Rev. Biol. Trop., 9(1):117-129, 1961

Evolutionary Trends in the Ventral Nerve Cord of the Stingless Bees (Meliponini)

(Received for publication, May 6, 1961)

by

Alvaro Wille*

A paper (WILLE, 3) dealing with the dorsal vessels of bees, published as a result of a preliminary study on the relationships of the genera and subgenera of the Meliponini, led to a comparative study among other bees. The present paper is a continuation of the same type of work, now dealing with the ventral nerve cord. However, since other investigators are working with the nervous system of the bees, the present work deals only with the Meliponini, although reference to other bees is made when necessary. The species examined are listed below by genera and subgenera.

Genus TRIGONA. Subgenus PLEBEIA: *Trigona beccarii* Gribodo, *Trigona cassiae* Cockerell, *Trigona denoiti* Vachal, *Trigona emerina* Friese, *Trigona remota* Holmberg, *Trigona saiqui* Friese. Subgenus PARATRIGONA: *Trigona subnuda* Moure. Subgenus SCAPTOTRIGONA: *Trigona mexicana subobscuripennis* Schwarz, *Trigona pectoralis* (Dalla Torre), *Trigona postica* Latreille. Subgenus NANNOTRIGONA: *Trigona testaceicornis perilampoides* Cresson. Subgenus PARTAMONA: *Trigoan cupira* Smith, *Trigona testacea musarum* Cockerell. Subgenus HYPOTRIGONA: *Trigona braunsi* Kohl, *Trigona buyssoni* Friese, *Trigona duckei atomaria* Cockerell. Subgenus OXYTRIGONA: *Trigona tataira mellicolor* Packard. Subgenus CEPHALOTRIGONA: *Trigona capitata zexmeniae* Cockerell. Subgenus LEPIDOTRIGONA: *Trigona terminata* Smith. Subgenus TETRAGONA: *Trigona apicalis* Smith, *Trigona carbonaria* Smith, *Trigona dorsalis* Smith, *Trigona hockingsi* Cockerell, *Trigona itama* Cockerell, *Trigona jaty* Smith, *Trigona mombuca aequinotialis* Ducke, *Trigona nigra paupera* (Provancher). Subgenus TRIGONA: *Trigona corvina* Cockerell, *Trigona fulviventris fulviventris* Guerin, *Trigona ruficrus* Latreille, *Trigona trinidadensis silvestriana* Vachal. Unnamed subgenus: *Trigona erythratogoensis* Sadelman.

---

* Departamento de Entomología, Facultad de Agronomía, Universidad de Costa Rica.

Genus DACTYLURINA. *Dactylurina staudingeri* Gribodo

Genus LESTRIMELITTA. *Lestrimelitta limão* (Smith)

Genus MELIPONULA. *Meliponula bocandei* Spinola

Genus MELIPONA. *Melipona beecheii* Bennett, *Melipona fasciata* (Latreille), *Melipona flavipennis* Smith, *Melipona marginata* Lepeletier, *Melipona schencki picadensis* Strand, *Melipona scutellaris scutellaris* Bennett.

METHODS

The specimens used in this study were preserved in Kahle's (Dietrich's) fixative. Dissections were done under water, and several specimens were dissected for every species examined. The entire study was based mainly on the worker caste. All the drawings were made diagrammatically. In presenting the data, Roman and Arabic numbers have been used for the thoracic and abdominal ganglia respectively. Furthermore, the terms mesoma and metasoma are not used in this paper except when referring to a specific metasomal segment, in order to avoid confusion with current literature on the nervous system. Ganglion 1 therefore is that of the propodeum (first abdominal segment); 2, of the first metasomal segment (second abdominal segment), etc.

THE VENTRAL NERVE CORD OF THE LARVA

The ventral nerve cord of the stingless bee larva (as represented by *Melipona schencki*) is, according to DIAS (1), similar to that of *Apis mellifera*. At hatching the larva has three thoracic and nine abdominal ganglia. These twelve body ganglia are located in their respective segments. The ninth abdominal ganglion represents the fusion of ganglia 9 and 10, and possibly the rudiments of ganglion 11.

In the older larva the abdominal ganglion 8 is incorporated into 9, so that there are three thoracic and eight abdominal ganglia.

Judging by the work of NELSON (2) and DIAS, the main differences between the nerve cord of the larva of the honey bee and that of *M. schencki* is that in the latter the abdominal ganglia 8 and 9 are very close to each other when the larva is newly hatched, becoming completely united when a little older (possibly at the second instar, according to DIAS). In the honey bee the two ganglia in question are well separated at hatching and it is not until the larva grows older that the two ganglia move closer together, becoming completely fused only when the larva is mature.

THE VENTRAL NERVE CORD OF THE ADULT

The nerve cord of the adult stingless bee presents various modifications from that of the larva. There are, in relation to the number of ganglia, three main types found in the adult: 1) those which have two ganglia in the thorax and five in the abdomen (Fig. 1, A), 2) those which also have two ganglia in the thorax but only four in the abdomen (Fig. 1, D), and 3) those which have three ganglia in the thorax and four in the abdomen (Fig. 1, E). Judging by the evolutionary trends of the ventral nerve cord in the genus *Melipona,* there is a possibility that a fourth type may exist: One with three ganglia in the thorax and three in the abdomen. Although no one has been found as yet with this type, the species *Melipona scutellaris scutellaris* approaches it very closely. Intermediate types between those listed exist.

While the most anterior ganglion of the thorax is ganglion I, the second thoracic ganglion represents ganglia II and III plus the abdominal ganglia 1 and 2 (Fig. 1, A). The third thoracic ganglion found in *Melipona* (type 3) is abdominal ganglion 3, which had moved into the thorax during pupation.

The last abdominal ganglion is ganglion 7, which represents the fusion of ganglia 7, 8, and 9 of the larva. However, in some stingless bees there is a further union of the 7 with the preceding ganglion (type 2).

Finding the exact location of the abdominal ganglia in relation to the segments has been a difficult task. The difficulties concern mostly the last three ganglia. The dissections of only one or two specimens for every species may give the wrong impression as to the location of the ganglia. This is partially due to the differences in the degree of contraction or telescoping of the abdominal segments, and partially to the twisting or shrinking of the ventral nerve cord in some of the preserved bees. Nevertheless it has been possible, after the long series of dissections was accomplished, to make the following generalizations: In most workers of *Trigona, Dactylurina, Lestrimelitta,* and *Meliponula,* each ganglion lies only one segment ahead from its respective segment, except the last one, or ganglion 7, which is located in the fifth abdominal segment (fourth metasomal segment), together with ganglion 6. The reason of this is that in most of these species there is a trend toward the fusion of abdominal ganglion 7 with 6. Therefore, 7 is usually close to 6 or else fused with it. One exception is *Trigona fulviventris,* which has a generalized type of ventral nerve cord, with ganglia 6 and 7 well separated, and the latter located in the sixth abdominal segment (fifth metasomal segment). It should also be mentioned that among ten specimens of *Trigona remota,* nine had ganglion 6 in the fourth abdominal segment, but one specimen had the usual type of location, that is, ganglion 6 in the fifth segment. Are the nine specimens cases in which the nerve cord has been slightly shrunken? or are those specimens indicative of the real location of the abdominal ganglia in *Trigona remota?.* Fresh specimens are needed in order to answer those questions. A similar case was found in *Trigona capitata,* but here the twelve specimens dissected had, as in *Trigona remota,* ganglion 6 located in the fourth abdominal segment, and ganglion 7, which is almost fused with 6, in the anterior section of the fifth abdominal segment, close to the border line of the fourth segment. Finally, DIAS (1) has described the ventral nerve cord of *Trigona ruficrus* as having ganglia, 5, 6, and 7 located in the fourth abdominal segment. Unfortunately, all the specimens of *T. ruficrus* examined by me had the cord twisted and it was not possible to tell the exact location of the ganglia.

In most workers of *Melipona* each ganglion lies two segments ahead from its respective segment, except the last one, or ganglion 7, which is located in the fourth abdominal segment (third metasomal segment), together with ganglion 6. One exception is *Melipona flavipennis,* which has a very specialized type of ventral nerve cord, with the ganglia 6 and 7 located in the third abdominal segments (second metatosmal segment). A similar case was reported by DIAS (1) in *Melipona quadrifasciata anthidioides.*

As noted by DIAS the ventral nerve cord of workers of Meliponini differs from that of the closely related tribes, Apini, Bombini, and Euglossini, in that the cord is not well extended posteriorly in the abdomen. Furthermore, the terminal ganglia of meliponids are never in direct contact with the oviducts, and all the lateral nerves of the abdomen run above the median ventral muscles. On the other hand, in Apini, Bombini, and Euglossini, the nerve cord is well extended posteriorly in the abdomen and the terminal ganglia are in contact with the oviducts. Moreover, in the workers of Apini the lateral nerves of the abdomen (except those to the first metasomal segment) run under the median ventral muscles. These nerves in Bombini and Euglossini are above the muscles, as in Meliponini.

EVOLUTIONARY TRENDS IN TRIGONA

Since the small genera *Dactylurina, Lestrimelitta* and *Meliponula* are actually in the same general line of evolution as *Trigona,* those genera are regarded here, for the purpose of discussion, as one group, the *Trigona* line.

There in one major trend in the evolution of the ventral nerve cord in the *Trigona* line. This trend is toward the fusion of ganglion 7 with the preceding abdominal ganglion. In order to accomplish this, ganglion 7 migrates from the sixth abdominal segment to the fifth, where it finally fuses with ganglion 6. These events occur independently in the several subgenera of *Trigona,* with a series of intermediate types.

Although I have never had an opportunity to dissect a queen of a stingless bee, it is evident from the work of DIAS (1) that the queens of these bees possess a more generalized type of ventral nerve cord than the workers. Thus, in the queen of *Trigona ruficrus,* according to DIAS, "the cord is not so shortened as among the workers, so that each ganglion lies only one segment ahead from its respective segment". This type of ventral nerve cord was also found among the workers of *Trigona fulviventris.* Of all the species dissected, this is actually the only one which has ganglia 3, 4, 5, 6, and 7 in the second, third, fourth, fifth, and sixth abdominal segments respectively, with ganglia 6 and 7 well separated (Fig. 1, A). This generalized type of ventral nerve cord can be taken as a starting point for both *Trigona* and *Melipona.*

Following the evolutionary trend in the *Trigona* line, the next step is found in *Trigona hockingsi, T. erythratogoensis* and *Dactylurina staudingeri,* in all of which ganglion 7 has migrated from the sixth abdominal segment to the fifth (Fig. 1, B). In these forms ganglion 7 is now closer to 6, but they are sitll fairly well separated (Fig. 3, B).

The next level is found in *Trigona denoiti, T. cupira, T. testacea, T. carbonaria, T. jaty, T. saiqui, T. beccarii,* and *T. dorsalis,* all of which have ganglia 7 and 6 very close (Fig. 3, C). There are still others, such as *Trigona remota, T. tataira, T. postica, T. pectoralis, T. trinidadensis, T. mexicana,* and *Meliponula bocandei,* in which ganglia 7 and 6 appear still colser (Fig. 3, D).

The nearly complete fusion of ganglia 7 and 6 is found in *T. emerina, T. subnuda, T. terminata, T. mombuca, T. apicalis, T. clavipes, T. capitata, T. corvina,* and *T. ruficrus.* In these species, however, there is a small hole and a constriction between ganglia 7 and 6 (Fig. 3, E).

Complete fusion of ganglia 7 and 6 is found in *Lestrimelitta limão, Trigona itama, T. testaceicornis* and *T. nigra,* but in these species the single ganglion shows a slight median constriction indicating its compound nature (Fig. 3, F).

Finally, in the three species dissected of the subgenus *Hypotrigona (braunsi, duckei* and *buyssoni*) and in *Trigona cassiae,* the fusion of ganglia 7 and 6 is more complete since the slight median constriction has virtually disappeared. The ganglion of *T. braunsi* and *T. duckei* is still elongated (Fig. 3, G), but that of *T. buyssoni* and *T. cassiae* is rather oval in shape and is very similar in gross structure to the other abdominal ganglia (Fig. 3, H).

It should be pointed out that dissection of several specimens for each species studied reveals occasional cases which differ somewhat from the normal types. Thus, one specimen of *Trigona jaty,* which normally has ganglia 7 and 6 very close, appeared with those ganglia fairly well separated. Similarly, in *Trigona subnuda,* which normally has ganglia 7 and 6 nearly fused, occasional specimens appear with those ganglia separated. Furthermore, in *Trigona cupira,* which has normally ganglia 7 and 6 very close, but separated, and in *Lestrimelitta limão,* which usually has ganglia 7 and 6 completely fused, occasional specimens appear with those ganglia nearly fused, with a small hole in the middle.

EVOLUTIONARY TRENDS IN MELIPONA

There are two trends in the evolution of the ventral nerve cord in *Melipona.* One trend is toward cephalization; the second trend, as in *Trigona,* is toward the fusion of ganglion 7 with the preceding abdominal ganglion.

The most interesting trend in the genus *Melipona* is toward cephalization. Originally, the bee or bees which gave origin to *Melipona* had probably a ventral nerve cord of the type found in *Trigona fulviventris,* that is, with each abdominal ganglion lying one segment ahead from its respective segment (Fig. 2, A). Among other things, the origin of *Melipona* must have been marked by the first important step toward the cephalization of the ventral nerve cord. This was accomplished by the migration of the abdominal ganglia to one more segment ahead from the position mentioned, so that each ganglion lies two segments ahead from its respective segment (Fig. 2, B). As a result of this, ganglion 3, which in primitive forms was located in the second abdominal segment (first metasomal segment), has moved well inside the thorax. Of the many bees that I have dissected, only in *Melipona,* Bombini and Euglossini was abdominal ganglion 3 located in the thorax.

The first step in the cephalization of the cord is represented by the queens of *Melipona.* Thus, in the queen of *Melipona quadrifasciata anthidioides,* according to DIAS, the cord "extends as far as segment 5". Each ganglion lying two segments ahead from its respective segment. Therefore, ganglion 7 is located in the fifth abdominal segment ,Fig. 2, B). Although DIAS described ganglion 6 in segment five, it is possible that ganglion 6 actually belongs to the fourth segment and not to the fifth. A slight stretching of the nerve cord may give such impression. Furthermore, this view is supported by DIAS's statement that "The anterior part of ganglion 6 is actually over sternum 4".

The next stage in the cephalization is found in *Melipona marginata* and *M. schencki,* in which ganglion 7 has migrated from the fifth abdominal segment to the fourth. As a result, ganglion 7 is now closer to 6, but they are well separated (Fig. 2, C).

A further migration of the ganglia toward the head is found in *Melipona fasciata scutellaris,* so that, according to DIAS, "Ganglia 4 and 5 are in segment 2, ganglia 5 and 6 in segment 3 and ganglion 7 + in between segments 3 and 4". Ganglion 5 has been placed by an error in both the second and third abdominal segments. It is possible that it belongs to the second (Fig. 2, D).

The culmination of the cephalization of the ventral nerve cord ir found in *Melipona quadrifasciata anthidioides,* described by DIAS, and in *M. flavipennis.* In these forms the last ganglion has been displaced four segments ahead. Therefore, the cord extends in the abdomen only as far as the third abdominal segment (second matasomal segment), and the distribution of the ganglia is as follows: Ganglia 7 and 6 in the third abdominal segment, and ganglia 5 and 4 in the second or first metasomal segment (Fig. 2, E). According to DIAS, the cord was possibly able to move cephalad because of the lack of a functional sting and because the lateral nerves run above the median ventral abdominal muscles.

The second trend in the evolution of the ventral nerve cord in *Melipona* is toward the fusion of ganglion 7 with ganglion 6. Starring with *Melipona marginata* (Fig. 4, B and Fig. 1, F), the next step is found in *Melipona beecheii* and *M. fasciata both* of which have ganglia 7 and 6 very close (Fig. 4, C).

The nearly complete fusion of ganglia 7 and 6 is found in *Melipona scutellaris.* However, this form still has a small hole and a constriction between ganglia 7 and 6 (Fig. 4, D).

The complete fusion of ganglia 7 and 6 was not found in any of the species dissected, but there exists the possibility that further studies may reveal one having those ganglia completely fused.

SUMMARY AND CONCLUSIONS

There are, in relation to the number of ganglia, three main types of ventral nerve cords in the adult stingless bees: 1) Those which have two ganglia in the thorax and five in the abdomen, 2) those which have two ganglia in the thorax and four in the abdomen, and 3) those which have three ganglia in the thorax and four in the abdomen. Intermediate types between those listed exist.

The most generalized ventral nerve cord was found in the workers of *Trigona fulviventris,* where each ganglion lies only one segment ahead from its respective segment (Fig. 1, A). When this generalized type of nerve cord is taken as a starting point, there are two major recognizable evolutionary trends among the stingless bees (Fig. 1). One trend is toward the fusion of ganglion 7 with the preceding abdominal ganglion. This occurs independently in the several subgenera of *Trigona,* with a series of intermediate steps (Fig. 3, A to H). Among some of the species of *Melipona* there is also a tendency of fusion of ganglion 7 with ganglion 6 (Fig. 4, A to D) but none of the species of *Melipona* dissected was found with those ganglia completely fused.

The second trend noted is toward cephalization of the nerve cord (Fig. 2). This occurs only in *Melipona.* Here the abdominal ganglia migrate from two to four segments ahead from their respective segments. As a result, ganglion 3, which in primitive forms was located in the second abdominal segment (first metasomal segment), has moved well inside the thorax. The presence of ganglion 3 in the thorax is characteristic of all the species of *Melipona.* The highest type of cephalization is found only in a few species, such as *Melipona flavipennis,* in which ganglia 4 and 5 have moved into the second abdominal segment, and ganglia 6 and 7 into the third. Therefore, in this type, the cord extends in the abdomen only as far as the third abdominal segment (second metasomal segment, Fig. 2, E). There are, of course, intermediate types.

RESUMEN Y CONCLUSIONES

El trabajo presente consiste en un estudio comparativo de la cuerda nerviosa ventral entre las abejas melipónidas.

En relación al número de ganglios, se distinguen tres tipos principales de cuerdas nerviosas ventrales entre los adultos de estas abejas: 1) los que tienen dos ganglios en el tórax y cinco en el abdomen; 2) los que tienen dos ganglios en el tórax y cuatro en el abdomen; 3) los que tienen tres ganglios en el tórax y cuatro en el abdomen. Existen tipos intermedios entre ellos.

La cuerda nerviosa ventral más generalizada se encontró en las obreras de *Trigona fulviventris,* donde cada ganglio se encuentra localizado un segmento más adelante de su respectivo segmento. De esta forma los ganglios abdominales 3, 4, 5, 6 y 7 se encuentran en el segundo (primer segmento metasomal), tercero, cuarto, quinto y sexto segmentos abdominales respectivamente. Esta situación se representa en la figura 1, A. Si tomamos este tipo generalizado de cuerda nerviosa como punto de partida, se pueden reconocer dos tendencias evo-

lucionarias importantes entre las abejas melipónidas. Una tendencia es hacia la unión del ganglio 7 con el ganglio abdominal que le precede. Para que esto suceda, entre las especies de *Trigona,* el ganglio 7 emigra del sexto segmento abdominal al quinto, donde finalmente se une con el ganglio 6. Esto sucede independientemente en los varios subgéneros de *Trigona,* con una serie de grados intermedios (Fig. 3, A a H). Entre algunas de las especies de *Melipona* existe también una tendencia de unión entre el ganglio 7 con el 6 (Fig. 4, A a D), sin embargo, ninguna de las especies de *Melipona* disectadas se encontró con dichos ganglios completamente unidos.

La segunda tendencia evolucionaria es hacia la cefalización de la cuerda nerviosa (Fig. 2). Esta tendencia se observó solamente en *Melipona.* Para que esto ocurra, los ganglios abdominales emigran de dos a cuatro segmentos más adelante de sus respectivos segmentos. Como resultado, ganglio 3, que en formas primitivas estaba localizado en el segundo segmento abdominal (primer segmento metasomal), se trasladó dentro del tórax. La presencia del ganglio 3 en el tórax es característica de todas las especies de *Melipona.* El tipo más avanzado de cefalización se encuentra en unas pocas especies, tal como en *Melipona flavipennis,* donde los ganglios 4 y 5 han emigrado al segundo segmento abdominal, y los ganglios 6 y 7 al tercero. En este tipo, por lo tanto, la cuerda nerviosa se extiende en el abdomen solamente hasta el tercer segmento abdominal (segundo segmento metasomal, figura 2, E). Existen, desde luego, tipos intermedios. La cefalización extrema, representada por *M. flavipennis,* es el tipo más evolucionado de la cuerda nerviosa ventral que se encontró entre las abejas melipónidas. Este movimiento hacia adelante de los ganglios abdominales fue posible seguramente debido a la falta de aguijón en estas abejas, y también a que los nervios laterales se extienden sobre los músculos abdominales ventrales de la parte central.

ACKNOWLEDGMENTS

I am especially indebted to Dr. C. D. Michener, of the University of Kansas, and to Dr. R. L. Rodríguez, of the University of Costa Rica, for reading the manuscript and offering some suggestions, and to Padre J. S. Moure, C. M. F., of the University of Paraná for indentifying most of the species used in this work. Thanks are also due to the following individuals who generously gave preserved material for this study: C. D. Michener, J. S. Moure, W. E. Kerr, P. Nogueira-Neto, V. de Portugal-Araujo, W. J. Hanson, C. W. Rettenmeyer and W. L. Ramírez.

LITERATURE CITED

1. DIAS, D.
1958. Comparative notes on the ventral nerve cord of certain Apinae bees. *An. Esc. Sup. Agr. Luiz de Queiroz* (Piracicaba, Brazil), 32: 279-289.

2. NELSON, J. A.
1915. *The embryology of the honey bee.* 282 pp. Princeton University Press, Princeton.

3. WILLE, A.
1958. A comparative study of the dorsal vessels of bees. *Ann. Ent. Soc. Amer.,* 51: 538-546.

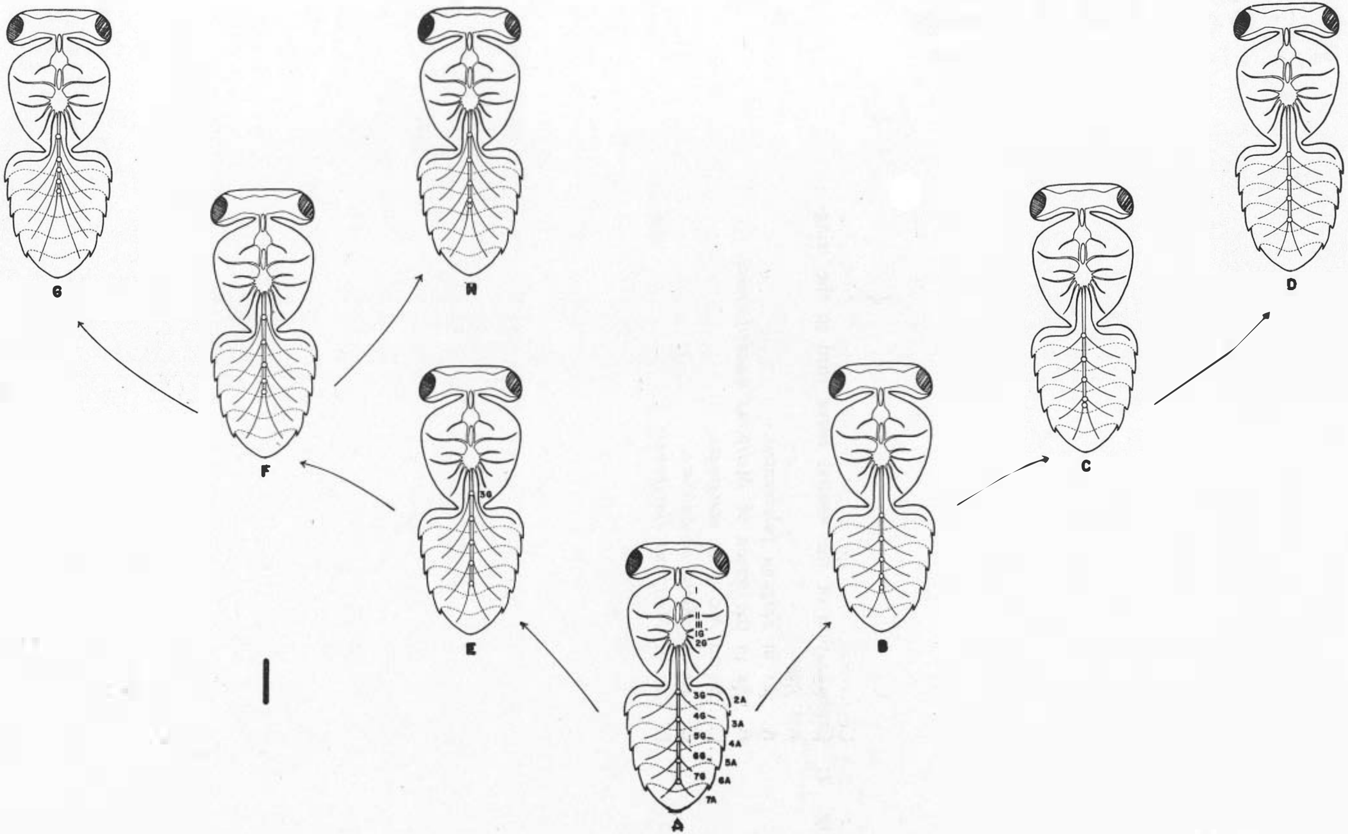
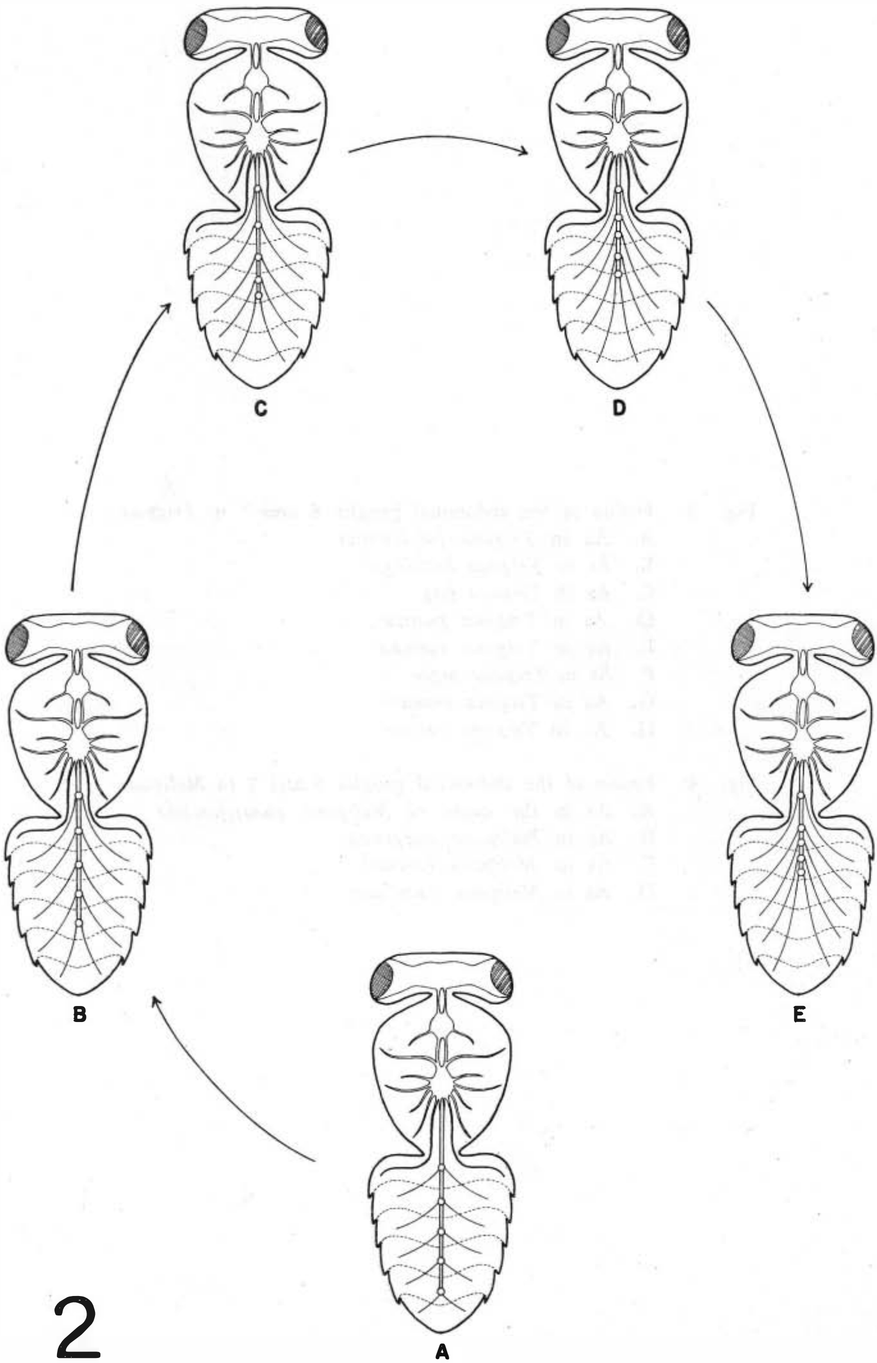


Fig. 1: Evolutionary trends of the ventral nerve cord in the stingless bees. A. Generalized ventral nerve cord, represented by *Trigona fulviventris* *. I to III thoracic ganglia, 1 G to 7 G abdominal ganglia, 2a to 7a abdominal segments. B. As in *Trigona hockingsi*. C. As in *Trigona jaty*. D. As in *Trigona cassiae*. E. As in the queen of *Melipona quadrifasciata*. F. As in *Melipona marginata*. G. As in *Melipona flavipennis*. H. As in *Melipona scutellaris*.

* All references are to the worker caste, unless otherwise specified.

Fig. 2: Cephalization of the ventral nerve cord in the stingless bees.

A. As in *Trigona fulviventris.*
B. As in the queen of *Melipona quadrifasciata.*
C. As in *Melipona marginata.*
D. As in *Melipona fasciata.*
E. As in *Melipona flavipennis*



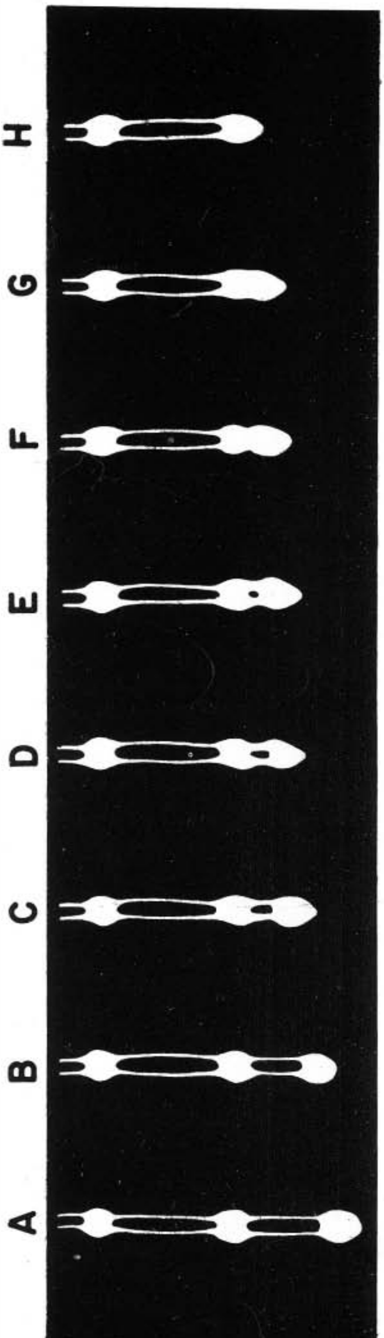
2

Fig. 3: Fusion of the abdominal ganglia 6 and 7 in *Trigona.*

A. As in *Trigona fulviventris*
B. As in *Trigona hockingsi*
C. As in *Trigona jaty*
D. As in *Trigona postica*
E. As in *Trigona corvina*
F. As in *Trigona nigra*
G. As in *Trigona braunsi*
H. As in *Trigona cassiae*

Fig. 4: Fusion of the abdominal ganglia 6 and 7 in *Melipona*

A. As in the queen of *Melipona quadrifasciata*
B. As in *Melipona marginata*
C. As in *Melipona beecheii*
D. As in *Melipona scutellaris*



3

4