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# NEUROSECRETION IN SOME HYMENOPTERA

BY

MATHIAS THOMSEN



København

i kommission hos Ejnar Munksgaard

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## Introduction.

The concept of neurosecretion is especially due to ERNST and BERTA SCHARRER and to HANSTRÖM. It is not necessary to cite here all the earlier papers on neurosecretion, as the literature has been repeatedly reviewed in recent years (see BARGMANN and E. SCHARRER 1951, B. SCHARRER 1948 and 1952c, and B. SCHARRER 1954); a few facts, especially with regard to neurosecretion in insects, however, ought to be mentioned.

WEYER (1935) was the first to observe neurosecretory cells in the brain of an insect, the honey-bee (*Apis mellifica*), and this observation was confirmed by B. SCHARRER (1937), who also found similar cells in *Bombus* sp. HANSTRÖM described secretory cells in the brain of the hemipteran *Rhodnius* (1938), and these cells were again pictured by WIGGLESWORTH (1940), who showed that they secrete a hormone connected with moulting.

Later, cells containing secretory material have been described in the nervous system of a number of insects belonging to different orders (HANSTRÖM 1940, 1943, DAY 1940a and b, PEREZ 1940, B. SCHARRER 1941 and later, VOGT 1942, WILLIAMS 1948, M. REHM 1950, E. THOMSEN 1948 and 1952, M. THOMSEN 1951 and 1954, DUPONT-RAABE 1951 and 1952, L'HÉLIAS 1950 and 1952).

Important progress in the staining technique was made by BARGMANN'S detection (1949) that the chrome-hematoxylin-phloxin stain of GOMORI is of value to the study of the neurosecretory cells of the vertebrates; these cells, which are situated in the diencephalon, and their axons going to the neurohypophysis, assume a very distinct dark blue colour with the chrome-hematoxylin, while the surrounding tissue stains light red.

During the last few years several papers have appeared which are based on the use of the chrome-hematoxylin-phloxin stain in insects. B. SCHARRER (1951) used it for the blattid *Leucophaea*; STUTINSKY (1952) studied *Gryllus*, *Blatta*, *Periplaneta*, *Carausius*, and *Dytiscus*; ARVY and GABE investigated *Odonata* (1952) and *Ephemeroptera* (1953); ARVY, BOUNHIOL and GABE (1953) *Bombyx mori*; HANSTRÖM (1953) described the conditions in the apterygote insect *Petrobius*; and NAYAR (1953) showed the occurrence of neurosecretory cells in *Iphita* (*Hemiptera*).

In most cases the neurosecretory cells occur in the dorsal part of the protocerebrum, where they generally form two medial and two lateral groups, though the latter may be less distinct and sometimes have not been found at all. The medial cells are situated in the pars intercerebralis.

As found by HANSTRÖM (1940) and later confirmed by other investigators the fibre bundles comprising the axons of the two medial groups after crossing inside the brain leave it ventrally to form the nervi corporis cardiaci I of Hanström, while the axons of the two lateral groups, taking a simpler course through the brain, form the nervi corporis cardiaci II. These nerves innervate the corpus cardiacum.

In some cases neurosecretory cells have been described in other parts of the nervous system (suboesophageal ganglion and other ganglia, DAY (1940a), B. SCHARRER (1941), ARVY and GABE (1952), BOUNHIOL, GABE and ARVY (1953)).

Already in 1941 HANSTRÖM (1941a) pointed out the analogy between the pars intercerebralis-cardiacum-allatum system of insects and the hypothalamus-hypophysis system of vertebrates. In 1944 B. and E. SCHARRER extended this comparison by adding that neurosecretory granules migrate along the axons from the neurosecretory brain cells to the c. cardiacum in insects and to the neurohypophysis in vertebrates. They further advanced the hypothesis that the neurosecretory cells and the corpus cardiacum should be regarded as one neuro-endocrine complex. At that time neurosecretory granules had only been observed in the axons of two insect species, *Petrobius brevistylis* (described by HANSTRÖM 1940), and the blattid *Leucophaea maderae* studied by BERTA SCHARRER, but some years later CAZAL (1948) made similar observations in the adult *Tipula* and perhaps other insects, and M. THOMSEN (1951) figured neurosecretory granules along the medial (internal) bundle of neurosecretory nerve fibres in the larva of *Tabanus*.

During a stay in the United States in the summer of 1951 the author got hold of a few specimens of the giant digger-wasp *Sphex speciosus*, in America called "the cicada-killer" as it uses the big cicadas (*Cicada septendecim* and others) as its prey. Two brains were dissected out and fixed in Bouin's fluid. Later study showed that in this insect the neurosecretory material in the brain cells and their axons stands out in an extraordinary clear way, and could be traced down into the c. cardiacum. It was therefore decided to investigate also other species of *Hymenoptera*, preferably large ones, but it proved difficult to obtain suitable material in Denmark. However, through the generous help of Mr. H. STENHOLT CLAUSEN, cand. mag., lecturer of zoology, University College, Ibadan, Nigeria, and Mrs. STENHOLT CLAUSEN, cand. mag., I received an ample collection of African species of *Hymenoptera*, fixed in Bouin's fluid. I am highly indebted to Mr. and Mrs. Clausen for their kind efforts, which proved of extreme value to my studies.

The African and American material has been supplemented by the study of a few Danish species, but so far only representatives of a few families have been considered.

Some of the papers recently published, especially those of STUTINSKY (1952) and ARVY and GABE (1952, 1953), have given results which are similar to those found by me in the *Hymenoptera*. Still I venture to say that among insects the *Hymenoptera* are exceptionally well suited for a histological study of neurosecretion, for in some of the species neurosecretory material occurs in unsurpassed quantity and distinctness.

### Material and Technique.

The following species, all belonging to the *Hymenoptera aculeata*, have been studied:

- Superfam. *Sphecoidea*. Fam. *Sphecidae*. *Sphecius speciosus* (Drury). From Harvard University, Massachusetts, U. S. A. The genus *Sphecius* is sometimes referred to a special family, *Stizidae*.
- Superfam. *Vespoidea*. Fam. *Vespidae*. *Eumenes* sp. Ibadan, Nigeria. Specimens were hatched from a laterit-nest on a stone.
- Synagris (Paragris) calida* (L.). Ibadan, Nigeria. Like *Eumenes* a solitary wasp, building laterit-nests.<sup>1</sup>
- Belonogaster* sp. (probably *junceus* Fabr.). Ibadan, Nigeria. A semi-social species, making paper-nests.
- Vespa vulgaris* L. Workers. From North Zealand, Denmark.
- Superfam. *Apoidea*. Fam. *Megachilidae*. *Megachile (Gronoceras) cincta* Fabr. Ibadan, Nigeria. Solitary bee, making laterit-nests.
- Fam. *Apidae*. *Apis mellifica* L. Workers. Copenhagen, Denmark.

As mentioned above, the African species were collected or hatched from larvae by Mr. and Mrs. STENHOLT CLAUSEN at Ibadan in West Africa. After anaesthetizing the insect by means of cold or chloroform the head was cut off, the mouth parts removed, and the head and body placed in Bouin's fluid, in which the material was shipped to Copenhagen. Here the brains with the adhering endocrine organs were dissected out under the binocular, as the cuticle is too hard to allow sectioning of whole heads. The brains were taken through increasing strengths of alcohol up to 90 per cent. and then through two changes of butylic alcohol into paraffin wax. Sections were cut at 7  $\mu$ . The American and Danish material was mostly treated in a similar way, although in some cases the brain was partly or totally dissected out before fixation. This method is rather difficult owing to the fragility of the brain tissue, and fixation before dissection is preferred and as a rule gives a satisfactory fixation of the brain, etc.

Allen's modification of Bouin's fluid and Helly's fluid were used in some cases.

Most of the material was stained with Gomori's chrome-hematoxylin-phloxin method (see BARGMANN 1949). A few series were stained with Masson's trichrome stain.

The photographs were taken with a Zeiss "Phoku" camera and a Zeiss "Lumi-pan" microscope, using Perutz "Silbereosin" plates (orthochromatic) and an orange filter. In a few cases a red filter gave better results and—contrary to expectation—it

<sup>1</sup> The specimens when received were labelled *Synagris negusi*, and this name was used in a short earlier publication (M. THOMSEN 1954). Some material was later sent to Mr. I. H. H. YARROW, British Museum, London, who determined it as belonging to *S. calida* (L.). Mr. Yarrow also checked the determinations of *Belonogaster junceus* and *Megachile cincta*. I am very much indebted to Mr. Yarrow for his valuable help.

did not prolong the exposure unreasonably (fig. 2 – 40 seconds, fig. 5 – 4 minutes). All the photographs show sections stained with Gomori's chrome-hematoxylin-phloxin stain. The original photos were not reduced in reproduction.

I am very grateful to Mr. N. HAARLØV, mag. scient., for his assistance with the photographic work, and to Mr. E. RASMUSSEN, mag. scient., for help with the drawings.

Further I want to express my sincere gratitude to the Carlsberg Foundation, which has supported the work financially.

### The Morphology of the Endocrine Organs in the Hymenoptera.

The early history of the discovery of the endocrine organs of insects has been recorded by NABERT (1913), CAZAL (1948), and others, and it will not be repeated here. Only it seems appropriate to mention that what is probably the first figure of the corpora allata of a hymenopterous insect was given by MEINERT in his "Bidrag til de danske Myrers Naturhistorie" (Contributions to the Natural History of the Danish Ants) published in the transactions of this society in 1861. He designated them as "gaadefulde Legemer" (enigmatic bodies) or corpora incerta.

Of more recent publications in which conditions in the *Hymenoptera* are considered, reference should first be made to that of NABERT (1913). He gave an extensive description of the anatomy of the corpora allata and c. cardiaca ("Pharyngealganglia") and the topographical relations between these organs and the brain, the aorta, the oesophagus, etc., in several *Hymenoptera* (*Lasius*, *Vespa*, *Chalicodoma*, *Bombus*, and *Apis*). He regarded the c. allata as endocrine glands, which are innervated by nerves coming from the c. cardiaca, while each of these is innervated by a nerve coming from the brain.

NELSON (1915) described the embryological development of the corpora allata and the stomatogastric nerves including the "pharyngeal ganglia" (= corpora cardiaca) in the honey-bee (*Apis*).

Mention should further be made of de LERMA (1937), who studied the innervation and histology of the corpora cardiaca of *Vespa crabo*. REHM (1939) briefly described the stomatogastric nervous system of the bee; and STÄRCKE (1939) gave some information on the c. allata and c. cardiaca in ants, unfortunately containing some misunderstandings.

HANSTRÖM (1941b) in his survey of the corpora cardiaca and allata of insects recorded his own observations on two species of *Hymenoptera*, *Apis mellifica* and *Vespa crabo*. He found that each c. cardiacum is innervated by two nerves from the brain, the nervi corporis cardiaci I and II, and he supposes that the n. c. cardiaci I takes its origin from the neurosecretory cells of the pars intercerebralis which had been discovered by WEYER (1935). He further described the histology of the c. allata and cardiaca, mentioning the two sorts of cells in the c. cardiacum.



Observations on the corpora allata of ants have been published by HULTIN (1947), of *Bombus* by PALM (1948), and of *Apis* by PFLUGFELDER (1948).

In his well-known monograph of the retrocerebral endocrine organs of insects CAZAL (1948) has a section on the *Hymenoptera* based on the study of one representative of the *Symphyla* (*Selandria*) and a number of species belonging to the *Apocrita*. His diagram of the topography of the organs in *Selandria* is redrawn in text-fig. 1. It is seen that the corpora cardiaca form parts of the lateral walls of the aorta, while the c. allata are placed more posteriorly and laterally. The nervi corporis allati are very short, almost wanting. CAZAL states that each corpus cardiacum is only innervated by one cardiac nerve, which, however, has two roots inside the brain, an internal and an external one. A ganglion hypocerebrale is said to be present only in the *Symphyla* and the ants.

A short description of the endocrine organs of the larva of the honey-bee was given by SCHALLER (1950). The c. cardiaca are less developed than in the adult bee, while the c. allata of the last stage attain the size found in the imago. The author could not find the two roots of the nervus corporis cardiaci stated by CAZAL to be present.

The same subject was independently treated by L'HÉLIAS in a similar short paper from the same year (1950). Her results, while mainly in accordance with those of SCHALLER, differ from his on certain points. Thus she states very precisely that the single-nervus corporis cardiaci rises from two intracerebral roots, the internal root coming from the large neurosecretory cells of the pars intercerebralis, the external one from "un groupe de grandes cellules analogues aux cellules de la pars intercerebralis, en position latéro-interne par rapport au nid de cellules du futur lobe pédonculé." Outside the brain the n. corporis cardiaci is stated to anastomose with the "nerf stomacal" (= n. oesophageus) of the same side and then go to the c. allatum. The c. cardiacum is faintly developed, consisting of few cells.

In 1952 L'HÉLIAS described the post-cerebral endocrine glands of the larva of *Lophyrus* (*Tenthredinoidea*). Also in this insect she found that the cardiac nerve originates from two roots which show a similar intracerebral course as in the honey-bee larva.

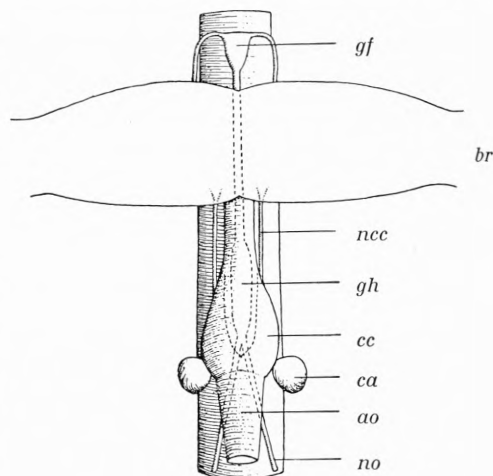


Fig. 1.

Diagram of stomatogastric nervous system and endocrine organs of *Selandria*. ao aorta (below this the oesophagus); br brain; ca corpus allatum; cc corpus cardiacum; gf ganglion frontale; gh ganglion hypocerebrale (on nervus recurrens); ncc nervus corporis cardiaci; no nervus oesophageus.

(After Cazal).

*Own observations.*

With regard to the topography of the endocrine organs in the adult *Hymenoptera* investigated, my results are in accordance with those of several other recent workers. CAZAL's general diagram is applicable also to the types studied by me, though there are some differences between the species.

The two corpora cardiaca are well-developed organs, which are intimately connected with the lateral walls of the aorta. In *Vespa* they virtually constitute this wall, as already shown in de LERMA's semi-schematic figure (1937, fig. 16); the c. cardiaca meet dorsally for most of their length, but caudally they are separate dorsally, but united ventrally by a narrow bridge. In other types, such as *Eumenes* (Pl. VI, fig. 21) and *Megachile* (Pl. VII, fig. 28), only the dorsal portion of the c. cardiacum forms part of the aortic wall, while the narrower ventral part adjoins the oesophagus. In *Megachile* the two corpora cardiaca are connected ventrally below the oesophagus by a strand of tissue (fig. 28 *vc*); a similar condition has been described by CAZAL (1948) in the bee *Xylocopa*.

The corpora allata are globular or egg-shaped bodies lying below the corpora cardiaca and leaning against the wall of the oesophagus.

Each corpus cardiacum receives only one nervus corporis cardiaci from the brain. In some cases the nerve—i. e. the extracerebral part of the fibre bundle—is extremely short or almost absent (f. inst. *Sphecius*, Pl. II, fig. 8, and *Vespa*, Pl. VII, fig. 26), while in other types it is longer (*Megachile*). The nerve enters the c. cardiacum laterally and in the *Vespidae* it can be followed as a well-defined bundle of nerve fibres inside the c. cardiacum; this is shown in *Synagris* (Pl. IV, fig. 16) and *Eumenes* (Pl. V, fig. 19). But in *Megachile* the fibre bundle can hardly be said to be inside the c. cardiacum; it runs down along the lateral side of this organ, sending fibres into it (Pl. VII, fig. 28 *ncc*).

In all species the fibre bundle continues into the corpus allatum as the nervus corporis allati, but again this nerve differs in length; while it is rather well developed in *Eumenes* (Pl. VI, fig. 21–23) and *Synagris*, it is almost absent in *Sphecius*, where the c. cardiacum and allatum lie very close together.

The nervus recurrens as usual runs along the dorsal side of the oesophagus. In the species investigated the ganglion hypocerebrale is absent or vestigial, i. e. only indicated by a small collection of nerve cells, which can be seen in transverse sections; it is most distinct in *Megachile* (Pl. VII, fig. 28), where there is a slight swelling at the point where these nerve cells occur and the recurrent nerve divides into the two nervi oesophagei. Like HANSTRÖM (1941) and CAZAL (1948) I have not been able to find any nervous connection between the recurrent nerve and the c. cardiaca nor the c. allata.

### The Neurosecretory Cells.

The neurosecretory cells observed by me in the brain of the *Hymenoptera* are situated in the anterior and dorsal part of the pars intercerebralis which connects the right and the left halves of the protocerebrum (Pl. I, fig. 1, Pl. III, fig. 9 and Pl. VIII, fig. 29). The cells mostly lie close together around the median plane, virtually forming one large group (Pl. V, fig. 17 and Pl. VII, fig. 27). It is obvious that this group corresponds to the two medial (internal) groups found in most insects, but in the *Hymenoptera* the two groups have practically fused. The cells form several layers, the superficial ones lying just below the perineurium, which is rather thin in this region (Pl. V, fig. 17 and 18). In frontal sections it is seen that the group tapers downward towards the fibre bundle, the greater number of cells lying near the surface.

The region of the brain containing the neurosecretory cells receives two tracheae which penetrate the perineurium and branch inside it. Some of the branches follow the fibre bundle of the neurosecretory cells running between the axons, while others take an oblique course into other parts of the brain.

My search for the lateral groups of neurosecretory cells gave a negative result. It is true that in *Synagris* 5–6 neurosecretory cells may be observed which lie scattered at a distance from the main group between this and the ocellar nerve fibres, i. e. posterior to the medial group. They lie very near the median plane, but may perhaps be said to form two groups. A close scrutiny of the slides revealed, however, that fine axons containing delicate blue granules extend from these cells parallel to the surface of the brain on to the large medial group where they bend downwards joining the main bundle of neurosecretory fibres. So these cells cannot represent the lateral group, but must be regarded as belonging to the medial group.

In the medial group many cells stain dark blue with the chrome-hematoxylin of the Gomori stain. This is due to their content of distinct bluestained granules, which differ somewhat in size and number in various species. They are beautifully seen in *Sphecius*, *Synagris*, *Eumenes*, and *Vespa* (cp. fig. 2, 3, 4, 11, 12, 18 and 25), i. e. in the species belonging to the *Vespidae* and *Sphecidae*, while in *Megachile* they are visible, but much less distinctly stained. The same is the case in *Apis* (workers caught and fixed in autumn). My material is not comprehensive enough to decide whether this is indicative of a general difference in the neurosecretory systems of bees and "wasps".

In the single species the granules differ in size from minute particles to distinct, discrete bodies (cp. the photographs). At first it was thought that the larger bodies, which are more or less spheroid, arise by gradual growth of the small granules. But in the best slides (*Synagris*) it could be discerned that more likely the larger inclusions are aggregates of small granules; their surface is not even and smooth, but verrucose or knotty (cp. also E. and M. THOMSEN 1954). This does not mean, however, that the small granules are all of the same size; they seem to vary *inter se*.

Among the cells with blue-stained granules there are usually some which only contain a few such granules; and furthermore there are cells—sometimes about half of the cells in the group—without any granules at all, the cytoplasm of these being phloxinophilic (see f. ex. Pl. V, fig. 18). The shape and position of the last-mentioned cells make it highly probable that they, too, are neurosecretory cells, which at the moment of fixation were in a phase of secretion in which no formed granules were present.

In most of the species investigated all granules of the neurosecretory cells appeared blue, being stained by the chrome-hematoxylin, but in *Belonogaster junceus* both blue and red inclusions occurred. The two sorts of inclusions were mostly localized in separate cells which differed somewhat in appearance. The cells with red inclusions were larger and more pear-shaped, while those with blue granules were somewhat smaller and rounded or angular, the blue granules mostly occurring as a cap-like collection above the nucleus. The individual red bodies were larger and fewer than the blue granules and spherular in shape, i. e. they resemble droplets, while the blue inclusions seem to be solid granules (Pl. VIII, fig. 31–32). Sometimes cells were found which contained a number of red spherules beside a majority of blue granules, while the reverse relation was not observed. The red droplets might occur in the thick proximal portion of the axon, which is rather conspicuous in these cells, but they were not observed in the axons farther away from the cell body.

In *Sphecius speciosus* a similar phenomenon was observed. Only a few cells contained red spherules, which were themselves fewer in number, but somewhat larger than in *Belonogaster*, looking very much like droplets.

Apart from my own observations of phloxin-stained neurosecretory cells in the brain of the adult *Calliphora* (M. THOMSEN 1954), no other similar cases seem to have been recorded in insects.

Obviously the occurrence of the phloxinophilic inclusions could be explained in two different ways. Either the red material is a second neurosecretory substance, chemically and physiologically different from the blue granules, or it is only another phase in the secretory cycle of the usual blue substance, perhaps representing a liquefaction of the material.

The latter alternative seems the more likely because: (1) red spherules only occur in two of the species; (2) they are found in cells which resemble the “empty” neurosecretory cells of the other species; (3) blue granules and red spherules may occur in the same cell. However, this evidence is only circumstantial and a decision must await further studies.

In the vicinity of the neurosecretory cells or even among them some larger nerve cells occur which are certainly not neurosecretory cells (Pl. V, fig. 18). I have not been able to identify these with any cells described in the papers of KENYON (1896) or HALLER (1905), which deal with the brain of *Apis* and other *Hymenoptera*.

The number of neurosecretory cells in the *Hymenoptera* is very great. In *Eumenes* sp. I have counted the cells with distinct blue granules in four individual brains.

The numbers found were: 120 — 129 — 136 — 142. To avoid counting the same cell twice I have included only cells in which the nucleoli were distinct, so the counts should be rather reliable. On the other hand all cells without unquestionable granules were excluded, as it is difficult to distinguish with certainty the neurosecretory cells in the non-granular phase from other nerve cells. This means that the numbers given above are too low, and presumably they should almost be doubled, so that the total number of neurosecretory cells can roughly be estimated at 200—250 in this species. Some counts from *Synagris calida* gave similar results.

The nuclei of the neurosecretory cells resemble those of other nerve cells. They are rather pale, but contain conspicuous nucleoli which stain red with the phloxin. There are mostly two or more (3—5) nucleoli, which generally lie close together forming an aggregate or more rarely are scattered in the nucleus; they may differ in size in the same nucleus. Such multiplication of the nucleolus is considered to be characteristic of highly active cells.

In *Synagris* 2—3 cells with blue granules (after the Gomori stain) were also observed in the suboesophageal ganglion, but their possible connections with other cells or organs could not be established. In the other species no such cells were seen.

In this connection it should be mentioned that the chrome-hematoxylin of the Gomori stain is not absolutely specific for the neurosecretory material, but also stains some other structures. Thus non-cellular membranes, such as the neural lamella of the brain (cp. B. SCHARER 1939) and the covering membranes of the corpus cardiacum and allatum, are generally dark blue. Similarly the cuticular wall of tracheae is also stained blue, and this fact sometimes makes it difficult to distinguish between fine tracheae and neurosecretory nerve fibres inside the brain.

In some cases the perineurium, which covers the whole surface of the brain like an epithelium, contained blue structures when stained with chrome-hematoxylin. These inclusions appear as blue granules or fine moniliform filaments which seem to wind between the cells. Especially in *Synagris* they resembled nerve endings in a rather delusive way, but no connection with nerve fibres of the underlying brain tissue could be detected. In one case they seemed to be extensions of the neural lamella, and this is probably the most likely explanation.

Furthermore it should be mentioned that the nuclei should be red in the Gomori-stained slides, but rather often they stain blue. This is the case when the slides remain too long in the hematoxylin, especially when rather fresh hematoxylin is used, and in such cases a prolonged differentiation in acid alcohol may not be able to destain the nuclei before also the blue colour of the neurosecretory material disappears.

### **The Neurosecretory Nerve Fibres and the Nervi Corporis Cardiaci.**

As all insect neurons the neurosecretory cells are unipolar nerve cells. Their axons extend downwards in the brain either directly or after making a more or less conspicuous curve (cp. figures).

The axons from all the neurosecretory cells converge to form a well-defined tract of nerve fibres. Dorsally the fibres still lie somewhat scattered, but they converge more and more, and in the ventral part of the brain they form two distinct cords (Pl. III, fig. 9). *Belonogaster junceus* differs somewhat from the other species, as the neurosecretory nerve fibres dorsally are unusually dispersed and seem to take a rather irregular course. Below the chiasma, however, they concentrate and form two definite bundles.

In some of the types studied, notably *Sphecius*, *Synagris*, and *Eumenes*, axons emerging from neurosecretory cells which contain distinct blue granules, do themselves contain similar blue material in their whole course through the brain and onwards. In such cases the bundle of neurosecretory nerve fibres stands out very clearly in the sections as a blue band on a red background, reminiscent of the tractus hypothalamo-hypophyseus in vertebrates.

Often the proximal portions of the axons are indistinct, but in some cases, especially in *Sphecius* and *Synagris*, also these parts of the axons are well stained (Pl. I, fig. 2—4). The cell tapers conically into the axon which gradually attenuates. The broader part nearest to the pericaryon (the "Zellstiel" of some authors) contains very fine granules, which are sometimes seen to form two convergent or parallel rows, obviously indicating that in reality the granules lie in the superficial layer of an axon cut longitudinally by the microtome knife. This is visible in one of the photographs only (Pl. I, fig. 3), but has repeatedly been observed. STUTINSKY (1952) has noticed the same in his material, and BARGMANN (1949) has given photographs of similar cases in vertebrates.

At a short distance from the pericaryon the axons appear as delicate filaments where fine blue granules are still visible, but owing to the thinness of the fibre the granules as a rule no longer form two rows, but fill the whole axoplasm. Such fine fibres are seen on some of the photographs of Pl. I and II. Using a high magnification and changing the focus it is sometimes possible to follow a single nerve fibre for a long distance. This is of course difficult to show in a photograph, but Pl. II, fig. 5 pictures rather a long portion of such a fibre, though not one of the thinnest. The diameter of this axon varies, in some parts there is more blue material, which causes the axon to swell, such swellings gradually continuing into extremely thin, thread-like portions.

In the central and lower parts of the protocerebrum swellings become very pronounced and numerous, and therefore this region, especially in sagittal sections, is very conspicuous on account of its dark blue colour (Pl. I, fig. 1 and Pl. III, fig. 9).

There are some differences in detail between the species investigated. In *Sphecius speciosus* the blue fibres are very striking. The single axon is swollen for a shorter or longer distance and then again may get thin and fine. Such elongate thickenings seem to recur several times in the same axon (Pl. II, fig. 6—7). Besides there are also roundish blue lumps or bulbs which occur just around the main tract and probably are connected with this by means of fine filaments which are difficult to trace. Similar

fine fibres, which leave the main bundle and go out into the surrounding brain tissue, were often observed in the other *Hymenoptera* investigated. As they are generally very thin, it is as a rule impossible to decide where they end, but in some cases it seems that they only make a sort of detour into the surrounding tissue and then return to the main route. Such a case is seen in Pl. IV, fig. 13 (*Synagris*), where it could be photographed on account of the bead-like swellings of the fibre. Whether these fine diverging fibres are complete axons or branches of axons could not be decided. I did not succeed in observing any convincing case of branching.

In *Synagris* the swellings are not so long and gradual as in *Sphecius*, but generally appear as short fusiform or sausage-shaped lumps connected by fine filaments. But besides there are round bulbs and also fine moniliform fibres (Pl. IV, fig. 13). In the most successful slides (*Synagris*) it could be distinctly seen that the swellings and bulbs are not uniform, but granular in structure. Thus it seems that they are really formed by accumulations of small granules like those observed in the pericaryon and in the proximal part of the axons. In *Eumenes* and *Vespa* the moniliform fibres predominate, and this also applies to *Apis* and *Megachile*.

In several insects it has been observed that the two fibre bundles which arise from the two medial groups of neurosecretory cells cross in the anterior part of the brain, and this is rightly considered typical. Owing to the fusion of the two medial cell groups in the *Hymenoptera* their axons likewise join to form one median nerve tract, as evident in transversal sections (Pl. V, fig. 17 and Pl. VII, fig. 27). Even so it is possible to observe that the nerve fibres do cross in a similar way as in other insects, though it could not be decided whether all fibres cross. In the above-mentioned photographs (especially Pl. VII, fig. 27) it should be possible to see some evidence of this chiasma in the lower part of the picture. Also other nerve fibres from the right and left parts of the protocerebrum cross in the same region.

Just below the chiasma the fibre tract divides into two, which may remain very close together (as in *Eumenes*) or become more separate (as in *Megachile* and *Apis*). In the antero-ventral region of the brain the fibre tracts curve and proceed in a posterior direction lying very near to the ventral wall of the brain, below the perineurium. This is best seen in sagittal sections (Pl. III, fig. 9 and 10). In the ventral part, which comprises about half of the length of the whole fibre tract, the axons run close together, and no fibres are seen to leave the general course. The swellings show almost the same picture as in the middle of the brain.

Near the posterior surface of the brain the two neurosecretory tracts diverge more, and just before they leave the brain the axons swell considerably. This is very striking in *Eumenes*, *Vespa* (Pl. VII, fig. 26), *Synagris*, and *Sphecius* (Pl. II, fig. 8), where there are big collections of blue material in this place, bigger even in some slides which were not photographed. One cannot help getting an impression that this region forms a mechanical obstruction, which somehow dams up the regular flow of secretory material through the nerve fibres. The swelling of the axons in the central part of the brain might similarly be explained as caused by the curving

of the fibres in the antero-ventral region which slows down the flow of the axoplasm carrying the neurosecretory substance.

In most of the species studied I was unable to observe any lateral (external) root of the nervus corporis cardiaci; only in *Belonogaster*, where I got some obliquely horizontal sections, could this root be found (Pl. VIII, fig. 30). It contained blue, moniliform axons and in some cases also what seemed to be phloxinophilic fibres.

The fibre tracts from the neurosecretory cells extend from the brain as the nervi corporis cardiaci, which, as already mentioned, are short, especially in *Vespa* and *Sphecius*, where the corpora cardiaca almost adhere to the brain. Where the nerves are longer, the chrome-hematoxylin positive axons can be distinctly seen. This is impressively illustrated by the sections of *Synagris* shown on Pl. IV, fig. 14 and 15. In this case the blue, rope-like fibres almost fill the nerve, and one cannot escape the notion of witnessing a copious flow of neurosecretory material from the brain down into the corpus cardiacum.

However, it should be noted that not all axons are blue; some of them are phloxinophilic and mostly thin; perhaps the blue material passes now through some, now through other axons. But it seems that also the red axons may sometimes appear swollen.

### The Corpora Cardiaca.

The two corpora cardiaca are oviform or pear-shaped organs lying behind the brain.

The nervus corporis cardiaci, as already mentioned, enters the c. cardiacum laterally, and the axons of the nerve usually form a remarkable blue strand which runs through the c. cardiacum near its lateral surface (Pl. IV, fig. 16 and Pl. V, fig. 19; as to *Megachile* cp. p. 8).

From the fibre bundle ("nerf basal" of CAZAL) the axons diverge, finding their way between the cells of the c. cardiacum and tending—as it seems—towards the surface of the organ. Whether the axons also branch in the c. cardiacum or whether they continue undivided, could not be decided with certainty, though branching was probably observed in a few cases.

Inside the c. cardiacum the axons show many large swellings which are fusi-form, ovoid or spheroid in shape. In accordance with STUTINSKY (1952) and ARVY and GABE (1952a and b) it was found that the nerve fibres containing the blue-stained material lie between the cells; though some doubtful cases occurred I could never convince myself that nerve fibres entered cells or connected with them.

In the central part of the c. cardiacum delicate fibres with rather small and regular, bead-like swellings are often seen, but also larger globular or ovoid bulbs (see especially Pl. V, fig. 20). The bulbs somewhat resemble the "Herring-bodies" of the neurohypophysis in vertebrates, and like these they are swellings of nerve fibres caused by local accumulations of neurosecretory material. Although these blue



bulbs may occur almost everywhere in the *c. cardiacum* they are most numerous near the medial surface, which turns against the aorta and the oesophagus. In some cases this region is literally crammed with blue material. Just as is the case in the brain the bulbs and swellings in the *c. cardiacum* after suitable differentiation can be seen to consist of smaller elements, which are combined into granular structures.

As found also in other insects the *c. cardiacum* contains two sorts of cells. The large cells are rounded or polygonal, phloxinophilic cells which vary much in size; the cell borders are distinct. Along the lateral surface they are arranged in a single layer resembling an epithelium (Pl. V, fig. 19); they also make up much of the central and posterior parts of the *c. cardiacum*, where the cells either occur singly or form roundish clusters between which the blue nerve fibres are seen. They have large spheroid nuclei with one or several conspicuous phloxin-stained nucleoli and small red granules, probably chromatin. I have not been able to detect any cellular processes, so it seems that these cells are not nerve cells.

STUTINSKY (1952) observed a phloxinophilic secretion in the cells of the *c. cardiacum* of *Carausius*, and ARVY and GABE described a similar phenomenon in *Ephemeroptera* and *Odonata* (1952a and b). These authors therefore regard the large cells as secretory cells. In my material the cytoplasm did not contain definite granules, but in several cases irregular or rounded red masses—one might call it a phloxinophilic colloid—were seen between the cells. It is possible that this "colloid" might represent a secretion produced by the large cells. Such red masses are especially distinct in *Vespa*, where they occur in the region closest to the brain and—what is more surprising—also just inside the brain, but only at the place where the neurosecretory fibres leave (Pl. VII, fig. 26). This observation is a warning not to disregard the alternative possibility that the red colloid might be a product of the brain which, like the blue substance, migrates into the *c. cardiacum*. In this connection we should remember the occurrence of red droplets in certain neurosecretory cells (p. 10) and the presence of red nerve fibres in the *nervus corporis cardiaci* (p. 14). Inside the *c. cardiacum* the red colloid seems to occur intercellularly and not to be confined within the axons. The final decision as to its origin must await further investigation.

The small cells occur in a rather irregular way between the groups of large cells, and besides they almost exclusively form the medial side of the *corpus cardiacum*, where they are interwoven by the nerve endings containing the blue neurosecretory material (Pl. V, fig. 19–20, Pl. VI, fig. 23–24). Mostly it seems that these cells are almost devoid of cytoplasm, only consisting of a nucleus, somewhat varying in shape and size and containing several small phloxinophilic granules. In other cases, however, the nuclei appear to be situated in vacuolated cytoplasm without definite cell borders, thus forming a sort of syncytium. Several authors have described these cells as glia cells, and it is true that they do resemble glia cells, though this designation is perhaps to some degree suggested by the hitherto prevailing concept of the large cells as nerve cells. Furthermore not all small nuclei of the *c. cardiacum* are of identical nature. Tracheae enter the *c. cardiacum* from the surface, and there-

fore some of the more elongate nuclei belong to the tracheal cells. And along the nerve fibres of the nervus corporis cardiaci some very small and thin, fusiform nuclei can be found which probably belong to "neurilemma cells" entering the c. cardiacum together with the nerve fibres.

The preceding description of the morphology of the c. cardiacum is mainly based on sections of *Synagris* and *Eumenes*. In the other species studied the appearance of the organ is somewhat different and not quite so clear. In *Megachile* the number of small cells much exceeds that of the large ones, which are mostly confined to the anterior end of the c. cardiacum. In *Sphecius* (Pl. II, fig. 8) and in *Vespa* (Pl. VII, fig. 26) the c. cardiacum looks highly vacuolated and the single cells are difficult to distinguish, but here again the small nuclei seem to predominate in number. The blue neurosecretory material occurs in smaller quantity in the c. cardiaca of these three forms than in *Synagris* and *Eumenes*.

The c. cardiacum of *Apis* is still more peculiar. Most cells are small, highly vacuolated and without distinct borders, only dorsally a few large cells occur with a phloxinophilic, finely granular cytoplasm; these, like the small cells, seem to form a syncytium; the nuclei contain several red granules. Among the cells are found numerous fine, partly moniliform, blue threads, which at first were taken to be nerve fibres with neurosecretory material. A closer study revealed, however, that at least some of these threads are connected with the cuticula-like membrane covering the surface of the organ; in reality the c. cardiacum is subdivided into lobes by fine lamellae descending from the outer covering. Similar blue lamellae are seen to surround the lobes of the c. allatum of *Apis* and the c. cardiacum and c. allatum of *Sphecius*. In this insect unmistakable nerve fibres with neurosecretory material can be observed in the c. cardiacum besides the "cuticular" structures (Pl. II, fig. 8), but this was not the case in the honey-bee. As, however, the intracerebral fibres of the nervus corporis cardiaci in *Apis* show the typical appearance of blue swollen axons, it is possible that the apparent lack of neurosecretory material in the c. cardiacum of the bee only represents a temporary stage, perhaps due to age or season. The specimens sectioned were workers caught in late autumn. No doubt the neurosecretory cells and endocrine organs of the honey-bee deserve a more detailed study.

### The Corpus Allatum.

The corpora allata show a much more uniform structure in the *Hymenoptera* investigated than do the c. cardiaca. They are globular or oviform organs connected with the lower or posterior part of the c. cardiacum. They are typically solid organs, but abnormally a small cavity may occur (Pl. VI, fig. 24). The c. allatum consists of rather a restricted number of cells, which vary considerably in size. The size of the nuclei varies still more, the largest ones mostly occurring at the dorsal (anterior) end of the c. allatum. The nucleus generally encloses one big nucleolus and a number

of small granules and threads, probably chromatin. The cytoplasm in the Bouin-fixed sections looks vacuolated or reticular and stains red with the phloxin; as in most other insects the cells of the *c. allatum* do not show any morphological signs of being secretory, though such a function must be assumed to occur.

The dorsal or anterior end, nearest to the *c. cardiacum*, has a hilus, through which the *nervus corporis allati* enters the *c. allatum*. This nerve is a direct continuation of the *nervus corporis cardiaci*, of which not all the fibres end in the *c. cardiacum*, but some continue through the whole length of this organ, keeping laterally, and leave the *c. cardiacum* ventrally (or posteriorly) as the *nervus corporis allati*.

It is of some importance to decide whether neurosecretory material is transported along these nerve fibres on to the *c. allatum*. This was stated to occur in blattids and *Gryllus* by STUTINSKY (1952), and in *Bombyx* by ARVY, BOUNHIOL and GABE (1953).

In *Synagris* and *Eumenes* the existence of blue secretory material in the *nervus corporis allati* could be observed with great clearness. Transversal sections like those shown in the photographs on Pl. VI are best adapted for demonstrating the connection between the *c. cardiaca* and *allata*. The free portion of the *nervus corporis allati* is very short; the nerve winds somewhat, but perhaps this appearance is augmented by the shrinkage caused by the Bouin fixation. The segment of the nerve inside the *c. cardiacum*—as repeatedly mentioned—is conspicuous on account of the abundant neurosecretory material present in the axons. Bulbs and swellings are also seen in the axons just leaving the *c. cardiacum* (Pl. VI, fig. 24), and they continue down into the *c. allatum* (Pl. VI, fig. 22—23). In the actual sections it is seen better than in the photographs that the blue material is contained inside axons of the *nervus corporis allati*, which at intervals are dilated by the substance, although the swellings are much smaller than many seen in the *c. cardiacum*. In the *c. allatum* the nerve divides into branches which ramify between the cells, the finer branches being difficult to follow. Occasionally a few blue granules could be observed among the cells of the *c. allatum*, but on the whole the neurosecretory material somehow seems to disappear in the *c. allatum*.

In the other *Hymenoptera* studied the *c. allatum* lies so close to the *c. cardiacum* that practically no free nerve can be found between them. No secretory material was observed in the *c. allatum* of these species.

### Discussion.

The preceding description shows the existence in the *Hymenoptera* of a typical neurosecretory pathway which agrees in all essentials with the diagram set forth by B. and E. SCHARRER (1944 and later). Neurosecretory cells, localized in the *pars intercerebralis* of the brain, contain stained granules which can be traced

also in the whole course of the fibre bundle comprising the axons of these cells and innervating the corpus cardiacum.

In 1944 such an idea might seem a rather bold generalization as few insects had in fact been studied in this respect, but, as mentioned in the introduction, during the last few years a number of cases have been described which confirm the hypothesis of the Scharrers.

The material presented in this paper seems to show convincingly that such transport occurs, at least as far as stained sections can evince that an active movement takes place. The recent studies of B. SCHARRER (1952a and b) on *Leucophaea* and E. THOMSEN (1954a and b) on *Calliphora* substantiates the hypothesis experimentally, for they found that either by cutting (*Leucophaea*) or ligaturing (*Calliphora*) the nervous connection between the brain and the corpus cardiacum, could the flow of neurosecretory material be blocked. Of course the crucial proof would be the direct observation of moving particles in living nerve fibres, as made by CARLISLE (1953) in preparations of the X-organ connective of the crustaceans *Lysmata* and *Dromia*, but so far this has not been possible in insects.

The original diagram of B. and E. SCHARRER can be amended by adding that neurosecretory material also reaches the corpus allatum, as clearly seen in *Eumenes* and *Synagris*. Probably this occurs in many (perhaps all) insects, for it has been observed also in the living nervi corporis allati of the fly *Calliphora* (E. THOMSEN 1954) and in stained sections of other insects (cp. p. 17). These results suggest the possibility that the c. allatum is activated by means of neurosecretory material produced in the pars intercerebralis. The experiments of E. THOMSEN (1952) on the adult *Calliphora* have already indicated that the c. allatum is activated from the medial neurosecretory cells of the brain.

The corpus cardiacum in the *Hymenoptera*, when stained with chrome-hematoxylin-phloxin, presents a striking picture described on the preceding pages. There is no doubt that a copious amount of neurosecretory material is drained down into the c. cardiacum through the nervus corporis cardiaci. This material seems to be stored for some time in the c. cardiacum, probably still remaining inside the nerve fibres, and finally to be discharged through the surface of the organ into the blood stream. Most of the neurosecretory material collects along the medial surface of the c. cardiacum, from where it may ooze out into the aorta. Here it is at once diluted by the blood so that it is no more possible to show its presence by staining methods.

In the experiments of E. THOMSEN (1952) referred to above it was shown that the c. cardiacum could to some extent be substituted for the neurosecretory brain cells and vice versa. This can be explained by the storing of neurosecretory material in the c. cardiacum.

It is likely, however, that the c. cardiacum is not exclusively a storage organ for a substance produced in the brain. During the last few years morphological evidence has been presented that the large cells of the c. cardiacum do themselves function as secretory cells (STUTINSKY 1952, ARVY and GABE 1952). The phloxinophilic colloid

found between the cells in some of the *Hymenoptera* is perhaps a secretory product of the cells, but so far the possibility cannot be excluded that this substance is also produced by neurosecretory cells of the brain and transported down into the c. cardiacum.

The physiological role of the small cells of the c. cardiacum is unknown. As already mentioned, they have often been spoken of as glia cells, but this designation does not convey much information about their real significance.

The concept of the structure of the c. cardiacum commonly held for some years was introduced by PFLUGFELDER (1937) and further elaborated by CAZAL (1948). According to these authors the c. cardiacum consists of chromophile and chromophobe cells. The chromophile cells—corresponding to our large cells—were described by CAZAL as provided with pseudopodia-like prolongations, often ramified and of considerable length, and besides he found so-called “formations chromophiles”, closely resembling the prolongations, but not connected with cells.

There is hardly any doubt that the osmic acid impregnation used has led to a misconception of the structure. The “prolongements chromophiles” and the “formations chromophiles” are in all probability the same elements, viz. nerve fibres more or less dilated by neurosecretory material which forms local swellings and bulbs. In the *Hymenoptera* it is clear that there is no connection between these structures and the cells of the c. cardiacum, and no prolongations of the cells were ever observed. STUTINSKY (1952) and ARVY and GABE (1952a and b) came to a similar conclusion. Thus, although the c. cardiaca may have originated as ganglia (HANSTRÖM 1940), it seems that in present-day insects the cells have no axons or other processes and thus lack the typical characteristic of nerve cells.<sup>1</sup>

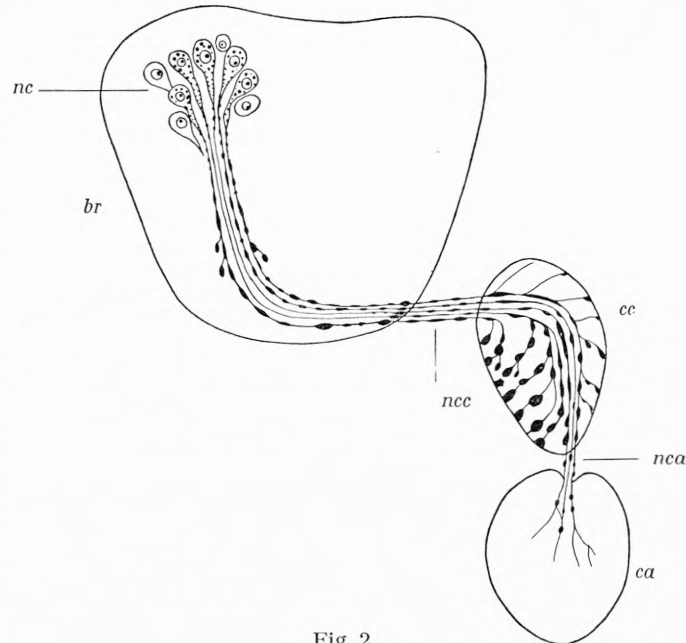


Fig. 2.  
Diagram of the neurosecretory pathway in the *Hymenoptera*.  
*br* brain; *ca* corpus allatum; *cc* corpus cardiacum; *nc* neurosecretory cells; *nea* nervus corporis allati; *ncc* nervus corporis cardiaci.

<sup>1</sup> In an earlier publication (M. THOMSEN 1951) I have described “axonlike processes” from cells of the c. cardiacum of the *Ptychoptera* larva. This observation is open to the same objections as those of CAZAL, as I used the same technique, and the material ought to be reinvestigated.

The revised concept of the neurosecretory pathway according to the preceding discussion is schematically illustrated in text-figure 2, which is modelled after a figure in B. and E. SCHARRER's paper from 1944.

The secretory material included in the neurosecretory cells of various animals is generally described as granular, but sometimes cells occur which in addition contain a homogeneous colloid often staining differently (cp. B. SCHARRER 1941 and other papers). The neurosecretory cells of the *Hymenoptera* mostly contain small discrete granules which may combine into bigger aggregations; they stain blue with the hematoxylin of the Gomori stain. In two species also phloxinophilic inclusions were observed, which seem to be droplets; they are thought to represent another stage in the secretory cycle of the same material, but this has not been proved.

In the nerve fibres the same structure of the blue neurosecretory material can be demonstrated. The swellings, bulbs, etc., are not homogeneous, but, at least in the sections best fixed and stained, show a granular structure indicating that they are composed of particles. In the thinner regions of the axons the material consists of separate granules lying in a single row. In the proximal, thicker part of the axon the granules form a superficial layer.

These observations suggest that in the *Hymenoptera* the neurosecretory material is mostly in a solid state and forms discrete granules. It is possible, that such granules may occasionally be subdivided into still smaller particles, thereby assuming colloid properties, and this may be connected with the change in staining properties from blue to red (cp. CARLISLE 1953 and PASSANO 1954). S. W. SMITH regards similar minute granules in various vertebrates as "relatively dehydrated, very viscous coacervate particles," which may coalesce due to hydration so that hyaline masses are formed. This explanation only applies to the blue-stained material; the phloxinophilic inclusions sometimes present in the neurosecretory cells he provisionally regards as "qualitatively distinct from the CHP-positive type." In the *Crustacea* studied by CARLISLE and PASSANO there is good evidence that the blue and red staining material is qualitatively identical.

### Summary.

1. The neurosecretory cells and the retrocerebral endocrine organs have been studied in several species of *Hymenoptera aculeata*, in most cases on sections stained with Gomori's chrome-hematoxylin-phloxin stain.

2. The medial neurosecretory cells mostly contain dark blue granules which form aggregates of varying size. In *Belonogaster* and *Sphecius* also phloxinophilic droplets occurred.

3. The axons of the medial neurosecretory cells contain blue-stained material which in some of the species is very abundant, forming swellings, moniliform strings or lumps. The fibre bundle is very distinct in these species.

4. Lateral neurosecretory cells were not localized; the lateral root of the nervus

corporis cardiaci was only observed with certainty in *Belonogaster*, but probably occurs in the others, too.

5. The nervus corporis cardiaci contains blue axons, which continue into the corpus cardiacum, where most of them deviate from the main bundle (the "nerf basal"), tending towards the surface. Both in the free part of the nerve and inside the c. cardiacum the nerve fibres show more or less conspicuous swellings and bulbs, which in the most developed cases convincingly demonstrate the flow of abundant neurosecretory material from the brain into the c. cardiacum.

6. In several cases the c. cardiacum also contained a phloxinophilic colloid, which may be a secretion of the large cells of the c. cardiacum, although the possibility of its cerebral origin could not be excluded.

7. Some of the nerve fibres of the nervus corporis cardiaci pass through the c. cardiacum and form the short nervus corporis allati. Blue neurosecretory granules occur in the axons of this nerve, but are very rare inside the c. allatum.

8. The results of the present study are in full accordance with the diagram of B. and E. SCHARRER (1944) which can be amplified by adding that not only the corpus cardiacum, but also the c. allatum receives neurosecretory material. This substance is produced by definite cells of the brain and transported in the axons of these cells to the organs mentioned.

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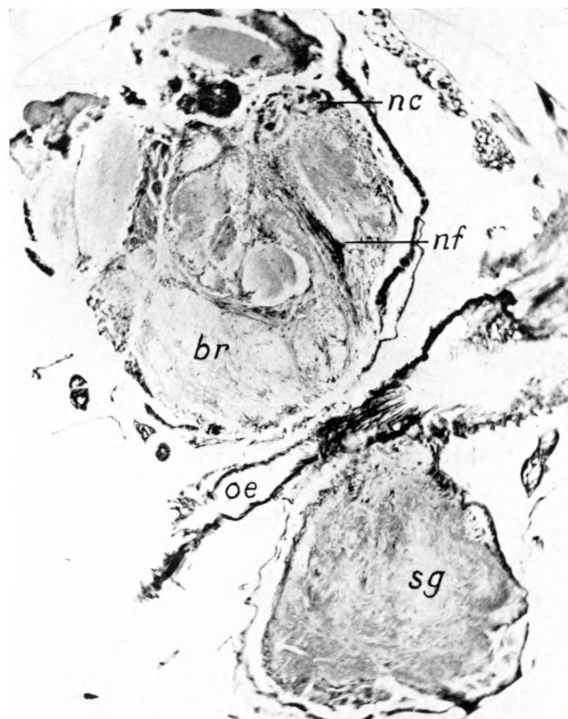
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**PLATES**

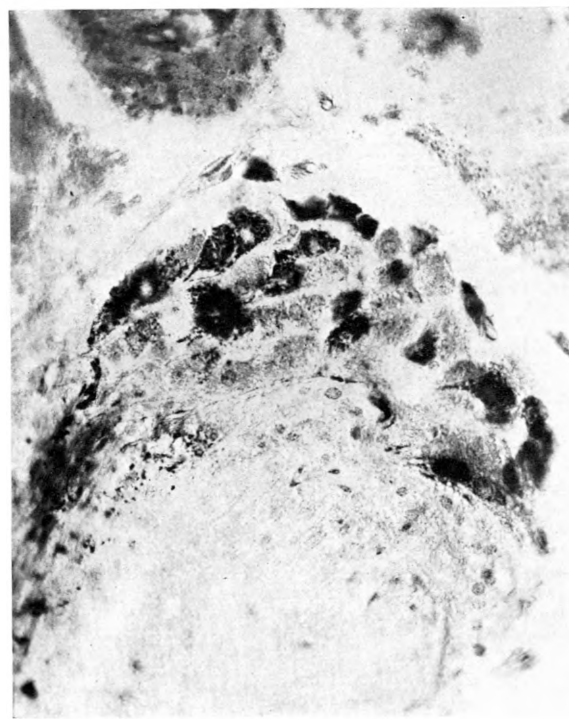
PLATE I

*Sphecius speciosus.*

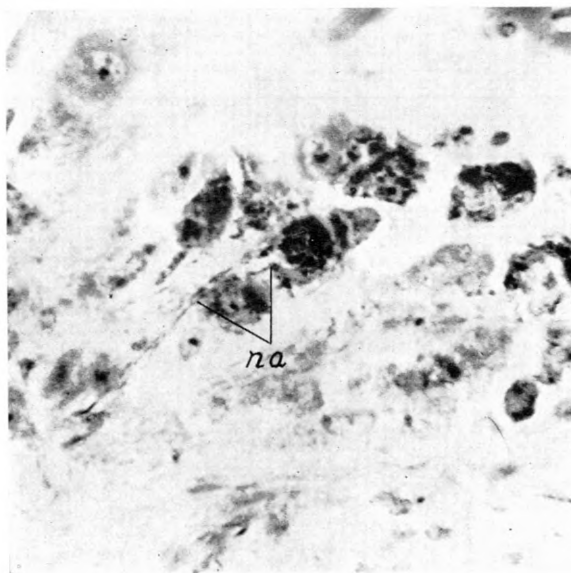
- Fig. 1. Sagittal section through brain (*br*) and suboesophageal ganglion (*sg*), anterior part to the right in the picture. *nc* group of neurosecretory cells; *nj* fibre bundle consisting of axons from neurosecretory cells containing abundant neurosecretory material, the ventral and posterior portion of the bundle not seen in this section; *oe* oesophagus; *sg* suboesophageal ganglion 60 ×.
- Fig. 2. The same group of neurosecretory cells as shown in fig. 1. Note the dark-blue granules, abundantly present in many cells, and the thin axons. Red filter. 300 ×.
- Fig. 3. Neurosecretory cells highly magnified. *na* proximal part of axon with granules at surface appearing as two rows. Other axons faintly seen. 720 ×.
- Fig. 4. Neurosecretory cells, one of them showing axon. 540 ×.



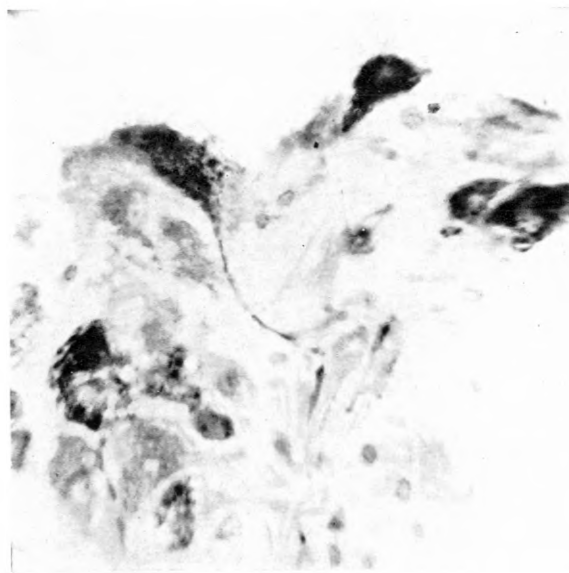
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## PLATE II

### *Sphecius speciosus.*

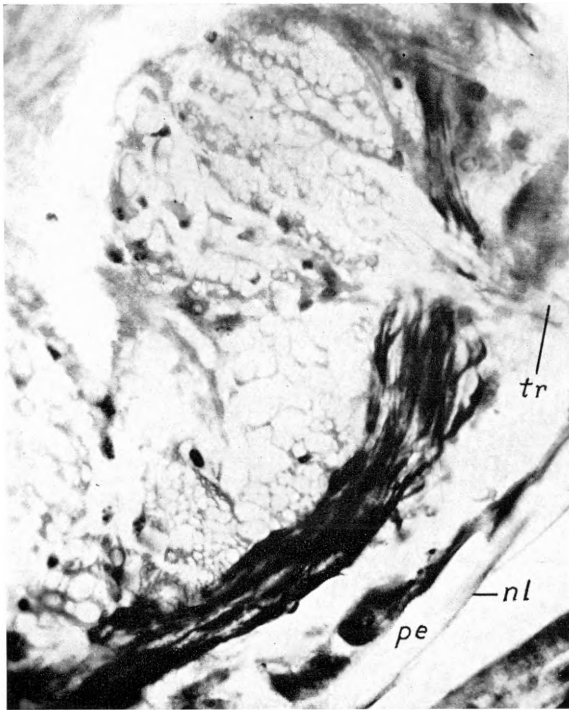
- Fig. 5. Single axon with neurosecretory material from dorsal part of brain, showing elongate swellings connected by delicate filaments. On the right other axons are visible. Red filter. 900  $\times$ .
- Fig. 6. Portion of intracerebral fibre bundle formed by the axons from the neurosecretory cells. Some axons are swollen and contain abundant blue material, others appear as fine filaments with bead-like thickenings. 500  $\times$ .
- Fig. 7. The fibre bundle, coming from above, curves backwards when approaching the ventral wall of the brain seen on the lower margin of the picture. Note the swellings of the single axons. *nl* neural lamella; *pe* perineurium cell; *tr* trachea, around which the fibre bundle bends. 500  $\times$ .
- Fig. 8. The corpus allatum (*ca*) and the corpus cardiacum (*cc*) lying behind the brain (*br*, the letters being placed in an artificial break of the section). *ncc* nervus corporis cardiaci, which is very short in this species; *sm* secretory material in highly swollen axons of the nervus corporis cardiaci just before it leaves the brain. Some few blue axons are visible in the nervus corporis cardiaci, and blue droplets in the corpus cardiacum proper. Sagittal section. 300  $\times$ .



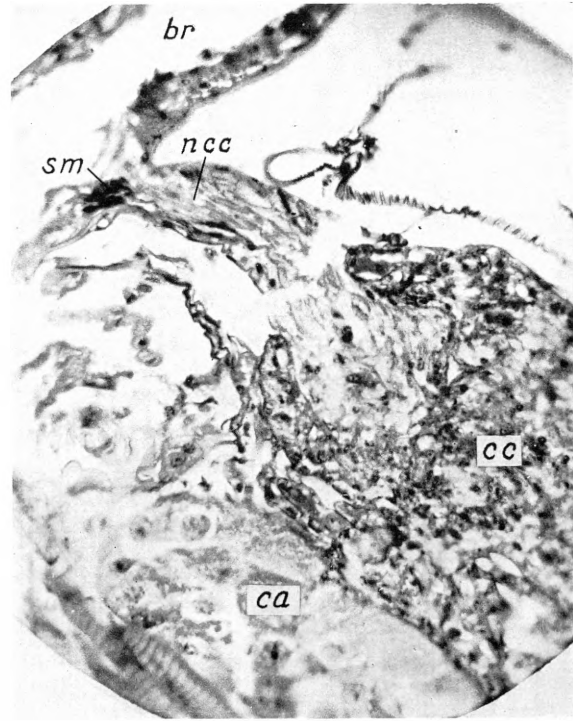
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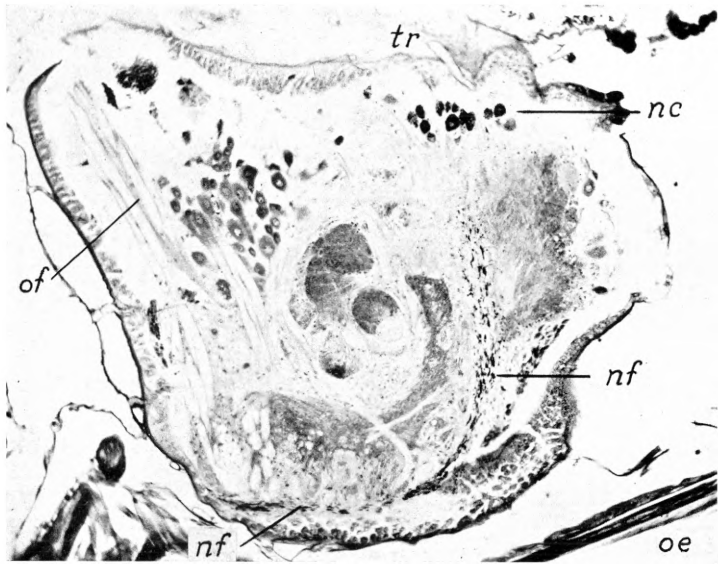
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PLATE III

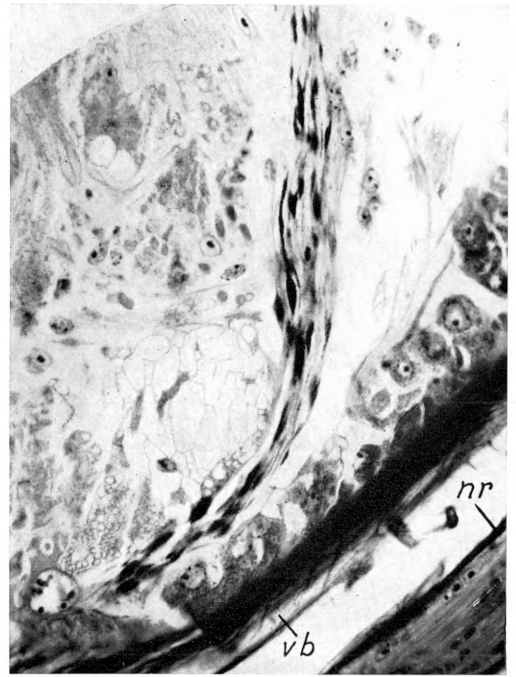
*Synagris calida.*

- Fig. 9. Sagittal section through the pars intercerebralis of the brain; anterior part on the right in the picture. *nc* group of neurosecretory cells; *nf* fibre bundle formed of axons from neurosecretory cells, containing blue material; *oe* oesophagus; *of* fibres from median ocellus; *tr* trachea entering brain. 100  $\times$ .
- Fig. 10. Portion of neurosecretory fibre bundle near ventral wall of brain, from another section of the brain shown in fig. 9. Axons with definite swellings caused by the great amount of neurosecretory material. *nr* nervus recurrens; *vb* ventral wall of brain. 540  $\times$ .
- Fig. 11. Group of neurosecretory cells from the pars intercerebralis. *nf* axons with neurosecretory material. 300  $\times$ .
- Fig. 12. Neurosecretory cells with distinct granules. 540  $\times$ .

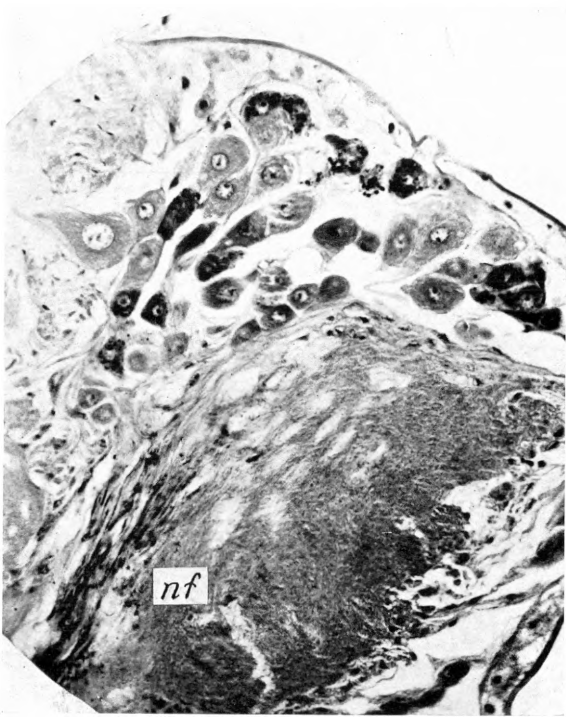




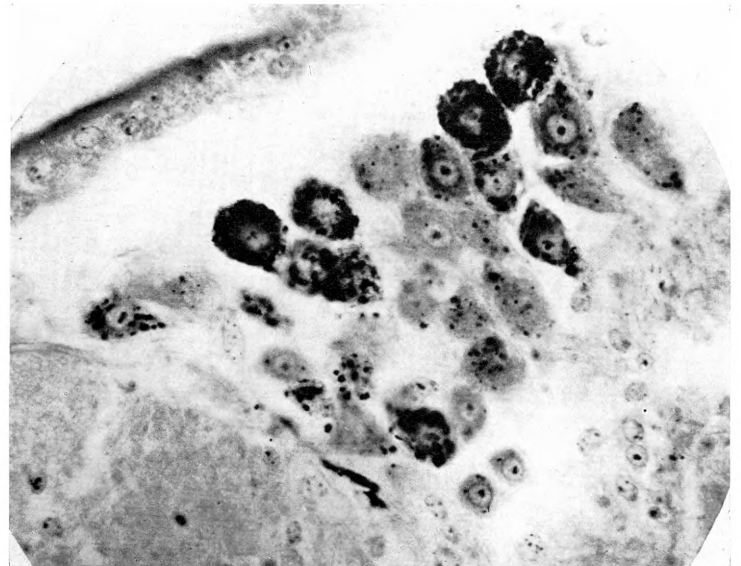
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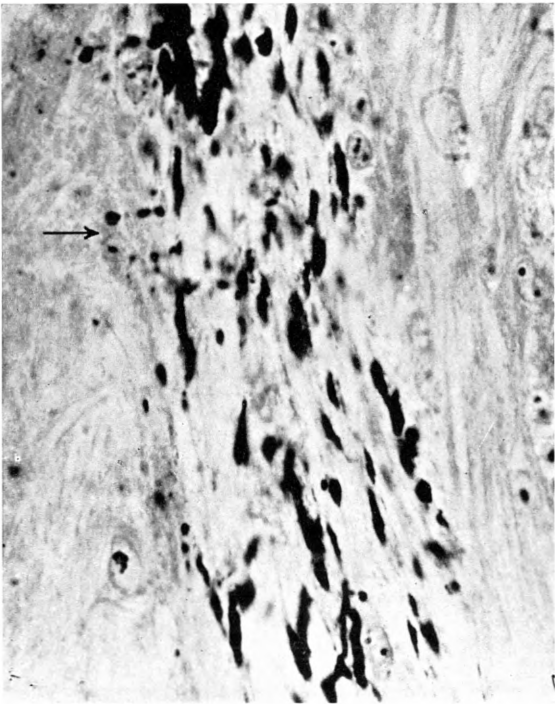


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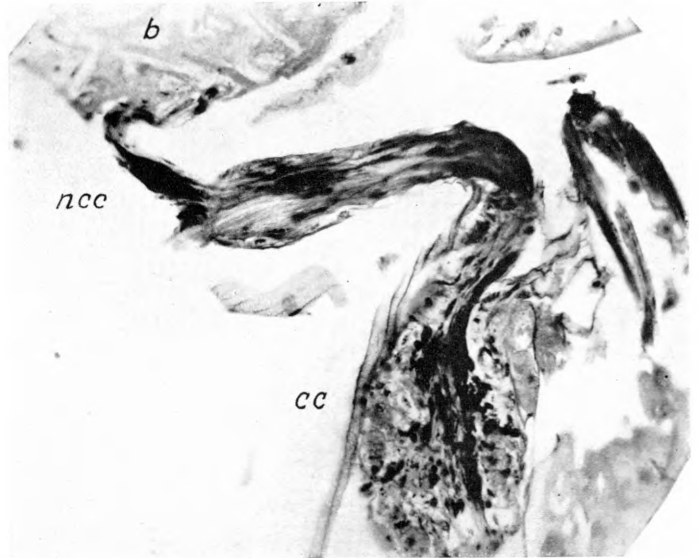
PLATE IV

*Synagris calida.*

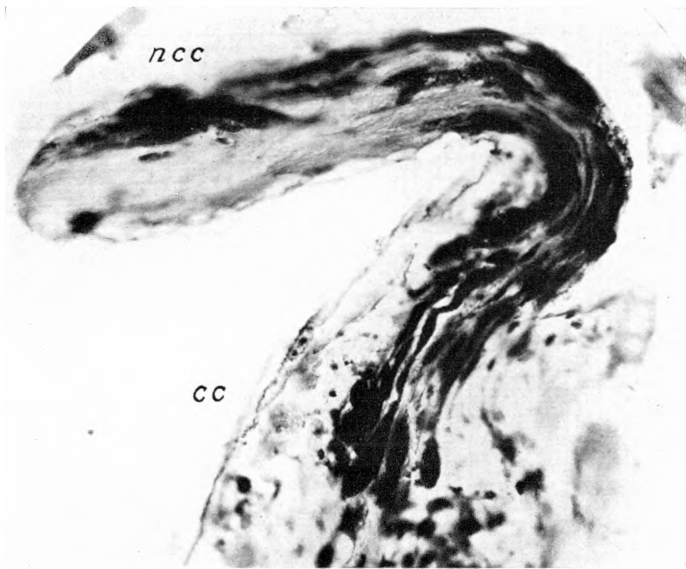
- Fig. 13. Small portion of the neurosecretory fibre bundle inside the brain, numerous axons with swellings are seen; the arrow on the left points to a moniliform fibre making a loop. 900  $\times$ .
- Fig. 14. The nervus corporis cardiaci (*ncc*) leaving the brain (*b*); the nerve has been slightly torn where the letters *ncc* are placed; *cc* corpus cardiacum. The heavily stained and swollen axons are distinctly seen. Sagittal section 300  $\times$ .
- Fig. 15. Neighbouring section at higher magnification. The axons of the nervus corporis cardiaci (*ncc*) contain a substantial quantity of neurosecretory material which is flowing down into the corpus cardiacum (*cc*). 540  $\times$ .
- Fig. 16. The second corpus cardiacum of the same specimen as shown in figs. 14—15. The axons coming from the neurosecretory brain cells form a well-defined bundle with numerous swellings and bulbs. Note also the large rounded cells of the c. cardiacum. *ncc* nervus corporis cardiaci. 300  $\times$ .



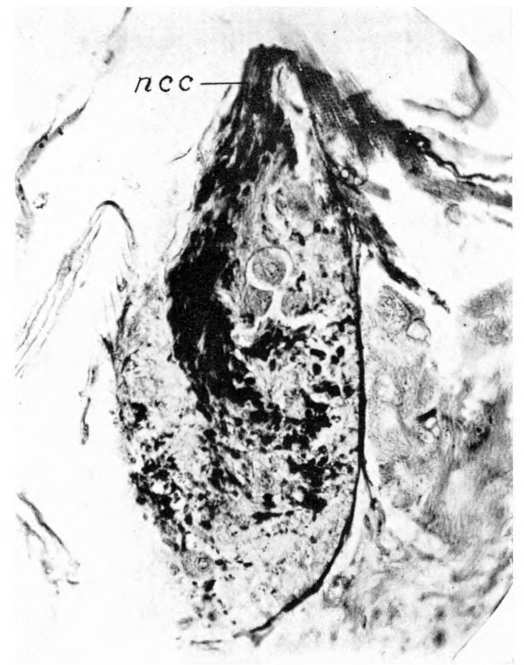
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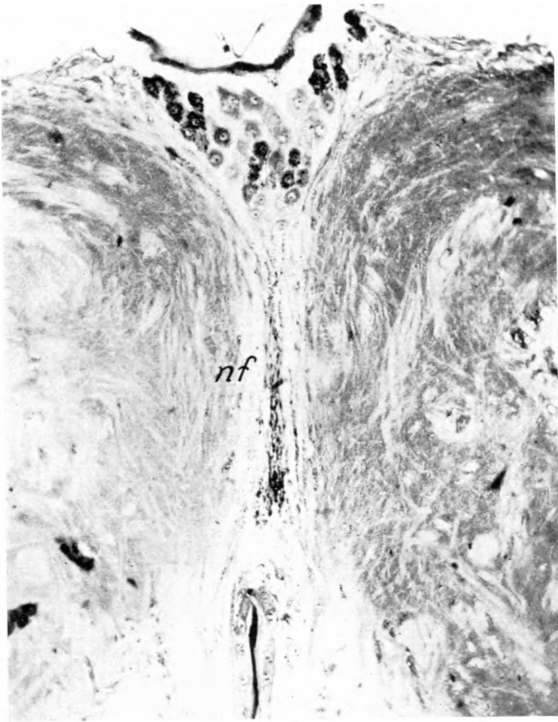


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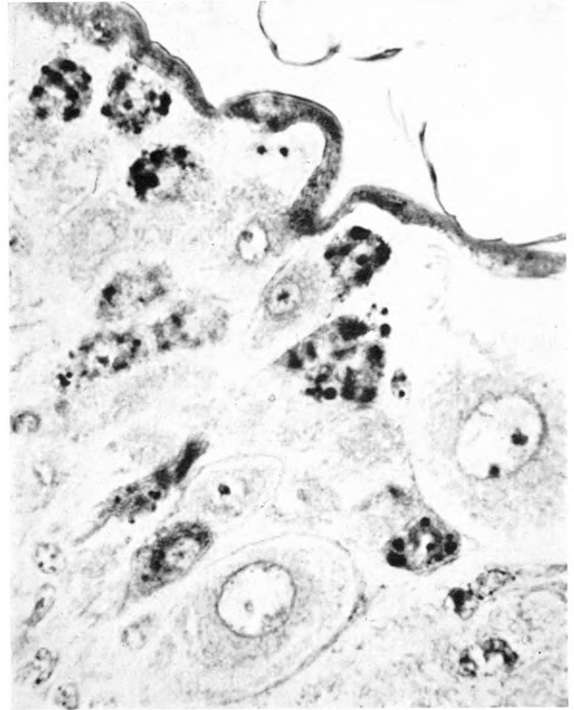
PLATE V

*Eumenes* sp.

- Fig. 17. Transversal section of brain showing dorsal part of the pars intercerebralis with the neurosecretory cells constituting one medial group; the blue stained axons (*nf*) run towards the ventral part of the brain. Section no. 86 of the series. 200  $\times$ .
- Fig. 18. Neurosecretory cells from a sagittal section of the brain. The light medium-sized cells between those with dark granules are probably phloxinophilic neurosecretory cells in another phase of secretion. Below and on the right two large nerve cells. 900  $\times$ .
- Fig. 19. Section of the corpus cardiacum with large cells in the upper and central parts and small cells at bottom. The axons of the nervus corporis cardiaci continue inside the organ near its latero-caudal side (right in picture) and fan out between the cells. Abundant neurosecretory material near antero-medial surface. 540  $\times$ .
- Fig. 20. Posterior part of corpus cardiacum with abundant neurosecretory material. In upper and central part of picture large corpus cardiacum cells and between these moniliform axons 900  $\times$ .



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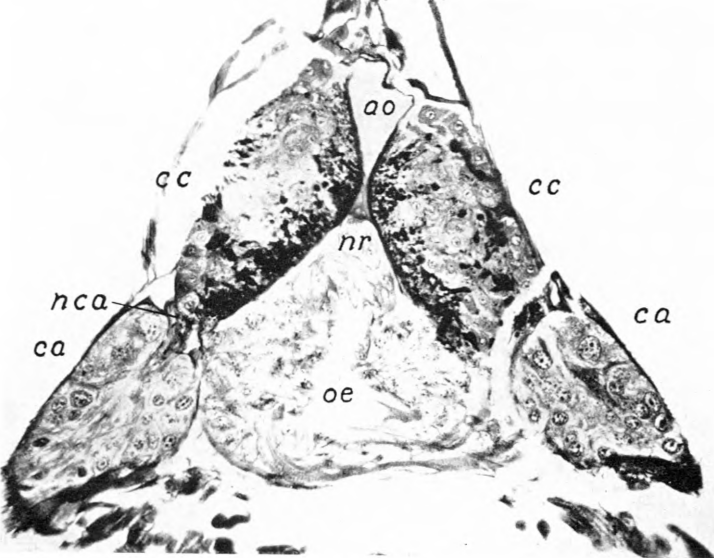


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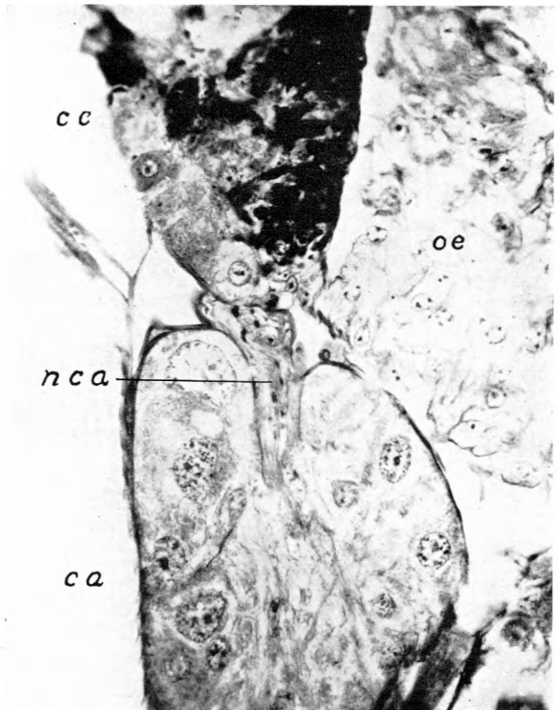
## PLATE VI

### *Eumenes* sp.

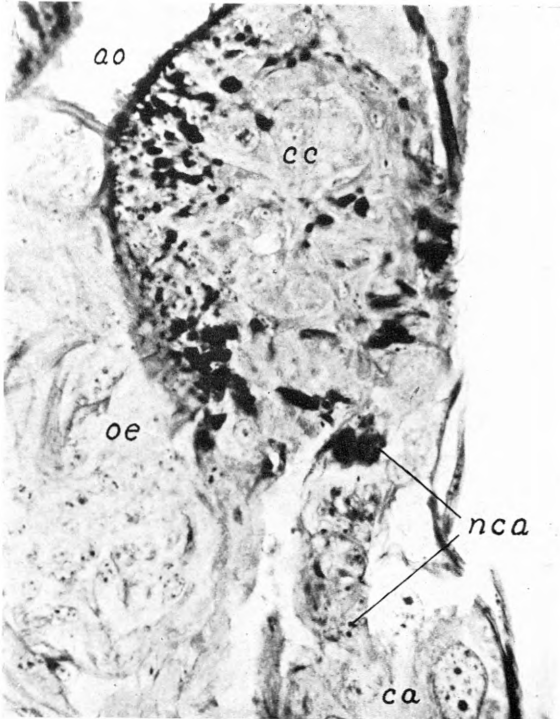
- Fig. 21. Transversal section of the retrocerebral endocrine organs (section no. 21 from the same series as fig. 17). The neurosecretory material in the corpora cardiaca is mostly collected at the mediad surface. *ao* aorta, probably the lumen has contracted somewhat due to the fixation; *ca* corpus allatum; *cc* corpus cardiacum; *nea* nervus corporis allati, only cut on the left side; *nr* nervus recurrens; *oe* oesophagus. 200  $\times$ .
- Fig. 22. Left side of the section shown in fig. 21, at higher magnification. *ca* corpus allatum; *cc* corpus cardiacum; *nea* nervus corporis allati containing blue material; *oe* oesophagus. 500  $\times$ .
- Fig. 23. The connection between the corpus cardiacum and the c. allatum on the right side. Same series, section no. 23. *ao* aorta; *ca* corpus allatum; *cc* corpus cardiacum; *nea* nervus corporis allati; *oe* oesophagus. Note the neurosecretory material in the nervus corporis allati. 500  $\times$ .
- Fig. 24. Section no. 19 of the same series. *fb* the fibre bundle inside the corpus cardiacum which continues as the nervus corporis allati (cp. fig. 22). Other letters as in preceding figures. 540  $\times$ .



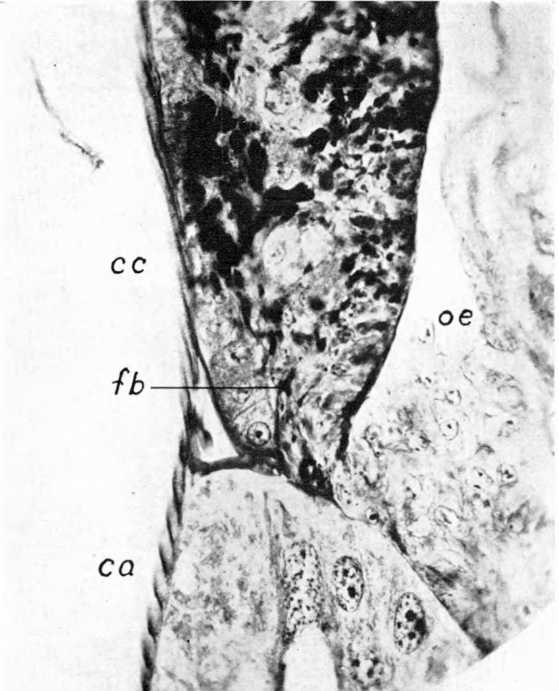
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PLATE VII

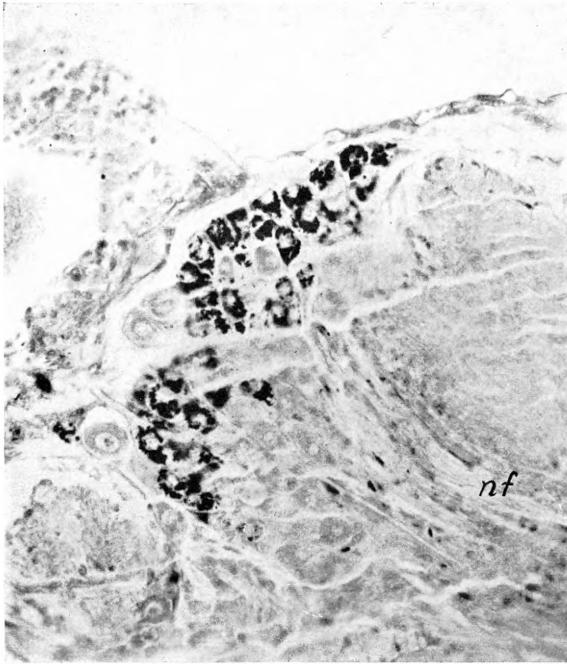
*Vespa vulgaris.*

- Fig. 25. Neurosecretory cells from the pars intercerebralis; sagittal section. *nf* axons. A few tracheae are visible. 300  $\times$ .
- Fig. 26. The connection between the brain and the corpus cardiacum (*cc*); sagittal section. *na* blue stained axon in c. cardiacum; *sb* collection of blue and red secretory substance in the brain; *sc* blue axons and red colloid in the c. cardiacum. The blue parts appear black in the photograph, the red ones grey. 500  $\times$ .

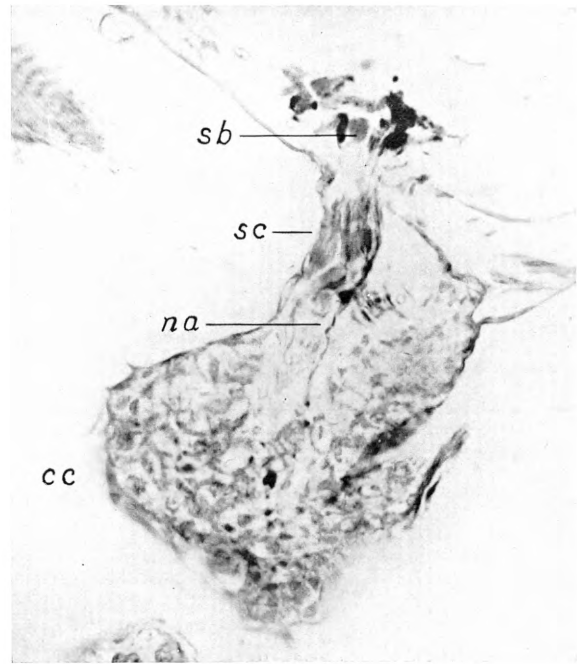
*Megachile cincta.*

- Fig. 27. Transversal section of the brain showing the group of neurosecretory cells (below *nc*). *cp* corpus pedunculatum (calix internus); *nf* crossing axons from the neurosecretory cells. 200  $\times$ .
- Fig. 28. Transversal section of the retrocerebral endocrine organs of another specimen. *ao* aorta; *ca* corpus allatum; *cc* corpus cardiacum; *ha* hypocerebral ganglion; *mu* muscles; *ncc* nervus corporis cardiaci; *oe* oesophagus; *vc* ventral bridge connecting the two corpora cardiaca. 200  $\times$ .

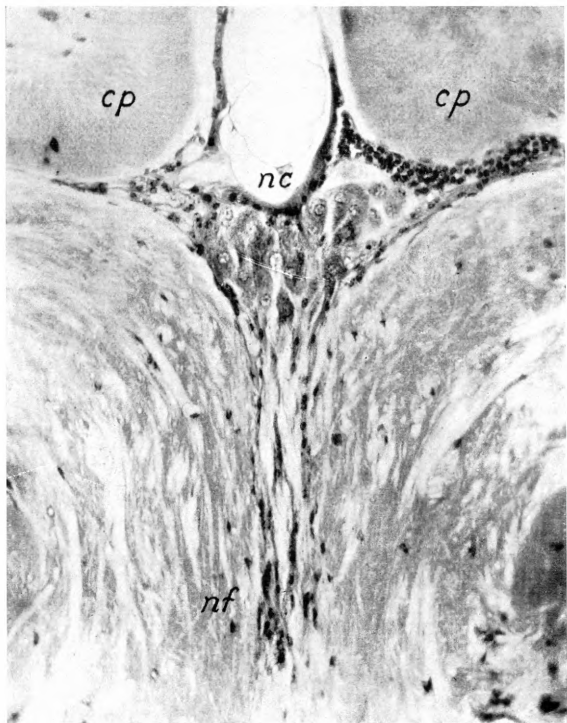




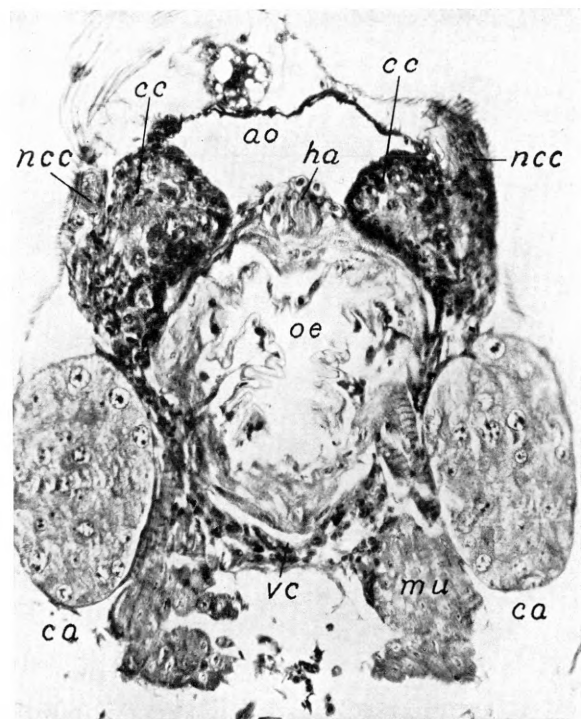
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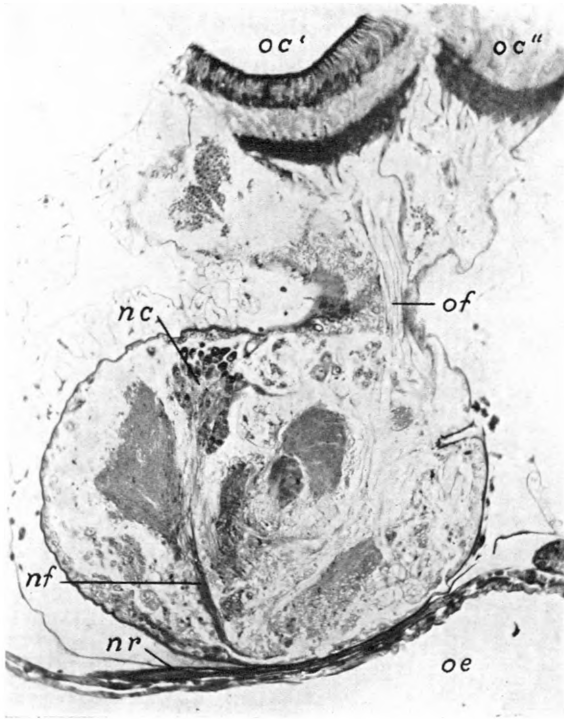


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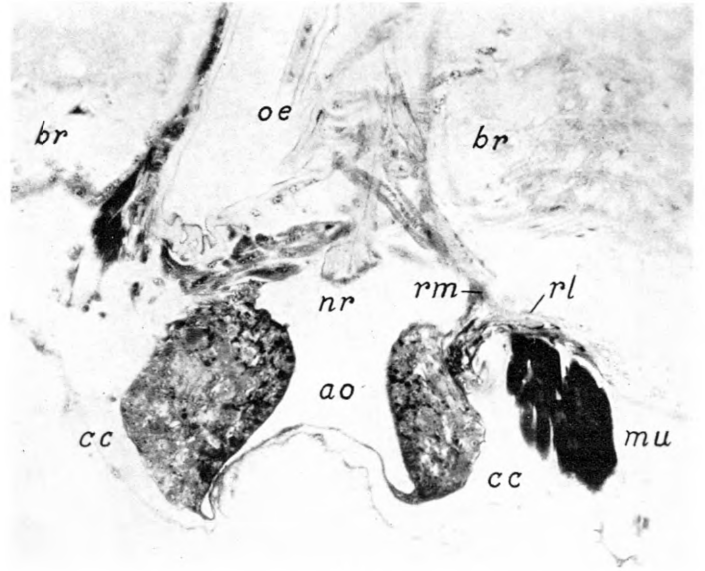
## PLATE VIII

### *Belonogaster junceus.*

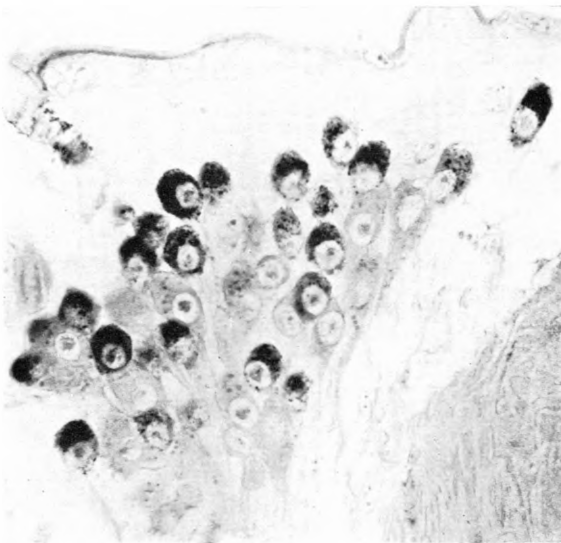
- Fig. 29. Sagittal section through the pars intercerebralis of the brain; anterior part left in picture. *nc* group of neurosecretory cells; *nj* fibre bundle constituted of the axons from these cells; *nr* nervus recurrens; *oc'* median ocellus; *oc''* lateral ocellus; *oe* oesophagus; *of* nerve fibres from ocellus. 100 ×.
- Fig. 30. Obliquely horizontal section through the postero-ventral part of the brain (*br*). *ao* aorta; *cc* corpus cardiacum; *mu* muscle; *nr* nervus recurrens; *oe* oesophagus; *rl* lateral root of nervus corporis cardiaci; *rm* medial root of same. 200 ×.
- Fig. 31. Group of neurosecretory cells from the pars intercerebralis, sagittal section. Smaller cells with blue granules (black in the photograph), and larger cells with red spherules (grey in the photograph), cp. the text p. 10. Red filter. 500 ×.
- Fig. 32. Part of same group highly magnified. The red spherules are best seen in cells marked with arrows. The blue granules mostly form cap-like accumulations above the nuclei. Red filter. 1000 ×.



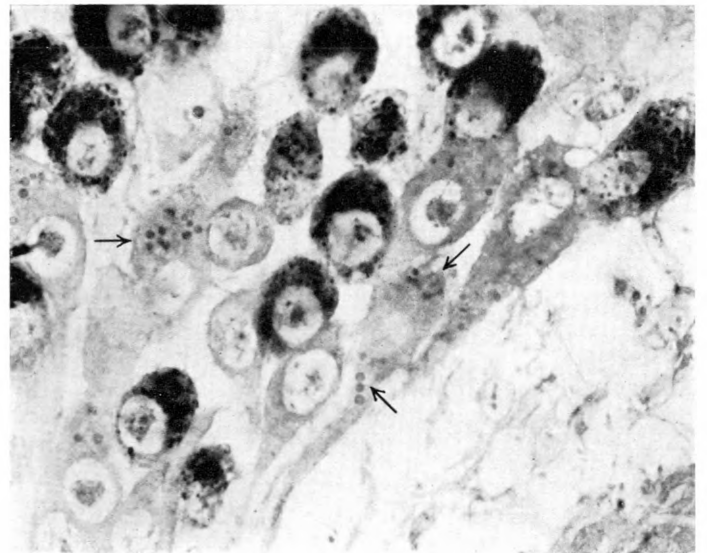
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