the neuropteran thoracic muscular pattern is only a variant of the one described in the orthopteran representative.

(I) PECULIARITIES OF THE THORACIC MUSCULAR PATTERN IN THE MECOPTERAN TYPE - (Vide Plate Nos. 57, 58, 59; Chart No. 2, Col. 13).

(a) The thoracic muscular pattern in the mecopteran representative is a reduced version of the one described above in the case of the neuropteran type; because in the former only a few muscles of each category have been found compared to the condition in the latter.

(b) As is the case in the neuropteran representative, the prothoracic tergo-anapleural and tergo-ketapleural muscles are characteristically present in the mecopteran type also. The observations recorded by Maki (1938),
Hasken (1939), Fuller (1955) and Mickoleit (1967, '68) in the various mecopteran insects confirm the present finding.

Obviously, this is a primitive synapomorphic character in the representatives of the Mecoptera and Neuroptera, perhaps indicating the closer relationship of the two groups.

(c) As in the neuropteran type, two muscles of the third axillary sclerites occur in the mecopteran representative also. The presence of this feature is shared synapomorphically by all the other holometabolous representatives as will be discussed later.

(d) In the mecopteran type, both the direct and indirect wing muscles are well-developed. Further, some of the leg muscles also serve to operate the wings as is the situation described above in the orthopteran type.

Inspite of this, however, the flight in the mecopteran type is not efficient, as mentioned in the case of the neuropteran type due to the equal sized pterothoracic segments with similar peteolate wings and concomitant occurrence of equally well-developed flight muscles. This feature leads to the production of maximum phase-difference between wing strokes ultimately effecting primitive 'flapping' mode of flight, as is described earlier in the cases of the orthopteran and neuropteran representatives. (Sotavolta 1952; Weis-Fogh & Jensen 1956).
(J) PECULIARITIES OF THE THORACIC MUSCULAR PATTERN IN THE COLEOPTERAN TYPE. (Vide Plate Nos. 49, 50, 51; Chart No. 2, Col. 12).

(a) Compared to the condition in neuropteron type, the thoracic muscular pattern in the coleopteran representative exhibits considerable reduction in number of muscles, which is evident in the absence of the tergo-ketapleural and the tergo-anapleural (Muscles 10 and 11; t-p and t-pl of Matsuda); the second tergosternal muscle (Muscle 32; t-s 7, 8, 10 of Matsuda); the second and third pleurosternals (Muscles 45 and 47; p-sl and p-s5 of Matsuda); the first and second sternal remotors of the coxa (Muscles 52 and 53; S-cxl, and S-cx-5 of Matsuda); the second and third pleural remotors of the coxa (Muscles 61, 62; P-cx 7 and P-cx 9 of Matsuda).

Maki (1938), Saxena (1953), Larsen (1954,'66) and Balfour-Browne (1967) have also recorded similar features in the different coleopteran representatives they worked on.

The above-alluded degeneration in the thoracic musculature of the coleopteran type, presumably, is a result of the increased sclerotization of the exoskeleton; strongly sclerotized exoskeleton as Matsuda (1970) maintains - "simply can not serve as a functional surface for small muscles".
(b) In the mesothorax, the muscles concerned with the movements of the elytra are:

(i) the median dorsal longitudinals which (Muscle 1; t-14 of Matsuda) by their tonic contraction hold the elytral margin locked into the metanotal groove, when at rest. This confirms the interpretations of Herbst (1952).

(ii) the contractions of the oblique dorsal longitudinal muscles (Muscle 2; t-12, -13 of Matsuda), the first tergo-episternal muscle (Muscle 8; t-p 3 of Matsuda), and the tergal depressor of the trochanter (Muscle 63; t-tr 1 of Matsuda), raise the mesocutum and simultaneously extend and elevate the elytra. This is in agreement with postulations of Stellwaag (1914a,b) Herbst (1952) and Larsen (1966) as regards to the click mechanism.

(iii) As is shown by Larsen (1966), the epimero-subalar muscle (Muscle 20; t-p 16 of Matsuda) is found to effect the rearward movement of the elytra over the back. The two muscles of the third axillary sclerite (Muscles 17 and 18; t-p 13 and t-p 14 of Matsuda) act as the flexors of the elytra in a similar way as in other insects.

(iv) According to Larsen (1966), the mesothoracic pleurotrochantinals (Muscle 58; p-cx2 of Matsuda) and subalar-coxals (Muscle 38; t-cx 8 of Matsuda) also are
concerned with the movements of the elytra, because they are absent in the forms that have greatly reduced elytra. However, experimental evidences are lacking in this regard.

(c) In the metathorax, the usual indirect flight muscles, the median dorsal longitudinals (Muscle 1; t-14 of Matsuda), the fourth tergo-pleural muscles (Muscle 13; t-p5 and 6 of Matsuda) and the oblique dorsal longitudinals (Muscle 2; t-12 of Matsuda) are very well-developed. As usual the first one depresses the wing, whereas the latter two act as its levators.

Besides, the tergo-trochantinal muscles (Muscle 35; t-cx 1, 2, 3 of Matsuda) and the pleurotrochantinal muscles (Muscle 58; p-cx 1, 2, 3 of Matsuda) are set free of their normal action of operating the legs and are found to be characteristically modified into most effective indirect wing muscles. The tergo-trochantinals act as the wing levators, while the pleuro-trochantinals bring about their the pronation-depression and pronation-extension.

Furthermore, the third pleural or the basalar muscle (Muscle 41; p3 of Matsuda), as shown by Larsen (1966), also, co-acts in the pronation-depression and pronation-extension of the wing. On the other hand, the subalar-coxal muscle (Muscle 38; t-cx8 of Matsuda) functions as a supinator of the wing, during an upstroke since it depresses
the posterior margin of the wing. This is done by virtue of the connection of the subalar (to which this muscle is attached) with the second and third axillary sclerites. (Doyen 1966; Larsen 1966). According to Evans (1961), there is no such connection between the subalar and the axillary sclerites in the Atomaria sp..

Thus, as is pointed out by Ruschkamp (1927) and Pringle (1957), in the use of the direct muscles, - the basalar and subalar, - as the phasic muscles to assist in wing depression, the Coleoptera resemble the Orthoptera and are distinguished from the Diptera and Hymenoptera, in which all the power for wing strokes is provided by the indirect muscles as will be described later.

The corroborating observations regarding all the foregoing features are obtainable in the investigations of Maka (1938), Saxena (1953), Evans (1961) and Larsen (1966) on various species of the Coleoptera.

It may be pointed out here, that the aforementioned curious functional modification of the leg muscles into the flight muscles in the coleopteran type is obviously due to the reversal of their primary origins and insertions in correlation with the increased incorporation of the coxal bases into the body wall in the group as is convincingly explained by Chadwick (1953).
Larsen's (1966) histological and histochemical studies have proved beyond doubt that the various above described metathoracic flight muscles of the Coleoptera are of fibrillar type, in striking contrast to their mesothoracic counterparts which are of tubular type. This is a further affirmation of the fact that the leg muscles in the Coleoptera are modified to move the wings. Menon and Joshi (1957-58) also convincingly showed the fibrillar nature of the tergotrochantinal muscles in a buprestid beetle and asserted that these muscles act as the flight muscles.

It is clear therefore, that in the metathorax of the Coleoptera, the musculature is adapted to accomplish more efficient wing movements. Simultaneously, however, the leg mobility is very much restricted.

(d) Among the metathoracic dorsal tergopleural muscles as is shown by Larsen (1965) -

(i) the third teropleural (muscle 12, t-p4 of Matsuda) bends the pleural process medially;

(ii) the second tergobasalar muscle (Muscle 15p t-p 8 of Matsuda) controls the pronation - depression actions of the third pleural muscle (Muscle 42; p3 of Matsuda) and the pleurotrochantinal muscle (Muscle 58 p-cx 1,2,3 of Matsuda);
(iii) the epimero-subalar muscle (Muscle 20; t-p 16 of Matsuda) has a controlling effect on the position of the second axillary sclerite,

(iv) the two muscles of the third axillary sclerites (Muscles 17 and 18; t-p 13 and t-p-14 of Matsuda) are the usual wing flexors;

(v) the first pleuro-sternal muscle (Muscle 44; p-sl of Matsuda) has no effect upon the click mechanism, although Pringle (1957a) attributed the click mechanism to this muscle in another species.

(e) In striking contrast to the situations in the other insectan types, in the coleopteran type the mesothorax and its muscles are genetically reduced. Thus, the main motive power for flight is derived from the concomitantly well-developed metathoracic muscles.

Furthermore, the important indirect dorsoventral levator complements - the fourth tergopleural muscles (Muscle 13; t-p5 and 6 of Matsuda) - are absent in the mesothorax of the coleopteran type. Consequently, the elytra are not moved up and down, though they have an important role in the aerodynamics of flight (Pringle 1957).

Concurring observations are found in the studies of Maki (1938), Saxena (1953), Larsen (1954, '66) on various coleopteran insects.
As is explained by Stellwag (1914), and Herbst (1952), in the Coleoptera, the elytra are held during flight in a position 30° to 45° above the horizontal plane, where they are maintained by the tonic contractions of indirect muscles and by a system of self-locking apodemes at the base.

Eventually, the implication is that the interaction between the pterothoracic segments and of phase-difference between contractions of the fore- and hindwing muscles are of little or of no significance during the flight. Thus the flight in the Coleoptera is of "fast flapping" or of "Horsefly" type (Weis-Fogh and Jensen 1956).

(f) An allusion may be made to an interesting feature that in some aquatic macropterous Coleoptera, the flight muscles are more or less atrophied. Jackson (1952) suggested that beetles with abnormal development of the flight muscles are those in which the normal development of wing muscles and their supports has been arrested at an early stage. Histological and histochemical studies of Tietze (1963) and Smith (1964) amply support Jackson's hypothesis. According to Tietze (1963), the degeneration of flight muscles in the macropterous forms represents the first evolutionary step towards wing rudimentation and wing polymorphism.
(K) **PECULIARITIES OF THE THORACIC MUSCULAR PATTERN IN THE LEPIDOPTERAN TYPE.** (Vide Plate Nos. 61, 62, 63; Chart No. 2; Col. 14).

(a) The thoracic muscular pattern in the lepidopteran type is a reduced and modified version of the one described in the case of the mecopteran representative. Its reduction is very evident in the absence of the tergo-ketapleurals (Muscle 10; t-p of Matsuda), the tergoanapleurals (Muscle 11; t-p of Matsuda); the muscles of the axillary sclerite (Muscle 16; t-p 10, 11 of Matsuda); the pleuro-subalar muscle (Muscle 21; t-p 19 of Matsuda) and the first sternal remotor of the coxa (Muscle 55; s-cx2 of Matsuda), which occur well-developed in the case of the mecopteran type. The observations recorded by Nuesch (1953), Treat (1959), Srivastava (1961, '62), Ehrlich and Davidson (1961), Ehrlich and Ehrlich (1963), Dierl (1964), Demus (1965a), Krammer (1967), Kristensen (1968), Mitchell and Seabrook (1970, '71), Eaton (1970), Macfarlane and Eaton (1973) also show the absence of these muscles in the other lepidopteran species.

Mickoleit (1966), however, has recorded the presence of the muscle of the first axillary sclerite (Muscle 16; t-p 10 of Matsuda) in some species of Lepidoptera.
(b) The third tergopleural muscle (Muscle 13; t-p^4 of Matsuda) is found to occur in both the meso- and meta-thorax of the lepidopteran type investigated here. This contradicts Sharplin's postulation (1963 a, b, c; 1964 a, b) that the mesothoracic third tergopleural muscle in the Ditrysia - the higher Lepidoptera, is replaced by the tergopleural apodeme.

(c) All the direct and direct and indirect wing muscles are better developed in the lepidopteran representative, when compared to the situation in the mecopteran type. The indirect wing muscles - the dorsal longitudinal muscles (Muscles' 1; t-14 of Matsuda) and the fourth tergo-pleural muscle (Muscle 13; t-p 5, 6 of Matsuda) however, exhibit pronounced hyperdevelopment. Similar feature is also observed by Huesch (1953), Srivastava (1961, 62), Krammer (1967), Kristensen (1968), Eaton (1970), Mitchell and Seabrook (1970, '71), Macfarlaine and Eaton (1973).

(d) Besides, very conspicuously, many of the leg muscles in the lepidopteran type are functionally modified into wing muscles due to increased incorporation of the leg-bases into the body wall and heavy sclerotization of the pleuron and the pleuro-coxal junction portions (Madden 1944; Michener 1952, Ehrlick 1958, Matsuda 1960a). As is stated by Chadwick (1953) this secondary development reverses the
primary origins and insertions of several of the dorso-ventral muscles which makes them highly effective depressors of the tergal margin and hence levators of the wings. In the lepidopteran type, the tergotrochantinals and the tergal promotors of the coxa (Muscles 35, 37; t-cx 1, 2, 3 and t-cx 5, 6, 7 of Matsuda), the pleurotrochantinals and the pleural promotors of the coxa (Muscles 58, 59; p-cx 1, 2, 3 and p-cx 45 of Matsuda), and the subalar coxal (Muscle 38; t-cx 8 of Matsuda) represent this stage of modification. These muscles have no influence on the leg mobility which therefore is very much restricted. Treat (1959). Observations of Nuesch (1953), Srivastava (1961, '62), Krammer (1967), Kristen sen (1968), Mitchell and Seabrook (1971), Macfarlaine and Eaton (1973) in this regard are essentially similar.

Mention may be made here, in passing, that the above described state of affairs has a parallel in the metathorax of the coleopteran type alone, as described earlier.

Thus it may be reasonably concluded that in the use of direct muscles, the basalars and subalars, as phasic muscles to produce wing depression and also in the functional modification of the leg muscles into flight muscles, the Lepidoptera resemble the Coleoptera and remain distinguished from the Hymenoptera and Diptera, which derive their motive power from the indirect muscles alone (Pringle 1957).
(e) In the case of the lepidopteran type, in striking contrast to the condition in the coleopteran type, the hindwing, metathorax and its muscles are reduced in size. However this is less important in the flight of the lepidopteran representative since both the wing pairs function simultaneously because of the wing-coupling mechanism. As a result, the 'lift' and 'thrust' are in a great measure unlike the cases in other insects investigated.

Thus as an advancement over the Coleoptera, this feature perhaps makes the Lepidoptera the good fliers even at higher altitudes. The flight being of 'fast-flapping' type or of 'Horse-fly' type. (Setavalta 1952, '54; Weis Fogh-Jensen 1956; Pringle 1957).

L) PECULIARITIES OF THE THORACIC MUSCULAR PATTERN IN THE HYMENOPTERAN TYPE- (Vide Plate Nos. 53, 54, 55; Chart No. 2, Col. 11).

a) The presence of the pleuro-subalar muscle, (Muscle 21; t-p 19 of Matsuda) is unique feature in the hymenopteran type, shared by the mecopteran type alone. This character in the representatives of the two groups can be reasonably regarded as a synapomorphic feature, since this muscle is lacking in all the other insectan types investigated here.
On the other hand, the absence of the muscle of the first axillary sclerite (Muscle 16; t-p 10 and 11 of Matsuda) and the presence of the second tergo-episternal muscle (Muscle 9; t-p 12 of Matsuda) are features shared by the neuropteran and the hymenopteran representatives. This perhaps is symplesiomorphic character in these insects. Observations recorded by Maki (1938), Duncan (1939), Snodgrass (1942, '56), Alam (1951), Wille (1956), Saksena (1959), Daly (1964), and Markl (1966) in the various hymenopteran species amply confirm these findings.

Based on the above evidences, Hymenoptera may be regarded as a sister group of the Neuroptera and Mecoptera as is aptly pointed out by Matsuda (1970). It appears that the Hymenoptera departed early from the common stock and perhaps their automorphic characters have been very rapid and strong to obscure their relationships with the modern Neuroptera and Mecoptera (Snodgrass 1910, Matsuda, 1970).

The aforementioned interpretation supports the postulations of Crampton (1919) and Ross (1936, '37, '55), which maintain the origin of Hymenoptera from the Megaloptera-Mecoptera stem based on the similarities in wing venations.

(b) In the case of the hymenopteran type, the main motive power for flight is derived from the mesothoracic indirect wing muscles. According to Pringle (1961), "even
power for moving the hind-wing is drawn from the mesothoracic indirect wing muscles to an extent controlled by the mesophragmal retractor muscle (median dorsal longitudinals; Muscle 1; t-14 of Matsuda) of the metathorax.

(c) In the hymenopteran type, (Weber 1925, Duncan 1939; Snodgrass 1956; Pringle 1961) the first axillary sclerite articulates anteriorly with the ante-notal wing process and humeral complex. Its caudal end has a ligamentous connection with the fourth axillary sclerite. This unique development of the first axillary sclerite is important in the wing movements of the hymenopteran type as explained before.

As is experimentally proved by Pringle (1957a), the force of contraction of the median dorsal longitudinals (Muscle 1; t-14 of Matsuda) is transmitted to the first axillary sclerite through the combined and concerted actions of the scutellar arm, postnotal wing process, mesonotal suture and the ante-notal wing process. The upper part of first axillary sclerite turns forwards and downwards; since this is attached to the humeral complex, the wing is thereby pronated and depressed. The further depression of the wing in a pronated attitude is caused by the combined rotary actions of the first and second axillary sclerites and the anterior and posterior notal processes, as the median dorsal longitudinal muscles (Muscle 1; t-14 of Matsuda) contract further.
At the beginning of the upstroke, the contractions of the oblique dorsal longitudinals (Muscle 2; t-13 of Matsuda) and the fourth tergopleural muscles (Muscles 13; t-p 5, 6 of Matsuda) move the scutum downwards and backwards which causes the reverse movements of first and second axillarsclerites and hence the wings are supinated during elevation.

Thus, on the whole the arrangement of the indirect muscles and sclerites ensures the pronation and supination in the correct phasing to the depression and elevation.

Similar observations are also recorded by Alam (1951), Snodgrass (1956) and Saksena (1959) in the different species of Hymenoptera.

(e) Again, as is experimentally proved by Pringle (1961), in the hymenopteran type, the second and third pleural muscles (the basalars - Muscles 40 and 41; P2 and P3 of Matsuda); the furco-subalar (Muscle 30; t-s4, 5 of Matsuda); the subalar-coxal muscle (Muscle 38; t-cx8 of Matsuda); the pleuro-subalar muscle (Muscle 21; t-p19 of Matsuda); and the median dorsal longitudinal muscles (Muscle 1; t-14 of Matsuda); alter the setting of the sclerites so that the amount of pronation varies at different instants during downstroke, giving control of balance in the planes of 'pitch and yaw'; the upstroke is almost invariant with full supination.
The third pleural muscle (Muscle 41; p3 of Matsuda) and the intersegmental tergo-sternal muscle (Muscle 28; t-sl of Matsuda) control the power generated by the fibrillar indirect muscles - the dorsal longitudinal (Muscles 1 and 2; t-14 and t-13 of Matsuda) and the fourth tergo-pleurals (Muscle 13; t-p5 and 6 of Matsuda), Darwin and Pringle (1959); Daly (1963); Smith (1964).

(f) In striking contrast to the condition in the representatives of the specialized orders like Heteroptera, Coleoptera, and Lepidoptera, in the hymenopteran type the tergocoxal and the tergo-trochanteral muscles have undergone an extreme reduction in number. Only one tergocoxal muscle - the subalar-coxal muscle is present (Muscle 38; t-cx of Matsuda). In effect, therefore, the mobility of the legs in the hymenopteran type is very much restricted.

The observations reported by Morison (1927), Duncan (1939), Snodgrass (1942, '56), Alam (1951), Wille (1956), Saksena (1959), Daly (1964), Mark (1966) in the various hymenopteran insects are also essentially in agreement with the character noted above.

The functional change of the leg muscles into flight muscles has never taken place in the evolution of Hymenoptera. It is partly because of this peculiar evolutionary trend of the leg muscles that the indirect flight muscles, as
Pringle (1957a, '61) has very aptly shown, have come to assume such a dominant role in the flight of the Hymenoptera.

(g) It is very pertinent to mention in passing, that much like the condition in the lepidopteran type, the coupling of fore- and hind-wings is important in the flight mechanism of Hymenoptera (Weber 1925). Consequently, the reduction in the size of hindwings, metathorax and its muscles is of less importance during the flight of the hymenopteran type. Since the wing pairs function simultaneously, the 'lift' and 'thrust' produced are decidedly on a larger scale. As a result, the flight in the hymenopteran type is also of a 'fast-flapping' type or of 'Horse fly' type (Weis-Fogh and Jensen 1956). This feature, perhaps, enables the Hymenoptera to be good fliers.

(M) PECULIARITIES OF THE THORACIC MUSCULAR PATTERN IN THE DIPTERAN TYPE. (Vide Plate Nos. 65, 66, 67; Chart No. 2, Col. 15).

(a) The thoracic muscular pattern in the dipteran type is a reduced and modified variant of the one described in the mectopteran representative. However, its reduction is altogether in a different plane and very evident in the absence of the epimero-subalar muscle (Muscle 20; t-p15 of Matsuda); the pleurosubalar muscle (Muscle 21, t-p 19 of
Matsuda); the first intersegmental pleurosternal (Muscle 46; p-s3 of Matsuda) and the second pleural levator of the trochanter (Muscle 66; p-tr 2 of Matsuda).

Thus in the dipteran type, the only persistent muscle attached to the pleuron and the sternum is the first pleuro-sternal muscle.

Conversely, the muscle of the first axillary sclerite (Muscle 16; t-p 10, 11 of Matsuda), the first muscle of the third axillary sclerite (Muscle 17; t-p 13 of Matsuda), the second muscle of the third axillary (Muscle 18; t-p 14 of Matsuda) and the muscle of the fourth axillary sclerite (Muscle 19; t-p 15 of Matsuda) exhibit increase in the number of fasciculi. Presumably, this is due to the enlargement and subsequent splitting of muscles that were originally smaller in size (Matsuda 1970). Concurring observations as regards to these various features are recorded by Mihalyi (1936), Maki (1938), Zalokar (1947), Bonhag (1949), Miller (1950), Sara and Smerdel (1953), Smart (1959), Nussbaum (1960) and Mickoleit (1962) in the different species of Diptera. These various aforesaid tergopleural muscles and the second pleural muscle (the pleuro-basalar, muscle 40; p2 of Matsuda), which in its turn has also become enlarged in the dipteran type, are the direct flight muscles. As is most appropriately pointed
out by Matsuda (1970), the presence of such powerful and
massive direct muscles in the representative of the
Diptera forms a culmination of their development in the
evolution of the pterygota.

(b) Similar to the situation in the hymenopteran
type, in the dipteran type also the main motive power for
flight is derived from the extremely well-developed
mesothoracic indirect muscles. According to Schneider
(1953) and Danzer (1956) even the haltere is propelled by
the mesothoracic muscles.

As is experimentally shown by Boettiger and
Furshapan (1952) and Pringle (1957), in the mesothorax of
the dipteran type the median dorsal longitudinals (Muscle
1; t-14 of Matsuda) and the first pæuro-sternal muscle
(Muscle 44; p-sl of Matsuda) control the clicking of the
wing into its down position. Conversely, the fourth tergo-
pleural muscles (Muscle 13; t-p 5 and 6 of Matsuda) and the
oblique dorsal longitudinals (Muscle 2; t-13 of Matsuda) are
responsible for bringing about clicking of the wing back
into the up-position.

(c) As is convincingly explained by Bonhag (1949),
the direct muscles of the wings are found to function as
follows -
Muscles of the first, third and fourth axillary sclerites and those inserting on the post-median notal wing process, (Muscles 16, 17, 18, 19; Muscles t-p 10, 11, 13, 14 and 15 of Matsuda) are the effectors of the wing flexion movement, since by their concerted action the wing is drawn into the back of the fly when at rest.

The second pleural muscle (pleuro-basalar Muscle; Muscle 40 p2 of Matsuda) pulls the baslar ventrally and inward and thus accounts for the ventral deflection and forward thrust of the anterior margin of the wing during downstroke.

Deflection of the posterior margin of the wing during the up-stroke is accomplished by the two fasciculi of the muscle of the fourth axillary sclerite (Muscle 19; t-p 15 of Matsuda), which insert on the post-median wing process.

The third tergo-pleural muscle (Muscle 12; t-p4 of Matsuda) causes extension of the wing from its resting position over the back.

The first tergo-basalar (Muscle 14; t-p 7 9 of Matsuda), acts antagonistically to the third tergo-pleural muscle and retracts the wing over the back.
The third tergo-pleural muscle (Muscle 12; t-p of Matsuda) apparently serves to stabilize the pleural wing process during flight.

In addition to the various preceding direct and indirect wing muscles, some of the tergocoxal muscles also enter into the flight machinery, as is the situation in the coleopteran and lepidopteran types. The functional modification of the tergocoxal muscles into the indirect wing levators is caused by the reversal of their primary origins and insertions, which is entailed by the increased sclerotization and incorporation of the leg-bases into the body wall and the ventral approximation of such leg bases (Chadwick 1953).

In the dipteran type, this stage of bifunctional modification is represented by the tergotrochantinal muscle (Muscle 35; t-cx 3 of Matsuda) and the tergal remotor of the coxa (Muscle 37; t-cx 7 of Matsuda).

Corroborating observations are recorded by Miller (1950), Sara and Smerdel (1953), Smart (1953, '59), Nussbaum (1960) and Mickoleit (1962).

Mention may be made here that Bonhag (1949) erroneously termed these tergotrochantinals and the tergal remotor muscles of the coxa as pleurocoxal muscles in the case of Tabaenus sulcifrons, since he misinterpreted the antero-lateral and postero-lateral notal areas as the pleural

(e) In the dipteran type, a true case of double function is seen in the mesothoracic tergal depressor of the trochanter (Muscle 63; t-tr 1 of Matsuda). The primary function of this muscle is to extend the trochanter with force to effect the jumping action. A jump into the air is advantageous at the beginning of the flight as is maintained by Williams and Williams (1943), Boettiger and Furshpan (1952) and Smart (1958,'59). This muscle produces the initial upstroke after and hence acts as a 'starter' in flight. (Pringle 1957a).

It may pointed out at this juncture that the prothoracic tergal depressor of the trochanter in the case of T. sulcifrons is wrongly termed as the pleurotrochanteral muscles by Bonhag (1949), since his interpretation of the antero- and postero- lateral part of the scutum as the pleural area itself is erroneous. (Matsuda 1970).

(f) In the metathorax of the dipteran type, in accordance with the plausible explanations of Mickoleit (1962), the haltere is found operated by the following muscles -

(1) The fourth tergopleural muscle (Muscle 13; t-p5, 6 of Matsuda) is the elevator of the haltere as is obviously expected of it.
(ii) The subalar coxal muscle - (Muscle 39; t-cx 8 of Matsuda) functions as the depressor of the haltere. It also presumably has a pronating action on the haltere.

(iii) The second pleural muscle (the pleurobasalar muscle 40; p2 of Matsuda) and the second tergobasalar (Muscle 15; t-p8 of Matsuda) muscles serve to bring about the rotary movements of the haltere.

(g) Thus it is evident from all the aforementioned account that in the dipteran representative, all the direct and indirect wing muscles are extremely well-developed.

And besides, Miller (1950), Telgs (1955) and Smith (1964) have convincingly proved that all the indirect wing muscles which provide main motive power for flight are of fibrillar asynchronous type. Smart (1957, '59) investigated that even some of the direct muscles, invariably the coxo-subalar muscles (Muscle 38, t-cx 8 of Matsuda) are of a fibrillar type. Hinton (1959a) showed that in Psychodid genus, the tergal depressor of the trochanter (Muscle 63; t-tr 1 of Matsuda) also is of a fibrillar nature.

To add to this, the interaction between the two pterothoracic segments and the phase-difference between the wing strokes are very insignificant during the flight of the dipteran type, since it is well known that in the reduced metathorax of the group, haltere is a gyroscopic organ of
the equilibrium (Pringle 1948, 57a; Sotavalta 1953, Horridge 1956).

It can be reasonably inferred, therefore, that Diptera have attained the ultimate in the indirect wing mechanism by reducing metathorax and its muscles and by eliminating the hindwings as organs of flight, and at the same time by highly developing mesothorax and its muscles to motorize the single pair of wings. (Snodgrass 1958).
PART III: THE MUSCULATURE OF THE PREGNATAL ABDOMEN AND ITS ROLE IN LOCOMOTION, RESPIRATION, CIRCULATION AND OVIPOSITION.

The salient features of the muscular patterns of the pregenital abdominal segments in the presently-investigated insectan types, are comparatively—discussed in the following pages—

(A) PECULIARITIES OF THE MUSCULAR PATTERN IN THE PREGNITAL ABDOMEN OF THYSANURAN TYPE—

(a) All the complements of the dorsal longitudinal musculature in the thysanuran type—viz the M. dorsales interni medialis (dim of Snodgrass 1935), the M. dorsales interni laterales (‘dl’ of Snodgrass 1935), the M. dorsales externi medialis (dem’ of Snodgrass 1935) and the M. dorsales externi laterales (‘del’ of Snodgrass 1935)—are well developed and oriented longitudinally. Of these, the first two complements—the M. dorsales interni groups—occupy the inner tergal area all along the segmental length, whereas the latter two, viz the M. dorsales externi groups occur as short strips of muscles located in the posterior half of the segment external to the first two groups.

All these muscles in the thysanuran type, not only bind and brace the abdominal terga but also serve to produce
traction and lateral undulations of the abdomen while trailing along the substratum because of the concomitantly weak limbs, weakly sclerotized body segments and the flexible intersegmental membranes in the group (Snodgrass 1935, '38).

In conformity with the above features, the different complements of the ventral longitudinal musculature - viz the M. ventrales interni mediales ('Vim' of Snodgrass 1935), the M. ventrales interni laterales ('Vil' of Snodgrass 1935), the M. ventrales externi mediales ('Vem' of Snodgrass 1935), the M. ventrales externi laterales ('Vel' of Snodgrass 1935) are also equally well-developed and oriented parallel to the dorsal longitudinal muscles. Of these, the first two muscles the ventrales interni groups, are fused to form massive flat fasciculi that occupy the inner sternal area all along the segmental length. On the other hand, the latter two - the ventrales externi groups are short strips of muscles located in the posterior half of the segment external to the first two groups.

As is the case with the dorsal longitudinals, all these ventral longitudinals also serve to produce traction and lateral undulation in the abdomen in addition, while trailing along the substratum.

This afore-described production of the traction and lateral flexion by the dorsal and ventral longitudinal...
muscles in the abdomen is of immense importance in the locomotion of the thysanuran type, since as aptly explained by Manton (1949-56, '72) like many other terrestrial arthropods it does not fully stand up on its legs but 'hangsdown' from them. Consequently the traction and lateral undulations produced in the abdomen (and thorax) assist its weak pairs of legs in locomotion that usually takes place in short bursts. Thus in effect, the abdominal dorsal and ventral longitudinals in the thysanuran type are essentially locomotary in function. They do not cause the respiratory movements as in the cases of the pterygotes to be discussed later.

Similar features regarding the traction and lateral flexion are noted by Manton (1952a, 1953, '72) and Gruner (1953) in myriapodans also. As such, this character can be reasonably regarded as symplesiomorphic in both these groups of Arthropoda.

The aforesaid feature provides overwhelming support to the views of Crampton (1916), Imms (1936), Lemche (1940), Wigodzinsky (1941), Ewing (1942), Remington (1954), Carpenter and Richardson (1958), and Manton (1972) that the Thysanura is an archaic group which diverged from the protohexapoda much earlier to the origin of the pterygota. Simultaneously it decisively disproves the hypothesis of Handlirsch (1930) that the Thysanura represent neotenous wingless pterygotes.
(b) The lateral muscles (M. laterales; '1' of Snodgrass 1935) in the pregenital abdomen of the thysanuran type are the well-developed M. laterales interni ('li' of Snodgrass 1935) and M. laterales externi ('le' of Snodgrass 1935). Of these, the first complement is made up of a single intrasegmental muscle bundle, whereas the second complement comprises of several intersegmental fasciculi obliquely disposed. Both the complements are represented reduced as the vertical tergo-sternal muscles in correlation with the genetically rudimentary nature of the abdominal appendages in the group.

The above described tergo-sternal lateral muscles on contraction, bring about the vertical compression of the abdomen, which causes the expiratory movement in respiration. Conversely, the relaxation of the abdomen brings about inspiration. Thus, these abdominal lateral muscles are responsible for the breathing movements in the thysanuran type.

(c) The abdominal transverse dorsal muscles (M. transversi dorsales of Snodgrass 1935) in the thysanuran type, arise at the anterolateral part of the terga and fan out mesally to attach along the ventral wall of the heart and thus form the "alary muscles". Presumably, these muscles are the effectors of the cardiac diastole. (Snodgrass 1935; Richards and Davies 1964).
Incidentally, these muscles along with the enclosing connective tissue membranes form the pulsating dorsal diaphragm which separates the pericardial sinus from the perivisceral sinus, and helps in maintaining of the course of haemocoelic blood circulation (Snodgrass 1935, Richards and Davies 1964).

(d) The abdominal transverse ventral muscles (M. transversi ventrales, ('tv' of Snodgrass 1935) in the thysanuran type are represented by a series of horizontally continuous compact slender muscles-strips attached on the apophyses at the lateral extremities of the sterna. The pulsating ventral diaphragm and the consequent ventral sinus are not found in the thysanuran type, unlike the condition in some of the pterygotes to be discussed later. However, the abdominal transverse ventrals bring about the horizontal (lateral) compression of the abdomen and thus supposedly help in expiration and also in maintaining of circulation.

(B) PECULIARITIES OF THE MUSCULAR PATTERN IN THE PREGENITAL ABDOMEN OF THE EPHEMERID TYPE.

(a) Much similar to the situation in the thysanuran type, in the ephemerid type also, all the complements of the dorsal longitudinals are well-developed. The M. dorsales
interni groups, however, have fused to form a massive flat strip extending the length of the segments, whereas the M. dorsales externi groups occur as the short slender strips in the posterior part of the segments.

The various component muscles of the ventral longitudinals - the M. ventrales interni mediales ('Vim' of Snodgrass), the M. ventrales interni laterales ('vilj of Snodgrass) the M. ventrales externi mediales, ('VeM' of Snodgrass) and the M. ventrales externi laterales ('Vel' of Snodgrass) - exhibit exactly the similar features like their dorsal counterparts.

Very curiously, despite their resemblance to the thysanuran type, the use of these various complements of the dorsal and ventral longitudinals in the ephemerid type is restricted mainly to hold the abdomen lifted above the resting surface by their tonic contraction. This anamoly can be explained only on the basis that in the genetically predominant aquatic nymphal ephemerids, due to the weak sclerotization of their body segments and the intersegmental membranes, the highly developed dorsal and ventral longitudinal musculature serve to produce only lateral undulations of the abdomen. This perhaps, helps the weak thoracic legs to propel the body in the water. Interestingly, it may also be recorded at this juncture that similar condition is observed
in the zygopteran nymph also. Since such a feature occurs in the thysanuran type as described earlier, perhaps this is a symplesiomorphic character in all these groups suggesting their archaic origin. The affinities of these groups, however, are obscured by their strong automorphic trends during the evolution.

Alternatively, this aforesaid feature may also be considered as coenogenetic in the ephemerid and zygopteran nymphs.

Thus, in striking contrast to the condition described in the thysanuran type, in the ephemerid representative, despite their well-developed nature the function of the dorsal and ventral longitudinals is restricted to hold the abdomen lifted above the substratum by their tonic contractions. Incidentally, they also produce retraction of the abdomen which effects the expiratory movement. The protraction of the abdomen immediately after retraction is, however, accomplished by the general elasticity of the muscles and abdominal integument.

(b) The abdominal lateral muscular pattern in the case of the ephemerid type does not differ at all both anatomically and functionally from the one described in the thysanuran type. As a result in this case also the vertical
compression of the abdomen i.e., the expiratory movement is brought about by the various complements of the lateral muscles, whereas the dilation of the abdomen immediately after compression causes the inspiratory movement, assisted by the general elasticity of the abdominal integument.

(c) Likewise, the abdominal transverse dorsal and ventral muscular patterns in the ephemerid type also do not differ in any respect from their counterparts in the thysanuran representative described earlier.

(C) PECULIARITIES OF THE MUSCULAR PATTERN IN THE PREGENITAL ABDOMEN OF ZYGOPTERAN TYPE.

Compared to the situation in the thysanuran and ephemerid types, the pregenital abdominal muscular pattern in the zygopteran type is a degenerated one, perhaps in correlation with the greater sclerotization of the genetically narrow abdominal segments in the group. This degeneration is manifested in various degrees in many of its complements as follows:

(a) The abdominal dorsal longitudinals are represented by reduced muscle strips forming the M. dorsi alia mediales, which occupies the posterior portions in the terga. The more lateral strips of this muscle exhibit oblique disposition with an anterior outward slant.
On the other hand, the ventral longitudinals consist of the *M. ventrales interni mediales*, *M. ventrales interni laterales* and *M. ventrales externi mediales*; of these, the first two are made up of a single slender muscle strip running along the length of the sterna. The last one comprises two short muscle strips, of which one occupies the anterior part of the sternum whereas the other is located in the posterior part. Both these strips arise on the sternal apodemes in the mesal region and extend obliquely backwards to insert on the lateral sternal area; consequently, they are secondarily intrasegmental in attachments. Very similar observations regarding the ventral longitudinals are recorded by Whedon (1918) in *Calopteryx* sp.

Thus in effect, the dorsal and ventral longitudinals produce feeble retraction of the abdominal segments and hence help feebly in the expiratory movements. Simultaneously, the obliquely disposed *M. ventrales externi mediales* group produces horizontal lateral compression of the abdomen assisting the expiration. The relaxation movements of the abdominal segments, which help inspiration appear to be due in all cases to the general elasticity of the abdominal muscles and intersegmental membranes and hence are on the whole slow.
The slow and feeble respiratory movements in the zygopteran type are in correlation with its less oxygen demand, which in turn appears to be consequent upon the low metabolic rate, weak and slow flight in the group. (Tannert 1958, Richards and Davies 1964).

(b) The abdominal lateral muscles are entirely lacking in the zygopteran type as in the anisopteran one in striking contrast to the condition in the thysanuran and ephemerid representatives described earlier. Consequently, no vertical compression and dilation of the abdomen are produced in this case, resulting in the absence of vertical respiratory movements.

(c) Very peculiarly, in the zygopteran type as also in the anisopteran only the abdominal transverse dorsal and ventral muscles do not show any degeneration. On the contrary they resemble very closely their counterparts in the thysanuran and ephemerid representatives, from the anatomical and consequently the functional viewpoint also.

(D) **PECULIARITIES OF THE MUSCULAR PATTERN IN THE PREGENITAL ABDOMEN OF THE ANISOPTERAN TYPE:**

The pregenital abdominal muscular pattern in the anisopteran type is a more degenerated and modified variant
of the one described above in the zygopteran representative. This extreme degeneration and the modifications in the case of the anisopteran type, are obviously correlated with the heavy sclerotization of the abdominal segments in the group; and they are reflected very conspicuously as follows -

(a) The entire complement of the dorsal longitudinal musculature is made up of only one reduced muscle, the *M. dorsales externi mediales*. On the other hand, the ventral longitudinal musculature is composed of both the complements, the *M. ventrales externi mediales* and the *M. ventrales externi laterales*, which however are reduced in size.

The *M. ventrales externi mediales* group is represented by two muscle-strips. Of these, one is located at the anterior sternal area exhibiting obliquely vertical disposition as it connects the tip of the furcal apodeme and the lateral sternal area. Conversely, the other is situated in the posterior sternal part and is horizontally disposed, since it connects the mesal and lateral sternal areas. Thus, these muscles secondarily become intrasegmental in attachments.

It is significant that unlike in the zygopteran type, the *M. ventrales externi laterales*, occurs as a single strip with normal longitudinal disposition.
Thus, it is very clear that due to the extreme degeneration of the abdominal longitudinal musculature, the part played by these muscles in the retraction of the abdomen is not much. The reverse movements of the abdomen involving inspiration, take place due to general elasticity of the abdominal integument.

The aforesaid feature in the anisopteran type is very enigmatic in the face of immense oxygen demand by this insect consequent upon its active flight and high rate of metabolism. (Richards and Davies 1964). This curious feature can be accounted for on the assumption that, the longitudinal muscles in the abdominal segments of the anisopteran type function in the postero-anterior direction, enabling expiration to be effected through the anterior spiracles. Understandably, this keeps the inspiration and expiration continuous. At the same time as they help the drive the air in the trachea anteriorly towards thorax, they also bring about anteriorly-directed haemocoelic blood pressure. This, probably helps in adequate and faster measure, the aeration process.

(b) Similar to the condition in the zygopteran type, in the anisopteran type too the lateral abdominal muscles are lacking. Consequently, no vertical compression and dilation are produced in this case resulting in the
absence of vertical respiratory movements. However, this perhaps is compensated by the unique faster and continuous respiratory movements in the longitudinal plane by lateral compression described in the preceding paragraph.

(c) In keeping with all the aforementioned features, the transverse abdominal musculature in the anisopteran type also exhibits degeneration, which is quite unmistakable in the absence of the transverse ventral musculature. Eventually, as a result, no trace of the ventral diaphragm is formed.

The transverse dorsal musculature which forms the alary muscles however, resembles both anatomically and functionally its counterparts in the thysanuran, ephemerid and zygopteran types.

(3) PECULIARITIES OF THE MUSCULAR PATTERNS IN THE PREGENITAL ABDOMINAL SEGMENTS OF THE DICTYOPTERAN, ISOPTERAN, ORTHOPTERAN, AND MECOPTERAN TYPES.

The abdominal muscular pattern in the dictyopteran, isopteran, orthopteran and mecoptera types is only a modified version of the one described earlier in the case of the ephemerid representative. These modifications are as follows -
(a) In the cases of the dictyopteran, alate swarming isopteran and orthopteran and mecopteran types, the various complements of the dorsal and ventral longitudinal musculature - viz the M. dorsales interni mediales, the M. dorsales externi laterales, the M. ventrales interni mediales, the M. ventrales interni laterales, the M. ventrales externi mediales, the M. ventrales externi laterales, - occur in the form of well developed, horizontally spread out strips, perhaps in correlation with the concomitantly broader abdomen in these groups. The dorsales interni and the ventrales interni groups are of segmental length, whereas the dorsales externi and the ventrales externi groups form the short strips occupying only the posterior sternal areas.

In all these cases, the various aforementioned muscles have disposition parallel to the longitudinal axis, except in the queen of isopteran, and orthopteran representatives, wherein the dorsales externi group has maximum oblique disposition with an anterior outward slant.

Strangely, in spite of their better developed nature as mentioned above, the retraction of the abdomen and hence the expiratory movement caused by these various longitudinal muscles is not much pronounced. This feature in all these types excepting the queen of the isopteran representative
appears to be correlated with the higher degree of sclerotization of the intersegmental membranes in their abdomen. The regaining of the original pose by the abdomen, during the inspiration, is caused by the general elasticity of its integument and the muscles.

*M. dorsales externi* are obliquely disposed groups in the case of the orthopteran type, and act as the torsion muscles serving to import a partial transverse rotation of the abdominal segments on each other. This is a special feature of the arthopteran type.

Similar observations as regards to the abdominal musculature are recorded by Snodgrass (1935), Vishnoi (1962), Maill and Denny (vide Richards and Davies 1964) in the cases of the different species of Dictyoptera, Isoptera and Orthoptera. No such previous record is available in the mectopteran type.

It is worthwhile to mention here in passing, that very peculiarly, in the queen of the isopteran type, the various aforedescribed abdominal muscles are extremely well-developed and produce a continuous peristalsis that takes place anteroposteriorly. This, perhaps, helps in the maintenance of the faster rate of oviposition. Incidentally, it also drives the air in the trachea posteriorwards by creating haemocoelic blood pressure directed backwards.
In such a movement of the abdomen in the queen of the isopteran type, the **M. dorsales externi muscles** effect transverse movements of the abdominal segments they exhibit a maximum obliquity almost attaining horizontal disposition. As a result, they become secondarily intrasegmental both in attachments and function to effect the horizontal compression of the abdomen and in a measure to antagonise the normal actions of the other abdominal longitudinal muscles.

(b) The abdominal lateral musculature in the cases of the dictyopteran, alate swarming isopteran, orthopteran and mectopteran representatives shows further modification from the pattern met with in the case of the ephemeral type. This modification has reached its climax, in that, some of the more lateral fasciculi of the **M. laterales externi** group arise on the lower anterior angle of the terga and insert on the upper outer tip of the lateral sternal apodeme. Thus, they have reversed origins and insertions to act as the vertical dilators of the abdomen instead of functioning normally as the vertical compressors. Because of such a state of affairs, the vertical movements of the abdomen - both the compression and dilation - are very efficient, and consequently the expiration and inspiration both form the active phases of respiration in striking contrast to the situation in the ephemeral and odonatan-zygopteran types described earlier.
On the whole it may be inferred from the entire preceding account that in the cases of the dictyopteran, alate swarming isopteran, orthopteran and mecopteran types, the chief ventilatory movements occur in the vertical plane. The ventilatory movements due to lateral compression are very feeble.

(c) The abdominal transversal ventral and dorsal muscular patterns in all these insectan representatives resemble very closely their counterparts in the ephemerid type both from the anatomical and functional view points.

(F) PECULIARITIES OF THE MUSCULAR PATTERN IN THE PREGENITAL ABDOMINAL SEGMENTS OF THE GYMNOCERATE HETEROPTERAN TYPE.

Compared to that in the representatives of the Dictyoptera, and Orthoptera the muscular pattern in the pregenital abdomen of the gymnocerate heteropteran type is extremely degenerated, perhaps in correlation with the very heavy sclerotization of the abdominal segments and intersegmental membranes. This degeneration is quite unmistakable in its following characteristics -

(a) The longitudinals in the gymnocerate very peculiarly heteropteran type are restricted only to the abdominal segments No. 1, 2, 3, and 6. They are absent in the other abdominal segments. These muscles in the
other abdominal segments. These muscles in the first segment are represented by the strips of the \textit{M. dorsales interni mediales}, and \textit{M. dorsales interni laterales} groups, whereas in the segments 2, 3 and 6 they comprise only the slender bands of \textit{M. dorsales interni mediales}.

The \textit{M. dorsales externi} group is entirely lacking in this case.

In conformity with the above feature, the ventral longitudinals also have a restricted distribution. In the first abdominal segment, they are composed of the strips of \textit{M. ventrales interni} groups, whereas in the sixth abdominal segment, they consist of strips of \textit{M. ventrales externi} group.

In effect, therefore, the longitudinal mobility of the abdominal segments is meagre to directly help in respiration in striking contrast to the conditions described previously in the other insectan types.

(b) The lateral abdominal muscular pattern in the gymnocerate type is very similar to its counterpart in the dictyopteran, isopteran and orthopteran types, both from anatomical and functional view points.

Consequently the vertical ventilatory movements are very conspicuous, and they form the only breathing movements in the gymnocerate type, since no longitudinal mobility of
the abdomen occurs in this case described above.

(c) The abdominal transverse musculature in the gymnocerate type, also shows degeneration, which is conspicuous in the absence of the transverse ventral muscles.

The transverse dorsals, however, are similar to those in the dictyopteran and orthopteran types both from anatomical and functional aspects.

(c) PECULIARITIES OF THE MUSCULAR PATTERN IN THE PREGENITAL ABDOMEN OF THE CRYPTOCERATE HETEROPTERAN TYPE.

Compared to that in the gymnocerate heteropteran type, in the cryptocerate type, strangely the degeneration and modifications in the pregenital abdominal muscular pattern are altogether in a different plane. Likewise, different grades and planes of degeneration and modifications are recorded by Akbar (1958), David (1967) and Kaushik (1972) in different species of gymnocerate and cryptocerate types. Thus, it appears that in the Heteroptera, the pregenital abdominal muscular pattern, perhaps, has undergone numerous variations depending upon the mode of respiration and habitat at large.
The degeneration and modifications in the investigated cryptocerate type are obviously as follows:

(a) The dorsal longitudinals are present in all the pregenital abdominal segment of the cryptocerate type and their complement consists of only the highly reduced *M. dorsales externi* groups. This is in striking contrast to the situation in the gymnocerate type, wherein the dorsal longitudinals are restricted to certain abdominal segments and are made up of the reduced *M. dorsales interni* groups.

Further, the aforesaid dorsal longitudinals in the case of the cryptocerate type exhibit a very peculiar disposition. They insert on the elongated apodemes from the succeeding phragma and assume the form of a pair of pinnate muscles, wherein the muscle strips have almost transverse disposition with the posteriorly directed slant (vide Plate No. 41) towards their insertions. As a result, these muscles become intrasegmental functionally serving to effect the horizontal lateral compression of the abdomen. Incidentally, they also bring about a very feeble retraction of the abdomen due to their posteriorly directed obliquity.

In conformity with all the above, the ventral longitudinals also occur in all the pregenital abdominal segments of the cryptocerate type and are made up of the
M. ventrales externi group alone. This is in striking contrast to the condition in the gymnocerate type, wherein the ventral longitudinals are restricted only to certain segments in the abdomen and are composed of the M. ventrales interni groups.

Further, these ventral longitudinals insert on a single median apodeme from the succeeding furca to form a sort of single median pinnate type of muscle, wherein the muscle-strips have horizontal disposition. Thus, these muscle-strips functionally become intrasegmental and serve to bring about the horizontal lateral compression of the abdomen.

The reverse movement of the abdomen i.e. regaining of the original pose by the abdomen in this cryptocerate type, however, is due to general elasticity of the abdominal wall. This effects a slow inspiratory movement.

(b) Very peculiarly, both the complements of the abdominal lateral musculature - the M. laterales interni and the M. laterales externi groups - are represented as tiny slender strips distributed along the length of the segments. This state of affairs has no parallel in any of the insectan type investigated in the present work.

These muscle-strips, obviously bring about the uniform vertical compression of the abdominal segments,
which effect the expiratory movement. The reverse movement of the abdomen i.e. regaining of the original pose by the abdomen is effected by the general elasticity of its wall. This brings about the slow inspiratory movement.

It is very clear from all the above account that in the cryptocerate type, the compression and dilation of the abdomen occur in both the vertical and horizontal lateral planes. Presumably, such movements take place in a postero-anterior succession, driving the air in the trachea anteriorly. Obviously, this facilitates the sucking in of the air through the respiratory siphon, at the hind end.

(c) In both the cryptocerate and gymnocerate types, the abdominal transverse musculature exhibits very similar degeneration, since in both cases, the ventral transverse muscles are lacking in the abdomen. However, the dorsal transverse muscles in abdomen of these types, resemble their counterparts in the orthopteran representative both anatomically and functionally.

(E) PECULIARITIES OF THE MUSCULAR PATTERN IN THE PREGENITAL ABDOMEN OF THE NEUROPTERAN TYPE.

The pregenital abdominal muscular pattern in the neuroptera type is a reduced variant of that described
earlier in the orthopteran and mecopteran representatives.
This feature in the neuropteran type appears to be correlated with the greater sclerotization of the concomitantly narrow abdomen in the group. However, the reduction in this case is comparatively less and is manifested as the following peculiarities -

(a) The abdominal dorsal longitudinals in the neuropteran type are represented by single slender strips of each M. dorsales interni mediales and M. dorsales interni laterales groups; both the M. dorsales externi groups are absent. This is in striking contrast to the situation described previously in the orthopteran and mecopteran types, wherein all these dorsal longitudinal complements are well-developed and comprise several muscle-strips.

On the other hand, the abdominal ventral longitudinals in the neuropteran type comprise single slender strips of M. ventrales interni mediales, M. ventrales interni laterales, and M. ventrales externi mediales groups; the M. ventrales externi laterales groups are absent. This again is in striking contrast to the condition in the orthopteran and mecopteran types, wherein all the above groups of ventral longitudinals comprise several well-developed muscle-strips.
Thus, the horizontal longitudinal mobility of the abdominal segments is less, which is further attenuated by the more sclerotization of the abdominal segments and intersegmental membranes.

(b) The abdominal lateral musculature in the neuropteran type, however, resembles that in the orthopteran and mecopteran representatives both from anatomical and functional view points.

Consequently, in the neuropteran type also, the chief respiratory movements are brought about by the vertical compression and dilations of the abdomen.

(c) Likewise, the abdominal transverse ventral and dorsal musculature also resembles its counterpart in the orthopteran and mecopteran type anatomically and functionally as well.

(I) PECULIARITIES OF THE MUSCULAR PATTERN IN THE PREGENITAL ABDOMEN OF THE COLEOPTERAN TYPE.

The muscular pattern in the pregenital abdomen of the coleopteran type, again is also a reduced version of the one found in the cases of the orthopteran and mecopteran representatives. This reduction in the case of the coleopteran type is comparatively less than that in the
mecopteran type and appears to be correlated with the heavy sclerotization of the abdominal wall in the group. It, however, is unmistakably in a different plane as is mentioned below -

(a) The abdominal dorsal longitudinals in the coleopteran type are made up of the *M. dorsales interni mediales*, the *M. dorsales interni laterales*, the *M. dorsales externi mediales*, which occur in the form of muscle bands distributed horizontally in each segment of the pregenital abdomen.

The *M. dorsales externi laterales* group, which is very well-developed in the orthopteran and mecoptera types, however, is absent in the coleopteran representative.

On the other hand, the abdominal ventral longitudinals in the coleopteran type are peculiarly restricted only to segments No. 1, 2, 6 and 7, whereas they are lacking in the other abdominal segments. Further, in the segments No. 1, 6 and 7, they comprise all the complements - viz the *M. ventrales interni mediales*, the *M. ventrales interni laterales*, the *M. ventrales externi mediales* and the *M. ventrales externi laterales*, which occur in the form of well-developed strips. In contrast to this, in the segment No. 2, they are made up of only the *M. ventrales externi mediales* and the *M. ventrales externi laterales*; the *M. ventrales interni* groups being absent.
Very similar observations as regards to these features are recorded by Evans (1961) and Termier (1970) in the other species of Coleoptera also.

In effect, therefore, the longitudinal mobility of the pregenital abdominal segments is too meagre to cause any horizontal longitudinal breathing movements.

(b) The lateral and the transverse dorsal and ventral muscular patterns in the abdomen of the coleopteran type resemble very closely their counterparts in the orthopteran and mectopteran representatives, both anatomically and functionally. Consequently, the main respiratory movements in this case also are the vertical compressions and dilations of the abdomen.

(J) PECULIARITIES OF THE MUSCULAR PATTERN IN THE PREGENITAL ABDOMEN OF THE LEPIDOPTERAN TYPE.

The muscular pattern in the pregenital abdomen of the lepidopteran type also exhibits degeneration, which, however, is in a quite different plane again, compared to the conditions in other degenerated patterns described earlier. This feature in the lepidopteran representative is obviously correlated with the sclerotization of the abdominal wall, and is manifested in the following manner -
(a) In the first abdominal segment of the lepidopteran type, the dorsal and ventral longitudinal muscles are represented by the \textit{M. dorsales interni mediales} and \textit{laterales} and the \textit{M. ventrales interni mediales} and \textit{laterales} respectively. All these muscles are well-developed strips of segmental length.

In striking contrast to this, in the abdominal segments No. 2-7, the complements of the dorsal and ventral longitudinals are the \textit{M. dorsales externi mediales} and \textit{laterales} and the \textit{M. dorsales externi mediales} and \textit{laterales} respectively. These muscles also occur as well-developed strips which are short, and occupy the posterior tergal and sternal areas.

It is very clear from the above account that the longitudinal horizontal mobility of the abdominal segments is very feeble.

(b) The lateral and the transverse dorsal and ventral muscular patterns in the lepidopteran type, however, resemble very closely their counterparts in the orthopteran and mecopteran representatives both from anatomical and functional view points. Eventually, the main respiratory movements in this case also are the vertical compressions and dilations of the abdomen.
PECULIARITIES OF THE MUSCULAR PATTERN IN THE PREGENITAL ABDOMEN OF THE HYMENOPTERAN TYPE -

The muscular pattern in the pregenital abdomen of the hymenopteran representative is extremely degenerated and remarkably modified at the same time. These features in the case of the hymenopteran type are conspicuously exhibited as recorded in the following paragraphs -

(a) The abdominal dorsal longitudinal muscles in the hymenopteran type are made up of the M. dorsales interni and mediales, the M. dorsales externi laterales. Each one of these muscles is represented by a single well-developed muscle-strip.

In a unique way, the M. dorsales interni mediales has an oblique disposition with a mesad slant posteriorly towards its insertion. Conversely, the M. dorsales externi laterales shows obliquity that has an outward slant posteriorly towards its points of insertion. Such an arrangement of muscles in the hymenopteran type, in company with the concomitantly flexible and very less sclerotized intersegmental membranes in the group, is mainly responsible for effecting the characteristic telescoping of the abdomen. Incidentally, this feature in the hymenopteran type is of immense importance in many of its life activities like respiration, circulation, copulation, oviposition and self-defense involving the use of the sting. It also, perhaps,
serves to reduce the 'drag' of the abdomen during the flight of the hymenopteran type. (Pringle 1957a).

In striking contrast to all the above, the M. dorsales externi mediales, exhibits the reversal of its origin and insertion, since it arises on the posterior mesal area of the tergum of its segment and extends anteriorly to its insertion on the overlapping under surface of the anterior apophysis of the succeeding tergum (vide Plate No. 53). The M. dorsales externi, therefore are the protractors of the terga, inasmuch as their contraction serves to separate the tergal plates. This, incidentally, helps in the inspiratory movement.

As for the abdominal ventral longitudinal musculature, it may be recorded here that its complements are the single strips of each M. dorsales interni mediales and the M. dorsales interni laterales. Of these, the former has an oblique disposition with a mesad slant posteriorly towards its points of insertion. Conversely, the latter shows obliquity that has an outward slant posteriorly towards its point of insertion. Such an arrangement of ventral longitudinal muscle serves to effect the telescoping of the abdomen described above. Observations of Snodgrass (1942, '56) and Saksena (1959) in the other hymenopteran species are also essentially similar in this matter.
(b) The abdominal lateral muscular pattern in the hymenopteran type, however, is very similar to its counterpart in the orthopteran and mecopteran representatives anatomically and functionally as well. Consequently, the vertical compressions and dilations of the abdomen involving the expiration and inspiration respectively are quite pronounced in this case also.

On the whole, therefore, it appears that understandably the vertical compressions and dilations and likewise, the retraction and protraction of the abdomen bring about the expiration and inspiration respectively.

The wave of these movements, presumably occurs in posteroanterior succession and thus the air in the trachea is driven anteriorly towards the thorax to ensure faster aeriation of the body during flight.

The intermittent telescoping of the abdomen may help in reducing the air space of the air sacs.

(c) The abdominal transverse dorsal musculature in the hymenopteran type is essentially similar to its counterpart in the orthopteran and mecopteran types both anatomically and functionally.

The abdominal ventral transverse musculature, however, is very peculiar in that it forms a pulsating
ventral diaphragm along with the intervening connective tissue fibers. This is a unique feature of the Hymenoptera. The ventral diaphragm separates the ventral sinus from the perivisceral sinus and hence serves in controlling and maintaining the course of circulation. Incidentally, it also perhaps helps in respiration by effecting horizontal compression of the abdomen.

(L) **PECULIARITIES OF THE MUSCULAR PATTERN IN THE PREGNITAL ABDOMEN OF THE DIPTERAN TYPE.**

The muscular pattern in the pregenital abdomen of the dipteran type is an extremely degenerated one. The degeneration in this case again is in an altogether different plane and is very evident as shown below:

(a) The dorsal longitudinals in the first abdominal segment of the dipteran type comprise the M. dorsales interni mediales, the M. dorsales externi mediales and the M. dorsales externi laterales. Each one of these muscles is represented by a single strip.

On the other hand, in the abdominal segments No. 2-7, the dorsal longitudinal complements are only the M. dorsales externi mediales and the M. dorsales externi laterales.
The \textit{M. dorsales externi mediales}, is represented by two muscle-strips - one occupies the normal posterior position in the tergal areas exhibiting an oblique disposition with an anteriorly outward slant, whereas the other occupies the anterior tergal areas with a usual longitudinal disposition. These muscles as usual act as the retractors of the abdomen.

The \textit{M. dorsales externi laterales} is made up of single muscle strip, but in striking contrast to the former, arises on the posterior lateral area of the tergum of its segment and extends anteriorly to its insertion on the overlapping phragma undersurface of the succeeding segment. Consequently, these muscles have reversed their origins and insertions and hence serve to protract the abdomen.

In keeping with the above features, the ventral longitudinals in the abdomen of the dipteran type are also reduced, since they are made up of the \textit{M. ventrales externi mediales}, and the \textit{M. ventrales externi laterales}, which occur as single muscle strips. The former is obliquely disposed with the outward slant posteriorly, while the latter has obliquity with outward slant anteriorly. Such an arrangement of muscles, perhaps, brings about more efficient retraction of the abdomen.

(b) The abdominal lateral musculature, and the abdominal dorsal and ventral transverse musculature in the
dipteran types resemble very closely their counterparts in the other insectan types investigated, both anatomically and functionally as well.

Observations of Bonhag (1951), in *Tabanus sulcifrons* are almost similar with regard to all the above features.

On the whole, therefore, the compressions and dilations and likewise the retractions and protractions of the abdomen appear to effect the expiration and inspiration respectively.

The wave of such abdominal movements presumably occurs in postero-anterior succession, driving the air in the trachea anteriorly towards the thorax to ensure the faster aeriation of the body.

These above features reflect in a way the condition in the hymenopteran representative described earlier.