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Notes on the morphology of the musculature of the salivary syringe and neck region of bees

by

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The present paper is a continuation of a former work on the thoracic musculature of bees (WILLE, 7). The main purpose of this study is to shed light on the evolutionary trends of muscles which may also provide, indirectly, clues as to the relationships among certain groups of bees.

Like most works of this type, the scope of the study has been limited by the relatively small numbers of specimens available for dissection. The specimens dissected are as follows:

FAMILY COLLETIDAE: *Ptiloglossa mexicana* (Cresson), *Colletes punctipennis* Cresson, *Hylaeus cressoni* (Cockerell), *H. modestus* Say.

FAMILY HALICTIDAE: *Lasioglossum imitatum* (Cresson), *Pseudaugochloropsis graminea* (Fabricius), *Augochloropsis diversipennis* (Lepeletier), *A. sparsilis* (Vachal), *Agapostemon radiatus* (Say), *Pseudagapostemon divaricatus* (Vachal), *Halictus ligatus Say, Megalopta genalis* Meade-Waldo, *Dufourea marginata* (Cresson), *Nomia heteropoda* (Say), *N. melanderi* Cockerell, and *N. apacha* (Cresson).

FAMILY ANDRENIDAE: *Andrena bipunctata* Cresson, *A. argemonis* Cockerell, *Perdita lacteipennis* Swenk and Cockerell, *Psaenythia mexicanarum cockerelli* Dunning and *Oxaea flavescens* Klug.

FAMILY MEGACHILIDAE: *Megachile brevis* Say, *Anthidium maculosum* Cresson, and *Dianthidium sayi* Cockerell.

FAMILY ANTHOPHORIDAE: *Exomalopsis solani* Cockerell, *Ancylosceles armata* Smith, *Paratetrapedia oligotricha* Moure, *Nomada* sp., *Diadasia enevata* (Cresson), *D. diminuta* (Cresson), *Ptilothrix sumichrasti* (Cresson), *Melitoma euglossoides* Lepeletier and Serville, *Xenoglossa fulva* Smith, *Florilegus condignus* (Cresson), *Melissodes coloradensis* Cresson, *Svastra obliqua* (Say), *Thygater*

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analis (Lepeletier), *Centris lanosa* Cresson, *Epicharis elegans* Smith, *Xylocopa virginica* (Druny), *Ceratina dupla* Say.

FAMILY APIDAE: *Bombus fraternus* Smith, *B. Medius* Cresson, *B. ephippiatus* Say, *B. volucelloides* Gribodo, *Euglossa igniventris* Friese (=*cupreiventris*). *E. cordata* (Linnaeus), *E. (Euglossa)* sp., *Euplusia coerulescens* (Lepeletier), *Eulaema dimidiata* (Fabricius), *Apis mellifera* L. and *Trigona nigra paupera* (Provancher).

METHODS

The specimens were preserved in Dietrich's fluid (Kahle's fixative) for several days, and then kept in 80 percent alcohol. Dissections were done under water. Most direct muscles of the head were studied by cutting open the anterior ventral area of the thorax. The indirect muscles of the head were best observed by dorsal and lateral dissections of the thorax. When possible more than one specimen was dissected for each species studied.

Since the anatomy of the honey bee, *Apis mellifera,* has been adequately described (MORISON 2, 3, 4; SNODGRASS 5, 6) this species can serve as the standard type for comparison with other bees. For the terminology of the skeletal structure, that of MICHENER (1) has been adopted, but, to avoid confusion, the structural names used by SNODGRASS (5) in the honey bee have been indicated in parentheses. For the muscle terminology, that of SNODGRASS (5) has been followed.

It is to be understood that in most cases there is a right and left set of muscles. For this reason, any particular muscle is likely to occur as one pair: one muscle to the right and the other to the left of the median plane. One exception among the muscles studied in this paper is the *inferior phragmatic levator of the head,* which is usually just one branched muscle situated medially on the back of the head. Any specific pair of muscles, either the right or left set, has been treated as singular throughout the paper.

OBSERVATIONS

THE SALIVARY SYRINGE: The salivary ejection apparatus is called the salivary syringe. It consists of a wide, flat, triangular chamber at the base of the ligula (glossa and paraglossa). The floor of this chamber is slightly concave and is continuous at its distal angle with the inflected ends of the ligular arms of the prementum. It is rather rigid, while the roof is flexible and elastic. This chamber has a wide aperture situated anteriorly at the distal end of the prementum. The salivery duct opens at the inner end of the chamber. There are two muscles inserted on the salivary syringe:

1) *Dilator of the salvary syringe* (Fig. 1). A flat muscle arising on the lateral margin of the prementum, usually close to, or associated with, the ligular arm. The muscle is inserted medially on the anterior wall of the salivary syringe.

2) *Compressor of the salivary syringe.* This is the largest muscle in the prementum, arising at the posterior part of the prementum and inserted distally on the lateral margins of the salivary syringe. This muscle varies little in bees.

The comparative study of the musculature of the salivary syringe has shown that only the dilator muscle has undergone important modifications among the bees. Since this muscle is usually associated with the ligular arms, and since these arms vary considerably, both structures are discussed in detail. The ligular arms (Fig. 1) are sclerotic bands arising from the anterior margins of the premental plate. The arms are curved inward and are continuous medially with the distal angles of the salivary syringe. The distal parts of the ligular arms are usually elastic and whitish in color, being apparently of the same nature as the glossal rod.

In the family Colletidae the ligular arms are well developed, strongly arched, elastic, and frequently whitish throughout their whole length. Starting at the margins of the premental plate, the arms are bent first dorsomesad then curve ventrad and at the same time diverge slightly; at the base of the ligula they are inflected laterad of the salivary opening, and are then continuous with the distal angles of the salivary syringe. The dilator of the salivary syringe originates on the posterior half of the ligular arm. It should be pointed out that in the wasp *Bembix,* the ligular arm (one on each side) is also very arched, but the posterior half of the arm, where the dilator muscle originates, is not elastic like the anterior half.

In the family Halictidae the ligular arms are represented by two long and narrow sclerotizations on the dorsal part of the labium, with different stages of fusion to the premental plate according to the species. Each dilator of the salivary syringe originates posteriorly on one of these long sclerotizations.

In the family Andrenidae the ligular salivary syringe is essentially the same as in the family Halictidae. In *Andrena,* however, the ligular arms are shorter and slightly arched, and the dilator muscle is attached to the proximal or non-elastic portion of the arms. In *Perdita* and *Psaenythia* the ligular arms are straight and the dilator muscle originates on the posterior margin of the prementum.

In the family Megachilidae the ligular arms are very short. Almost immediately after arising from the anterior and dorsal margins of the premental plate, they curve inward toward the salivary syringe. The arrangement of the dilator of the syringe is also different from that of the previous families. The muscle curves around the other muscles and extends basally to its origin, which is below the anterior lateral margin of the prementum.

In the family Anthophoridae the ligular arms are very short, like those of the family Megachilidae, except that in *Centris,* the arms are longer. In most of the species studied the dilator of the salivary syringe was also similar to that of Megachilidae, in which the muscle makes a curve around the other muscles. In *Xylocopa* the arrangement of the dilator was found identical to that of Megachilidae. In other species, however, the muscle differs slightly in that it is attached more posteriorly and well below on the lateral margin of the

prementum. In Megachilidae and *Xylocopa* the muscle arises more anteriorly. A less specialized type of dilator muscle was found in *Diadasia, Xenoglossa, Florilegus* and *Ceratina.* In these bees the muscle originates on or close to the border of the prementum, for which reason the dilator does not make a curve around the other muscles. In this family the dilator may arise anteriorly, as in *Diadasia,* or posteriorly, as in *Xenoglossa, Florilegus* and *Ceratina.*

In the family Apidae the ligular arms are very short, being curved inward toward the salivary syringe. In Bombini and Euglossini the dilator of the syringe curves around the other muscles (Fig. 1) and extends basally to its origin well below on the lateral margin of the prementum, as in most species of Anthophoridae. In Meliponini and Apini, on the other hand, the dilator originates on the anterior lateral margin of the prementum, close to the ligular arms.

THE NECK REGION: The neck or cervix of bees is a narrow membranous region between the head and the thorax. It is concealed within the concave median area of the posterior region of the head. The cervical membrane attaches anteriorly to the head, just outside the margin of the foramen magnum, and posteriorly to the prothorax. The anterior side of each propleuron is produced into the mesally bent occipital process, which supports the cervical membrane and serves as an articulating point with the corresponding occipital condyle of the head. The cervical sclerites are apparently fused with the propleura. According to MICHENER (1), cervical sclerites are present in some bees such as *Andrena, Halictus, Megachile, Triepeolus, Xylocopa* and *Apis.* These sclerites, which have apparently developed independently in the various groups of bees, are secondary sclerotizations of the cervical membrane just below the occipital processes of the propleura. There are no muscles inserted on these sclerites, they merely serve to strengthen the cervical membrane.

The musculature of the neck consists of those muscles which move the head. They can be divided into two groups: 1) muscles that move the head directly, and 2) muscles that move the propleura, which indirectly affects the movements of the head.

DIRECT MUSCLES OF THE HEAD: These muscles are attached on the margins of the foramen magnum. They include two levators, two rotators (which may act as levators also) and one depressor muscle. The levators are attached on the dorsal margin of the foramen and consist of one median muscle, the *inferior phragmatic,* at either side of which is attached the other levator, the *superior phragmatic.* The rotators of the head are attached laterally on the dorsal margin of the foramen, one pair is the *pleural* and the other the *endosternal.* The depressors consist of a pair of muscles attached on the ventral margin of the foramen. Since the head is articulated on a transverse axis between the occipital processes or cephaligers of the propleura, it has mainly up and down movements by the opposed action of the levator and depressor muscles.

1. *Inferior phragmatic levator of the head.* (Fig. 4). This is a two- or four-branched muscle, the branches originating laterally on the first phragma. It is inserted medially by a common tendon on the dorsal angle of the foramen magnum. In a few bees this muscle appears as one pair.

2. *Superior phragmatic levator of the head.* (Fig. 4) This is a two-branched muscle, shaped like a V or Y. The inner branch originates near or along the midline of the first phragma. The outer branch follows closely the outer branch of the *inferior phragmatic levator.* The *superior phragmatic* is inserted laterally on the dorsal margin of the foramen magnum, lateral to the insertion of the *inferior phragmatic.*

3. *Pleural levator or rotator of the head.* This is a three-branched muscle which arises on the propleuron and attaches laterally on the dorsal margin of the foramen mangnum.

4. *Endosternal levator or rotator of the head.* This is a single unbranched muscle, its wide base arises on the horizontal apophyseal bridge (supraneural bridge of prothoracic endosternum), and attaches laterodorsally on the margin of the foramen magnum.

5. *Depressor of the head.* This is a two-branched muscle which arises on the horizontal apophyseal bridge, beneath the *endosternal levator,* and attaches to the ventral margin of the foramen magnum.

INDIRECT MUSCLES OF THE HEAD: These muscle are attached on the anterior part of the propleura. Since the propleural plates lack any fixation on the prosternum and are articulated posteriorly on the prosternal apophyseal arms (prothoracic endosternal arms), and since the occipital axis between their anterior ends is short, the propleural plates are well adapted to give partial rotatory movements to the head, aided by the antagonistic action of the strong right and left sets of muscles attached to their anterior parts. These muscles are the following:

6. *Phragmatopleural muscle of the prothorax.* (Fig. 4) This muscle may have the shape of a slender ribbon, a V or a fan. It arises on the first phragma, and is inserted on the posterior ramus of the occipital process (cervical apodeme of the propleuron).

7. *Tergoepisternal (tergopleural) muscle of the prothorax.* (Fig. 4) (Since the division of the propleuron into episternal and epimeral regions is not conclusive, the muscle should be called *tergopleural of the prothorax).* This is a large strap-like muscle which arises mesally on the posterior inflection of the pronotum, although apparently it may seem to originate on the first phragma. It then diverges forward above the *inferior* and *superior phragmatic levators of the head* to the transverse propleural brace (horizontal apodeme of propleuron).

8. *Adductor of the propleuron.* Spindle shaped muscle, from the anterior process of the inner crest of the apophyseal arm (apodeme of prothoracic endosternum) to the posterior ramus of the occipital process.

DISCUSSION

The comparative study of the neck musculature of bees shows that only a few of these muscles present important modifications. Among these muscles, the *inferior phragmatic levator of the head* and the *phragmatopleural muscle of the prothorax* show the most interesting variations. In the Meliponini, for

instance, the *inferior phragmatic levator* is V-shaped, and splits close to its insertion at the dorsal angle of the foramen magnum. The two diverging branches originate on the medial area of the first phragma, and like all neck muscles, they are long and slender (Fig. 4). In the Bombini and Euglossini this muscle is similar to that of Meliponini, except that in Bombini the muscle is Y-shaped because it is inserted by a long apodeme (Fig. 5A), and in Euglossini the two branches originate farther apart (Fig. 6A). In the Apini the situation is quite different, the *inferior phragmatic muscle* is four-branched instead of two-branched. The two inner branches originate on the medial areas of the first phragma and the two outer branches laterally on the same phragma (Fig. 3A). SNODGRASS (5) regarded this muscle as being two-branched in the honeybee, or, as he called it, a pair of long muscles. However, several specimens were dissected and all were found to be four-branched. The question of considering this muscle as one or as a pair is a relative one. Obviously it must be regarded as one muscle in the Bombini and possibly in most bees in which there is a small common insertion. In others, as in *Colletes* (Fig. 2A), it can be regarded either as one or two muscles. A comparative study of this muscle shows that the four-branched condition is found in the more primitive bees, such as in *Colletes* sp. (Fig. 2A), *Ptiloglossa mexicana, Augochloropsis sparsilis, Pseudaugochloropsis graminea, Halictus ligatus, Megalopta genalis, Dufourea marginata* and *Andrena argemonis.* On the other hand, the two-branched condition (Fig. 4) is found in the more specialized bees, such as: *Nomia apacha, Oxaea flavescens, Anthidium maculosum, Megachile brevis, Paratetrapedia oligotricha, Diadasia enevata, Melissides coloradensis, Centris lanosus* and *Xylocopa virginica.*

The *superior phragmatic levator of the head* is a Y- or V-shaped muscle which varies little among the bees. The inner branch always originates near or along the midline of the first phragma. The outer branch follows closely the outer branch of the *inferior phragmatic* and varies as does the latter. The *superior phragmatic levator* is inserted laterally on the dorsal margin of the foramen magnum lateral to the insertion of the *inferior phragmatic levator of the head.* This muscle was also regarded by SNODGRASS (5) as simple or unbranched in the honeybee. However, it is actually branched in *Apis,* as well as in all other bees examined (Figs. 2, 3, 4, 5, 6).

The *phragmatopleural muscle of the prothorax* is also Y- or V-shaped in most bees. The inner branch closely parallels the *tergoepisternal muscle of the prothorax.* The outer branch arises laterally and the inner one medially on the first phragma. It is inserted anteriorly on the cervical apodeme of the pleuron (Fig. 5C). Although the same type of muscle is found in the honeybee (Fig. 3C), SNODGRASS (5) misinterpreted its relation. He traced the outer branch and part of the inner branch correctly but he considered the latter to be a part of the *tergoepisternal muscle of the prothorax.* He describes the situation as follows: "A small prothoracic muscle attached close to 46 (phragmatopleural muscle) on cervical apodeme of pleuron may be a branch of 48 (tergoepisternal muscle), though its fibers appear to run along the underside

of the latter" (page 104, muscle number 47). Two such modifications of the *phragmatopleural muscle* were found among Apoidea. In *Colletes* sp. the outer branch is missing (Fig. 2C), and in Euglossini the outer and inner branches seem to be fused into one large triangular muscle (Fig. 6C).

CONCLUSIONS

The present study shows that certain muscles of the salivary syringe and neck region underwent important modifications during the evolution of bees.

The evolutionary trend of the *dilator of the salivary syringe* can be easily traced. Apparently the muscle underwent a definite shift in its origin in the following sequence:

1. Origin on the ligular arms of the prementum, as found in Colletidae, Halictidae and most Andrenidae.
2. Origin on the anterior lateral margin of the prementum, as found in *Diadasia,* Meliponini and Apini.
3. Origin on the posterior lateral margin of the prementum, as found in *Perdita, Psaenythia, Xenoglossa, Florilegus* and *Ceratina.*
4. Origin below the anterior lateral margin of the prementum, thus making a curve around the other muscles, as found in Megachilidae and *Xylocopa.*
5. Origin well below the posterior lateral margin of the prementum, for which reason the dilator makes a curve around the other muscles (Fig. 1), as found in Euglossini, Bombini and most Anthrophoridae.

The *inferior phragmatic levator of the head* is perhaps that of the muscles which presents the most interesting evolutionary tendency in the neck region of bees (Fig. 7). Originally the *inferior phragmatic* consisted of a pair of v-shaped muscles, inserted very close to each other (Fig. 2A). Next, both muscles became fused together at the insertion level, thus forming a four-branched muscle (Fig. 3A). Finally two of the branches, possibly the outer ones, were suppressed, thus forming a two-branched muscle (Fig. 4). The actual sequence is as follows (Fig. 7):

1. A pair of v-shaped muscles, arising laterally on the first phragma of the mesonotum, are inserted very close to each other in the dorsal angle of the foramen magnum. The paired condition is found in *Colletes* sp.
2. These muscles are fused together at the insertion, in the dorsal angle of the foramen magnum, forming a large four-branched muscle. The outer branches of this muscle arise far apart laterally on the phragma, while the inner branches originate closer to the median area of the phragma. The four-branched condition is found in most Colletidae, Halictidae, Andrenidae and *Apis.*
3. The four-branched muscle becomes reduced by the elimination of the outer branches, forming in this way a two-branched or v-shaped muscle. Since the branches of this muscle usually arise not far apart from the median

area of the phragma, it has been assumed that the missing branches are the outer ones. The two-branched condition is found in Nomiinae, Oxaeinae, Megachilidae, Anthophoridae and most Apidae.

4. The V-shaped muscle becomes inserted by a long apodeme, forming in this way a Y -shaped muscle. This condition is found in Bombini (Fig. 7D).

As can be observed from the evolutionary trend of the inferior *phragmatic levator of the head, Apis mellifera* retains the primitive condition, a four-branched muscle, in spite of the fact that it belongs to one of the most specialized groups of bees. This is perhaps not very surprising since several other characters, which have been considered primitive, are also found in the honey bee. It is also interesting to point out that among the families Halictidae and Andrenidae, the Nomiinae and Oxaeinae exhibit this two-branched condition, found among the more advanced bees. In some features of the thoracic musculature (WILLE, 7) and the dorsal vessel (WILLE, 8) the Nomiinae and Oxaeinae also agree with more specialized families of bees.

The *phragmatopleural muscle of the prothorax* shows three tendencies:

1. A V- or Y-shaped muscle from the cervical apodeme of the pleuron, with both branches arising far apart on the first phragma, as in most bees.

2. The outer branch missing, forming in this way a flat, ribbon-like muscle, as in *Colletes* sp.

3. The branches fused together, forming a large triangular or fan-shaped muscle, as in Euglossine.

It should also be mentioned that the *intersegmental dorsal muscle of the prothorax* is a semicircular muscle arising on the pronotum and inserted on the first phragma (Fig. 3D). Although there is little variation in this muscle, it is usually large and elongated in the Euglossini (Fig. 6D).

The probable trends of specialization of the *dilator of the salivary syringe, the inferior phragmatic levator of the head,* and the *phargmatopleural muscle of the prothorax* are shown in the following table.

Unspecialized	Specialized
1. Origin of the *dilator of the salivary syringe* on the ligular arms.	1. Origin of the *dilator of the salivary syringe* well below on the posterior lateral margin of the prementum, for which reason the dilator makes a curve around the other muscles of the prementum.
2. The *inferior phragmatic levator of the head* consists of a pair of v-shaped muscles or a four-branched muscle.	2. The *inferior phragmatic levator of the head* is two-branched or V-shaped.
3. *Phragmatopleural muscle of the prothorax* V- *or* Y-shaped.	3. *Phargmatopleural muscle of the prothorax* ribbon-like or fan-shaped.

Many bee groups, such as genera, tribes, subfamilies and even families, may show similar musculature. However, more specimens should be dissected

to prove or disprove the apparent homogeneity that some of the groups show in relation to certain musculature regions. In the genera in which only one species was dissected, it is impossible to predict whether additional species have similar or different musculature.

SUMMARY

In a comparative study of the musculature of the salivary syringe and neck region of bees, forty genera, representing six families, were dissected. Some interpretations of the phylogeny of the muscles are discussed. Evolutionary tendencies and probable trends of specialization were found in the following three muscles: *dilator of the salivary syringe, inferior phragmatic levator of the head,* and *phragmatopleural muscle of the prothorax.*

RESUMEN

En un estudio comparativo de la musculatura del aparato eyaculador de la saliva y de la región del cuello de las abejas, se hizo la disección de más de 100 ejemplares, representando 6 familias, 40 géneros y 52 especies. Se encontró que ciertos músculos, tales como el *dilator del aparato eyaculador de la saliva, el elevador fragmático inferior de la cabeza* y el *músculo fragmatopleural del protorax,* muestran tendencias evolutivas y grados de especialización bien definidos. También fue posible indicar algunas interpretaciones de la filogenia de esos músculos.

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Fig. 1. Musculature of the salivary syringe of *Bombus fraternus* Smith.

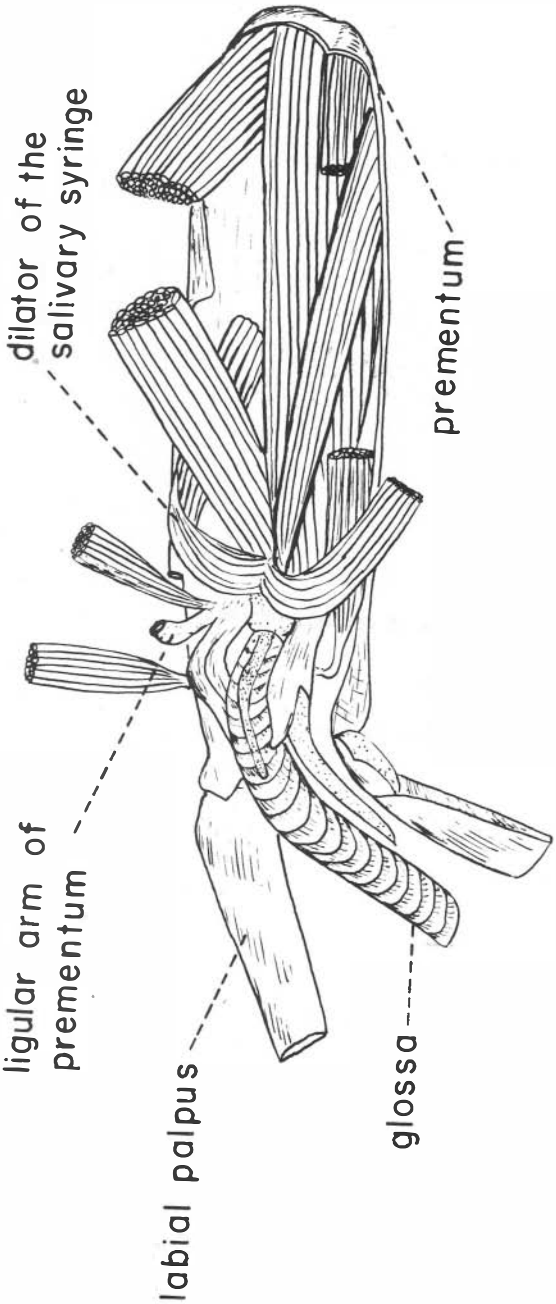
dilator of the salivary syringe
prementum
ligular arm of prementum
labial palpus
glossa

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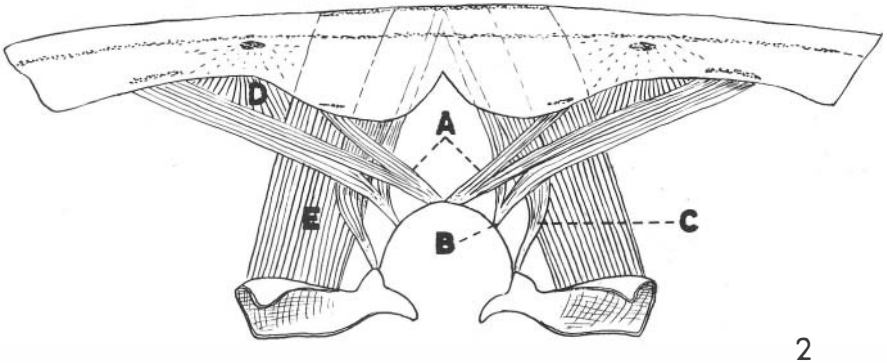
Fig. 2-6. Musculature of the neck region.

Fig. 2. *Colletes* sp.

Fig. 3. *Apis mellifera* Linnaeus.



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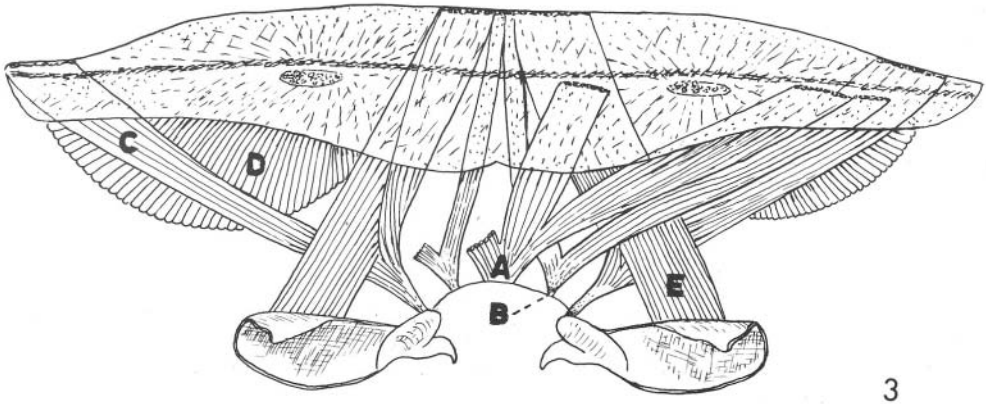

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Fig. 4. *Trigona nigra paupera* (Provancher).

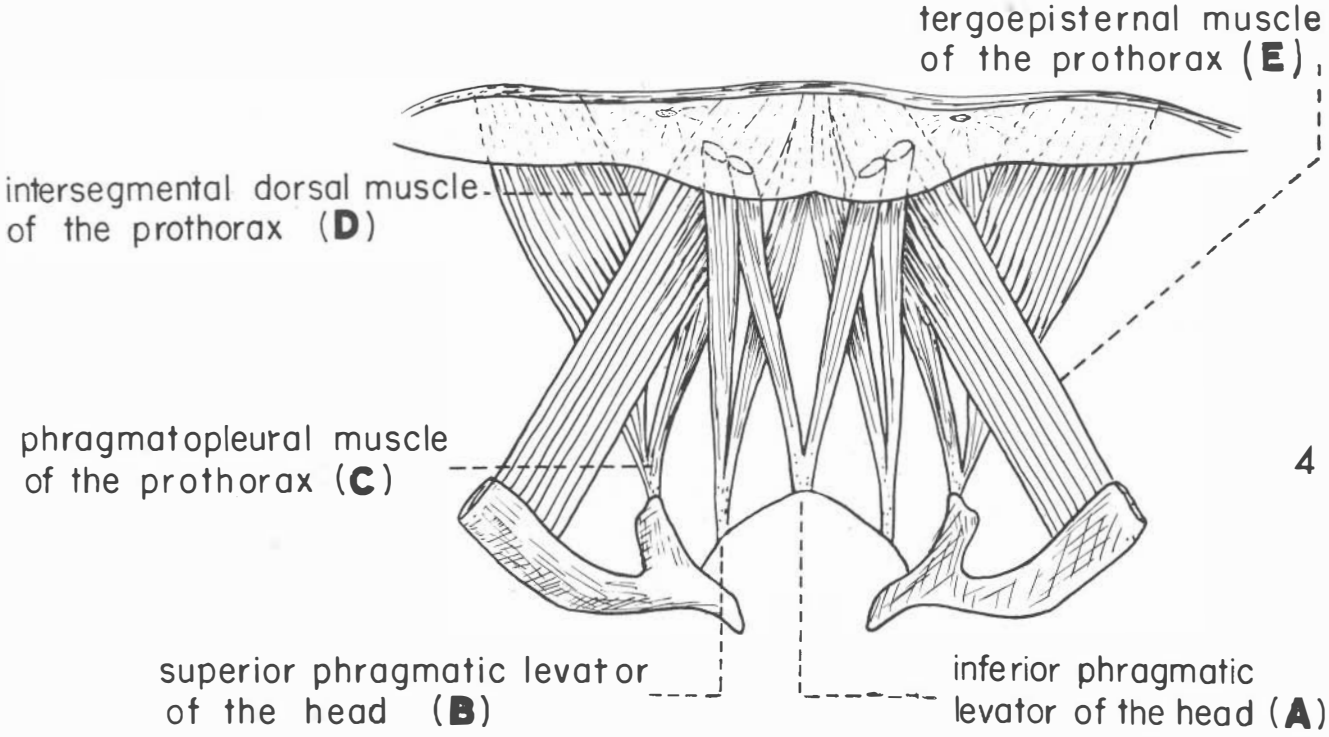
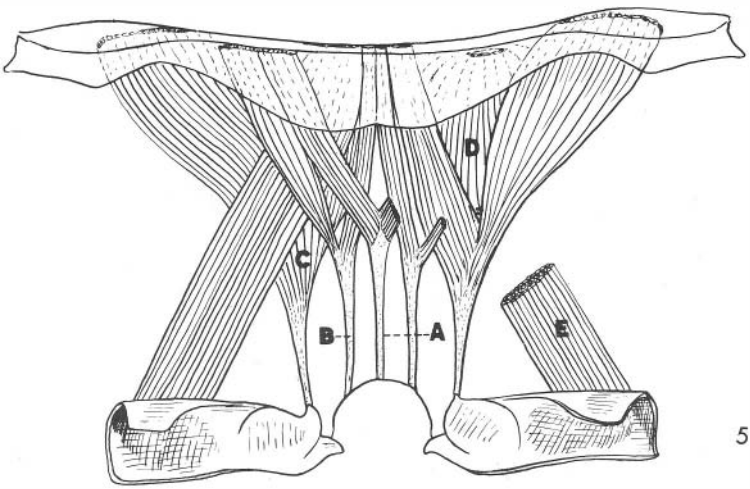

tergoepisternal muscle of the prothorax (E)
intersegmental dorsal muscle of the prothorax (D)
phragmatopleural muscle of the prothorax (C)
4
superior phragmatic levator of the head (B)
inferior phragmatic levator of the head (A)

Fig. 5. *Bombus fraternus* Smith.

Fig. 6. *Euglossa cordata* (Linnaeus).



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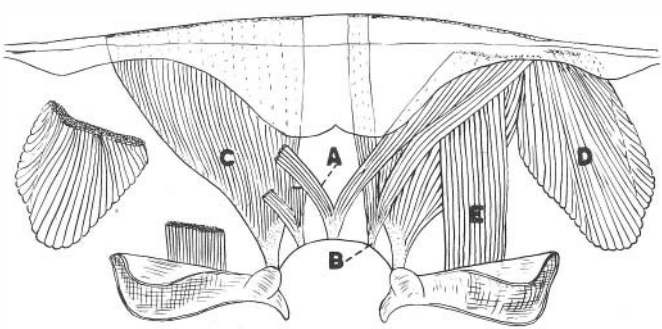

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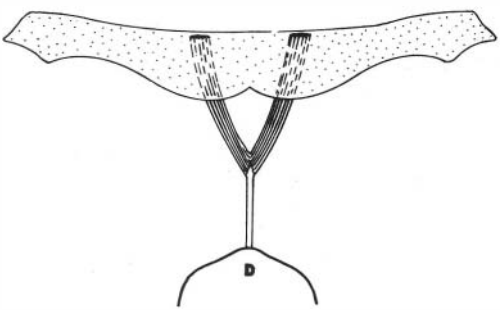
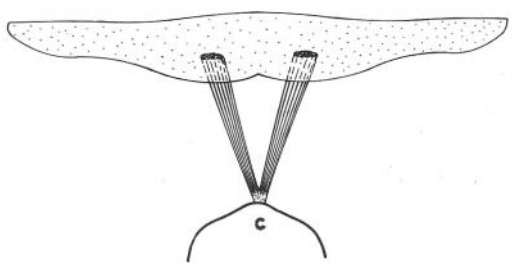
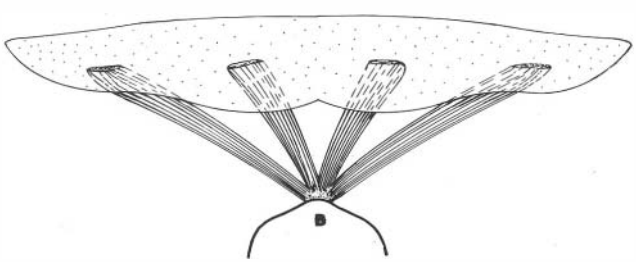
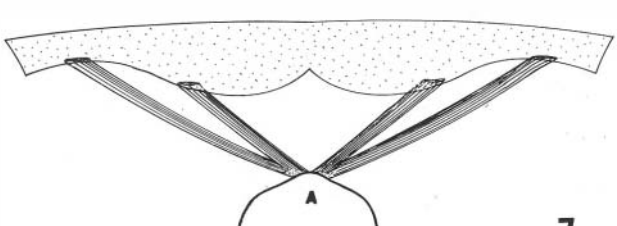
Fig. 7. The evolutionary trend of the inferior phragmatic levator of the head.
A. *Colletes* sp.
B. *Apis mellifera* Linnaeus.
C. *Trigona nigra paupera* (Provancher).
D. *Bombus fraternus* Smith.









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