COMPARATIVE NOTES ON THE VENTRAL NERVE CORD OF CERTAIN APINAE BEES

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INTRODUCTION

On the course of a study on the alimentary canal of **Bombus**, the author (DIAS, 1953) dissected, among other bees, workers of **Melipona quadrifasciata anthidioides** (Lep.), **Lestrimelitta limão** (F. Smith) and **Trigona ruficrus** (Latreille). It was observed at the time that the terminal ganglia of the ventral nerve cord of these stingless bees were not in close contact with the oviducts as in **Bombus** and **Apis**, but were located forward in the abdomen. It was also noticed that in **Melipona** there were three ganglia in the thorax as in **Bombus**, and not two as in **Apis**, and the other stingless bees examined. These observations were left at that until early in 1956 when through a CAPES research fellowship, part of a joint CAPES-ROCKEFELLER FOUNDATION project for the study of bees, it was possible to pursue further on the matter at the laboratory of Professor Pe. J. S. MOURE, C. M. F. at the University of Paraná in Curitiba. At Curitiba, and since then at the author's laboratory in Piracicaba, several bees have been investigated, and the postembryonic development of the ventral nerve cord of **Melipona s. schencki** (Gribodo) has been followed. The detailed results of these studies will be published separately as soon as completed, however, it has been found convenient to put forward a brief comparative summary of what is already known.

The nerve cord of several bees have been described by BRANDT (1879) which, however, only includes a few **APINAE** bees of two genera : **Bombus** and **Apis**, and of the latter only one species, the common honey bee.

MATERIAL AND METHOD

Apinae bees are here understood as comprising the tribes **EUGLOSSINI, BOMBINI, APINI** and **MELIPONINI** as given by MICHENER (1944) plus the tribe **TRIGONINI** as given by MOURE (1951), which now includes his then separate **LESTRIMELITTINI** tribe. **A-FINI** bees are here referred by their more commonly accepted designations, and the reader is directed to the paper by MAA (1953) for a throughout discussion on the systematics of the group. For our present purpose all above tribes are groupped under two major headings : 1) APINAE BEES WITH FUNCTIONAL STING, which includes **EUGLOSSINI**, **BOMBINI**, and **APINI**; and, 2) APINAE BEES WITH NON FUNCTIONAL STING. which includes the so-called stingless bees **MELIPONINI** and **TRIGONINI**.

Live specimens were fixed in either of the following fixing solutions : Bouin, Dietrich, Carnoy 3:1 or Formol, and stored mostly in 70% alcohol. Dissections were done in weak alcohols, and in the case of **Melipona s. schencki** (Gribodo), serial sections of eggs, immature forms and adults were cut from 8 to 20 microns, stained in Shortt's Hematoxylin, and counterstained with Erythrosin following SCUDDER's (1953) fast technic.

The thoracic segments are here indicated by Roman and the abdominal by Arabic numerals, as well as their corresponding ganglia.

Segment 1 in the adult corresponds thus to the **Propodeum.** A distinc ganglion will be considered here as such when, either it is a single ganglion, or when it is made up of the union of more than one ganglion, and no connective between the component ganglia can be detected from gross examination, or what seems to be connectives are present but are so shortened and united longitudinally, and with no space separating them, that they are here considered as non existent. When the component ganglia, or group of component ganglia, of a given composite ganglion can be identified by means of the constrictions between them, the numbers corresponding to the components, or group of components, are separated in the formulas by a comma.

When no constriction is present, the numbers corresponding to the component ganglia are united by a plus sign. In the case of the terminal ganglion, the number of the last identified component is followed by a plus sign indicating that it also corresponds to all remaining ganglia of the chain, which, during development have become incorporated to the terminal ganglion and lost their identities. In the cases where no component of the terminal ganglion can be told apart, then the whole ganglion is referred by the number corresponding to its most anterior component ganglion, followed by a plus sign. All composite ganglia have their formulas expressed in brackets. Except otherwise specified. all statements refer to the adult worker bee and by VNC (ventral nerve cord) it is meant the entire cord minus the suboesophageal ganglion.

GENERAL CONSIDERATIONS

The VNC of the adult bee is the end product of a series of gross and histological changes that take place during the development of the insect, particularly during pupation. Here at least two types of associated gross changes take place in the cord : 1) displacement of certain ganglia from their respective segments, and 2) union of certain ganglia into composite ganglia. This process is in part a repetition and continuation of what takes place earlier in the embryo when certain head ganglia unite to form the brain and the suboesophageal ganglion, and of what happens later in the embryo and larva when certain other ganglia unite to form the terminal ganglion of the chain. Among bees, displacement of a given ganglion from its original segment is not necessarily followed by union with another ganglion, and displacement from a segment to another is in general cephalad as in most insects. As stated by SNODGRASS (1935), it is a well established fact that among insects the nerves from a given ganglion "consistently go to the segment in which the ganglion had its origin. Hence, morphologically, a ganglion should be numbered according to the segment it innervates..." Thus, the imaginal ganglion of the bee expressed here by the formula [II + III + 1 + 2], indicates a composite ganglion made up of the original ganglia belonging to the thoracic segments II and III plus the abdominal ganglia of segments 1 and 2 of the larva.

As a basis for our dicussion about the VNC of the various bees, it follows a brief description of the cord of **Apis mellifera mellifera** L. . The larva of the common honey bee, according to NELSON (1915), hatches from the egg with twelve body ganglia, three thoracic and nine abdominal, each in its respective segment. The 9th abdominal being a composite ganglion made up of the ganglia corresponding to the 9th, and 10th abdominal segments plus the rudiments of the 11th. The same author (1918) sums up the situation in the larva as follows : "In the newly hatched larvae the last three abdominal ganglia, including the rudimentary 11th abdominal, unite to form a compound ganglion situated in the 9th abdominal segment. As the larva grows older the compound terminal ganglion and the ganglion of the 8th abdominal segment move closer together and both come to lie in this segment. In mature larvae (4-5 days old) the ganglion of the 8th abdominal segment finally becomes incorporated in the terminal compound ganglion, which has then the same composition, as regards number of ganglia, as the terminal ganglion in the imaginal ventral nerve cord." The remaining ganglia do not change position during larval life.

The VNC of aduld worker honey bee, however, has only seven ganglia, two in the thorax and five in the abdomen. The 1st ganglion is in the prothorax and innervates this segment, thus did not move from its original position during larval and pupal development. The 2nd ganglion, the largest of all, lies under the arch of the united meso and meta-thoracic endosterna and innervates the meso and metathorax, **Propodeum** (= 1st true abdominal segment) and the 2nd abdominal segment (the 1st following the constriction). Thus, as already described by BRANDT (1879), this is a composite ganglion made up of the 4 ganglia originally belonging to the 2nd and 3rd thoracic plus the 1st and 2nd abdominal segments of the larva. This is ganglion [II + III + 1 + 2] present in all bees known to the author, and most certainly characteristic of bees in general. The 3rd ganglion of the adult bee lies in abdominal segment 2 but innervates segment 3, thus during pupation moved to the segment ahead. The 4th ganglion lies in segment 4 and not 3 as stated by SNODGRASS (1910. 1925, 1956), thus did not move from its original segment. The 5th ganglion also lies in its respective segment. The 6th ganglion lies in segment 6 but innervates this and segment 7; during pupation the ganglion belonging to segment 7 moved forward to segment 6 and united with the 6th ganglion. This is ganglion [6 + 7]. The last ganglion in the chain, the 7th, lies over the anterior part of **Sternum** 7 and innervates all the remaining abdominal segments, thus during pupation it changed only in position, from segment 8 of the larva to the next in the adult. This is ganglion [8 +].

THE VNC OF APINAE BEES WITH FUNCTIONAL STING

The VNC among these bees extend posteriorly in the abdomen and the last terminal ganglia are in contact with the oviducts.

EUGLOSSINI - BOMBINI

The VNC of these two close related tribes are very similar. The cord consists of eight ganglia, three in the thorax and five in the abdomen. The 1st and 2nd being essentially as above described for the honey bee. Among these two tribes, however, there is an extra ganglion in the thorax. This is the 3rd abdominal ganglion which has moved into the thorax during pupation. Among the males and females of these bees, the lateral nerves to segment 2 and following abdominal segments run above the abdominal median ventral muscles.

EUGLOSSINI

In this tribe, as seen in the females of **Euglossa cordata** (L.) and in the females and males of **Euplusia violacea** Blanch. the 3rd abdominal ganglion is barely inside the thorax, lying over the membranous **Sternum** 1, just cephalad of the anterior rim of **Sternum** 2. The next three ganglia in the chain lie, each, one segment ahead from their original segments; thus, ganglion 4 lies in segment 3, ganglion 5 in segment 4, and ganglion 6 in segment 5. All distinct abdominal ganglia (3 to 6) lie directly against the **Sternum**, except, ganglion 7, which lie against the anterior end of the common oviduct. This ganglion can have its position in relation to the **Sternum** only approximately determined, depending whether the sting is retracted or not. In the former case it is over **Sternum** 6 and in the latter, partially over this, and partially over segment 7. As in the honey bee, the terminal ganglion of the chain is ganglion [8+], which lies well above the common oviduct, and is definitely over abdominal segment 7. The VNC of the male **Euplusia violacca** consists of only seven ganglia, three in the thorax, as above described for the female, and four in the abdomen; all from 4 to 6 equally located. The terminal ganglion here, however, is ganglion[7+] which lies against the anterior margin (gonobase) of the genitalia, over the anterior portion of **Sternum** 6.

BOMBINI

In this tribe ganglion 3 is much closer to ganglion [II + III +**1** + 2] than in **EUGLOSSINI.** It is definitely over thoracic **Sternum III**, midway over the median ridge of the **Metasternum.** The abdominal ganglia 4, 5 and 6 lie respectively in segments 3, 4 and 5 as in **EUGLOSSINI.** Both ganglia 7 and [8+], the ones in contact with the oviducts, are definitely over **Sternum** 6. The terminal ganglion of the queen and male **Bombus** is ganglion [7,8+]. BRANDT (1879), however, considered ganglion 7 as distinc from ganglion [8+] in the female, and because of that stated that there are six abdominal ganglia in the queen bumblebee (counting the one which has moved into the thorax).

APINI

The description given above, for the VNC of the common honey bee, stands, except for minor details, for the workers of all **APINI** bees examined. This includes, besides **Apis mellifera mellifera** L., its African sub-species **A. m. adansonii** Latr., and **A. m. capensis** Eschoscholts, the native honey bees of South Asia : **A. indica** Fabr., **A. dorsata** Fabr., and **A. florea** Fabr.

The VNC of the workers of all these bees consists of seven distinct ganglia, two in the thorax and five in the abdomen, thus one less than in the preceding two tribes. Here ganglion 3 has not moved into the thorax but only as far as segment 2. Ganglia 4 and 5, as previously described for the common honey bee, remain in their respective segments. Thus, there is no ganglion in segment 3. The following ganglion in the chain lies in segment 6, and innervates this, as well as, segment 7. Just as in **EUGLOSSINI** and **BOMBINI** ganglion 7 moves during pupation to segment 6, but here unites with ganglion 6 which in **APINI** does not move to the segment ahead, thus forming ganglion [6+7]. The terminal ganglion of the chain, as in **EUGLOSSINI** and **BOMBINI**, is ganglion [8 +], which in all cases lies over the oviduct in segment 7, except in **A. m. adansonii** where it seems to have been somewhat displaced forward along with the internal organs of reproduction and come to lie with ganglion [6+7] in segment 6.

The VNC of queens and males is not as uniform from species to species as above described for the worker bees. Here, vary the location of the ganglia and the degree of union between the components of the terminal ganglion.

The VNC of the queens of the above species consists of only six distinct ganglia, two in the thorax and four in the abdomen. Ganglia I, [II + III + 1 + 2], 3, 4 and 5 are as above described for the worker bees. It is the terminal ganglion which differs from the workers, and which varies from species to species among the queens. The terminal ganglion of queens and males of **BOMBINI** is glanglion [7,8 +]. The terminal ganglion of **APINI** queens is ganglion [6+7,8+] which even though including an extra component ganglion, mantains the same relationship between the components 7 and [8 +], as indicated by the above two formulas, that is, they touch each other with no distinct connectives between them. This is the case among the queens of all above species, except for the queens of **A. m. capensis,** where the terminal ganglion is an elongated, tubular shaped single structure with no visible constrictions between the component ganglia [6 + 7] and [8 +]. This is then ganglion [6 +], since the remaining component ganglia can not be told apart.

Among all queen bees, however, the terminal ganglion, whatever the degree of union between its component ganglia, lies over the oviduct above the posterior and anterior portions of **Sterna** 6 and 7 respectively.

Among all female **APINI** bees (workers and queens) the lateral nerves to segments 3, 4, 5 and 6 go under the two lateral bundles of the **V** shaped abdominal median internal ventral muscles (Nos. 141, 152, 163 and 174 of SNODGRASS 1942). Thus, among the female bees only the lateral nerves to segment 2 go over a median ventral muscle (No. 130 of above author).

The VNC of all male **APINI** bees examined (**A. m. mellifera, A. m. adansonii, A. indica** and **A. florea)** consists of only six distinct ganglia, just as among the queen bees, and except for the male of **A. florea,** ganglia I, [II + III + + 1 + 2], 3, 4, and ganglion 5 are equally located as above described for the worker bee. The cord of the male of **A. florea,** however, has been displaced forward so that each ganglion, except the first two, moved one segment ahead. Thus, ganglion 3 is over the membranous **Sternum** 1, ganglion 4 is in segment 3, ganglion 5 in segment 4 and ganglion [6+] in segment 5. In the male **A. florea** then, there is no ganglion in segment 2.

The degree of union between the components of the terminal ganglion of the male **APINI** bees also varies as among the queens. The terminal ganglion of the male of the common honey bee is ganglion [6,7+]. Even though this is a single ganglion it shows a constriction between the component glanglia 6 and [7+] of the larva. It lies mostly in segment 6 with only its posterior portion over **Sternum** 7. The components of the terminal ganglion of the male of **A. indica** and of **A. florea** are much more closely united together than in the male of **A. m. mellifera.** Among the formers there is no visible constriction between them and the resulting ganglion is an elongated tubular shaped structure, very similar to the terminal ganglion of the queen of **A. m. capensis.** As far as degree of union among the components of the terminal ganglion is concerned, the terminal ganglion of **A. m. adansonii** is in between that of. **A. m. melifera** and the two above species. In **A. m. mellifera** it lies in segment 6 and 7, as above described, in **A. m. adansonii** in segment 6, in **A. indica** in between segments 5 and 6 and in **A. florea** as already mentioned, in segment 5.

Among the males of **A. m. mellifera, A. m. adansonii** and **A. indica** only the lateral nerves to segment 4, 5 and 6 go under the respective abdominal median internal ventral muscles. The lateral nerves to segments 2 and 3 go over these muscles. In the male of **A. florea,** however, the lateral nerves to all abdominal segments, not only to segments 2 and 3, as above, run over the median ventral muscles. Thus, the cord of the male of **A. florea** resembles very closely the cord of the male of **Euplusia.**

APINAE BEES WITH NON FUNCTIONAL STING

The VNC of the bees of this group differs from those of the preceding one in that it does not, as a rule, extend so far posteriorly in the abdomen and the two distinct terminal ganglia are never in direct contact with the oviducts, and the lateral nerves to all abdominal segments run, in all cases examined, above the median ventral muscles.

MELIPONINI

The VNC of the hatching worker larva of **Melipona schencki schencki** (Gribodo), as that of the hatching larva of **Apis m. mellifera**, consists of twelve ganglia, three thoracic and nine abdominal. As in the honey bee, they all are single ganglia and lie in their respective segments except the 9th, which is a composite ganglion made up of the ganglia corresponding to the 9th and 10th abdominal segments. This ganglion also must include the rudiments of the 11th ganglion, as described by NELSON (1918) for the honey bee. In the newly hatched larva the terminal glanglion lies over **Sterna** 9 and 10, and is at this early stage already very close to ganglion 8. In a little older larva, probably of the second instar, the 9th ganglion has already moved forward to segment 8 and united with its ganglion, thus forming an elongated ganglion which tapers over **Sternum** 9, under the ventral loop of the hind-intestine. At this stage, this ganglion is midway over the transverse trachea of segment 8. As the larva grows older, the terminal ganglion moves forward so that most of it comes to lie ahead of the transverse trachea of segment 8. No other gross change in the cord is to be detected up to pupation. The terminal ganglion of the **Melipona** larva is, then, ganglion [9+] in the newly hatched larva, and ganglion [8+] during the remaining larval stages. With pupation, the cord which had kept almost unchanged during larval life, iniciates a phase of very active transformations. During the very early stages of pupation (early prepupa), abdominal ganglion 1 moves into the thoracic segment III and becomes incorporated with ganglion III, thus forming ganglion [III + 1]; a little later ganglion 2 also moves in and becomes incorporated with ganglion [III+1], thus forming ganglion [III+1+2]. During pupation, ganglion II and ganglion [III + 1 + 2] move close together and form the definitive imaginal ganglion [II + III + 1 + 2] of bees in general. During the pupal development of **Melipona,** as in **EUGLOSSINI** and **BOMBINI,** ganglion 3 also moves into the thorax, remaining, however, a distinct ganglion, and occupying the same position as in **Bombus.** At the time ganglion 1 is uniting with ganglion III in the metathoracic region, ganglia 7 and [8+] begin to move close together and soon forms the terminal ganglion of the adult bee. During pupal development, all abdominal ganglia are displaced two to three segments ahead from their original positions.

The VNC of the adult worker of **Melipona s. schencki** consists, thus, of only seven ganglia, three in the thorax, the same three as in **EUGLOSSINI** and **BOMBINI,** and four in the abdomen. Ganglion 3 lies in the thorax, as above stated, and ganglia 4, 5 and 6 respectively in segments 2, 3 and 4. The terminal [7+] ganglion of the adult bee also lies in segment 4, along with ganglion 6.

The VNC of the worker of **Melipona quadrifasciata anthidioides** (Lep.) is much shorter than the cord of **M. s. schencki.** Here the whole cord extends in the abdomen only as far as segment 3, and reminds the cord of some of the syrphids illustrated by KUNCKEL D' HERCULAIS (1881): a very short chain of closely spaced ganglia sending off a spreading array of nerves, like stretched fingers, reaching for the segments. Here, ganglia 4 and 5 are in segment 2 and ganglia 6 and [7+] in segment 3. The cord of **M. fasciata scutellaris** (Latr.) is in between that of **M. s. schencki** and the cord of **M. quadrifasciata anthidioides** Lep. Ganglia 4 and 5 are in segment 2, ganglia 5 and 6 in segment 3 and ganglion [7+] in between segments 3 and 4.

The cord among the queens of **Melipona** is not so short as among the workers, and consequently extend a little farther back in the abdomen. Thus, the cord of the queen of **M. quadrifasciata anthidioides** extends as far as segment 5 against segment 3 among the workers, and its ganglia are located as follows: ganglia 4 and 5 in segments 3 and 4 respectively, and ganglia 6 and [7+] in segment 5. The anterior part of ganglion 6 is actually over **Sternum** 4. In all cases examined, whatever the variation in the positioning of ganglia 4 to [7+], ganglion 3, among all three castes of **Melipona,** is well inside the thorax.

TRIGONINI

The VNC varies a great deal among the bees of this tribe. The typical **TRIGONINI** cord, if one can speak of such, consists of seven ganglia, just as in **MELIPONINI**, however, ganglion 3 is never in the thorax. The cord of **Trigona (Trigona) ruficrus** (Latr.) might be taken as an example. The thoracic ganglia, as among other bees, are ganglion I in the prothorax and ganglion [II + III + 1 + 2] which lies under the arch of the united meso and meta-thoracic endosterna, just as above described for the honey bee. Ganglia 3 and 4 are in segments 2 and 3, ganglia 5, 6 and [7+] in segment 4. In the queen, the cord is not so shortened as among the workers, so that each ganglion lies only one segment ahead from its respective segment. Thus ganglia 3, 4, 5, 6 and [7+] are in segments 2, 3, 4, 5 and 6 respectively. The terminal ganglion of the **Trigona** cord, then, is ganglion [7+], just as in **Melipona.** In some cases, as in **Plebeia (Mourella)** sp. the terminal ganglion is ganglion [6,7+] which lies in between segments 5 and 6.

CONCLUSIONS

Only a few generalizations and conclusions can be made at the present phase of the work :

1. The ventral nerve cord among Apinae bees, as among Hymenoptera in general, as already observed by BRANDT (1879), varies not only from species to species but even among the castes of a same species.

2. A primitive type of imaginal cord, in terms of number and position of the ganglia in relation to the cord of the embryo, is not necessarely associated with a primitive type of adult insect, as illustrated by **Apis** which has one of the most primiteve type of nerve cord among bees.

3. The lack of functional sting, and the fact that the lateral nerves run above the abdominal median ventral muscles among **MELIPONINI** and **TRIGONINI**, might explain why the cord among the bees of these tribes has been able to move cephalad. That lateral nerves above the median ventral muscles allow the cord to move cephalad is illustrated by the male of **Apis florea.**

4. The cord of the queen **Bombus** and **Apis** represents a step ahead in the development of the worker cord. Among the queens, the ganglia corresponding to the two distinct terminal ganglia of the worker come closer together, and form a single more complex terminal ganglion. This is not only expected, as simple to explain, once among these two genera the workers are produced by means of differences in quantity and quality of the food received during larval development. This, however, is not the case with

MELIPONINI and TRIGONINI where the cord of the queen is not a step ahead from that of the worker. Here, it is the worker cord which seems to be the one a step ahead in development. In **Melipona** this might be explained in terms of the genetic diferences between workers and queens (KERR, 1948, KERR and LAIDLAW, 1956). The situation in **TRIGONINI**, with workers and queens produced by means of food differences as in **Bombus** and **Apis**, remains to be explained.

5. The presence of ganglion 3 in the thorax of **EUGLOSSINI-BOMBINI** and **MELIPONINI** seems to be a case of parallel evolution.

6. The association of the terminal ganglia with the female internal organs of reproduction in **EUGLOSSINI - BOMBINI** and **APINI** also seems to be a case of parallel evolution.

7. Whatever the evolutionary paths followed by the ventral nerve cord among Apinae bees, and whatever the relationship among them, some of the foregoing differences in the nerve cord might prove, however, of immediate taxonomic value.

ACKNOWLEDGMENTS

The author has been able to undertake the present series of studies, on the ventral nerve cord, through the cooperation of several persons who have kindly contributed with fixed bee material. In this connection he wants to mention Dr. HENRY E. FERNANDO of the Department of Agriculture of Ceylon and Dr. M. LINDAUER of the University of Munich, Germany for the material of **A. indica, A. dorsata** and **A. florea**, Dr. PAULO NOGUEIRA-NETO of São Paulo for most of the Brazilian stingless bee material used, and Dr. WARWICK E. KERR of this School for the stingless bee and honey bee material brought by him from Africa. The author also wants to extend thanks to Professor CHARLES D MICHENER of the University of Kansas, U. S. A. for his interest and bibliographic material and to the Campanha Nacional de A perfeiçoamento do Pessoal de Nivel Superior (CAPES) of Rio de Janeiro for the financial support of the early phase of the study. Finally the author wants to register his gratitude to Professor Pe. JESUS S. MOURE, CMF of the University of Paraná, Curitiba, who made possible the start of the present series of studies, at his laboratory in Curitiba.

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