

NEUROHEMAL ORGANS IN MYRIAPODA AND PHYLOGENY

by

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ABSTRACT

Comparisons of neurohemal organs in Insecta and Myriapoda are made. The structure of the corpora cardiaca, the paraesophageal bodies and the blood sinus formations are paralleled. Some Diplopoda possess three protocerebral systems, among which the paraesophageal bodies - blood sinus formations system and the basic myriapodan lateral one. Diplopod paraesophageal bodies and blood sinus formations are reminiscent of the insect "aortal complex" system. Chaudonneret's idea of two primitive lateral cords inherited from an annelid ancestor is adopted. His homology of corpora cardiaca and paraesophageal bodies is defended. The present study supports the view that Myriapoda and Hexapoda have a common ancestor.

LIST OF ABBREVIATIONS USED

CA	— corpus allatum
CC	— corpus cardiacum
CG	— cerebral gland
gl	— globulus
GO	— Gabe organ
NCC	— nervus corporis cardiaci
NH-EO	— neurohemal-endocrine organ
NHO	— neurohemal organ
NS	— neurosecretion
NSC	— neurosecretory cell
PB	— paraesophageal body
PNHO	— protocerebral neurohemal organ
PNS	— protocerebral neurosecretion
PNSC	— protocerebral neurosecretory cell
PW	— pathway
S	— blood sinus formation

INTRODUCTION

It seems that individualized extracerebral neurohemal organs (i.e. separate anatomical

entities) have begun to appear in Arthropoda. In Annelida and Mollusca only neurohemal areas occur here and there. A "neurohemal area" is a storage and release site, located inside the nervous system (often close to small vessels), invested with neurosecretory axons.

In arthropods the most simple neurohemal organ (NHO) consists solely of axon terminals. It possesses neither glial cells (according to Cassagnau & Juberthie, 1983), intrinsic secretory cells nor connections with an endocrine organ. Such a simple organ occurs only in Symphyla (Juberthie-Jupeau, 1983). In pselaphognathe millipedes some glial processes are also in evidence (Seifert & El-Hifnawi, 1972), but there are apparently no nuclei (?).

The NHO of the protocerebral neurosecretory system has been termed the Gabe organ (GO) in Diplopoda (Sahli, 1963, 1966). For convenience in this discussion the term will be retained for the NHO of Symphyla. For the same reason I will call protocerebral neurohemal organs (PNHO), those NHOs the axons of which (all or only a part of them) originate from the protocerebral neurosecretory cells (PNSC). Arthropods possess several neurosecretory systems. As this is a brief discussion I shall deal only with the protocerebral neurosecretory system.

Probably in all chilognathe millipedes GOs consist of axon terminals and glial cells. Intrinsic secretory cells are never present (Seifert, 1971; Juberthie & Juberthie-Jupeau, 1974; Sahli & Petit, 1972). In the Julida, Spirobolida, Callipodida and Paradoxosomatidae (Diplopoda) the GO (or the GO nerve) is connected with a neurohemal-endocrine organ (NH-EO),

termed the paraesophageal body (PB) (Sahli, 1963). NH-EOs contain both intrinsic secretory cells and extrinsic axon terminals (cf. Gupta, 1983b). In Penicillata (Diplopoda) the GO system is connected with two paired nerves (Nguyen Duy, 1973) originating from the subesophageal mass and only by one in Julida (Sahli, 1966).

In addition, swellings occur on the periesophageal sinus wall: they have been called blood sinus formations (S1, S2, S3, S4, Sahli, 1966). Like the PBs, they are NH-EOs.

In this paper we shall only compare the myriapod protocerebral neurosecretory system with the protocerebral neurosecretory systems of apterygote and pterygote insects. For a better understanding we shall first sum up our present knowledge in apterygote insects. Collembola have been well studied, mainly due to the accurate investigations of Denis (1928), Cassagnau & Juberthie (1967), and Juberthie & Cassagnau (1971). Recently the topic has been dealt with in an excellent paper by the latter (Cassagnau & Juberthie, 1983). PNHOs of some Collembola consist of only axon terminals without glial cells (type 1), as in Symphyla. Others show glial cells in addition (type 2), as in Chilognatha. Finally, some others like the collembolan *Hypogastrura* exhibit axon terminals, one intrinsic secretory cell and no glial cells (type 3). It must be emphasized that in Collembola PNHOs seem to be always in more or less close nervous connections with an endocrine organ, the corpus allatum. *Campodea* (Diplura) and Machilidae (Thysanura) presumably belong to the Collembola type 2. Japygidae (Diplura) possess a formation with glial cells, one intrinsic secretory cell but no axonal endings. This formation might be a rudimentary corpus cardiacum without a neurohemal part. Curiously, up to now no PNHO has been described in Japygidae.

In Lepismatidae (Thysanura) the situation is complex and still confused, even contradictory. Well-developed organs called "CC", with numerous secretory cells, are always present. They lie on either sides of the aorta, sometimes very close to it. In *Thermobia*, according to

Cassagnau & Juberthie (1983, fig. 8.16), the CC are widely separate. Only the protocerebral nerves corresponding to the NCC I of Pterygota carry neurosecretion material (no secretory product occurs in the NCC II). The PNHO (i.e. the storage region, which is distinct from the CC) may receive the NCC I directly. PNHOs correspond to the posterior aortic nerves of Chaudonneret (1950). The organ called CC is an endocrine (or at least mainly endocrine) organ, homologous to the glandular intrinsic part of CC. It lies lateral to the PNHO and may receive axons from the NCC II, according to Watson (1963). It is closely connected with a circumesophageal sinus. According to the most accurate investigations of Chaudonneret (1950) nervous prolongations of the CC extend around the sinuses and join ventrally beneath the esophagus (as the blood sinus formations S4 do in julid millipedes, vide infra).

Cassagnau & Juberthie (1983) suggest that in Apterygota the primitive PNHOs have evolved by the addition first of one, then of numerous intrinsic secretory cells. Gupta (1983a) came to the same conclusion in assuming that intrinsic secretory cells became incorporated into primitive PNHOs later on in evolution.

COMPARISONS BETWEEN INSECTA AND MYRIAPODA

1. Localization of PNHOs or CC in Insecta and GO or CG in Myriapoda

In Apterygota and Pterygota PNHOs or (and) CC are often located close to the aorta. CC are typically paired organs on or in the lateral walls of the aorta. Cazal (1948) considers the location of the CC within the aorta wall to be a primitive one. According to him CC lost their direct connections with the aorta and have been "lateralized" in different pterygote groups (in fact they are slightly lateralized). Generally speaking we are entitled to state that insect PNHOs and CC belong to what one may call an "aortal complex system". There is an exception in the collembolan *Orchesella kervillei* Denis (cf. Cassagnau & Juberthie, 1967). The PNHO is here located in the "lateral posterior

part of the head". Its situation is a bit reminiscent of that of the GO in Juliformia (Diplopoda) and Symphyla.

In Myriapoda the Gabe organs of Diplopoda and Symphyla and the cerebral glands (CG) of Chilopoda are never close to the aorta. In reality they are a long distance away from it (fig. 1). PNHOs are located sometimes on each side of the subesophageal nervous mass of the brain, sometimes near the optic lobes, sometimes peripherally near the integument, etc. (Sahli, 1981). The route of the PNHO nerves is consequently very different of that of the NCC I and NCC II.

2. Release of secretion products

As a result of their location, the PNHOs (and the CG) of Myriapoda do not release their secretion products into the aorta but into the hemocoel. It is odd and surprising that even PB and blood sinus formations (e.g. S 3) located close or within the sinus wall send at least a part of their own intrinsic secretory material towards the GO, via the PB nerve, instead of releasing it directly into the periesophageal sinus. PNHOs are not closely associated to a blood sinus in most of the Myriapoda. Sometimes "blood vessels" are found in association with the cerebral gland, as in Chilopoda (Joly & Descamps, 1968).

3. Protocerebral neurosecretory cells

Basically there are two symmetrical groups of protocerebral neurosecretory cells in Apterygota (fig. 1B): one group called "median cells" is located on each side of the medioposterior area of the brain; this part is considered homologous to the pars intercerebralis in Pterygota, in spite of the fact that in the latter the median NSCs lie classically in the forebrain (viz. the anterior part of the pars intercerebralis) (fig. 1C). The other group called "lateral cells" is situated in each lateral lobe of the protocerebrum. NSC axons of the pars intercerebralis give rise to the nervi corporis cardiaci I (NCC I) (after decussating inside the brain) on the one hand, and those of the lateral

cells to the nervi corporis cardiaci II (NCC II) on the other.

In Pterygota the pars intercerebralis is a most complicated area. NCC I exhibit axons originating from six different places and NCC II from three (Grassé, 1975). Only certain median cell axons decussate in the brain while others do not (fig. 1C).

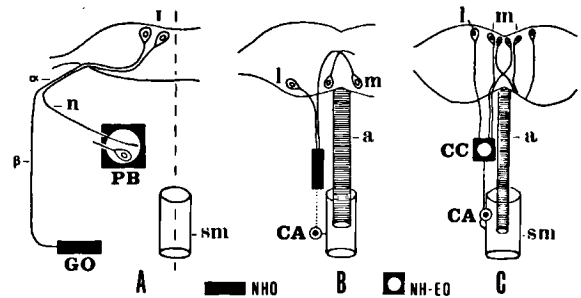


Fig. 1. Diagram of the PNS systems in Diplopoda Julida (A), primitive Apterygota (B) and Pterygota (C). In A two systems are showed; periesophageal sinus formations and pathway between paraesophageal bodies (PB) and Gabe organ (GO) not represented. B is inspired (among others for the location of m and l) by Cassagnau (1969) and Cassagnau & Juberthie (1983). I, gl I NSC; α and β , axons inside the α and β parts of the GO nerve (not shown); a, dorsal aorta; l, lateral neurosecretory cell; m, median neurosecretory cell; n, axon inside the PB nerve (not shown); sm, subesophageal nervous mass.

In Myriapoda protocerebral NSCs are frequently located near the globuli. In Diplopoda (Petit & Sahli, 1977) and probably in Chilopoda as well (see Sahli, 1977) an important group of NSCs is associated with the globuli I (= gl I NSC). In Diplopoda it is situated on the dorsal and slightly anterior part of the brain. The gl I NSC axons constitute the GO nerve. In Julidae the gl I NSCs are numerous and small. Their axons do not decussate inside the brain (Sahli, 1966). Axons of PNSC giving rise to the GO or CG nerves never decussate in Myriapoda, as already stressed by Juberthie & Cassagnau (1971).

In Chilognatha (Diplopoda) and Chilopoda NSCs occur also in the medioposterior part of the brain (viz. near the globuli III in Julidae). In Chilopoda they have been considered

homologous to the pars intercerebralis of Pterygota.

In addition few (e.g. 1-3 in *Tachypodoiulus*) lateral NSCs occur in each lateral lobe, close to the globuli II in Chilognatha. In Pterygota the lateral NSCs are often located near "the globuli of the corpora pedunculata" (Gabe, 1967) and their axons run directly to the corpora cardiaca via the NCC II. Are the lateral NSCs in Diplopoda and Apterygota homologous? The question remains open. In Julida axons presumably originating from the gl II NSC (= lateral NSC according to Sahli) and gl III NSC (= pars intercerebralis NSC?) fuse at the "K" commissure level (Sahli, 1966) and give rise to what I named the "TR IV" pathway (= PW IV; fig. 2); their axons run downwards into the connective, then into the subesophageal nervous mass and finally backwards into the ventral nerve cord. The "K" commissure is probably a neurosecretory axon chiasma area (decussating axons were observed by Holmgren, 1916, at this place). In Symphyla axons of NSCs of the lateral and posterior lobe give rise to a pathway homologous to the Diplopoda PW IV. This pathway and its PNSC constitute a PNS system of its own, different from the PNHO lateral system (= GO system). It can be considered a primitive myriapodan (or arthropodan?) system with its own NHOs, viz. the connective bodies present at least in modern Paradoxosomatidae (Prabhu, 1959; Sahli, 1962; Sahli & Petit, 1974).

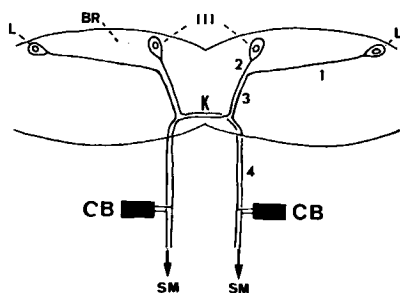


Fig. 2. Diagram of the Diplopoda "PW 4" system (connective not shown): 1, 2, 3, 4, neurosecretory pathways; III, globuli III NSC; BR, brain; CB, connective body; K, K commissure (= an axon chiasma area); L, lateral NSC; SM, subesophageal nervous mass.

In Annelida three globuli are present (Holmgren, 1916) but no evidence could be provided that NSCs are in the vicinity of the globuli.

Drawing homologies between the globuli of different Arthropoda is very difficult and can be fraught with pitfalls. Homologies made by different investigators are often contradictory.

Are median neurosecretory cells of insects homologous to the globuli I NSC and their equivalent in the frontal lobes in *Lithobius*? They might well be. But the term "pars intercerebralis" has probably been misused in arthropod literature.

4. Presence or absence of corpora allata

Emphasis must be placed on the fact that Apterygota and Pterygota always possess corpora allata (CA). They belong to the mandibular and maxillar segments (Chaudonneret, 1950). In Collembola they may be distinct organs; CA are often closely associated with the PNHOs, what is considered an evolved condition. CA are always innervated by a nerve (the nerve of Hoffmann or a branch of it) which arises from the subesophageal mass. Juberthie & Cassagnau (1971) underline the presence of CA in Insecta and their absence in Myriapoda. Indeed no CA have been described hitherto in the latter. Nevertheless organs of similar function might exist in Diplopoda (Sahli, unpubl. data).

5. Components of the corpora cardiaca, parasophageal bodies and sinus formations

When the PNHOs possess one or several secretory cells they are called corpora cardiaca in Apterygota and Pterygota. But pure PNHOs on the one hand and "CC" consisting of only intrinsic secretory cells on the other have also been named corpora cardiaca in a confusing way in insect literature. CC are compound organs in most cases. The axon terminals of extrinsic NSCs and the intrinsic secretory cells may either be intermingled or they may build up two distinct parts in the same organ. In some

Diptera independent organs with only (or a few?) intrinsic secretory cells have been described. This has led Normann (1983) to another concept of CC. He redefines them as "endocrine glands situated on or near the cephalic aorta and containing intrinsic NS cells with hormonal functions". According to several authors (cf. Gupta, 1983b) the aortal wall, rather than the CC would be the principal NHO in many Pterygota, axons from the brain NSC bypassing the CC. The same situation occurs in Lepismatidae: the aortal wall or the posterior aortic nerves are the unique or at least the main storage site.

The location of the paraesophageal bodies in Diplopoda is strikingly similar to the location of the CC in the 92-hour embryo of the heteropterid insect *Oncopeltus fasciatus* (Dall.) according to Mori & Ando (1983).

The components of the PBs and blood sinus formations (S) are similar. PBs and S possess both intrinsic secretory cells and some extrinsic axon terminals (called ax 1 in Julida, Sahli & Petit, 1973; 1979 and unpubl. data). These axons may originate from the protocerebral NSC and run to the PB via the part of the GO nerve and the PB nerve as illustrated in figs. 1A and 4C. In Glomerida Juberthie-Jupeau (1973) suggests that the PB may receive PNSC material via the GO and the PB nerve. If so, some Diplopoda possess three protocerebral systems: the "PW IV" system, the basic myriapodan lateral one (GO) and in addition the "PB-S" system, reminiscent in some extent of an insect "aortal complex" system (fig. 1). Besides there are resemblances between the S2-S3-S4-PB complex on the one hand and the circumesophageal complex in the lepismatid *Thermobia* on the other hand (vide supra). One (among others) difference between insect and myriapod systems is that in Insecta all (or nearly all) axons end within the aortal complex (sensu lato), while in Diplopoda only a few terminate within the PB-S complex, most of them ending in the lateral GO system.

The presence of extrinsic neurosecretory axon terminals within the PB-S complex constitutes a morphological basis for the existence

of a neurohemal mechanism controlling PB-S functions.

Besides intrinsic secretory cells, the PB probably sends at least a part of its own secretion products to the GO (fig. 4C), as suggested in Julidae by Sahli (1966, 1979), Sahli & Petit (1973, 1979), and Petit & Sahli (1975), in Glomerida by Juberthie-Jupeau (1973) and in Paradoxosomatidae by Prabhu (1962).

DISCUSSION

It is worth noting that PB intrinsic cells possess features in common with neurons and glandular cells. Among others, this is an evidence in support of Chaudonneret's remarkable theory (1950, 1978). He supposes that Arthropoda inherited two primitive lateral cords from an annelid ancestor. He advances the hypothesis that the two lateral cords have given rise to most NHOs and NH-EOs in Arthropoda. The posterior part of the lateral paired chain is often lacking. He assumes that neurons of the lateral ganglions have evolved into secretory cells and consequently the original ganglions into endocrine organs. One can imagine that the primitive lateral chain has been deeply modified in evolution: some ganglions have disappeared, some others fused together, perhaps migrated; finally their cells have evolved into neurosecretory or secretory cells.

In my opinion these cells might have constituted a target area where extrinsic neurosecretory axons could end. In this way a protocerebral NH-EO (like PB of CC, etc.) can result by close association of neurosecretory axon terminals with secretory cells originating in primitive ganglion cells.

Concerning the PNHO nerves and PNHOs one can choose from several alternatives. One can for instance assume that some PNHO nerves have nothing to do with a hypothetical lateral chain. One can also assume that some PNHO nerves derive from the longitudinal connective nerves between each primitive ganglion; in other words that they are parts of a vestigial cord from which, at least in some

cases, all the ganglions have disappeared and neurosecretory axons appeared. In this way simple PNHOs might result (fig. 3).

In Apterygota PNHOs often look like nerves and in fact they have been previously described as such, using the light microscope. This is the most simple situation. Perhaps the first PNHOs in arthropods used to look like nerves (fig. 3B).

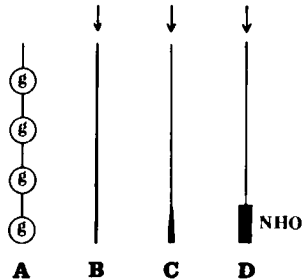


Fig. 3. How a NHO may originate from a hypothetical primitive lateral cord. Only four ganglions (g) are shown (A); they disappear (B, C, D) and neurosecretory axons (arrows) appear into the remaining nerve. B represents the most simple situation in modern arthropods.

Chaudonneret (1978) considers that PBs and CC may be homologous; both may result from the fusion of several first ganglions (fig. 4 A and B). Chaudonneret's homology is defensible if one takes into account only the intrinsic secretory part of PBs and CC and if one admits an arthropodan basic "plan of organization". I would not be surprised if intrinsic parts of CC and PBs had a same embryological origin.

Another theory has been put forward (Cassagnau & Juberthie, 1983; Gupta, 1983a). According to these authors at first only NHOs occur in Arthropoda. NH-EOs appear as new distinctive specializations later on; according to Gupta this hypothesis does not need to invoke homology and nervous origin of all NHOs and NH-EOs in Arthropoda. But in Chaudonneret's opinion (pers. comm.) not all arthropodan NHOs have derived from a primitive lateral cord. As an example we can mention the connective bodies in Diplopoda.

In my opinion the evolution of ganglions into endocrine organs may be regarded as new specializations. In addition to these, further

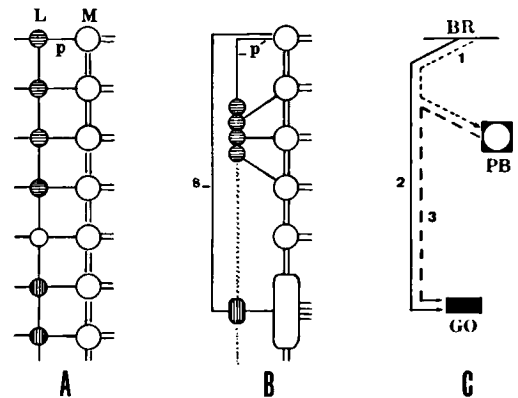


Fig. 4. A: Diagram of the primitive lateral (L) and main (M) cords.

B: Possible evolution in Myriapoda. Only the left half is shown. The four first lateral ganglions fuse and give rise to the PB (or CC), the fifth (mandibular one) disappears, the sixth and seventh fuse and give rise to the GO (or CA); p, primary connection; s, secondary connection between the protocerebrum and the GO.

C: 1, PB system; connection 1 corresponds to the p one in B (sinus formations not shown); 2, GO (myriapodan lateral) system in Diplopoda; connection 2 corresponds to the s one in B; 3, additional connection between PB and GO which is not exhibited in B; BR, brain.

A and B: courtesy of Prof. J. Chaudonneret, C: after the author's point of view.

specializations have also occurred, originating independently from a lateral chain.

Diplopoda lacking PBs are very sensitive to heat and dry atmospheres (for instance Chordeumatidae, Craspedosomatidae, Polydesmidae). They die quickly under unfavourable conditions. Perhaps Diplopoda with PBs are better adapted to dry and/or hot conditions than Diplopoda missing PBs. The presence or absence of PBs might be in connection with paleogeographical environmental conditions. Among other functions, PBs (or the PNS-CC system) might regulate the water loss and produce an antidiuretic substance. If so, the PBs and CC might not only be "morphologically" homologous, but they still have preserved the same function.

CONCLUSIONS

The location of PNHOs in primitive Myriapoda may have been similar to that of the

GO in modern Juliformia (fig. 5A), i.e. an organ located far behind the brain (= extended type), almost in a ventral position, on either side of the subesophageal mass, perhaps innervated by several metameric nerves arising from it and near bundles of tracheae. In Myriapoda, we can tentatively suggest the scenario illustrated in fig. 5.

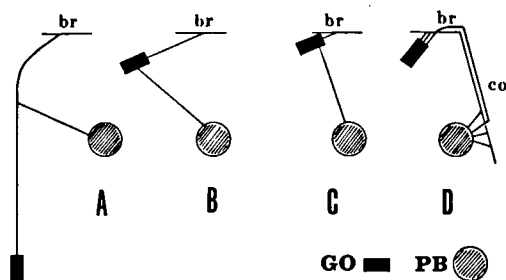


Fig. 5. Myriapodan GO and PB systems. A: GO extended type in *Tachypodoiulus*; B, C, D: condensed type (after the GO has migrated upwards) in *Callipus*, *Glomeris* and *Oxidus*, respectively; br, brain; co, connective.

PBs, if present, have occupied a constant position in all groups. Unlike PBs (linked to sinus formations in some groups) the PNHOs have migrated upwards and forwards toward the brain with a reduction of GO nerve length. This leads to a condensed type (fig. 5B, C, D): the PNHO is now near the brain as in Polydesmidae, Trizonia, Glomerida and Chilopoda.

After the migration of the PNHO toward the brain, PNHO and PB are now directly connected by the PB nerve as in Glomerida and Callipodida. In Paradoxosomatidae, as a result of this condensation, the majority of the PB nerve has become incorporated into the brain (fig. 5D) but in spite of this "cerebralization" the PB has not moved away from its old location.

Unlike the PNHOs of all other Myriapoda that of all Chilopoda possess intrinsic secretory cells. Where do they come from? We know that in *Scolopendra* the Tömösváry organ of Heymons (1901) is the frontal organ of Holmgren (1916) which is the cerebral gland of Fahlander (1938) and more recent authors. According to the data

of Heymons (in Scheffel, 1961), the formation of the cerebral glands and the frontal lobes are closely connected in *Scolopendra*. Ectodermal cells from the hypodermis in the vicinity of the frontal lobes migrate into the cerebral glands. During embryonic development further hypodermal cells continuously migrate into the cerebral gland "Anlagen". These cells may represent the secretory part of the cerebral gland. The "Anlagen" may constitute a target area (cf. Mori & Ando, 1983) for PNSCs. Perhaps something like a nerve growth factor (NGF) exists in Arthropoda. The cerebral gland may result from the fusion of the secretory cells with a PNHO. The great last new event in the evolution of the PNS system in Myriapoda is the acquisition of a NH-EO in Chilopoda. The extrinsic neurohemal part of the CG belongs to the myriapodan lateral system. By reason of Heymons' data one can assume that the intrinsic secretory part of the CG is a new acquisition and therefore a chilopodan specialization (sensu Gupta) and that this part does not derive from some primitive annelid ganglions.

In comparison with Symphyla and Diplopoda an important change occurs in Chilopoda: endocrine cells are fused with the PNHOs and there are no PBs. On the other hand, the cerebral gland nerve receives axons from the "pars intercerebralis" (Jamault-Navarro & Joly, 1977; Jamault-Navarro, 1981). Such axons do not occur in the GO nerve. Diplopoda and Symphyla develop a PNSC-PW 4 system, absent (or most rudimentary?) in Chilopoda. There are three protocerebral neurosecretory systems in some Diplopoda and apparently only one in Chilopoda.

There is probably a common basic plan to PNHOs/PNH-EOs in Arthropoda. From this plan several major patterns have derived: for instance an apterygote pattern (to the exclusion of Lepismatidae?), a pterygote pattern, and a myriapod pattern. The myriapod pattern can be subdivided into two (one symphylian-diplopodan and one chilopodan) or four (one symphylian, two diplopodan and one chilopodan) subtypes.

There is an important gap in our knowledge of neurohemal organs. In Myriapoda for instance we lack investigations on Pauropoda and numerous orders and families in Diplopoda.

This study supports the view that Myriapoda and Hexapoda may have a common ancestor, as for instance stressed by Manton (in Dohle, 1974, her fig. 4, p. 196). Concerning Chilopoda, Dohle's standpoint (1974, his fig. 2, p. 192) is not incompatible with the ideas developed in the present paper. Although it may be an old-fashioned view, it is likely that Arthropoda originate from one (or several) annelid ancestor(s), as assumed by many zoologists, like for instance Vandel (1949) or Grassé (1973).

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REFERENCES

- CASSAGNAU, P., 1969. La phylogénie des Collembolés à la lumière des structures endocrines rétro-cérébrales. Simposio internacional Zoofilog. Fac. Ciencias, Univ. Salamanca: 333-349.
- CASSAGNAU, P. & C. JUBERTHIE, 1967. Structures nerveuses, neurosécrétion et organes endocrines chez les Collembolés. II. Le complexe cérébral des Entomobryomorphes. Gen. comp. Endocr., 8: 489-502.
- & —, 1983. Neurohemal organs in Apterygota. In: A. P. GUPTA ed., Neurohemal organs of arthropods: 281-318 (Charles C. Thomas, Springfield, Illinois).
- CAZAL, P., 1948. Les glandes endocrines rétro-cérébrales des Insectes (étude morphologique). Bull. biol. Fr. Belg., Suppl. 32: 1-227.
- CHAUDONNERET, J., 1950. La morphologie céphalique de *Thermobia domestica* (Packard) (Insecte Aptérygote Thysanoure). Annls. Sci. nat., (Zool., 11) 12: 145-302.
- , 1978. La phylogénèse du système nerveux annélide-arthropodien. Bull. Soc. zool. Fr., 103: 69-95.
- DENIS, J. R., 1928. Etudes sur l'anatomie de la tête de quelques Collembolés, suivies de considérations sur la morphologie de la tête des Insectes. Archs. Zool. exp. gén., 68: 1-291.
- DOHLE, W., 1974. The origin and inter-relations of the myriapod groups. Symp. zool. Soc. Lond., 32: 191-198.
- FAHLANDER, K., 1938. Beiträge zur Anatomie und systematischen Einteilung der Chilopoden. Zool. Bidr. Upps., 17: 1-148.
- GABE, M., 1967. Neurosécrétion: 1-1091 (Gauthier-Villars, Paris).
- GRASSÉ, P.-P., 1973. L'évolution du vivant. In: Sciences d'aujourd'hui: 1-477 (Albin Michel, Paris).
- , 1975. Le système nerveux des Insectes. In: P.-P. GRASSÉ ed., Traité de zoologie, 8: 321-510 (Masson, Paris).
- GUPTA, A. P., 1983a. Neurohemal and neurohemal-endocrine organs and their evolution in arthropods. In: A. P. GUPTA ed., Neurohemal organs of arthropods: 17-50 (Charles C. Thomas, Springfield, Illinois).
- (ed.), 1983b. Neurohemal organs of arthropods. Their development, evolution, structures and functions: 1-629 (Charles C. Thomas, Springfield, Illinois).
- HEYMONS, R., 1901. Die Entwicklungsgeschichte der Scolopender. Zoologica, Stuttgart., 33: 1-224.
- HOLMGREN, N., 1916. Zur Vergleichenden Anatomie des Gehirns von Polychaeten, Onychophoren, Xiphosuren, Arachniden, Crustaceen, Myriapoden und Insekten. K. svenska VetenskAkad. Handl., 56: 1-303.
- JAMAULT-NAVARRO, C., 1981. Cellules neurosécrétrices et trajets axonaux protocérébraux chez *Lithobius forficatus* L. (Myriapode Chilopode). Etude ultrastructurale. Archs. Biol., Paris, 92: 203-218.
- JAMAULT-NAVARRO, C. & R. JOLY., 1977. Localisation et cytologie des cellules neurosécrétrices protocérébrales chez *Lithobius forficatus* L. (Myriapode Chilopode). Gen. comp. Endocr., 31: 106-120.
- JOLY, R. & M. DESCAMPS, 1968. Etude comparative du complexe endocrine céphalique chez les Myriapodes Chilopodes. Gen. comp. Endocr., 10: 364-375.
- JUBERTHIE, C. & P. CASSAGNAU, 1971. L'évolution du système neurosécréteur chez les Insectes; l'importance des Collembolés et des autres Aptérygotes. Revue Ecol. Biol. Sol, 8: 59-80.
- JUBERTHIE, C. & L. JUBERTHIE-JUPEAU, 1974. Etude ultrastructurale de l'organe neurohémal cérébral de *Speleoglomeris doderoi* Silvestri Myriapode Diplopode cavernicole. Symp. zool. Soc. Lond., 32: 199-210.
- JUBERTHIE-JUPEAU, L., 1973. Etude ultrastructurale des corps paraoesophagiens chez un Diplopode Oniscomorphe *Loboglomeris pyrenaica* Latzel. C. r. hebdom. Séanc. Acad. Sci., Paris, (D) 276: 169-172.

- , 1983. Neurosecretory systems and neurohemal organs of Myriapoda. In: A. P. GUPTA ed., Neurohemal organs of arthropods: 204-278 (Charles C. Thomas, Springfield, Illinois).
- MORI, H. & H. ANDO, 1983. Embryonic neurohemal organs in arthropods. In: A. P. GUPTA ed., Neurohemal organs of arthropods: 5-16 (Charles C. Thomas, Springfield, Illinois).
- NGUYEN DUY, M., 1973. Contribution à la connaissance de l'anatomie céphalique, des formations endocrines et du développement post-embryonnaire de *Polyxenus lagurus* (Diplopodes, Pénicillates): 1-148 (Thèse Sci., C.N.R.S., A.O. 8186).
- NORMANN, T. C., 1983. Cephalic neurohemal organs in adult Diptera. In: A. P. GUPTA ed., Neurohemal organs of arthropods: 454-480 (Charles C. Thomas, Springfield, Illinois).
- PETIT, J. & F. SAHLI, 1975. Cytochemical and electron-microscopic study of the paraoesophageal bodies and related nerves in *Schizophyllum sabulosum* (L.) (Diplopoda Iulidae). *Cell Tiss. Res.*, **162**: 367-375.
- & —, 1977. Etude ultrastructurale des cellules neurosécrétrices protocérébrales des globuli I chez *Schizophyllum sabulosum* (L.) (Diplopoda, Iulidae). *Bull. Soc. zool. Fr.*, **102**: 431-437.
- PRABHU, V. K. K., 1959. Note on the cerebral glands and a hitherto unknown connective body in *Jonespeltis splendidus* Verhoeff (Myriapoda, Diplopoda). *Current Sci.*, **28**: 330-331.
- , 1962. Neurosecretory system of *Jonespeltis splendidus* Verhoeff (Myriapoda, Diplopoda). *Neurosecretion, Mem. Soc. Endocr.*, **12**: 417-420.
- SAHLI, F., 1962. Sur le système neurosécréteur du *Polydesmoïde Orthomorpha gracilis* C. L. Koch (Myriapoda, Diplopoda). *C. r. hebd. Séanc. Acad. Sci., Paris, (D)* **254**: 1498-1500.
- , 1963. Sur le système neurosécréteur des Myriapodes Diplopodes. *Proc. 16th int. Congr. Zool., Washington*, **2**: 149.
- , 1966. Contribution à l'étude de la périodormorphose et du système neurosécréteur des Diplopodes Iulides: 1-226 (Thèse Sci., **94**; Bernigaud & Privat, Dijon).
- , 1977. Sur les cellules neurosécrétrices des globuli I et sur la voie neurosécrétrice protocéphalique des Myriapodes Diplopodes. Premières observations chez les *Polydesmida Platyrrhacidae*, les *Nematophora Lysioptelidae*, les *Spirostreptida* et les *Spirobolida*. *C. r. hebd. Séanc. Acad. Sci., Paris, (D)* **284**: 815-817.
- , 1979. Different types of neurosecretory system in Diplopoda. In: M. CAMATINI ed., *Myriapod biology: 279-285* (Academic Press, London, etc.).
- , 1981. Aspects of the neurosecretory system relevant to the classification of the juliform millipedes. Ms. 5th. int. Congress Myriapology, August 1981, Radford, U.S.A.
- SAHLI, F. & J. PETIT, 1972. Observations sur l'ultrastructure des organes de Gabe des *Polydesmidae* et des *Iulidae* (Diplopoda). *C. r. hebd. Séanc. Acad. Sci., Paris, (D)* **275**: 2017-2020.
- & —, 1973. Observations sur l'ultrastructure des corps paraoesophagiens des *Diplopodes Iulides*. *C. r. hebd. Séanc. Acad. Sci., Paris, (D)* **276**: 2019-2022.
- & —, 1974. Observations sur l'ultrastructure des corps connectifs (organes neurohémaux céphaliques) d'*Orthomorpha gracilis* (C.L.K.) (Diplopoda, *Polydesmoidea*). *C. r. hebd. Séanc. Acad. Sci., Paris, (D)* **279**: 2055-2058.
- & —, 1979. The latero-oesophageal complex in *Iulidae* (Diplopoda). In: M. CAMATINI ed., *Myriapod biology: 308-313* (Academic Press, London, etc.).
- SCHEFFEL, H., 1961. Untersuchungen zur Neurosekretion bei *Lithobius forficatus* L. (Chilopoda). *Zool. Jb., (Anat.)* **79**: 529-556.
- SEIFERT, G., 1971. Ein bisher unbekanntes Neurohämälorgan von *Craspedosoma rawlinsii* Leach (Diplopoda, *Nematophora*). *Z. Morph. Ökol. Tiere*, **70**: 128-140.
- SEIFERT, G. & E. EL-HIFNAWI, 1972. Die Ultrastruktur des Neurohämälorgans am Nervus protocerebralis von *Polyxenus lagurus* (L.) (Diplopoda, *Penicillata*). *Z. Morph. Ökol. Tiere*, **71**: 116-127.
- VANDEL, A., 1949. Embranchement des Arthropodes; généralités, composition de l'embranchement. In: P.-P. GRASSÉ ed., *Traité de zoologie*, **6**: 79-158 (Masson, Paris).
- WATSON, J. A. L., 1963. The cephalic endocrine system in the *Thysanura*. *J. Morph.*, **113**: 359-374.