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THE CEPHALIC NERVOUS SYSTEM
OF THE CENTIPEDE ARENOPHILUS
BIPUNCTICEPS (WOOD) (CHILOPODA,
GEOPHILOMORPHA, GEOPHILIDAE)

(WITH FIVE PLATES)

By

MICHAEL A. LORENZO

Woodstock College
Woodstock, Md.



(PUBLICATION 4425)



CITY OF WASHINGTON
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THE CEPHALIC NERVOUS SYSTEM OF THE
CENTIPEDE *ARENOPHILUS BIPUNCTICEPS*
(WOOD) (CHILOPODA, GEOPHILOMORPHA,
GEOPHILIDAE)¹

By MICHAEL A. LORENZO
Woodstock College, Woodstock, Md.

(WITH FIVE PLATES)

I. INTRODUCTION

This paper deals primarily with the gross and microscopic anatomy of the cephalic nervous system of a geophilomorphous centipede. In contrast to the voluminous literature concerned with the neuroanatomy of other arthropods, little work has been done on the class Chilopoda, and virtually nothing is known about the order Geophilomorpha. Inasmuch as valid interpretations of phylogenetic relationships must be based on the varied studies of numerous workers, a knowledge of the neuroanatomy of this hitherto neglected group is desirable.

GENERAL CONSIDERATIONS

Centipedes are terrestrial arthropods which lead a cryptozoic existence. Nocturnal habits and dark hiding places during the day make their biotic presence unfelt. They exercise little influence on man's economy and have eluded the interest of most biologists. The chilopods, however, are regarded with reverential fear by many of the lower organisms, especially the insects. Characteristically they possess prehensors, which contain a poison gland. Unlike their myriapod kin, the millipedes, they are carnivorous and rapid runners. Predaceous even to the habit of cannibalism, centipedes are capable of inflicting fatal "bites," and some mammals have succumbed to their attack. There are many exaggerated tales of their attacks on the human species. Some of the larger scolopendromorphs² of the eastern world, however, attain the formidable length of over 12 inches; and the death

¹ The research for this paper was completed at St. Louis University, St. Louis, Mo.

² *Scolopendra gigantea*.

of several human beings, indeed, has resulted from the venom injected by their poison claws. Less common is the morbidity known as chilopodiasis, which is the invasion of a sinus by a centipede.³ As a zoogeographical fact, however, western civilization is spared all but the occasional horror of seeing *Scutigera*, the common house centipede, caught by surprise running across a tile floor.

The Chilopoda are recognized as a class of the phylum Arthropoda and include only the opisthgoneate centipedes, which bear one pair of legs per segment. The progoneate millipedes, easily distinguished by the presence of two pairs of legs per segment, belong to the class Diplopoda. At one time both classes were grouped together in the Myriapoda, a term erected by Latreille in 1802, but, though still in use, it no longer has taxonomic status.

All centipedes fall into one of two classes: Notostigmophora and Pleurostigmophora (Verhoeff, 1925) or Anamorpha and Epi-morpha (Attems, 1926). The classificatory schemes of three taxonomists serve to define the position of the Geophilomorpha and will be of historical as well as systematic interest. Pocock (1902) considered the Geophilomorpha the most primitive stock and gave the following classification:

- Subclass Pleurostigma.
 - Orders:
 - Geophilomorpha.
 - Scolopendromorpha.
 - Craterostigmophora.
 - Lithobiomorpha.
- Subclass Notostigma.
 - Order Scutigermorpha.

Stressing the importance of an embryological character not known to Pocock, Verhoeff (1925) further refined the classification by erecting two superorders in the Pleurostigmophora. His scheme is inverted to reflect the primitive condition of the Scutigermorpha. The summary of his classification is as follows:

- Subclass Notostigmophora.
 - Order Scutigermorpha.
- Subclass Pleurostigmophora.
 - Superorder Anamorpha.
 - Orders:
 - Lithobiomorpha.
 - Craterostigmophora.

³ Wilson (1929) gives the history of a patient who sneezed an arthropod into his handkerchief, promptly relieving a nasal congestion of several years. The article erroneously refers to the organism as an insect, but the photograph clearly identifies it as a geophilomorph.

Subclass Epimorpha.

Orders:

Scolopendromorpha.

Geophilomorpha.

Count Carl von Attems (1926), however, makes several modifications. He does not consider the Scutigermorpha worthy of subclass rank on the basis of its gross anatomical features alone but respects the embryological evidence as justifying his division of the order into the subclasses Anamorpha and Epimorpha. He further relegates the Craterostigmophora to subordinal rank. His is the following classification:

Subclass Anamorpha.

Orders:

Scutigermorpha.

Lithobiomorpha.

Suborder Craterostigmophora.

Subclass Epimorpha.

Orders:

Scolopendromorpha.

Geophilomorpha.

The classification of Attems appears to be the more natural and is the scheme which we have adopted for our discussion in the light of the following evidence:

Anamorpha.—Postembryonic development is by hemianamorphosis—that is, the young leaves the egg with only seven fully formed trunk segments and seven pairs of legs; the eggs are laid singly by the parent female and she broods neither the eggs nor the young. The adults of both orders possess 15 pairs of ambulatory appendages. The Scutigermorpha is the only order of the class possessing compound eyes, and the external respiratory openings (stomata) are dorsally situated and unpaired. The Lithobiomorpha have simple ocelli, when visual elements are present, and the external respiratory openings (stigmata) are lateral and paired.

Epimorpha.—Postembryonic development is by epimorphosis—that is, the young animal leaves the egg with the adult complement of pedal segments and pairs of legs; the eggs are laid in groups, and the female broods both the eggs and the young. The Scolopendromorpha have either 21 or 23 pairs of walking legs, and this number is constant within the species. The antennae have at least 17 articles. The Geophilomorpha, on the other hand, possess no less than 31 pedal segments and may number as high as 183 with intraspecific variation.⁴ The antennae constantly have 14 articles.

⁴ It should be remarked that, exclusive of the prehensors, the number of pairs

The order Geophilomorpha includes 10 families and over 120 genera. Typically a long, vermiform arthropod, geophilomorphs are found under rocks, in loose soil and forest litter, under the bark and in the wood of decaying trees, and occasionally under drying dung hills. They share with their chilopod relatives the outdoor life and cryptozoic customs. The geophilomorphs have neither ocelli nor Organs of Tömösvary. The antennae are the principal sense organs of the head. The body tergites, unlike those of the other chilopod orders, are homonymous. A single pair of mandibles, first and second maxillae, comprise the mouth parts, which are in part concealed by strongly developed prehensors. With the exception of the anterior and posterior extremities of the animals, the trunk is a repetition of almost identical segments. Each body segment has its own ganglion joined to its neighboring ganglia by paired connectives. The ganglia and connectives comprise the ventral nerve cord. The alimentary canal is a long continuous tube beginning at the mouth and ending in an anal opening on the terminal body segment. A pair of Malpighian tubules empties into the hind gut. There is a single elongate testis in the male and paired seminal vesicles which communicate at the single genital opening located ventrally on the penultimate segment. The female reproductive organs are similarly an unpaired ovary, paired ducts, and a single opening situated on the penultimate segment.

Arthropod neuroanatomy.—Since the chilopod nervous system follows the pattern of that of the typical arthropod, a brief review of the structure of the brain and nerve cord will not be without profit.

The neurons, the essential cellular components of nerve tissue, are grouped together into masses called ganglia. The axons of these cells emerge from the ganglia as nerves, or course within the ganglia as fiber tracts. Other cells are present in the ganglia which are non-nervous supporting elements. These are called neuroglial cells, or simply neuroglia. The axons of invertebrates are generally considered to be nonmedullated, but there is present a submicroscopic lipoprotein sheath not unlike myelin. The central nervous system and the emerging nerves are clothed in a connective tissue covering composed of an acellular "neural lamella" and a cellular "perilemma." The two are referred to as "neurilemma."⁵

of walking legs in all centipedes is never an even count. A tentative explanation for intraspecific variation in the Geophilomorpha is that segments may be added in successive molts and that variation in pedal counts may be a function of age. (Crabill, private communication.)

⁵ The term "neurilemma" is used differently by mammalian histologists.

Typically there is a pair of ganglia for each body segment but, in most of the arthropods, the pair is fused. The ganglia are interconnected by longitudinal and transverse connectives and commissures respectively. In the higher insects the ganglia of adjacent segments are so concentrated as to be indistinguishable as individual entities. This coalescence reaches an extreme in the Diptera, where the single thoracic ganglion is in reality an amalgamation of many segmental ganglia.

Transverse sections reveal the typical ganglion as being composed of an inner core of nerve fibers, termed the neuropile, and an outer cortex of neurons. This arrangement is the reverse of that found in the vertebrate spinal cord, where the fibers are located in the cortical white matter, and the nerve cells in the medullary gray matter. Since sensory neurons are situated in the epidermis, the neurons contained within the central nervous system are either motor or internuncial in nature, and are typically unipolar. Multipolar and bipolar cells are found in the vicinity of the receptors. Within the fibrous neuropile are found varying amounts of neuroglial cells.

The central nervous system consists of a brain, or supraesophageal ganglion, the subesophageal ganglion, and the ventral nerve cord. The brain is the dorsal aggregation of nerve tissue in the cephalic capsule situated either anterior or dorsal to the esophagus, depending on the shape of the head. According to the terminology of Viallanes (1887), the brain is divided anatomically into three regions known as the protocerebrum, deutocerebrum, and tritocerebrum. The regions, however, are not always clearly defined externally. In most insects the greater portion of the protocerebrum is associated with the visual apparatus. Where eyes are absent or poorly developed, this region is reduced.⁶ The protocerebrum is further divided into protocerebral lobes and optic lobes. The second region of the brain, the deutocerebrum, innervates the antennae. For the most part, it is sensory and internuncial in function but may contain some motor elements associated with the antennal musculature. Efferent fibers may emerge from the antennal lobes independent of the sensory roots and are sometimes called accessory antennal nerves. The third region, the tritocerebrum, is represented as the ventral portion which communicates directly with the subesophageal ganglion by way of the circumesophageal connectives. It is through the tritocerebrum that the central nervous sys-

⁶ Power (1946a) has found that, although quantitative differences exist, there are no detectable qualitative architectural modifications in the brain of eyeless *Drosophila* mutants. There is no correlation between the inability to see with a qualitative hypoplasia of the central nervous system.

tem makes connection with the stomatogastric, or "sympathetic," nervous system. A pair of lateral roots emerges from the tritocerebrum and enters what appears to be the central center of the stomatogastric system, the unpaired frontal ganglion. It is from this ganglion that the median recurrent nerve emerges.

The subesophageal ganglion innervates the mouth parts and contains both motor and sensory components. There are often present in this ganglion "giant cells," which are specialized nerve cells with neurosecretory significance. The subesophageal ganglion communicates with the supraesophageal ganglion by means of the circumesophageal connectives, which circumvent the esophagus and may be notably long or almost nonexistent. In the latter case the brain appears to adjoin the subesophageal ganglion directly.

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II. REVIEW OF THE LITERATURE

Investigations of the chilopod nervous system began early in the 19th century (Treviranus, 1817; Leon-Dufour, 1824). Until methods of microtomy were introduced in the second half of that century, studies were confined to gross dissections and a few *in toto* staining procedures. The smaller species of centipedes and the Geophilomorpha were given very little attention.

Newport (1843) was the first worker to study the nervous system of a geophilomorph (*Geophilus*[†] *subterraneus* Leach). Having recognized the importance of a comparative invertebrate neurology as "an aid in resolving problems of life in higher animals," Newport studied the abdominal ganglia of three chilopod types: a lithobiid, a scolopendrid, and a geophilid. He described the pedal nerves and the manner in which they emerged from the central ganglion. More noteworthy, however, is the footnote which appeared on page 245. He remarked that in the embryo of the geophilomorph *Necrophloeophagus longicornis* (Leach)—

[†] = *Stigmatogaster subterraneus* (Leach).

at the moment of bursting its shell, the brain is composed of four double ganglia, the centers of the corresponding number of segments, which are then becoming aggregated together to form the single movable portion of the head in the perfect animal; so that the brain of the myriapod, and probably of all the higher Articulata, is in reality, composed of at least four pairs of ganglia.

This was a precocious observation, for Newport was seeing for the first time in a geophilomorph the protocerebra, deutocerebra and tritocerebra of the brain and the subesophageal ganglion located in the cephalic capsule.

Saint Remy (1887), employing the microtechniques of Dietl (1876), was the first to make an intensive investigation of the centipede brain. Two geophilomorphs, *N. longicornis* and *S. subterraneus* (Leach), were studied in addition to other centipedes, various millipedes, araneids, and insects. Illustrations made from sectioned material appear in 14 plates containing 155 figures. His work is a notable contribution to the field of comparative invertebrate neurology. Several discrepancies, however, have been discovered in his work by other investigators (Hörberg, 1931; Fahlander, 1938), who, in demonstrating inaccuracies regarding other species, have jeopardized an appreciation of the exactness of his observation on the geophil brain. In the light of some of the more recent studies, Saint Remy's treatment of the brain of *longicornis* is brief; some of his interpretations are questionable. He described, for example, a small nerve emerging inferiorly from the posterior part of the frontal lobe (see pl. 6, fig. 68) and called it the "nerf de Tömösvary." Whether he mistook this nerve for one innervating the Organ of Tömösvary—which is lacking in the Geophilomorpha—or whether he considered it a vestigial homologue of the nerve to that organ in other centipedes, could not be determined by the present author.⁸

The paper of Crabill (1951) is of interest in that it suggests a close affinity of the species *N. longicornis*, studied by both Newport and Saint Remy, and the geophil selected for this study, *Arenophilus bipuncticeps* (Wood). While examining the four type specimens on which Meinert (1886) based the new species *Geophilus huronicus*, Crabill discovered that two of the centipedes are assignable to *longicornis*, a geophil widely distributed throughout Europe, and the others to the North American *bipuncticeps*. The four were considered conspecific by Meinert.

Although other workers have studied the chilopod nervous system (Child, 1892; Adensamer, 1893; Duboscq, 1899; Haller, 1905;

⁸ It is now known that this nerve innervates the "cerebral gland" and has neurosecretory significance (Gabe, 1952).

Holmgren, 1916; Verhoeff, 1925; Hanström, 1928; Hilton, 1930; Hörberg, 1931), it was not until Kjell Fahlander (1938) had completed his doctoral dissertation that geophilomorph neuroanatomy was again treated in the literature.

In a general treatment of the anatomy of representatives of the four orders of centipedes, Fahlander devoted a large portion of his research to a detailed study of the nervous system. He described more cephalic nerves than had hitherto been reported and homologized them on the basis of an intensive study of a scutigermorph, *Thereuopoda clunifera*. The cephalic ganglia and nerves of *Lithobius forficatus*, *Scolopendra cingulata*, and the geophilomorph from Japan, *Scolioptanes*⁹ *hirsutipes*, were described and clearly illustrated. The internal histology and disposition of fiber tracts were thoroughly investigated in the scutigermorph, but the geophilomorph was given little more than gross study. Fahlander's work encountered some opposition from the late G. F. Ferris (1953), but a critical review of both papers will reveal that Ferris had misunderstood Fahlander on several crucial points. The points of disagreement will be treated in another section of this paper.

A bibliography of the microscopic anatomy of the geophilomorph brain is nonexistent. Saint Remy (1887) describes briefly the cortical structure of the three neuromeres of the subesophageal ganglion. This is the only existing work known to the present author. It is necessary, therefore, to draw from the reports of workers on other arthropods (Hörberg, 1931; Snodgrass, 1935; Scharrer, 1939, 1941; Wigglesworth, 1953; Gabe, 1952; Imms, 1957; Hess, 1958).

Since the present investigation is concerned with the geophilid *Arenophilus bipuncticeps* (Wood), a brief resumé of the taxonomy of this organism is indicated.

The genus *Arenophilus* was created by R. V. Chamberlin (1912). A year later Gunthorp (1913) reported that *A. bipuncticeps* was common in Kansas. Crabill (1955) collected specimens of this species in three counties of Missouri and in eight localities in and around St. Louis. Johnson (1952), who studied the distribution of centipedes and millipedes in Michigan, gives the following synonymy:

Arenophilus bipuncticeps (Wood), 1912

Geophilus bipuncticeps Wood, 1862, Journ. Acad. Nat. Sci. Philadelphia, vol. 5 (ser. 2), p. 45.

Geophilus latro Meinert, 1870, Naturh. Tidschr., vol. 7 (ser. 3), p. 79.

Geophilus georgianus Meinert, 1885, Proc. Amer. Philos. Soc., vol. 23, p. 219.

Arenophilus bipuncticeps Chamberlin, 1912, Canadian Ent., vol. 44, p. 66.

⁹ = *Strigamia hirsutipes*.

III. MATERIAL AND METHODS

HISTOLOGICAL PROCEDURE

Specimens assignable to *Arenophilus bipuncticeps* (Wood) were collected in the late spring and summer in the vicinity of Florissant and Bellefontaine, Mo., when these arthropods were most abundant. Most of the centipedes were found under flat rocks which had a "good bite" on the ground. Some were collected under the loose bark of felled trees. It was found expedient to kill and fix the collections in the field, or soon after capture in the laboratory. Because of their cannibalistic habits, they were placed in individual containers along with some of their immediate environment when it was necessary to keep them alive. Sensitive to sudden changes in temperature and humidity, they are not amenable to culture.

A variety of fixatives was used. Dietrich's (Kahle's), Carnoy's, Sinha's (1953), Bouin's, hot alcohol, and cupric trinitrophenol were employed with varying degrees of success. A mixture (1:1) of aqueous and alcoholic Bouin's solutions was found to give best results antecedent to silver impregnation (see Bodian, 1937). The harsher fixatives (Sinha's, Carnoy's) required narcotization and were abandoned. The modification of Bouin's fixative was neither too slow nor too drastic and was used routinely.

A graded series of ethanol mixed with increasing volumes of n-butyl alcohol (Stiles, 1934) was used for dehydration of tissue previous to paraffin imbedding. Terpeneol (oil of lilac) was employed as a clearing agent. This did not harden the cuticular material so as to complicate sectioning. To facilitate infiltration the tips of the poison claws and the distal 10 or 12 antennal articles were excised with iridectomy scissors under the dissecting microscope.

The imbedding medium was prepared by melting together nine parts of Fischer tissue mat (60°-63° C.) and one part of bayberry wax. This mixture was heated over a low flame for several hours and filtered to insure better texture and cutting quality.

Material cleared in terpeneol required about five changes of fresh infiltration medium. When the odor of lilac is no longer detectable, infiltration is complete. Although heat hardens cuticle which has been treated with the more common clearing agents (i.e., xylol, toluol, etc.), terpeneol-cleared tissue left in the oven for over eight hours did not harden appreciably. Rapid infiltration in vacuo tended to distort and collapse material and was abandoned when the advantages of terpeneol were discovered.

Serial sections were cut with a Spencer rotary microtome. Dry ice

in a plastic funnel placed above the microtome blade and object carrier was used to lower the temperature during the actual microtomy. Because of the minute size of the material, crooked ribbons were almost useless. A device was designed to prevent this nuisance (Lorenzo, 1959), and it greatly improved the condition of the ribbon. Transverse, horizontal, and longitudinal sections were cut at 10 micra.

Albumenized water was used as an adhesive. One drop of Mayer's Egg Albumen was added to ten milliliters of distilled water. The water was first boiled to expel gases which might form bubbles under the sections. Because of the consistency of the imbedding medium, stretching of ribbons was kept to a minimum. The excessive adhesive was drained off, the slides were chilled briefly under dry ice, and gently blotted, face down, on filter paper. Drying was continued on the warming table for about an hour and completed in a desiccator before staining. The slightest trace of moisture under the sections caused loss of material in the subsequent steps of deparaffinizing and hydrating. After the paraffin had been removed from the tissue, 5-minute immersion in 0.1-percent celloidin followed by a brief (no longer than 60 seconds) drying in air was employed as an added precaution against section loss.

Hansen's trioxymethatein counterstained with picrofuchsin (Richins, 1938) was found to be a good general stain. Muscle tissue stains yellow, connective tissue and neurilemma red, and nuclei dark brown.

Several silver impregnation methods were tried without success. Controlling the pH of impregnation solutions (Samuel, 1953a; Peters, 1955) gave inconsistent results with the silver nitrate method of Holmes (1943). Both chilopod and vertebrate nervous tissue was affixed to the same slide for comparison of results. While the vertebrate nerve fibers were impregnated well with this technique, the chilopod tissue was not. The protargol method of Bodian (1936) was adopted and proved most effective. Several "protargol" products, however, were erratic. The Chroma¹⁰ silver protein, manufactured especially for use in Bodian staining, produced consistent success and was used throughout the present study.

The procedure outlined by Bodian was followed with slight modifications. Best results were always obtained with gold toning in 1.0-percent aqueous gold chloride without acetic acid. In the toning procedure, best contrast was given when slides were kept in 0.25-percent aqueous oxalic acid four times longer than in gold chloride. The time ratio, therefore, of gold chloride to oxalic acid was 1:4. Fifteen sec-

¹⁰ The registered trade mark for the West German products originally known as "Gruebler" stains.

onds in gold chloride and one minute in oxalic acid produced optimum results. Cresyl violet (0.25-percent aqueous) was used as a counter-stain after toning for demonstrating the neuronal cytoplasm. The microtechnical schedules found most effective are given as follows:

Paraffin method.

1. Kill and fix in modified Bouin's no longer than 12 hours, no less than 8. Decapitate and remove antennae, tips of poison claws.
2. Wash in several changes of 50-percent ethanol for 1 hour.
3. Dehydrate in ethanol/*n*-butyl series, combined as follows:

<i>Ethanol</i>	<i>n-butyl</i>		
(a) 25 ml. of 50 percent	4 ml.	1½ hr.	
(b) 20 ml. of 70 percent	6 ml.	1 hr.	
(c) 17 ml. of 80 percent	9 ml.	2 hrs.	
(d) 11 ml. of 95 percent	14 ml.	2½ hrs.	
(e) 6 ml. of 95 percent	19 ml.	6 hrs.	(2 changes)
(f)	25 ml.	6 hrs.	(no longer)

4. Complete dehydration and clearing in terpeneol, at least overnight. (Several days are not injurious.)
5. Infiltrate with paraffin-bayberry wax (9:1) in oven at 59°C. about five changes, or until the odor of lilac disappears, in the course of about 6 hours. (Material left longer does not harden appreciably.)
6. Block in paper boats, orient specimen quickly and cool; harden in cooled water.
7. Block is trimmed, squared after being affixed to wooden carrier, and sectioned at 10 micra.
8. Serial sections placed on clean slides, flooded with albumenized water, and placed on warming table (47°C.). Ribbons are stretched only if necessary.
9. Drain off excess fluid (much of the picric acid will be removed from tissue at this stage!); reorient ribbons; chill slide under dry ice for about a minute and blot gently, face down, on filter paper.
10. Continue drying on warming table; complete in desiccator for several hours before deparaffinizing.
11. To eliminate section loss, place slides in 0.1-percent celloidin in ether-alcohol (1:1) for 5 minutes after the second alcohol rinse in the deparaffinizing series.
12. Remove slides from celloidin solution, drain, and dry in air no longer than 1 minute; continue hydration as usual, omitting 95 percent alcohol.

Hansen's iron trioxihematein.

1. Steps 1 to 12, above.
2. Hansen's hematein, 3 minutes.
3. Wash in water, 10 minutes.
4. Aqueous picrofuchsin (10-percent acid fuchsin, aqueous: picric acid, saturated aqueous: distilled water (23:77:77)—no longer than 10 seconds.
5. Dehydrate rapidly, clear in xylol, and mount.

Silver impregnation procedure (Bodian's, modified).

Precautions: *All glassware must be scrupulously clean.* (Soak all glassware overnight in detergent, rinse in distilled water just before use.) *Use only chloride-free distilled water.* (Drop small crystal of AgNO_3 in sample of water. If precipitate forms, water is unfit for use.) *Use bone or plastic forceps only.* (Avoid use of any metal instruments or containers whatsoever.)

1. Steps 1 to 12 above.
2. Hydrate slides in at least four changes of distilled water for about $\frac{1}{2}$ hour.
3. Place slides in 1.0-percent silver protein solution, prepared as follows:
 - (a) Into 100 ml. of distilled water, place about 15 grams of metallic copper, which has been thoroughly washed in 70-percent alcohol (10 changes) and in distilled water (12 changes); and spread evenly on bottom of staining dish.
 - (b) Sprinkle 1 gm. of "silver protein, strong, highest purity for Bodian staining"¹¹ onto surface of water. (Do not stir while powder is on surface; let it dissolve without agitation.)
 - (c) Place slides gently into staining dish, cover and place in total darkness in incubator (37°C.) for 19 hours.
4. Remove staining dish from incubator, wash slides quickly in distilled water, rubbing debris from slides with finger.
5. Develop in the following reducing solution, made up fresh immediately before use, for 10 minutes:

¹¹ Catalogue No. M 773 p.

Hydroquinone	1.0 gm.
Sodium sulfite	5.0 gm.
Distilled water	100.0 ml.

6. Rinse slides (2-4 changes) in distilled water several minutes.
7. Gold tone immediately as follows:
 - (a) 1.0-percent gold chloride (*without* acetic acid), 15 seconds.
 - (b) Rinse briefly in distilled water, several dips.
 - (c) 0.25-percent oxalic acid, 60 seconds.
 - (d) Rinse in distilled water, about 30 seconds.
 - (e) 5-percent thiosulfate, 5 minutes.

(The gold chloride may be used repeatedly for about 100 slides; the oxalic acid and sodium thio-sulfate solutions should be made up fresh before use.)

8. Wash thoroughly in at least 12 changes of distilled water over a period of 1 hour.
9. Counterstain in 0.25-percent aqueous cresyl violet (Coleman and Bell Co.) for 6 minutes at 57°C. (Just before use add 15 ml. of 10-percent acetic acid to every 90 ml. of solution, heat gently and filter.)
10. Rinse in several changes of distilled water, dehydrate rapidly, clear in xylol, and mount.

RECONSTRUCTION TECHNIQUES

During the preparation of the microscopic material care was taken to avoid distortion of the internal structures. Efforts were made to orient the tissue blocks so that nearly perfect transverse, longitudinal, and horizontal sections were obtained. A dissecting microscope was often employed to orient the centipede heads in melted paraffin, since the cephalic capsule is about 1 mm. in length.

Photography of the stained sections greatly facilitated a study of each serial section and aided in the interpretation of relationships. All photographs were taken with a single lens reflex, 35-mm. Exakta camera and a compound microscope with apochromatic objectives. An illuminator with a ribbon filament, 6-volt tungsten lamp was employed. A green filter was used to increase contrast in the silver preparations. Panatomic-X film developed in FR X-22 was used, and enlargements were printed on F-4 Kodabromide paper developed in Kodak Dektol (1:2).

A number of adjacent photographed sections seen at a glance could be evaluated and examined without the distractions accompanying mechanical manipulation of the microscope. The finer details were, of course, checked and filled in from a direct observation of the microscopic preparations under the microscope. A stage micrometer, photographed at the same time and under the same conditions as the sections, afforded a method of accurate measurement, regardless of the enlargement factor. Occasionally tracings were made directly from the photographic enlargements using transillumination. Rapid sketches could be made with little effort and provided handy work sheets of structure outline. The photographic negatives furnished a permanent record of the series, and additional prints could be made when necessary.

Graphical reconstructions were also made directly from the microscopic material. By means of a microprojection apparatus, the dorsal, ventral, and sagittal views of the brain of *bipuncticeps* were thus constructed (figs. 1, 2, 3). With the aid of a stage micrometer, the apparatus was adjusted so that the diameter of the sections corresponded to the known thickness (10 micra) of the sections. Each division on the graph paper used (10 divisions to the linear inch) was made equivalent to 10 micra. Equal magnification of each section, the most important condition for accurate reconstruction, was thus insured. The reconstruction procedure was as follows: The image of a section was projected onto the graph paper. Pencil dots marked the limits of the anatomical entities which were to be reconstructed. The adjacent section was then brought into position, and dots were made on the next line of the graph paper. Additional sections were plotted until the entity being reconstructed was completely delimited. The dots were then connected by continuous lines, and the resulting outline was shaded for perspective effects in accordance with the observed contours in the microscopic sections. The bilateral symmetry of the brain exhibited in the transverse sections facilitated the selection of a reference point in each section. Alignment of reference points on a center guideline drawn on the graph paper insured accurate reconstruction. Only one aspect, obviously, can be reconstructed at a time.

IV. OBSERVATIONS

GROSS ANATOMY OF THE CEPHALIC NERVOUS SYSTEM

The cephalic nervous system of *bipuncticeps* is a small mass divided into an anterior supraesophageal and a posterior subesophageal

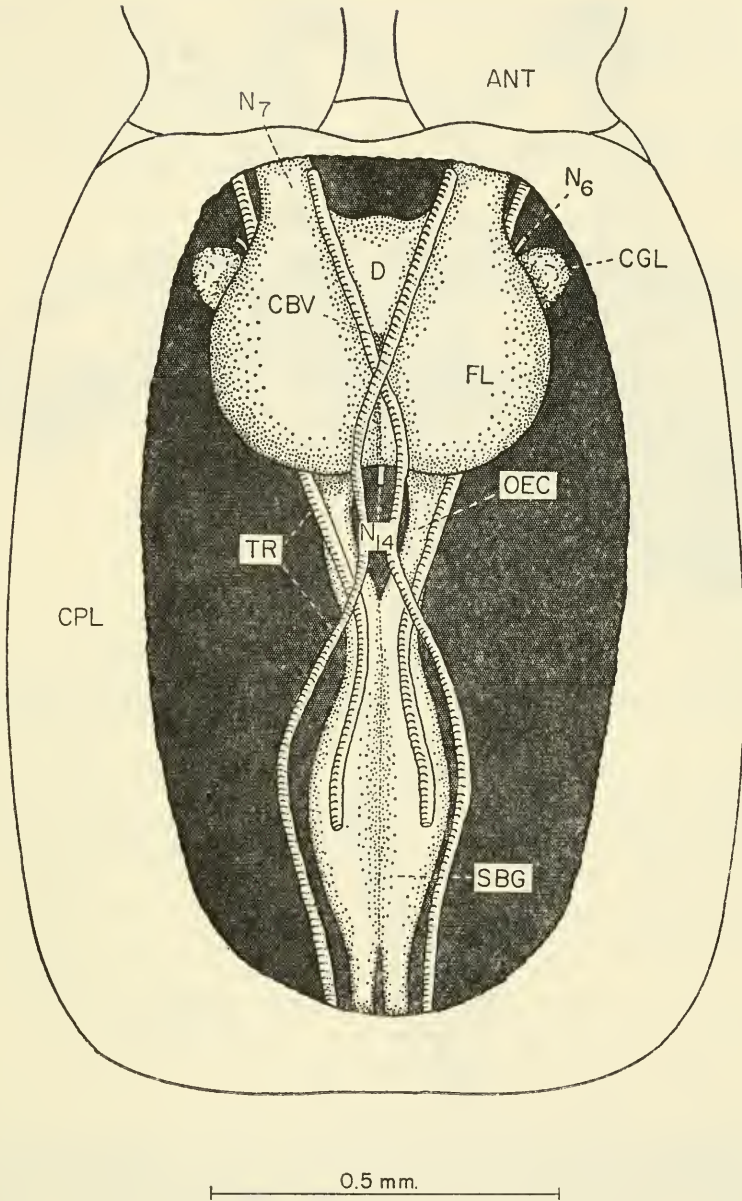


FIG. 1.—*Arenophilus bipuncticeps* (Wood), dorsal view of the head with part of the cephalic plate removed showing the cephalic nervous system. Note the position of the cerebral glands (CGL) and the cerebral haemolymph vessel (CBV). The latter is indicated by shading as emerging anterior to the crossed tracheae (TR), which served as reference points in the reconstruction procedure. (Graphically reconstructed from transverse serial sections.)

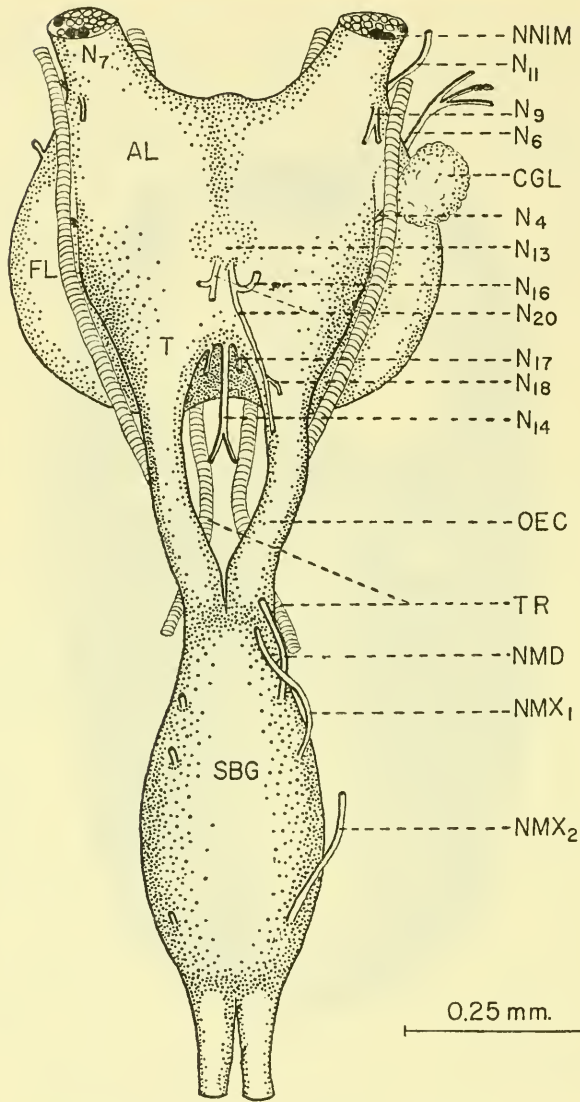


FIG. 2.—*Arenophilus bipuncticeps* (Wood), ventral view of the cephalic nervous system. The majority of cephalic nerves emerge from the brain and subesophageal ganglion ventrally. The three nerve fiber bundles in N₇ represented in section innervate the intrinsic antennary musculature (NNIM). See also plate I, inset, and text for explanation. (Graphically reconstructed from transverse serial sections.)

ganglion. Cordlike circumesophageal connectives join the two ganglia, and both ganglia are located within the cephalic capsule (fig. 1). The

posterior ganglion is more ventrally situated than the anterior one. The esophagus passes between them and is bounded laterally by the circumesophageal connectives, which run in an anterodorsal-posteroventral direction (fig. 3).

Viewed from the dorsal aspect the supraesophageal ganglion is relatively simple and almost circular. Transversely it is slightly wider

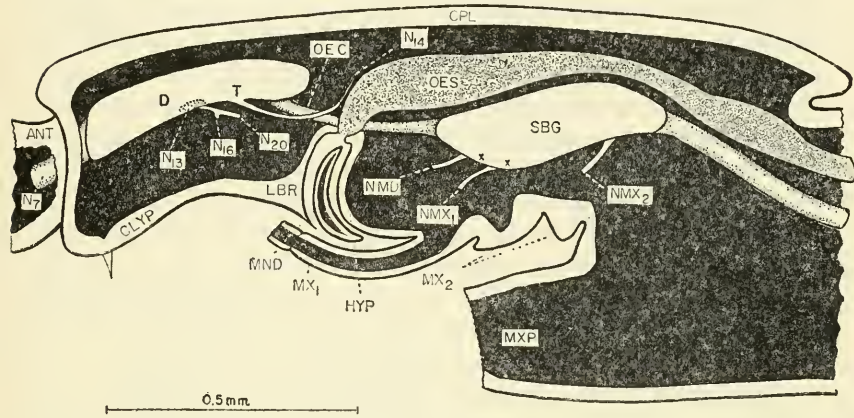


FIG. 3.—*Arenophilus bipuncticeps* (Wood), sagittal view of the head, showing the cephalic neural mass in relation to the exoskeletal structures and the esophagus (OES). The position of the two pairs of giant cells located in the subesophageal ganglion (SBG) is indicated by x's.

than it is long by a ratio of 9:7. The lateral and posterior borders are rounded in a smooth arc. The antennal nerves emerge anteriorly and are more widely separated than the posterior circumesophageal connectives. In the median plane a depression is seen anterior to the crossed dorsal tracheae (fig. 1). This is the exit of a canalicular structure, the "cerebral artery," which courses in an oblique posteroventral direction (see fig. 5, B, and pls. 3 and 4).

The most striking feature on the ventral surface of the supraesophageal ganglion is a pair of circumesophageal connectives. These are continuous with the tritocerebrum which is poorly developed (fig. 2). The cerebral gland is laterally situated and projects beyond the lateral margin of the frontal lobe. A small nerve (N_4) innervates this gland (fig. 2). A larger nerve (N_6) emerges from the frontal lobe adjacent to the cranial border of the gland. The median recurrent nerve (N_{14}) emerges between the tritocerebral lobes and is closely associated with several other small nerves. These are described in the following section.

The subesophageal ganglion is an elongate mass located ventral to

the esophagus and overlying the roots of the mouth parts (fig. 3). The anterior margin of this ganglion is continuous with the circumesophageal connectives. It is located at a point where imaginary transverse and sagittal midlines intersect on the dorsum of the cephalic plate (fig. 1). Nerves innervating the mandibles and maxillae emerge lateroventrally (fig. 2).

It is conventional (following the terminology of Viallanes, 1887) to divide the supraesophageal ganglion into three portions: protocerebrum, deutocerebrum, and tritocerebrum. Since these neuromeres are fused into a single mass in the brain of *bipuncticeps*, it is impossible to delimit their extent in whole mounts. The protocerebrum is poorly developed as contrasted with the brains of higher chilopods. In centipedes with well-developed eyes, i.e., the Scutigermorpha and some of the Lithobiomorpha, this region is large and distinctly delimited from the underlying deutocerebrum and tritocerebrum (fig. 4, A and B). A typical arthropod protocerebrum, however, is not present in the Geophilomorpha (fig. 4, D). It is represented only by the frontal lobes. The term "protocerebrum," nevertheless, will be employed to refer to the posterodorsal portion of the brain.

The deutocerebrum constitutes the major bulk of the brain of *bipuncticeps*. The two antennary lobes are distinctly separated in the brains of the other orders of centipedes (fig. 4, A, B, C) but in the geophilomorphs are fused at the midline (fig. 4, D). The deutocerebrum is mainly sensory and associational in function, as indicated by its connection with the antennae, but several motor nerves to the antennal musculature emerge from this region.

The poorly developed tritocerebral lobes begin as a fused central mass anteriorly but diverge at their posterior extensions as continuations of the circumesophageal connectives. The median recurrent nerve emerges between these two pyriform lobes and is flanked on either side by two smaller nerves which innervate the labrum (fig. 2, N₁₄). No free tritocerebral commissure was observed in this species.

CEPHALIC NERVES

The sites where the cephalic nerves emerge from the central neural mass were observed, but it was not always possible to trace the fibers to their terminations. The delicacy of the fibers, the thickness of the sections, and the varying degree of staining intensity of the surrounding tissue obscure the terminal endings. They seem to end in more than one structure. In a coordination center as complex as the cephalic nervous system this is not surprising. Rather than attempt

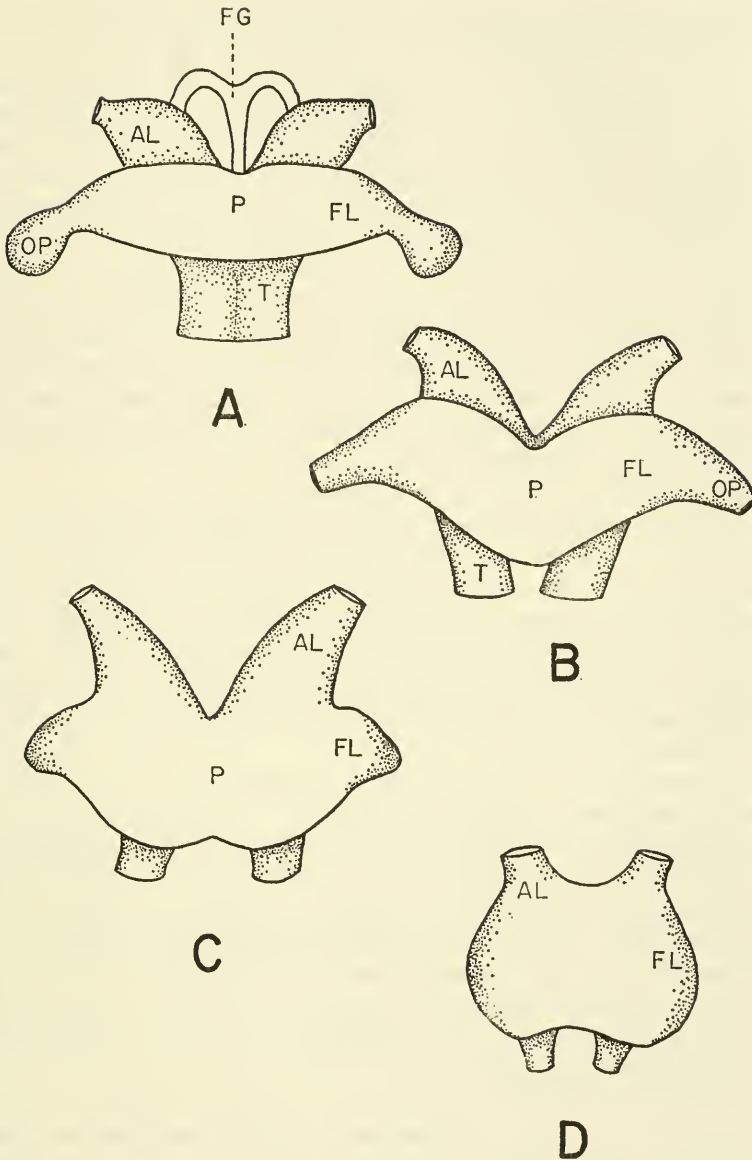


FIG. 4.—Schematic illustration, dorsal aspects, of the brains representative of the four orders of the class Chilopoda. A, The scutigermorph brain. The optic lobes (OP) and the frontal ganglion (FG) are well developed. B, The lithobiomorph brain. C, The scolopendromorph brain. D, The brain of *Arenophilus bipuncticeps* (Wood), representative of the geophilomorph. The protocerebrum is represented only by the frontal lobes (FL). (A, B, C, modified, after Fahlander, 1938.)

to develop a new terminology for the cephalic nerves of *bipuncticeps*, the numerical designations of Fahlander (1938) are used.

1. *Nerves of the protocerebrum*.—The nerve to the cerebral gland, N_4 , is present in *bipuncticeps*. This nerve emerges from the ventral surface of the brain as a minute filament. It is concealed by a trachea and a haemolymph vessel which are associated with the cerebral gland (fig. 2, and pl. 2, fig. 2.) The cells of origin of this nerve are located in the dorsal cortex of the frontal lobe. According to Scharrer (1941) and Gabe (1952), these cells are neurosecretory in other genera. The cytoplasm contains round granules which have a marked affinity for the acid dyes; acid fuchsin stains these granules a deep red (Gabe, 1952). In *bipuncticeps*, however, these cells show no such granules when stained with picric acid and acid fuchsin. Some pink granules were demonstrated in the tissue of the cerebral gland but not in the neuronal cytoplasm.

Arenophilus bipuncticeps is devoid of eyes and the Organ of Tömösvary. The optic nerve (N_1) and the nerve to the Organ of Tömösvary (N_3) are, therefore, absent. A small sensory nerve (N_2) to the dorsal integument of the cephalic plate, which was described by Fahlander (1938) in the Scutigermorpha and Lithobiomorpha, was not observed. A nerve, called *nerf viscéral pair* by Saint Remy (1887) and reported to be deutocerebral in *Necrophloeophagus longicornis*, was not demonstrated in the present study and did not appear in Fahlander's material.

A sensory nerve enters the lateral portion of the frontal lobe and will be considered tentatively as protocerebral until its homology can be established. The fibers originate from the neurons peripherally situated in the lateral clypeus. Two or three distinct branches merge into a single nerve which enters the central neural mass (fig. 2, N_6). In the scutigermorph this nerve enters the brain dorsomedially at a groove dividing the protocerebrum from the deutocerebrum. In lithobiomorphs and scolopendromorphs, it enters the frontal lobe proximal to the optic nerves. Fahlander, nevertheless, classified N_6 as a deutocerebral nerve.

2. *Nerves of the deutocerebrum*.—The largest cephalic nerve in *bipuncticeps* is N_7 , the antennal nerve. At its base there are from 15 to 18 bundles of fibers separated from one another by connective tissue (fig. 2). Three of these bundles may be traced to a group of neurons located in the ventromedial portion of the antennal lobes about 60 micra posterior to the anterior limit of the brain (pl. 2, fig. 2). Two of these fiber bundles are ventral in position, and one is lateral (pl. 1, inset). Since the distal articles of the antennae were

removed to facilitate infiltration, the fibers were not traced beyond the proximal articles. The fibers are probably motor since they are noticeably thicker and more heavily stained than those of the adjacent bundles, and they seem to originate from the nucleus which also gives origin to the fibers of N_9 . Thus they probably innervate the intrinsic antennary musculature. The remaining bundles of fibers in N_7 stain less intensely and are undoubtedly sensory to the antennae.

Two nerves, N_9 and N_{11} , innervate the extrinsic musculature of the antennae (fig. 2). This musculature is divided into a ventral and dorsal group which insert on the proximal articles of the antennae. The muscles originate on the cephalic plate and the tentorium. The ventral antennary muscles are innervated by N_9 which emerges from the ventrolateral surface of the brain medial to the large trachea (fig. 2) and about 60 micra posterior to the anterior limit of the brain. The nerve sends fibers anteriorly to terminate in finer branches in the ventral antennary musculature. The nucleus of origin of N_9 is adjacent to the group of neurons which are associated with the intrinsic antennary motor nerve (pl. 2, fig. 2).

In *bipuncticeps*, only one nerve, N_{11} innervates the dorsal musculature (fig. 2). It emerges from the lateral surface of the antennal lobes. N_{10} , which is a branch of N_{11} in *Strigamia hirsutipes* (see Fahlander, 1938, p. 89), was not observed. The fibers of N_{11} do not continue into the antennae with fibers of N_7 but are clothed in their own neurilemma.

3. *Nerves of the tritocerebrum.*—The tritocerebral lobes and the stomatogastric bridge are continuous with the antennal lobes anteriorly and the circumesophageal connectives posteriorly in *bipuncticeps*. The only vestige of an unpaired frontal ganglion is a mass of fibers and a few cells ventrally situated. The slight bulge which this structure makes on the ventral surface is likely to be overlooked in a gross dissection, since it is only about 50 micra in extent (fig. 2, N_{13} , pl. 3, fig. 3, STG). The stomatogastric bridge is formed from the frontal ganglion and the frontal connectives. The stomatogastric bridge represents the first anterior fibrous interconnection between the two sides of the brain. It occurs about 190 micra posterior to the anterior limit of the supraesophageal ganglion.

Fibers which contribute to the formation of N_{20} originate in the neuropile of the tritocerebrum. After this nerve emerges from the ganglionic mass, it gives rise to a branch (N_{16}) (fig. 2). This branch innervates a longitudinal group of muscles located on either side of the clypeal midline. Another branch (N_{18}) arising caudal to the first branch, proceeds laterally to terminate on each side of the anterior

portion of the oral opening. A nerve to the hypopharynx (N_{19}) described in *S. hirsutipes* by Fahlander was not observed in *bipuncticeps*. Neither did N_{20} exchange fibers with its fellow of the opposite side. A free tritocerebral commissure, therefore, does not appear in *bipuncticeps*.

The unpaired recurrent nerve N_{14} , emerges 50 micra caudal to the roots of N_{20} . The recurrent nerve is dorsal to and runs between the *levator pharyngis* muscles which insert on the pharynx (pl. 4, figs. 1-3). On each side of this nerve the labral nerve, N_{17} , is observed. These three nerves and a pair of tracheoles emerge simultaneously from the ventral surface and form a "sort of tuft." This expression was used by Saint Remy (1887) in describing the same site in *Necrophloeophagus longicornis*. The recurrent nerve continues caudad for about 100 micra and bends sharply dorsad onto the esophagus (fig. 3). The nerve then branches into two nerves on the dorsal surface of the esophagus. They were not traced beyond the point of bifurcation.

4. *Nerves of the subesophageal ganglion.*—Three pairs of nerves emerge from the lateroventral aspect of the subesophageal ganglion. The mandibular nerve (fig. 2, NMD) emerges anteriorly. It is closely followed by the nerve to the first maxilla (NMX_1). The nerve to the second maxilla (NMX_2) emerges from the ganglion posteriorly. In *bipuncticeps* the nerves to the first and to the second maxillae are widely separated. The three nerves are sensory to the receptors and motor to the intrinsic muscles of the mouth parts.

HISTOLOGY OF THE CEPHALIC NERVOUS SYSTEM

The histology of the nervous system of *bipuncticeps* is typically arthropod in appearance. The ganglia and the nerves outside of the ganglia are covered with a connective tissue sheath called neurilemma. The neurilemma of the ganglia was previously thought to have the same construction as that enveloping the peripheral nerves and connectives. Recent studies, however, reveal that the nerves have a connective tissue layer and a Schwann cell layer, while the ganglia have a thicker connective tissue layer, a perilemmal cellular layer, and neuroglial cells (Hess, 1958).

1. *Neurilemma and neuroglia.*—The neurilemma is composed of an outer homogeneous covering called the neural lamella, and an inner cellular layer called the perilemma. This neurilemma may vary in thickness within the same species. In *bipuncticeps* the ventral surface of the brain has a thicker neurilemma than the dorsal surface. It may vary from about 2 to 8 micra in thickness.

The neural lamella stains bright pink with picrofuchsin. There are no cells present in this homogeneous sheath. In sections which are distorted it is seen to consist of several laminae. The cells in the underlying layer are thought to produce the neural lamella.

The cells of the perilemma are differentiated in silver and cresyl violet preparations. At least three nuclear types are distinguishable on the basis of shape and staining properties (pl. 5, fig. 1). One type (*a*) of nucleus is almost spherical. It is almost opaque and the cell has very little cytoplasm. A second type (*c*) has an oval nucleus whose chromatin stains a bluish black and is heavily distributed throughout the nucleus. A third type (*b*) stains light pink. Its chromatin is aggregated along the nuclear membrane. A clump of chromatin, probably a nucleolus, is eccentrically placed against the nuclear membrane. The third type resembles one of the neuroglial cells which occur within the cortex and neuropile in that it stains pink and has similarly distributed chromatin. The cell types found in *bipuncticeps* are similar to those described in the thoracic ganglion of *Periplaneta* (Hess, 1958).

The neuroglial nuclei are smaller than those of the neurons and stain less intensely. Two types of "glial" cells can be differentiated on the basis of their nuclear properties. Both nuclei are ellipsoidal (3×5 micra) but occasionally assume different shapes, which may be the effect of fixation or position in the ganglia. They are generally kidney shaped in the neuropile. Dark and light staining cells are present in silver and cresyl violet preparations. The dark cells have a great abundance of chromatin which is distributed in clumps and strands throughout the nucleus and which stains black. The light cells have less chromatin. This is aggregated near the nuclear membrane and stains pink. Eccentric nucleoli less than a micron in diameter are present. The two types of glial cells are represented in plate 5, figure 2.

2 *Cellular cortex*.—The brain of *bipuncticeps* consists of an outer cellular cortex and an inner fibrous core. The cortex contains the cell bodies of the neural elements, and the fibrous core, also called the neuropile, neurospongium, or, by some European authors, "punktsubstanz," contains the cell processes or nerve fibers. Routine histological stains, such as haematoxylin and eosin, trichrome stains, etc., do not reveal the precise fibrous nature of the neuropile; special silver-staining techniques are required. The cortex and neuropile exhibit a precise bilateral symmetry. Even the number and location of the nuclei reflect this symmetry.

Sensory neurons have not been demonstrated in the ganglia of

arthropods. They are located near the receptors in the epidermis. The cell bodies located in the cephalic nervous system of *bipuncticeps* fall into three categories: motor neurons, internuncial, or associational neurons, and neuroglial (supporting) cells.

The motor neurons are typically pyriform, unipolar nerve cells which are rich in cytoplasm. A moderate amount of chromatin is present in the nucleus. The single "stalk" or cell process usually projects radially inward into the neuropile. The main process gives off a collateral in the neuropile but continues uninterrupted to the effector which it innervates. The collateral makes numerous connections with the other elements in the neuropile and cortex, principally with the associational components.

The majority of cells found in the cortex of the brain are association neurons. They are usually smaller than the motor neurons, and their spherical nuclei are heavily stained in silver preparations. In certain areas of the brain, particularly in the posterior cortex, these cells are so crowded together that their nuclear membranes appear to be touching. Very little cytoplasm surrounding a dark spherical nucleus usually identifies the cell body as an associational neuron.

Typical neurosecretory neurons were not observed in the frontal lobes or in any other part of the supraesophageal ganglion with the stains employed. In the subesophageal ganglion, however, four large cells were discovered which may have neuroglandular significance. The main center of neurosecretory activity has been found to be located in this ganglion in a number of arthropods (Scharrer, 1941). In *bipuncticeps* these large cells occur 70 to 100 micra posterior to the anterior limit of this ganglion. They are ventrally situated on either side of the midsagittal plane (fig. 3 indicated by x's.).

The cells are pyriform and unipolar and have a large amount of cytoplasm. The single stalk is directed dorsad and enters the neuropile. Their dimensions are approximately 12×20 micra. The nucleus is ellipsoidal and measures 5.7×6.9 micra. A dark, spherical nucleolus about 1.5 micra in diameter is present and is eccentric in position (pl. 5, fig. 3). These cells are probably the largest found in the nervous system of *bipuncticeps* and are considered "giant cells."

In addition to the neuronal cells located in the cortex, neuroglial cells occur. These may be found in the neuropile as well as in the cortical layer. They have already been described.

An abundance of tracheoles and tracheal fibers penetrate the neural substance. These have been mentioned for two reasons: (1) They are easily mistaken for nerve fibers in some "unsuccessful" silver impregnations; (2) they are accompanied by elongate and flattened

cells (pl. 5, fig. 1) which may be confused with neuroglial or perilemmal elements. These cells adhere to the surface of the tracheoles and may be observed at the site where certain nerves (e.g., N_{14} and N_{17}) emerge from the central neural mass.

3. *The neuropile*.—The histology of the neuropile is more revealing in the present study than is that of the cortex. The three neuromeres of the brain of *bipuncticeps* are easily homologized with these entities as they are exhibited in other arthropods by a study of the neuropile. The limits and extent of the protocerebrum, deutocerebrum, and tritocerebrum are poorly outlined in gross dissections as they are extremely reduced. Silver impregnations reveal, however, that the medullary substance is arranged according to a definite pattern, and the apparent radical departure of the geophil brain from the typical arthropod plan is clarified.

The protocerebrum is identifiable by the presence of the "frontal lobes." These lobes are weak, lateral outbulgings of the neuropile (pls. 3 and 4). The deutocerebrum is represented by the antennal lobes situated anteriorly. These are two bilaterally symmetrical bodies which are separated by an area of cortical cells located in the midline for the major portion of their extent (pl. 2, fig. PI [AL]). Only a microscopical study reveals this separation. The deutocerebrum is ventral to the protocerebrum posteriorly and is continuous with the tritocerebrum and the circumesophageal connectives. Fibers interconnect each of these neuromeres and distinct fiber tracts are traceable.

In naming the fiber bundles in the brain of *bipuncticeps* we have attempted to recognize homologies with the entities previously described in other centipedes. Invention of a new terminology would be confusing and tends to overlook the significance of biological affinity. The names employed are subject to correction if additional information makes this necessary.

The fiber groups in the brain of *bipuncticeps* were carefully studied with the intention of determining probable interconnections and spatial interrelations before names were assigned. This appeared to be the only logical approach to the problem. If it be assumed that the supraesophageal ganglion of this centipede is homologous with that of *Thereuopoda*, whose tracts were studied by Fahlander, then some order can be found in the neuropile of the geophil brain.

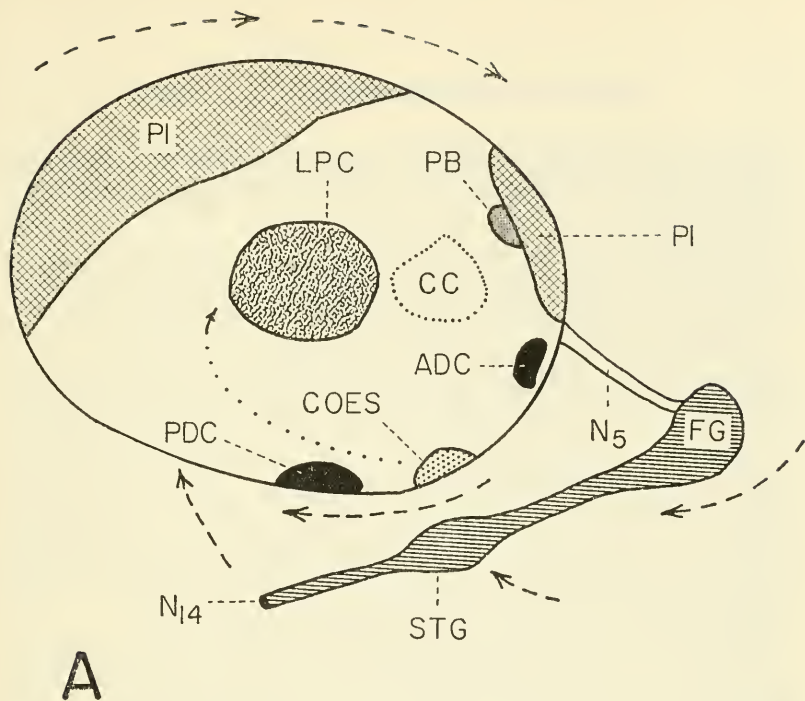
The head of the scutigermorph is roughly globose, resembling in certain respects the head of an insect; the head of *bipuncticeps*, however, is extremely compressed dorsoventrally. If one imagines the ventral portion of the brain of the scutigermorph to be shifted posteriorly and the dorsal portion anteriorly, and the relocated structures

flattened (fig. 5, A, indicated by broken arrows) the resulting brain would resemble that found in the geophil head capsule. The free frontal ganglion and the stomatogastric ganglion are now incorporated in the neural mass instead of having their own neurilemma. The antennal lobes are joined at the midline while still separated by a cellular cortex, and the protocerebrum is compressed. Figure 5, B represents a schematic sagittal section through the supraesophageal ganglion of *bipuncticeps*. Terms can now be assigned, tentatively, to the various glomerular elements in the brain of *bipuncticeps*.

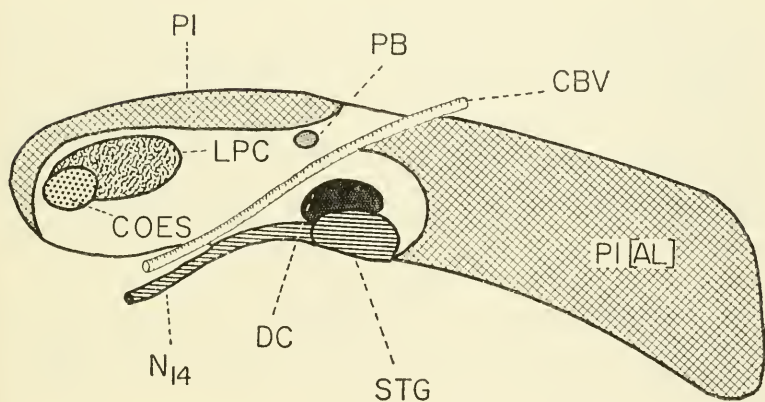
The deutocerebrum is considered first. About 60 micra posterior to the base of the antennal nerves, a marked indentation of the neuropile, approximately 40 micra in length, exists. This suggests the presence of a medial and a lateral lobe (pl. 2, fig. 3, Dl, Dm). Between these lobes courses a fibrous structure which is probably homologous to the "corpus lamellosum" (clm) found in the other three orders of chilopods. As the name suggests, this glomerulus consists of densely aggregated parallel fibers. This tract consists of fibers which run between the medial and lateral lobes in a dorsolateral-ventromedial direction. The tract bends abruptly caudad about 100 micra from the anterior margin of the brain. It continues into the circumesophageal connectives. It receives fibers from the cells of the "pars intercerebralis" (pl. 3, fig. 1). Whether the tract of the opposite side sends fibrous connections by way of the region of the stomatogastric bridge is not certain. The fibers lose optical individuality in this region and cannot be followed with precision.

A bundle of fibers in the lateral lobe of the deutocerebrum follows a path parallel to the tract just described. It assumes a position lateral to the corpus lamellosum in the circumesophageal connectives. These two pathways undoubtedly establish connections between the antennae and the subesophageal ganglion. Whether they are motor or sensory or both cannot be determined in the present study. The evidence that connections exist is indirect and is suggested by the manner in which this species "cleans" its antennae with its mouth parts.

In addition to a large glomerulus ventrally situated at the rostral limit of the antennal lobe (pl. 2, fig. 1, *glom*), two small adjacent dorsolateral glomeruli are present in the medial lobe of the deutocerebrum. These are most probably the "antennal glomeruli" described by other authors. In a brain of this size they may be easily overlooked. Saint Remy mentioned the presence of "glomerular concentrations" in *Necrophloeophagus longicornis* but gave little attention to their histology. The antennal glomeruli in *bipuncticeps* lack the scalloped appearance of the antennal glomeruli in the higher arthro-



A



B

FIG. 5.—Diagrammatic sagittal section through the brains of A, a scutigeromorph (modified, after Fahlander, p. 57, fig. 23), and B, *Arenophilus bipuncticeps* (Wood). Homologies are represented by the same shading patterns. The antennal lobes, separated in the scutigeromorph (see fig. 4, A), do not appear in section. The central complex (CC) is lacking in *bipuncticeps*. The anterior (ADC) and posterior (PDC) commissures of the deutocerebrum are not separate entities in *bipuncticeps* but represented as fused (DC). Note that the frontal ganglion and stomatogastric ganglion are separated from the central neural mass in A, and indicated only by STG in B. (See text for explanation of broken arrows.)

Pods and are not easily identified. In silver preparations the matrix of these entities is amorphous, but a few dark fibers are seen scattered throughout it.

It is generally accepted that this homogeneous ground substance is made of innumerable fine, branching, arborizing fibers interwoven and matted together, but . . . they are not visible as separate entities. (Power, 1946b, p. 488.)

Another tract associated with the glomeruli of *bipuncticeps* may be called the "olfactorio-globularis" tract. Hanström (1928) considered this to be one of the most primitive tracts in the arthropod brain having antecedents, perhaps, in the Annelida. Its presence may be expected, therefore, in the geophilomorph brain. Like so many fibers in our preparations, those associated with this tract are extremely difficult to follow. It is most probable, nevertheless, that some of the fibers cross to the opposite side by way of a small commissure located dorsoposteriorly in the protocerebrum (pl. 3, fig. 2, PB).

There are no structures in the cephalic nervous system of *bipuncticeps* which can be homologized with the "corpora pedunculata" or with the "central complex" of the scutigeromorph and higher forms. These components are well developed in the higher arthropods with compound eyes, especially the social insects (Kenyon, 1896; Thompson, 1913; Power, 1943) and are, in large part, fibrous entities. They are poorly developed in the Lithobiomorpha and Scolopendromorpha (Fahlander, 1938). In *bipuncticeps* the "pars intercerebralis" consists of a cellular cortex and occupies the greater extent of the midline between the frontal and antennal lobes. The first anterior continuity of the neuropile in the median plane occurs in the anterior half of the tritocerebrum. This however, has already been identified as the stomatogastric bridge. A diffuse array of fibers which probably represent a fusion of the anterior and posterior commissures of the deutocerebrum (fig. 5, DC=ADC+PDC) is dorsal to this bridge and slightly caudal. Fibers run, it appears, in every direction. It is highly improbable, therefore, that either of these represent vestiges (or Anlagen!) of the corpora pedunculata or central complex of the higher arthropods.

A commissure occurs between the frontal lobes about 40 micra caudal to the stomatogastric bridge. It is dorsal and posterior to the canalicular space containing the median cerebral vessel. This narrow file of fibers is considered to be the "protocerebral bridge" (pl. 3, fig. 2).

A large mass of commissural fibers is observed about 30 micra caudal to the protocerebral bridge. Its dimensions are enormous in contrast to the other commissures mentioned (pl. 4, figs. 1-3). Begin-

ning about 90 micra anterior to the caudal end of the brain this transverse file extends almost to the posterior boundary of the ganglion. Heavily stained fibers interconnect the frontal lobes, the deutocerebral lobes, and the bases of the tritocerebral lobes. Connections are also made between the circumesophageal connectives at their anterior end (pl. 4, fig. 2). This large commissure is obviously the most important association area in the brain of *bipuncticeps*. Although connections with fibers derived from the three neuromeres are made at every level, there is a pattern which can be resolved by resorting to the postulated shifting of commissures (fig. 5).

The majority of fibers which cross the large commissure in the anterior portion are derived from the lateral portion of the frontal lobes (pl. 4, fig. 1). This morphological observation identifies the anterior portion of the tract as the "large protocerebral commissure" of other authors. Fibers which are clearly derived from the deutocerebral region are seen farther caudally. These fibers arch dorsally above the cerebral vessel. Fibers from the dorsal bases of the tritocerebral lobes, where the circumesophageal connectives take origin, are located still more caudally. Arcuate fibers intercommunicate the tracts in the connectives. This has been named the "commissure of the circumesophageal connectives" (pl. 4, fig. 2, *COES*).

The position of the "commissure of the circumesophageal connectives" is the only radical displacement of commissural elements in the brain of *bipuncticeps*. The translocation of this commissure—from a position (in the scutigermorph brain) anterior and ventral to the "large protocerebral commissure" (fig. 5) to one posterior to it—is difficult to reconcile. The difficulty, however, is only spatial. The fiber interconnections which are observed in the neuropile warrant the homology.

V. DISCUSSION

THE GANGLIA

The geophilomorph has a simply organized cephalic nervous system and is the least complex of the chilopod brains. The spadelike cephalic capsule has resulted in a wide separation of the supraesophageal and subesophageal ganglia with a lengthening of the circumesophageal connectives. The connectives are longer than those found in the other chilopod orders. In the scutigermorphs and insects the two ganglia are practically one, and the esophagus courses through what appears to be a single neural mass; the connectives are short, if present at all as observable entities. In *bipuncticeps*, however, the connectives are long, thin, and cordlike. Its cephalic nervous system superficially

resembles that of the Annelida. This similarity to the annelid system was recognized about a century ago by at least two workers (Newport, 1843; Walter, 1863).

The protocerebrum is virtually lacking; only the frontal lobes exist. The absence of light receptors and of the Organ of Tömösvary results in a reduction of the size and number of neural components in this region of the brain. The deutocerebrum, on the other hand, is well developed. The majority of fibers associated with the deutocerebral lobes originate from the sensory neurons in the antennae and the associational neurons of the cortex. The tritocerebrum is extremely reduced and modified in structure, as compared with the other orders of centipedes. The frontal ganglion and its connectives and the stomatogastric ganglion in the Scutigermorpha are separated and clothed in their own neurilemma. In *bipuncticeps* these elements are incorporated into the central neural mass so as to be indiscernible. They are aggregated at the site of the "stomatogastric bridge."

THE CEPHALIC NERVES

The protocerebral nerve to the cerebral gland (N_4) is concerned with neuroglandular activity. Fahlander was the first to hint at the true nature of this nerve. It had been called "nerf de Tömösvary" (Saint Remy, 1887), "der Nerv der ursprünglich zweiten Antenne" (Haller, 1905, p. 199), and the "nerve of the frontal organ" by other authors. Holmgren (1916) followed its intraganglionic path using the methylene blue technique but considered it the "Nerv des Frontalorgans." The data given by Fahlander and the name he used, "Nerv zur Gehirndrüse," are most valid and appropriately indicate its neurosecretory nature, as supported by the work of Gabe (1952). In our material, moreover, the presence of a haemolymph vessel passing through the tissue of the cerebral gland supports the high probability that it has an endocrine function. Fahlander compared this gland with the corpora allata of insects and the X-organ of crustaceans. Gabe (1952) disagrees and claims that the histological data warrant comparison with the corpora cardiaca and the sinus gland.

Fahlander grouped N_6 , a nerve from the lateral clypeus, with the deutocerebral nerves in *Thereuopoda*, but expressed a doubt that it was. In the other orders, this nerve is clearly associated with the protocerebrum and emerges from the proximal end of the optic lobe. This nerve is considered to be protocerebral in *bipuncticeps*.

The descriptions of the motor antennal nerves of the deutocerebrum of *bipuncticeps* do not follow Fahlander's account of their arrangement in *Strigamia hirsutipes*. He did not distinguish between in-

trinsic and extrinsic antennal musculature. The motor antennal nerves in *bipuncticeps* originate from a nuclear group ventrally situated in the antennal lobes. Motor fibers were identified in N_7 and traced to the same nucleus of origin as the fibers of N_9 and N_{11} , the nerves to the extrinsic antennal musculature. Fahlander reported that N_{10} , a branch of N_{11} , innervated the dorsal musculature in *S. hirsutipes* and that N_{11} continued into the antennae with the fibers of N_7 . In *bipuncticeps* however, N_{10} is absent and N_{11} itself innervates the dorsal extrinsic musculature of the antennae. Fahlander may have mistaken the fibers of one of the intrinsic motor nerves for those of N_{11} .

No "free tritocerebral commissure" is present in *bipuncticeps*. Saint Remy (1887) was not able to demonstrate it in *Necrophloeophagus longicornis* and said that its absence is well explained by the concentration of the tritocerebral ganglion. Fahlander admitted that he did not find a continuity between N_{20} of one side and that of the opposite side but still did not "doubt that the Geophilomorpha concur in this respect with the other chilopod orders." His effort to homologize the four orders of centipedes hindered him from conceding that a free tritocerebral commissure, which he had demonstrated in the other three orders, could be absent in the geophilomorphs.

It is customary to consider a *dorsal* motor and a *ventral* sensory root in a typical arthropod ganglion (Wigglesworth, 1953). This arrangement is inverted, however, with reference to the antennal motor nerves in *bipuncticeps*. Their nuclei of origin are ventral in position. In the subesophageal ganglion efferent neurosecretory neurons are also ventral in position. Most of the neurons, in fact, are ventrally aggregated in this ganglion. Experimental studies of nerve degeneration and chromatolysis, as performed by Vowles (1955), would probably indicate that the ventral surface of the subesophageal ganglion is a motor area. It is hoped that this may be investigated in the future.

The nerves which innervate the mouth parts of *bipuncticeps* emerge from the subesophageal ganglion, and in general, agree with the arrangement in *Strigamia hirsutipes*. The nerves to the mandible, first, and second maxillae, in *S. hirsutipes*, are equidistant from one another; in *bipuncticeps* the nerves to the mandible and first maxilla are anteriorly located while the nerve to the second maxilla is considerably more posterior in position. This is probably related to the fact that the ganglion of *S. hirsutipes* is spherical while that of *bipuncticeps* is elongate. The entire cephalic capsule of *bipuncticeps* is, in fact, longer than that of *S. hirsutipes*.

CELL TYPES

The types of nerve cell bodies observed in *bipuncticeps* resemble those of other arthropods with reference to relative size and shape. The motor, associational, and neuroglial nuclei may be differentiated on the basis of size and the nuclear properties already described. The cells described by Gabe (1952) were not observed in the frontal cortex, probably because specific stains for secretory granules were not employed. In a preparation in which a contaminated metachromatic dye was accidentally used, however, some evidence of neurosecretory activity was seen, not in the cells of origin but in the tissue of the cerebral gland. This requires further investigation.

NERVE TRACTS

The difference between the glomerular entities in the neuropile of *bipuncticeps* and those of other centipedes, particularly the Scutigero-morpha, are probably due to phylogenetic modifications. Homologies undoubtedly exist. The scutigero-morph head is domed and resembles that of an insect, in that the antennae are dorsally placed and the mouth is pushed forward so that the labrum and clypeus form the front boundary of the head. In *bipuncticeps* the head is flattened dorsoventrally so that the mouth, clypeus, and labrum are ventrally located. The antennae are rostrally situated. The general configuration of the cephalic capsules accounts for many of the differences between the geophilomorph and scutigero-morph brains. The positions of the antennal lobes and tritocerebral components in the brain of *bipuncticeps* become intelligible. The reduction of the protocerebrum is related to the absence of eyes and the Organs of Tömösvary, and the absence of the corpora pedunculata and of the central complex follows logically. The other tracts may be homologized on the assumption that the shapes of the heads are correlated with a spatial displacement of fibers.

THE FAHLANDER-FERRIS CONTROVERSY

Fahlander's contribution to chilopod neuroanatomy has proved a most reliable source in this study, but a single statement found in Ferris (1953) is sufficient to jeopardize the value of the former's research. "It is not a criticism of the author of this work [Fahlander, 1938] to say that as far as the nervous system is concerned the work fails." (Ferris, 1953, p. 12.)

After World War II, G. F. Ferris began a study of the comparative

morphology of the Annulata (=annelid-arthropod complex). In a paper entitled "The Contradictions of the Insect Head," he stated:

The processes of change which have produced the millions of species, living and dead, that belong and have belonged to the super-phylum Annulata have left the central nervous system basically unaltered. A system that must have been established in the Precambrian has come down to the present time so little altered that a point-by-point correspondence may be shown to exist on even some of the smaller details throughout the vast group that has been derived from Annelid-like ancestors.

This is the fundamental significance of the facts that will be presented. (Ferris, 1947, p. 64.)

This concept is the starting point from which Henry (1947, 1948) undertook the study of the "Nervous System and the Segmentation in the Annulata," which appeared under that title in five articles. She considered the problem of segmental homology in the oligochaete annelids up through the insects. Included in her work is a brief treatment of a large gosibiid centipede, *Pseudolithobius megaloporus* (Stuxberg). She interpreted the segmentation of the chilopod head and the disposition of the cephalic nerves in the light of her investigations on the nervous systems of the Polychaeta, Onychophora, and Crustacea.

Applegarth (1952) continued the program with a study of the cephalic musculature and innervation of the same lithobiomorph. He interpreted his findings in accord with the principles outlined by Ferris (1948) and the conclusions given by Henry (1948). The bibliographies of these workers did not include Fahlander (1938) until Applegarth (1952) had completed his doctoral dissertation. In a supplementary note, he wrote:

it appears that Fahlander's paper contains numerous errors, small in themselves, but of such a nature as to preclude the development of any understanding of the relation of the muscles of the head region to the segmentation of that area. (P. 143.)

Ferris (1953) summed up the work he had initiated and defended his morphological principles. He concluded a section devoted to the Chilopoda with a bitter criticism of Fahlander's efforts. Comparison of the various areas of controversy revealed the following discrepancies:

(1) Fahlander described a short, thin, motor nerve (n_8) which innervates a part of the *levator pharyngis* muscle and which arises from the deutocerebrum. Ferris, on the other hand, said that no such nerve existed in his material. A nerve corresponding in position occurs but goes to the integument between the bases of the antennae.

Ferris failed to emphasize that Fahlander was describing the nerve as it occurs in the scutigermorph *Thereuopoda*. Fahlander made no mention of this nerve's occurrence in the other species he studied—either in the text or in the figures.

(2) Fahlander described a nerve (n_5) which originates between the protocerebrum and deutocerebrum whose destination is the frontal ganglion. Ferris denied its existence: "No such nerve appears in our material. No such nerve should be present. If the generalizations previously offered are valid no such nerve can be present." (P. 12.) Fahlander was still, however, referring to the organization of the brain of *Thereuopoda*. The nerve in question is conspicuously absent in the other three representatives he described and illustrated.

(3) Fahlander described still another nerve (N_{17}):

Die Labralnerven gehen vom Tritocerebrum gleichzeitig mit den Frontalkonnektiven ab und bilden einen Plexus praefrontalis ganz kranial in Kopf. Von dort gehen Nerven für die clypeale Muskulatur sowie die sensorischen Nerven des Labrum aus. (P. 81.)

Ferris criticized him principally on the basis of a definition of muscle origin and insertion which first appeared in Applegarth (1952, p. 132). Fahlander made no reference to origin or insertion in the clypeal musculature. It is clear, furthermore, from his own words and from the German idiom, that he was referring primarily to the *plexus praefrontalis* and not to a direct branch of the labral nerve as Ferris described it. On the contrary, Fahlander wrote, concerning *Lithobius*:

Der Frontalnerv (n_{16}), welcher unpaar ist, aber eine doppelte Wurzel besitzt, verläuft in kranialdorsaler Richtung und innerviert die Clypeusmuskulatur. Er hat *keinerlei Verbindung mit den Labralnerven* (n_{17}), die vom kaudalen Teil der Brücke abgehen und *sensorisch sind*. Ausser zum Labrum schicken die Labralnerven Äste zur lateralen Partie des Clypeus. (P. 85.) (*Italics mine.* M.A.L.)

Fahlander is beyond reproof on this point of Ferris's criticism.

(4) Fahlander described a free tritocerebral commissure in *Lithobius* (p. 86 and fig. 29). It is represented as a dorsal and ventral doublet having connections with two other nerves. Ferris, however, denied that such a commissure existed in his material. He suggested that paired stomodaeal nerves innervating the esophagus may have been mistaken for a free tritocerebral commissure. Fahlander was aware that this structure was a subject of controversy and Ferris admitted that it may be present in some species and not in others as had been shown in the insects. Both authors could be correct since they concerned themselves with different species of lithobiomorphs.

(5) Fahlander claimed that nerves proceeding from the commis-

sure in question innervate the hypopharynx. Ferris disagreed repeatedly throughout his article with Fahlander's description of hypopharyngeal innervation but added: "There are present a pair of nerves . . . corresponding in position to Fahlander's n_{20} but which innervate the muscles of the hypopharynx with a branch proceeding laterally of the mouth opening." (P. 12.) Fahlander's n_{20} is the tritocerebral commissure!

It at once becomes clear to one who has studied both articles that the interpretation given by Ferris to Fahlander's descriptions do not seem to be accurate. On the contrary, the reliability of Fahlander's work has been enhanced by the study of the points of disagreement uncovered by his antagonist.

CONCLUDING COMMENTS

The results of this paper do not allow broad speculation on the problem of chilopod evolution; general conclusions are impossible without considering all the morphological features as a whole. This research was initiated on the supposition that the nervous system of the Geophilomorpha might furnish evidence conducive to a solution of the problem of their disputed position on the chilopod tree. Some authors have considered the scutigermorph as primitive and the geophilomorph as degenerative; others have looked upon the modern centipedes as offshoots of a geophiline stock.

In the course of the study of the nervous system of *bipuncticeps*, the relevant literature was consulted and it was found that in each order of the class there is an admixture of features, some presumably conservative, others theoretically highly derivative. The presence of compound eyes in the scutigermorph, the shape of the head capsule and position of the antennae, the peculiar scape organ of the antennae—found nowhere else among the centipedes—set this order apart from the rest of the Chilopoda and closer to the higher insects. The geophilomorph, on the other hand, with its absence of eyes and of the Organs of Tömösvary, its homomerism and intraspecific variation of the number of segments, manifests a simplicity only vaguely hinted at in the Scolopendromorpha. It is indeed a difficult task to answer the question: Which of the present-day chilopod orders has the closest affinity to the primitive condition of the hypothetical "Ur-Chilopoda"?

Homomerism and high and variable number of tergites have been considered primitive characteristics; the Geophilomorpha alone approximate this condition. Heteromerism with a low and fixed number of tergites has also been called primitive; the other three orders mani-

fest these characteristics. The compound faceted eye is regarded as highly specialized by most entomologists, but some regard its presence in the scutigermorph as primitive. The absence of a visual apparatus is degenerative or primitive depending on the taxonomic scheme one favors. Anamorphosis and epimorphosis are simultaneously the primitive postembryonic state!

Are the simplicity of the geophil brain and the absence of photoconductor elements in the neuropile conservative or specialized? Fahlander's aversion to more than one parallel evolution seems to be the prime reason for his refusal to admit that the geophilomorph may represent the primitive stock of the Chilopoda. Although his argumentation is sound, it rests on an undemonstrated "principle of economy" and is undoubtedly influenced by his selection of Verhoeff's system of classification. The dismissal of difficulties of variation by attributing them to "adaptations to a modus vivendi" seems to be evading the issue. Evolutionary mechanisms are being better understood today to make that line of argument more and more tenuous. It is the author's hope that the neglected chilopods will receive more attention in the future. Only then will the existing arguments about their phylogeny be tested.

VI. SUMMARY

1. The anatomy of the cephalic nervous system of *Arenophilus bipuncticeps* (Wood) was studied. Serial sections were prepared and studied with trichrome and silver impregnation techniques. Graphical reconstructions were made to demonstrate the more gross relationships. Photographic methods aided in the interpretation of microscopic relationships.

2. The brain, or supraesophageal ganglion, is composed of a protocerebrum, a deutocerebrum, and a tritocerebrum, which may be distinguished histologically. Grossly, however, they are fused into a single mass. The brain is connected to a subesophageal ganglion by long, cordlike circumesophageal connectives. Both ganglia are composed of a cellular cortex and a fibrous core. The constituents are bilaterally symmetrical in number and position.

3. The cephalic nerves emerge from the three neuromeres of the brain and subesophageal ganglion and are homologized with those of other chilopods. A cerebral gland is associated with the frontal lobes of the protocerebrum. The nerve to the gland exhibits possible neurosecretory significance. Nerves supplying the intrinsic and extrinsic musculature of the antennae were traced to their nuclei of origin located ventrally in the deutocerebrum. The recurrent nerve

emerges from a stomatogastric bridge which is poorly developed and incorporated in the ventral portion of the brain. Other nerves emerging from the supraesophageal and subesophageal ganglia are described.

4. The neurohistology of *bipuncticeps* was studied. The cellular cortex of the ganglia contains cells whose processes turn inward to form part of the fibrous medullary neuropile. The neurilemmal elements consist of an outer homogeneous "neural lamella" and a cellular "perilemma" containing at least three types of cells. Motor neurons, associational neurons, and neuroglial cells may be differentiated on the basis of staining qualities. Four "giant" cells, possibly of a neuroglandular nature, are present in the anteroventral portion of the subesophageal ganglion.

5. Fibrous entities in the neuropile were examined and homologized. "Antennal glomeruli," the "corpus lamellosum," and "olfactorio-globularis tract" are identified. Connections between the antennal lobes and subesophageal ganglion are observed. The "corpora pedunculata" and "central complex" do not appear in *bipuncticeps*, and it is highly improbable that there exist vestiges or Anlagen of these complex elements in the geophilomorph brain. The commissures located in the median plane are homologized with the named commissures of higher chilopods.

6. The cephalic nervous system of *bipuncticeps* is simply organized and less complex than those in the other orders of the Chilopoda.

ABBREVIATIONS USED ON THE FIGURES

a,b,c, three types of perilemmal nuclei.	D, deutocerebrum.
ADC, anterior commissure of D.	DC, deutocerebral commissure.
AL, antennal lobe.	DI, Dm, lateral, medial lobe of deutocerebrum.
ANT, antenna.	exo, exoskeleton.
ax, axon of giant cell in SBG.	ff ₁ , fibers of nerve to intrinsic antennary musculature emerging from the neuropile.
bv, haemolymph vessel associated with the cerebral gland.	ff ₂ , fibers from nucleus of origin of N ₆ .
bn, black-staining neuroglial nucleus.	ff ₃ , fibers from the pars intercerebralis.
CBV, cerebral haemolymph vessel.	ff ₄ , fibers from frontal lobe in the large protocerebral commissure.
CC, central complex.	FG, frontal ganglion.
CGL, cerebral gland.	FL, frontal lobe.
clm, corpus lamellosum.	gcn, giant cell nucleus.
CLYP, clypeus.	
COES, commissure of circumesophageal connectives.	
CPL, cephalic plate.	

- g1, portion of medial buccal gland.
- glom, large antennal glomerulus.
- HYP, hypopharynx.
- LBR, labrum.
- LPC, large protocerebral commissure.
- mm, muscle fibers.
- MND, mandible.
- MX₁, first maxilla.
- MX₂, second maxilla.
- MXP, prehensor.
- N₄, nerve to cerebral gland.
- N₅, nerve from brain to frontal ganglion.
- N₆, sensory nerve to clypeus.
- N₇, antennal nerve.
- N₈, nerve to ventral extrinsic antennary musculature.
- N₁₁, nerve to dorsal extrinsic antennary musculature.
- N₁₃, stomatogastric bridge.
- N₁₄, recurrent nerve.
- N₁₆, nerve to longitudinal clypeal musculature.
- N₁₇, labral nerve.
- N₁₈, nerve to lateral portion of oral opening.
- N₂₀, nerve from which N₁₈ and N₁₉ originate.
- NMD, nerve to mandible.
- NMX₁, nerve to first maxilla.
- NMX₂, nerve to second maxilla.
- NNIM, nerve bundles to intrinsic antennary musculature.
- np, neuropile.
- OEC, circumesophageal connective.
- OES, esophagus.
- OP, optic lobe.
- P, protocerebrum.
- PB, protocerebral bridge.
- PDC, posterior commissure of D.
- PI, pars intercerebralis.
- PI[AL], PI of antennal lobe.
- pn, pink-staining neuroglial nucleus.
- SBG, subesophageal ganglion.
- sp, neurosecretory product (?) in giant cell.
- STG, stomatogastric ganglion.
- T, tritocerebrum.
- TR, trachea.
- tr, tracheole.

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EXPLANATION OF PLATES

PLATE 1

The cephalic nervous system of *Arenophilus bipuncticeps* (Wood) showing the levels at which the sections seen in the following photomicrographs were taken. *Inset*, transverse section of the right antennal nerve showing the three nerve bundles which innervate the intrinsic antennary musculature. The two ventral bundles and one dorsolateral bundle are more heavily stained and enclosed in their own neurilemma (not seen in silver preparations but verified in general trichrome stains).

PLATE 2

- FIG. 1. Transverse section through the antennal lobes, showing the fibers (ff_1) of the ventral bundle of nerves which innervate the intrinsic antennary musculature. The large antennal glomerulus (glom) is ventrally situated.
- FIG. 2. Transverse section through the antennal lobes showing the fibers (ff_2) from the nucleus of origin of N_3 (located immediately to the left of ff_2). PI[AL] is the pars intercerebralis of the fused antennal lobes.
- FIG. 3. Transverse section showing the lateral and medial lobes of the deutocerebrum (DL, Dm). The interior of the corpus lamellosum (clm) is weakly stained but can be identified by its arrangement of parallel fibers.

PLATE 3

- FIG. 1. Transverse section through the deutocerebral lobes showing the fibers (ff_3) from the cells in the pars intercerebralis (PI) entering the corpus lamellosum (clm).
- FIG. 2. Transverse section showing the narrow band of fibers of the protocerebral bridge (PB) forming a commissure dorsal to the cerebral blood vessel (CBV). The frontal lobe is dorsal and lateral to the deutocerebrum (D). The stomatogastric ganglion, ventral to the cerebral blood vessel is damaged and out of focus.
- FIG. 3. Section immediately following that illustrated in figure 2. The stomatogastric ganglion (STG) sends fibers into each of the cerebral hemispheres, intercommunicating the two halves of the deutocerebrum.

PLATE 4

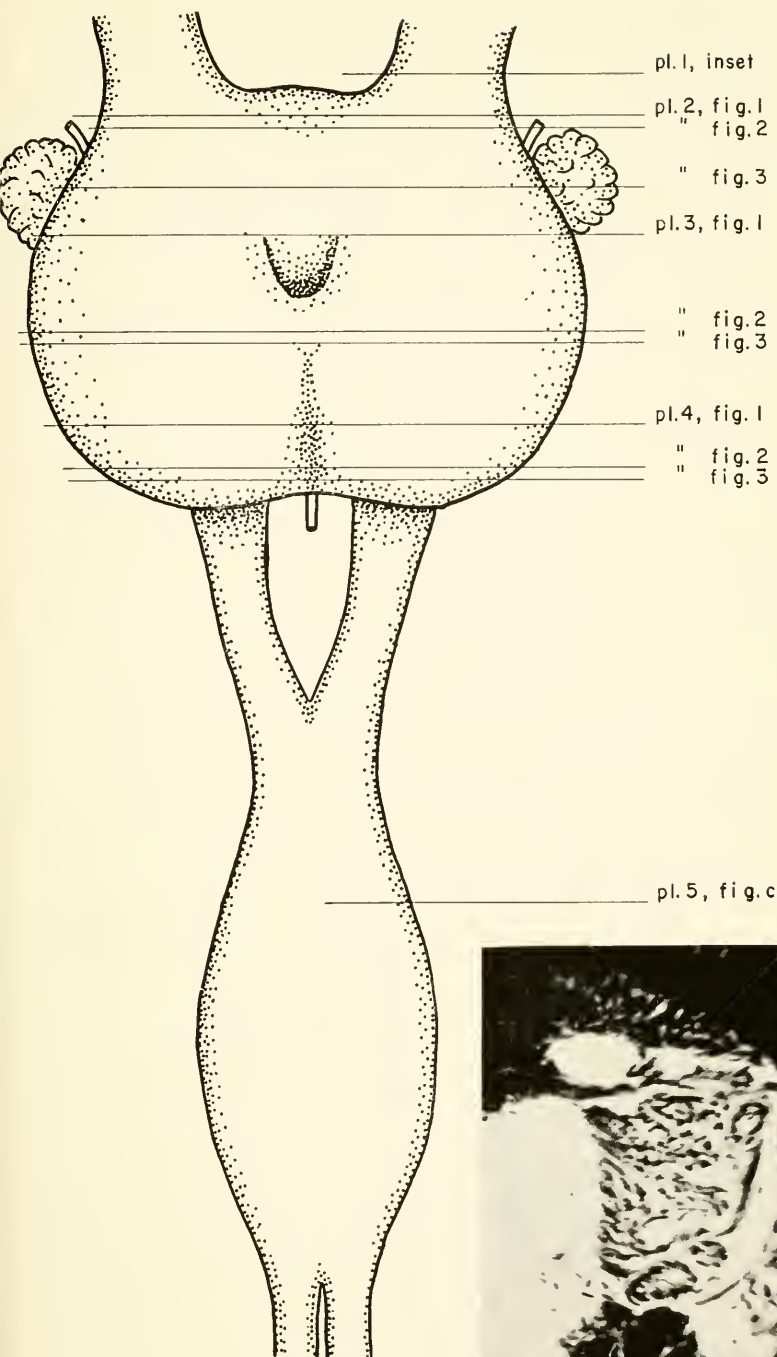
- FIG. 1. Section through the large protocerebral commissure (LPC) showing fibers (ff_4) intercommunicating the frontal lobes. Seen in cross section are muscle fibers (mm) of the *levator pharyngis* immediately ventral to the median recurrent nerve (N_{14}).
- FIG. 2. Section showing the recurrent nerve (N_{14}) flanked by the paired labral nerves (N_{17}). The arcuate fibers dorsal to the cerebral blood vessel are those of the commissure of the circumesophageal connectives (COES).
- FIG. 3. Section showing the base of the brain and the circumesophageal connectives (OEC). Note that the cellular cortex is beginning to envelop the neuropile of the connectives dorsally, thus delimiting them from the caudal portion of the supraesophageal ganglion.

PLATE 5

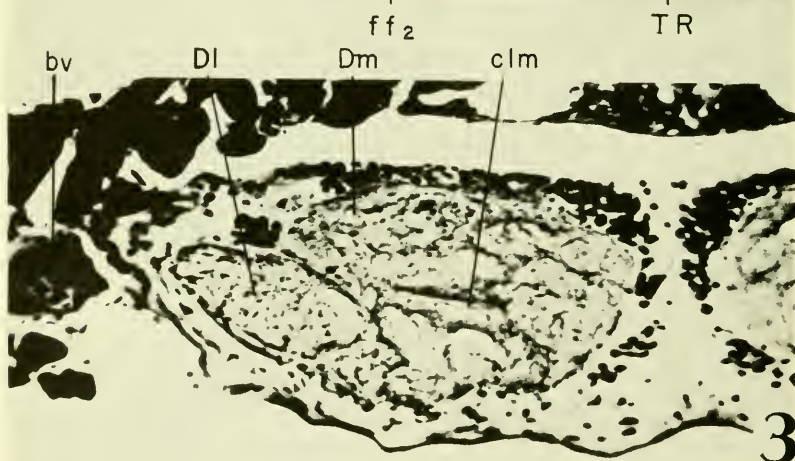
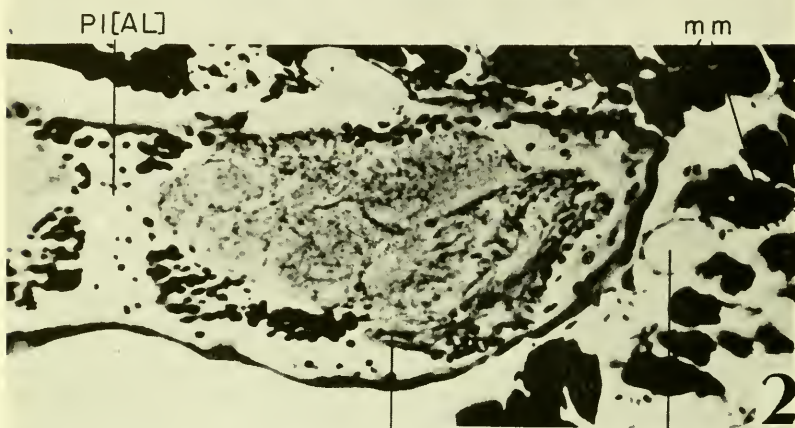
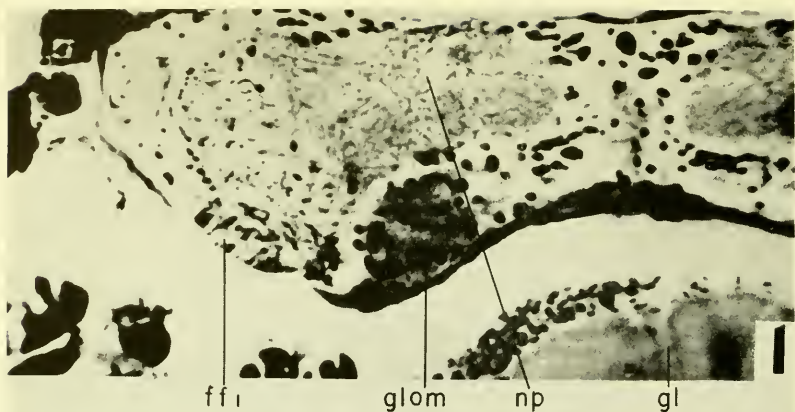
FIG. A. Showing the three types of nuclei (*a, b, c,*) found in the inner cellular perilemmal portion of the neurilemma. A portion of a tracheole (*tr*) is seen to the left with its small nucleus (out of focus) adhering to the periphery.

FIG. B. The two types of neuroglial nuclei in the neuropile. One type (*pn*) has pink staining chromatin with an exocentric nucleolus; the other (*bn*) has densely aggregated black staining chromatin. The dimensions of the first type may serve as a scale for this and the preceding figure (3×5 microns).

FIG. C. A transverse section through a giant cell located in the subesophageal ganglion. The large nucleus possesses a centrally situated clump of chromatin (*gcn*). A tracheole (*tr*) which may be mistaken for a second giant cell process is seen to the left of the axon (*ax*). The mass of material ventral to the nucleus (*sp*) may be a secretory product of the giant cell. The dimensions of the nucleus are approximately 12×20 microns.

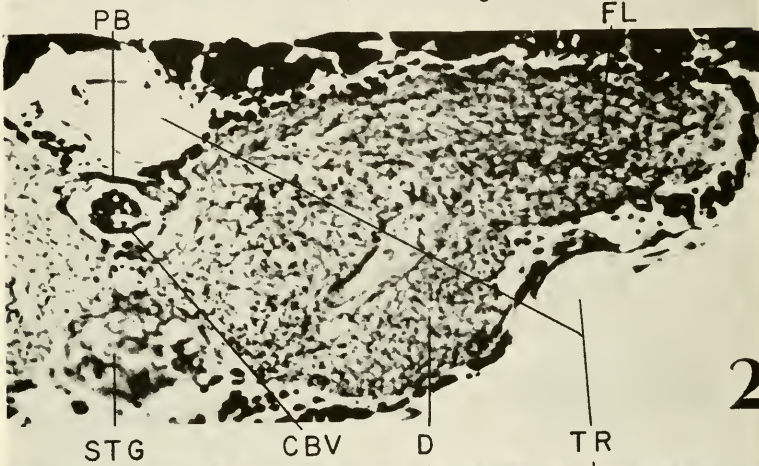


(See explanation of plates at end of text.)



1 sc. div. = 10 μ

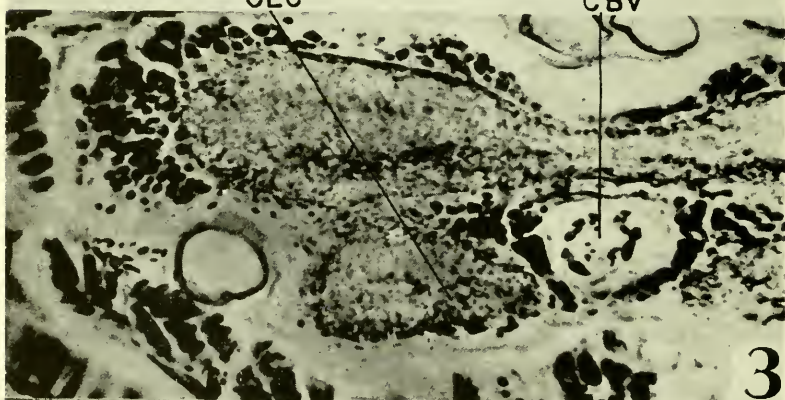
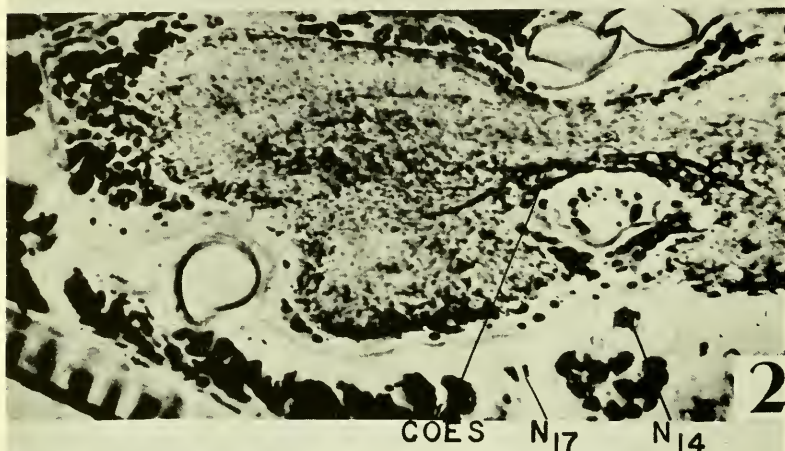
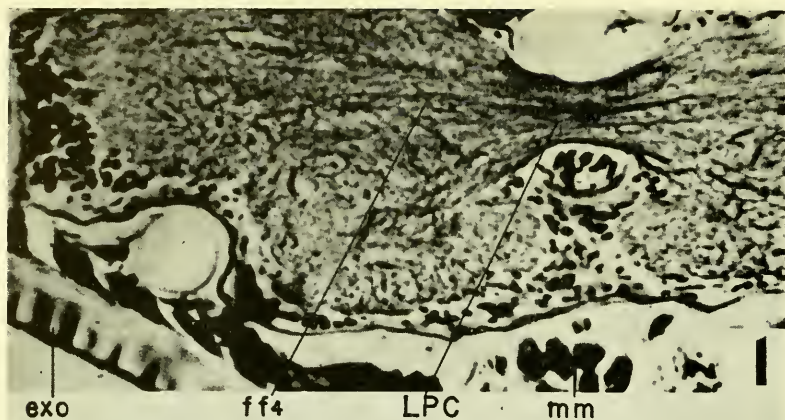
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1 sc. div. = 10 μ



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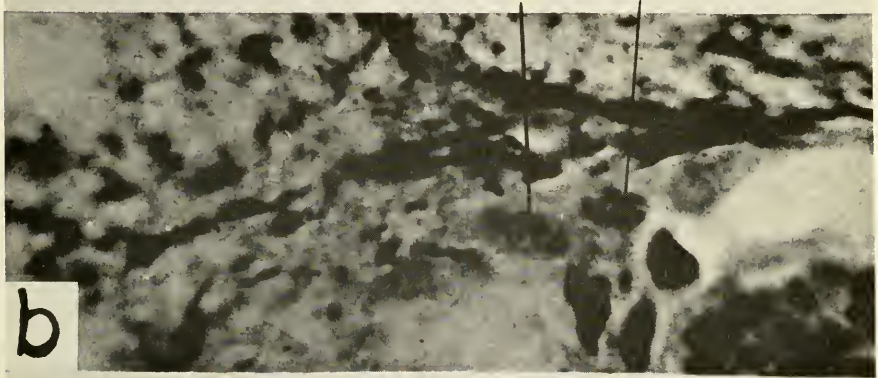
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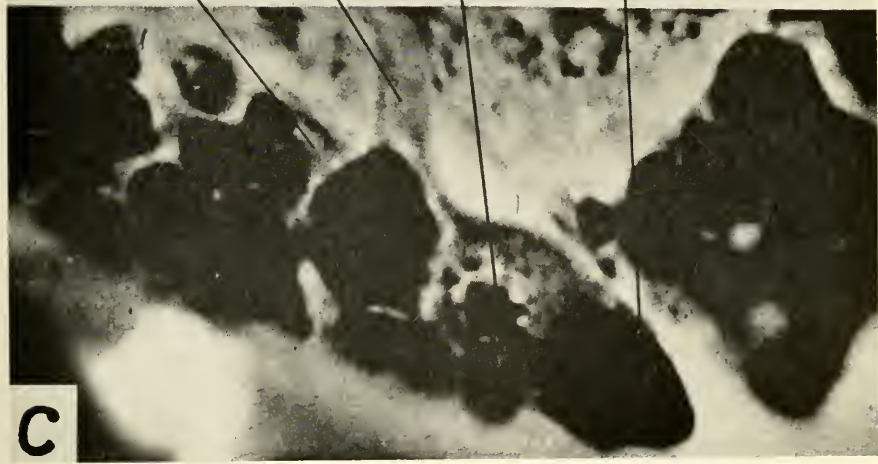
a

tr a b c
pn bn



b

tr ax gcn sp



c

(See explanation of plates at end of text.)